

## Essay Review

# Darwinism About Darwinism

### **Darwinian Populations and Natural Selection**

Peter Godfrey-Smith

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Ernst Mayr (1959) coined the term “population thinking” for what he regarded as a much overlooked third great insight we owe to Charles Darwin, the other two being the evidence for evolution from common descent and the principle of natural selection (Mayr 1976). Mayr used “population thinking” as part of a dichotomy with “typological thinking.” The latter characterizes what he regarded as a misguided, pre-Darwinian practice. For the typologist, variation between individuals is an aberration from the underlying type. For the population thinker, types are mental abstractions and variation among individuals is real and important. No variation, no natural selection.

In the introduction to *Darwinian Populations and Natural Selection*, Peter Godfrey-Smith tells us that one of his aims is “to extend and re-assert the power of the perspective on the living world that Mayr gave partial expression to with his concept of population thinking” (p. 15; all page numbers in this essay refer to the book reviewed here). One might fear that with such aims, G-S is about to start skating on ice that is getting increasingly thin. After all, recent work in the history of science has shown that Mayr’s claims that pre-Darwinian thought was essentialist and typological are, to say the least, contentious (see, e.g., Amundson 2005; Winsor 2006; Wilkins 2009). But this is not what G-S’s plea for population thinking is aimed at. It will come as a surprise for the population thinker that G-S sets out to reassert and extend population thinking within

Darwinian evolutionary theory itself. In fact, he claims to have detected substantial typological thinking in representations of the main component of evolutionary theory: natural selection.

The book can be divided into two parts. In the first five chapters the organizing theme of “Darwinian populations” is developed. The Darwinian populations framework is the vehicle G-S uses to rethink Darwinism. The last three chapters apply these new ideas to theorizing about selection at different levels and in different domains. An appendix is included with some formal elaborations and extensions of topics discussed in the eight chapters of the book.

One strand of argument that runs through the book is a criticism of (a broad interpretation of) typological thinking: our tendencies to think and talk—overtly or unconsciously—in terms of types, essences, and agents when we talk about evolution by natural selection. Representing natural selection by positing agents of a certain type is most prominent in the replicator approach. Like many other biologists and philosophers, G-S is highly critical of replication thinking. Unlike many others, he is also critical of the “classical approach” in describing evolution by natural selection. Under this approach fall “summaries” of natural selection that consist of a small set of conditions—usually some combination of the presence of variation, heredity, and fitness differences. Acting in concert, these conditions are often proclaimed to be necessary and sufficient; they pin down the *essence* of natural selection. This approach goes back all the way to Darwin’s *Origin*, but nowadays it is often associated with Lewontin’s (1970) triad of “Darwin principles.”

G-S devotes a large part of Chapter 2 to showing that it is mistaken to think that the classical summaries actually state the essence of natural selection. Contrary to common understanding, the conditions that make up these summaries are not components of logical machines; they do not describe an algorithm (Dennett 1995: 50) or a syllogism (Gould 2002: 125). Instead, natural selection summaries are *idealizations*; they are *false* representations of the real process under study, but accurate representations of imagined simpler relatives

of that process (cf. Wimsatt 1987). Because the summaries idealize, there will be cases where they get things wrong. G-S gives several insightful examples of cases in which all conditions are satisfied but no evolution by natural selection occurs, as well as cases in which some conditions are not satisfied but natural selection ensues nevertheless. Different natural selection summaries give slightly different conditions, reflecting different idealizations. The result is that one summary may recognize a process as an instance of natural selection, whereas another one doesn't. Not a single one of them captures all cases we like to think of as showing natural selection at work. So what the summaries can do is different from what they are advertised as being able to do. They are advertised as *abstractions*, as omitting details to give a foundational description of natural selection. What they actually do is to give an *idealized recipe* that applies in some cases, but that does not cover all cases of natural selection. It would be misguided to try to dissolve this tension by constructing better summaries, by trying to combine different idealizations to turn them into abstractions. There are good reasons to think that is a lost cause. For instance, the notion of fitness, which appears in all summaries, cannot be expressed as one and the same parameter for predicting change in all possible cases. The notion of fitness we should employ to predict change will depend on the circumstances, which means that there is no single set of conditions that will tell us what is needed to get natural selection going.

