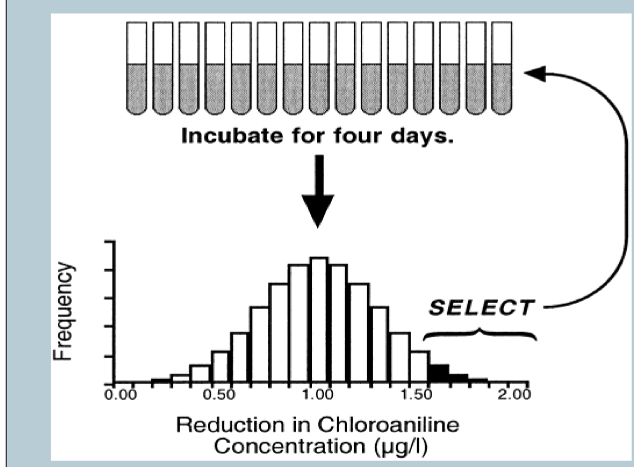
Artificial selection of simulated microbial ecosystems

Recent work with microbial communities has demonstrated an adaptive response to artificial selection at the level of the ecosystem. The reasons for this response, and the level at which adaptation occurs, are unclear: does selection act implicitly on traits of individual species, or are higher-level traits genuinely being selected? We used simulations to approach this important question.

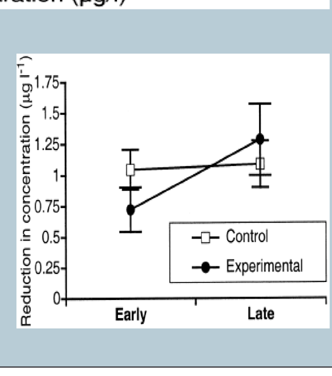
Background

Artificial ecosystem selection experiments on an individual-based evolutionary simulation model of microbial ecology showed a similar response to that seen with real ecosystems. We found that a significant fraction of artificially selected ecosystem responses cannot be accounted for by implicit lower-level selection of a single type of organism within the community, and that interactions between different types of organism contribute significantly to the response in the majority of cases. However, when the ecological problem posed by the artificial ecosystem selection process can be easily solved by a single dominant species, it often is.

Artificial ecosystem selection

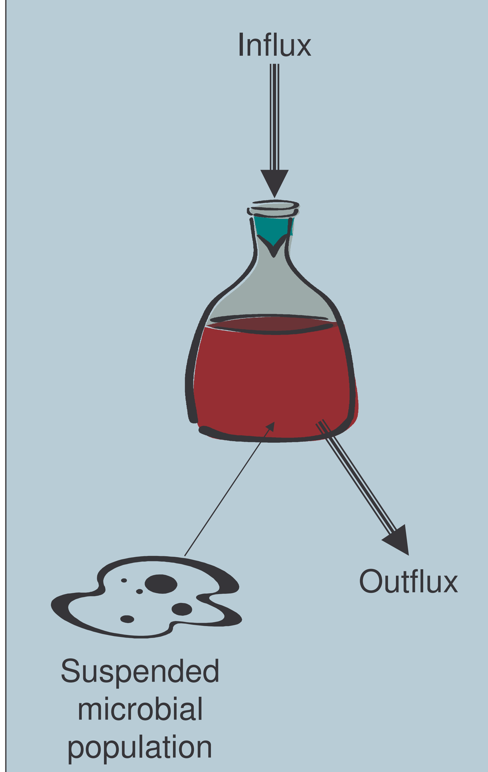


15 test tubes of 1ml inoculum + 29ml broth, 1 generation = 4 days. Plot shows reduction in 3-chloroaniline (mean±SD) over 4 runs in selected (experimental) and non-selected (control) lines, measured early (gen. 4-8) and late (gen. 25-30).



