The problem of ephemeral identity in evolving metacommunities and using organisational character to define higher-level units of selection

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Multilevel selection considers selective pressures acting at different levels in the biological hierarchy. Selection may be effective across levels, that is, selection at one level in the hierarchy can have fitness consequences for units at another level. Here we use an abstract individual-based model of an evolving microbial ecosystem to explore community-level selection in artificial and natural selection scenarios. We then speculate about one approach to defining community-level units of selection.

We performed artificial selection experiments on model ecosystems and observed a robust response (Williams & Lenton, 2007), similar to that reported elsewhere for real microbial communities (Swenson et al, 2000). The mechanisms of this response and the level at which adaptation occurred were unclear for the real communities -- did the community-level selection process act implicitly on traits of individual species, or were higher-level traits genuinely being selected? Careful analysis allowed us to elucidate the level of adaptation in our model system. We found that genuine community-level adaptation occurred in a significant fraction of cases. However, when the ecological problem posed by the artificial selection process could be easily solved by a single dominant species, it often was.

In another series of experiments, we showed that spatial structure and environmental feedbacks on growth can create conditions for a limited form of community-level natural selection to operate (Williams & Lenton, 2008). Local communities that improve their environmental conditions achieve larger populations and are better colonizers of available space, whereas local communities that degrade their environment shrink and become susceptible to invasion. The spread of environment-improving communities has a genetic basis in environment-altering traits of individuals, even though these traits are neutral at the individual level.

Overall, our modelling work shows that under certain conditions selection at the level of the community can be an important evolutionary mechanism. In the artificial selection scenario the unit of selection is externally defined by the selection intervention, although the level at which adaptation occurs (that is, the level at which phenotypic character change is observed) depends on the selection conditions. The means of transmission is also externally imposed in the artificial selection experiments and is designed to preserve associations between species, thus avoiding one of the problematic aspects of multilevel natural selection. The case of natural community-level selection is far more conceptually challenging, as here neither the unit of selection nor the means of transmission are externally defined.

In the natural selection scenario, it is clear that some form of selection above the level of the individual is active (as evidenced by systematic changes in allele frequency at loci which are neutral at the individual level) and that this selection depends on the spatial structure of the metacommunity (as evidenced by an observed dependence on inter-community mixing rate). However, it is not straightforward to define a higher-level entity on which selection might act. An obvious candidate is the local community at each patch, suggested by the semi-discrete spatial structure in the model. However, mutations and mixing of individuals between neighbouring patches continually change the species composition of each local community, while ecological and lower-level selection processes alter species abundances. Thus the identity of each local community is ephemeral. This poses the key conceptual question of how selection pressures above the level of the individual can be effective when the best candidate higher-level unit of selection has a shifting identity?

One possible solution to this difficulty is to alter our definition of higher level units away from the standard perspective suggested by the biological holarchy: rather than define higher units by their nested lower-level components, it may be useful to base our definition on functional organisation. The higher level unit is then not simply a set of lower level entities, but a persistent pattern of ecological organisation. We tentatively define the *organisational character* of a community at a point in time as the network of ecological interactions supporting the flow of material and energy around the ecosystem. This definition avoids the problem of continual changes in species composition (the ephemeral identity problem) by positing a persistent pattern of organism-mediated material/energy flow, in which species membership may change as long as functional roles are conserved. An analogous definition might define the organisational character of an organism in relation to its cellular components; constituent cells may be continually replaced but the identity of the organism is conserved if its pattern of functional organisation remains the same.

If the notion of organisational character is to provide a useful framework with which to consider the existence of community-level units of selection, then we must seek to establish whether or not communities (phenotypically defined by their organisational character) can satisfy the three conditions for evolution by natural selection: phenotypic variation, differential fitness, and heritability (Lewontin, 1970).

Variation in the organisational character of communities can clearly occur if the abundance or type of individuals/species making up the community are varied, but our definition requires changes in the *functional types* of organism making up the community for a change in organisational character. [A functional type is defined as a class of organism/species that performs a distinct functional role. Functional types are often defined in terms of biogeochemical function (e.g., photosynthesisers, nitrogen-fixers, ...) (Le Quere et al, 2005). Distinct organisms/species may belong to the same or different functional types depending on the breadth of the functional characteristics being considered, e.g., all plants are photosynthetic, but not all fix nitrogen.]

Differential fitness based on organisational character is observed if some character types become more dominant than others as a result of their functional differences. Since communities are rarely (if ever) discrete, it may be better to consider differential proliferation rather than differential production of new units in allocating fitness. Thus the fitness of an organisational character type depends on the rate at which it can spread to occupy available resource-space (which may be physical space, nutrient/water supply, etc.).

Heritability is the most problematic of Lewontin's three conditions for the organisational character concept. In previous work we have characterised community organisation in terms of nutrient recycling, using a graph-based formalism to characterise nutrient flow in an ecosystem as a network of cross-feeding relationships between species (Williams & Lenton, submitted). Here we extend this formalism to include aspects of the abiotic environment and thus give a more complete representation of community organisational character. By observing the resulting character-networks of local communities at different locations in our spatial model, we can track the spread of organisational character types across the metacommunity. Changes in organisational character can then be quantified via the level of isomorphism between the character-networks of local communities. Using this technique we are able to establish a measure of heritability during inter-patch colonisation.

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