With this criticism of the classical approach the stage has been set to launch the second strand of argument, which will become the core of the book. This is the constructive project of developing an alternative representation of natural selection, the Darwinian populations framework. To get a better grip on the understanding of natural selection, G-S argues that we should start by looking at populations, which have characteristics that make them more or less "Darwinian." The more Darwinian a population is, the larger its capacity to undergo evolution by natural selection. We can align populations on a gradient from the most Darwinian ones, the *paradigm* Darwinian cases, all the way to those about which we are hesitant to say that natural selection can occur in them in any meaningful sense, the *marginal* cases. A population of non-reproducing entities would be an example of a *very* marginal Darwinian population. Then there are *minimal* Darwinian populations. These are the "dull" cases. They can undergo selection, but will produce variations on an existing theme, unlike the paradigm cases, which tend to evolve complex adaptations. The right way to understand the concepts of marginal, minimal, and paradigm populations is as placeholders on a continuum that ranges from the very marginal to the obviously paradigm. Nowhere on that gradient can we find the starting point for *real* cases of natural selection, but natural selection starts playing a more prominent role as we move toward the end of the paradigm.

## Populations, Parameters, and Spaces

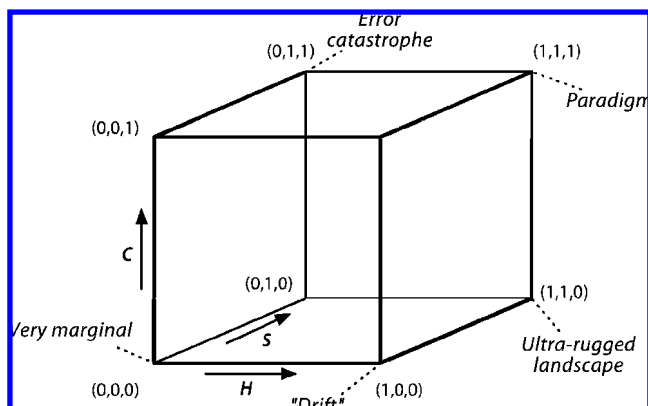
Chapter 3 is the heart of the book. It is devoted to fleshing out what makes a population Darwinian. This is done by scoring a given population on a variety of parameters, such as  $H$ , the fidelity of heredity, and  $V$ , the abundance of variation. So, instead of saying that a population *must have* heredity and variation—in the vein of the classical approach—the Darwinian populations framework ranks populations according to *how much* it possesses of each.

The  $H$  and  $V$  parameters are familiar; they are derived from the classical summaries. The other parameters are less obvious. G-S discusses several important ones, but notes that these do not exhaust the options; other parameters may also be important in judging how Darwinian a population is. The new parameters that are discussed at some length are  $\alpha$ , defined as the competitive interaction with respect to reproduction,  $C$ , for "continuity" or smoothness of the fitness landscape, and  $S$ , the dependence of reproductive differences on "intrinsic character." I will briefly discuss two of these parameters,  $C$  and  $S$ .

The concept of continuity was introduced by Lewontin as the principle that "small changes in a characteristic must result in only small changes in ecological relations" (Lewontin 1978: 169). G-S extends this principle, and turns it into a parameter. One way to understand  $C$  is as the smoothness of the fitness landscape. The smoother the fitness landscape, the higher the value  $C$  takes for the population under consideration.  $C$  is determined by causes of both internal and external nature. Internal influences stem from the organism's physiology and development. External influences on  $C$  are location, and interaction with others. G-S assigns the internal/external difference its own parameter,  $S$ , for "intrinsic character." The higher a population's score on  $C$  and  $S$ , the more Darwinian are the individuals it is composed of.

