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BOOK REVIEW

Okasha's evolution and the levels of selection: toward a broader conception of theoretical biology

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Abstract The debate about the levels of selection has been one of the most controversial both in evolutionary biology and in philosophy of science. Okasha's book makes the sort of contribution that simply will not be able to be ignored by anyone interested in this field for many years to come. However, my interest here is in highlighting some examples of how Okasha goes about discussing his material to suggest that his book is part of an increasingly interesting trend that sees scientists and philosophers coming together to build a broadened concept of "theory" through a combination of standard mathematical treatments and conceptual analyses. Given the often contentious history of the relationship between philosophy and science, such trend cannot but be welcome.

Keywords Multi-level selection · Theoretical biology · Price equation · Evolutionary theory

Discussions about the levels of selection have marked evolutionary biology during the second part of the twentieth century, with the debate often taking on acrimonious tones combined with a significant amount of conceptual confusion. Okasha's (2006) book will probably not put a stop to the mess, but it should: no serious discussion of group selection, and more broadly of multiple levels of selection, should take place without serious consideration of this book. This is, of course, not to say that I did not find anything objectionable concerning specific claims or arguments presented in the book, but the treatment of the subject matter is

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so thorough and clear, that this will have to be a reference landmark for many years to come.

While in what follows I will discuss some aspects of Okasha's book, I am actually less interested in the specifics of the multi-level selection debate—as important as the latter is—than in using the book as an example of what I think theoretical biology is becoming, or should become. I will argue that philosophers of science have a crucial role to play in evolutionary theory broadly conceived, and that the latter should expand its tools beyond the current emphasis on mathematical analytical treatment and computer simulations. It is not that biologists should not do math, but rather that they should reclaim that broad concept of "theory" that characterized the field from Darwin to the Modern Synthesis. It is time to stop referring disdainfully to philosophy of science and theoretical biology *sensu lato* as "armchair speculation," as if mathematics where not done, largely, while sitting on armchairs.

Conceptual distinctions vs. mathematical representations

Two core pairs of concepts underlie much of Okasha's book, and together they represent an excellent example of the distinction I am trying to make between theory understood as mathematical formalism and the broader conceptualization of "theory" that should bring together philosophers and biologists. The first pair of concepts is the distinction between Multi Level Selection-1 (MSL1) and Multi Level Selection-2 (MLS2). The second distinction concerns the famous Price (1970) equation, an early and much discussed approach to provide a general model of natural selection, and contextual analysis, an alternative conceptualization of natural selection.

Let us start with the MLS1/MLS2 distinction, originally introduced by Damuth and Heisler (1988), and which provides the backbone to Okasha's book. Damuth and Heisler argued that theorists had up to that point conflated two distinct processes under the general label of "multiple levels of selection." For instance, traditional discussion of group selection were framed in terms of the evolution of individual traits (such as altruism) by selection at the level of groups. This in an example of MLS1, where the focus is on the "particles" (e.g., individuals) that are embedded in a given "collective" (e.g., a population). In MLS1, we are concerned with the evolution of particle-level traits, and the collective can be thought of as part of the environment that influences such evolution. Take, however, the very different process of species selection (Stanley 1975). Here the focus is on the collectives themselves (in this case, the species) and their evolution.

This distinction between MLS1 and MLS2 goes hand in hand with a parallel distinction between fitness-1 and fitness-2, again the first one referring to particles, the second one to collectives. As Okasha (2006, pp. 56–57) points out, this immediately makes sense of Wilson's (1975) concept of "trait groups" in the context of the evolution of altruism. According to this model, although altruists have lower fitness *within* groups, groups containing a higher proportion of altruism may leave more individual offspring, which means that their fitness1 may be higher than that of individuals embedded in other groups. This neatly accounts for the fact that Wilson's model contrasts individual and group selection, with the evolutionary outcome depending on the balance between the two processes. In the case of species selection, on the other hand, it is fitness2 that counts, and what one wishes to explain is how species (not individuals) with certain characteristics become more common, one of the classic examples being Jablonski's (1987) suggestion that some taxa of late Cretaceous mollusks became more common because of species-level traits, such as average geographic range.

