THE EVOLUTION OF DIVERSITY IN TWO-LEVEL SELECTION

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ABSTRACT. Though many evolutionary processes tend to decrease genetic diversity in populations throughout time, empirical studies often find unaccounted-for diversity in genomes within many populations. While there have been several mechanisms proposed to explain this phenomenon, this paper explores the concise and direct proposal of "social heterosis" in which diversity is evolutionarily beneficial to all members of a given group. We use a dynamical (PDE) model of two-level selection to explore possible effects of group level diversity.

1. INTRODUCTION

Directional selection, which favors a specific gene over all others, and genetic drift, which eliminates genes from the sampling pool due to stochastic variation among generations contribute to strong selection against diversity within a population. However, in many populations genetic diversity has been maintained at a very high level. In light of this, Nonacs & Kapheim (2009) proposed the mechanism of *social heterosis*, by which groups experience benefits due to a diverse gene pool. They explain that there are many examples where group-level diversity is evolutionarily beneficial. If a population includes species that can occupy separate ecological niches, it can increase the carrying capacity of a specific environment. If a population maintains diverse immunological defenses, it can better withstand or prevent a widespread infection. These examples may require groups of individuals to possess mutually exclusive characteristics for the desired group-level effect, meaning that evolutionarily advantageous mixtures of traits must be selected on the group-level.

We continue this line of research by constructing and finding numerical solutions to a dynamical model (PDE) of two-level selection (closely modeled after Simon 2010) that affirms the group-level benefits of diversity within a population.

2. ENVIRONMENT AND GROUP CONSTRUCTION

We take as fundamental the notion that within an environment, there exist distinct types or species of organisms. These types are set apart in any number of ways, but including different types is a prerequisite to an evolutionary process. In this paper, we consider an environment with $n > 1$ individual types of organisms. In order to explore the benefits of diversity, we must work with a model that considers the role of groups in selection (a so-called two-level selection model). We model their compositions as vectors that change in time.

Definition 2.1. The *state of a group* is a vector $\vec{x}(t) = (x_1(t), ..., x_n(t)) \in \mathbb{R}^n_+$, where, if $1 \leq i \leq n, x_i(t)$ is the number of type i individuals at time t. The composition of a group changes throughout time in ways that will be described in this paper.

Definition 2.2. The *state of the environment* at time t is a density function $\theta_t : \mathbb{R}_+^n \longrightarrow \mathbb{R}_+$, where $\theta_t(\vec{x})$ is a measure of the number of all groups within the environment that very closely resemble $\vec{x}(t)$, i.e., if $A \subset \mathbb{R}_+^n$ and $d\vec{x} = (dx_1, \ldots, dx_n)$, then:

$$\int_A \theta_t(\vec{x}) d\vec{x}$$

is the number of $\vec{u}$ groups such that $\vec{u} \in A$.

This function very closely resembles the classical probability density function but $\int \theta_t d\vec{x} = G(t)$,[1] where $G(t)$ is the total number of groups in the environment at time t and $G(t)$ not necessarily is equal to 1, as it would be in a probability density function. When this is understood, we find that the function $\frac{\theta_t(\vec{x})}{G(t)}$ is analogous to the multivariate probability density function.

Another useful statistic that may be derived from this function is the number of a specific type of organism within the environment. For example, at time t the number of type i organisms is equivalent to $\int x_i \theta_t(\vec{x}) d\vec{x}$.

3. Birth and Death Rates Within Groups

The fundamental characteristic of a specific species in our model is its birth rate, which determines the individual rate of success at reproduction. We will be denoting the birth rate of a type i organism as b_i. On the other hand, we fix the death rate $d(\vec{x})$ of all types as proportional to the population of the group:

$$d(\vec{x}) = c \cdot \sum_{i=1}^{n} x_i \tag{3.1}$$

where c is a constant.

The birth rate of an individual species is dependent upon its type, while its death rate is equivalent to that of other species in its group, so birth rate is sometimes referred to as a species's fitness. From these developments, we can describe the dynamics of individual species within a group. For any i such that $1 \leq i \leq n$, the dynamics of the type can be stated as:

$$\frac{dx_i}{dt} = x_i(b_i - d(\vec{x})) \tag{3.2}$$

In all biological populations, mutation plays a role in evolutionary dynamics. We will consider mutation as the rate of birth of a type j species from a type i parent. To specify all these rates, let M be a $n \times n$ "mutation matrix" where M_{ij} is the probability of mutation from i to j, that is, the probability that a type i parent gives birth to a type j offspring. To lend familiarity to this concept, we recognize that $M_{ii} \leq 1$ is the probability of a "normal" birth. Additionally, for all i, we say that $\sum_{j=1}^{n} M_{ij} = 1$, as we assume that all parents must given birth to offspring of a known type.

