

Darwinian populations and natural selection, by Peter Godfrey-Smith, New York, Oxford University Press, 2009. Pp. viii+207.

Darwinian populations and natural selection deals with the process of natural selection and the best way for us to apprehend it. It asks whether an abstract description of this process is desirable, and how it should be done. It is assuredly desirable: though Darwin himself offered a rather concrete account of natural selection, it soon appeared that an abstract description enabled a better understanding of the process itself, and its extension to new entities (from organisms to genes, groups, etc.) and new fields (cultural change, genetic algorithms, etc.). Peter Godfrey-Smith (henceforth PGS)'s key question is how to best achieve this abstract account, this 'recipe' of what is essential for the process of evolution by natural selection (henceforth ENS). This project is certainly not original, as it has been worked on by many biologists and philosophers in the last forty years. But PGS's way of examining it is revolutionary and extraordinarily illuminating. His strategy is to develop a *gradualist* conception of a Darwinian population (moving from the question 'Is this process Darwinian?', to 'How much is it Darwinian?'), which leads him to distinguish *minimal*, *paradigm* and *marginal* cases, and then to use this conception to shed light on key questions such as levels of selection and evolutionary transitions, the gene's eye view, and cultural evolution.

This book is at once a major contribution to biology, philosophy of biology, philosophy of science (in contrast with much recent philosophy of biology, focused on problems quite isolated from those of general philosophy of science), and philosophy in general.

Epistemology of Natural Selection

PGS starts with classic accounts of the 'recipe' for having a population evolve by natural selection. This recipe has three ingredients: variation, fitness differences, heritability (Lewontin, The Units of selection, *Annual Review of Ecology and Systematics* 1970, 1: 1-18). Though PGS wants to build on this classic account, he describes its flaws, showing especially that there can be variation, fitness differences and heritability without evolutionary change.

To account for the problems met by the classic view, PGS offers a diagnosis, which pertains to the epistemology of scientific knowledge, and constitutes an important contribution to *general philosophy of science*. There is an underappreciated tension, or trade-off, between two ways of conceiving of 'abstraction' in classic accounts: *inclusion* and *modelization*. First, the goal can be to offer a general, maximally inclusive account of cases of ENS. Second, it can be to determine ideal, pure examples of ENS (real or fictional cases), and then use them as models that other processes will approximate. When insisting on inclusion, the risk is to blur our understanding of the very process of ENS; when insisting on ideal cases, the advantage is simplicity (a causally transparent account), but the risk is to lose interesting borderline cases. It might seem obvious that the solution is to combine the two; this is indeed what PGS does, but this, precisely, presupposes the new analysis of Darwinian processes he offers.

With this diagnosis, PGS reactivates a major debate in epistemology, that between Locke and Berkeley on abstraction. Locke defends the role of abstraction in human understanding, while for Berkeley no general abstract idea exists, and the human mind

relies on idealization (e.g. one particular idea of a triangle, not the idea of a triangle in general) rather than abstraction. PGS shows that we need both abstraction and idealization, but that each approach has its difficulties, and that combining the two can be thorny.

In this analysis, PGS also makes a crucial move towards the integration of philosophy of biology into general philosophy of science, where the questions of modelization and idealization have become crucial in the last decade (Giere, *Explaining Science*. Chicago, IL: Chicago University Press, 1988). PGS's look at the epistemology of scientific knowledge in evolution thus constitutes a major contribution to the indispensable 'de-provincialization' of philosophy of biology.

The Darwinian Space

After his diagnosis, PGS suggests a cure, which is to develop a *gradualist* conception of a Darwinian population. This framework can be pictured by a 'Darwinian space', a spatial representation of ENS. This part of the argument is the major contribution to both *biology* and *philosophy of biology*.

PGS shows that ENS is *multifactorial* and comes in *degrees*. He distinguishes *minimal* (characterized by variation, fitness differences, heritability), *paradigm* (a subset of the minimal cases, characterized in addition by novel, complex, adapted traits) and *marginal* (cases that only approximate the minimal requirements) concepts of a Darwinian population.

The spatial representation makes vivid the idea that a process is *more or less* Darwinian. The position of a population in the space depends on how it scores on several factors: fidelity of heredity (H), abundance of variation (V), competitive interaction with respect to reproduction (α), continuity of fitness landscape (C), dependence of reproductive differences on intrinsic character (S). Figure 1 shows a representation of populations according to three of these factors.

This representation sheds light on key evolutionary concepts, such as drift – described here as low C and low S, and not as an independent evolutionary force, nor a reflection of our ignorance.