Perhaps most interestingly, toward the end of the book Okasha (2006, Chap. 8) moves beyond the simple idea that the MLS1/MLS2 distinction is a dichotomy, and turns it into a continuum that helps make sense of the so-called major transitions in evolution (Maynard-Smith and Szathmary 1995). The starting point here is that most of the debate on multiple levels of selection is framed in a synchronic fashion, that is on what is happing now, as opposed to a diachronic framework that takes into account how things change over long time spans. From a synchronic perspective, MLS1 and MLS2 are indeed clearly distinct because of their different focus. However, asks Okasha (2006, p. 229), which type of multi-level selection is going on during a major transition, say the origin of multi-cellular life forms? Intuitively, the answer should be MLS2, given its focus on collective, rather than particle, characters, and that a major transition often results precisely in the emergence of a new kind of collective. But Okasha is surely right when he argues that a *transition*, by its very nature, will more likely start as an MLS1-type process, and end up in the realm of MLS2. In other words, shifting from a synchronic to a diachronic perspective simultaneously makes sense of what kind of processes evolutionary transitions are, and of the distinction between different types of multi-level selection theory. Now, that is what I would call a major conceptual contribution to evolutionary theory.

Things are more debatable, I believe, in the case of the other major thread running through Okasha's book, his discussion of the relative merits of the Price equation and the so-called contextual analysis of selection. The Price (1970) equation is a general mathematical formalism aiming at describing natural selection while making no assumptions about the specifics of biological systems. One formulation takes the following form:

$$\Delta Z = \mathrm{cov}(\omega, z) + E_w(\Delta z) \tag{1}$$

where ΔZ is the change in average trait value from one generation to the next; $\mathrm{cov}(\omega, z)$ is the covariance between relative fitness (ω) and trait values (z), and E_w (Δz) is the average of the change in z, weighted by the fitness value. Okasha (2006, p. 29) then interprets the two components of the Price equation as formalizing the change due to selection (first term of the right-hand side of Eq. 1) and the change due to transmission bias (second term of the RHS of Eq. 1) or, under simplifying assumptions (p. 33) the change due to drift. A major reason why Price's equation lends itself naturally to a treatment of multi-level selection is that the fitness and trait terms appearing in it can be applied to whatever level(s) one happens to be interested in, lending a high degree of flexibility to the approach. The following is the Price equation in the general case of multi-level selection:

$$w_a \Delta Z = \operatorname{cov}(W, Z) + E(\operatorname{cov}_k(w, z)) \quad (2)$$

which expresses the fitness-weighed change in particle traits, $w_a \Delta Z$, as a result of selection at the collective level (first term of the RHS) and selection at the particle level (second term of the RHS) (note that capital vs. small letter "w" and "z" indicate fitness and trait means at the collective and particle levels, respectively).

This flexibility notwithstanding, Okasha identifies situations where the Price equation produces counterintuitive and somewhat questionable results. Without entering into too much detail, one such case is presented by what Okasha (2006, pp. 84–85) calls "cross-level by-products" in the case of MLS1. These by-products arise any time there is a spurious covariance between group-level fitness and group-level traits, despite the fact that all the action is going on among individuals within groups. The classic example (due to Sober 1984) is a situation when taller organisms have higher fitness than shorter ones. Natural selection here acts within groups, and group structure is irrelevant. However, it will likely be the case that, due to random fluctuations, some groups will have a higher proportion of taller organisms. This will mean that some groups will be, on average, more fit than other groups, and the Price equation will in fact detect a non-zero cov(W, Z). But a sensible biologist would conclude that such covariance is spurious, not causal, thereby identifying a set of cases where the Price equation misses the mark.

