Natural Selection and Loop Analysis

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1   Introduction

Although much remains obscure, and will long remain obscure, I can entertain no doubt, after the most deliberate study and dispassionate judgment of which I am capable, that the view that each species has been independently created is erroneous.

—Charles Darwin, 1809–1882

Natural selection: a historical misconception

It is a common misconception that the theory of *evolution* is the same as the theory of *natural selection*. This is not so. Biological theory of evolution refers to temporal changes in the proportion of genes for various traits. Evolutionary changes can occur for different reasons. Natural selection, by far, is the most important mechanism of evolutionary changes[1].

Long before the publication of *The Origin of Species* in 1859 [1], most scholars had abandoned the notion of fixity of species through time, and had accepted the notion of change through some process of evolution. The modern theory of evolution as to explain *how* these changes are brought about, however, is due to Darwin. Darwin's theory of evolution by way of natural selection is based on three principles:

1. **Principle of variation.** Organisms within any species are qualitatively different.

2. **Principle of heredity.** Some of the existing variation among individuals is hereditary.

3. **Principle of selection.** Among the existing variants, some forms are more successful at surviving and reproducing.

The process of evolution through natural selection, as described by Darwin, can be better understood by drawing a parallel to the process of domesticating wild plants and animals by man through *artificial selection*. In the plant population, for instance, some plants have a higher yield than others. Taking advantage of the existing variability in yield, the plant breeder then selects the highest-yielding plants from the current generation and make them parents of the next generation of plants. If such high-yielding characteristics are indeed heritable, the next generation of plants should have a higher yield as well. While artificial

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[1]Other possible mechanism of evolution include the inheritance of acquired characteristics, gene flow, meiotic drive, and genetic drift.

selection dates back only as far as the time when people began to domesticate wild plants and animals, natural selection has been around since the beginning of life on earth. Hence, it was no accident that Darwin termed his model of evolution natural selection. In 1859, he wrote: "As man can produce a great result with his domestic animals and plants by adding up in any given direction individual differences, so could natural selection, but far more easily from having incomparably longer time for action" [1].

Although natural selection operates on the phenotypic characteristics of species, for natural selection to change the composition of population of a species, such phenotypes must be heritable and hence transmittable from generation to generation. Natural selection takes place when the individuals of the different genotypes either have different probabilities of survival or produce different numbers of offspring, or both; hence the reason for some genotypes to spread further in the population relative to the others.

If the population size is growing, all genotypes could be expanding in absolute numbers even as their relative proportions are changing. If the population size is more or less constant, then the spread of some genotypes must mean that others are declining.

For readings in the history, development, and implications of the theories of evolution and natural selection, see [1, 2, 3, 4, 10, 11, 13, 14, 16, 17].

In this paper, we focus on some other existing misconceptions about natural selection that are much more subtle in nature than the one addressed here. In particular, we will pay attention to the popular myth that natural selection works in the direction of stabilizing communities and making species more efficient and abundant. Using the qualitative method of loop analysis, as introduced in section 2.2, we will examine such assertions and will demonstrate that natural selection can work in ways that are by no means intuitively obvious, and that there is indeed no justification for such naive anticipations.

2 Loop analysis: signed digraphs

There is a one-to-one correspondence between loop models and systems of differential equations, where a system of n differential equations represents a community of n interacting species. The variables of the system represent either species abundances, or some by-product of species such as toxicity or predation intensity. Let X_i be the ith variable. Then we define the rate of change, or the growth rate of X_i as follows:

$$\frac{dX_i}{dt} = f_i(X_1, X_2, \ldots, X_n; C_1, C_2, \ldots) \tag{1}$$

where C_h represents a potential parameter of the system, such as biological properties of the component species, or the environmental factors such as temperature. If we assume that a system (community) is at or near equilibrium, we can then examine its local stability properties of when $\frac{dX_i}{dt} = 0$, $i = 1 \ldots n$.

Loop models are signed directed graphs, constructed from the structure of the interaction matrix, or the so called community matrix in ecology, of coefficients of X_i's evaluated at equilibrium[2]. Given a community matrix $\mathbf{A}$ as follows:

$$\mathbf{A} = \begin{pmatrix} \dfrac{\partial f_1}{\partial X_1} & \dfrac{\partial f_1}{\partial X_2} & \cdots & \dfrac{\partial f_1}{\partial X_n} \\ \vdots & \vdots & \vdots & \vdots \\ \dfrac{\partial f_n}{\partial X_1} & \dfrac{\partial f_n}{\partial X_2} & \cdots & \dfrac{\partial f_n}{\partial X_n} \end{pmatrix}$$

$$= \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & \vdots & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{pmatrix}$$

where a_{ij} is the coefficient of X_j in f_i, i.e. the effect of variable X_j on the growth rate of variable X_i, one can translate the community matrix $\mathbf{A}$ uniquely into a signed digraph. The variables of the system are the vertices of the graph, and the coefficients of the community matrix are the edges or links of the graph (see figure 1).

2.1 Definitions and notations

2.1.1 Links and their signs

The coefficients a_{ij} of the community matrix are readily taken to translating into the effect of the variable X_j on the growth rate of the variable X_i. Depending on the sign of such coefficients in the matrix, there will be two types of links in the signed digraph. If the sign of a_{ij} is negative in the original matrix, there will be a negative link from X_j to X_i, represented by the symbol —○. If the sign of a_{ij} is positive in the original matrix, meaning X_j has a positive impact on the growth rate of variable X_i, then there will be a positive link from X_j to X_i, represented by the symbol ⟶ (see figure 1).

