

The Role of Non-Genetic Change in the Heritability, Variation, and Response to Selection of Artificially Selected Ecosystems

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Abstract

A response to selection on the level of the ecosystem has been demonstrated in artificial selection experiments, and poses interesting challenges to concepts of heritability, variation and phenotype in biological systems. We use ecosystems modeled as Lotka-Volterra competition systems, and subject to an ecosystem-level selection process, to illustrate and discuss the potential, and possible mechanisms, for ecosystem-level evolution without genetic change of the component species. A limited positive response to selection is demonstrated by the selection of alternative stable ecosystem states.

Introduction

The ability of whole ecosystems to respond to selection has recently been demonstrated in artificial selection experiments, (Swenson et al., 2000b; Swenson et al., 2000a). However the concept of ecosystem selection remains controversial; artificial selection experiments demonstrate only the phenomenon of ecosystem-level evolution and not the mechanism by which it occurs (Johnson and Boerlijst, 2002). A common question concerns the fact that an ecosystem has no genome and hence should not be able to respond to selection. In fact the requirements for a response to natural selection are general properties, not restricted to any particular level of the biological hierarchy, or indeed systems with their own genomes in the conventional sense (Lewontin, 1970). In “The Units of Selection”(1970), Lewontin set out three fundamental conditions which a population of units must satisfy in order to respond to natural selection:

1. Phenotypic variation amongst units.
2. Fitness consequences of phenotypic variation.
3. Heritability of fitness.

If ecosystems were to act as units of selection then they would need to fulfil all these requirements, including the implicit assumption of the individuality or separateness of units. For communities “in the wild” this would present significant problems. (The possibility of self-organised spatial structures allowing selection between subcommunities has

been addressed elsewhere (Johnson and Boerlijst, 2002).) In the artificial selection experiments however, two of the properties are imposed by the experimenters. A population of ecosystems is provided by the experimental setup, and the fitness consequences of the measured “ecosystem-level” phenotypic variation are imposed. Selected ecosystems are reproduced by sampling the medium of the “parent” ecosystem (eg soil, pond water), and inoculating new sterile medium. This still leaves two important criteria to be satisfied. In order to respond to selection the ecosystems must still vary phenotypically one from the other, and this variation must be at least partially heritable. The concepts of phenotype, variation and heritability at the ecosystem level are far from straightforward, and deserve further exploration. In particular, Wilson and Swenson have suggested that when whole ecosystems are subject to artificial selection on an ecosystem-level property, the response to selection could be due to change in species composition of the community only, without species genetic change (Wilson and Swenson, 2003). In previous work, (Penn, 2003), we showed that ecosystems with simple dynamics responded to ecosystem-level selection if genetic change was allowed. Here we wish to investigate the possibility of evolution without genetic change in a simple model. This paper will explore the ideas and implications of variability, heritability and phenotype in self-contained experimental ecosystems (microcosms), and discuss the feasibility of evolution at the ecosystem level without genetic change in the constituent species.

Evolution at the Ecosystem Level

What is an ecosystem “phenotype”?

The term ecosystem phenotype refers to the measured property of the experimental microcosm that is selected for. As examples of ecosystem phenotypes, Swenson and Wilson chose above-ground plant biomass of *Aribidopsis thaliana* for a soil ecosystem, and pH and rate of biodegradation of 3-chloroaniline, for aquatic, microbial ecosystems. Their choices of phenotype were based on their definition of an ecosystem as the “interactions of the species with each other

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and their physical environment". Because the traits pH and biodegradation of chloroaniline are properties of the physical environment and the trait of plant biomass "is likely to be mediated through effects on the physical environment", they claim that their experiments qualify as ecosystem-level selection.