It is at this point that Okasha calls on a different approach, originally imported in this context from the social sciences by Heisler and Damuth (1987): contextual analysis. This uses linear regression models, and considers a collective-level trait as part of the "context" relevant to each particle within that collective. The basic equation looks like this:

$$w = \beta_1 z + \beta_2 Z + e \quad (3)$$

where w is the particle's fitness, z is the particle-level trait, Z is the collective-level trait, β indicates regression coefficients, and e is the error term. If β_2 is non-zero, then the contextual analysis reveals collective-level selection. Equation 3 handles Sober's example very well, because it explains all particle-level fitness at the particle level (β_1 is non-zero, but β_2 is not). As a bonus, the contextual approach is the same as the Lande-Arnold (1983) multiple regression formalism of natural selection, in the general case in which it includes selection on correlated characters. Since the Lande-Arnold formalism is by far the dominant approach used by both theoretical and empirical biologists to study natural selection, it would seem that we have a clear winner.

But, alas, things are not so simple, in part for reasons Okasha himself addresses, in part because of additional problems that he does not discuss. It turns out that there are instances where it is the turn of the contextual approach to yield awkward results, while the Price equation gets it right (p. 154–156). One such instance occurs if we wish to treat the problem of genic vs. genotypic selection in population genetics as a potential case of multi-level selection. Consider, for instance, a simple case when the fitnesses of three diploid genotypes (all possible combinations of two alleles at a given locus) are identical, while the fitnesses of the two alleles vary depending on which other allele happens to combine with them to produce the diploid genotype. Here, the Price equation will correctly lead one to conclude that there is selection only at the genic level, not the genotypic one (because all genotypes have the same fitness); but, interestingly, the contextual approach will end up detecting some collective-level selection because differences in genotype will in fact predict (statistically) differences in genic fitness.

Okasha, then, reaches an important conclusion about the Price-contextual approach contest, one that will be somewhat unpalatable to philosophers, but downright revolting to biologists:

> “Since the Price approach sometimes works better than the contextual approach, theoretical arguments for the latter notwithstanding, there cannot be a fully *general* [emphasis in the original] solution to the problem of causally decomposing the total evolutionary change in an MLS1 scenario. Secondly, the fact that two fitness structures can be formally isomorphic, yet generate different intuitions about the levels of selection, shows that the biological interpretation of the fitness structure is also crucial” (p. 157).

Indeed, but one wonders why we should expect either the Price equation or the contextual approach to get things right all the time. After all, they are statistical formalisms independent of biological content, not causal models of actual biological systems.

Statistical formalism vs. causality, revisited

One of the recurring issues in evolutionary theory is the relationship between statistical formalism and causal analysis. A classic example is the beautiful paper by Lewontin (1974) on what the analysis of variance, arguably the most frequently used statistical technique in organismal biology, can tell us about what we really want to know, the analysis of causes. As it turns out, in the case discussed by Lewontin, which deals with heritability and phenotypic plasticity, analyses of variance end up telling us very little. More recently, Kaplan and I (Pigliucci and Kaplan 2006, Ch. 4) have argued that the complex issues raised by causal interpretations of quantities such as variances and covariances—which are at the core of the evolutionary quantitative genetic approach—are too often conveniently swept under the rug by biologists. To his credit, Okasha addresses the issue directly in several places in the book, though in a way that I feel still leaves much room for debate.

Okasha readily acknowledges (e.g., pp. 25 and 94) that both the Price equation and contextual analysis are “inherently statistical in nature,” and that “at most one of them can constitute a correct *causal* decomposition” (original emphasis). Indeed, the problem arises even for different formalizations of the Price equation: “there is a genuine distinction between statistical and causal decomposition, or partitioning. Equations 1.2 and 1.3 [two forms of the Price equation] both provide correct *statistical* decompositions of ΔZ, for both equations hold true by definition; but it still makes sense to ask which if either provides the correct *causal* decomposition” (p. 27, original emphasis). This strikes me as a rather strange question, since statistical quantities do not *provide* causal decompositions, the latter derive from the user's interpretation of the quantities manipulated by the statistical analyses, and therefore requires knowledge external to the statistical analyses themselves. The question only makes sense once the physical system is specified and the actual causal pathways determined.

