

SELECTION CONTROVERSIES IN AND OUT OF EQUILIBRIUM
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The relationship between selection, costly behaviors and population structure –to include kinship and groups– has been a central debate in evolutionary theory for the last forty years. This is often defined in terms of those conditions favoring the emergence of altruism. There remains substantial uncertainty about the mathematical relationship of models supporting altruism based on kinship (inclusive fitness), group selection and individual selection to one another, and the extent to which these selection structures are truly alternatives, or are instead, members of a statistical family all of which can be derived from more fundamental equations of evolutionary dynamics.

The most recent insight into the consequences of selection in structured populations comes from Nowak et al. (Nowak, Tarnita, Wilson, 2010). Nowak and colleagues show that there are a large number of mathematically related statistical frameworks that can account for the persistence of altruistic traits (traits that cause donor fitness to decrease and recipient fitness to increase) in equilibrium systems, and that Hamilton’s popular kin selection theory, sits in this space along with several alternative expressions (Nowak et al. 2010, SI; see also Nowak, 2006; Lehmann, Keller, West, Roze, 2007; Traulsen, 2010). Nowak et al’s paper has drawn fire because it suggests that inclusive fitness theory makes rather strong assumptions, including weak selection, employs rather unnatural methods of accounting, and that the conditions supporting kin selection solutions are stringent and likely to be rare in nature.

Although there will be countless arguments about this paper - largely focused on its rhetoric - the essential insight, as we see it, is not that kin selection completely fails as an explanation for eusociality. It is that that much of multilevel selection theory has been based on equilibrium solutions operating on posited, aggregate variables. This has generated some cumbersome calculation frameworks that are in need of updating. In Hamilton’s theory, for example, these aggregate variables correspond to the terms benefit - b , cost - c and relatedness - R . R in particular is problematic because it is more often than not interpreted statistically as a measure of association or correlation, rather than as a parameter describing genetic properties (Grafen, 1984). Treatments of kin and group selection have thereby been founded on statistical variables in largely non-mechanistic and non-dynamical frameworks. A key limitation is that these variables are often not provided with the same units of measurement, and the experiments required to make precise measurements, are required to span many generations of observation.

One advantage of the statistical approach is that it has promoted a wealth of experimental investigations into the relationships among these variables, and helped to elucidate many empirical phenomena that remained mysterious, such as the division of labor in social insects, or more recently, cellular diversity in multicellular organisms. One disadvantage, is that without knowledge of the dynamics generating the aggregate variables of the theory, we do not know whether they are “natural” or “nominal”.

Here we point out an analogy with physics, where a similar debate prevailed until a new theoretical framework was established. This debate began with thermodynamics - an equilibrium theory treating aggregate variables - and terminated with the maturation of statistical mechanics - a dynamical theory treating microscopic variables.

Thermodynamics is the study of the macroscopic behavior of systems exchanging work and heat with connected systems or their environment. The theory was developed before the atomic theory of matter, and is silent on dynamics. The four laws of thermodynamics, all operate on average quantities defined at equilibrium - temperature, pressure, entropy, volume and energy. These macroscopic variables exist in fundamental relationships with each other, as expressed in the ideal gas law. Thermodynamics is an extremely powerful framework as it provides experimentalists with explicit recommendations about what variables should be measured and how they are expected to change relative to each other.

Statistical mechanics seeks to provide the microscopic basis for the macroscopic variables in thermodynamics, and to establish when the equilibrium relations are no longer valid or expected to apply. The essential intellectual technology behind much of statistical mechanics are powerful tools for counting possible microscopic configurations of a system and connecting these to macroscopic averages. In other words, moving from dynamical many body formalisms, to equilibrium descriptions with a few favored macroscopic degrees of freedom.

This should now sound familiar to evolutionary biologists, as what Nowak et al. (see Nowak et al. 2006, SI), and others (e.g. Traulsen, 2010), are presenting, is in spirit an evolutionary analogue to statistical mechanics that complements the evolutionary thermodynamics that has prevailed for the last half century. Under this broader perspective, the standard Hamilton’s rule, expressed in the inequality $bR > c$, and related inequalities generated by alternative sorting principles, can be said to resemble an attempt at the form of an ideal gas law $PV = nRT$, in that all express dependencies among measurable, macroscopic variables of state. Obviously the thermodynamic law has accrued huge empirical support and can be shown to be the correct coarse-grained representation of equilibrium microscopic dynamics. In the case of the evolutionary inequalities, such a consensus does not yet exist. Whereas the Nowak et al. paper has been interpreted primarily as an assault on kin selection, it can be more broadly read as one approach at a derivation of the conditions where the kin selection macroscopic law is justified, and ascertaining those conditions where alternative regularities, including other kinds of assortativity, are expected. The conclusion of the Nowak et al. paper is that inclusive fitness theory is more restrictive than had previously been supposed, and in the space of possible inequalities, likely to be rather rare.

This transition between an evolutionary thermodynamics and an evolutionary statistical mechanics is not just a matter of historical interest. It relates to one of the significant weaknesses of many evolutionary models. Early evolutionary thermodynamic-style theory has been largely phenomenological, and where it has been suggestive of mechanism - such as in kin selection theory which suggests an explicit dependency on genetic mechanisms of inheritance - this has often been short hand or code for assortativity through common descent rather than the proportion of genome shared through common descent.

This suggests a deep need for a more fundamental mechanical theory, from which to derive the particular meaning and value of this and related parameters. The field of population genetics offers one such approach within evolutionary theory where dynamical, microscopic principles have been emphasized over coarse-grained equilibrium concepts. Without this bottom-up derivation we can not be sure we are not dealing with a misleading nominal variable in our statistical theory. And without the statistical theory we lose the utility of compressed representations which are required for effective experimental research which can not hope to measure and record all the microscopic observations. As Nowak et al. point out, the critical question is how different kinds of assortativity promoting these social selection effects arise - whether their basis lies in genetic or spatial constraints. This can only be established starting from microscopic observation.

The greater complexity of biological systems over physical systems, and their strong historical dependencies, makes for a veritable zoo of biological macroscopic laws - not just one ideal gas law but many multi-level selection principles - each of which has its adherents and disciples. The great promise of an evolutionary statistical mechanics is that it should allow us to enumerate the full space of possible fundamental evolutionary inequalities (Nowak, 2006). We hope that the Nowak et al. paper will be read not simply as an attack on what has been a highly generative and approximate effective theory in biology, but as a means of deriving more explicitly the conditions of its applicability, and making us aware of new, potentially more powerful, macroscopic selection laws.

1. REFERENCES

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