

Title:

Making the most of clade selection

Abstract:

Clade selection is unpopular with philosophers who otherwise accept multilevel selection theory. Clades cannot reproduce, and reproduction is widely thought necessary for evolution by natural selection, especially of complex adaptations. Using microbial evolutionary processes as heuristics, I argue contrariwise, that (1) clade *growth* (proliferation of contained species) substitutes for clade reproduction in the evolution of complex adaptation, (2) clade-level properties favoring persistence – species richness, dispersal, divergence, and possibly intraclade cooperation – are not collapsible into species-level traits, (3) such properties can be maintained by selection on clades, and (4) clade selection extends the explanatory power of the theory of evolution.

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1. Introduction. One might intuit that there are two ways to create something useful. First, conceive the thing's purpose in advance and somehow determine, top-down, how it should be built – “intelligent design”. Second, generate (somehow) many possible solutions and choose among them those that work best for the purpose at hand – selection. The culling of failed structures repeated many times over (“iterated variation-and-selection” [Godfrey-Smith 2015]), each time starting with successful products of the last, will hone the fit to whatever use. It is a tribute to the tyranny of the belief in a purposeful universe and its Creator that the idea that the second way to create provides a fully coherent “how possibly” explanation for the exquisite fit of organisms to their environments is scarcely 150 years old, and still not widely accepted. Nevertheless it accomplishes, in Maynard Smith's (1969, 82) words, “The main task of any evolutionary theory ... to explain *adaptive complexity*, i.e. to explain the same set of facts which Paley used as evidence for a Creator.”

Arguably, those 150 years have left us with a too narrow version of that second way of thinking, the narrowing being the downside of one reason for the success among biologists of Darwin and Wallace's broad theory. Depew and Weber (2011, 89) interestingly assert that “... natural selection, would probably have gone the way of other grand nineteenth century ideologies or “meta-narratives” if it had not been turned in the first half of the twentieth century into a mathematized science. In this respect, Darwinism's fate contrasts with that of two other seminal nineteenth and early twentieth century discourses, Marxism and Freudianism”. But the almost exclusive focus of this mathematization on allele frequency changes in conspecific sexual populations [Smocovitis 1992; Gould 1983; Pigliucci 2008a]), to the general neglect of trans-species macroevolutionary modeling, asexuals and prokaryotes, biased the synthesis towards “bean-bag genetics” (Rao and Nanjundiah 2011) and ultimately selfish gene centrism (Dawkins 1976). George Williams spoke for the majority in the mid 1960s when he wrote that “In explaining adaptation, one should assume the adequacy of the simplest form of natural selection, that of alternative alleles in Mendelian populations, unless the evidence clearly shows that this theory does not suffice...” (Williams 1966, 4).

It was not until the last decade of the last century that many of evolutionary biology's prominent theorists were willing to seriously take on board that evolution by natural selection (ENS) ensues of logical necessity for any entities exhibiting *heritable variation in fitness* (as in Lewontin's [1970] formulation). Such entities can be found at the levels of genes, cells, organisms and species (multi-level selection or MLS theory). There are, however, several good reasons not to extend ENS to the next higher level of the genealogical hierarchy, genera or more generally supra-specific clades, in spite of a seeming fit to intuition. Indeed, clade selection (CS) – defined here as the *differential persistence of clades due to clade-specific properties* – maps imperfectly to Lewontin's three-part recipe, and whether or not we consider it a form of ENS is a matter of choice. But a coherent CS theory *is* possible, can be shoehorned into our intuition about creation, and does do some explaining about how things are in the living world.

2. Imagine no genetics. It is instructive in this context to contemplate a counterfactual history of Darwinism after 1900, one in which Mendel's work remains undiscovered, R.A. Fisher sticks to agricultural statistics, and Watson and Crick never even meet. We'd still have paleontology, biogeography and phylogenetics (at least protein sequence-based), "meta-narratives" already considerably more mathematized than Marxism or Freudianism (Hunt et al 2015 and work cited therein). In such an alternative universe our ENS paradigm might be *species selection*.

Species selection was first championed by paleontologists (Stanley 1979; Arnold and Fristrup 1982; Vrba and Eldredge 1984; Jablonski 2008) and is the easiest sort of supra-individual ENS for evolutionists in the universe we actually do inhabit to accept, especially when arguments for it are uncoupled from disputes around the evolution of altruism within species that take up so much of the literature. The former type of theory (called MLS2) addresses the differential reproduction of groups while the latter (MLS1) looks at the reproductive advantages accruing to individuals from group membership (Damuth and Heisler 1988; Okasha 2001, 2006). Many biologists would now accept that speciation and extinction are – for sexual species – the species-level equivalents of organismal birth (reproduction) and death, that daughter species resemble their parent species (exhibit heredity), and thus that variable traits that enhance *diversification* (increase speciation or suppress extinction) will be selected for at the level of species. The academic and popular paleontological literature focuses as much on extinction (and thus, indirectly, survival) as on speciation (e.g. Van Valen 1994; McKinney 1997; Raup 1991; Jablonski 2001; Longrich et al. 2012; Wagner and Estabrook 2014), perhaps because it is easier to observe, and more dramatic. In contrast, the gene-centric Modern Synthesis, though touting "survival *and* reproduction", values the former only insofar as it serves the latter.

