

Darwinian Populations and Transitions in Individuality

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1. Introduction

John Maynard Smith and Eörs Szathmáry (1995) used the phrase "major transitions" to refer to a set of evolutionary events with particular importance in the history of life. In their original count, eight such transitions were recognized. In many of their cases, though not all, the "transition" involved the appearance of a new kind of entity or biological unit, formed by the merging or combination of simpler ones. These new biological entities include eukaryotic cells, multicellular organisms, and insect societies. Michod (1999) uses the phrase "transitions in individuality" to refer to this particular kind of transition, and those are the ones I will discuss in this paper. But I will reach that topic by way of a general discussion of evolutionary processes.

There is a long tradition of giving abstract summaries of what is essential to evolution by natural selection. These summaries have two roles. One is describing the core of evolutionary theory – or rather, one aspect of the core – in a concise way. The second is

guiding the application of evolutionary concepts to new phenomena and problem cases. We see that second goal in the most-cited summary of this kind, given by Lewontin (1970). Lewontin summarizes what he calls "Darwin's scheme" in the form of a recipe for change that can be applied, in principle, to systems of all kinds.

As seen by present-day evolutionists, Darwin's scheme embodies three principles...

1. Different individuals in the population have different morphologies, physiologies, and behaviors (phenotypic variation).
2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness)
3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable).

These three principles embody the principle of evolution by natural selection. While they hold, a population will undergo evolutionary change. (1970, p. 1)

This is one of family of such summaries and recipes (see also Endler 1986, Maynard Smith 1988). All known formulations are subject to counterexamples or problems of other kinds (Godfrey-Smith 2007). This is because they tend to be the products of a trade-off between two theoretical goals that pull in opposite directions. One goal is capturing all genuine cases. The other is describing a causally transparent machine. Nonetheless, the approach I take continues this tradition, as I think the Lewontin-style summaries are on the right track. The first idea I will use is what I call the *minimal concept* of a *Darwinian population*. This is a population in which the constituent individuals show variation in character, differences in reproductive output, and heritability (in the statistical sense). Though the presence of these features does not, as it is sometimes thought, guarantee that change will occur, we can think of these as the basic components in any Darwinian process. The term "Darwinian individual" will be used for any member of a Darwinian population.

The minimal concept has a problematic concept at its heart: reproduction. We need to know what reproduction is in order to work out whether there are fitness differences and heritability, but the concept of reproduction is one surrounded by puzzle cases. Some of those will be discussed later. It is worth noting right away, though, that I do not use the concept of a *replicator*, the reproduction-like concept often favored in this sort of discussion. Maynard Smith and Szathmáry themselves discussed evolutionary transitions using the concept of a replicator. Sometimes replicator-based analyses are treated as more-or-less equivalent to three-part summaries in the style of Lewontin, and sometimes they are seen as

competitors, depending on how narrowly the idea of "replication" is understood. Maynard Smith and Szathmary understand the concept broadly, but I believe that the Lewontin-style summaries provide a better starting point. Replication is one kind of parent/offspring relationship, but not the only that suffices for evolution by natural selection (Godfrey-Smith 2000). The conception of reproduction being developed by Griesemer (2000, 2005), which requires "material overlap" between generations and the capacity for development, is too narrow to use here as well.

The minimal concept gives us a definite starting point, but my aim is to develop a framework which emphasizes gradient concepts, approximations, and the idea that theoretical ideas often work by picking out paradigm cases which are surrounded by a cloud of more marginal ones. This is especially so in a Darwinian context. This idea can be illustrated by looking at a criticism sometimes directed at formulations like my minimal concept. This criticism is seen in one form in Sterelny and Griffiths' *Sex and Death* (1998). According to this criticism, familiar three-part summaries do not capture the features of evolution by natural selection that make the process scientifically important, because they include both the powerful processes that give us eyes and brains, and also dull and trivial cases of sorting of fixed types. So maybe our summary of natural selection should be designed to capture a narrower class, something like the category of *cumulative* selection processes. These involve high heritability, ample variation, a fitness gradient, and perhaps other things as well.

My response is to hang onto the minimal concept, which has its own role, but locate it as part of a family of concepts. I use the following terminology. *Paradigm* Darwinian populations are the ones that generate novel, complex, and adaptive traits. The *minimal* concept is a broader category, picking out all populations with variation, fitness differences, and heritability, including the paradigms but including many others. I also use a third concept, that of a *marginal* Darwinian population. These are not the "dull" cases within the minimal category. Rather, they are cases that do not clearly satisfy the minimal requirements, but only approximate them. Darwinian patterns of description get some purchase on phenomena that do not pass a classical test, though Darwinian descriptions can also be misleading in those cases. The distinction between minimal-sense, paradigm, and marginal cases can be applied to Darwinian individuals as well.

2. A Darwinian Space

One way to investigate the relations between these concepts is with a spatial approach, locating different Darwinian populations in an abstract space characterized by evolutionarily important parameters. This requires that we find a range of features which can be represented numerically. Each feature is associated with one dimension of the space. A population, in virtue of how it scores on each dimension at a time, occupies a point in the space. We can then ask whether the paradigm cases cluster in one part of the space and the marginal cases in another. The minimal criteria are supposed to pick out a large region, covering the paradigm cases and shading into the marginal ones. Once the space is constructed, though, the specific categories of paradigm, minimal, and marginal should fade in significance.