Now, we'll formulate the "effective birth rate" of a type i species. First, its birth rate b_i determines the total birth rate of the parents, but $b_i \cdot M_{ii} \leq b_i$ is the birth

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[1] When writing $\int$ for the remainder of this paper, we are denoting an integral over the non-negative quadrant. Additionally, we may omit t in formulas that do not explicitly require it.

rate of i type offspring from i parents, as it is the proportion of i births that do not mutate into other types. Additionally contributing to the growth of x_i are other types with mutant i offspring. For example, $b_j \cdot M_{ji}$ is the number of i offspring with j parents. Therefore, across all species, we have $\sum_{j \neq i}^{n} b_j \cdot M_{ji}$ being the rate of i births due to such favorable mutations. Returning to the above equation, we revise the dynamics of an individual type:

$$\frac{dx_i}{dt} = x_i(b_i - d(\vec{x})) \tag{3.3}$$

$$= x_i \left(b_i \cdot M_{ii} - c \cdot \sum_{i=1}^{n} x_i \right) + \sum_{i \neq j} x_j \cdot b_j \cdot M_{ji} \tag{3.4}$$

$$= \sum_{j=1}^{n} x_j \cdot b_j \cdot M_{ji} - x_i \cdot c \cdot \sum_{i=1}^{n} x_i. \tag{3.5}$$

Now, let's consider the dynamics of an individual group with $n = 2$ types before we formulate group level events. From the equation above, we have:

$$\frac{dx_1}{dt} = x_1 \cdot b_1 \cdot M_{11} + x_2 \cdot b_2 \cdot M_{21} - c(x_1 + x_2) \tag{3.6}$$

$$\frac{dx_2}{dt} = x_2 \cdot b_2 \cdot M_{22} + x_1 \cdot b_1 \cdot M_{12} - c(x_1 + x_2). \tag{3.7}$$

However, as $M_{11} + M_{12} = 1$ and $M_{21} + M_{22} = 1$, we simplify the above to state:

$$\frac{dx_1}{dt} = x_1 \cdot b_1 \cdot (1 - M_{12}) + x_2 \cdot b_2 \cdot M_{21} - c(x_1 + x_2) \tag{3.8}$$

$$\frac{dx_2}{dt} = x_2 \cdot b_2 \cdot (1 - M_{21}) + x_1 \cdot b_1 \cdot M_{12} - c(x_1 + x_2). \tag{3.9}$$

We numerically solved these equations using Euler's method in MATLAB and have included and discussed our results in the appendix [Fig. 1].

4. Extinction and Fissioning Rates Within the Environment

As mentioned before, a critical aspect of this model is that it rewards diversity. We will measure a group's diversity in terms of its "information entropy," using Shannon's Diversity index. We use this index due to its consideration of both the number and evenness of a given group's types as well as its widespread acceptance as a standard metric in the field of ecology (Krebs 1989). For any state of a group, $\vec{x}$, the probability that an individual is type i is

$$p_i = \frac{x_i}{\sum_{i=1}^{n} x_i}.$$

Then, the "entropy," or diversity of a group $\vec{x}$ is

$$E(\vec{x}) = \sum_{i=1}^{n} (p_i \ln p_i). \tag{4.1}$$

As most $p_i < 1$, we notice that $E(\vec{x})$ will generally have a negative value, with the more highly negative values being attributed to more diverse populations.

Additionally, we must also consider other natural factors which may have a detrimental effect on a group's survival rate. Naturally, as the number of groups in an environnment increases, resources become more scarce, decreasing the likelihood that any individuals will be able to reproduce successfully.

Now, we'll use the concept of diversity to give diverse groups an evolutionary benefit in the environment. Let the extinction rate $e_t(\vec{x})$ be the chance over a given time period that a group (and all of its members) is destroyed in a catastrophic event, such as an infection. Now, as $G(t) \geq 0$ and $E(\vec{x}) \leq 0$, let e_1, e_2 be postitive constants and let the extinction rate of a group be:

$$e_t(\vec{x}) = e_1 \cdot G(t) \cdot e^{e_2 \cdot E(\vec{x})}. \tag{4.2}$$

This construction rewards diverse groups as $e_2 \cdot E(\vec{x})$ will be increasingly negative as a group becomes more diverse. Additionally, as e_t is directly proportional to the number of groups in the environment, it also respects the increased probability that groups go extinct as the environment becomes more crowded.