PGS applies the same multifactorial and gradient reasoning to *reproduction*. Reproduction is usually seen as the production of a new individual via the causal role of some preexisting individual(s) of the same kind. Exploring a rich 'menagerie' (plants, clonal organisms), PGS shows that ingredients of reproduction are the possession of a bottleneck, reproductive specialization ('germa'/'soma' distinction), and overall integration (Figure 2). He gives a new, relaxed, conception of a biological *individual*. Here an individual is a member of a Darwinian population; it can be an organism, but also a gene or a cell; it is not necessarily genetically homogenous, unique and physiologically unified.

Insisting that ENS comes in *degrees* sheds light on the *levels* of natural selection. A Darwinian individual often contains a Darwinian population (e.g. cells in a multicellular organism), which leads PGS to support *hierarchical* conceptions of ENS. Yet biological entities at different levels can be 'Darwinian' to different degrees, scoring differently on the factors described earlier. For example, cells in our bodies constitute a Darwinian population, but lost a significant part of their Darwinian character.

This analysis also allows us to understand *moves* within the Darwinian space. A

population can become more or less paradigmatically Darwinian through evolution. In particular, building on recent literature on evolutionary ‘major transitions’, PGS shows that the *emergence of a new individual* often presupposes a ‘De-Darwinization’ – the partial suppression of competition among lower-level constituents. Several processes, for example, suppress the subversive proliferation of tumour cells in multicellular organisms.

Using the same framework, PGS examines the renewal of the debate over group selection. He offers a very illuminating account of *altruism*, *kin selection*, and *multilevel selection*. One of the important conclusions of this analysis is that genetic similarity is not per se a necessary component of the evolution of altruism.

Overall, this analysis in terms of degrees, levels and increasing/ decreasing Darwinization is a major contribution to evolutionary biology and its philosophical understanding.

Critique of Replicators and of the Gene’s Eye View

A direct consequence of the Darwinian space is a critique of what can be called *synecdochic* approaches to evolution: because of the failure to think about ENS in a gradient way, biologists and philosophers have often mistaken a part for the whole. The most striking example is that of replicators. In contrast with many (Dawkins, Hull, Sterelny...), PGS claims that ENS does not require *replicators* (faithfully copied entities), but only that reproduction leads to parent-offspring similarity. This similarity *can* take the form of a faithful ‘copying’, but does not *need* to. The replicator view insists on the persistence of entities, instead of the construction of new entities, resembling their parents to some extent, at each generation (Oyama, *The Ontogeny of Information*, Cambridge: Cambridge University Press, 1985), whereas it is entirely possible to conceive a process of ENS without any entity that persists and is transmitted.

Unsurprisingly, another synecdochic approach criticized by PGS is the famous *gene’s eye view*. If this view means that evolution can be *represented* in genetic terms, it is true, but this is just one representation among many. If, however, it means that evolution is always a contest between replicators, with genes being almost the only replicators (Dawkins, *The Selfish Gene*, Oxford: Oxford University Press, 1976), then this claim is totally different, and wrong as it stands. PGS shows that a Darwinian competition between *selfish genetic elements* can exist in real biology (transposons, homing endonuclease genes, meiotic drive), but is the exception rather than the rule. In addition, the gene is not a persistent, well-delimited entity. In most cases, thus, genes are *marginal* Darwinian individuals.

Put the Blame on Memes, Boys!

The final chapter, particularly enlightening, deals with cultural evolution. Is cultural change Darwinian? Do changes in behaviours, ideas, words, etc. obey the Darwinian ‘recipe’? PGS applies the same strategy, asking ‘Why not?’, and then ‘How much?’

PGS distinguishes two conceptions of cultural evolution. In the first, the reproducing entities are *biological* entities, and cultural traits are simply one type of phenotypic trait. This, in fact, is a *direct* application of ENS: ENS does not specify a mechanism of inheritance, therefore if offspring tend to resemble their parents in a high fitness behaviour, then we can have ENS. The problem is that this conception accounts only for *vertically* transmitted traits (from parents to offspring), while cultural change is

often driven by *horizontal* transmission (you imitate your neighbour, friend, priest, etc.)

In the second conception, the reproducing entities are *cultural variants themselves*. Ideas, words, behaviours, artefacts would reproduce and be selected. This approach has been dominated by the ‘*meme*’ view, a ‘*meme*’ being a *cultural replicator*. PGS shows that several cultural phenomena may *look* Darwinian without being truly so. For cultural phenomena to be Darwinian, it is important that i) we deal with a *population*; ii) the parent has a clear *causal responsibility* for the offspring; iii) the offspring is not simply *modified* by the parent, but comes into being largely because of its parent. Using this gradient analysis, PGS concludes that *some* cultural phenomena express *some* Darwinian features, and constitute *marginal* Darwinian populations.