The list of dimensions we could include, the *smorgasbord* offered by recent work on evolutionary transitions and evolvability, is huge. I will pick just a few to look at here. I won't discuss some obviously important factors, like population size and structure, sexual as opposed to asexual reproduction, and various others. Some features are not easily representable in numerical terms, and those are not thereby less important.

In Figure 1, I include one very familiar dimension, one often discussed but handled differently here, and a newer one. I imagine this as a 3-dimensional projection of a higher-dimensional space.

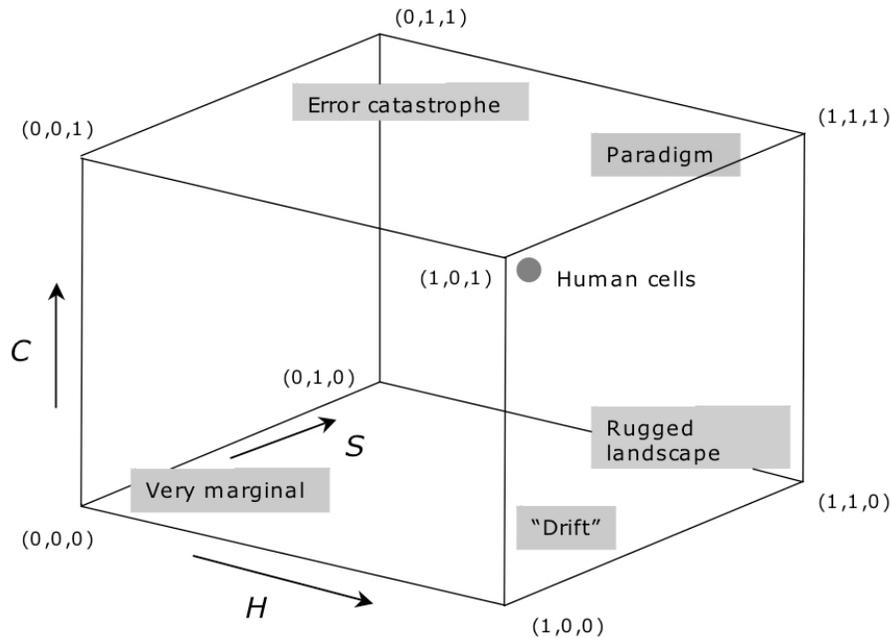


Figure 2. Three dimensions of the Darwinian space, (H,S,C) .

H is an absolute measure of the fidelity of inheritance (not the comparative measure used in the minimal concept). When H is high, "cumulative" selection is possible. When H is low, the products of one round of evolution tend to be lost on the next, and do not reliably reappear later on. In the case of a sexual and polymorphic population like our own, it is sometimes said that there is low-fidelity inheritance at the level of organisms, but high-fidelity inheritance of genes. I resist the idea that we, as organisms, are low-fidelity inheritors in the sense relevant here. The contrast is with cases in the top-center of Figure 1, where an "error catastrophe" makes it impossible to retain what evolution has built (Eigen and Schuster 1979). Clearly we do not see that with humans. The faithful copying of stretches of genetic material is part of the mechanism by which these organism-level properties are achieved.

Dimension S is newer. I define S as the extent to which differences in realized fitness (actual reproductive output) in a population depend on differences in the *intrinsic* character of the members of the population. Intrinsic features – basically, internal make-up and structure – are contrasted with *extrinsic* ones, which involve relations to other things. Location is an example of an extrinsic property (though location may be a causal consequence of an intrinsic property, such as a preference).

Here is an initial justification for including S . Mutation and recombination, the paradigm sources of evolutionarily important variation, affect the intrinsic properties of organisms. To the extent that reproductive differences in a population are dissociated from intrinsic characteristics, they cannot be tracking the subtle intrinsic differences that mutation generates. Extrinsic properties such as location are themselves variable among organisms, can generate reproductive differences, and can be heritable (Odling-Smee, Laland, and Feldman 2003, Mamei 2004). Extrinsic factors of organisms are obviously very important in evolution – where an organism lives and who it interacts with largely determine *which* intrinsic features are worth having. But the evolutionary role of extrinsic phenotypic features *per se* is limited. In Figure 1, the occupant of the area corresponding to a low value of S but high values of the other parameters is labeled "human cells." I will explain this in section 5 below.

The third dimension, C , represents, roughly speaking, the smoothness of the fitness landscape (Wright 1932, Gavrillets 2004). C is high when near-variants with respect to phenotype are similar with respect to (realized) reproductive output. The symbol comes from Lewontin's term "continuity," used in an early discussion of these issues (1985).

The evolutionary importance of continuity, or reasonable smoothness of fitness landscape, is widely recognized. But S and C also make possible a new treatment of the relation between selection and "drift." I assume that in real populations, differences in realized fitness will almost always exist, and will have some causal basis or other. Given that there are reproductive differences in a population, the question is where they come from, and what they are correlated with. Suppose S and C are both very low. As S is low, reproductive differences are largely due to extrinsic differences. These extrinsic factors are real features of the organisms; they are part of what fitness is treated as a function of, in the determination of C . Extrinsic factors, like intrinsic ones, may have a role that is robust, or one that is fine-grained and chaotic. When S and C are both very low, reproductive differences are due to factors that are both extrinsic and chaotic. These are the cases that induce talk of "drift"; recall the familiar example of two intrinsically similar organisms, one struck by lightning. (The label "drift" can also seem appropriate to some extent when only one of S or C is low, but those are not the clearest cases.)

