Leads on mechanisms for the evolutionary selection of cooperative structures

James K. Hazy
Adelphi University

Abstract

Recent research in evolutionary biology offers insights into the evolution of cooperative communities. Although the work related to insect colonies, it has implications for the advanced cooperative structures in human systems such as the division of labor and non-reproductive life-choices. In particular, in an August 2010 article in *Nature*, Norwak, Tarnita and E. O. Wilson argue that kin selection and the mechanism of inclusive fitness, where indirect fitness associated with the survival of related individuals is counted along with the direct fitness of the individual, is unnecessary to explain the emergence of altruistic behavior. A five stage evolutionary process is proposed. A key prerequisite in this theory is the differentiated access to resources - in particular, a "defensible nest" - which provides survival advantage to members of the group.

Introduction

The question of how human interaction dynamics (HID) relates to large-scale human cooperative activities like social, cultural, political and economic systems is a fundamental one. Of particular ontological and epistemological interest is the appropriate unit of selection for individual and collective altruistic and pro-social behavior because these behaviors enable the requisite complex organizing that undergirds human systems. Interestingly, this question is also at the center of a theoretical dispute in evolutionary biology that erupted as a consequence of the cover article in the journal *Nature* that was written by a group that included the prominent evolutionary biologist Edward O. Wilson.

The article, *The evolution of eusociality* by mathematical biologists Martin A. Nowak and Corina E. Tarnita as well as Wilson purports to describe the mechanisms whereby altruism and eusociality - social collectives like insect colonies where adult members are divided into reproductive and non-reproductive castes - emerges through evolutionary selection. In particular, the question addressed is whether *kin selection*, the idea that altruistic behavior has survived evolution because it supports the genes of closely related others through a mechanism that is called *inclusive fitness*, is even necessary to demonstrate the presence of altruism, a hallmark of human evolutionary development. Although unstated, the ontological question addressed in the article is whether evolution acts only on the gene alone, or whether it also acts at group and community levels, a process called multi-level selection (Okasha, 2006).

Nowak, Tarnita and Wilson (2010) argue that kin selection, which the authors equate with the more general notion of inclusive fitness, is actually an unnecessary construct. They make the case that there are more parsimonious mathematical explanations that rely on standard natural selection theory and multi-level selection, and that these ideas are all that are needed to directly imply the emergence of altruistic interactions including eusociality. They propose a five stage model for the evolution of cooperative structures.

Five stages of emergence for cooperative structures

The five stage selection process proposed by Norwak, Tarnita and Wilson (2010) can also be interpreted in human terms (**Figure 1**).

The first stage occurs when individuals form into groups as they freely mix across the population. Although at this earliest stage, groups may not persist, it is not surprising that groupings of individuals form within social networks. This is particularly true in human social networks due to the need to cope with rapidly expanding interaction complexity (Goldstein, Hazy & Lichtenstein, 2010). Groupings by themselves do not imply the emergence of persistent social structures, but they create a necessary substrate upon which high level cooperative structures can emerge (Hazy, 2008). The formation of groups also creates the potential for increased micro-diversity among individuals (Allen, 2001).

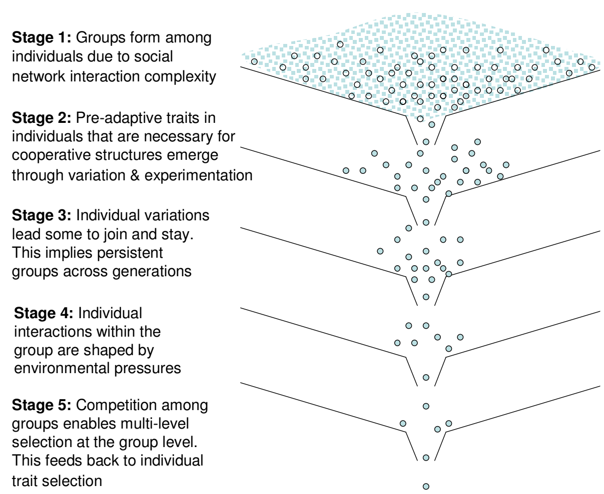

Figure 1. Nowak, Tarnita and Wilson (2010) argue that complex cooperative systems can evolve in a five stage process. Examples at each stage are much rarer that the previous one.