Another way that groups can transform is through the process of fissioning, which is described by a rate and a density. We consider this event the "death" of an individual group and the "birth" of other groups. First, let the fissioning rate be chance that an $\vec{x}$ type group will fission over a given time period. We suggest that this chance is directly proportional to the size of a given group. Hence:

$$f_t(\vec{x}) = m \cdot \sum_{i=1}^{n} x_i. \tag{4.3}$$

Now, we must describe *how* a group fissions. For the sake of simplicity, we suppose that all groups fission into two new distinct groups. When a group fissions, we say that each individual in the group randomly decides which group to join by flipping a fair coin. To do this with precision, we define the fissioning density, which represents the expected number of $\vec{u}$ type groups that result from the fissioning of a $\vec{x}$ type group.

Definition 4.4. The fissioning density is an integrable function $h(\vec{x}, \vec{u})$ where $\vec{u}, \vec{x} \in \mathbb{R}^n$ which satisfies $0 \leq u_i \leq x_i$ and:

$$\int u_i h(\vec{x}, \vec{u}) d\vec{x} \leq x_i$$

for all $i = 1, \ldots, n$.

This ensures that the resultant groups from a fissioning event do not exceed the size of the original group. In this case, we assume that the expected value for each type in the new group u_i is normally distributed with mean $\frac{x_i}{2}$, and variance $\frac{x_i}{4}$, as individuals from each type flip a fair coin to determine group membership. As normal distribution curves are specified only by mean and variance, our fissioning density is described by:

$$h(\vec{x}, \vec{u}) = 2 \cdot \prod_{i=1}^{n} \frac{\exp\left[\frac{-2 \cdot (\frac{x_i}{2} - u_i)^2}{x_i}\right]}{\sqrt{\frac{1}{2}\pi x_i}}. \tag{4.5}$$

In the two dimensional case ($n = 2$), we find:

$$h(\vec{x}, \vec{u}) = 2 \cdot \prod_{i=1}^{2} \frac{\exp\left[\frac{-2\cdot(\frac{x_i}{2} - u_i)^2}{x_i}\right]}{\sqrt{\frac{1}{2}\pi x_i}} \tag{4.6}$$

$$= 2 \cdot \frac{\exp\left[\frac{-2(\frac{x_1}{2} - u_1)^2}{x_1}\right]}{\sqrt{\frac{1}{2}\pi x_1}} \cdot \frac{\exp\left[\frac{-2(\frac{x_2}{2} - u_2)^2}{x_2}\right]}{\sqrt{\frac{1}{2}\pi x_2}} \tag{4.7}$$

$$= \frac{4\exp\left[\frac{-2(\frac{x_1}{2} - u_1)^2}{x_1}\right]\exp\left[\frac{-2(\frac{x_2}{2} - u_2)^2}{x_2}\right]}{\pi\sqrt{x_1 x_2}}. \tag{4.8}$$

As this equation describes a normal distribution, a small amount of probability mass is sometimes lost beyond the boundary of the first quadrant. We simply interpret this mass as individuals who die during the fissioning event.

5. Dynamical Equation

Now, we tie together all of the equations that we have formulated to create a general partial differential equation of θ as it changes in time. First, to track the creation of $\vec{x}$ type groups from the fissioning of (larger) $\vec{u}$ type groups, we let

$$\rho_t(\vec{x}) = \int_{\vec{u} \geq \vec{x}} h(\vec{x}, \vec{u}) f(\vec{u}) \theta(\vec{u}) d\vec{u}.$$