So S and C have general importance; their use is motivated mainly by what happens at non-extreme values. But then we can note that at extremely low values, we find one famous kind of non-Darwinian phenomenon, "drift"-like change.

Figure 1 does not include any measure of the abundance of variation, but this is obviously crucial and several different measures of variation seem relevant. One is the amount of variation present at a time – the immediate raw material of evolutionary change. Another is the dispositional property a system may have, of reliably tending to produce new variation as it is consumed by selection. As discussed later, it is also common to emphasize some kind of "quasi-independence" of variation, or "modularity" in the effects of variation on the phenotype. Yet other important features are the size of a typical deviation and the absence of bias. But here I will only make use of the most basic of these features. V will represent the amount of variation in a population at a time.

Some parameters we would want to include are not independent of each other, either at extreme values or more generally. For example, if H is perfect, no new variation appears, though existing variation will be retained. There is also a variety of causal relationships between the features.

In this section I have shifted emphasis away from the discrete categories introduced earlier (paradigm, minimal, marginal), to a network of relations between populations, with respect to their evolutionarily important parameters. And as a population evolves, it not only changes the characteristics of the organisms within it, it also changes how it evolves in the future. Populations move through the space. A population can evolve a higher or lower H , by evolving better or worse suppression of mutation via DNA editing. It can evolve heat-shock proteins that increase C . It can move to a new environment full of capricious and lethal risks that reduce both C and S .

3. Forms of Reproduction

Earlier I noted the role of the concept of reproduction, which figures in the minimal concept. What *is* reproduction? We might give an initial analysis by saying that reproduction involves (i) the production of a new individual, (ii) of the same general kind as other members of the population, (iii) primarily via the causal role of particular pre-existing individuals in that population. Reproduction can then be contrasted with (i) growth of the same individual, (ii) the production of waste and artifacts, and (iii) production of a new

individual without it being the product of particular parents. This is a "shallow" analysis of reproduction. It uses terms that are themselves problematic, and may have to be revised under the influence of theory later on. But it is a start.

There are two well-known families of problem cases to grapple with.

(i) *Reproduction versus growth*: When is the production of new biological *material* the production of a new biological *individual*? The problem is most acute with plants and colonial organisms, and in the absence of sex.

(ii) *Collective entities*: When does the production of a new collective entity (such as a colony, herd, or symbiotic association) count as reproduction at that higher level?

In addressing these problems, I avoid making any particular criteria essential to reproduction. Instead, I apply the gradient approach used in the previous section. Owing to the role of several biological features, cases of reproduction can be clearer or more marginal. This analysis may then be connected to the analysis used in the previous section; marginal Darwinian processes often involve marginal forms of reproduction.

Returning to the contrasts between reproduction and other phenomena introduced earlier, a case of reproduction might be marginal because: (i) it is not clear that new individuals are being produced, as opposed to new parts of old individuals, or because (ii) the population is made of dubious higher-level entities that have little standing as individuals in their own right. Alternatively, it might be because (iii) the causal relation linking "parent" and "offspring" is not clear. (That last possibility applies often in the case of cultural evolution.) At different places in the tree of life, we find lots of different reproduction-*like* phenomena. This is for Darwinian reasons; the forms taken by the creation of new biological material from old are consequences of contingencies of ecology and history on different parts of the tree.

I will discuss three reproduction-related features. They are designed to deal with the families of problems raised above: distinguishing growth from reproduction, and recognizing reproduction in higher-level entities. The two problems are linked, as growth-versus-reproduction problems usually involve either modular organisms or colonies (aspen, corals, fungi, etc.), and certainly the problem will usually arise when there is at least multicellularity present. So the treatment given here may apply generally to all cases of "collective

reproducers" (Godfrey-Smith 2009), though they may not give a framework appropriate for some other sorts of cases.

The first parameter I will use is *B*, where *B* stands for "bottleneck." A clear case of reproduction, at least when we are dealing with collectives rather than things like cells, has a narrowing to mark a divide between generations. This might be understood absolutely, or as some measure of the relation between propagule and adult size. A bottleneck enables a process of growth and development to begin anew, so a localized mutation can have a multitude of downstream effects (Harper 1977, Dawkins 1982). I understand *B* as coming in all degrees, not as marking a distinction between one-celled beginnings and everything else.

The second feature is *G*, which stands for "germ/soma," but is understood more broadly as the degree of reproductive specialization seen in the collective's parts. When *G* is high, many parts of a reproducing entity are unable to become the basis of a new entity of the same kind. Only a few parts have that role. This feature seems particularly relevant when analyzing reproduction in colonies, as will be discussed further below. The third feature I will use is *I*, which stands for "integration." This one is vaguer. It involves such features as division of labor (aside from the kind involved in *G*), mutual dependence of parts with respect to viability, and maintenance of a boundary between individual and environment.

In another work (2009) I give a three-dimensional chart that categorizes various cases according to *B*, *G*, and *I*. Here I will just discuss two dimensions, *G* and *I*, and will use an example with special relevance to questions about evolutionary transitions.