PGS is critical of the meme approach, championed by Dawkins (op. cit) and Dennett (*Darwin’s Dangerous Idea: Evolution and the Meanings of Life*, New York, NY: Simon & Schuster, 1995). First, cultural evolution does not need cultural *replicators*. Second, one of the main motivations for introducing memes has been that memes are *selfish* cultural variants, and that cultural change is the contest of hidden *agential* cultural units (e.g. religious ideas). For PGS, there is no evidence in favour of this view, and it can be altogether misleading to believe that revealing a hidden agenda explains a phenomenon.

Worldview

Based on this new account of ENS, the book offers a worldview. This is a contribution to *general philosophy*, in the form of what PGS calls ‘philosophy of nature’ – the philosophical elaboration of a scientifically informed worldview, without taking science in its raw form. PGS offers a critique of some of our psychological habits when describing the living world, and shows what a truly Darwinian view of it would be.

First, reviving key philosophical convictions of Darwin, PGS defends a *populational, nominalist, strictly non-essentialist* view of the living world. ENS is possible even if every biological entity is unique, and grouping of living individuals into ‘types’ is always conventional. Darwin has shown the necessity of replacing types by populations, but this battle must constantly be re-fought, because of our psychological tendency to think in terms of essences and types. In PGS’s framework, the term ‘Darwinian population’ is at once a scientific contribution to how ENS should be understood, and a philosophical contribution to a Darwinian worldview.

Second, PGS offers a critique of our *anthropomorphic, often axiological*, tendencies when describing the living world. This includes the agential view, examined in discussions on replicators and memes, which often leads to ‘Darwinian paranoia’ – the tendency to think about evolution in terms of hidden vicious intentions (Francis, *Why Men Won’t As for Directions*, Princeton, NJ: Princeton University Press, 2004). The agential view has undesirable consequences for evolutionary biology, prompting us to search for persistence instead of similarity, to ask ‘*cui bono?*’ instead of adopting a multilevel analysis, and to insist on a genetic criterion when defining biological individuals.

Contrary to PGS, I would add to the anti-anthropomorphic picture the necessity of rejecting the idea of biological ‘complexity’. This raises the question of how PGS defines *paradigm* Darwinian populations. PGS says they are those in which novel, adapted, complex structures emerge, like eyes and brains. I agree ENS needs to offer an

explanation of the origin of *evolutionary novelties*, but not an explanation of ‘complexity’. PGS pictures adaptation of bacteria to antibiotics as paradigmatic. I agree this is a good example of evolutionary *novelty*, but I think most people will tend to call ‘complex’ only fascinating metazoan traits such as, precisely, brains and eyes. The insistence on brains and eyes is a misleading remainder of natural theology, which has certainly inspired Darwin, but should not inspire us today.

PGS’ ‘Darwinian picture’ says something crucial about our place in the world as human beings. But this, precisely, presupposes that we do not see the world through excessively ‘humanized’ lens.

The Causality of Heredity

I will close this review with an objection to PGS’s analysis of heredity. He insists that heredity must not be defined by the reliable transmission of a structure (*replicator*), but as parent-offspring similarity, and therefore favours the statistical concept of ‘heritability’. He then insists that ENS necessitates a *causal* role of the parents in the production of the offspring. But I think a deeper analysis of the causality of heredity is necessary. The replicator view was an *explanation* of similarity, so it cannot be *replaced* by the very notion of similarity, but by a new analysis of the causality of heredity, a new explanation for parent-offspring similarity. It is all the more necessary because replication is usually easier to track than similarity, and it is not at all clear that humans are competent to establish similarities. We all know that causality is a difficult, highly debated concept in philosophy of science. But PGS’s excellent analysis makes indispensable a deep reflection on the causality at work in ENS.

Conclusion

This book will be a classic, in philosophy of biology and beyond. It shows that Darwinian processes should be seen as coming in *degrees*. Real biological processes can be *more or less* Darwinian, and can *become* more or less Darwinian through evolution. This view illuminates natural selection and constitutes a remarkable tribute to Darwin himself, 150 years after the publication of the *Origins*. But this book also makes a decisive contribution in integrating philosophy of biology into the general framework of philosophy of science. I see it as a complete success, and a model for research to come in philosophy of biology.

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