

# Does global niche construction lead to environmental regulation?

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Ecological models often ignore the interaction between the biota and the environment. For example, Lotka-Volterra population models (Lotka, 1925; Volterra, 1926) and replicator equation models (Hofbauer and Sigmund, 1998) typically look only at the interaction between species. The external environment, where it is modelled at all, is usually taken only as a source of food; other aspects that may affect the growth and reproductive success of organisms are ignored. However, it is increasingly recognised that there is a constant and significant interaction between living things and the abiotic environment that extends beyond food web dynamics. Ideas of niche construction (Laland et al., 1996; Laland et al., 1999) and the extended phenotype (Dawkins, 1982) highlight the importance of the environment in evolutionary dynamics, while the increasingly accepted Gaia theory (Lovelock, 1979) suggests that not only do organisms affect their environment, they do so in a way that regulates the biosphere to conditions that are suitable for life. Proposed Gaian phenomena include the regulation of local climate by marine algae that influence the formation of clouds over the oceans (Charlson et al., 1987; Lovelock, 1997; Liss et al., 1997; Andreae and Crutzen, 1997), global temperature regulation by biotic enhancement of rock weathering (Schwartzman and Volk, 1989; Schwartzman and Volk, 1991), and the maintenance of constant marine salinity and N:P ratios by the aquatic biota (Redfield, 1958; Lenton and Watson, 2000; Volk, 1998).

Given this recognition of the bi-directional feedback between life and its physical environment, we can now ask how the entire coupled system will evolve over time. We can study the effects of a variety of mechanisms that act to shape the environment over a variety of spatial and temporal scales, from purely physical processes through to ecological and evolutionary dynamics. We can begin to explore questions concerning the overall result of the combined actions of these mechanisms: will the coupled system reach an equilibrium state? what kinds of state might it tend towards?

Purely abiotic processes are constrained by immutable physical laws, meaning that the components of the biosphere that can adapt (and thus have the potential to steer system

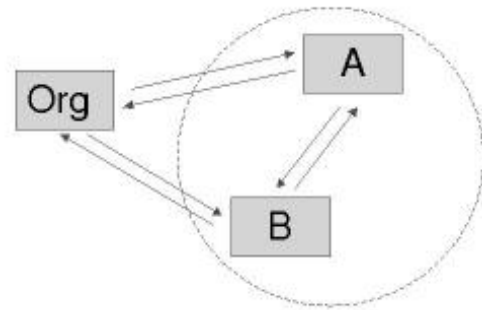


Figure 1: Every organism has an environment (dotted circle) which consists of both abiotic (A) and biotic (B) components. There is two-way feedback between the organism and all of these components, as well as between the components and each other.

dynamics in different directions) are the biological components: living organisms. Every organism has an environment made up of both biotic components (e.g., other organisms) and abiotic components (e.g., temperature, chemical fluxes, geography, salinity). The organism interacts with all of these components, which also interact with each other, and the nature of this interaction determines the selection pressure it experiences. As species evolve, it is possible that selection may occur on their environment-altering traits so that traits are favoured which change the environment in some beneficial way. The same physical laws that constrain abiotic processes also constrain biology, meaning that many organisms share similar basic preferences for certain aspects of the environment (such as temperature, pH, etc.). This potentially gives a shared 'target' for selection on environment-altering traits, raising the question of whether the collective niche construction activities of all species can result in regulation of the abiotic environment to conditions suitable for growth.

Here we present results from a new model which has been developed to examine the hypothesis that environmental regulation can result from natural selection on environment-altering organismal traits. The Flask model (Williams,

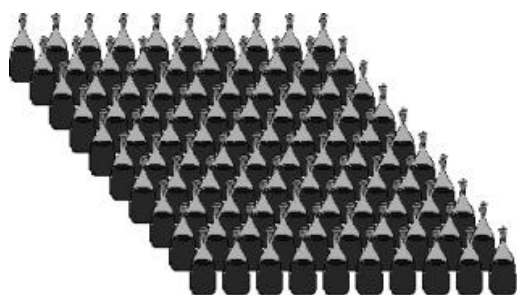


Figure 2: The Flask model. Ecological and evolutionary dynamics mean that microbial communities within flasks may be more or less successful depending on initial conditions. If migration is possible between flasks this raises the possibility of colonisation or invasion by more successful communities.

2006) consists of a spatial array of flasks containing a liquid medium and supplied with a constant flow of nutrients. Each flask contains a population of microbes, which can grow, reproduce and mutate, so that stable food webs may be formed by ecological and evolutionary interaction. Microbes have an effect on their abiotic environment and the abiotic environment has an effect on growth, so that a two-way feedback exists between the microbial community and its abiotic environment. The community determines the composition of the abiotic environment and the abiotic environment influences the rate of microbial growth. There is limited migration between flasks, allowing the possibility of colonisation or invasion of a neighbouring flask by a community. We would expect more populous communities to be better colonisers, and since the effect of a microbial community on its abiotic environment will be key to its growth and population size, it is possible that higher-level selection effects will lead to the evolution of communities that regulate their environment around the optimal conditions for growth.

Results from the model show that multi-level selection on environment-altering traits can lead to the evolution of stable microbial communities that consistently alter their abiotic environment toward an arbitrary pre-defined state. When the environment affects microbial metabolism, the result is a strong causal relationship between the state of the environment and the success of the microbial population. These results suggest that spatial structure and multi-level selection can lead to environmental regulation by the biota in a manner consistent with established evolutionary theory.

The Flask model is a computational thought experiment designed to examine the hypothesis that natural selection can lead to environmental regulation. If we accept that life both affects and is affected by its environment, then in the presence of physical constraints on metabolism life has the power either to maintain its environment in a habitable state or to degrade its environment such that life is no longer vi-

able. Our results suggest that there may be a tendency for life to maintain habitability. The collective construction of a habitable world is surely one of the most fundamental ways in which organisms engage in environment construction.

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