2.1.2 Path and loops

A *path* is a sequence of links starting at a source variable and ending at a sink variable without going through any variable twice. A *loop* is a path where the sink variable is the

[2]The relationship between graphs and matrices have been developed independently by different researchers in different contexts. Samuel Mason at MIT [12] developed such models to compute gain in electrical circuits; Sewall Wright [18] used similar techniques to calculate statistical correlations among relatives of different breeding systems; Richard Levins [6] developed loop models to examine qualitative questions in ecology.

same as the source variable. Hence, in a loop, only the starting variable is met twice on the path. A loop that begins and ends on the same variable without going through any other intermediate variables is a *self-loop*.

A self-loop with a negative link is called *self-damped*. A self-loop with a positive link is called *self-accelerating* (see figure 1).

The *length* of a path or a loop is the number of links constituting the path or the loop. Consequently, a self-loop is a loop of length one.

The *sign* of a path or a loop is the product of the signs of the constituent links in the path or the loop.

2.1.3 Conjunct loops and disjunct loops

In a signed digraph there are two types of loops: *conjunct* loops and *disjunct* loops. Conjunct loops consist of those loops that have at least one variable in common. Disjunct loops have no variable in common.

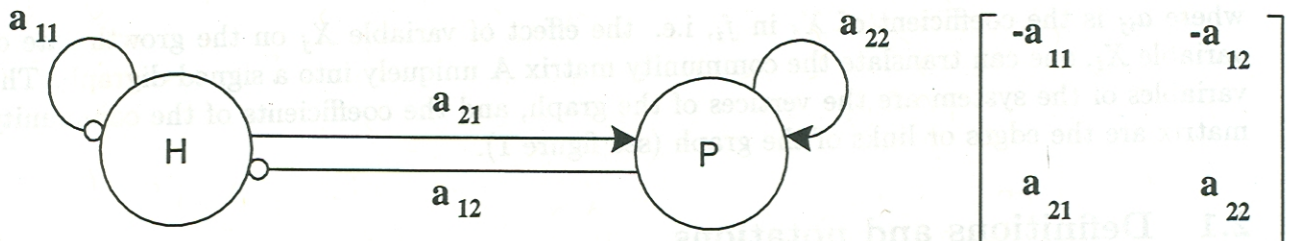Figure 1 provides a definitional illustration of loop models.

$$\begin{bmatrix} -a_{11} & -a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$

Figure 1: A predator-prey system with a self-damped herbivore (H), and a self-accelerating predator (P), and its community matrix.

2.2 Conditions for stability

The stability properties and the local behavior of systems of differential equations in the neighborhood of their critical points have been well studied. Here, we relate the general conditions of stability, as understood in systems theory, to the notion of the feedback of a system.

The characteristic polynomial, $p(\lambda)$ of a community matrix $\mathbf{A}$, is defined as $|\mathbf{A} - \lambda \mathbf{I}|$, where $\mathbf{I}$ is the identity matrix. For instance, the characteristic polynomial of a 3×3 matrix is the following:

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$$p(\lambda) = \begin{vmatrix} a_{11} - \lambda & a_{12} & a_{13} \\ a_{21} & a_{22} - \lambda & a_{23} \\ a_{31} & a_{32} & a_{33} - \lambda \end{vmatrix}$$

Expanding the determinant we get:

$$\begin{aligned} p(\lambda) = {} & \lambda^3 - [a_{11} + a_{22} + a_{33}]\lambda^2 + \\ & [(a_{11}a_{22} - a_{12}a_{21}) + (a_{11}a_{33} - a_{13}a_{31}) + (a_{22}a_{33} - a_{23}a_{32})]\lambda - \\ & [a_{11}(a_{22}a_{33} - a_{23}a_{32}) - a_{12}(a_{23}a_{31} - a_{21}a_{33}) + a_{13}(a_{21}a_{32} - a_{22}a_{31})] \quad (2) \end{aligned}$$

Equation 2 can be generalized for an n dimensional matrix as follows:

$$p(\lambda) = \lambda^n + \sum_{k=1}^{n-1} (-1)^k D_k \lambda^{n-k} \tag{3}$$

where D_k is the sum of all principal determinants of order k, corresponding to subsystems of k variables. But every such D_k can also be written as a sum of products of disjunct loops as can be investigated from equation 2. That is, we have:

$$D_k = \sum_{m=1}^{k} (-1)^{k-m} L(m,k) \tag{4}$$

where $L(m,k)$ is defined as the product of m disjunct loops with k variables. Note that for an $n \times n$ matrix, D_n is the determinant of the square matrix. We then transform this value into the measure of the feedback of a matrix. Specifically, we define the notion of "*feedback at level k*" as follows:

$$\begin{aligned} F_k ={} & (-1)^{k+1} D_k & \text{for } k = 1 \ldots n \\ ={} & (-1)^{k+1} \sum_{m=1}^{k} (-1)^{k-m} L(m,k) & \text{by equation 4} \\ ={} & \sum_{m=1}^{k} (-1)(-1)^{2k-m} L(m,k) \\ ={} & \sum_{m=1}^{k} (-1)^{m+1} L(m,k) & \text{since } (-1)^{2k-m} = (-1)^{-m} = (-1)^m \quad (5) \end{aligned}$$

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where feedback at level 0 is defined as $F_0 = -1$.

In this way, feedback at level k is the the net feedback of all the subsystems of k variables in a system of n variables, where $k = 1 \ldots n$.

