
Individuals and groups in evolution: Darwinian pluralism and the multilevel selection debate

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Outlined here is an updated review of the long-standing ‘kin selection vs group selection’ debate. Group selection is a highly contentious concept, scientifically and philosophically. In 2012, Dawkins’ attack against Wilson’s latest book about eusociality concentrated all the attention on group selection and its mutual exclusivity with respect to inclusive fitness theory. Both opponents seem to be wrong, facing the general consensus in the field, which favours a pluralistic approach. Historically, despite some misunderstandings in current literature, such a perspective is clearly rooted in Darwin’s writings, which suggested a plurality of levels of selection and a general view that we propose to call ‘imperfect selfishness’. Today, the mathematically updated hypothesis of group selection has little to do with earlier versions of ‘group selection’. It does not imply ontologically unmanageable notions of ‘groups’. We propose here population structure as the main criterion of compatibility between kin selection and group selection. The latter is now evidently a pattern among others within a more general ‘multilevel selection’ theory. Different explanations and patterns are not mutually exclusive. Such a Darwinian pluralism is not a piece of the past, but a path into the future. A challenge in philosophy of biology will be to figure out the logical structure of this emerging pluralistic theory of evolution in such contentious debates.

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1. Introduction

Group selection: Anatomy of a betrayal

Recent debates about individuals and groups in biological evolution, and about the eternally contentious concept of ‘group selection’, have been unfortunately dominated by the controversy between Edward O Wilson and Richard Dawkins (Dawkins 2012). It is useful to point out what exactly Wilson proposes in his latest book on the matter, *The Social Conquest of Earth* (EO Wilson 2012). Despite what some critics wrote, focusing just on the obsessively debated concept of group selection, Wilson’s integrated frame is the following:

- (W-a) Human sociality is a kind of eusociality (strong co-operation rather than reproductive division of labour), showing parallels with the scenarios of animal eusocial evolution.
- (W-b) The two main roads to eusociality (insects and humans) differ in some degree in terms of historical

contingencies (such as physical constraints, evolutionary timetable, co-evolution with ecosystems, the role of instincts, the kinds of social intelligence, presence or not of sterile castes).

- (W-c) More significantly, the two main roads to eusociality differ in terms of the combination of evolutionary forces involved: a standard natural selection queen vs queen (with the sterile castes as extended phenotypes of the queens and extrasomatic projection of their genome) and then a between-colony selection, in insects; and a multilevel selection (with a stronger interplay between individual selection and group selection) for human-specific eusociality.
- (W-d) The dialectic between individual and group selection produces two ambiguities of human nature: trade-offs between selfish attitudes (by individual selection) and cooperative attitudes (by group selection); contradictions between unselfish and socially conservative behaviours inside the group (to

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the extremes of tribalism) and aggressive behaviours between groups (to the extremes of xenophobia and war).

- (W-e) The theoretical role of kin selection (mathematically and biologically failing according to Wilson, so reversing his ideas exposed in previous books) must be replaced by multilevel selection, tuned case by case in the field. The ‘narrow focus’ on relatedness, studying social behaviours in nature, should be replaced by integrated scenarios with multiple selective forces acting.

Dawkins’ furious reaction concentrated on just point (W-e), reaffirming the elegance of kin selection theory, his 1970s version of which talked about replicators (genes) and vehicles (organisms), and extrapolated everything else from the genetic level. Dawkins’ criticism against group selection is twofold: (1) it is irrelevant because reducible to individual or parental fitness; and (2) it is wrong because groups do not replicate like genes and do not reproduce like organisms. But (2) is not the point defended by Wilson and (1) seems incorrect in at least some cases. Mostly, the subtly contradictory criticism does not consider the real interpretation of group selection proposed by Wilson, as follows:

- (W-1) Group selection is an important but very rare force: it works for eusociality because in those cases it is able to win (at least partially) over the behaviours previously established by selfish individual selection (as already shown in George Price’s equation and Hamilton’s later works).
- (W-2) Being part of an adaptively competitive group gives advantages to the individual fitness as well, and vice versa, individual behaviours reflect on the group fitness.
- (W-3) Individual selection and group selection refer to the ‘targets’ (traits and behaviors) on which the multilevel selection process acts, but the fundamental evolutionary ‘unit’ remains the whole genetic code of the individual, the queen in the case of Wilson’s model (i.e. groups are another kind of ‘vehicles’ for genes, and despite the old-fashioned criticism repeated by Dawkins, this mechanism can be framed also in terms of selfish gene theory, as attempted by Pagel 2012).
- (W-4) Group selection starts gradually, given particular environmental and social conditions (namely, population structure and ecology), in evolutionary processes where standard individual natural selection provided the necessary pre-adaptations (the selfish advantage of fertile queens with reproductively differentiated offspring, as in the original hypothesis proposed by Darwin).
- (W-5) Group selection favours group-level emergent and heritable traits (products of interactions between individual members) but no evolutionary ‘jumps’

are needed. Opposing the alleged abstractness of inclusive fitness theory, Wilson presents sets of empirical cases involving single mutations with conditional effects in strategies already provided by phenotypic plasticity, and wider consequences in social behaviours. Thus, Wilson’s model is gradualist, normally ‘gene-centered’ but not ‘worker-centered’, and based on standard selection equations.

- (W-6) So described, group selection is based on standard models of population genetics and a new mathematical model built by Harvard biologists and mathematicians Martin Nowak and Corina Tarnita (able to dismantle, they think, the efficacy of kin selection as explanation mainly based on relatedness) (Nowak *et al.* 2010, p 1061).

This mathematically updated hypothesis (Tarnita *et al.* 2009) in philosophical terms has not much to do with the old and theoretically more radical version of ‘group selection’ originally formulated by Vero Copner Wynne-Edwards (quoted again rhetorically, as a straw man, by Dawkins), that is self-regulation of population size connected with group-level adaptations such as reproductive rates, foraging strategies and strict population localization (Borrello 2010).

Moreover, Wilson’s group selection is a process working strictly inside the species; thus, it has nothing to do with ‘species selection’, species sorting or competitive exclusion between species. A group is neither a metaphysical entity nor a new kind of ontological hyper-individual nor a holistic organized whole that suppresses the individual (as its opponents suspect): for group selection to work, it is a coordinated collection of individual organisms with emergent behaviours produced by the interactions between members and favoured by the differential contribution of the group to the overall population of the species. The group is a context of relationships that make adaptive sense to individual behaviours, in most cases pre-adapted by classic natural selection.

Thus, we can fix a first point: we have a new, integrated, disputable version of group selection in the field (based on population genetics and behavioural ecology). Dawkins’ reaction is a misrepresentation. The alleged ‘betrayal’ of Wilson is just related to the role of kin selection and its compatibility or not with group selection. Wilson’s thesis is not ‘group selection’; it is ‘multilevel selection’, with varying combinations of selective processes case by case.

2. Darwin’s solution: Imperfect selfishness

Another frequent worry about group selection is its theoretical impact on the Neo-Darwinian theory of evolution. In his harsh review of Wilson’s book, Dawkins wrote that Darwin spoke about group selection only in ‘one anomalous passage’. This is historically false. A detailed analysis of the six

editions of *The Origin of Species* – together with *The Descent of Man*, private writings and correspondences – shows a much less simplified theoretical frame in the founder of evolutionary theory by natural selection. As a matter of fact, the advantage for the single individual is the Darwinian background position: survival and reproduction are related to organisms, the basic units of evolution; ‘no good for the species’ as a whole or between species is tolerated. Nevertheless, above this level we can appreciate the typical Darwinian pluralism:

- (D-1) (background position 1) According to the background individualistic position, when the selective advantage seems collective or devoted to other species, we should consider, as a first hypothesis, the reduction to underlying individual advantages: there could be reciprocal interests or trade-offs between advantages and disadvantages, but summing up, any trait must have a dominant individual utility (in *Origin*: the rattles of snakes; the mutual services of aphides and ants; the selfishness of the cuckoo and the tolerance from parasitized species; the enslaved ants; and other cases).
- (D-2) (background position 2) If no individual selective advantage is detectable, a second option is the collateral effect, like in the hard case of the non-selective origin of hybridism when two varieties are diverging: in the progressive sterility of hybrids, there is neither individual advantage nor innate adaptation at the level of species (as in Wallace’s hypothesis), but for Darwin (after long ruminations) just an incidental collateral effect of increasing differences in the reproductive systems of the two parental species. Then, no individual fitness, no natural selection.
- (D-3) (collective advantage) Darwin acknowledges that nature is full of traits apparently disadvantageous for individuals and adaptive at the level of groups and colonies; why does selfish natural selection promote sociality? In *Origin*, we see the case of the suicidal stings of some bees: the death of the individual finds a reason in the advantage for the communities (protection from enemies, through a re-adaptation of the sting). Darwin is very clear about the point: if the sting is effective against enemies and useful for the community, all the criteria for natural selection are satisfied, even though the individual is dead. It is a sacrifice for the whole beehive.
- (D-4) (group selection) The sterility of whole castes inside a species is one of the most important difficulties of his theory, he famously confessed: there is a good for the group, disadvantageous within the group.