$C$  and  $S$  not only tell us something about what makes individuals more Darwinian, they also serve as a replacement for another vexed notion in evolutionary theory: drift. Selection is often contrasted with drift; change may be due to selection and/or drift. G-S suggests that the  $C$  and  $S$  parameters dissolve this dichotomy. What we take to be drift is in fact a combination of low values of  $C$  and/or  $S$ . So drift and selection are not two distinct factors, but are "distinctions along the gradients of  $S$  and  $C$ " (p. 61).

After having discussed some of the parameters, G-S introduces a spatial framework of three-dimensional "Darwinian spaces" as a tool for further analysis. Along each of the three axes of a Darwinian space, we can put a parameter, on which a score from 0 to 1 can be obtained. For instance, if we put the  $H$ ,  $C$ , and  $S$  parameters along the axes and start scoring populations, one that scores close to (0,0,0) is very marginal, and one that sits close to (1,1,1) is a paradigmatic Darwinian



**Figure 1.** A Darwinian space representing three of the parameters ( $H$ ,  $S$ ,  $C$ ) (redrawn from Figure 3.1, p. 64).

population. Scoring somewhere in between will make it a minimal Darwinian population (see Figure 1).

So far it has been unclear what things actually form populations. Organisms obviously do, but G-S intends his framework to extend to other individuals. He takes a liberal view on what other individuals can be recognized, which is crucial to make the framework useful in applying it to the topics of the later chapters. Not just organisms can form populations but so can cells, colonies, and chromosomes. Cells are examples of *simple reproducers*; they have all the reproductive machinery internal to them. Organisms and groups of organisms are *collective reproducers*; they are made up of parts—simple reproducers—that can themselves reproduce. Chromosomes, genes, and cultural entities fall in the category of *scaffolded reproducers*; their reproduction depends on some kind of external scaffolding. For collective reproducers, G-S introduces a new set of parameters and another spatial framework to adapt the moral about natural selection to reproduction: it comes in degrees, ranging from marginal cases of reproduction to paradigmatic ones. The parameters are the degree of the presence of a bottleneck,  $B$ ; a germ/soma specialization  $G$ ; and some measure of overall integration,  $I$ . Just as the parameters of the Darwinian populations framework can be employed to sketch a Darwinian space, the reproduction parameters can be used for reproduction space. Scoring high on all parameters makes something a well-integrated and individuated reproducer. The lower the score gets, tending to the marginal end, the less reason there is to speak of one collective reproducer instead of a loose collective of simple reproducers.

### De-Darwinization

When two sets of parameters—one for measuring how Darwinian a population is, the other for measuring reproduction—are linked up, their application to debates about the levels of selection and transitions in individuality becomes clear. In the classification of reproduction, G-S has built in the

observation that the biological world is hierarchically organized. Collective reproducers (multicellular organisms) are composed of simple reproducers (cells), and collectives of collective reproducers (e.g., eusocial insects) can be found at yet another level higher up. All simple reproducers are members of Darwinian populations; they are Darwinian individuals. But higher-level Darwinian individuals—i.e., collective reproducers—can at the same time be thought of as Darwinian populations. Take a multicellular organism. It is an instance of a Darwinian individual in a Darwinian population of organisms. At the same time an organism is itself a Darwinian population of the cells it is composed of. Usually, individuals at two distinct levels do not have the same Darwinian status *qua* individuals. Comparing a herd of fleet deer with a fleet herd of deer makes this clear. When we speak of a herd of fleet deer, we assert something about the deer as Darwinian individuals that make up a Darwinian population—the herd. When we speak of a fleet herd of deer we focus on the herd, which is of course part of a population of herds (of deer). If we compare how Darwinian a population of deer is to how Darwinian a population of herds of deer is, we will often see that the former scores much higher on the parameters than the latter. Individual deer score high on the reproduction parameters, and populations of deer are paradigmatically Darwinian. Instead, a herd of deer will score low on the reproduction parameters, and populations of herds will usually be only marginally Darwinian.

