A great number of contemporary philosophers are concerned about the relationship between the facts of evolutionary science and the positions that they hold dear. Since philosophy tends to address foundational questions about the kinds of creatures that human beings are and the world that they occupy, and evolution along with its driver natural selection have deeply shaped the human experience, we might say that any serious philosophical project must at some point address evolutionary theory. However, the details of evolutionary theory are arcane and, much like the data of philosophy itself, often reveal themselves only to
those engrossed in the weeds of their respective disciplines. Thus, it’s essential for philosophers interested in the implications of evolutionary science to get their hands on *rigorous yet accessible* discussions of that science.

To this end, *Cooperation and its Evolution* ought to be on the reading lists of a great many philosophers. It is a rich and varied collection of essays by biologists and philosophers working at the cutting edges of evolutionary science and the crossroads between that science and philosophy. Given the fact that the book is an imposing tome, weighing at around 600 pages, I hope that this review can serve as a guide for interested philosophers, as well as those in other related fields. I do this by providing a narrative overview of the essays, drawing connections and extending ideas where I see fit.

II.

The existence of altruism is often seen by evolutionary biologists as a puzzle. Since altruism is defined as some creature A sacrificing its own interests for the benefit of some other creature (or set of creatures) B, then why would altruism improve the reproductive fitness of A? As Ronald Noë and Bernhardt Voelkl explain the problem, natural selection favors traits and behaviors that promote the fitness of the creature who has them, and altruistic behaviors don’t do this, then it seems like cooperation should never have evolved (Noë and Voelkl p. 131). Yet clearly it did evolve! So we need to give an account of how it could be that cooperation could have evolved despite the uncompensated costs it requires individuals to bear.

The shadow of group selection theory looms large over this collection of essays. A growing number of contemporary biologists have tried to solve this puzzle by arguing that
natural selection can work on groups in the same way that it works on individuals, by selecting group characteristics that promote the fitness of the group. The trouble, of course, is that individuals are the carriers of genes, the data that selection works on. Even if group selection can be a helpful piece of the puzzle, one might think that a story needs to be told that can account for the relations between individuals and the groups that they constitute. This problem, it seems, can be most readily solved by appealing to the sorts of cooperation mechanisms found in insect societies, as Deborah Gordon does in her essay “What We Don’t Know about the Evolution of Cooperation” (Gordon p. 197). Ant colonies, for example, reproduce as group units. Very few individual ants reproduce. Rather, ant colonies have specialized queens that do the reproducing. This means that the queen ant which is most likely to survive to reproduce is the queen ant that produces offspring which do the things most likely to allow the survival of the queen, and as a consequence we get ants which sacrifice their interests without hesitation when doing so is in the interest of the survival of the colony and the queen. The fitness that a particular action produces to an individual ant is irrelevant to understanding which behaviors will be selected for; rather, and this is Gordon’s primary point, we need to think ecologically when we try to get clear on what exactly the causes of the evolution of altruistic behavior are (Gordon pp. 200-1). We need to ask: what benefits do ants provide to the fitness of the colony? If we look only at fitness at an individual level, the existence of cooperation is often far more mysterious than if we’re willing to look at fitness on a group level.

This answer, however, is incomplete. What makes Gordon’s account work is that ant colonies, in the body of the queen, and not individual ants, are the site of selection. What, however, should we say when it is individual
creatures themselves that do the reproducing? Why is it adaptive for, say, some sort of bird, to assist in the reproduction of other birds with whom it has not itself reproduced? It’s not so obvious that Gordon’s ecological solution can be applied here, at least without significant qualification. Andrew Cockburn discusses the problem of ‘cooperative breeding’ in more advanced animals in his chapter “Cooperative Breeding in Birds: Toward a Richer Conceptual Framework.” Cockburn notes that numerous species of birds have individual tendencies to partake in the care of offspring which are not their own, which is surprising given the aforementioned puzzle of cooperation. If it’s costly for a bird to take care of offspring which are not their own, with no correlative with no reproductive benefit, then how would this tendency have evolved? In the *Malurus*, the species of bird discussed here, there tend to be a great number of less equally reproductively desirable male birds who never have the opportunity to reproduce, given the competition over female birds. Yet if each bird themselves has an evolved tendency to care for young, then birds which never have young of their own will tend to play that out with any young that they can (Cockburn p. 236). So we need not be puzzled by the existence of cooperative breeding in these species; it’s simply a function of the facts that these birds have a disposition to care for young and that there tend to be a great number of bachelor birds available to aid biological parents.