In the early 1980s, when species-selection seemed a radical notion linked to punctuated equilibria, its major proponents cautiously and conservatively focused on identifying speciation-promoting (or extinction-deferring) traits that could be cast as *emergent* at the level of species (Vrba 1983; Vrba and Gould 1986, Grantham 1995, Gould and Lloyd 1999; Lieberman and Vrba 2005). Parameters like population size, sex ratio or geographic distribution of populations would be such traits. On the other hand, features common among species because they are commonly beneficial to organisms within species would not count. The higher-level consequences of such "aggregate traits" would be considered mere *byproducts* or *effects*, even when such effects also enhance species diversification (positive *effect macroevolution*). Indeed, only when an emergent trait selected for at the species level is for that reason common among organisms in spite of being detrimental to them as individuals ("downward causation"), was species selection to be invoked. Sex, supposedly wasteful for individuals but good for species, would be a paradigmatic example of such a trait (Maynard Smith, 1988).

More recently though, several theorists have come to accept positive *effect macroevolution* – that even traits that might be selected for among individuals within species can have independent speciation-promoting or extinction-discouraging effects, and

thus are subject to selection at both levels (Damuth and Hiesler 1988; Jablonski 2007, 2008). The prevalence of such traits *within species* reflects the benefit to individuals, while the *prevalence of species* whose members exhibit such traits may reflect additional speciation-promoting or extinction-discouraging effects. Determining the relative strengths of these collaborating forces might of course be very difficult, but as David Jablonski nicely summarizes the current state of play ...

The growing acceptance of species selection (in the broad sense [including effect macroevolution]) as a potential evolutionary force derives in part from an expansion in the range of evolutionary questions being addressed. The focus is no longer so exclusively on changes in allele frequencies and how those might drive the origin of features such as eyes and horns, but instead it more actively includes the frequencies of such features among clades (how many species have horns), the fates of those features (how long do horns last, in evolutionary terms), and origination and extinction rates of species and clades (why do clades wax and wane, and do horns determine clade dynamics ... (Jablonski 2008, 502).

4. Major transitions theory and other reasons why CS is interesting but problematic.

In the current century, interest in MLS theory has been rekindled by the recognition that most “major transitions in evolution” (MTE; Maynard Smith and Szathmary 1995) such as the origin of cells, of eukaryotes, multicellularity, and eusocial species – involved surrendering (at least partially) the evolutionary interests of lower-level reproducing entities in favor of those of a higher-level collective reproducer (Okasha 2005). If in fact MLS was itself necessary for establishing the hierarchy of genes, cells, organisms and species in the first place, it is surely worth our serious attention. But the MTE connection also points out one of the several problems in extrapolating upward from species selection to “genus selection” or more generally to CS (see Fig. 1 for a definition of ‘clade’). Species in a genus or higher-level clade, (and, as we shall see, bacteria in a clone) do not surrender their evolutionary interests to a higher-level collective: they do not depend on each other for reproduction *or* survival in the quite direct way that genes in a genome, cells in a multicellular organism, or organisms in a sexually reproducing species do. Nor, unlike lower-level entities (arguably including species), are clades collectively “interactors” conforming to a formulation first fleshed out by Hull (1980). Damuth (1985, 1132), who is also opposed to species selection but not to a form of community selection, noted that “Clades are not localized, their members do not share an environment, and they cannot be said to respond to local selective regimes.” Certainly, members of a clades are more likely to occupy the same “adaptive zone” in Simpson’s sense (Arnold 2014), but this is not required by the definition of ‘clade’. Moreover, Haber and Hamilton (2005) note that clades lack the cohesion-generating relationships (such as interbreeding) that help define at least some species as individuals.

There is also a simple reproductive process issue, encapsulated in the aphorism attributed to Michael Ghiselin by Hamilton and Haber (2006, 382): “Individuals copulate, and species speciate, but genera do not generate”. The means by which multicellular (sexual) individuals reproduce is different than that by which their constituent cells reproduce, and

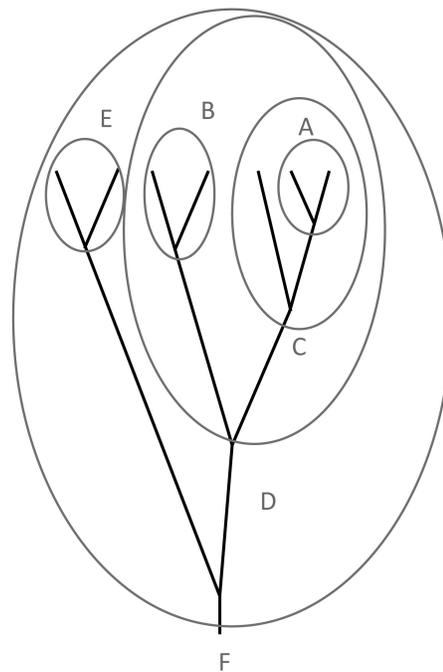


Fig. 1. Clades within clades

Lines represent species. Clades comprise a common ancestral species and all and only its descendant species (as surrounded by ellipses in this figure). Each clade is necessarily *part* (a “subclade”) of a more inclusive clade (as A is part of C, and C part of D in Fig. 1), the subclade/clade distinction being relational. I use “clade” to refer to the most inclusive entity relevant in a specific context. Whether or not clades correspond to recognized supra-specific taxa such as genera or families is irrelevant: the hierarchy shown is rank-free (Okasha 2011). Genes replicate, organisms reproduce and species speciate, but by definition a clade cannot “cladiate” because all included subclades (and *their* subclades and individual species) remain parts of the clade. Clades can however *grow* (by comprising more species) and *die* (by the extinction of all contained species). Growth is one (but not the only) way in which chances of clade survival might be enhanced, but in the view presented here (*contra* Van Valen 1989), is not by itself a measure of a clade’s evolutionary success.