As an example for the calculation of feedback terms, consider the predator-prey system of figure 1. At level 1, $F_1 = -a_{11} + a_{22}$; and at level 2,

$$F_2 = (-1)^2(-a_{12})(a_{21}) + (-1)^3(-a_{11})(a_{22}) = -a_{12}a_{21} + a_{11}a_{22}$$

Equipped with our definition of feedback at level k, as in equation 5, We can rewrite equation 3 as follows:

$$
\begin{aligned}
p(\lambda) &= \lambda^n + \sum_{k=1}^{n-1} (-1)^k (-1)^{k-m} L(m,k) \lambda^{n-k} \\
&= \lambda^n - \sum_{k=1}^{n-1} F_k \lambda^{n-k} \quad \text{by equation 5}
\end{aligned}
\tag{6}
$$

The characteristic polynomial resulting from equation 6 involves the feedback terms as coefficients. Although, one may not be able to generally solve polynomials of higher orders, one can determine the sign of $\text{Re}(\lambda_i)$ using the coefficients of such polynomials. By the Routh-Hurwitz theorem, for the system to be locally stable, i.e. for $\text{Re}(\lambda_i) < 0$, $i = 1 \ldots n$, the coefficients of the polynomial must satisfy two conditions [5]:

1. $F_k < 0$, $\forall k$.

2. Alternate Hurwitz determinants up to order n must be positive.

If the roots of the polynomial are real, then condition 1 alone suffices and guarantees that all the roots are negative, and hence the system is stable. But if some or all of the roots are complex, then conditions 1 and 2 together imply that the system is oscillatory, but returns to equilibrium through damped oscillations, and hence stable. The second condition needs more elaboration. A Hurwitz determinant of order k, H_k, is defined as follows:

$$
H_k =
\begin{vmatrix}
-F_1 & -F_3 & -F_5 & \cdots & -F_{2k-1} \\
-F_0 & -F_2 & -F_4 & \cdots & -F_{2k-2} \\
0 & -F_1 & -F_3 & \cdots & -F_{2k-3} \\
0 & -F_0 & -F_2 & \cdots & -F_{2k-4} \\
0 & 0 & -F_0 & \cdots & -F_{2k-5} \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 0 & 0 & \cdots & -F_k
\end{vmatrix}
$$

6

This means that for instance, for a system of 3 variables, where only the sign of H_2 needs to be checked, $H_2 = F_1 F_2 + F_3 > 0$ implies that negative feedback coming from shorter loops, in this case levels 1 and 2 combined, must be stronger than the negative feedback coming from the longer loops, in this case feedback at level 3. Since, in equation 6, lower order feedbacks are paired with the higher orders of λ, intuitively this means that if λ is small, we get slow damping, and fast damping if λ is large.

To date, there is no general form for H_n; for the purpose of this article test of positivity of H_2 will be sufficient.

3 Natural selection: not a virtuous force

It is often assumed that natural selection operates in the direction of stabilizing the communities. Furthermore, it is taken for fact that the abundance of a species undergoing selection is generally increased. This sometimes unspoken, false notion of evolution of communities, has persisted throughout the past century since the publication of Darwin's *The Origin of Species* in 1859. Why is that?

Darwin often spoke of natural selection as a "good" force, an "efficient" force, a "truer" force, a "serving" force, etc. In fact, chapter IV of *The Origin of Species* is full of such references. For example, "It may metaphorically be said that natural selection is daily and hourly scrutinizing, rejecting those that are *bad*, preserving and adding up all that are *good*, silently and insensibly working, ..." (emphasis not in the original); or "Although natural selection can act only through and for the *good* of each being, yet characters and structures, which we are apt to consider as of very trifling importance, may be acted on." (emphasis not in the original); etc. Of course, there are much more references that portray natural selection as a positive force throughout the book, and it is no surprise that the title of the chapter itself reads: *Natural Selection; or the Survival of the Fittest.*

But such references are only made with regards to the effect of evolution on the particular species undergoing selection, and hence, they cannot be generalized to the situations outside the domain of its action. What is the implication of such actions for a community of species as a whole and for the abundance of the coexisting species? In fact, it turns out that there are no obvious answers to these questions.

Using the method of loop analysis [6, 7, 15], we will examine such assertions as the "maximizing effects of natural selection" and will demonstrate otherwise. In particular, we will show that "there is no justification for the belief that natural selection results in greater *efficiency* or *stability* or in any other civic virtue" [6] (emphasis not in the original).

3.1 Natural selection and stability

What is the impact of selective pressures within each species of a community on the stability of the community as a whole?

It has been falsely presumed, within biological communities, that natural selection is an stabilizing force. That communities have always evolved and will continue to evolve in the direction of becoming more efficient and stable. Let's examine this assertion more closely.

Natural selection changes the composition of the genotypes of species by operating on those phenotypic characteristics that are heritable. Mathematically, this means that when a genetic variant arises in a species under selective pressures, a parameter C_h from equation 1 is ultimately altered. The parameters C_h are assumed to consist of those characteristics that depend on the genotype of species, such as fecundity or heat tolerance or any other heritable traits. Suppose that species i in a community consisting of n interacting species is undergoing selection. Then since the genetic variant that is altering parameter C_h is selected for, we must have that:

$$\frac{\partial f_i}{\partial C_h} > 0 \tag{7}$$

which means that the direction of selection solely depends on the growth-rate of species i, f_i. However, in what follows, we will demonstrate that the evolutionary consequences of that selection for the community depend on the entire ensemble of species in the community and the dynamics of their interactions, since f_i itself depends on such ensemble (see equation 1).