We may consider ecosystem-level properties as those that cannot easily be attributed to one species in the assemblage. Rather they will be consequences of the complex interactions of the many species present, (as well as the particular environmental conditions which they are subjected to.) If we consider that it is possible to represent the ecosystem as some sort of state vector of species composition, species numbers and genotypes, then the particular measurable phenotype in which we are interested would be some sort of function on this vector (given for the moment a constant environment). From this perspective, stable phenotypes would correspond to attractors in the ecosystem's state space¹. A further complicating factor is the possible form of this "phenotype function" with respect to the underlying dynamics and ecosystem state, which will have a significant effect on the response to selection. Phenotype could be an additive or non-additive function of ecosystem state. Many to one mappings from ecosystem state to phenotype value are probable, leading to areas of selective neutrality.

Variation

In order for selection to act there must be variation between the "phenotypes" of the ecosystems in a population. This can, broadly speaking, be generated in two ways: by variation between offspring and parent ecosystems caused by the sampling process; and by variation arising during the ecosystems' development stage during an experimental "ecosystem generation". Variation in either of the stages could be heritable or non-heritable, because in ecosystem reproduction there is no distinction between germ and soma. The heritability of any variation arising depends on its reliability of transmission not only via the sampling procedure, but also after being subject to another "generation" of ecosystem development.

According to Swenson and Wilson (Swenson et al., 2000b; Swenson et al., 2000a), ecosystems are complex systems, sensitively dependent on initial conditions, and it is this that can potentially give rise to wide phenotypic variation from small variations due to sampling error when ecosystems are reproduced. This position implicitly assumes that the important sources of variation in ecosystem phenotype are endogenously generated, that is, have at their root natural variability of the population dynamics. Such behaviour has been shown in both models and experimental

microcosms with chaotic dynamics, (Schefer et al., 2003), in which small initial differences in numbers of each of several species competing for resources give rise to different stable outcomes after a period of transient chaos.

However, there are many other potential sources of variation which could alter the state of the ecosystem phenotype when it is measured. Amongst others: sampling error on community composition when ecosystems are reproduced; heterogeneous spatial distribution of species within the microcosm potentially magnifying sampling error; environmental stochasticity; and species' own effects on the abiotic environment. In addition, given sufficient diversity within a population of ecosystems, "sexual" recombination, i.e. mixing, of ecosystems could perform a similar role. The pertinent question about all of this variation from the perspective of selection is, is it heritable?

Heritability

In order for evolution to occur we require partially heritable phenotypic variation. The phenotype in question is whatever function of the community composition that we define, measured at the end of an ecosystem generation. This could be an instantaneous or cumulative value. Heritability of the phenotype will depend on the reproducibility of an ecosystem's state at time T from the process of taking a sample of that system and using it to seed an offspring system.

To try and express this in a more formal fashion, if we imagine the ecosystem state at the end of a generation, E , as a vector of species numbers, then heritability requires that the combination of 2 vector operators, sampling and development (ecosystem dynamics plus additional sources of variation), on E produces the same end state E . (For ease of description, and to suit the purposes of this paper, we ignore intra-species genetic variation and change.) Variation requires that either the sampling or development operator acts so as to produce E' rather than E . The response to selection depends on the balance between these two outcomes with given sampling and development operators.

So, for an ecosystem phenotype to be heritable, it must be robust to the operations of sampling and development. This implies that heritability depends upon the existence of attractors in the ecosystems' state space, and evolvability on the existence of multiple stable attractors. In order for a sustained response to ecosystem selection to be possible, a network of attractors of varying stability is required. The attractors must be reachable via the variation incurred during the sampling and development stages. The heritability of a given phenotype then, will depend on the nature and extent of the basin of attraction of the ecosystem's state at the end of the generation. It is interesting to note that, unlike selection at the level of the organism, ecosystem selection must search for phenotypes that are not only fit, but also stable.

¹Even limit cycles could produce a stable ecosystem phenotype if the cycle length was short with respect to the length of the ecosystem generation, and the selected trait was a cumulative rather than an instantaneous function of the ecosystem state.