the means by which (sexual) species reproduce (speciate) is different than that by which the individuals making them up reproduce. In contrast, the only way a genus or higher taxon can “give birth” to another of the same rank is as a consequence of the speciation of a constituent species: there is no distinct genus- or higher clade-level reproductive mechanism. Similarly, asexual species (and bacterial clones) have no means of reproduction other than that enjoyed by the individuals (or bacterial cells) that make them up, and thus are incapable of species selection, evolving as do clades, detailed below. (Most theorists of species selection focus on sexually reproducing organisms conforming to the “Biological Species Concept”: few if any discuss asexuals or bacteria.)

Finally, there is an insurmountable logical problem. As Okasha (2003, 740, see also Rieppel 2008)) puts it “Clades do not have what it takes to be units of selection in the first place”. Reproduction of any sort is inconsistent with the very definition of the term! The reasoning here seems ironclad. Since a clade comprises an ancestor and all its descendants, it cannot have descendants that are not part of it (Fig. 1). A clade can *grow* (by having more of its species alive at any one time) and it can *die* (if all its species go extinct). And it can survive variously long, thanks to the survival of one or more of its lineages. But it cannot – by the rules of logic which are at the base of my argument in this essay – reproduce.

Where I differ from Okasha and with the usual representations of ENS, however, is in my claim, fleshed out in the next sections of this essay, that *differential persistence alone can support a process that we cannot dismiss as a form of ENS*, unless we stipulate by fiat that ENS *must* involve reproduction of the selected entities. Many discussions of clade-level evolutionary processes, particularly in the paleontological literature, imply selection, to be sure (McKinney 1997; Finnegan et al. 2012; Longrich et al. 2012). But most fail to offer any sufficiently explicit MLS formulation or to distinguish between species-level and higher-level processes, paying little attention to the problem of non-reproduction of clades more inclusive than species, the problem I focus on here. In this my arguments parallel those of Frédéric Bouchard (2008, 2011, 2014, see also Dussault and Bouchard 2016), whose emphasis has been on the persistence of clonal individuals and ecosystems. And although my thesis might seem to some to depend too much on a mere convention – cladist rules of naming – there are interesting and useful consequences to thinking this way.

5. Why reproduction? That ENS is indeed most often taken to entail some sort of reproduction of the target entities seems unarguable. “How else could such entities exhibit heritability?”, one automatically asks. Even when ENS is cast as “*survival of the fittest*”, survival is useful only because it allows time for reproduction, understood to underwrite selection in one of three ways. First, when resources limit populations, one individual’s having more progeny entails others having fewer. *Reproductive competition* drives selection in this case. Second, even when there is no resource or population size limitation, more fecund variants will (all else being equal) eventually come to dominate. A third way, having little to do with giving favored mutants the numerical edge, is as *replenishment*. It is only (or overwhelmingly most often) through a succession of selections on mutations of small effect that “complex adaptations” might arise and realize natural selection’s full creative potential, according to the Modern Synthesis. So after each step of selection, the favored mutant must proliferate in order to create a population in which the next mutation is likely to occur.

An experimentally tractable analogy that exemplifies such reproduction-as- replenishment is the sequential selection of bacteria resistant to increasingly high levels of an antibiotic (Toprak et al. 2011). Sensitive bacteria die at each step because they are killed by the antibiotic, not because resistant mutants have stolen their resources or crowded them off the Petri plate. There is no reproductive competition, but growth at each higher level of

antibiotic requires a sizeable population of organisms resistant to lower amounts of antibiotic in which subsequent mutations to resistance at higher amounts might occur.

6. A model for CS. Visualizing selection without reproduction – through differential persistence of clades alone – requires some perspectival re-orientation. The entities under selection, though differing in survival potential synchronically (horizontally in Fig.1) are not delimitable diachronically (vertically), and there are no discrete generations as in the microbial example above. The hierarchy of clades is “rank- free” in the sense of Okasha (2011), comprising nested individuals, indefinite in number. Although species reproduce and go extinct, clades (that is, ancestral species together with their descendant species) can only survive (with or without growth) or go extinct. The survival of a single species makes the nested set of clades to which the species belongs a success, as far as persistence goes, but is not necessarily a mark of CS. If survival is due only to “chance” (independent of the properties of surviving species *or* clades) then this is merely species “sorting” (Vrba and Gould 1986). If survival is due solely to individual or species-level properties (organismal tolerance to environmental challenges or broad geographical distribution of the species’ populations, for instance), that would also be non-selective at the clade level. If however it is a *property of the clade* that its species are numerous, widely separated from each other (dispersed) geographically or divergent ecologically (see below), and such a property explains why at least one species survives (why the clade has greater survival potential), then this *is* CS.