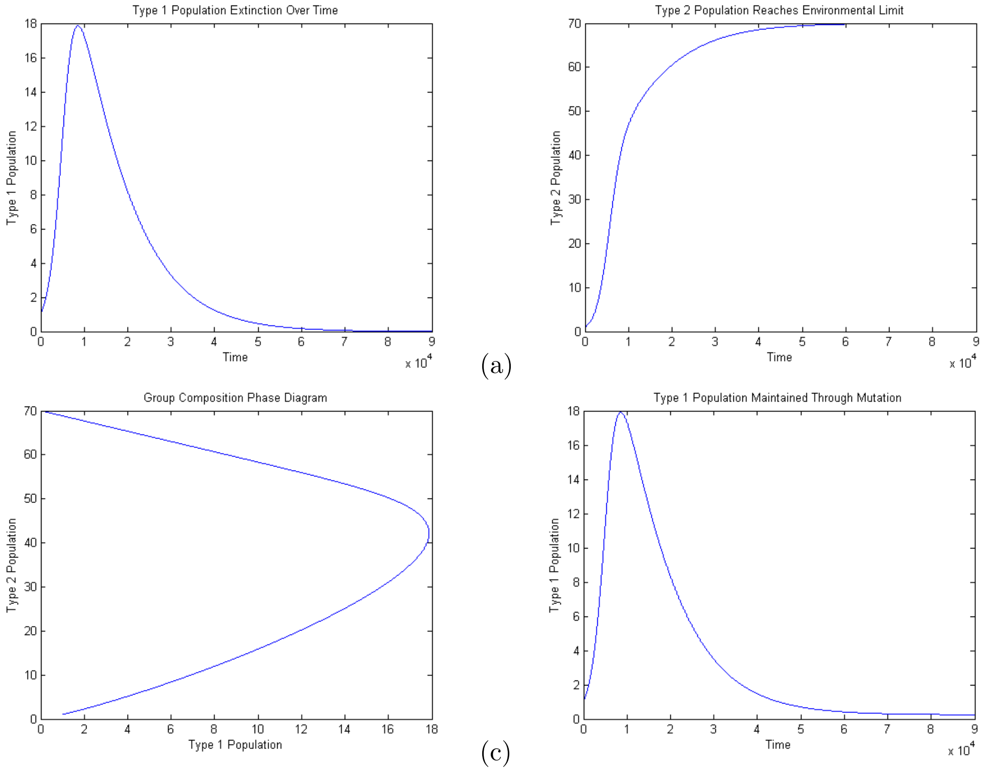
From this, we find:

$$\frac{\partial \theta_t}{\partial t}(\vec{x}) = \rho_t(\vec{x}) - \left(e_t(\vec{x}) + f_t(\vec{x})\right)\theta_t(\vec{x}) - \sum_{i=1}^{n} \frac{\partial(\theta_t x_i)}{\partial x_i}(\vec{x}). \tag{5.1}$$

This takes into account the extinction rate, fissioning rate and rates of change in individual groups. We numerically solved this PDE using MATLAB with $n = 2$, and have included results in the appendix [Fig. 2].

6. Appendix

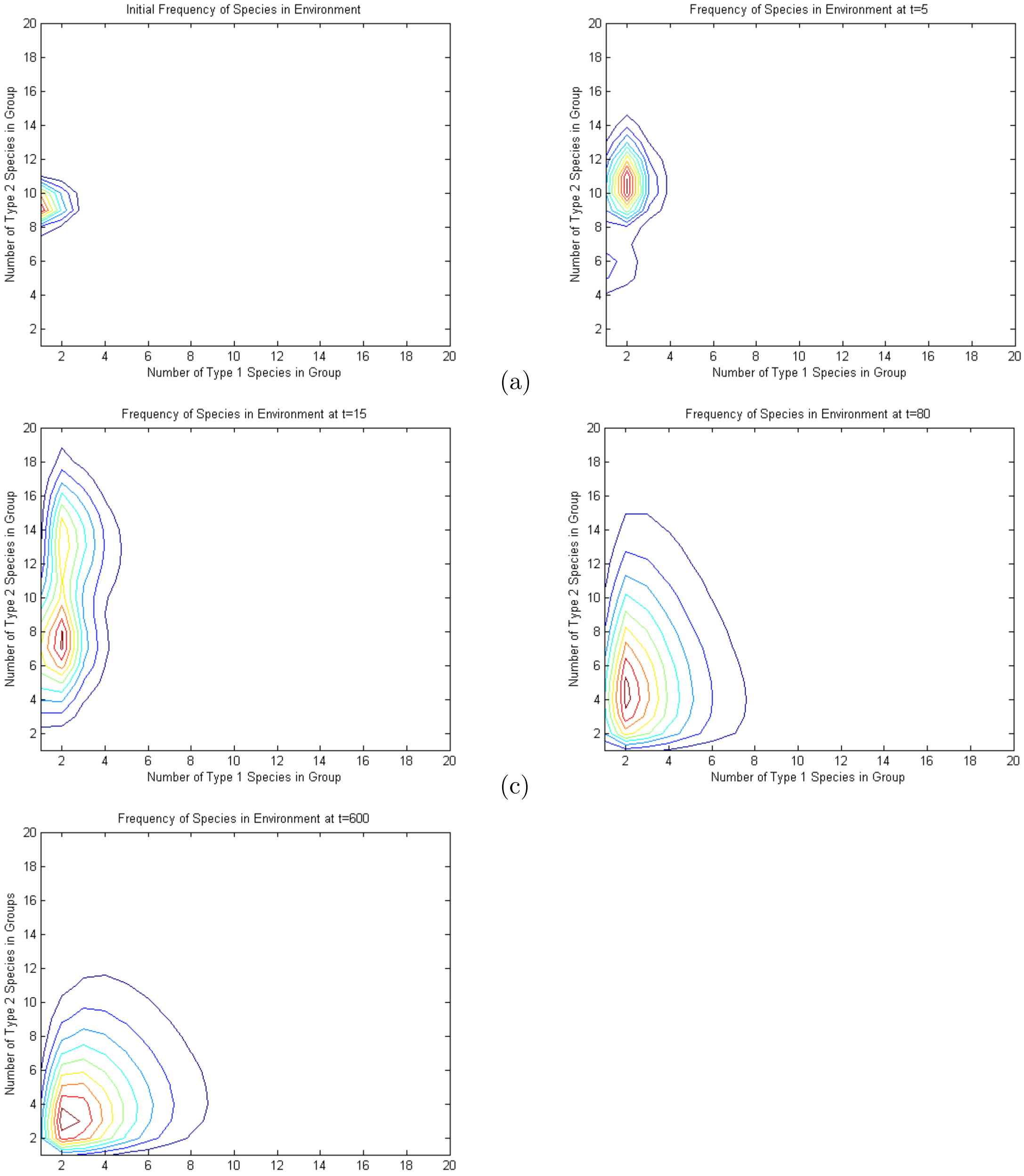
In Fig. 1, we show the results of our numerical analysis of Equation 3.8-9. We found that when mutation probabilities are 0, the species with the lower birthrate eventually goes extinct (a-c). Using small mutation probabilities, we find that the less fit species is maintained at a low population over time (d).