Evolution without genetic change

Wilson and Swenson, (Wilson and Swenson, 2003), note that evolution at the phenotypic level of the community could theoretically occur either through genetic changes in the constituent species, changes in the species composition of the community, or both. That is, that evolution could occur without changes in the genes of the species present. They emphasize that changes in species composition or population numbers of species in a community literally are changes in gene frequency at the level of the community. In the context of the ideas of heritability and variation discussed above, evolution of a community without genetic change would be possible if that community possessed multiple stable states. Sampling error during reproduction, or noise or chaotic dynamics during development could be enough to knock the community into different basins of attraction, and hence allow evolution to occur.

Model

In order to investigate the possibility of this mode of evolution occurring, we use a simple, yet widely-used, model of basic ecological dynamics, and subject it to an ecosystem selection procedure. No genetic change within species is allowed. As an initial simple approximation, the within-ecosystem dynamics are modeled using the generalised Lotka-Volterra competition equations (MacArthur, 1972), these equations potentially have multiple stable equilibria and so are suitable for our purposes. We make the assumption that, as under laboratory conditions, ecosystems are closed after sampling. That is, unlike the model of Ikegami and Hasimoto, (Ikegami and Hasimoto, 2002), species that have been eliminated from the population cannot reappear.

$$N_{i,t+1} = N_{i,t} \left[1 + \frac{R_i}{K_i} \left(K_i - \sum_{j=1}^S N_{j,t} \alpha_{ij} \right) \right]; \quad (1)$$

Where $N_{i,t+1}$ is the density of species i at the next time step, S is the total number of species, K_i is the carrying capacity of species i , R_i is the rate of increase of species i , and α is a matrix of interaction coefficients representing the per capita effect of each species on every other (α_{ij} is the per capita effect of species j on species i). Source ecosystems for each selection run were randomly initialised with K_i 's set at uniform random in the range 100:1000, R_i 's at uniform random 1.5:2.5, and each α_{ij} set randomly on a skewed distribution in the range 0:2, unless $i = j$ and then $\alpha_{ij} = 1$. The α_{ij} 's were drawn from the distribution $\alpha_{max} x^{1.5}$, where x is randomly chosen from 0:1. This gives a weakly skewed interaction matrix with many weakly interacting species and fewer strongly interacting ones. Note that although all direct interactions are competitive ($\alpha_{ij} > 0$), indirect effects may give rise to mutualisms or commensualisms. The initial populations for the source ecosystems are set at uniform random in the range 0:100

Ecosystem reproduction involves taking fixed-size samples from a selected parent ecosystem (eg samples of soil or water containing the microbial ecosystem (Swenson et al., 2000b)) and using them to inoculate or "seed" offspring ecosystems. Reproduction is asexual, that is, samples from different parent ecosystems are not mixed before being used to inoculate new ecosystems. In real ecosystem selection experiments, the process of sampling can introduce variation between offspring both in species genetic composition, and initial species population sizes. In this model only variation in population size is considered. The initial population size for each species in an offspring ecosystem is calculated on the assumption that a sample contains individuals chosen at random from the parent ecosystem, thus the expected frequency of a species in a sample is equal to its frequency within the sampled ecosystem. Since species population sizes are continuous variables, sampling was modeled using the standard Gaussian approximation to a binomial distribution. Thus, N_i , the size of the species in the new sample, was generated at random from a Gaussian distribution with mean, Bp_i , and standard deviation, $\sqrt{Bp_i(1-p_i)}$, where p_i is the frequency of the species in the parent ecosystem, and $B = 100$ and $B = 10$ were the mean sample sizes.

Each ecosystem was run for 50 time steps which constituted an ecosystem generation. During this "developmental stage", developmental noise was added to the dynamics by multiplying each of the $N_j \alpha_{ij}$ interaction terms by a number drawn from a uniform random distribution in the range 0.5:1.5.