The colonial green algae in the clade that includes the "Volvox" organisms are often seen as a very informative case for the study of the evolution of multicellularity (Kirk 1998 & 2005, Michod et al. 2003, Michod 2005). These organisms, which are found commonly in ponds, have both sexual and asexual reproduction. A sexually produced cell divides repeatedly to produce a colony, which may be of various sizes and degrees of organization. The colonies swim using their members' flagella, migrating to shallow water during the day and collecting nutrients in deeper water at night. When food is plentiful the colonies reproduce asexually – new colonies are formed inside the old from single initiating cells. The new colonies bud off or are released from inside the old colony. When food becomes scarce they enter a sexual cycle, producing "zygospores" which lie dormant until times are better. Here I consider only their asexual mode of reproduction.

In Figure 2, all the colonies are formed from a single-celled bottleneck – all share a high value of B . They differ with respect to G and I . (A version of this figure was sketched initially by Rick Michod. That should not be taken to imply that he endorses the framework used here.)

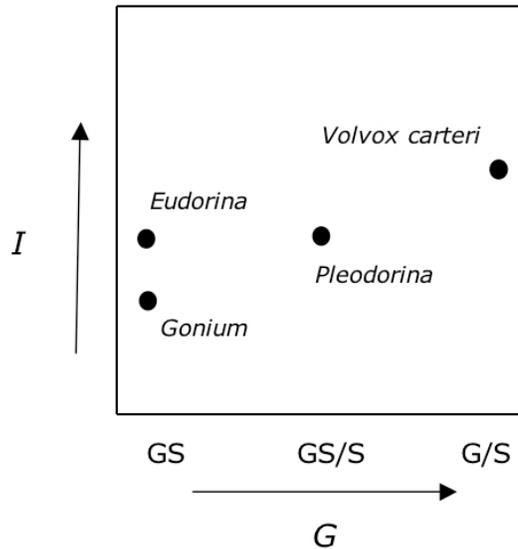


Figure 2. (G, I) comparisons for some colonial green algae

The distinctions between "GS," "GS/S," and "G/S" states on the G axis follow Michod's framework (with apologies for my double use of the letter "S" – I have not italicized the letter in this second use). A GS colony has no reproductive division of labor at all; all cells carry out a similar mix of "somatic" and reproductive roles, though not simultaneously. In these organisms, a central non-reproductive function is locomotion, via the action of the flagella. A particular cellular structure (basal body) is needed for both cell division and use of the flagella, so this determines a trade-off (Buss 1987), which is temporally organized in GS organisms. In the GS/S case, we have somatic cells plus cells that play both roles. Typically, the dual-role cells act "somatic" in locomotion first and then become reproductive. In the G/S cases on the right, there is a definite distinction between somatic and germ-line cells.

Gonium, on the far left, consists of loosely organized colonies of 8 to 16 cells. *Gonium* is basically a flat clump of cells, but with some spatial organization of flagella action.

Eudorina, in contrast, has 32 cells and is spherical, with a distinction between inside and

outside. Both organisms are GS.¹ *Pleodorina* colonies consist of 64 to 128 cells. They have the partial GS/S reproductive division of labor, and the somatic cells are localized to one part of the structure. *Volvox carteri*, on the right, is larger (2^{12} cells) and more integrated – many would say it counts clearly as an organism. It also has a clear germ/soma distinction, with the vast majority of cells allocated to a purely somatic role early in development.

It would be possible to add more cases, though their plotting on the chart might be controversial. *Volvox rousseletii* is larger than *carteri*, as it has 2^{15} cells. These colonies are GS/S, like *Pleodorina*, but might be distinguished with respect to dimension *G* because the reproductive cells in *V. rousseletii* only have flagella for a very short time, less than a day, before abandoning this set of functions. *V. rousseletii* is a more adept swimmer than *V. carteri*. It also has cytoplasmic bridges linking the cells when mature, which are lost during development in the case of *V. carteri*. These might be seen as a mark of higher integration than we find in *V. carteri* (though Michod, personal communication, is wary of that comparison). So it would be possible to plot *V. rousseletii* as higher than any other case with respect to *I* and intermediate, with *Pleodorina*, with respect to *G*. But perhaps it should be intermediate between *Pleodorina* and *V. carteri* with respect to *G*, and it is not clear that it is higher than the *V. carteri* with respect to *I*. So I included only the clearer cases in the figure.

4. Comparison with Sterelny

In this section I will compare my framework to one that Sterelny has discussed in several papers (2001, 2004), and revisits in his contribution to this volume. Sterelny's aim is to describe "enriched Darwinian environments... the characteristics of individuals, populations and environments in which the evolution of novelty and disparity is possible." Sterelny is more focused on the "high end" of the range of cases that I am discussing, and treating that region in more detail. But there are some relevant points of comparison. His conditions for "enrichment" of Darwinian processes are as follows:

¹ Kirk qualifies this. Under most circumstances all *Eudorina* cells divide, but "under some circumstances" the four anterior ones remain somatic (2005, p. 305).

Anti-Outlaw Conditions

(1) Replicators should be transmitted vertically. Replicators should flow from parents to offspring, and to them alone.

(2) Replicators should be transmitted simultaneously.

(3) The transmission of the replicator set should not be biased. Either all an organism's replicators are transmitted to each descendant, or each replicator has an equal chance of being transmitted to each descendant.