The second stage occurs when a series of pre-adaptations occur at the individual level. As Peter Allen (2001) argues, this increase in micro-diversity within the population is enabled by the protective shield of group or colony life. He describes the diversity of marine life in protected areas or coves in the North Atlantic. Many variations among individual traits can coexist when a collective is somewhat insulated from the harsh survival pressures of the open sea. These pre-adaptation experiments represent the potential that can become cooperative structures when the requisite conditions come together (Goldstein, Hazy & Lichtenstein, 2010).

An example of a pre-adaptation of this type in insect colonies allows individuals to segment and compartmentalize their activities into sequential steps, only beginning a task after the prior one is completed (Nowak, Tarnita & Wilson, 2010). This adaptation, along with others, would enable individuals to observe tasks being completed by others and then skip certain tasks that were already completed or are being completed by others, a primitive form of specialization. Other pre-adaptations that might be repurposed in support of cooperative structuring include communication skills and systems of external memory such as scent trails in insects and symbol systems in humans.

The third stage is when groups persist across generations. This occurs when offspring branch into two types: those that leave the community and head off on their own, and those that stay in the community. This latter case can lead to the formation of persistent groups. More specifically, some offspring are drawn to remain with their groups so these groups can regenerate with younger participants as older ones leave or die out. The offspring that leave are also necessary because they can lead to the colony's reproduction as other colonies are formed from a like gene pool. Even if these individuals do not seed an entirely new colony, they can also provide a source of diversity for recombination in other communities.

Stage four involves a community that is shaped by environmental pressures like disease and predation. As described for insects by Nowak, Tarnita and Wilson (2010), the critical enabler of eusociality is a "defensible nest". Community members who are protected within a defensive boundary accrue survival benefits of being insulated from an otherwise harsh environment. For humans, an analogue to a "defensible nest" could be a shared resource store, a fresh water spring or fuel source for example, that can be accessed more effectively through cooperation.

In the fifth and final stage which is particularly relevant in understanding human interaction dynamics (HID), evolutionary selection operates across disparate groups, some of which demonstrate survival advantage over others. Competition among groups might relate to establishing a preferential position in relation to other groups with respect to access to necessary resources such as water or fossil fuels. Here we find relevance for questions of leadership (Hazy, 2008) and innovation (Goldstein, Hazy & Lichtenstein, 2010) in human terms.

What is selected when cooperative structures emerge?

The Nowak, Tarnita and Wilson (2010) work and the inferences for human systems described in the previous section highlight an important question for science: Is it useful to resort to inclusive fitness as a theoretical argument because it aims to reduce the unit of selection to the physical human genome? Is reduction to a gene-selection model a requirement to explain the emergence of reciprocal and other forms of altruism? This ontological and epistemological question is important since these behaviors are at the core of human cooperative associations, and thus ultimately they are keys to the emergence of cooperative institutional structures that are the scaffolding of social, political and economic systems.

Although multi-level selection arguments like that of Nowak, Tarnita and Wilson imply that perhaps one does not necessarily have to limit evolutionary selection to variation and recombination of physical genes embedded in DNA, these approaches do not in and of themselves offer an alternative explanation that links human cultural, political and economic structures to chemical and physical processes in the same way that alternative approaches like inclusive fitness models of selection seek to do. At the same time, it is difficult to generalize the simple inclusive fitness argument to large scale human systems.

The basic question of how information is gathered, physically encoded, used, and selected in evolutionary processes, together with the follow-on questions that devolve as cooperative structures emerge along a trajectory of ever increasing scale, is a fundamental area of science that needs focused research and development.

Implications for HID research

To further explore the evolutionary selection mechanisms of cooperative structures in human organizing, the following questions, among others, must be asked and answered: Can the explanation for large scale human systems ultimately be reduced to the mechanisms of gene-selection alone? If evolutionary selection occurs outside of the human genome, then where is the selected information physically stored? To what does the selected information pertain? How is it encoded? How is information passed along with fidelity across generations? How is it replicated with variation or recombination? Finally, by what mechanisms are the information stores instantiated into the physical environment with sufficient fidelity such that selection pressures in the environment could be interpreted, even loosely, as differentiating on the basis of relative fitness?

These questions are important because arguably natural selection as an explanatory mechanism for the emergence of cooperative structures in HID is only relevant if its operation serves to somehow *encode, preserve, and select* information about successful instantiations of action in the environment, and if those previously successful instantiations can be repeated with fidelity in the present circumstance. Until an evolutionary theory that is supported by empirical evidence makes this link from informational and interpretive to physical and objective, and does so convincingly, the question of whether the mechanisms at work within human systems are ontologically distinct from those that drive biological evolution remains an open one.

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