Selection is for the maximization of a random linear function of the population sizes, normalized to the range 0:1.

$$F = \sum_{i=1}^S N_i \beta_i; \quad (2)$$

Where the β_i are randomly generated coefficients in the range -1:1. This is an appropriate ecosystem-level fitness function because, as is likely to be the case with macroscopic properties of real ecosystems, the optimal strategy for each species to achieve maximum ecosystem fitness is context dependent. That is, dependent on the dynamics and population levels of the other species within the community.

Results

With both the larger ($B = 100$, smaller sampling error,) and smaller ($B = 10$, larger sampling error), sample size we see a small positive response to directed selection, and a slightly negative or no response to random selection. Figures 1 and 2, show the mean response to directed and random selection respectively, of 30 randomly generated ecosystem populations, $B = 10$. Each population is created from a different randomly initialised source ecosystem with different interaction coefficients, carrying capacities and growth rates, and 20 species. Figures 3 and 5 show the final species population

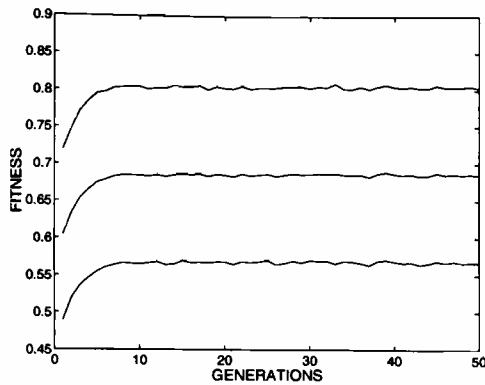


Figure 1: Directed Selection: Mean fitness (+ and - Std Dev) of 30 ecosystem populations, $B = 10$, over 50 generations.

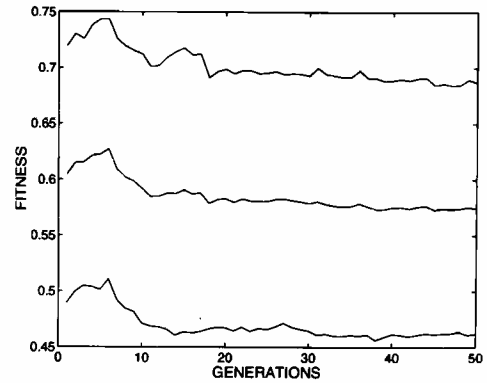


Figure 2: Random Selection: Mean fitness (+ and - Std Dev) of 30 ecosystem populations, $B = 10$, over 50 generations.

states for the best ecosystem in population 1 over 50 generations, under directed and random selection respectively. Note that this is in fact the same set of ecosystem parameters in both cases, effectively the same “ecosystem” under a different selective regime. We can see that two different stable attractors have been reached. Although not shown, in the case $B = 100$, the same “ecosystem” also falls into two different stable attractors under selection and random selection, both of which have a different species composition to either of those seen when $B = 10$. These dynamics are typical of the majority of our randomly generated ecosystems. Figures 4 and 6 show the corresponding fitness values over the course of 50 generations for the ecosystem populations in figures 3 and 5. Best, worst, mean and upper and lower quartiles are shown to give an indication of the diversity within the population. It is evident that under both selection and random selection the fitnesses undergo a period of change and then settle to a stable value with the diversity of the population reduced. This is particularly noticeable in the case of the randomly selected population (fig.6). Here fitness does in fact increase, but to a low stable mean value, and only after a prolonged period of change caused by the dynamics of a 2-species transient (fig.5). When one species is eliminated from the ecosystem, it has reached a stable point and the fitness jumps to a new steady value. In figure 4, directed selection, we see the same dynamic of fitness change during a transient period (fig.3), then settling to a stable, higher, value when a stable attractor in the ecosystem state space has been reached. In this case the attractor consists of 2 species. Variation in their dynamics is simply caused by the added developmental noise. If it is removed it can be seen that the ecosystem has reached a fixed point.