Quite interestingly, his solution was very different from that of sterility of hybrids between two incipient species. In this case Darwin has no doubts about the role of community (the queen and her worker daughters) as a unit of selection. The incidental emergence of variations which cause sterility in a part of the progeny, and subsequent division of labour, could have had a beneficial effect for the group. The incipient stages of the process (with many individuals losing their reproductive abilities) could be explained by the individual selective advantages between the parents, specifically the queens (like in Wilson’s model, as Wilson correctly acknowledges in his book). Then, the adaptive role for the group will consolidate the behaviour. Summing up: natural selection does not work on sterility/fertility of the offspring, but on the differential reproductive strategies of the queens (with a trend to produce sterile offspring). This solution – in Darwin, translated by analogy with the models of artificial parental selection – is compatible today both with kin selection and group selection: the sterile castes (gradually evolving) contribute both to the reproduction of the queen, and to the fitness of the whole community (thanks to the division of labour). In Darwin’s words, natural selection applies not only to individuals but also to ‘families’ and groups. There is a differential survival of communities (proportional to the degree of division of labour, in Darwin), thanks to the different reproductive strategies of the fertile members. Parental selection (between queens) gradually creates the conditions for group selection (between colonies).

- (D-5) (group selection in human biological evolution) In *The Descent of Man* we read in several passages that in human evolution, because of special conditions in population structure and ecology (like in Wilson’s model), natural selection can act also between families and ‘tribes’, favouring cooperation and altruism inside groups at the same time as aggressiveness and violence between groups (confirming the ambivalence of human nature stressed also by Wilson and many others today, like Samuel Bowles 2008).
- (D-6) (group selection in human cultural evolution) In *The Descent of Man* we read that the human species is able to produce such high intellectual faculties that the competition between groups is fueled also by cultural traits, like social conformism, moral judgments and religion. There is interplay between biological and cultural evolution which results in the evolution of human moral virtues.

Nothing could be more distant from ‘one anomalous passage’. This shows how, for ultra-Darwinians like Dawkins,

the founding father has become an idealized icon. What is historically real is the flexible theoretical pluralism of Darwin. Considering (D-1) to (D-6), Darwin is pointing out that natural selection is basically individualistic and any benefit for the group should be also a benefit for the members, but in special conditions (maybe rare, but crucial in natural history), we have both exceptions (the stings of the bees, the sterile workers devoted to the queen) and selection acting directly via competition between colonies and groups. In these cases, more efficient swarms (as for defence of the nest, reproduction of queens, resource founding, architectural skills) can transmit their variations to new swarms.

We can even appreciate a progressive trend towards group selection and ‘for the good of the community’ in the subsequent six editions of the *Origin* (Sober 2010). Darwin’s background is individualist, but with explanatory pluralism about the levels of selection in terms of different ‘individuals’ and degrees of complexity in the organization of biological entities. There is never explanatory ‘monism’ in Darwin. We would define his position as ‘imperfect selfishness’, or ‘multilevel selfishness’.

3. Criteria of compatibility between kin selection and group selection

A modern reading of Darwin is compatible both with parental selection and inclusive fitness (considering a group of genealogically related members) and group selection (considering the group as a unit of selection in special conditions). According to David Sloan Wilson (DS Wilson 2012), this is the consensus of the many also among contemporary biologists involved in researches in the field. Leaving aside the too personalized fight between famous scientists, compatibility is the background landscape of current literature in the matter. Here we see the weak side of the new theoretical model proposed by Nowak, Tarnita and Wilson, which hypothesizes incompatibility, based on mathematical results and game theory.