Stability Conditions

(4) The copy-fidelity of the generation of replicators from generation to generation should be high.

(5) The replicator/organization map should be robust. To the extent that the causal channel from replicator to organization depends on context, both internal and external, that context should be stable and predictable.

Generation of Variation

(6) The array of possible replicator sets should be very large; possibly even unbounded.

(7) The effect of a replicator on the biological organization of its carrier should normally be well-behaved. That is, the replicator/organization map should be smooth. A map is smooth if a small change in the replicator set generates a small change in biological organization; and the smoother the map, the more evolvable the lineage using that inheritance channel. Moreover, the relationship between phenotype and fitness should be smooth: if T^* is fitter than T , and $T^\#$ is phenotypically intermediate between T^* and T , its fitness should be intermediate, too.

(8) The generation of biological organization from the replicator set should be modular. The replicators as a whole should not generate the biological organization of the organism as a whole. Rather, replicators, or small sets of replicators, should be designed so that they make a distinctive contribution to the generation of one or a few traits, and relatively little distinctive contribution to others.

One difference between us is that Sterelny assumes a replicator framework – not that the organisms in an evolving population are replicators, but that their inheritance mechanisms work through the physical transfer of replicators. If this is an application of the idea that Darwinian phenomena in general require replicators, then I think it is a mistake, even on a liberal conception of replication. Alternatively, Sterelny might be assuming, in the background, that *significant* evolutionary processes all involve replicators. In that case, "inheritance works via the transfer of replicators" becomes his condition zero, the first big distinction between different Darwinian phenomena. Either way, the treatment of replicators

has the consequence that, from my point of view, Sterelny is discussing the relations between two Darwinian populations at once: a population of organisms and a population of underlying replicators which undergo their own evolutionary activities. His "outlaw conditions" are concerned with such relations. There is no mention of bottlenecks or germ lines here; later I will discuss their role as "anti-outlaw" mechanisms. In fact, his (3) must be understood carefully if it is not to be incompatible with a germ-line requirement; it must mean all the replicators *initially* present. There is trouble if the replicators transferred are representative of changes during ontogeny.

Sterelny's (4) and (5) together yield high H in my sense. We have faithfully copied replicators, with stable effects on phenotype. So Sterelny breaks H into two components. His (6) is a standard condition on variation that I would also include in some form.

His (7) and (8) are both linked to my C . Specifically, the last part of (7) *is* my C . The early parts of (7) are *means* to C . This recalls Lewontin's original discussion of "continuity"; he said that similar phenotypes should yield similar "ecological relations," in turn yielding a smooth fitness landscape (Lewontin 1977).

Condition (8) seems to me to duplicate part of (7). This is because modularity has the consequence that a small change to what is inherited implies a local change to phenotype. So I worry that Sterelny may be treating parts of a causal chain involved in C as if they were distinct requirements. Modularity is one means to a situation in which small changes to inherited resources imply small changes to phenotype. That, in turn, is a good way to ensure that similar organisms have similar fitness. Some of these connections are near to deductive, others looser. Given the loose connections, Sterelny may be right that many these factors are worth listing separately. But I suspect there is probably some partial duplication of criteria having to do with smoothness of fitness landscape, through separately requiring both the outcome and some of its preconditions.

5. Transitions in Individuality

I now turn to the "major transitions in evolution." Most of these transitions, but especially what Michod calls "transitions in individuality," involve the appearance of new Darwinian populations from old. Often this occurs via collective entities acquiring a genuine status as Darwinian individuals – as members of Darwinian populations.

The analysis I have in mind works like this: we take a permissive attitude to the concept of a Darwinian population itself. Many can be recognized – some inside of others, some that look like mere byproducts of the activities of lower-level populations, some with odd shapes and boundaries. In many cases, it may appear that the "real" evolutionary action is going on somewhere else. And action elsewhere may indeed be going on. But these dubious cases will often nonetheless pass or at least approximate the minimal Darwinian criteria discussed above.

So Darwinian populations exist at many different levels.² Returning to the spatial analysis in section 3, there are all sorts of dubious and apparently artifactual cases that can be located *somewhere* in such a space. But populations also move through the space, as a consequence of the evolution of new genetic and phenotypic features in the individuals themselves. This may include movement from marginal to paradigm status, or from paradigm to marginal. Movement of that kind is often a consequence of evolutionary change to how reproduction works. What were formerly mere collections of lower-level entities can become significant Darwinian individuals in their own right. As I will argue, movement of a higher-level population into "better" parts of the space often goes via movement of another population – the lower-level one – into a "worse" part of the space.

Let us imagine a schematic evolutionary transition, having the flavor of a transition to multicellularity, of the kind discussed by Maynard Smith, Szathmáry, Michod, and others. We assume a population of lower-level entities that come to interact in collectives, either by association or by failure to separate after reproduction. Their association may initially be loose. But cooperation develops. Cooperation requires overcoming subversion problems. This may lead to the appearance of a series of adaptations that suppress lower-level competition.

