# Adaptive units of selection can evolve complexes that are provably unevolvable under fixed units of selection

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Symbiosis, the collaboration of multiple organisms from different species, is widespread amongst prokaryotes. As symbiotic associations become more absolute, an inseparable union can result (symbiogenesis). This union would typically be considered a new unit of selection once a set of symbionts became reproductively inseparable. However we consider a macroevolutionary model within which new units of selection are formed gradually from maturing symbiotic relationships, without the need for symbiogenic events to be complete. We find that these adaptive units of selection can evolve complexes that are provably unevolvable under fixed units of selection.

We perform experiments in several structured rugged landscapes (including spin glasses) in which there only few global optima amongst many local optima. Importantly, the number of initial conditions that must be sampled to find one of these global optima by individual selection is exponentially large (i.e., their basins of attraction are small).

Selection on individual species only has the ability to evolve to locally optimal configurations. Selecting on groups at the level of entire ecosystems requires an exponentially large number of ecosystems to be created to find optima of globally maximal fitness. Since this level of selection cannot utilise gradient information, global optima are only guaranteed to be found by enumerating all possible ecosystem configurations.

We model an ecosystem, in which species have variable length genotypes. Every species has the potential to develop a symbiotic association with any other species. Initially all species specify a single gene and have no associations. The ecosystem is sub-divided into several semi-independent demes, each evolving to local attractors via individual selection. Symbiotic associations between the entities that are present in the local attractor discovered by each deme are modified to reflect their frequency of co-occurrence in the attractors across all of the demes: when entities are repeatedly found to be successful with the same partners, the symbiotic relationship is strengthened. Strong associations between entities biases the likelihood of their future co-occurrence. These two phases are repeated, resulting in coalitions of increasing size, stability, and co-dependence. Selection starts at the level of the individual, when local optima are discovered. However, the unit of selection adapts as composites gradually develop. Some composites are favoured at the expense of other composites, leading to the discovery of higher fitness optima. These composites consist of co-adapted groups that are locally optimal under individual selection, and not random configurations of large sets of entities. Thus, although the groups can contain many entities, the number of competing complexes is small: the configuration space is reduced as symbiotic relationships are strengthened.

We demonstrate the adaptive significance of these processes by applying them to provably difficult optimisation problems. In general, optimisation problems frequently have some structure that can be exploited, but only with an appropriate mechanism that can recognise that structure. When locally optimal configurations contain some information that is congruent with globally optimal solutions, such as when local optima are created from the frustration of a large number of low-order fitness interactions, the process described above can provide automatic problem decomposition.

When composite entities evolve through the intensification of symbiotic coalitions, the units of selection adapt causing the configuration space dimensionality to be collapsed. We show that this can result in complexes that are unevolvable when the units of selection are static.