Consider, for instance, the classic case of a phenotypic covariance between two quantities, let's say the width and length of the leaves measured in several individuals belonging to a particular species of plants. Assume further that we know that these plants have different genotypes and that they were grown in different environments. Given the proper experimental design, it is possible to partition the phenotypic covariance between the two traits into several *statistical* components:

$$\mathrm{covP}_{w,l} = \mathrm{covG}_{w,l} + \mathrm{covE}_{w,l} + \mathrm{error} \tag{4}$$

where cov indicates a covariance, P, G and E are phenotypic, genotypic and environmental effects, and error indicates the residual unexplained variance (the subscripts w and l indicate width and length of the leaf, respectively). The term $\mathrm{covG}_{w,l}$, for instance, tells us that there is a statistical component of the phenotypic covariance that is *associated with* known differences among genotypes. This, however, does not mean that genotypic differences *caused* the observed $\mathrm{covG}_{w,l}$ quantity. The latter is a possible interpretation of the statistical partition, but other interpretations are available (for instance, different genotypes may have been sampled from different environments, in which case the "genotypic" variance is actually a reflection of the heterogeneity in the environments of provenance of the different plants, sometimes referred to as a "maternal" effect). To further unravel the causal basis of the observed covariances one has to gather additional empirical information, for instance by carrying out an experimental design that makes it possible to partition covariances between truly genotypic and maternal "carryover" environmental effects. Even so, the filtered genotypic effects could be further dissected causally by additional modifications or iterations of the experimental design, and so on and so forth.

This is the sort of reason why, as Okasha points out, neither the Price equation nor contextual analysis are optimal under all causal scenarios involving multiple levels of selection: since covariances are a high-level summary of complex data, they can be generated by a variety of causal scenarios, and they may not be suitable to shed light on the specific causes underlying a given situation. This problem has actually been widely debated in the literature precisely in the case of what Okasha considers, on balance, the preferable approach, contextual analysis (p. 99). As Okasha points out (p. 88), contextual analysis is actually a special case of the Lande-Arnold approach to selection analysis (Lande and Arnold 1983), which in turn is a specific application of multiple regression analysis. Kaplan and I (2006, Ch. 2) have devoted some effort to show why the Lande-Arnold approach cannot function as anything more than a very preliminary indication of whether selection is operating, and that it actually provides no insights at all about causal pathways, even under the best circumstances.

Briefly, some of the problems with the Lande-Arnold approach have been well known to biologists for some time, and indeed several of these problems have been anticipated by Lande and Arnold themselves in their original paper—which did not prevent many biologists from going on and ignoring them in practice. For instance, like any regression analysis, the L-A approach to measuring selection suffers from the possibility that one did not include in the model additional causal factors that actually play a role, which will then result in spurious covariances not indicative of real causal pathways. This is not fatal if one treats multiple regression techniques (including Okasha's contextual analysis) as exploratory data analyses, or as Mitchell-Olds and Shaw (1987) put it, "primarily as a tool for suggesting hypotheses about the forces of selection." But what the Price equation and contextual analysis (and, unfortunately, the common use of the Lande-Arnold approach) are used for is much more than just an exploratory statistical tool: there is a tendency to consider them as overarching mathematical formalisms of causal pathways to selection, a task for which they are not well suited at all.

There is a different technique that is well known to perform much better when it comes to representing complex causal models: structural equation modeling, of which the path analysis used by ecologists, some evolutionary biologists, and especially social scientists is a special case. It seems surprising that there is no mention of structural equation modeling in Okasha's book, although the reasons may have at least in part to do with why few biologists themselves use it in place of the L-A multiple regression approach. For starter, structural equation modeling provides too much flexibility to the user: one can specify as many levels of interacting variables, and as many causal paths between variables, as one likes. This flexibility ought be a crucial advantage, since one is trying to model multiple levels of selection with potentially complex and multi-layered causal pathways; however, the disadvantage is that structural equation modeling is not user friendly, and its output is much less neat than the simple Price equation, or the flat causal structure implied by contextual analysis, with the result that it is difficult to generalize from specific applications to broad principles concerning the action of selection.