Swenson et al [1] incubated pond water ecosystems in the laboratory. After 4 days they measured the reduction of the pollutant 3-chloroaniline to give a \`fitness' score used to rank the test tube ecosystems. The fittest ecosystems were sampled to inoculate a new batch. After several \`generations' a significant improvement in the ability to degrade 3-chloroaniline was observed. Other experiments successfully selected pond water communities for the ability to alter environmental pH and soil communities for the enhancement of above-ground plant growth [2]. However, the underlying mechanisms and level of adaptation were unresolved.

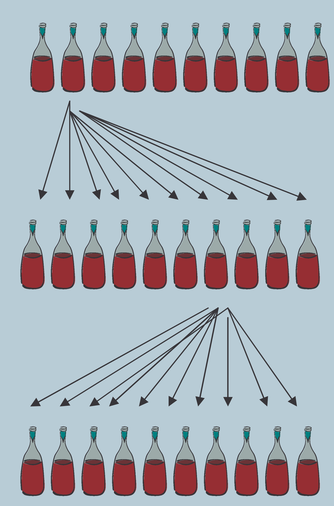
The Flask model



An individual-based simulation model of microbial evolutionary ecology. Continuously cultured microbes are suspended in well-mixed liquid medium supplied with a steady flow of nutrients. Microbes have a fixed genotype which determines metabolic reaction. Growth occurs by conversion of consumed nutrients to biomass. Reproduction is by splitting above a certain biomass threshold. Offspring receive copy of the parental genotype with low probability of mutation. Bidirectional feedback exists between organisms and environment: The environment (nutrient levels and abiotic factors such as pH, temperature, etc.) affects microbe growth rate, while microbes consume nutrients and alter abiotic factors as a by-product of metabolism. See [3] for details of model and evolutionary/ecological dynamics.

Artificial selection in Flask

1. Seed initial batch of flasks with random microbial inocula.
2. Allow flasks to develop for fixed period.
3. Assign \`fitness' score to each flask.
4. Sample fittest flasks to inoculate new batch.
5. Repeat 2-5.



Select (viable) ecosystems on the distance, Φ, of their abiotic environmental state from an arbitrary target state:

- High line: maximise Φ
- Low line: minimise Φ
- Control line: random choice

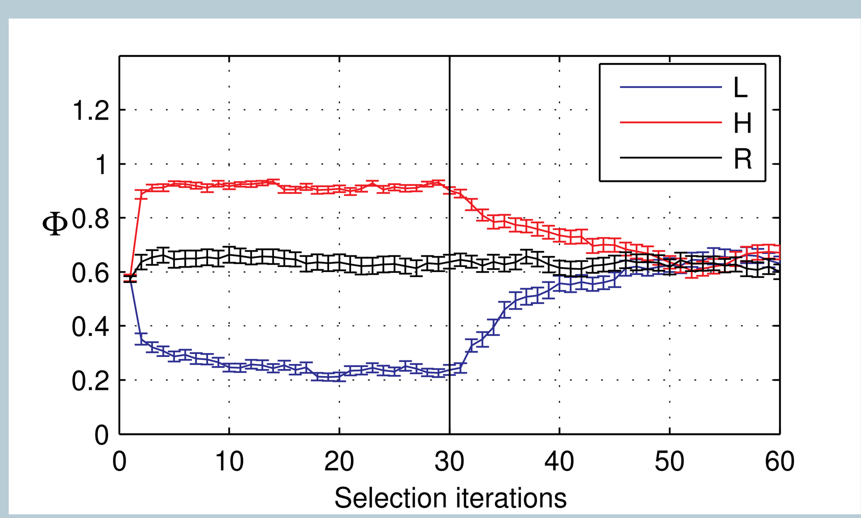
See [4] for full details.

$$\Phi = \sqrt{\sum_{i=1}^{A} (\bar{a}_i - \hat{a}_i)^2}$$

$\bar{a}_i$ = normalised level of abiotic factor a_i
$\hat{a}_i$ = target normalised level of a_i
A = number of abiotic factors

Response to selection

Artificial ecosystem selection produces a strong adaptive response. High (H) and low (L) lines quickly diverge from the randomly selected control line (R). When directed selection is replaced by random selection after iteration 30, the high/low selected lines relax to the non-selected control condition. The response is robust to different targets and sampling methods. Size of response is inversely related to mutation rate (P_{mut}) and propagation time (T_{prop}).