Discussion

In the results above we see a combination of two types of variation, “instantaneous variation”, and variation caused by movement to a different basin of attraction. Instanta-

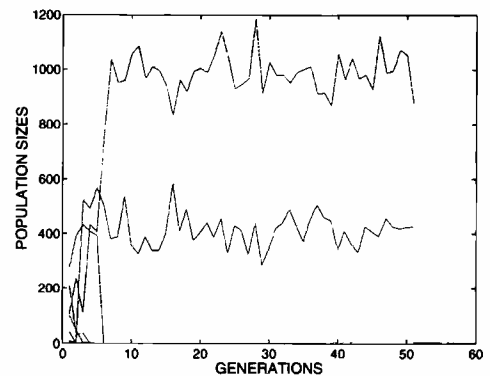


Figure 3: Final species population states for the best ecosystem in population 1 over 50 generations, directed selection.

neous variation” is the phenotypic variation of ecosystems in a population which may be following different trajectories but are ultimately destined for the same attractor. Stochastic sampling from a point on a particular trajectory will still tend to lead to the same attractor if the basins of attraction are broad and attractors widely spaced in state space. If species are close to an alternative equilibrium point/basin of attraction then variation due to sampling error or developmental stochasticity could allow the community access to a new stable state corresponding to a different phenotypic value, and potentially a higher fitness. In this way the community could increase its fitness. Even in systems subject to random rather than directed selection this effect could lead to change in fitness and more stable community compositions via a “ratchet” effect. The key issue for ecosystem evolvability is the reachability of those different basins of attraction. Our simple models show that fitter attractors can be selected at an early stage before the community reaches equilibrium. However, once these attractors are reached the perturbations due to sampling error and developmental noise are not large enough to allow a progression to attractors cor-

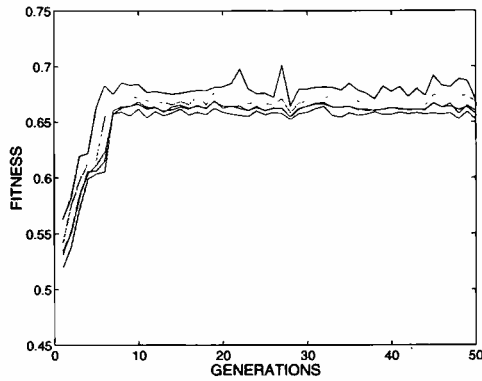


Figure 4: Fitness, best, mean, worst, and upper and lower quartiles, for ecosystem population 1 over 50 generations, directed selection.

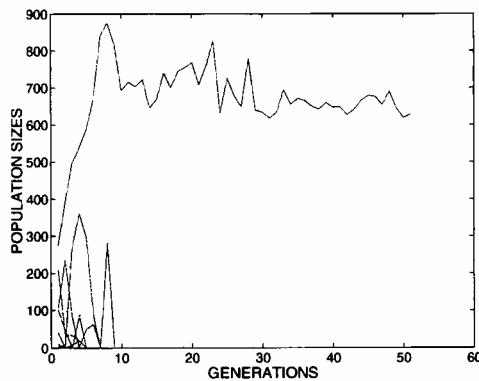


Figure 5: Final species population states for the best ecosystem in population 1 over 50 generations, random selection.

responding to higher fitness. Thus, the ecosystems' evolvability with these dynamics is very limited. The only option to increase fitness is by attractor switching in the early non-equilibrium stages, when we assume that the population sizes of the species within each ecosystem may be close to many different attractor boundaries.

Properties of Lotka-Volterra competition equations

In an N species Lotka-Volterra competition system there are 2^N possible stable equilibria corresponding to presence or extinction of each of the species. In any given system the number of realisable attractors will in fact be much less as many of the non-zero species values at equilibrium will correspond to negative numbers and hence not be allowed. If we assume that the probability of any non-zero valued species in an attractor being positive or negative is 0.5, then the expected number of equilibria with only positive or zero species sizes will be $(1 + 0.5)^{10} - 1 = 56$. However, not all of these potential equilibria will be stable. Limit cycles and chaotic dynamics are also possible although the latter