For Darwinian populations to come into existence at a higher level, a transition to that level is needed. The Darwinian populations framework comes to full expression in explaining what happens during such transitions. In brief, a transition is a combination of two synchronized “movements” in two Darwinian populations—one at a level above the other—in Darwinian space. The population at the higher level moves gradually toward the more paradigmatic end, while at the same time “de-Darwinizing” the population below. Darwinization at higher level and de-Darwinization at the lower level go together, for when the higher-level reproducers increase their score on the reproduction parameters such as  $B$ ,  $G$ , and  $I$ , this can only mean that the individuals at the lower level become more restricted in their evolutionary potential.

In the discussion about levels and transitions, genes do not appear at a separate level. One reason is that genes are better seen as scaffolded reproducers, rather than simple or collective reproducers between which transitions can occur. They rely on a complex cellular environment that empowers them. Without such external scaffolding genes cannot “do” anything, and certainly cannot make copies of themselves—contrary to misleading, loose talk of genes as “self-replicating.” Other reasons make it even more questionable to think of genes as reproducing. On the Darwinian populations framework, something needs to be a Darwinian individual to be

reproducing. But there are good reasons related to the crossing over of chromosomes, which make it problematic to think of genes as Darwinian individuals at all.

In a lucid chapter on what has become known as the “gene’s eye view,” G-S gives reasons to think that we should dethrone the gene from the position gene selectionists have assigned it. They have obscured the problems G-S identifies, by presenting genes as unproblematic individuals, or worse, as the only individuals that really matter in evolution. On top of that, some gene selectionists have added a mix of a methodology and a marketing strategy. They suggest that we can think of genes as pursuing certain goals and having interests. In a local context this may indeed be a useful tool, but it becomes a different matter if the gene is taken to be “the fundamental unit of self-interest” (Dawkins 1976: 33). G-S’s view on such language can hardly be misunderstood when he labels it “Darwinian paranoia”—an explanatory scheme of small, sub-personal agents “pursuing agendas that cross-cut or oppose our interests” (p. 144). Interestingly, G-S suggests that there may be a psychological pull to think along these lines, and looks for support in the research on folk biology and folk psychology. Indeed, there is some support for the idea that thinking in terms of hidden agents has particular salience (e.g., Boyer 2003). If G-S is right, the ironic explanation for why so many readers report to be left with a feeling of amazement upon reading *The Selfish Gene* is not that it states fundamental truths but because we (and not just our genes!) have evolved to be attracted to its metaphors.

Dawkins and Co. will likely object that it continues to escape their critics that talk of “interests” and “selfishness” of genes should be read as metaphorical, and that we can always “translate back into respectable, if longwinded terms” (Dawkins 1976: 89). They are right, we sure can. G-S’s book is a *tour de force* that constitutes this translation, and in less than 200 pages it turns out not to be that long-winded, while covering a much richer set of phenomena than the narrow gene’s eye view captures. Moreover, as a consequence of putting the “respectable terms” back in, we see that little conceptual space is left for the way of thinking advocated by the gene’s eye view.

### Foundations and Parameterizations

G-S is appropriately cautious about the status of his constructive project. In various places he puts up warning signs for taking his presentation of the Darwinian populations framework to be complete as it has been presented. He explicitly mentions other parameters that could be adopted as features of Darwinian populations, such as niche construction or the distinctive contributions of sex. These parameters could be integrated into the framework to make more fine-grained distinctions between marginal, minimal, and paradigmatic populations, but that is not G-S’s aim. His aim is “to mark an initial distinction

between trivial Darwinian processes and important ones. Once we get past the coarse-grained distinctions made here, the question of where various kinds of significant cases are located in the space becomes an open question” (p. 66). In the nominalist spirit that guides G-S throughout the book, there is nothing about these parameters that captures the *essence* of what makes something more or less Darwinian. But surely there is a reason why G-S has chosen *these* parameters and not others as the basic underpinnings of his Darwinian populations framework.