Again, bacterial genetics provides a usefully analogous model (Fig. 2): the chemostat. In a continuously operated constant-volume chemostat, the number of cells is kept constant by balancing discharge of culture with input of fresh sterile medium. Assume that at time t_0 there are N cells, each reproducing by fission every m minutes. Because culture discharge randomly and continuously eliminates cells, roughly one-quarter of these N cells will have two daughters remaining in the chemostat at $t_0 + m$ minutes, while half of them will have only one daughter, and one quarter will have none. Lineages derived from original cells will continue to be lost until, at some time in the future, all cells in the chemostat will be descendants of only one of the original N cells, constituting a single *clone*. If mutants arise that more efficiently make use of the chemostat’s resources (and thus leave more than the average of one surviving daughter every m minutes), such mutants will more quickly and more certainly become the exclusive ancestors (founders) of a future population (achieve “fixation”) in the chemostat (Dykhuizen and Hartl 1983).

Although a takeover of the chemostat by more efficient resource utilizers depends on their differential reproduction, it is survival or persistence of the clone founded by the mutation (and thus of the deeper clones in which it is nested) that interests us. Should the chemostat suddenly suffer a loss of almost all of its contents (a “mass extinction”), being present in greater numbers should give our clone an advantage, a greater chance of having some surviving cells.

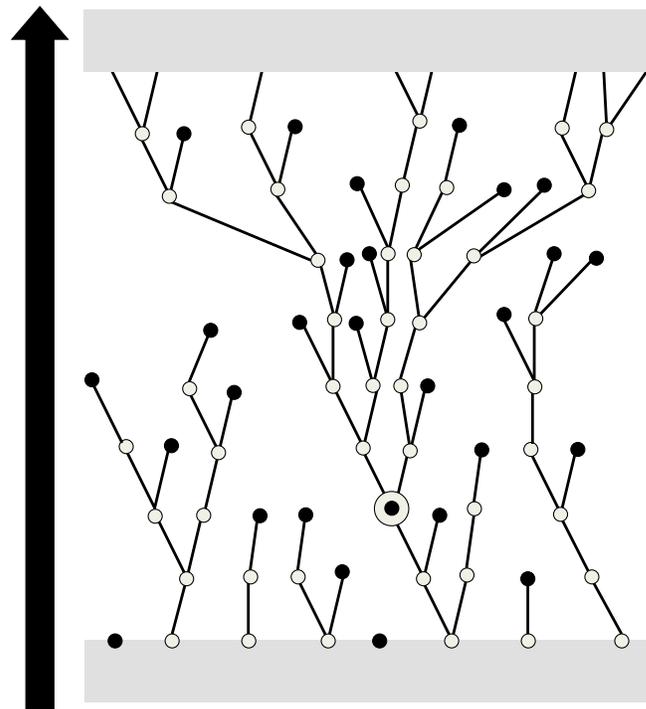


Fig. 2. Differential clone or clade persistence. A model either for a chemostat with a constant population of eight cells, or for clade growth in a similarly limited environment. Circles represent cells or species that can have either two, one or zero progeny cells (surviving chemostat discharge) or species (surviving extinction). Grey circles have one or two surviving progeny, black circles have none. The large double circle is the ancestor of the single lucky clone or clade that persists into the future. If there is no selection, the average time required for all descendents to be part of this single clone or clade is $2N$ “generations”, where N is the number of cells or species in the population (Zhaxybayeva and Gogarten 2004 and citations therein). “Fixation” is faster if there is selection. Vertical arrow is time, gray horizontal bars the past and present.

Another way to increase survival potential would be to diverge ecologically. Chemostats offer two niches, floating free in the middle or clinging to the walls: mutations favoring the latter are selected for because mutants are not washed out in discharges. Clones that more readily spawn lineages diverging ecologically like this, even if less fecund, will persist longer (Dykhuizen and Hartl 1983). Also favoring clone survival could be changes in mutation rates. In laboratory evolution experiments “mutator” alleles can be selected as “hitchhikers” on the favorable mutations they have fostered (Elena and Lenski 2003; Notley-McRobb and Ferenci 2000).

In the analogy I want to draw, bacterial cells in a chemostat correspond to species and clones correspond to (indeed *are*) clades. Clones can grow (through the reproduction of

the cells that are their parts) or die (through death of all cells), but they cannot reproduce. If, analogously, the biosphere is constrained in the number of species it can hold – if speciation and extinction are in even a rough balance – and if there are no differences in survival chances among species, the biosphere will of necessity eventually come to hold a single clade, corresponding to the single clone in the chemostat model. Indeed, this will eventually happen even in a continually expanding biosphere, as long as there is *some* extinction. And of course there *will* be differences in survival potentials because of intrinsic clade-level properties, hastening such a result.

7. Objections to the theory. Several objections can be raised against any claim that ENS can occur *via* differential clade persistence. Here I hope to counter five obvious ones.

7.1. First objection: Clades are not easily compared and relevant causal properties are hard to establish. The rank-free nature of clade hierarchies (Okasha 2011) and the asynchrony of speciation events make enumerations and comparisons problematic. In Fig. 1, for instance, is it the relative survival potential of B *versus* A or rather B *versus* C that selection addresses? Contemporaneity of clade ancestors might be a relevant parameter but hard to establish, and assessments of the relative abundances of species within clades will be dependent on contestable definitions of ‘species’ (Rabosky 2015). Genus-to-genus or phylum to phylum comparisons are even harder to defend. Moreover, “survival to our particular year or moment has no privileged ontological status (Van Valen 1994, 202).”

