Social Environment Construction Provides an Adaptive Explanation for New Levels of Individuality

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During a major transition, former free-living entities relinquish their own individuality and aggregate into groups, such that the group becomes an evolutionary individual in its own right (Maynard Smith and Szathmáry, 1995; Michod, 1999). Essential to this process is cooperation, for the group members must cooperate to contribute to the success of the higher-level unit, rather than pursue independent, competitive, interests. While it is well-known from social evolution theory that population structure can promote such cooperation (Hamilton, 1964; Wilson, 1975), little attention has been paid to how such structure can itself arise via adaptive evolutionary mechanisms. We postulate here a process by which selection on individual environment-modifying traits can create conditions favourable for the evolution of cooperation, and, in extreme cases, for a transition to a new level of individuality. We term such processes, by which an individual evolves an influence over with whom it interacts, "social environment construction", which can be viewed as a type of niche construction (Odling-Smee et al., 2003).

To support this argument, we have developed a two-locus model in which a trait for social behaviour evolves concurrently with a trait that affects group size (this trait could be, for example, the amount of extracellular matrix produced in a biofilm; Penn et al., 2008). We have then shown that a smaller initial group size can be selected for because it increases variance in fitness at the group-level, and hence brings about increased cooperation through group selection (Powers and Watson, 2009; Powers et al., 2007). Indeed, we have shown that if the advantages of increased cooperation are strong enough then this can occur even if there are some opposing advantages of larger size, demonstrating that the benefits of increased cooperation can dominate the selective pressures on the size locus. Significantly, this can occur despite the fact that selfish cheats are also present and can themselves influence group size. We view this model as being particularly relevant to the fraternal transitions (*sensu* Queller 1997, 2000), where trade-offs between individual and group reproductive output are likely to be the key issue, such as in the transition from single- to multi-cellular organisms (Michod, 1999). In particular, most multi-cellular organisms develop from a single cell (i.e., an initial group size of 1), despite benefits of larger size (such as better access to resources and predator defence). It is commonly held that this is adaptive because growth from a single cell allows cheater cells to be effectively purged through group-level selection, for it increases between-group variance and reduces within-group variance (Maynard Smith and Szathmáry,

1995; Michod, 1999). Our model illustrates a pathway by which such adaptations can evolve.

We have also modelled the evolution of traits that directly influence the types with which an individual interacts. The evolution of such assortative interactions is problematic if cooperation is altruistic, as exemplified by the Prisoner's Dilemma game (Axelrod, 1997), because cooperators and cheats would both like to form groups with cooperators. However, this is not an issue if cooperation involves coordination with other group members, rather than altruism, for then there are multiple evolutionarily stable states (ESSs, *sensu* Maynard Smith 1982) that can be selected between by group selection (Boyd and Richerson, 1990). In such cases group structure need not be assumed, but instead "marker" traits can evolve that control the types with which an individual interacts. The evolution of these markers creates assortative trait groups (*sensu* Wilson 1975) and hence effective group selection (Snowdon et al., 2009).

We view such coordination games (Van Huyck et al., 1990) as being particularly relevant to the egalitarian transitions (Queller, 1997), that is, those that involve the formation of symbioses of different species or types (for example, the packaging of genes onto chromosomes). A key difficulty in such cases is to ensure coordination of function, by evolving sets of compatible types. We suggest that types can evolve associations with other types that are beneficial to them (e.g., pollinating plants evolve adaptations to attract transport vectors, such as honey bees), and thus ensure that they carry on interacting with those types down through the generations. In particular, through modelling work based on a coordination game with many ESSs (leading to different group fitnesses) we have shown conditions under which specific groupings evolve whose members perform complimentary functions, thereby allowing group fitness to be increased (Watson et al., 2009; Mills and Watson, 2009, 2007). By evolving these groupings, individuals stabilise their selective environment, allowing coordination of function to evolve. This work provides theory that begins to characterise the structure of coordinated interactions that will evolve. Specifically, it argues that relationships between organisms change in a manner that follows Hebbian principles - behaviours that co-occur together under the same conditions 'wire' together such that they co-occur together more in future. This has the effect of forming an implicit associative memory at the ecosystem scale, such that the system 'recalls' past attractor states, enlarges high-utility ESSs in preference for low-utility ESSs, and generalises over local attractors to find higher-utility attractors that would not otherwise be visited.

Our models have also suggested that pre-existing environmental conditions may act as a support for the processes described here. For example, a population may from the outset exhibit some degree of interaction structure due to spatial localisation. This existing interaction structure can then scaffold the evolution of genetic traits that provide further structure and greater cooperation (Penn, 2006). This is significant because if there is already some structure and hence cooperation present, then it is likely that a mutation that increases this structure by only a small amount will lead to some increase in cooperation, and hence will

be selectively favoured (Powers and Watson, 2009). By contrast, if no interaction structure is present then a large modification of the environment may be required to produce any cooperation, and such a large adaptive modification may not be plausible by mutation (Powers et al., 2008; Powers and Watson, 2009). Another potential example of such a scaffolding process, which is significant to the major transitions, concerns the evolution of higher-level heredity. Some of our models (Penn and Harvey, 2004; Penn, 2006) have shown that where within-group interactions give rise to complex dynamics (for example, in Lotka-Volterra models), then the existence of multiple within-group attractors can act as a source of limited heredity, for offspring groups will tend to return to the same state as their parent, and selection can act between such stable states. We suggest that this limited heredity, given simply by ecological dynamics, could bootstrap the evolution of further heritability at the group level by processes analogous to those discussed here (Penn, 2006).

In conclusion, we have shown through a series of models how genetic traits that affect an individual's social environment can evolve in such a way as to produce conditions favourable for the evolution of greater cooperation. Thus, while most other work assumes the interaction structure that favours cooperation, we have shown how such structure can evolve under natural selection.

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