I want to suggest that there is something about the parameters G-S chose that makes them more basic than others he could have chosen. A parameter for the distinctive contributions of sex, for example, would not have fitted into the set of basic parameters. Sex is a generic label that covers a variety of processes that differ widely across the branches of the tree of life, which have different implications for evolvability in those different quarters. Moreover, sex is itself an *evolved* property (cf. Wilkins 2003). Thus, if we want to have a basic, foundational framework that applies to all Darwinian populations, it seems misguided to include sex as a parameter. This also appears in line with one of the goals G-S sets in the introductory chapter. He credits his colleague Glenn Adelson for aptly calling this attitude “Darwinism about Darwinism”:

Evolutionary processes, and the differences between them, *can be abstractly characterized*. But *the forms taken by these processes on earth are consequences* of the organisms (and the environments) that evolution has generated. In that sense, evolutionary processes are themselves evolutionary products. They vary across the tree [of life] in the same ways as organisms and kinds [e.g. species] do. (p. 15; italics added)

In contrast to sex, quasi-independence—or modularity, which enters G-S’s list as part of the variation parameter, *V*—and continuity, *C*, do seem to be more fundamental. Lewontin wrote the following about these concepts: “Continuity and quasi-independence are *the most fundamental characteristics* of the evolutionary process. Without them organisms as we know them could not exist because adaptive evolution would have been impossible” (Lewontin 1978: 169; my italics). Robert Brandon (2005), in a more philosophical spirit, called the argument for the existence of modularity “transcendental,” because modularity is argued to be necessary for the very existence of adaptation. So in contrast to sex, modularity and continuity are argued to be foundational for the evolution of adaptation. The same counts for the  $\alpha$  parameter, or the struggle for existence, which Lewontin introduced earlier in the article just mentioned as the “fourth principle” of Darwinian evolutionary theory. The three most basic principles are the ones G-S has described as the ingredients of the classical summaries of natural selection: variation, differential fitness, and heredity. Importantly, Lewontin says about these three principles: “[They] say nothing, however, about adaptation. In themselves they

simply predict change caused by differential reproductive success without making any prediction about the fit of organisms to an ecological niche or the solution of ecological problems” (Lewontin 1978: 165). Using G-S’s terms, Lewontin can be said to make the distinction here between minimal Darwinian cases and the interesting or paradigmatic ones. So, in fact, he carries out one of the aims G-S pursues with the Darwinian populations framework, and does not limit himself to the all-or-nothing approach G-S attributes to his classical summaries.<sup>1</sup> This is not to say that G-S has merely restated Lewontin’s principles. G-S’s main innovation is the spatial framework where the principles become parameters.

Although the spatial framework has its heuristic value, it may also lead to a loss of information. Lewontin divides his principles into a set of three basic ones for evolution by natural selection, and three others that are important for natural selection leading to adaptation. G-S’s parameters all appear to be on par within the spatial framework. But we could question whether each parameter is to be given equal weight, and whether they can be combined additively. Is a population that sits in the (0,1,1) corner of a space as Darwinian as one found at (1,1,0)?<sup>2</sup> I think there is a sense in which Lewontin’s division captures something that G-S’s spatial framework leaves out. Fitness differences, heritability, and variation capture some very basic tendencies of populations. Competitive interaction, continuity, and modularity are less basic; they inform us about properties that influence the basic features. The first triad is more basic because an absence of fitness differences, heritability, and variation is sufficient to guarantee that a population will not undergo natural selection, even if all the components of the second triad are present. Now take the opposite case. In the presence of the first triad, but in the absence of competitive interaction, continuity, and modularity a population can undergo change by natural selection, albeit of a marginal kind. The more components of the second triad are satisfied, the more paradigmatic the population undergoing change will be.