Biological causal properties will also be complex, theory-dependent and unverifiable, with forces leading to extinction often outside the apparent purview of selection (Leroi 2000). It is nevertheless nonsensical to assert that the biological features of clades have *no* influence on the relative likelihoods of persistence, and are not selected at the clade level. Clades are not arbitrary groupings, like the 26 “higher taxa” one could assemble by alphabetical ordering of species names. These too might be differently represented among extinct and surviving species, but not for biological reasons. That we do not know and may never be certain about causes does not mean that there are not causes, or that there is nothing to be gained by attempting to identify them.

7.2. Second objection: There are no clade-specific properties. In *The Structure of Evolutionary Theory*, Stephen Jay Gould writes:

I am not comfortable with this general argument, for no one has yet articulated firm and operational criteria for distinguishing true clade selection (based on irreducible fitness conferred by a clade-level property) from descriptive clade sorting (or differential survival) as an effect of lower-level properties belonging to species or organisms, but translating upwards to success or failure of a clade as a geologically persistent entity (Gould 2002, 713).

For sure, the persistence of a clade only because it possesses highly persistent species would not count as selection at the clade level. The size and habits of mammals might

have spared them the fate of the dinosaurs with selection only at the level of species and their individuals. No “emergent” or clades-level specific properties need necessarily be invoked. However, there *are* in fact “firm and operational” – *bona fide* emergent– clade-level properties, dependent on lower level properties only in the same sense that molecules depend on atoms, animals on their constituent cells, or species on individual organisms (see Okasha 2014). And these clade-level properties cannot but have consequences for clade persistence. In particular, clades with (1) more species, (2) species that are more widely dispersed geographically, or (3) species that are more divergent (different) ecologically are, *all else being equal*, unarguably more likely because of such properties to survive challenges that are, respectively (1) random, (2) geographically localized or (3) restricted in their environmental or biotic effects. One might break each of these three compositional properties down into subcategories to make the list seem richer: there are very many ways to generate ecological divergence for instance. But equally one might lump the myriad of organism-level properties normally considered selectable into a few, homeostasis, fecundity and robustness for instance.

Clades are indeed variously speciose (so very many beetles), dispersed (there are no marsupials in Europe) and divergent (many types of arthropods, few of tardigrades, though the latter are of equal or higher taxonomic rank) and must, *all else being equal*, variously survive because of this. Paleontologists commonly correlate clade persistence with such properties, and new methods for making causal inferences are under development (Mayhew 2007; Rabosky and McCune 2009; Wagner and Estabrook 2014; Hoehn et al. 2016). In an exemplary early study, Jablonski distinguished two sorts of extinctions in marine bivalves and gastropods, concluding that ...

During background times, traits such as planktotrophic larval development, broad geographic range of constituent species, and high species richness enhanced survivorship of species and genera. In contrast, during the end-Cretaceous and other mass extinctions these factors were ineffectual, but broad geographic deployment of an entire lineage, regardless of the ranges of its constituent species, enhanced survivorship (Jablonski 1986, 129).

Although such clade-level features do derive from properties that “translate upwards” from selection or drift at the levels of genes, cells, organisms and species, they are *not the same* as those properties and the functions for which such properties are selected at species and clade levels are different. Species selection for trait *t* might both relatively and absolutely increase the number of species with *t*. If but only if the latter happens, CS for species richness could then help explain why persistent clades are so frequently made up of species with *t* – connected but distinct explanans. Alternatively, a persistent clade might preferentially comprise species that are especially “evolvable”, but it is the resulting realized ecological disparity between the species, not the mechanisms diversifying them, that is the clade-level selected property. When a clade’s demise is attributable to its species collectively being too few, too geographically close or too ecologically similar, these are clade-level deficiencies. The shared traits that are too similar are organism-level or species-level properties: *that* they are too similar is the clade-level property.

This disconnection is a sort of “screening off,” given that clade persistence attributable to species richness, dispersal or divergence does not depend on how those properties are determined and that the determining lower-level processes are not foolproof (Sober 1992). Of course, selection on lower and clade-level properties can be fortuitously aligned, analogously to positive effect macroevolution for species. Uniquely, however, since clades are neither collective replicators nor interactors, there is no necessary “downward causation”. Species selection might be said to downwardly cause (in the sense that they would otherwise be absent) the presence of genes regulating sexual activity in sexually reproducing species. Sexually reproducing organisms necessarily need conspecific mates. But a beetle species does not similarly need any of the other 380,000 species in the clade Coleoptera; Smith and Marcot 2015). The causal arrow goes only one way. CS is thus a sort of limited positive “effect macroevolution” for non-reproducing entities.

What might over-ride this limitation, making for a fourth clade-level selectable property with potential downward causation, would be intraclade cooperation. Competitive exclusion (Hardin 1960) notwithstanding, there are evolved syntrophies and symbioses among species in many clades. Indeed, the recently articulated Black Queen Hypothesis makes it seem inevitable that this will happen in certain environments (Morris et al. 2012; Fullmer et al. 2015). Moreover, some clade-wide processes might be seen as collaborative strategies. Lateral gene transfer (LGT) for instance arguably increases the survival potential of strains within bacterial species, by establishing a “pangenome” of genes that can be drawn on as needed – what McNerney et al. (2011) call “the Public Goods Hypothesis”. Genes can in fact be shared between disparate species in the clade Bacteria (and with their archaeal sisters). Agents of gene transfer may well be “selfish” in origin, but that Bacteria have survived several billions of year on this planet is to some extent attributable to sharing genes and maintaining a library of shareable genes (the global pangenome). Since gene sharing requires commonalities of genetic systems (a universal genetic code, for instance) the presence of such features in most contemporary genomes might be seen to reflect downward causation at the time of LUCA. Vetsigian et al. (2006) have advanced something like this argument with respect to the code, as have Jankovic and Cirkovic (2016) in an even broader theory about the genetic apparatus in general.

