Formalizing the gene centered view of evolution

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ABSTRACT. A historical dispute in the conceptual underpinnings of evolution is the validity of the gene centered view of evolution (Dawkins, 1989; Sober and Lewontin, 1982). We transcend this debate by formalizing the gene centered view as a dynamic version of the mean field approximation. This establishes the conditions under which it is applicable and when it is not. In particular, it breaks down for trait divergence which corresponds to symmetry breaking in evolving populations.
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The gene centered view addresses a basic problem in the interplay of selection and heredity in sexually reproducing organisms. Sexual reproduction disrupts the simplest view of evolution because the offspring of an organism are often as different from the parent as organisms that it is competing against. In the gene centered view the genes serve as indivisible units that are preserved from generation to generation. In effect, different versions of the gene, i.e. alleles, compete rather than organisms. It is helpful to explain this using the "rowers analogy" introduced by Dawkins (Dawkins, 1989). In this analogy boats of mixed left- and right-handed rowers are filled from a common rower pool. Boats compete in heats and it is assumed that a speed advantage exists for boats with more same-handed rowers. The successful rowers are then reassigned to the rower pool for the next round. Over time, a predominantly and then totally single handed

rower pool will result. Thus, the selection of boats serves, in effect, to select rowers who therefore may be considered to be competing against each other. Other perspectives on evolution distinguish between vehicles of selection (the organisms) and replicators (the genes). However, a direct analysis of the gene centered view to reveal its domain of applicability has not yet been discussed. The analysis provided here, including all the equations, is applicable quite generally, but for simplicity it will be explained in terms of the rowers analogy[†].

The formal question is: Under what conditions (assumptions) can allelic (rower) competition serve as a surrogate for organism (boat) competition in the simple view of evolution. Formalizing this question requires identifying the conditions attributed to two steps in models of evolution, selection and reproduction. In the selection step, organisms (boats) are selected, while in the sexual reproduction step, new organisms are formed from the organisms that were selected. This is not fully discussed in the rowers model, but is implicit in the statement that victorious rowers are returned to the rower pool to be placed into new teams. The two steps of reproduction and selection can be written quite generally as:

$$\{N(s,t)\} \quad = \quad R\left[\{N'(s,t-1)\}\right] \tag{1}$$
$$\{N'(s,t)\} \quad = \quad D\left[\{N(s,t)\}\right] \tag{2}$$

The first equation describes reproduction. The number of offspring $N(s,t)$ having a particular genome s is written as a function of the reproducing organisms $N'(s,t-1)$ from the previous generation. The second equation describes selection. The reproducing population $N'(s,t)$ is written as a function of the same generation at birth $N(s,t)$. The brackets on the left indicate that each equation represents a set of equations for each value of the genome. The brackets within the functions indicate, for example, that each of the offspring populations depends on the entire parent population.

To formalize the gene centered view, we introduce a dynamic form of what is known in physics as the mean field approximation. In the mean field approximation the probability of appearance of a particular state of the system (i.e. a particular genome, s) is the product of probabilities of the components (i.e. genes, s_i)

$$P(s_1,\ldots,s_N) = \prod P(s_i) \tag{3}$$

In the usual application of this approximation, it can be shown to be equivalent to allowing each of the components to be placed in an environment which is an average over the possible environments formed by the other components of the system, hence the term "mean field approximation". The key to applying this in the context of evolution is to consider carefully the effect of the reproduction step, not just the selection step.

In many models of evolution that are discussed in the literature, the offspring

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[†] The rowers analogy may be considered a model of a single gene in an n-ploid organism with n the number of rowers, or a model of n genes with two alleles per gene and each pair labeled correspondingly. The formal discussion applies to complete genomes i.e. to homolog and non-homolog genes.

are constructed by random selection of surviving alleles (a panmictic population). In the rowers analogy the return of successful rowers to a common pool is the same approximation. This approximation eliminates correlations in the genome that result from the selection step and thus imposes Eq. (3), the mean field approximation, on the reproduction step for the alleles of offspring. Even though it is not imposed on the selection step, inserting this approximation into the two step process allows us to write both of the equations in Eq. (4) together as an effective one-step update

$$P'(s_j, t) = \tilde{D}\left[\{P'(s_j, t-1)\}\right], \tag{4}$$

which describes the allele population change from one generation to the next of offspring at birth. Since this equation describes the behavior of a single allele it corresponds to the gene centered view.

