BOOK REVIEW

Peter Godfrey-Smith, *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press (2009), viii+207 pp., $55.00 (cloth).

Peter Godfrey-Smith, in his newest book *Darwinian Populations and Natural Selection*, identifies himself as continuing in what he calls the 'classical' Darwinian tradition. This tradition, perhaps most often identified with Lewontin but also traceable back to Weismann and arguably Darwin himself, seeks to summarize which properties of a population will cause it to undergo change by natural selection. Typical summaries include three ingredients—variation, heredity, and variable reproduction. As Godfrey-Smith argues however, "The standard summaries have problems because they attempt to perform two theoretical tasks at once . . . (i) describing *all genuine* cases of evolution by natural selection, and (ii) describing a *causally transparent mechanism*" (20). One often encounters dilemmas of this sort in biological theory. On the one hand, conceptual clarity is desirable when attempting to understand complex biological processes and entities. On the other hand, the natural world tends to firmly resist attempts to neatly characterize it. A simple theory will inevitably fail to account for relevant phenomena. A theory that attempts to capture all relevant cases will be too unwieldy to provide insight or clarity.

Arguably the central contribution of Godfrey-Smith's book is a conceptual tool for understanding Darwinian change that satisfies both desiderata, providing conceptual clarity without excluding relevant cases. Godfrey-Smith achieves this by mapping populations to a multidimensional space whose axes correspond to various properties relevant to whether said populations will undergo change by natural selection. In this way, a population need not be judged as either possessing the three ingredients of change or not. Instead, populations are differentiated using a scale measuring their levels of these, and other, relevant properties. According to Godfrey-Smith, some areas of this conceptual space will house 'Darwinian populations', those with the potential to undergo change by natural selection. Some of these will be paradigmatically Darwinian (ones that can, e.g., evolve to produce novel, useful structures), others will be minimally so, and some others will display only marginal Darwinian qualities. In this way, unusual or borderline cases of populations undergoing something like change by natural selection can be accounted for in Godfrey-Smith's framework. Paradigmatic cases of Darwinian change, meanwhile, can be analyzed in finer detail. This space, which allows for greater flexibility and subtlety in capturing why a popu-

lation will undergo Darwinian change, is potentially a powerful conceptual tool.

The rest of this review will focus on Godfrey-Smith's Darwinian population space and its sister space, which similarly treats the concept of reproduction. I will lay out both spaces in more detail and elaborate how these two conceptual tools work together in Godfrey-Smith's account. Finally, I will bring up one potential doubt about the efficacy of these spaces. In focusing on these topics, the review will neglect a number of the book's important arguments. In particular, in his last three chapters Godfrey-Smith uses the insight established with his conceptual spaces to discuss three highly debated topics in evolutionary theory: the gene's eye view, levels of selection, and cultural evolution. Although not treated here, this discussion is well worth reading.

The Darwinian population space Godfrey-Smith proposes, as mentioned, is multidimensional, although he is somewhat agnostic as to how many dimensions it ought to have. The list of relevant traits Godfrey-Smith provides includes fidelity of heredity (H), abundance of variation (V), competitive interaction within the population (α), continuity of fitness landscape (C), and dependence of reproductive differences on intrinsic character (S). (This last property, especially, may be unfamiliar to readers. It refers to the degree to which intrinsic characteristics [i.e., limb length] of an individual determine its fitness as opposed to extrinsic features [i.e., a lightning strike].) Godfrey-Smith concludes this list by saying that it is "obviously incomplete" (63); that is, other properties of populations will be relevant to the character of Darwinian change they undergo. With a subset of this incomplete list (H, C, and S) Godfrey-Smith goes on to demonstrate how some regions of the space will contain paradigmatically Darwinian populations while others do not. The presence of a certain level of all three of these variables, for example, will correspond to paradigm cases of change, while low levels of any of the variables will pick out cases of change that are less paradigmatic, such as, for example, populations prone to 'error catastrophe'. In such a case, H is low, and excessive change between generations forestalls the possibility of a significant Darwinian process.

Godfrey-Smith provides a similar space to analyze the degree to which certain processes are cases of reproduction. Godfrey-Smith does not attempt to cover all cases of reproduction but rather focuses on understanding what he calls 'collective reproducers': entities that reproduce but are composed of lower-level entities that are themselves reproducers. The paradigm example is that of a multicellular organism composed of cells, although collectives like termite colonies or buffalo herds are also examples. In this second space, the axes of interest measure the level of bottlenecking during reproduction (B), the degree to which the germ line is segregated from the soma (G), and the level of integration seen in the new individual (I). This second conceptual