III.

The internal logic of group selection theory is undoubtedly powerful, as the last few paragraphs have shown. The interest in providing an explanation for the evolution of cooperation, however, does not end at accounting for cooperation in ants and birds. We want to know how cooperation developed in *humans*. What about the genetic
and phenotypic nature of human beings makes us so uniquely good at cooperation? The answer would seem to be quite obvious: humans have highly-developed cognitive faculties which allow us to do much that other related species cannot. For example, though humans tend to be shortsighted in deciding which states of affairs would be best to bring about, the ability to recognize that we have reasons to care about future states of affairs just as we have reasons to care about present states of affairs allows humans the ability to adapt their choices to ensure that future goods are not sacrificed disproportionately in favor of present goods (Kokko and Heubel pp. 85-6). Though humans have problems being motivated to pursue future goods, humans can at least consciously recognize the importance of pursuing future goods. It’s not obvious that, say, a fish could do the same.

As Felix Warnecken argues, humans can cooperate in ways that other animals can’t because humans have more advanced cognitive processes available for collecting social data from other organisms (Warnecken p. 412ff). We see this clearly when we note that non-human primates are capable of a high degree of cooperation, so long as the tasks at hand are simple enough for their relatively lesser cognitive capacities to comprehend (Warnecken pp. 409-11). Relatedly, Hugo Mercier argues against our common sense assumption that highly intelligent people are less amenable to influence by others. Less intelligent people tend to be less amenable to influence because they reject too much information without due consideration, but since accepting information tends to produce an adaptive advantage, as is the case in human societies, we should expect organisms to develop some kind of adaptation that allows them to accept information more reliably (Mercier p. 375). Thus, we can establish a convincing evolutionary
connection between higher cognitive capacities and the ability to form cooperative relations.

Humans are uniquely cognitively situated to defer their own interests for the benefit of others, even when they themselves do not obviously benefit. But certain aspects of human social functioning are puzzling in their own right. A number of essays in this volume are dedicated to accounting for the existence of stable social contracts and property norms, a pervasive feature of human societies. Kim Sterelny, in his chapter “Life in Interesting Times: Cooperation and Collective Action in the Holocene,” argues that the social contract that arose as a result of the Holocene revolution, where humans began to settle into permanent agricultural societies, ought not, from an evolutionary perspective, to have occurred. Pre-agricultural social contracts are stable, argues Sterelny, because no individual in that society has the ability to accumulate wealth past a very immediate level. In other words, pre-agricultural societies have a structural tendency toward egalitarianism (Sterelny p. 92ff). However, the Holocene revolution turned land into a heritable commodity: those who could acquire more land could leave it to their offspring (Sterelny p. 97). So we have the development of economic inequality. But part of what makes the pre-agricultural social contract stable is its egalitarian nature. Thus, we should be surprised when the Holocene social contract turns out to be stable, despite its inegalitarian nature. Now clearly this issue is easily answered in principle: ethical norms of property rights, as well as coercive power, reinforce the practical application of property rights. However, and this is Sterelny’s crucial point, these Holocene social contracts developed before the requisite coercive power and ethical norms were put in place. So an explanation of the Holocene social contract
desperately needs an account of how the Holocene social contract could develop without the existence of the functions necessary to hold it in place.

Paul Seabright attempts to sketch an answer to Sterelny’s challenge. Though he considers a number of possible responses, I think the one most worthy of note is his observation that hierarchical social contracts may exploit the existence of pre-existing human social impulses (Seabright p. 114), a theme which appears throughout Cooperation and its Evolution. People may have already had a tendency to sacrifice their own interests to further those of others in their group; perhaps elites in pre-agricultural societies were able to prey on this tendency to get people to accept economic inequality. Seabright rejects this possibility because he thinks that individuals are likely to act altruistically only when the benefits of that behavior are spread among many people and sufficiently salient to themselves, and that the benefits to Holocene inequality are unlikely to be salient and motivational in this way.