Example: Figure 2 illustrates an ecosystem consisting of blue-green algae (B); green algae (G); two nutrients: nitrate (N), secreted by blue-green algae and consumed by green algae, and phosphate (P), consumed by both the green and the blue-green algae; and an herbivore (H) feeding on the green algae. In addition, the blue-green algae produces a substance with a toxic effect on the green algae, represented by the negative link a_{GB}.

Using the methodology developed in section 2.2, we calculate the qualitative values of the feedback terms to examine the conditions for stability. At level 1, we have $F_1 = -a_{NN} - a_{PP} < 0$. Next we examine feedback at level 2:

$$
\begin{aligned}
F_2 &= (a_{GN})(-a_{NG}) + (a_{BP})(-a_{PB}) + (a_{GP})(-a_{PG}) + \\
&\quad (a_{HG})(-a_{GH}) - \overline{(-a_{PP})}(-a_{NN}) \\
&= -a_{GN}a_{NG} - a_{BP}a_{PB} - a_{GP}a_{PG} - a_{HG}a_{GH} - a_{PP}a_{NN} \\
&< 0
\end{aligned}
$$

What about feedback at level 3?

$$
\begin{aligned}
F_3 &= -(-a_{PP})(-a_{GN}a_{NG}) - (-a_{PP})(-a_{GH}a_{HG}) - (-a_{NN})(-a_{BP}a_{PB}) \\
&\quad -(-a_{NN})(-a_{GP}a_{PG}) - (-a_{NN})(-a_{GH}a_{HG}) + (-a_{PG})(-a_{GB})(a_{BP}) \\
&= -a_{PP}a_{GN}a_{NG} - a_{PP}a_{GH}a_{HG} - a_{NN}a_{BP}a_{PB} \\
&\quad -a_{NN}a_{GP}a_{PG} - a_{NN}a_{GH}a_{HG} + a_{PG}a_{GB}a_{BP}
\end{aligned}
$$

?

It is not clear whether $F_3 < 0$ or $F_3 > 0$! The loop of length 3, namely $a_{PG}a_{BP}a_{GB}$, contributes a positive term to F_3 that makes it ambiguous for a decision to be made. The same positive loop also enters into F_4 which makes it possible for F_4 to be positive as well.

Suppose now that there is selection pressure on the green algae towards becoming more resistant to the toxin released by the blue-green algae. Such pressure affects the system in the direction of weakening the link a_{GB} and making it less negative. This link that

$$\begin{bmatrix} -a_{NN} & 0 & a_{NB} & -a_{NG} & 0 \\ 0 & -a_{PP} & -a_{PB} & -a_{PG} & 0 \\ 0 & a_{BP} & 0 & 0 & 0 \\ a_{GN} & a_{GP} & -a_{GB} & 0 & -a_{GH} \\ 0 & 0 & 0 & a_{HG} & 0 \end{bmatrix}$$
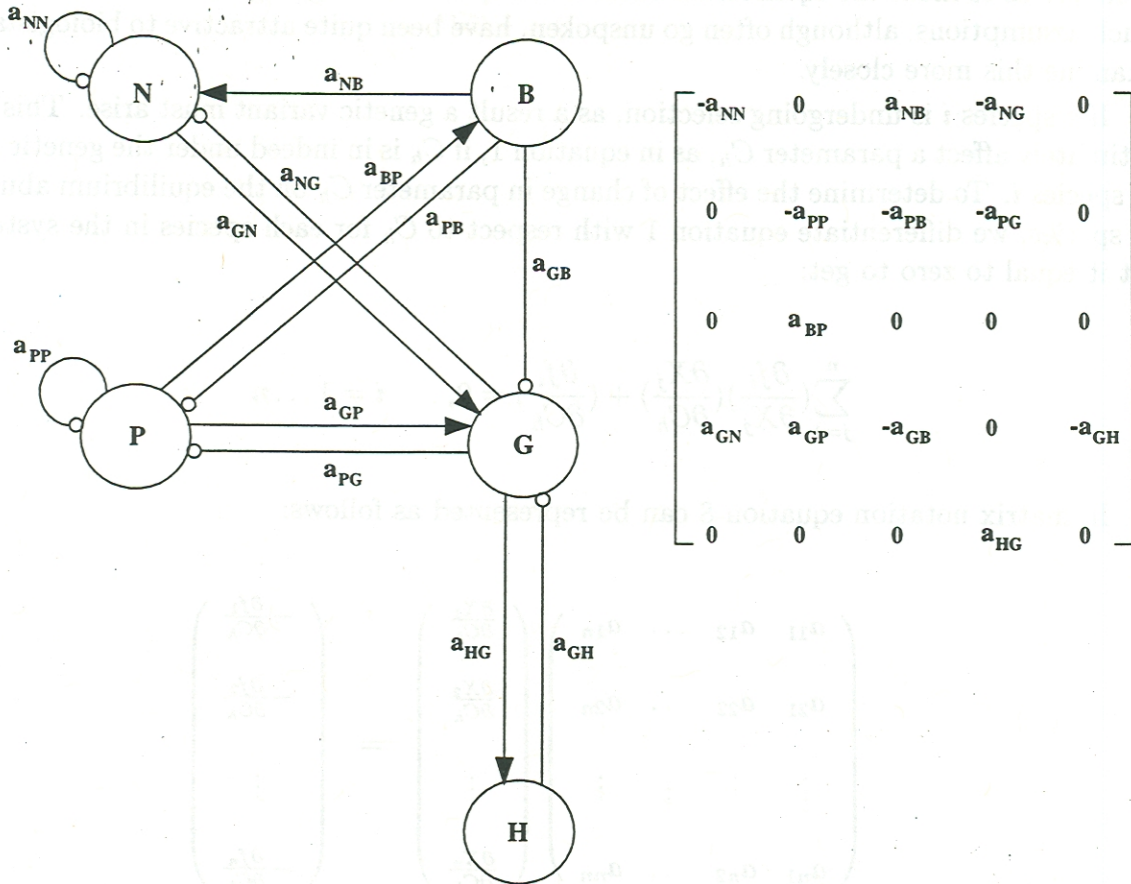
Figure 2: An ecosystem consisting of blue-green algae (B); green algae (G); two nutrients: nitrate (N), consumed by green algae, and phosphate (P) consumed by both the green and the blue-green algae; and an herbivore (H) feeding on the green algae. The system can be stabilized if selection is for toxin resistance within the green algae.