(a) (b) (c) (d)

Figure 1. For all the diagrams, we set $b_1 = 0.06, b_2 = 0.07$, and $c = 0.001$ for the initial conditions of $\vec{x} = (1, 1)$. In (d), we set $M_{12} = M_{21} = 0.0005$. In all diagrams, we ran the equation for 900 units of time.

In Fig. 2, we numerically solved Equation 5.1 with identical parameters as above for individual level phenomena (including mutation). We have shown $\theta_t(x_1, x_2)$ for $t = 0, 5, 15, 80, 600$ to relate how $\theta(x_1, x_2)$ changes over time. Initially, we set the group composition to have 0 Type 1 species and 25 Type 2 species, so the growth of Type 1 is initially due to mutation. Over time, the Type 1 species invades the population, being selected for on the basis of the group-level benefits of diversity.



Initial Frequency of Species in Environment

(a)

Frequency of Species in Environment at t=5

(b)

Frequency of Species in Environment at t=15

(c)

Frequency of Species in Environment at t=80

(d)

Frequency of Species in Environment at t=600

(d)

Figure 2. For all diagrams, we set $b_1 = 0.06, b_2 = 0.07, c = 0.001, e_1 = 1.5, e_2 = 9, m = 0.0015$ and $M_{12} = M_{21} = 0.0005$. We find that through mutation and group-level selection, the frequency and magnitude with which type 2 organisms appear in groups increases over time. Initially, groups grow as quickly as possible, and as type 1 organisms both have higher birth rates and representation in the population, they dominate the environment (t=0-15). However, large, imbalanced groups eventually begin to go extinct or fission into smaller groups (t=60), until finally the environment reaches an equilibrium state at t=600. At this point, there

are a total of 4.6 groups, 46.7 type 1 organisms, and 62.8 type 2 organisms. With diversity acting as a measure against group extinction, the less-fit type 1 organism is maintained at a relatively high level.

Acknowledgments. I would like to thank Professor Burt Simon for providing invaluable advice and expertise while helping me choose an interesting topic to explore, understand important concepts, and formulate this model. I would also like to thank my mentor, Evan Turner for spending time to work with me and all those who helped make UChicago's REU program such a supportive and encouraging environment in which to learn mathematics.

References

[1] Nonacs, P. & K.M. Kapheim. 2007. Social heterosis and the maintenance of genetic diversity. Journal of Evolutionary Biology vol 20, pgs 2253–2265.
This article forms the justification and basis for the diversity aspect of the model. Nonacs & Kapheim define social heterosis and make some calculations about possible effects it may have on a population's evolutionary dynamics.

[2] Simon, B. 2010. A dynamical model of two-level selection. Evolutionary Ecology Research vol 12, pgs 555-588.
This article's model on two-level selection acts as a general basis for the diversity model of selection developed here.

[3] Krebs, Charles (1989). Ecological Methodology. HarperCollins, New York.