Two characteristics are often discussed in this connection: bottlenecks and germ lines (Buss 1987, Grosberg and Strathman 1998, Michod 1999, Szathmáry and Wolpert 2002). Features like these can be visualized as producing two kinds of movement in a space defined by Darwinian parameters. First, the population of collectives, formerly marginal,

² When I talk of "levels" of selection here, roughly speaking I mean this in what is known as the "MLS2" sense, not the "MLS1" sense (Damuth and Heisler 1988, Okasha 2006). Group selection, for example, requires reproduction *of groups*, and heritability at the group level. We apply the standard Darwinian criteria at all levels and in all cases. So differential fitness as a feature of entities at level N involves differential reproduction of entities at level N .

moves closer to the paradigms. High values of B and G are associated with clearer instances of reproduction. The second change concerns the lower-level entities, which here we assume to be cells. The evolution of higher values of B and G at the collective level suppress or curtail evolutionary activities at the cell level. They make cells into a *less* significant Darwinian population, push them away from the paradigm region.

This happens in several ways. First, bottlenecks impose uniformity at start of the life cycle of the collective entities. This reduces the scope for evolution at the lower level. This is a reduction in variation (V) for the population of cells found within a multicelled organism. The only genetic variation that can arise has to appear by mutation from an initially uniform genotype, or perhaps by mitotic recombination or lateral gene transfer. Epigenetic variation can accumulate much more quickly.

Higher values of B reduce the *scope* for low-level evolution. Evolution of a germ line has the further effect of making certain kinds of within-collective evolution *irrelevant* to longer-term evolutionary processes.

In my framework, this is a reduction in S at the cell level. To see this, think about the situation fairly late in ontogeny for a multicellular organism like one of us. There is an array of cells with different genotypes as a consequence of mutation (and different epigenotypes as well). Which cells are fitter than others? Some may reproduce faster than others, commandeering more resources, and so on. But if we ask which cells have the chance of giving rise to a long lineage of descendants, then these intrinsic differences have limited importance. What matters instead is location, the extrinsic property of being, or not being, in the germ line.

So from the lower-level point of view, bottlenecks and germ lines are "de-Darwinizing" elements. They make the collection of lower-level entities into a less significant Darwinian population. Whether or not this is the evolutionary *function* of bottlenecks and germ lines, in the historical sense, it is something they in fact *do*.

Here I will not take sides on the many interesting questions about the evolution of bottlenecks and germ-lines, but I will discuss some features of the landscape of possibilities in a bit more detail. In an asexual population, there can in principle be either without the other. A bottleneck without a germ line is possible if there is spore-like or apomictic asexual reproduction. Reproductive specialization of the germ/soma kind without a bottleneck is also possible in principle; a large multicellular propagule might derive from a specialized

reproductive structure. We might wonder whether there is much point in high G without high B , however. Then there may be genetic variance within the propagule, even though somatic evolution after sequestration is irrelevant. The result is the continuation in a small and special arena of the same sort of competitive process that germ/soma specialization usually acts to suppress (Michod and Roze 2001). An organism would carry into the next generation a competition inherited from the previous one.

Things are different in a sexual population with fusion of gametes. In a sexual population of this kind, bottlenecks without germ lines are still possible. But a germ line without a bottleneck seems even more implausible than in the asexual case (Grosberg and Strathman 1998, Wolpert and Szathmary 2002). Even if all the cells in a particular parent contributing gametes to a large propagule were themselves very genetically similar, the gametes themselves would differ, owing to the many separate events of segregation and recombination. Sex magnifies the problem of internal conflict discussed above.

Both pairs of authors cited above raise other possible problems with the possibility of a large sexual propagule, unrelated to the problem of internal competition. Grosberg and Strathman suggest mechanistic problems with the coordination of cells during syngamy and early development. Wolpert and Szathmary claim that it would be hard for such organisms to have a coherent developmental program, as the organized differentiation of cell lineages in development requires that "all the cells have the same set of genes and obey the same rules" (p. 745). Slime moulds are, when we think of the multicellular fruiting body as the organism, highly sexual with many parents. But their developmental sequence is very simple indeed. Wolpert and Szathmary do not think that this argument from the possibility of complex developmental programs involves an inappropriate appeal to long-term consequences rather than short-term advantage, though they do gesture towards something like the culling of clades, rather than ordinary micro-evolution, for organisms with small propagules to prevail.³

Sex (in some form) is ancestral in all major multicellular lineages, though Grosberg and Strathman do not think this itself imposes too tight a constraint, and hold that a functional rationale for bottlenecks should still be sought. In any case, though all these

³ "[T]aking the broad view in evolutionary terms, organisms that develop from an egg would displace those that do not" (2002, p. 745).

discussions are presented as speculative, the upshot is that various arguments make it unsurprising that bottlenecks without high reproductive specialization are common, but not the converse.

In sum: some key adaptations on the road to complex multicellularity have the effect of moving collective entities towards paradigm status as Darwinian individuals, by giving them a clearer form of reproduction, and moving lower-level entities away from paradigm status. The lower-level entities are partially "de-Darwinized" by the transition process. In many cases (such as cells) the lower-level entities still engage in a clear form of reproduction, but they come to score lower in other ways.

6. Comparison with Michod

I will contrast the treatment above with some of Michod's recent ideas about evolutionary transitions (2005, 2006, this volume). Michod gives a foundational treatment in quite different terms from me, and the contrasts are informative about the different possible ways of setting things up.

Michod claims that an evolutionary transition in individuality (ETI) involves the "transfer" or "export" of fitness from the lower level to the level of the collective. The evolution of multicellularity is his main example.

