

Peter Godfrey-Smith, *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press, 2009. Pp. x, 207.

The core notion of Godfrey Smith's account is that of a 'Darwinian population', which is "a population—a collection of particular things—that has the capacity to undergo evolution by natural selection" (page 6). A 'Darwinian individual' is a member of such an evolving population. This sounds very broad, but the aim is a general characterization of the features that an ensemble of objects must have to be able to undergo selection-guided change. Indeed, Darwinian populations exist on different levels of organization. While some Darwinian populations are made up of organisms, others are collections of genes, cells, or organism groups.

In addition to a general construal of evolving things, Godfrey-Smith devotes substantial attention to marginal cases. There is not really an essence of Darwinian-population-hood. Rather, there are paradigmatic cases that clearly exhibit change by natural selection, but also borderline instances. To capture this conceptually, Godfrey-Smith considers five quantitative properties with respect to which Darwinian populations can differ. The three most important ones are the heritability H (the degree of parent-offspring similarity), the continuity and smoothness of the fitness landscape C (to which extent a small change in an individual's traits results in a small change in the individual's reproductive fitness), and the degree S to which reproductive fitness is determined by a fitness-bearer's intrinsic character (as opposed to extrinsic features having an influence). Different concrete Darwinian populations occupy different parts of this three-dimensional space with axes H , C , and S . If all three values are high, cumulative selection (where smaller steps gradually build up to long-term change in a certain direction) is possible, so that we are dealing with a paradigmatic Darwinian population. Several types of non-paradigmatic Darwinian populations exist, for instance when the heritability H is low, or instead the fitness

landscape is very rugged (low C)—both are different scenarios where selection occurs but change is hardly directional. Of particular interest is Godfrey-Smith's view on 'drift', whose interpretation has been hotly debated among philosophers. Often random drift is contrasted with selection, possibly by viewing drift and selection as two orthogonal forces whose strength can vary. Godfrey-Smith rejects this way of construing drift, and prefers his three-dimensional conceptual space, where low values of both C and S largely corresponds to what is usually judged a large 'influence' by drift.

An important part of the discussion pertains to the relation between reproduction and growth. Strawberries produce runners, so one may wonder whether this is growth of one individual rather than the production of a new individual. Whether a process is more reproduction than growth is treated with an eye on the degree to which it permits evolution by selection. Humans reproduce and form Darwinian populations, but the cells of an individual human do so to a lesser extent. Godfrey-Smith conceptualizes the reproduction of such entities (which have parts that themselves can reproduce) using three parameters: the bottleneck between the reproducing parent and the offspring's developmental starting point (multicellular organism but single fertilized cell), the degree to which germline and soma are separated, and the degree of causal integration among the parts of an individual. This is used to shed light on the major transitions in evolution (such as from single-celled to multicellular organisms) and the existence of Darwinian populations on different levels, where one Darwinian individual has parts that form a lower-level Darwinian population. Often a higher-level Darwinian individual (a multicellular organism or a bee colony) results from what Godfrey-Smith dubs 'de-Darwinization', where the higher-level entity restricts its lower-level constituent's ability to reproduce and thus to evolve, this due to a parent-offspring bottleneck and a germline-soma distinction.

Especially philosophers will be keen on considering Godfrey-Smith's critical stance on gene selectionism. While many have followed David Hull in distinguishing replicators and interactors (sometimes favoring replicators as the unit of selection), Godfrey-Smith views the very distinction as irrelevant. On his account, there are simply Darwinian populations, often on different levels, including groups of individuals. While acknowledging cases of gene selection (such as meiotic drive), he objects to redescribing cases of individual selection as instances of gene selection. For individuals can form genuine Darwinian populations that evolve due to the heritability of organismal traits—an issue not modified by the fact that there is something on lower levels that accounts for why there is this heritability. This argument has merit, yet a good deal of the levels of selection debate has centered on the causes of selection (where various preferred levels of selection have been defended in these terms); Godfrey-Smith's failure to address most of the literature and arguments surrounding the causes of selection is a flaw. But he is right that the notion of a replicator does not capture all instances of selection, as higher-level entities can exhibit heritability while the lower-level basis for this changes, so that there is no persistent lower-level replicator that copies its structure. Godfrey-Smith also addresses cultural transmission, which, depending on the empirical details, can be Darwinian. Richard Dawkins is known for his naturalistic interpretation and critique of religion, which highlights our psychological tendency to interpret complex natural events in terms of hidden intentional agents. The irony that Godfrey-Smith points to is that Dawkins's *Selfish Gene* ascribes agency to genes, falsely implying that for evolution by natural selection to take place there has to be an enduring entity that has interests and benefits from adaptation.

Without doubt, *Darwinian Populations and Natural Selection* ties into many philosophical and biological issues surrounding evolution and develops worthwhile perspectives and challenging points. However, in several spots the discussion could have been more explicit and

the arguments more elaborate. Given that his basic topic is of interest to a large audience, for readers not fully familiar with some of the philosophy of biology issues, Godfrey-Smith could have explained in more detail the debates he addresses and highlighted the import of his contribution vis-à-vis existing positions. His views are convincing, yet given various previous discussions and considerations, some stakeholders in these debates may want to see more developed defenses for Godfrey-Smith's views and criticism of rival arguments.

In the introduction Godfrey-Smith makes plain that his subject matter is at the same time (a) science, (b) philosophy of science, and (c) philosophy of nature. Yet in his concrete discussion it is left somewhat ambiguous whether a certain consideration concerns one primary subject matter, or in what way the discussion touches upon all three projects. Given that he does not develop new quantitative models and deliberately operates on a level more abstract than biological theories that are models for a limited range of phenomena, what exactly is his scientific contribution to issues in evolutionary theory? Are his philosophy of science insights meant to be of a metaphysical nature (about the ontology of biological entities and processes on different levels), or also of an epistemological nature (the character of evolutionary explanations, the role of metaphors of agency in biological reasoning)? In the context of philosophy of nature, Godfrey-Smith's account can clearly be seen—though he does not put it in these terms—as offering a more nuanced view than the 'universal Darwinism' advocated by Dawkins and Daniel Dennett, which offers a monistic vision of replicators as the fundamental biological entity and Darwinism as a principle transforming all of intellectual culture. At one point Godfrey-Smith defends his view as adequate for "Darwinian explanation" (page 106). If his scope was more broadly evolutionary explanation, at least then it would have been mandatory to make more explicit the variety of considerations beyond natural selection that are germane to evolutionary explanations, which would also have benefitted Godfrey-Smith's non-monistic philosophy of

nature. *Darwinian Populations and Natural Selection* develops a plethora of convincing points for philosophers and biologists alike; but sometimes it is left to the reader to infer their import.

Ingo Brigandt

University of Alberta