There is still a difficulty pointed out by Sober and Lewontin (Sober and Lewontin, 1982). The effective fitness of each allele depends on the distribution of alleles in the population. Thus, the fitness of an allele is coupled to the evolution of other alleles. This is apparent in Eq. (4) which, as indicated by the brackets, is a function of all the allele populations. It corresponds, as in other mean field approximations, to placing an allele in an average environment formed from the other alleles. For example, there is a difference of likelihood of victory (fitness) between a right-handed rower in a predominantly left-handed population, compared to a right-handed rower in a predominantly right-handed population. Since the population changes over time, fitnesses are time dependent and therefore not uniquely defined. This problem with fitness assignment would not be present if each allele separately coded for an organism trait. This is a partial violation of the simplest conceptual view of evolution, however, the applicability of a gene centered view can still be justified, as long as the contextual assignment of fitness is included. When the fitness of organism phenotype is dependent on the relative frequency of phenotypes in a population of organisms it is known as frequency dependent selection, which is a concept that is being applied to genes in this context.

A more serious breakdown of the mean field approximation arises from what is known in physics as symmetry breaking. This corresponds in evolution to trait divergence of subpopulations. Such trait divergence arises when correlations in reproduction exist so that reproduction does not force complete mixing of alleles. The correlations in reproduction do not have to be trait related. For example, they can be due to spatial separation of organisms causing correlations in reproduction among nearby organisms. Models of spatially distributed organisms are sometimes called models of spatially structured environments. However, this terminology suggests that the environment itself is spatially varying and it is important to emphasize that symmetry breaking / trait divergence can occur in environments that are uniform (hence the terminology "symmetry breaking"). In the rowers model this has direct meaning in terms of the appearance of clusters of mostly left and mostly right handed rowers if they are not completely mixed when reintroduced and taken from the rower pool. Trait related correlations in sexual reproduction (assortive mating) caused by, e.g. sexual selection, would

also have similar consequences. In either case, the gene centered view would not apply.

Historically, the gene-centered view of evolution has been part of the discussion of attitudes toward altruism and group selection and related socio-political as well as biological concerns (Sober and Wilson, 1998). Our focus here is on the mathematical applicability of the gene-centered view in different circumstances. While the formal discussion we present may contribute to the socio-political issues, we have chosen to focus on the mathematical concerns.

The problem of understanding the mean-field approximation in application to biology is, however, also relevant to the problem of group selection. In typical models of group selection asexually (clonally) reproducing organisms have fecundities determined both by individual traits and group composition. The groups are assumed to be well defined, but periodically mixed. Similar to the gene-centered model, an assumption of random mixing is equivalent to a mean field theory. Sober and Wilson (Sober and Wilson, 1998) have used the term "the averaging fallacy" to refer to the direct assignment of fitnesses to individuals. This captures the essential concept of the mean-field approximation. However, both the limitations of this approximation in some circumstances and its usefulness in others do not appear to be generally recognized. For example, it is not necessary for well defined groups to exist for a breakdown in the mean-field approximation to occur. Correlations in organism influences are sufficient. Moreover, standard group-selection models rely upon averaging across groups with the same composition. For this case, where well defined groups exist and correlations in mixing satisfy averaging (mean-field) assumptions by group composition, equations developed by Price (Sober and Wilson, 1998, see discussion on pp. 73-74) separate and identify both the mean field contribution to fitness and corrections due to correlations. These equations do not apply in more general circumstances when correlations exist in a network of interactions and/or groups are not well defined, and/or averaging across groups does not apply. It is also helpful to make a distinction between the kind of objection raised by Sober and Lewontin to the use of averaging, and the failure that occurs due to correlations when the mean-field approximation does not apply. In the former case, the assignment of fitnesses can be performed through the effect of the environment influencing the gene, in the latter case, an attempt to assign fitnesses to a gene would correspond to inventing non-causal interactions between genes.

The mean field approximation is widely used in statistical physics as a "zeroth" order approximation to understanding the properties of systems. There are many cases where it provides important insight to some aspects of a system (e.g. the Ising model of magnets) and others where it is essentially valid (conventional BCS superconductivity). The application of the mean field approximation to a problem involves assuming an element (or small part of the system) can be treated in the average environment that it finds throughout the system. This is equivalent to assuming that the probability distribution of the states of the elements factor. Systematic strategies for improving the study of systems beyond the mean field approximation both analytically and through simulations allow the inclusions of correlations between element behavior. An introduction to the mean-field approximation and a variety of applications can be found in Bar-Yam (Bar-Yam, 1997).

In conclusion, the gene centered view can be applied directly in populations where sexual reproduction causes complete allelic mixing, and only so long as effective fitnesses are understood to be relative to the prevailing gene pool. However, structured populations (i.e. species with demes–local mating neighborhoods) are unlikely to conform to the mean field approximation / gene centered view. Moreover, it does not apply to considering the consequences of trait divergence, which can occur when such correlations in organism mating occur. These issues are important in understanding problems that lie at scales traditionaly between the problems of population biology and those of evolutionary theory: e.g. the understanding of ecological diversity and sympatric speciation (Sayama *et al.*, in preparation).

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