During ETIs, the heritability of fitness for the new higher level must increase, while, at the same time, it must decrease for the lower-level units. This requires the *reorganization of fitness...*, by which we mean the transfer of fitness from the lower-level units to the new higher-level unit and the specialization of lower-level units in the fitness components of the higher-level unit. (2005, p. 968)

The evolution of cooperation is fundamental to ETIs, because it exports fitness from the lower level (e.g., its costs to cells) to the higher level (its benefits to the group) and in this way cooperation may create new levels of fitness. (2005, p. 969)

My first point is that this talk of export and transfer seems rather metaphorical. What is meant in more literal terms? So let us look at a more specific argument Michod makes about what happens to lower-level fitnesses as a transition occurs. When reproductive specialization occurs in a transition to multicellularity, the fitness of the lower-level entities (cells) goes to zero. That means they cannot engage in a Darwinian process.

Consider the case of multicellular organisms with complete G-S specialization. The germ cells specialize completely in reproductive functions and the somatic cells specialize completely in vegetative functions. The cell fitness of all cells must be zero (since fitness is the product of viability and reproduction and one of these is zero by the assumption of complete G-S specialization). Therefore, the fitness of the group is zero under MLS1, yet group fitness may be quite high under MLS2. (2005, p. 970)

Once the specialization is complete and the lower level units are specialized in one of the two major fitness components (viability or fecundity), they have no fitness by themselves and so group fitness in the sense of MLS1 is null, while group fitness in the sense of MLS2 may be quite high. (2005, p. 976)

For Michod, it is general fact that fitness is a combination of viability and fecundity, as discussed in life-history models. Specifically, it is the product of these. So if either of the two is zero, overall fitness is zero. The argument is that when we have complete germ/soma specialization, the fecundity of the somatic cells is zero, and the viability of the germ-line cells is zero. So there is no fitness present at the lower level, and hence no Darwinian process at that level.

I do not think it is true that when there is germ/soma differentiation, these cell-level viabilities and fecundities go to zero, on any natural kind of accounting. Germ-line cells do live for a time, and divide at the end of a period of remaining viable. Somatic cells do, in many cases, divide. They do not divide in the case of the *Volvox carteri* that Michod studies, but I assume he does not intend his argument to depend on that fact. I assume he sees the argument as applying generally to organisms with germ/soma specialization. But in general terms, surely both germ-line and somatic cells do the same sort of thing from a Darwinian point of view: both kinds of cells will live for a while, and then divide or die.

Of course, Michod does not intend to deny any those assertions about what germ-line and somatic cells do. He accepts that both kinds of cells in organisms like us are able to live and reproduce. What Michod is guided by is a functional difference between germ-line and somatic cells. But that functional contrast has to do with the effects of different cells on whole-organism fitness: the somatic cells aid in maintaining whole-organism viability (though not only that – they also support reproductive efforts). Germ-line cells do not contribute to maintenance of viability. This functional contrast has to do with the cells' relations to the collective's fitness, not their own.

Given that, I suggest that when we are considering the fitness and other Darwinian properties of lower-level entities, such as cells, we should assess the cells' relations to the standard criteria for being a Darwinian population *in their own right*, on their own terms. The functional contrast discussed above does not prevent cells in a multicellular organism from meeting, for a time, the criteria for making up a Darwinian population. It does not stop them from actually living, varying, reproducing, and potentially passing on – for a while at least – favored traits.

There are two ways of looking at cells in such a case, in fact. We can think of the cells within each organism as making up a small and short-lived Darwinian population, and we can also collect all human cells together and treat them as making up one larger population. Both kinds of analysis are possible. It is true that the cells in an organism like us are dependent on other cells in order to stay alive and reproduce; they have come to inhabit a particular kind of environment. But in that environment, they do in fact survive and reproduce – they engage in ordinary Darwinian activities. Some are fitter than others. With respect to their relationships to the basic Darwinian criteria, human cells are no different from bacterial cells and protists. When we look in more detail at what *kind* of Darwinian population the cells within you, or the totality of human cells, form, then we do find they have special features of the kind discussed in the previous section. But to acknowledge these evolved features is not to say that cells in organisms like us have, despite their ability to survive and reproduce, no fitness at all.

Michod's models are informative. They feature a germ/soma specialization pathway that does not go via the subversion problem, but goes via ecological trade-offs between reproduction and other functions. Might it be that subversion prevention is sometimes an incidental byproduct of a germ/soma specialization that tends to come about for other reasons? We are already used to that sort of byproduct explanation, as noted above, as a consequence of thinking about bottlenecks and their consequences. The models might be taken on board independently of Michod's commentary about them.

6. Conclusion

The project of this paper has been to start from a general and independently motivated analysis of Darwinian processes, extend it so it can accommodate some extra distinctions (paradigm and marginal cases, etc.) and then apply it to some problems raised by

evolutionary transitions. Many earlier discussions in this area have used the concept of a replicator, rather than a three-part summary in the more traditional style exemplified by Lewontin (1970). The three-part summaries are, I suggest, both superior in general and also quite useful for thinking about the major transitions. I have argued that attention to the concept of reproduction is particularly fruitful here. In many cases, the mechanisms of reproduction are crucial to the evolutionary properties of both higher-level Darwinian individuals, like multicellular organisms, and the lower-level Darwinian individuals from which they arose. Bottlenecks and germ lines, in particular, have complementary roles for each kind of entity, contributing at once to the Darwinization of the higher-level individuals and the partial de-Darwinizing of the lower.