Things look differently in the parameterization G-S proposes. He subsumes modularity under variation, and intrinsic character and continuity together seem to replace fitness. There is something unsatisfactory, though, about subsuming and substituting, instead of using two sets of principles as I suggested. A problem with the subsumption of modularity under variation is that a *population* can have lots of variation without being constituted by modular *individuals*.<sup>3</sup> So G-S’s variation parameter will have problems capturing both the properties of the population and of the individuals it is composed of at the same time. The substitution of intrinsic character and continuity for fitness is also problematic. To explain what these parameters amount to, G-S still needs to (and does) refer to a notion of fitness. So although fitness is not included as a parameter, it is needed to understand what other parameters mean. Continuity

is explicitly defined in terms of changes in fitness: “An evolving population exhibits continuity when small changes to an organism’s phenotype lead to small changes in its fitness” (p. 57). Alternatively, it can be understood as “a rough measure of the extent to which similar organisms in a population have similar fitness” (p. 58). Intrinsic character is also tied to fitness, although it need not be defined in terms of fitness. About the relation between intrinsic character and fitness, G-S says that “In the language of fitness, *S* is the extent to which ‘realized’ fitness differences in a population are tied to differences in intrinsic character” (p. 54). But two pages further we read that in organisms with a germline, “cell fitness is not very closely tied to intrinsic character” (p. 56). Instead, the location of a cell appears to be closely tied to its fitness. This seems to be a good reason to adopt locality as another feature of populations. Not giving locality its due is to miss out on what causes fitness to be differential at the cellular level. Nevertheless, G-S does not adopt locality as part of the basic features of the Darwinian populations’ framework.

Had fitness remained a basic parameter, it would have been possible to point out that at the cellular level locality is important to differential fitness, whereas at the organismic level intrinsic character and continuity might be more important. If the set of parameters is to be applicable at each level of organization, a general notion of fitness is required, instead of the incomplete set of components it is substituted with.

In conclusion, we can say that differential fitness stands to continuity and intrinsic character as variation stands to modularity. Continuity and intrinsic character tell us something about the fitness of an *individual*, but they are not required—or at least intrinsic character seems not to be—for fitness differences to exist at the level of the *population*. By turning basic features of populations and less basic features of individuals in those populations into equally-weighted parameters of Darwinian populations, G-S risks losing information that is important for determining how Darwinian a population is.

## Population Reification

It should be clear by now that populations play a central role in the book. It is therefore surprising that G-S is ambiguous about what counts as a population. In the introduction he states clearly: “A population is a physical object, bound by ancestry and other causal relation, internally variable at any time and changing over time” (p. 11). Some hundred pages later things appear to have changed. Instead of being physical objects in the world, populations have become perspectival:

Are we saying there is one Darwinian population of cells within me, and another within you—a collection of separate Darwinian populations—or is the idea that we can think of all the human cells as comprising one big Darwinian population? The answer is that we can see the situation in both ways; both kinds of collections qualify

as Darwinian populations . . . [B]oth kinds of analysis are possible, with the two kinds of populations having different evolutionary parameters. (p. 113)

Where we draw the boundaries between populations depends to some extent on our interests. So in a certain sense, populations are less than real.<sup>4</sup>

That populations are perspectival does not render them wholly arbitrary. Presumably, there is no meaningful population consisting of a kangaroo in Australia, two deer in Austria, and a dog in Great Britain. It seems that the limits of what counts as an appropriate population are not set by any further basic criteria, principles, or parameters, but by the course evolution has taken. A transition in individuality does not only give rise to new individuals but also to new ways of picking out populations.