On the contrary, compatibility seems rooted in two dimensions:

- (A) *The role of population ecology and population structure as tuning criteria for different compatible patterns, such as inclusive fitness and group selection, within the frame of a general theory of multilevel selection.* The purely theoretical possibility that between-group advantage (docility) could overcome within-group advantage (aggressiveness) was already contemplated by John Maynard Smith’s model of the ‘mice in the haystacks’ (with a negative solution at the end, as a matter of fact, in favour of kin selection alone in Maynard Smith). The main criterion in that model was the *structure of populations* of mice, divided into little groups among

the haystacks. Before him, JBS Haldane, S Wright and R Fisher considered similar models. T Dobzhansky wrote about the ‘physiology of populations’ (Borrello 2010). Price’s equation, and later Hamilton’s works about the differential contribution of kin groups to the global population, showed that between-group selection could in some cases (small groups, particular ecology) overcome within-group selection. As previously acknowledged by Nowak (2006, p 1563), Price’s equation was an early attempt to generalize interactions between individuals and groups with any form of phenotypic correlation (Harman 2010). In ‘first Wilson’s’ sociobiology, we saw the same model, with kin selection as a special case of group selection sensitive to genetic relatedness. Since relatedness can be understood as an aspect of population structure, inclusive fitness theory could be interpreted within the more general framework of multilevel selection theory, including group selection. Demographic and mathematical models confirm the role of population structure affecting evolutionary dynamics (Tarnita *et al.* 2009). Nowak’s definition of group selection (2006, 2011) is based on parameters of population structure (group size, number of groups, interactions): the effectiveness of the cooperative mechanism is proportional to the number of little groups. *Thus, population structures, demography and nonlinear interactive effects seem the main modulators of the different strategies of pro-social behaviours in nature.*

- (B) *The fuzzy boundaries of what we mean by ‘individuals’ in biology.* For instance, in Wilson the colony becomes an ‘individual’, a super-organism, made by the queens and the sterile servant castes. Then, if competition is between colonies, this is ‘individual’ selection in a classical sense and not ‘multilevel selection’; nevertheless, it depends on the terminology we use. In Wilson the two justifications are that: (1) in invertebrate ‘super-organisms’, we would not have antagonisms between internal selfish behaviours (like workers against workers, or workers against queens) and cooperative group-traits; (2) queens and workers have the same genotype, with different modulations of phenotypic plasticity. The colony is a whole, genetically and behaviourally. But in Nowak, Tarnita and Wilson’s paper, a super-organism is not exactly an individual, but ‘a distinct level of biological organization’ (2010, p 1057). So, it seems a special kind of group selection, namely ‘between-colony selection’ (quoted just two times in the paper). Group selection theory and super-organism terminology are somehow confusingly overlapping, but it is clear that ‘between-colony selection’ is only the advanced phase of a long process of cumulative (and altogether improbable) pre-adaptations.

The fact that groups are not replicators is quite irrelevant, because they are not ‘units’ of selection, but ‘targets’ of

selection: a group is a set of traits and behaviours on which the multilevel selection process could act (while the units are the genomes). There is nothing anti-Darwinian in saying that the targets of selection or the ‘vehicles’ of transmission of functional genes (like in Pagel 2012) could be distributed in several inclusive levels of organization (biological and cultural for human species). Since 1975, David Sloan Wilson’s ‘trait-group model’ (1975, 1987) and Michael Gilpin’s theory of group selection (Gilpin 1975) showed the role of multilevel selection as a frame of multiple evolutionary forces. In these models, kin selection and group selection are partially equivalent and reciprocally translatable (DS Wilson 2012). Group selection, whatever its frequency or rarity in natural history, is a real, empirically testable, pattern (Goodnight and Stevens 1997). The literature now offers several proposals of multilevel or hierarchical selection theories, each of them different from the others (Eldredge 1999; Gould 2002; Okasha 2006).

With respect to this pluralistic consensus, the Dawkins vs Wilson struggle is a step backward. ‘Second Wilson’s’ turning point (2007–2013, with the global rethinking of the foundations of sociobiology started in: Wilson and Wilson 2007) is now a (quite total) rejection of kin selection in favour of group selection, as if the two were incompatible. The new arguments for the refusal of inclusive fitness theory are:

- (1) the empirical failure of the haplodiploid hypothesis, since 1990;
- (2) the phylogenetic rarity of eusociality and its odd distribution;
- (3) the discovery of multiple selective forces (favouring genetic variability inside the colonies due to disease resistance, or working against the disruptive impact of nepotism within colonies and against the negative effects of inbreeding) that exist in groups and diminish the advantage of close kinship;
- (4) abstractness, because of the low contribution to empirical progresses in understanding eusociality;
- (5) mathematical limitations (lack of generality, too stringent assumptions, oversimplification of fitness relationships, no synergic effects included, and mostly the same conditions predicted by standard natural selection theory).