under equilibrium contributes a positive term to both F_3 and F_4 via the loop of size 3, under selection, could contribute a negative term and hence may have a stabilizing effect on the system. However, if selection within the green algae is for less susceptibility to the herbivore predation, then by weakening the link a_{GH} it may have a destabilizing effect on the community since it contributes a negative term to F_3.

Hence, depending on the dynamics of the interrelations between the species of a system, selection within the components may either stabilize or destabilize the community as a whole, in ways that are not intuitively obvious.

3.2 Natural selection and abundance of species

What is the impact of selective pressures within each species of a community on the abundance of the species itself and other coexisting species?

It has been naively presumed that the driving force of natural selection is generally di-

rected so as to make the equilibrium number of a species undergoing selection more abundant. Such assumptions, although often go unspoken, have been quite attractive to biologists. Let's examine this more closely.

If a species i is undergoing selection, as a result a genetic variant must arise. This should ultimately affect a parameter C_h, as in equation 1, if C_h is in indeed under the genetic control of species i. To determine the effect of change in parameter C_h on the equilibrium abundance of species, we differentiate equation 1 with respect to C_h for each species in the system and set it equal to zero to get:

$$\sum_{j=1}^{n}\left(\frac{\partial f_i}{\partial X_j}\right)\left(\frac{\partial X_j}{\partial C_h}\right) + \left(\frac{\partial f_i}{\partial C_h}\right) = 0, \qquad i = 1 \ldots n \tag{8}$$

In matrix notation equation 8 can be represented as follows:

$$
\begin{pmatrix}
a_{11} & a_{12} & \cdots & a_{1n} \\
a_{21} & a_{22} & \cdots & a_{2n} \\
\vdots & \vdots & \vdots & \vdots \\
a_{n1} & a_{n2} & \cdots & a_{nn}
\end{pmatrix}
\begin{pmatrix}
\frac{\partial X_1}{\partial C_h} \\
\frac{\partial X_2}{\partial C_h} \\
\vdots \\
\frac{\partial X_n}{\partial C_h}
\end{pmatrix}
=
\begin{pmatrix}
-\frac{\partial f_1}{\partial C_h} \\
-\frac{\partial f_2}{\partial C_h} \\
\vdots \\
-\frac{\partial f_n}{\partial C_h}
\end{pmatrix}
$$

By matrix algebra, we can then solve for $\dfrac{\partial X_j}{\partial C_h}$ as follows:

$$\frac{\partial X_j}{\partial C_h} = \frac{
\begin{vmatrix}
a_{11} & a_{12} & \cdots & -\frac{\partial f_1}{\partial C_h} & \cdots & a_{1n} \\
a_{21} & a_{22} & \cdots & -\frac{\partial f_2}{\partial C_h} & \cdots & a_{2n} \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
a_{n1} & a_{n2} & \cdots & -\frac{\partial f_n}{\partial C_h} & \cdots & a_{nn}
\end{vmatrix}
}{
\begin{vmatrix}
a_{11} & a_{12} & \cdots & a_{1j} & \cdots & a_{1n} \\
a_{21} & a_{22} & \cdots & a_{2j} & \cdots & a_{2n} \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
a_{n1} & a_{n2} & \cdots & a_{nj} & \cdots & a_{nn}
\end{vmatrix}
} \tag{9}$$

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Let's see if we can understand the intuition behind equation 9. The denominator of equation 9 is simply the feedback at level n, i.e. F_n. The numerator is more tedious and needs more elaboration before turning it into feedback notation. Note that the effect of substituting the jth column of the community matrix with $-\dfrac{\partial f_j}{\partial C_h}$ is of breaking all the closed loops that have the link a_{ij} in common. On expanding the numerator, we make the following observation: for an $n \times n$ matrix, the numerator is the sum of all $-\dfrac{\partial f_i}{\partial C_h}$, $i = 1 \ldots n$ each accompanied by a coefficient. The coefficient of $-\dfrac{\partial f_i}{\partial C_h}$ is the sum of all possible products of open paths between X_i and X_j, each multiplied by all the closed loops that share no variables with the open path considered. But this simply means that each open path is multiplied by the net feedback of the complement subsystem. Now, let $P_{ji}^{(k)}$ represent the open path from X_i to X_j consisting of k variables, and $F_{n-k}(comp)$ to represent the feedback of the complement subsystem of size $n - k$, i.e. the subsystem remaining after excluding the open path of k variables from the system. Then, equation 9 can be rewritten in terms of feedback loops as follows:

$$\frac{\partial X_j}{\partial C_h} = \frac{\sum_{i,k} (\frac{\partial f_i}{\partial C_h}) P_{ji}^{(k)} F_{n-k}(comp)}{F_n} \tag{10}$$

Equipped with equation 9 and an intuitive understanding of it, by way of equation 10, we are now ready to examine the question raised at the start of this section through some examples.