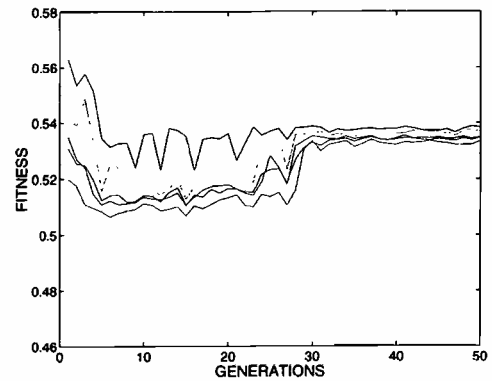


Figure 6: Fitness, best, mean, worst, and upper and lower quartiles, for ecosystem population 1 over 50 generations, random selection.

appear to be restricted to a fairly narrow parameter range (Vano et al., 2004). In theory, though, we should expect enough attractors to be present in a randomly generated set of ecosystem parameters to be able to achieve a response to selection.

One limitation of Lotka-Volterra dynamics is that the only possible change in attractor with asexual reproduction is via loss of species through competitive exclusion. This of course means that once we have reached a particular stable attractor with fewer species than the starting number, the attractors available to us are very much reduced in number, no matter how many might potentially exist. Additional noise, from environmental variation etc, could keep the populations out of equilibrium for longer, maintaining more species in the population, and allowing more attractors to be reached. In addition, more skewed interaction dynamics, with many more weakly than strongly competing species, and sparser connections, could both allow the maintenance of more species in the population and hence more potential for evolution. This sort of interaction distribution is often seen in natural ecosystems. Interestingly, we found no response to selection of ecosystems in which the interaction coefficients were generated from a uniform random distribution. The effects of the form of the interaction matrix on ecosystem evolvability deserve to be further investigated. Other options exist, however, given enough population diversity, sexual reproduction (mixing) could offer the opportunity to gain species and shift attractor that way.

Are there multiple stable states in nature?

Potentially, in real ecosystem dynamics the possibility exists of alternate stable states which do not involve complete competitive exclusion, but stability of different proportions of the same sets of species. Dynamics such as these would allow a much more flexible response to selection. The existence of multiple stable equilibria in natural populations

is still uncertain although several potential examples have been observed in marine ecosystems, both in competitive and predator-prey systems (Sutherland, 1981; Barkai and McQuaid, 1988). Both types of outcomes are seen, competitive exclusion and persistence at different proportional population sizes of the same species. In general however, the long time-series data needed to draw conclusions about the reality of these phenomena are not available. An additional cause of the existence of multiple stable states in ecosystems are environmental feedbacks, in which organisms affect their environment and alter it to their own preference. Such dynamics may play an important part in the ecosystem selection process in real ecosystems.

Conclusions

We have demonstrated a limited response to selection without genetic change in simple model ecosystems modeled as Lotka-Volterra competition systems. The response to selection depended on the skewed distribution of species interaction coefficients. Ecosystems were able to move between different attractors corresponding to phenotypes of varying fitness during the early stages of evolutionary runs. However, once stable attractors had been reached, the variation due to developmental noise and sampling error was not sufficient to allow movement to new attractors. It seems that evolution of whole ecosystems without genetic change is possible in principle. A requirement for such evolution is not only the potential for multiple stable (or locally stable) states in a particular ecosystem, but also the reachability of those states. In our model, evolution was limited by the competitive exclusion dynamics, which severely curtailed the number of available attractors once low species numbers were reached. In other more complex and realistic ecosystem dynamics this might not be the case. Our model is based on the restricted case of artificial, rather than natural, selection of ecosystems. Hence conclusions can only be drawn about the response to selection under a restricted set of circumstances, in which several of the requirements for a response to selection are enforced by the experimenter. This is an interesting and potentially useful topic in its own right. However, it is hoped that the results may ultimately be pertinent in considering the possibility of selection of communities outside the laboratory.

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