Thus, the general working theory should be standard natural selection. The basic problem for kin selection is that it applies to only a small subset of evolutionary models. But quite interestingly, ‘group selection’ or ‘between-colony’ selection or ‘multilevel selection’ (three terms involved in Wilson’s prose) is necessary for this criticism just in point 4 above, as explanation of the countervailing forces acting within groups independently from (or against) inclusive fitness.

Hard question: is relatedness the consequence or the cause of eusociality? The brief communication of 137 biologists to

Nature was, as a reaction, an effective empirical defense of kin selection (Abbott *et al.* 2010). The authors refused the sharp distinction between standard natural selection and inclusive fitness theory, both generating identical predictions: they confuted point (5) about limited assumptions; they firmly rejected the accusation of abstractness in point (4), giving an example of quantitative prediction (sex allocation), while point (1) (the empirical failure of the haplodiploid hypothesis) is defined as already known. But they admit that kin selection is valid only if correlated with certain ecological and demographical conditions. They counter-attacked that there are no novel predictions in Nowak, Tarnita and Wilson’s model. They do not mention group selection and Darwin’s pluralistic solution.

Both sides of the controversy seem to resist pluralism and to defend two reciprocal denials, with mirroring accusations of misrepresentation of the empirical literature. But the point of disagreement should be defined more rigorously. Nowak *et al.* are working on models in which population structures make inclusive fitness unnecessary, while a wider consensus claims that population structure is properly the parameter for multilevel selection (including kin selection). On the opposite side, some of the defenders of genetic relatedness seem still involved in the idea of forcing every experimental finding into a kin-selection framework. But a lot of pro-social behaviors, even in microorganisms, are insensitive to genetic relatedness (Kaushik *et al.* 2006; Smith *et al.* 2010).

Out of the line of this controversy, the growing consensus in the field is, instead, a pluralistic one, as matter of fact, especially in primatology and anthropology (Boehm 1999; Richerson and Boyd 2005). The transposition of the debate from *Nature* (where it was focused on the degree of limitations and predictions needed for kin selection to work) to the popularized fight between Wilson and Dawkins (diverted to group selection) introduced an oversimplification. Being each one a caricature for the other, they could be both wrong.

4. Discussion

Darwinian pluralism: A path into the future

As provisional conclusions, we could say that personalized controversies are not useful, because polarizations between misleading incompatibilities are against the reality of field research. Thus, we need a theoretical foundation of the pragmatic explanatory pluralism we see in the field, also about the topic of individuals and groups in evolution. As a proposal (Pievani 2012), the current theory of evolution could be seen as a progressive scientific research programme (in the sense of epistemologist Imre Lakatos and his methodology for detecting rival scientific research programmes), with a Neo-Darwinian extended core and a pluralistic protective belt made by open problems, auxiliary assumptions, *ad hoc* hypotheses, alternative models, etc.

The extended core is represented by four pluralistic basic patterns: multiple sources of genetic, epigenetic and developmental variation; multiple selective processes (multilevel selection); genetic drift and neutralistic factors; macro-evolutionary patterns. This evolutionary pluralism seems much needed in order to explain complex traits, behaviours and adaptations, at different levels of biological organization (Pievani 2011). We have to identify a plurality of coherent patterns and their differential frequencies in empirical evolutionary literature.

We should also clarify the extension of pluralism. More radical updating of the current evolutionary scientific programme comes from the growing explanatory role of cooperation, symbiosis and endo-symbiosis in early major evolutionary transitions. In those cases, the ‘associations for life’, with conflicting interests, appear not just as subsets of a multilevel selection theory (like group selection), but multilevel processes able to produce by themselves new forms of biological organization and new thresholds in evolvability (Okasha 2006). Are the kinds of ‘cooperation’ that lead to new levels of organization (between genes, cells, tissues, unicellular and multi-cellular individuals; with internal specializations and then new adaptive radiations) the same as we see in social interactions (between organisms and groups)? Do we need a revision and extension of the current theoretical evolutionary framework in order to include these advances?