Example: Figure 3 illustrates a community consisting of two competing self-damped prey species X_1, X_2; and a "keystone predator"[3] X_3 preying upon both species.

Suppose that selection for some trait C_1 within species X_1 increases its viability or fecundity. Since C_1 is selected for, we must have that:

$$\frac{\partial f_1}{\partial C_1} > 0, \quad \frac{\partial f_2}{\partial C_1} = 0, \quad \frac{\partial f_3}{\partial C_1} = 0 \tag{11}$$

We can now examine the effect of change in C_1 on the equilibrium levels of all three species. Note that for the system to be stable at all, $F_3 < 0$. Therefore, by equation 9 we have:

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[3] In ecology, a keystone predator refers to a predator that permits coexistence of several competing prey species.

$$\begin{bmatrix} -a_{11} & -a_{12} & -a_{13} \\ -a_{21} & -a_{22} & -a_{23} \\ a_{31} & a_{32} & 0 \end{bmatrix}$$
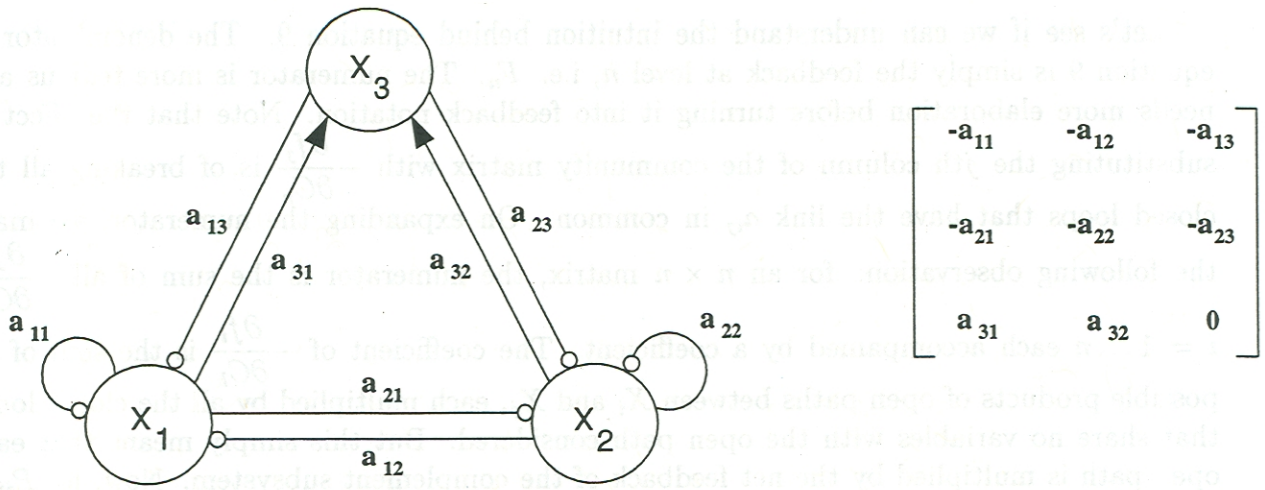
Figure 3: A community consisting of two competing self-damped prey species X_1, X_2; and a keystone predator X_3 preying upon both species. The introduction of the predator has a stabilizing effect on the community.

$$\frac{\partial X_1}{\partial C_1} = \frac{\begin{vmatrix} -\frac{\partial f_1}{\partial C_1} & -a_{12} & -a_{13} \\ 0 & -a_{22} & -a_{23} \\ 0 & a_{32} & 0 \end{vmatrix}}{F_3}$$

$$= \frac{-\frac{\partial f_1}{\partial C_1}(a_{23}a_{32})}{F_3}$$

$$> 0$$

$$\frac{\partial X_2}{\partial C_1} = \frac{\begin{vmatrix} -a_{11} & -\frac{\partial f_1}{\partial C_1} & -a_{13} \\ -a_{21} & 0 & -a_{23} \\ a_{31} & 0 & 0 \end{vmatrix}}{F_3}$$

$$= \frac{\frac{\partial f_1}{\partial C_1}(a_{23}a_{31})}{F_3}$$

$$< 0$$

$$\frac{\partial X_3}{\partial C_1} = \frac{\begin{vmatrix} -a_{11} & -a_{12} & -\frac{\partial f_1}{\partial C_1} \\ -a_{21} & -a_{22} & 0 \\ a_{31} & a_{32} & 0 \end{vmatrix}}{F_3}$$

$$= \frac{\frac{\partial f_1}{\partial C_1}(a_{21}a_{32} - a_{22}a_{31})}{F_3} \tag{12}$$

?

That is, selection within X_1 increases its own abundance, but decreases the abundance of X_2. As for X_3, the direction of change is not clear; it depends on the relative magnitude of the coefficients a_{21}, a_{32}, a_{22}, and a_{31}. For instance, if the predator preys more upon X_1, then its abundance may increase since it implies that $a_{31} > a_{32}$, and this makes the coefficients in the numerator of equation 14 more negative.