There is some tension in the book between the “population as object” mode of talking and the “population as perspective” mode. This is most clearly seen at the end of Chapter 5. At this point, G-S has already described the Darwinian populations framework in detail. The next chapter will be on transitions in individuality, where the perspectival notion of populations will be touched on. It is at this point that G-S summarizes what the Darwinian populations framework has brought us:

This account of Darwinism yields a particular picture of the world. One of the world’s constituents is a great range of Darwinian populations: paradigm cases and marginal ones, some clear and others obscure, some powerful and others suppressed. Some visible and obvious, others invisible. Some are inside others. They tread through their Darwinian behaviors on a great range of different scales in space and time. Some evolve via reproduction of a wholesale and definite kind, others evolve by coopting the biological scaffolding that results. Populations evolve as a consequence of their Darwinian properties, but also change the basis for their further evolution, moving through the imagined spaces of evolutionary parameters. . . . (p. 108)

The “picture of the world” G-S sketches here is part of doing “philosophy of nature,” as he calls it. Besides a work in (philosophy of) science, the book is also an exercise in philosophy of nature. This is what we do when we start with science and work out “what its real message is, especially for larger questions about our place in nature” (p. 3). I am skeptical about the use of such a project. A risk of sketching a “philosophy of nature” is that it is easy to take the resulting “world picture” too seriously. This is exactly what seemed to have happened—possibly in the most extreme form in modern-day science—with the gene’s eye view G-S criticizes vehemently. To a lesser extent, I think something similar happens when G-S outlines the philosophy of nature the Darwinian populations framework leaves us with. Not genes but populations are the actors in evolution according to this worldview. But if the concept of a population is in part perspectival, we should not reify populations as objects that

exist independently of us, and still less as threading through Darwinian behaviors and moving through spaces. I am *not* suggesting that the Darwinian populations approach is by any standard as paranoiac as the selfish gene approach; there is no sign of hidden drivers inside lumbering robots here. Nor is there any reason to think that if we aren’t careful, population talk might become as paranoid as selfish gene talk. It may therefore be considered unarmful. On the other hand, I think world pictures in general are better avoided, for the sake of critical thinking. The tensions—present within G-S’s book and outside it—surrounding the concept of populations are fertile ground for philosophical exploration, which may eventually affect how the concept will be used in science. Burying these tensions under an extra layer of metaphor in a “world picture” is not very helpful for making any progress on those fronts.

## Conclusion

I did a quick run through some of the main themes of the book, but G-S discusses a whole lot more interesting material that I haven’t touched on. The last chapter, on cultural evolution, is an example. The book is also packed with superb compact reviews of earlier attempts to tackle the issues G-S deals with. Chapter 4, for instance, discusses the myriad problems that have been encountered when trying to define reproduction. It is chock-full of biological examples but never becomes dull or obscure. And the chapter on levels and transitions contains an extremely clear seven-page overview of problems associated with cooperation and altruism.

The main theme—the Darwinian populations framework—is intelligible, useful, and raises lots of new interesting questions that make it a momentous achievement. Many sections have loose ends that need to be tied up, but nothing “aberrant” is swept under the carpet. I have raised some worries about how to refine and solidify the Darwinian populations framework, but these do not detract from the achievement of formulating such an inclusive framework in the first place. Profound insight inevitably gives rise to new questions.

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## Notes

1. G-S’s two main examples of classical natural selection summaries are taken from two of Lewontin’s other writings. One of them (Lewontin 1970) only gives the three conditions. The other, which G-S uses as his main example, discusses the notions of struggle for existence, quasi-independence, and continuity in a similar fashion as discussed here (Lewontin 1985: 76–80).
2. Similar observations were made by Griesemer et al. (2005) about a different, but partially overlapping set of evolvability conditions—but without a spatial framework—given by Sterelny (2001).

3. Populations of (simple) cultural entities may be the clearest cases.
4. The concept of a population is starting to gain some philosophical attention. Glennan (2009: 332), taking a mechanistic approach, states that “populations aren’t objects.” Millstein (in press 2009), on the other hand, thinks that populations are objects; they are individuals. Her main motivation is that if we do not define populations as having rough but objective boundaries, we run the risk of rendering natural selection and drift arbitrary.

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