As an example of possible theoretical updating, in Martin Nowak’s general theory of cooperation (2006), based on game theory, the answer is that a theory for the evolution of cooperation is possible. The background process is the selfish and competitive standard selection (increasing the relative abundance of defectors), but five disturbing mechanisms can constructively prevail in order to make cooperation possible: (1) kin selection (only among relatives), until 2011 accepted by Nowak as one of the evolutionary patterns for cooperation (Nowak, Highfield, 2011); (2) direct reciprocity (frequency-dependent); (3) indirect reciprocity (with reputation as social money); (4) network reciprocity or spatial selection (adding, in mathematical models, population structure and spatial structure); (5) group selection or multilevel selection. We can label this approach as ‘selective pluralism’: in other words, *natural selection + population structures + hierarchical and nested levels of targets*. Thus, in Nowak’s proposal natural cooperation is not ‘a third functional principle in evolution beside mutation and natural selection’ (as stated in his conclusions; Nowak 2006, p 1563), but just a set of special conditions of operation of classic selective processes. Apparently, there is nothing new on the horizon.

According to Stephen J Gould, instead, the structure of the forthcoming evolutionary theory will be a mix of extensions and revisions of the Neo-Darwinian synthesis (2002). This explanatory pluralism is silently working even in authors who did not recognize it. In the ‘second Wilson’, multilevel selection is just a piece of the new pluralistic

approach (Wilson and Wilson 2007; EO Wilson 2012). The Harvard entomologist stressed the role of ‘niche construction’ (that is a set of bidirectional adaptive relationships between organismal activities and environmental selective pressures), also for the interplay between biological and cultural evolution in hominin natural history. Moreover, the two roads to eusociality (in invertebrates and humans) are paved with long series of ‘pre-adaptations’: functional cooptations of traits evolved for previous adaptive reasons (without any anticipation of potential future roles for eusociality) and then converted for other functions in modified ‘social niches’ (another intuition leaking out from later Darwin’s writings). The evolution of sociality, namely, in the passage of altruistic behaviours from biological niches to human cultural niches, could have been strongly influenced by such ‘ex-aptations’ or functional shifts (Pievani 2012).

As shown in the current ‘individuals/groups’ debate, the hardening of the Modern Synthesis around natural selection acting only at the level of individuals seems to be definitely over. Different explanations and patterns are not mutually exclusive. It is quite surprising to see Stephen J Gould’s concept of ‘ex-aptation’, so crucial now for his historical opponent Edward O Wilson. Serendipic turning points and contingent thresholds in the evolutionary maze, as in Wilson prose, show how the strong adaptationism of sociobiology and evolutionary psychology has been replaced by integrated and interdisciplinary models, with convergent data coming from paleo-ecology, climatology, demography and biogeography, compared phylogenies, molecular biology and paleontology. It is meaningful that the scenario proposed by Nowak, Tarnita and Wilson (2010, pp 1060–1061) is truly historical: a sequence of pre-adaptations, starting with defensible nests, subsequent adaptive radiations, progressive provisioning, less migration outwards, etc. The rarity and odd phylogenetic distribution of eusociality in nature is explained by historical contingencies.

4.1 A philosophical implication

Waiting for the discovery of ‘eusociality genes’ (another weak side of Nowak, Tarnita and Wilson’s new model), this Darwinian pluralism about individuals and groups in evolution has also a major, purely philosophical consequence. After repeated oscillations between humans as a ‘killer ape’ and humans as an ‘empathic ape’, we catch the intrinsic ambivalence of human nature. Multilevel selection carries two paradoxical antagonisms: (1) trade-offs and uncertain balances between selfish attitudes provided by individual natural selection and altruistic behaviours provided by group selection; (2) inside the group selection processes themselves, conflicts between cooperation and conformism inside the groups and aggressiveness and violence between groups, both intrinsic in the competition of socially bound groups.

Neither altruism nor selfishness is the physiology or pathology of the human condition. Our inevitable tendency to use an anthropomorphic and teleological language depicting the pro-social vs selfish behaviours in nature does not help in understanding the diversity of evolutionary strategies. They are both the hallmarks of human chimerical contradiction. And this critique of the idea of 'nature' as a moral authority establishes a suggestive bridge linking biological evolution (the search for our evolutionary constraints) to the humanities (the realm of cultural evolution).

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