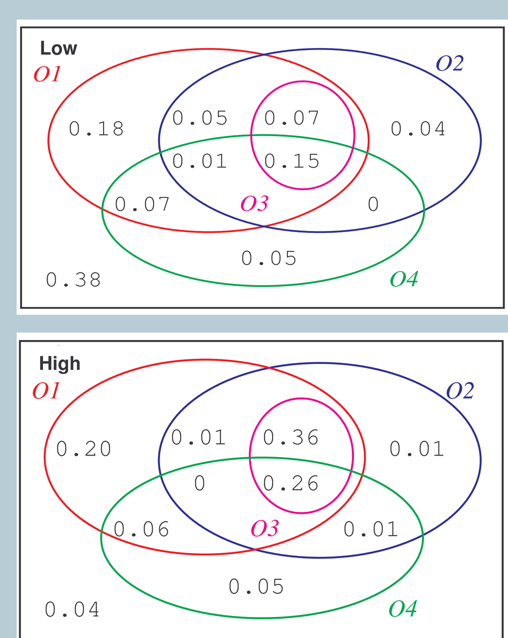
Mean Φ± 1SE plotted from 57 runs with propagule sampling, 3 abiotic factors, 3 nutrients, T_{prop}=5000, P_{mut}=0.01 at each locus. 30 iterations of directed selection followed by 30 iterations of random selection.

Decomposing the response

We tested the best artificially selected ecosystem in each run to determine how it achieved the target function. Were multiple species involved? If so, were ecological interactions between species important or did each species make an independent contribution? We used several observations to exclude cases where:

O1-O3: A single species performed as well or better than the intact community on the target function.
O4: The additive sum of independent species contributions (excluding interactions) was as good or better than the performance of the intact community (with interactions).

In any remaining cases, beneficial interactions between multiple species were necessary for the performance of the selected environmental function.



Fraction of 483 cases satisfying O1-O4. (O1 – test species better when grown in isolated monoculture, O2 – test species better when grown in the context of a wild type community, O3 – same species satisfies both O1 and O2.)

Our tests may be combined to test the proposition that the ecosystem selection process acts on traits above the level of individuals or species. We find a significant fraction of ecosystems where higher level selection has acted on higher level traits.

Almost all the high-selected ecosystems (91%) appear to have a selected function that is based on the strong contribution of a single species. A further 5% show no contribution of interactions, i.e., a response that could be due to the individual contributions of two or more species without interaction. Such solutions could be found by lower level selection methods, leaving only 4% cases where higher-level traits were selected. However with the low-selected ecosystems a significant number of cases (38%) have a selected function based on beneficial interactions between multiple species. Selecting for low Φ (target-hitting) is *a priori* a harder task, requiring more than one type of microbe to be present in the community, while a good high-Φ (target-avoiding) solution may be found with a single microbe type. The different kinds of solutions found to the high and low line problems show that while artificial ecosystem selection can act on higher-level properties when necessary, it will make use of simpler low-level solutions where available.

References:

[1] Swenson, W., Arendt, J. & Wilson, D.S. (2000) **Artificial selection of microbial ecosystems for 3-chloroaniline biodegradation.** *Environmental Microbiology* 2(5), 564-571.
[2] Swenson, W., Wilson, D.S. & Elias, R. (2000) **Artificial ecosystem selection**. *PNAS* 97, 9110-9114.
[3] Williams, H.T.P. & Lenton, T.M. (2007) **The Flask model: Emergence of nutrient-recycling microbial ecosystems and their disruption by environment-altering \`rebel' organisms.** *Oikos* In press.
[4] Williams, H.T.P. & Lenton, T.M. (2007) **Artificial selection of simulated microbial ecosystems.** *PNAS* 104 (21) 8918-8923.

Hywel T. P. Williams & Timothy M. Lenton
School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ / h.williams@uea.ac.uk