Now suppose that evolution within X_3 is so that a parameter C_3 is selected for. In principle alteration of parameter C_3 should increase some genotype related to the predator's viability or fecundity. Hence, this implies that we must have:

$$\frac{\partial f_1}{\partial C_3} = 0, \quad \frac{\partial f_2}{\partial C_3} = 0, \quad \frac{\partial f_3}{\partial C_3} > 0 \tag{13}$$

Let's examine the effect of change in C_3 on the equilibrium levels of all three species. Note that for the system to be stable at all, again $F_3 < 0$. Therefore we have:

$$\frac{\partial X_3}{\partial C_3} = \frac{\begin{vmatrix} -a_{11} & -a_{12} & 0 \\ -a_{21} & -a_{22} & 0 \\ a_{31} & a_{32} & -\frac{\partial f_3}{\partial C_3} \end{vmatrix}}{F_3}$$

$$= \frac{\frac{\partial f_3}{\partial C_3}(a_{12}a_{21} - a_{11}a_{22})}{F_3} \tag{14}$$

$$< 0$$

since the coefficient of $\frac{\partial f_3}{\partial C_3}$ in equation 14 is F_2 for the subsystem (X_1, X_2) which by definition must be positive if X_3 is a keystone predator. But this implies that $\frac{\partial X_3}{\partial C_3} < 0$! In other words,

selection on the predator for more viability reduces its abundance, and hence the stabilizing predator can select itself to extinction. This is not an intuitive result, and it should clarify the claim we made at the beginning of this paper that the direction of natural selection are not always predictable or intuitively obvious.

Next, if we examine $\dfrac{\partial X_1}{\partial C_3}$, we have:

$$
\frac{\partial X_1}{\partial C_3} = \frac{
\begin{vmatrix}
0 & -a_{12} & -a_{13} \\
0 & -a_{22} & -a_{23} \\
-\frac{\partial f_3}{\partial C_3} & a_{32} & 0
\end{vmatrix}
}{F_3}
$$

$$
= \frac{\frac{\partial f_3}{\partial C_3}(a_{13}a_{22} - a_{12}a_{23})}{F_3}
$$

$$
?
\tag{15}
$$

The direction of change for X_1 is not clear, and it depends on the relative magnitude of the coefficients a_{13}, a_{22}, a_{12}, and a_{23}. If $a_{23} > a_{13}$, that is, if the predator preys more on X_2 than X_1, then the change in the abundance of X_1 is likely to be positive; a rather intuitive result. A similar kind of analysis holds for the study of direction of change in the equilibrium level of X_2.

Hence, depending on the dynamics of the interrelations between the species of a system and with their environment, selection within the component species may either increase or decrease the equilibrium abundance of the species in the community.

4   Discussion

4.1   An extension

What happens when we leave the so called mendelian world of lower organisms, where evolution can occur in matter of hours, and enter populations of higher organisms such as those of humans?

For a mendelian population to be perpetuated, it may be sufficient to have a single surviving pair or a single individual. "Thus, when a bacterial culture containig billions of cells is exposed to a lethal concentration of antibiotics, such as streptomycin, the presence of a single resistant mutant cell is sufficient to perpetuate the strain." [10].

Where cultural and social measures have not interposed themselves between us and the physical environment, natural selection operates as it did before. Disease and diet are examples of areas where natural selection is still in work in the context of human populations. Not all populations are equally exposed to all diseases, and therefore nor are they equally

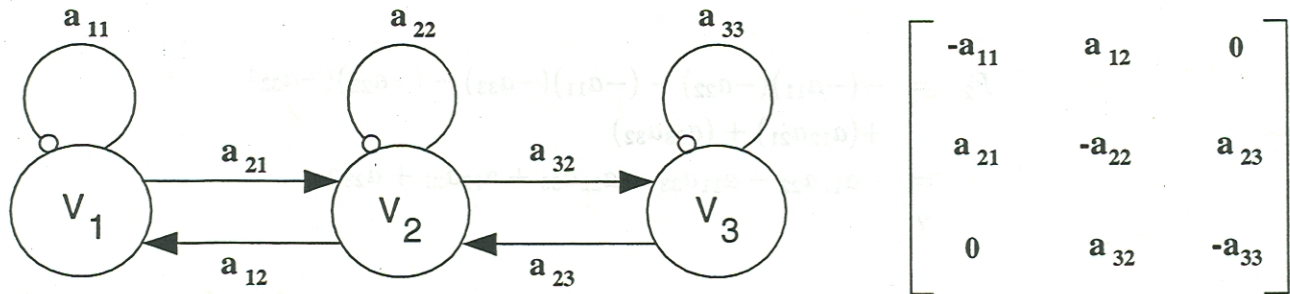$$\begin{bmatrix} -a_{11} & a_{12} & 0 \\ a_{21} & -a_{22} & a_{23} \\ 0 & a_{32} & -a_{33} \end{bmatrix}$$

Figure 4: A population cohort consisting of three vulnerability classes. The links between pair of classes indicate social mobility and/or movement of people by natural processes such as diseases or aging.

susceptible to all; malaria is one such disease, where a population of west Africans posses a protective genetic factor, namely the sickle-cell trait. Similarly, not every one can digest bean or milk as easily as some others.

Hence, we have not eliminated natural selection and evolution may still occur on geological time scales within human populations. But where we have created social environments, certain genetic differences become symbols of social behavior, and so we can speak of selection acting in a non-geological time scale[4]. For instance, skin pigmentation is an identifier of race and is a heritable trait, but there is nothing inherent in the melanin concentration in the skin which would influence the likelihood of getting arrested, as it is statistically a fact in the black population.

Every social measure taken within the human populations, therefore acts as selective pressures upon individuals; population cohorts identified by age, sex, race or ethnicity; or even psudo-populations such as organizations. As a result, there will be changes in the differential survival and reproductivity of those populations. Let's try to apply our loop methodology to two such populations.

Vulnerability and stability: Suppose that a human population cohort is distributed among 3 vulnerability classes, V_i, each associated with its own mortality rate. Here, "vulnerability" is defined with respect to the general health status of people. Furthermore, the degree of vulnerability is assumed to increase with index i. For example, V_3 is more vulnerable than V_2. Further, individuals in one class may move to another due to disease processes or natural processes such as aging, in which case the flow is to the adjacent higher vulnerability classes; but there is also some back flow due to social mobility and health-improvement policies, acquiring knowledge and skill, or good fortune, etc. This model is illustrated in figure 4.