I think Seabright ought to take this possibility more seriously, however, and indeed I think this possibility is a strong contender for solving Sterelny’s problem. Specifically, I think that the benefits of Holocene inequality are likely to be more significant and salient that Seabright estimates. One of the guiding assumptions of liberal economic theory is that inequality is one aspect of economic systems that makes all people better off. Further, in Sterelny’s view, inequality is the result of economic development. Though some people in Holocene society are better off than others, it’s likely that everyone will benefit materially, for example, in virtue of a steadier food supply and higher crop yields. Adam G. Hart’s discussion of task partitioning and division of labor further suggests this
move: developing a more complex, hierarchical form of social organization may lead to a higher degree of labor specialization, providing significant adaptive benefits in terms of productivity and flexibility (Hart pp. 203-207). It also seems quite reasonable to suppose that individuals in these societies would have felt in their own lifetimes their economic and material circumstances improve as a result of the development of agriculture, especially if we imagine the first people settling down and forming agrarian societies. If this is the case, then it’s straightforwardly beneficial to move to the Holocene agricultural social arrangement, even if some benefit disproportionately.

This account of the adaptive nature of stratified agricultural social arrangements is expanded by Herbert Gintis in his discussion of ‘loss aversion’, or the tendency of creatures to expend more to keep an already-held good than to acquire a previously-unheld good. Property equilibria can only be maintained when those who hold property are willing to fight to keep it more than others are willing to fight to take it away, because otherwise excessive costs would be paid by all creatures in seeking to stake their claims to a territory (Gintis p. 123). Applying this to Sterelny’s problem, it might turn out that it’s simply far more costly for the have-nots to fight with the elites over property, especially considering the possible distributed economic benefits of property that I considered above. Yet the problem here is that, once the have-nots unify against the elites, it surely becomes less costly to overtake the property of the elites than it is to maintain the stratified social system. Indeed, Sterelny himself notes this point (Sterelny p. 103). Thus, it seems like a Gintis-style answer would fail here; loss aversion cannot account for the stability of the Holocene social contract.
IV.

Though the answer proposed by Seabright is promising, we might review another possibility which Sterelny rejects out of hand, namely the possibility that ethical norms of property rights are responsible for the Holocene revolution. It might turn out that the economic answer is fragile, given that it isn’t clear whether it is actually in the interest of the have-nots to move to a stratified society, but if ethical norms worked on individuals in pre-agricultural societies in particular ways, then those ethical norms might have sufficiently pacified the have-nots to allow the elites to hold power over them. Now clearly norms of property rights are not evolutionarily free-standing, if they are evolutionarily constructed at all, since they did not simply appear at the time where they came to be implemented. Rather, they had to develop over time. Indeed, according to Matteo Mameli, our explicit cognitive moral concepts evolved to *co-opt* our intuitive normative impulses, since one can have a purely cognitive understanding that, say, the prohibition on murder is a moral norm, but unless one also have an intuitive moral concept which pushes them to make the decision, one will not act on the understanding of that norm (Mameli p. 542). Though the norms that we hold explicitly are essential to our moral self-understanding and can aid us in doing what we ought to, they are typically insufficient to guide and motivate action. Moral norms are only effective when they work in accordance with some other tendency.

Expanding on this, one way to explain the stability of cooperation after the Holocene transition is to show that respect for the property rights of others is parasitic on some other human tendency, meaning that because this
other tendency was already put in place by evolutionary processes, still other evolutionary purposes could be served by the application of that tendency to new problems and new situations. Gintis’s comments on loss aversion, already discussed above, are suggestive here. Further, in one of the most fascinating essays in this volume, Daniel Kelly discusses the relationship between the human disgust intuition and certain foundational ethical concepts that we hold. Disgust is a physiological response that developed in creatures to protect them from environmental hazards like parasites and pathogenic foods. However, disgust also comes along with certain physiological responses, like what Kelly and others have called the ‘gape face’, or the face that people make when they smell a toxic smell, which warns others that some object is worthy of disgust. Further, Kelly argues, the social needs of early human beings required us to produce signals that could communicate a broad variety of information to each other; in the case of disgust, group membership and purity, perhaps. It seems like it would be less evolutionarily costly to co-opt an already-existing capacity response to communicate information about group membership than to develop an entirely new one (Kelly p. 513). Thus, if the gape face served a social purpose, then that purpose could be seen to be parasitic on the intuition of disgust elicited by poisonous and parasitically-infested food. Similarly, Cecilia Hayes in her article “What Can Imitation Do For Cooperation?” discusses the fact that a great number of creatures engage in imitation with each other as a sort of ‘social glue’ which serves to differentiate members of a group from those not involved by creating shared experiences. Imitation is often unconscious and the signals that are sent are thereby quite difficult for those who are not members in that group to fake. Thus, from a biological process
which is seemingly non-normative we get a strong normative tendency (Hayes p. 326).