Moreover, path analysis does not lend itself to the calculation of the simple selection coefficients that readily result from the L-A approach (Scheiner et al. 2000), and it is these selection coefficients that play a crucial role in the currently mainstream quantitative genetics mathematical theory of evolutionary change. This, however, is more a reflection of the limitations of the quantitative genetic theory than of the desirability of the technique: the theory can provide a satisfactory account of how, broadly speaking, the interaction between the genetic architecture of a population and evolutionary factors such as natural selection may yield certain patterns of trait covariances; it also obviously provides researchers with convenient statistical summaries of a population's status; but it cannot and should not be used to generate long-term predictions about evolutionary trajectories, to infer the action of past selection, or to provide information about causal paths (Pigliucci 2006).

All of this is not to mean that I don't think Okasha's extensive discussions of both the Price equation and contextual analysis are not both on target and extremely valuable. They will represent the reference point for discussions of multi-level selection for several years to come. My hope, however, is that they will also turn out to be the starting point for the formulation of a more mature statistical-causal framework for natural selection, one that takes full advantage of the ability of structural equation modeling to flexibly generate (and, crucially, empirically test!) causal models of complex interacting phenomena (Shipley 2000).

Toward a broader view of theoretical biology

The relationship between philosophy and science has always been a difficult and asymmetric one. Ever since science has become an independent discipline from its origins as natural philosophy, philosophers have often been fearful of being relegated to irrelevance, and scientists have time and again been dismissive of "armchair speculation." This can be seen in print (just consider Sorell's (1991) essay on scientism and philosophy's infatuation with science, or physicist's Stephen Weinberg's (1992) infamous essay "Against Philosophy") and in the hallways of academia, where the common joke among scientists is that engaging in philosophy is what we do when we get too old to get grants, and hence—by implication—to do valuable research.

Even one of the main ideas underlying Okasha's book has an interesting history that touches on this war of the academic worlds. The distinction between MLS1 and MLS2 was put forth in papers by Damuth and Heisler in the mid-1980s. I have spoken to John Damuth recently, and he told me that the 1988 paper, published in *Biology and Philosophy*, had been rejected by a number of biological journals as too "speculative" and "philosophical" in character, even though, thanks to Okasha's contribution and elaboration, that paper deserves to be considered a landmark in the history of thought about multilevel selection theory.

The silver lining, I think, can however be found in a slow but increasingly evident trend of which Okasha's book itself is a perfect example. I am referring to a broadening of the concept of "theoretical" science, especially, but not exclusively, in biology. For a long time the word theoretical has implied mathematical formalism. Fisher (1930) devised his famous "fundamental theorem of natural selection" expressly using the second principle of thermodynamics as a model. He wanted to put biology on the same firm mathematical foundations as physics, and indeed, he succeeded as much as the state and intrinsic nature of the discipline itself allowed at the time. Yet, ever since Darwin (1859), conceptual analysis, or non-mathematical theory, has always played a major role, indeed arguably the major role in shaping the theoretical framework of the discipline. Not only was the original Darwinism non mathematical, but many of the crucial contributions to the Modern Synthesis were also of that nature.

This, of course, is not to say that mathematical formalism does not have an important role in science in general, and in biology in particular, but I increasingly see it as a subset of theory *sensu lato*, and this idea is perfectly embodied in Okasha's book. Okasha does not shy away from mathematical formalism, as his discussion of the Price equation in particular amply demonstrates. But the major contributions of the book come in the meticulous unpacking of the *meaning* of those equations, an unpacking that simply could not be done chiefly by mathematical formalism, especially if it is to be relevant to practicing (empirically oriented) evolutionary biologists. Let me briefly discuss two examples, the distinction between group and clade selection, and the relationship (or lack thereof) between emergence and group selection.