The biggest clade of all, “Life”, comprising LUCA and all its descendants, might be thought of as an individual in the sense that species are (Ghiselin 1974; Hull 1976), only older and much more loosely held together. The claim made here that clade-level properties – especially possible intraclade cooperation – are targeted by selection opens the door to claims that Life as an individual has adaptations, and thus to a naturalized version of the Gaia hypothesis (Doolittle 2014). One objection to Gaia has been that selection requires more than a single selected entity, especially if it is to accrue complex adaptations. Clade selection seems to get around this objection (next section). Furthermore, no theory of the origin of Life holds that LUCA was alone on the Earth, that there were not competing cells, species and thus whole clades that have left no surviving cellular lineages. So Life had its competitors: it just drove them all to extinction – it is the last clade standing.

7.3. Third objection: CS is not cumulative and thus not “interesting”.

Prominent philosophers of biology are not so much opposed to the notion of selection on survival alone as to the possibility that it plays a significant creative role in ENS. Okasha notes that defenders of clade selection ...

... concede that clades do not reproduce, but argue that differential extinction of clades might still occur. This is true enough. However, selection on entities that do not reproduce their kind is *not very interesting*, and *will not lead to adaptation* (Okasha 2006, 214, emphasis mine).

Okasha’s skepticism is based in large part on the non-reproduction of clades, as would be that of Peter Godfrey-Smith, who muses that ...

When we consider elements of the tree of life even larger than species, the idea of reproduction becomes even more tenuous, however. I see the logical difficulties that Okasha cites as a symptom, rather than the core, of the problem. There are probably ways of re-defining “clade” so that the idea of clade reproduction is at least coherent (Haber and Hamilton 2005), but it will be a very marginal kind of reproduction indeed. And clades might be differentially eliminated, but that is not enough for a significant Darwinian process (Godfrey-Smith 2009, 105).

A requirement for reproduction as replenishment is for Godfrey-Smith a general feature of ENS. He writes in a broader context that ...

In both biology and culture, successive rounds of undirected variation can yield significant design improvements, *provided that the successful variants in one generation proliferate* and provide many independent platforms at which further innovation can occur (Godfrey-Smith 2012, 2166, emphasis mine).

Similarly, Richard Dawkins describes as “one-off” selection the way that pebbles on a seashore are size-sorted by waves and contrasts it with biological evolution.

Complex adaptation requires many generations of cumulative selection, each generation’s change building on what has gone before. In one-off selection, a stable state develops and then is maintained. It does not multiply, does not have offspring. (Dawkins 2010, 370).

At first blush, selection without reproduction would indeed seem to be limited to the type of one-off selection Dawkins here dismisses. In this view, it might at best be like selection on crystal formation: crystal peculiarities can be passed on and may affect crystallization itself, but no one expects crystals to go on and acquire wings or spoken language (Bedau 1991).

However, though clades by definition lack offspring clades, they are not in fact bereft of “independent platforms at which further innovation can occur“ (to use Godfrey-Smith’s

language). Again a bacterial chemostat analogy may aid understanding (Fig. 3). Suppose a favorable mutation is approaching clonal fixation in an episode of “periodic selection” (Notley-McRobb and Ferenci 2000). As this proceeds, a secondary mutation that further enhances the reproductive advantage conferred by the first occurs, and a doubly mutant sub-subclone (black in Fig. 3) emerges within the spreading singly mutant (darkest gray) subclone. A multi-step “complex” adaptive process has begun, multiply ensuring the survival of the original clone (in an “improved” and further “improveable” form). Reproduction is involved here, but of cells not subclones, which instead decrease in number while growing in size and increasing in persistence. Similar models have been