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References

- Buss, L. W. (1987). *The Evolution of Individuality*. Princeton, NJ: Princeton University Press.
- Damuth, J. and Heisler, I. L. (1988). "Alternative Formulations of Multilevel Selection." *Biology and Philosophy* 3: 407-30.
- Dawkins, R. (1982). *The Extended Phenotype: The Gene as the Unit of Selection*. Oxford: W. H. Freeman and Company.
- Eigen, M. and Schuster, P. (1979). *The Hypercycle: A Principle of Natural Self-Organization*. Berlin: Springer-Verlag.
- Endler, J. A. (1986). *Natural Selection in the Wild*. Princeton, NJ: Princeton University Press.
- Gavrilets, S. (2004). *Fitness Landscapes and the Origin of Species*. Princeton, NJ: Princeton University Press.
- Godfrey-Smith, P. (2000). "The Replicator in Retrospect." *Biology and Philosophy* 15: 403-23.
- _____, (2007), "Conditions for Evolution by Natural Selection," *The Journal of Philosophy* 104: 489-516.
- _____, (2009). *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.
- Griesemer, J. (2000). "The Units of Evolutionary Transition." *Selection* 1: 67-80.
- _____, (2005). "The Informational Gene and the Substantial Body: On the Generalization of Evolutionary Theory by Abstraction," in M. Jones and N. Cartwright (eds.), *Idealization XII: Correcting the Model, Idealization and Abstraction in the Sciences* Amsterdam: Rodopi, 59-115.

- Grosberg, R. K. and R.R. Strathmann (1998). "One Cell, Two Cell, Red Cell, Blue Cell: The Persistence of a Unicellular Stage in Multicellular Life Histories." *Trends in Ecology and Evolution* 13: 112-116.
- Harper, J. L. (1977). *Population Biology of Plants*. London: Academic Press.
- Kirk, D. L. (1998). *Volvox: Molecular-Genetic Origins of Multicellularity and Cellular Differentiation*. Cambridge and New York: Cambridge University Press.
- _____, (2005). "A Twelve-Step Program for Evolving Multicellularity and a Division of Labor." *Bioessays* 27: 299 – 310.
- Lewontin, R. C. (1970). "The Units of Selection." *Annual Review of Ecology and Systematics* 1: 1-18.
- _____, (1985). "Adaptation," in R. Levins and R. C. Lewontin (eds.), *The Dialectical Biologist*. Cambridge, MA: Harvard University Press, 65-84.
- Mameli, M. (2004). "Nongenetic Selection and Nongenetic Inheritance." *British Journal for the Philosophy of Science* 55: 35–71.
- Maynard Smith, J. (1988). "Evolutionary Progress and Levels of Selection," in M. H. Nitecki (ed.), *Evolutionary Progress*. Chicago, IL: University of Chicago Press, 219-30.
- Maynard-Smith, J. and Szathmáry, E. (1995). *The Major Transitions in Evolution*. Oxford: W. H. Freeman.
- Michod, R. E. (1999). *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton, NJ: Princeton University Press.
- _____, "On the Transfer of Fitness from the Cell to the Multicellular Organism" *Biology and Philosophy*. 20:967-987
- _____, (2006). "The Group Covariance Effect and Fitness Trade-Offs During Evolutionary Transitions in Individuality," *Proceedings of the National Academy of Sciences (USA)* 103: 9113-9117
- Michod, R. E., Nedelcu, A. M., and Roze, D. (2003). "Cooperation and Conflict in the Evolution of Individuality IV: Conflict Mediation and Evolvability in *Volvox carteri*," *BioSystems* 69: 95-114.
- Michod, R. E. and Roze, D. (2001). "Cooperation and Conflict in the Evolution of Multicellularity." *Heredity* 81: 1-7.
- Odling-Smee, F. J., Laland, K. N., and Feldman, M. W. (2003). *Niche Construction: The Neglected Process in Evolution*. Princeton, NJ: Princeton University Press.
- Okasha, S. (2006). *Evolution and the Levels of Selection*. Oxford: Oxford University Press.
- Sterelny, K. (2001). "Niche Construction, Developmental Systems and the Extended Replicator," in R. Gray, P. Griffiths, and S. Oyama (eds.), *Cycles of Contingency: Developmental Systems and Evolution*. Cambridge, MA: MIT Press, 333-49.
- _____, (2004). "Symbiosis, Evolvability, and Modularity," in G. Schlosser and G. P. Wagner (eds.), *Modularity in Development and Evolution*. Chicago: University of Chicago Press, pp. 490-518.

- Sterelny, K. and Griffiths, P. E. (1999). *Sex and Death: An Introduction to the Philosophy of Biology*.
Chicago, IL: University of Chicago Press.
- Wolpert, L. and Szathmáry, E. (2002). "Multicellularity: Evolution and the Egg." *Nature* 420: 745.
- Wright, S. (1932). "The Roles of Mutation, Inbreeding, Crossbreeding and Selection in Evolution."
Proceedings of the Sixth International Congress of Genetics 1: 257-66.