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BOOK REVIEW

Darwinian Populations and Natural Selection

By Peter Godfrey Smith

Oxford University Press, 2009. x + 208 pp. £25.00

This ambitious book develops a novel framework for analysing putatively Darwinian populations and the extent to which their behaviours over time ought to match paradigm examples of evolution shaped by natural selection. Godfrey-Smith's approach is novel. He treats populations as conceptually prior to the individuals of which they are composed and develops a series of parameters for evaluating the extent to which individuals and populations match the standards for being 'Darwinian'. This enables him to model changing populations in a variety of state spaces of varying degrees of specificity and to set forth critical evaluations of the extent to which a population (or ensemble of populations) fits conditions for Darwinian evolution and various ways of departing from Darwinian expectations.

The book is admirable for clarity of exposition, the ease with which it passes between serious biological examples and abstract treatments of evolutionary thinking, and the extent of its coverage of standard positions in philosophy of biology. For example, Godfrey-Smith's apparatus handles, elegantly, 'gene's-eye' accounts of evolution; controversies over the units and levels of selection and evolution; issues surrounding evolutionary transitions and Darwinian analyses of social evolution; and analyses of such key concepts as *fitness*, *heritability*, *individuality*, *reproduction*, *replication*, *segregation of the germ line* and the like. Cumulatively, his analysis allows him to handle key disputes, first with simple models, then with increasing sophistication, as he develops his apparatus, gradually setting up his own views about some key problems in philosophy of biology.

Consider the following state space for analysing evolution of individuals in a population over time (first with rough qualitative measures, then, where appropriate, with quantitative parameterizations). A first dimension, **H**, is an analogue of the conventional concept of heritability, but, like Darwin's concept, is independent of genetics. (Darwin had no theory of genetics; he only required some degree of correlation of characters between parents and offspring.) A second dimension, **C**, concerns the continuity of changes in fitness values with changes in characteristics (or phenotypes) of individuals. This roughly mirrors the ruggedness or smoothness of a fitness landscape, especially when the characters considered are genetic states of a population of organisms. The third dimension, **S**, measures the dependence of reproductive success ('realized fitness') on 'intrinsic' versus 'relational' or 'extrinsic' characters of the parents. High **S** corresponds to reproductive success depending on intrinsic characters. This allows distinctions between 'accidental' success (one twin killed by lightning before reproducing, the other with numerous offspring) and success due to intrinsic features and is a crucial component of Godfrey-Smith's novel analysis of genetic drift.

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Proper construction of **S** helps characterize the role and limits of such 'intrinsic' characters as *genetic composition* in analysing evolutionary problems.

Paradigmatic Darwinian evolution occurs when the individuals in the population(s) in question have high (broad sense) heritability, when most changes in their intrinsic characters normally make only incremental changes in fitness, and when changes of intrinsic characters correlate closely with changes in fitness. These circumstances yield heritable variation in fitness such that arbitrary environmental changes do not overwhelm adjustments in fitness – i.e. evolution steered by selection (whether stabilizing or directional). As **H**, **C** and **S** depart from the paradigmatic value, the specific ways the population changes over time are altered. At one extreme – no heritability, a rugged fitness landscape and high dependence of reproductive success on circumstances – change will be unpredictable and the population unsustainable. When **H** is high, but **C** and **S** are low, circumstances will dictate which organisms survive and how widely their fitnesses will vary from their parents' – i.e. the population will face extreme drift. Accordingly, Godfrey-Smith argues that the supposed opposition between drift and selection as 'forces' or 'causes' of evolution is a mistake: differences between these supposed opposites are better analysed as differences in (more-or-less continuous) parameters affecting the behaviour of the population over time. This result exemplifies the power of Godfrey-Smith's state-space analyses as an analytical tool. I cannot go into detail here, but he connects his analyses to important biological examples, e.g. of the wide variety of modes of reproduction (including alternation of generations and serially distinct morphologies), covered persuasively, with wide-ranging knowledge of relevant biological literatures.

The state space just illustrated is the simplest (but most powerful) of Godfrey-Smith's analytical devices. The full apparatus, not yet deployed in this book, involves a state space of at least eight dimensions. Other parameters explicitly identified are $\boldsymbol{\alpha}$ (the extent to which direct competitive interactions affect reproductive success), **B** (the extent to which genetic or variational bottlenecks affect the population), **G** (the extent of reproductive specialization within the population – e.g. segregation of a germ line from a somatic line in a population of cells, or specialization of one member, e.g. a queen, as *the* reproductive member of a colony), **I** (overall integration of a collective, e.g. a multicellular organism or a colony, beyond the separation of germ and soma – e.g. division of labour, mutual dependence of parts and devices for maintenance of an inside/outside boundary) and **V** (the extent of variation in the population). Godfrey-Smith provides crude measures of these parameters to assign qualitative locations to populations in the relevant state space and indicates how they can be refined in appropriate cases to yield satisfactory quantitative parameterizations. The resulting apparatus provides a major tool with significant potential for 'locating' populations in a way that permits analysis of the sorts of historical trajectories accessible to populations and ensemble of populations.

I can only mention a few of Godfrey-Smith's own positions. Some follow from material presented above: e.g. replication à la Dawkins is not required for paradigmatic Darwinian evolution and full-fledged evolutionary scenarios do not require Darwinian populations. Others go further. For example, he argues that genes, unlike cells, are 'scaffolded' reproducers, entities that do not reproduce 'on their own' by drawing only on external resources, but are assisted by structures and processes internal to the cells (unscaffolded reproducers) in which they are embedded. Such distinctions contribute to Godfrey-Smith's treatment of varying kinds of

individuality, of reproduction, and of populations. The embedment of populations within one another (genes, organelles, cells, multicellular organisms, symbiotic associations, interacting groups, breeding populations, etc.) is the stuff of multi-level evolution. To characterize the different sorts of individuality, it is best to start from populations and work out how the individuation and reproduction of the component individuals contributes to the structure and potential trajectories of the population. Doing so reveals the damage caused by an 'agential' perspective: treatment of such entities as genes and cells as agents with aims, benefits, etc., that shape how they act or behave.

This is a rich book. The apparatus developed here needs to be explored in far greater detail than Godfrey-Smith has yet managed. But he has already made significant progress in going beyond the 'agential perspective', arguing that little but confusion is gained by holding that genes, cells and other such entities have aims and enjoy evolutionary benefits from their actions, which shape their behaviour. Even where he overreaches, Godfrey-Smith presents useful challenges to philosophers of biology and biologists. The new pathway he provides for working out the evolutionary trajectories of populations (study of the impact of parameters such as those explored in this book) should yield important advances the philosophy of biology.

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