The problem with interpreting Kelly and Heyes on this point is that the process is not simply one-directional. It’s not just that from imitation as a process we get its social cohesion function; the adaptive nature of that social cohesion function itself serves to further incentivize and reinforce imitation as a biological tendency. So in order to understand exactly what is going on here, it would be helpful to understand the ways in which genes influence the evolution of cultural norms, as well as the ways in which cultural norms influence the evolution and expression of genetic information. Maciek Chudek and coauthors, for example, note that human sociality creates a massive need for reliable and frequent information transmission: because humans work best in societies, and societies work best when individuals in those societies share information, we should think that humans have developed capacities and tendencies to share that information. So there’s a selection pressure on humans to create culture which provides adaptive benefits to those humans. In other words, the contingencies of human life create the need for culture. However, culture itself acts as a constraint on which sorts of genes are expressed and passed on and which are defeated by the evolutionary process (Chudek et al. pp. 438-9). This is just to say that, when looking at the evidence presented by Kelly and Heyes, we need to take it with a grain of salt, always keeping in mind that it’s not just biological processes which create norms; it works the other way around as well.

To motivate this point, we can see a similar pattern of environment/organism co-evolution with respect to the way that certain lifeforms control their environments, and are at the same time controlled by those environments. In
Jessica C. Flack and colleagues’ essay “Timescales, Symmetry, and Uncertainty Reduction in the Origins of Hierarchy in Biological Systems,” where the relations between coral reef systems and their environments are discussed, it is noted that, since ocean currents and temperatures play a significant role in the sorts of coral life that can develop, reefs often grow in ways that actually control currents and temperatures in a way that makes those systems more likely to flourish (Flack et al. pp. 62-4). In the same way that there is a bidirectional relationship between reefs and the environments which constrain the sorts of reefs that can grow, there is a bidirectional relationship between biological processes and ethical norms which arise out of those processes and constrain the ways that humans can behave.

From the perspective of Chudek, Flack, and their numerous coauthors, it might seem to be misplaced to ask whether culture or genetics is ‘prior’ to the other; to ask which one is primarily responsible for the existence of the other. The right answer to this question might be simply that there is no real answer; that it’s a hopeless ‘chicken and egg’ dilemma. Parallel to this point is Brett Calcott’s recognition that proximate explanations for an evolutionary phenomenon, whereby we explain the adaptation in terms of its benefit to individuals, and ultimate explanations for the phenomenon, whereby we explain the adaptation in terms of its benefits to the survival of the species itself, both have a rightful place in evolutionary theory, and that to preference one over the other as a matter of principle is myopic (Calcott pp. 251-2). If this is right, then the argument presented by Don Ross in his contribution to this volume, “The Evolution of Individualistic Norms,” needs to be amended. Ross argues that evolutionary biologists are guilty of assuming an individualistic framework when discussing evolution: we
look to what it is that individuals themselves do and benefit from to understand why things happen as they do. And, because of this, we get what he calls ‘normative individualism’, the view that individuals *ought* primarily to act to follow their own interests. This, according to him, is a mistake, because “genes in all multicellular organisms maximize the inclusive fitness of their bearers by entangling their fortunes with those of other genes” (Ross p. 22). We often have strong incentives to adopt altruistic norms, because our fortunes live and die with the fortunes of others. So a strict methodological individualism would seem to be a dogma that can be dispensed with. However, from the perspective of Chudek and coauthors, this might be seen as placing undue importance on the ‘culture’ side of the equation: though the evolutionary process is not individualistic in the sense Ross thinks many evolutionary theorists take for granted, the actions themselves can only be made sense of in terms of individual decisions and actions. For example, Ross cites evidence that individuals who know that their decisions will bind the group that they belong to end up choosing actions which are individually ineffective but collectively beneficial, but nonetheless see this as the correct choice to make (Ross p. 31). So in a sense these individuals sacrifice their own interests to those of the group, but in another sense, these individuals do what to them seems like the best course of action, all things taken into account. If Ross’s conclusion is simply that an individualist picture of evolution can’t account for everything perfectly, then he is right, but if his argument is that individualism is an errant approach (as he suggests at p. 37), then he is going too far. It might be better to follow Chudek and coauthors and simply say that there is no *complete* answer to be given here, though individualistic and collective frameworks might both be useful in certain cases.
V.