At level 1, we have $F_1 = -a_{11} - a_{22} - a_{33} < 0$. Next we examine feedback terms at leve 2 and 3:

---

[4]Selection simply refers to differential survival or reproduction or both, and is one of the three postulates that Darwin had for natural selection to cause genetic evolution.

$$F_2 = -(-a_{11})(-a_{22}) - (-a_{11})(-a_{33}) - (-a_{22})(-a_{33})$$
$$+(a_{12}a_{21}) + (a_{23}a_{32})$$
$$= -a_{11}a_{22} - a_{11}a_{33} - a_{22}a_{33} + a_{12}a_{21} + a_{23}a_{32}$$
$$?$$

What about feedback at level 3?

$$F_3 = (-a_{11})(-a_{22})(-a_{33}) - (-a_{11})(a_{23}a_{32}) - (-a_{33})(a_{12}a_{21})$$
$$= -a_{11}a_{22}a_{33} - a_{11}a_{23}a_{32} + a_{33}a_{12}a_{21}$$
$$?$$

The loops of size 2, namely $a_{12}a_{21}$ and $a_{23}a_{32}$ contribute positive terms to both F_2 and F_3, which make it ambiguous as to whether the system is stable or not.

Now suppose that there is selection for less vulnerability in V_3. This could occur, for instance, due to a new health policy by the government which affects mostly the poor and the elderly which by definition should reside in the highest vulnerability class. As a result some people from V_3 will move to V_2. This means that the link a_{23} is further strengthend, which in turn, unless the self dampings are strong, will destabilize the community since a_{23} contributes a positive term to F_2 and F_3. Similarly, any increased movement towards more vulnerable classes has a destabilizing effect as well, but that's rather intuitive. However, selection for preventing movements in any direction promotes stability. This is an intriguing result: increased social mobility could have devistating effects in a society that has reached equilibrium!

The dawn of Internet: Consider a technological system (techno-society) consisting of two competing computer companies, namely Microsoft (M) and Netscape (N), as in figure 5. Self dampings of the companies are possibly be due to implementation of occasional "bad" ideas. Let's examine the conditions for stability:

At level 1, we have $F_1 = -a_{11} - a_{22} < 0$. At level 2 we have:

$$F_2 = -(-a_{11})(-a_{22}) + (-a_{12})(-a_{21})$$
$$= -a_{11}a_{22} + a_{12}a_{21}$$
$$?$$

The sign of F_2 is ambiguous. Unless the self damping effect are very strong, F_2 may be positive and hence the system unstable. It is true that Microsoft's monopoly has been driving all other competing industries towards extinction in the direction of destabilizing

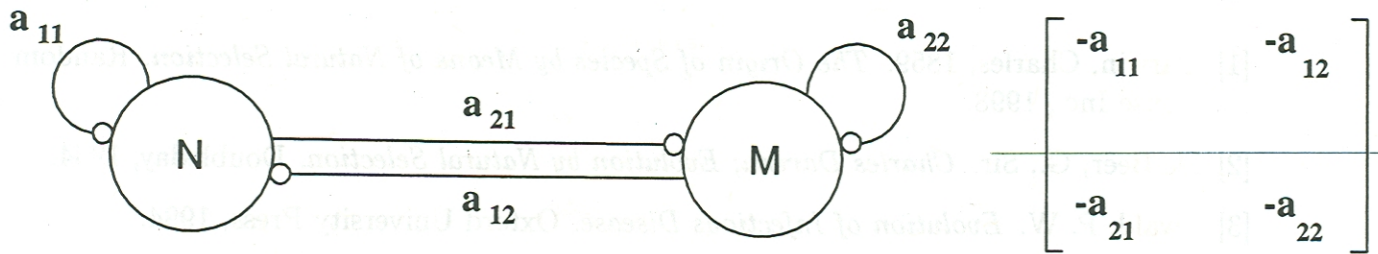$$\begin{bmatrix} -a_{11} & -a_{12} \\ -a_{21} & -a_{22} \end{bmatrix}$$

Figure 5: A techno-society consisting of two competing computer companies, Microsoft (M) and Netscape (N).

the entire techno-society. But in fact, this is an inherent outcome of any dynamical system of this sort. The bottom line is that competing species cannot "coexist" in the absence of an stabilizing factor. Thus far, this has been the outcome of the power struggle between Microsoft on one side and all the other competing companies on the other side. But then the government stepped in and assumed the role of a keystone, and so we get the same picture as in figure 3. Clearly, our keystone is aiming at stabilizing the system by establishing stronger tax laws, anti-trust regulations, and monitoring plans (represented as negative links in the digraph of figure 3). But the question is: By selecting for more regulations, can a goverment select itself to extinction? I leave this question open to brain storm.

4.2   Conclusions

1. The course of natural selection within species, may affect communities in ways that are not intuitively obvious and therefore not predictable. In particular, there is no justification for the popular assumption that natural selection generally make communities more stable and efficient.

2. It is by no means inevitable that natural selection serves to increase the abundance of the species undergoing selection. Moreover, it is not clear how the abundance of other coexisting species is affected.

3. There is potential for applying the methodology of loop analysis to structures within which selection forces operate. We have particularly argued for its applicability to problems pertaining to human populations. Specifically, we demonstrated through examples of social and technological nature that such qualitative approach can help unravel mysteries about stability of the societal structures within the human population.

Acknowledgment

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