space is important to Godfrey-Smith's project for several reasons. One is that the properties relevant to Darwinian change in a population, those that define the first space, often cannot be measured unless one is able to identify the individuals that make up the population in question. As Godfrey-Smith compellingly argues, there are a plethora of situations in the natural world in which this may be difficult to accomplish. As an example, he mentions groves of quaking aspens where each 'tree' arises from a common root system that connects what is arguably one large genetic individual. In providing a multidimensional space in which instances of reproduction are mapped using properties relevant to the extent to which the case is of reproduction or not, Godfrey-Smith creates a framework wherein problem cases of individuality can be considered with more subtlety as well (given that each case of reproduction involves the formation of a new individual from an old one). Furthermore, this second conceptual space allows Godfrey-Smith to introduce a compelling idea: that as higher levels of organization evolve in biological systems, populations at lower levels may evolve to lose their Darwinian character, or 'de-Darwinize'. It is no surprise that evolvability evolves. Godfrey-Smith contributes to this theme by arguing that certain properties of reproduction at a higher level of organization (i.e., sequestration of the germ line in multicellular organisms) directly influence the degree to which a lower-level population will be Darwinian (i.e., the fitness of cells in a multicellular organism will now be largely dependent on extrinsic factors, which is to say, S will decrease). These two spaces are thus complementary, each providing insight into how and why properties the other maps are important to understanding change by natural selection.

One potential complaint against these spaces that Godfrey-Smith himself brings up is as follows. The properties that identify the position of any particular population or case of reproduction in the spaces may be very difficult to measure. For example, consider an attempt to measure fidelity of heredity for a population (H). In general, the individuals in a population exhibit many traits; for some of these, presumably, fidelity of heredity may vary. How does one then measure H in a way that appropriately characterizes the whole set of traits in question? Averaging? Identifying minimum and maximum values? For that matter, how does one determine fidelity of heredity for each single trait? (To make things even stickier, how does one account for fidelity of heredity in sexual populations where traits may disappear and reappear in successive generations or exhibit a blend of parental characters?) Godfrey-Smith responds to this problem as follows, "When pressure is put on these measures, my response is to suggest successive moves away from precision. Perhaps they can only be scored with respect to high, intermediate, and low values; perhaps only high and low." He goes on to note that "the space is intended as a heuristic device. Many important features of Darwinian populations cannot easily be measured with a single number; that does not make

them less significant" (65). It seems from this that Godfrey-Smith avoids the problem by allowing his contribution in creating these spaces to be mainly a new way of thinking about things, rather than a completely developed framework in which real Darwinian populations are actually assigned numeric values corresponding to the properties in question.

It is not clear, however, that this response should alleviate worries about actually placing Darwinian populations in these spaces. In some cases it may not be possible to collapse meaningful information about the relevant properties into a single measurement—even a coarse-grained one. Consider C, the measure that corresponds to the continuity of the fitness landscape of a population. In a population with high C, small changes in phenotype will result in similarly small changes in fitness for the organisms in question. In a population with low C, small changes in phenotype will cause large changes in fitness. Imagine two populations, one in which the entire fitness landscape exhibits some moderate level of continuity and one in which about half the fitness landscape is entirely flat (phenotypic changes have no effect on fitness) and half is rugged. If C is taken as an average of the entire landscape, both populations could be mapped to the same value of C, although surely the continuity of their fitness landscapes differs in ways that are relevant to the types of Darwinian change that will be seen in the two populations. When highly complex data sets—like the levels of continuity throughout a fitness landscape—are compressed into single numbers (even if one chooses a method other than averaging), complexity will always be lost. This alone is not necessarily problematic. The problem in this case is that highly relevant complexity of the type that a conceptual tool aimed at differentiating the Darwinian character of populations ought to account for will be lost.

Coarse-graining does not provide a solution to this problem. It is not obvious that one of the two populations above should be 'high' and the other 'low' C given the details of their fitness landscapes. Instead, to distinguish these two populations with respect to C may require more measurements: two numbers, or four, or 20. The same worry applies to properties like fidelity of heredity (H), abundance of variation (V), and competitive interaction (α). Each is a complex and multifaceted property, and capturing the relevant aspects of these properties in a population with a single variable may not be possible.

One response to this worry could be as follows: the Darwinian population space is already multidimensional, why not add as many dimensions as are necessary to appropriately differentiate Darwinian populations? The same could be done for the reproduction space. Unfortunately, such a move would threaten one of these spaces' main virtues: that they are simple enough to provide conceptual clarity. Perhaps a better response is that one should simply pay careful attention to what these conceptual tools are used for. Although they may present sticky measurement problems, as a big picture

framework for understanding how and why certain populations undergo Darwinian change, Godfrey-Smith's spaces still provide insight. And given the difficulties of simultaneously meeting both desiderata mentioned at the beginning of this review, it may be that our best hope is to focus on collecting tools that allow us to understand natural selection without insisting that any particular tool or framework be successful for all tasks or in all contexts.

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