Though our normative capacities clearly play a hefty role in our ability to form cooperative systems, they cannot by themselves account for the existence of cooperation. Because it is often a significant burden on individuals to act altruistically, some will not do these actions unless they have some sort of external force motivating them to do so. Thus, an understanding of the evolutionary development of punishment and coercion is crucial to understanding how altruistic behavior can be maintained.

A number of authors in this volume address versions of this question. Ben Fraser, addressing the problem of ‘false advertising’, or organisms behaving in certain ways that trick others into thinking that the organism is a more desirable partner for cooperation than that individual really is, notes that there may be a few ways that this can be solved. First, obviously, we punish those who cheat evolution in this way; more detail on this point to come. Less obviously, however, groups often develop ‘commitment devices’ to disincentivize cheating. There are some societies where group membership is denoted by ritual scarring or tattooing; these signs can be quite difficult to fake convincingly and thus seem to prevent individuals from falsely denoting themselves as group members (Fraser p. 168). Daniel M. T. Fessler and Katinka Quintelier provide a painstaking and illuminating discussion of these commitment devices and the sorts of variety that they come in. One fascinating example they give is the modern institution of engagement rings: since women can no longer sue men who have broken off engagements, a norm of providing wedding rings as proof of one’s desire to marry has developed and become embedded quite deeply in our culture (Fessler and Quintelier pp. 471-2).
Commitment devices clearly have a role to play here, but they cannot play the entirety of the role that they would need to in order to explain the external forces which prevent defection from cooperative behaviors, because commitment devices are often explicitly and intentionally chosen by the organism in question. Sometimes, however, societies need to go against the wishes of individuals to preserve cooperative behaviors. Thus, societies have developed the institutions of punishment. Fiery Cushman, in a crucial essay “The Role of Learning in Punishment, Prosociality, and Human Uniqueness”, discusses these evolutionary mechanisms in detail. There, he tries to provide an account of punishment that does the most effective work in promoting prosociality. Specifically, he argues that we should expect ‘inflexible punishment’ strategies to develop, where individuals are punished regardless of whether punishment will tend to decrease their antisocial behavior. This is because punishment involves a highly cognitively simple connection between the antisocial action and the consequences imposed; in order to form the intended associations between antisocial action and external sanctions, punishment is most effective when it is swift and clearly understood. There is little room for ‘nuance’ in the relation between the behavior deserving of punishment and the organism who did it, since the tendency to be influenced by punishment is parasitic on our general capacities to be operantly conditioned (Cushman pp. 342-4).

VI.

As I said before, given the highly diverse nature of the essays presented in Cooperation and its Evolution, I am unable to discuss a number of interesting essays in detail here. In particular, Richard Joyce’s discussion of moral nativism is a valuable work on the implications for
metaethics of evolutionary science and will be particularly
interesting to those readers familiar with his previous work,
as it can be seen as a departure from some of his earlier
claims. Haim Ofek’s paper on biological differences which
can explain the unique human propensity to cooperate with
each other is also worth perusing.

Perhaps this book’s greatest strength is its diversity: in
providing such a great variety of viewpoints on biological
and philosophical issues involving the evolution of
cooperation, it is sure to appeal to a great number of readers
in subdisciplines across these fields. Ultimately, however,
this book’s greatest strength is also its greatest weakness:
the sheer size and variety that it contains makes it difficult
to get a handle on, from the perspective of the reader.
Indeed, it is a lengthy text; thus, readers need some idea of
what they’re interested in if they are to benefit most
efficiently from its cutting-edge evidence and
argumentation. The editor’s introduction is surely helpful in
this respect, and I hope that this review can aid other
readers in making this excellent book work for them.