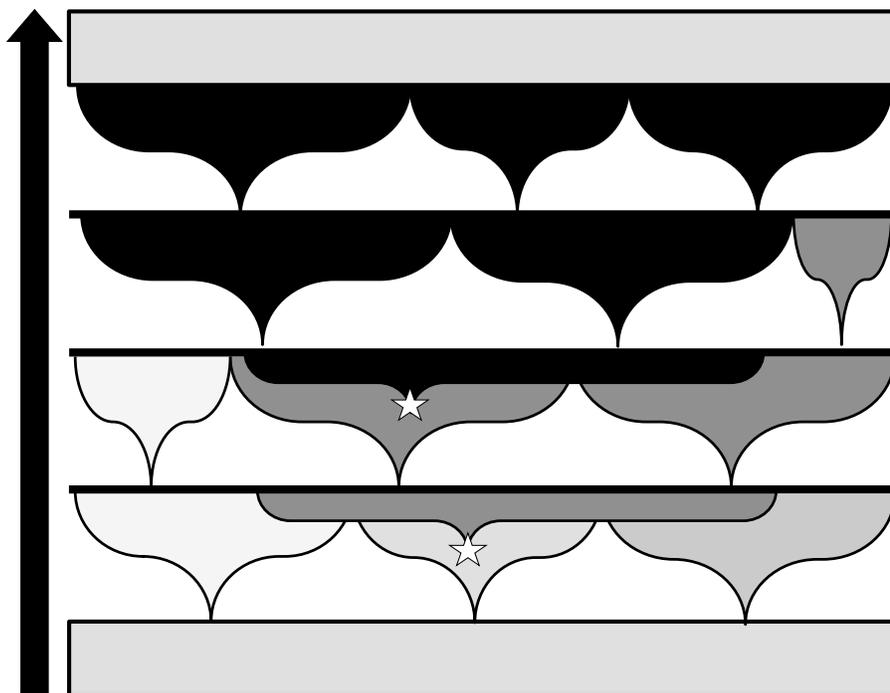


Fig. 3. Cumulative chemostat selection. Arrow, gray bars, as in Fig. 2. Black lines indicate flushings of the chemostat eliminating all but three randomly recovered cells. Stars indicate mutations to more efficient substrate use, selected for among cells. But, importantly, an efficient utilizer has no advantage over a less efficient sister in the random recovery process: there is at the clone level no selection based on efficiency, only on cell number whatever its cause. This model is directly relevant to the claim that clades (the analog of clones) with more species (the analog of cells) are more likely to survive extinctions that are “random” (independent of biology). The claim that clades whose species are more geographically dispersed or ecologically divergent are similarly favored by selection for persistence requires more complex microbial models.

proposed by the philosopher Frédéric Bouchard for the evolution through persistence of non-reproducing clonal biological individuals (Bouchard 2008, 2011, 2014) but his emphasis is on clonal individuals like aspen groves or communities as biological organisms and mine is on understanding clades above species as entities under selection within a MLS framework.

Analogously, within a growing clade each subclade and species lineage is potentially a platform for further innovation. When selective processes at the species level or below are more likely than not to enhance by “upward causation” species richness, dispersal or divergence, subclades bearing further innovations will assume dominance, and such innovations will be cumulatively encoded and more-or-less reliably passed on in the genomes of the responsible lineages. It is of course the heritability of traits in its reproducing parts that confers a heritability-like continuity of properties upon a clade.

All else being equal we do expect such a cumulative process to obtain much of the time. Species selection generally favors species richness and, through avoidance of local extinctions, geographic dispersal of species populations, which may subsequently speciate and diverge (Stanley 1979). Specific physical or behavioral traits that coincidentally increase species number, population dispersal and divergence are selectable within species. Species richness, dispersal and divergence are the indirect outcomes, selectable as traits at the clade level. Proposals that “evolvability has evolved” (increased) over time are credible if hard to prove, and often imply cumulative clade selection (Wagner and Altenberg 1996; Kirschner and Gerhart 1998; Pepper 2003; Pigliucci 2008b, Watson and Szathmari 2016). And the “Zero Force Evolutionary Law” (ZFEL; McShea and Brandon 2010) promises that even in the absence of any selection, organismal and higher-level complexity and divergence will inevitably increase with time within a clade. Older subclades not surprisingly have an advantage over younger, and, since Life is thought to have diverged from LUCA more than 3.5 billion years ago, ZFEL alone could make this biosphere more persistent than one on a younger planet.

A similar view to mine on cumulative clade selection has been endorsed by Kim Sterelny, who writes ...

Suppose a lineage survived an extinction event (meteor strike, climate change) because it happened to be a little more widespread, through range and niche, than its rivals. It then, as a result of the extinction event, has the chance to move into vacated range and niche, and hence is somewhat more widespread yet. The next extinction event it therefore survives, and the process repeats. *Now is that not honing by cumulative selection?* (Sterelny 2001, 142, emphasis mine).

7.4. Fourth objection: CS collapses into species selection. Superficially, what is proposed here resembles a re-formulation of ENS that Okasha (2003) entertains only to reject. He writes ...

Consider the clades marked A and B ... [comparable to the surviving and extinct clades in my Fig. 2], each containing two extant species. If clade A is fitter than clade B, according to the suggested re-definition, this means that A has a greater probability of becoming bushier in the future, i.e. coming to contain more subclades as parts. But cladogenesis only occurs when species lineages split, so this means that the species in A must have a greater probability of speciating than the species in B. (For example, perhaps the species in A are more ecologically specialised, which tends to promote speciation.) This means that clade selection, in the suggested sense, is entirely redundant: species selection can do all the work. Clade A has a higher probability of becoming bushy, but this is because the species in clade A have a higher species fitness (i.e. a higher probability of leaving offspring species) than those in clade B. Defining clade fitness as ‘probability of becoming bushy,’ and then invoking a process of clade selection is therefore pointless (Okasha (2003, 747).

But clade fitness in fact should *not* be re-defined as ‘probability of becoming bushy’. In Okasha’s scenario, species fitness becomes the ‘probability of becoming bushy’ due to something like species selection for specialization: there is a physical or behavioral trait that is selected for, in consequence of which there are more species with that trait and, quite possibly although not necessarily, more species overall. Clade fitness on the other hand depends on the actuality of being bushy, of a clade’s already having many species. What selection sees at the species level (specialization) is not what it sees at the clade level (bushiness itself). Mechanistically they are uncoupled (“screened off”), and we should not conflate a trait that is selected for with the outcome of that selection at an adjacent hierarchical level. A good analogy, one level down the hierarchy, may be floral symmetry, which Rabosky and McCune (2010) infer to be selected for within species because it reduces waste by pollinators but also between species (increasing speciation) because it increases the specificity of these pollinators. They write ...