Okasha (2006, pp. 206–209), together with many—though by no means all—evolutionary biologists, thinks that species selection is a legitimate contender in the arena of evolutionary theory, and in fact sees examples that Vrba (1989) considered macroevolution but not species selection as genuine instances of the latter. For instance, Vrba (1989) discusses the case of two African antelopes clades characterized by ecological specialists and generalists, with the former speciating more frequently than the latter. Vrba considers this macroevolution but not species selection, because the amplitude of the ecological niche can be treated as a side effect of individual characteristics. But Okasha points out that even according to Vrba the differences in species fitness among the African antelopes are *not* the result of differences in organismic fitness (although they can be traced to organismic characteristics—which is not the same thing at all), which leads him to conclude—correctly, I think—that this is indeed a case of species selection.

But here is the interesting bit: some authors, including Williams (1992), have attempted to extend the concept of species selection even further, to include clade selection, with Williams explicitly talking about cladogenesis as reproduction for clades. Except that Okasha elegantly shows that such an extension—as much as it may seem obvious—is not only unwarranted, it is based on a logical inconsistency. As Okasha (2006, p. 211) puts it: "Clades are by definition monophyletic, and as a matter of logic, monophyletic clades cannot stand in ancestor-descendant relations. … If we ask what the ancestor of … clade A is, then the answer can only be a *species*, not another clade" (original emphasis). Which means that species selection does all the work attributed to clade selection, and the latter is both a redundant and logically incoherent concept.

The second example of the sort of contribution that a broadened version of theoretical biology can make can be found in Okasha's illuminating discussion of the relationship between emergent properties and group selection: it turns out, to the surprise of many biologists I'm sure, that there is none. A full discussion of this issue is found in Chap. 4 of Okasha (2006), but some of the basics can be outlined here for the sake of my broader argument. Several authors (including Vrba 1989) have suggested that "emergent" characters are a necessary requirement for higher level selection to occur. This idea is intuitively appealing: just as organismal selection operates on individual traits, so group selection ought to operate on genuine group-level traits. But intuitive appeal can be a dangerous thing. First of all, it is not easy to draw a clear conceptual distinction between truly emergent characters and "aggregate" ones (those that are "mere sums of the parts," p. 113). Although Okasha does in fact discuss how to operationalize emergence so that it becomes a useful concept in biology (essentially, using departure from additivity as evidence of emergence), he also points out that to claim that one type of character (aggregates) cannot causally affect fitness of the group (MLS2) or of its constituent particles (MLS1)—which is what would disqualify aggregate characters from playing a role in group selection—is to make a rather unsubstantiated metaphysical claim, one that biologists surely are not prepared to defend.

Where, then, does the confusion come from? Again Okasha shows how a philosophical/conceptual analysis is more useful than most biologists would be ready to grant. In Okasha's view, the problem here stems from failing to separate what are two distinct questions: (a) whether a certain character-fitness covariance is the result of a lower-level causal process; (b) whether that covariance is an effect of selection at a lower level. It is the latter question that is relevant to adjudicate whether we are facing an instance of group selection or not. The first question, in some trivial sense, always has a positive answer, because it is always the case that higher-level outcomes are affected by lower-level processes—indeed, it would be rather surprising if they weren't. At the (very) bottom, all living organisms are made of quarks, but that doesn't imply that the best level of analysis to understand organismal processes is the quantum mechanical one.

For a long time the interaction between philosophy of science and science itself has been a difficult one, fostered mostly by the rare forays of philosophically inclined scientists who occasionally published in philosophical journals. More recently, philosophers have began to author (or co-author with scientists) papers published in mainstream science journals, for instance in fields like ecology and evolutionary biology. While philosophy of science certainly has its own raison d'être independent of its contribution to science, several authors have called for the recognition of a borderline field of interaction between science and philosophy, a conception of some area of philosophy of science as "a continuation of science by other means" (Chang 2004).[1] Similarly, the recently launched journal "Biological Theory," expressly appeals to both scientists and philosophers by consciously putting forth the broader conception of "theory" that I am endorsing here. Okasha's book should be read by anyone interested in multi-level selection theory because it is not "just" a philosophical book, it is a (broadly construed) theoretical work on one of the most stimulating subject matters at the interface between science and philosophy.

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[1] See also the March 2008 issue of the *Quarterly Review of Biology*, dedicated to the further exploration of the borderline between science and philosophy, with particular reference to ecology and evolutionary biology.

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