Selection at the individual level contributes to trait variation between species by transforming intraspecific variation into species differences that might result in species selection. However, the mechanism by which a trait becomes fixed within a species, whether through selection or drift, need not be the same as the mechanism by which the trait influences diversification (Rabosky and McCune 2010, 70).

Admittedly, even in CS as here conceived, evolutionary success entails an increase in the *relative* number of selected-for entities. But a relative increase can occur either through differential reproduction *or* differential persistence, the latter entailing *dwindling* populations (Doolittle 2014). In the case of clade selection, dwindling is the only option – all Life becomes a single clade.

Recently, Doolittle (2014) suggested that planetary biospheres (ours in particular) can be said to evolve through differential persistence, those with adaptations for survival making up a larger and larger fraction of a population of biospheres that diminishes over time. Critics might be troubled not only by this dwindling but by the implied existence of a large number of undetected alien biospheres, mostly failed. However, in an interesting elaboration of a similar line of thought, Chopra and Lineweaver (2016) have just this year proposed that the fact that we only know one kind of life (Life) is not due to life's failure to start on other planets but to its failure (elsewhere than here) to persist through a "Gaian bottleneck" requiring evolution of intraclade cooperation of the sort mooted above.

In any case, what recasting Doolittle's (2014) argument as CS does is make such speculation unnecessary. Selection for persistence indeed entails dwindling in the number of entities under selection, but this does not hinder further innovation, as detailed above. As time advances, in either the chemostat or the world depicted in Figs. 2 and 3, there will be fewer and fewer surviving maximally inclusive clades – ultimately there will be only one. But new subclades and species that are part of this expanding and ultimately-to-be victorious clade are continuously generated and can compete with each other at all levels of inclusiveness. So as the number of maximally inclusive clades decreases, the number of species lineages in which clade-preserving innovations can occur increases. Clade growth is a fire that never consumes its fuel.

7.5 Fifth objection: CS produces adaptedness but not adaptation. Another sense in which CS might be thought "uninteresting" is this. Even though clade-specific properties of species richness, dispersal and divergence may be very complexly instantiated in the biological and ecological characteristics of constituent species, such complexity is generated by lower level selection processes. All CS does, in effect, is "rubber stamp" the results, increasing the probability of persistence of clades. It maintains at the level of clades that which originates at the level of species.

Since "adaptation" as a claim about the history of a trait and "adaptedness" as a measure of the suitability of an entity's properties to the situation in which it finds itself are so often defined in terms of realized or potential differential reproduction (Amundson 1996, Forber 2013) it is unclear how to apply them to non-reproducing entities. Re-defining 'adaptation' for clades as an *increase over time in the propensity to survive, in consequence of selection on the biological and ecological characteristics of constituent species*, seems arguably appropriate.

Generalizing this, we would hold that a trait is an *adaptation* for any entity just in case that entity has proportionately higher numerical representation among entities of its type because of its prior possession of the trait, and that such higher representation can be achieved either by differential reproduction (as normally contemplated) *or by differential persistence*. In CS (as in Fig. 2 and 3) clades achieve proportionately higher numerical representation because the denominator in the ratio [selected clades]/[total clades] (Fig. 2) decreases rather than because the numerator increases. Whether or not a clade as large and as old as Life has adaptations for persistence, as in the popular "Gaia hypothesis"

(Doolittle 2014) then become a matter for empirical rather than philosophical investigation (Tyrrell 2013).

8. Summing up. What good, then, is CS? First, it makes a particular kind of biological sense of questions like “Why are there so many species of beetles?” or “Why did the dinosaurs go extinct?”. These are similar to questions David Raup asks about the extinct class Trilobita in his popular *Extinction: Bad Genes or Bad Luck?* “...

Did the trilobites do something wrong? Were they fundamentally inferior organisms? Were they stupid? Or did they just have the bad luck to be in the wrong place at the wrong time? (Raup 1991, 5).

But they are not exactly the same sorts of questions, insofar as each trilobite species might have independently succumbed because of its bad genes or bad placement. If *all* had the same bad genes (lack of clade divergence) or all happened to be living in the *same* wrong place (lack of dispersal) then CS would provide a useful additional explanatory framework. If extinction of clades is the explanandum, then it seems important to make such a distinction in explanans. “Why did Trilobita go extinct?” is not the same question as “Why did trilobites go extinct?”.

Second, although fueled by reproduction of its parts (species, and their parts, organisms), the persistence of a clade and its subclades fits poorly into popular formulations equating ENS with heritable variation in fitness, at least as these are implemented in population genetic models of the Modern Synthesis. To the extent that clades are expected to become more persistent with time as a result of ZFEL and/or of lower-level selection as in 7.3, CS could expand ENS beyond the existing frameworks of discrete entities with definable reproductive processes (Godfrey-Smith 2009). We could include a range of phenomena conforming to our intuitions about the second way to create something useful, but involving gradual “improvement” over time in single entities. One of these phenomena may be learning. Watson and Szathmari suggest that evolutionary and learning theories might be mutually informative, writing that ...

Learning and evolution share common underlying principles both conceptually and formally ... This provides access to well-developed theoretical tools that have not been fully exploited in evolutionary theory (and conversely suggests opportunities for evolutionary theory to expand cognitive science). Learning theory is not just a different way of describing what we already knew about evolution. It expands what we think evolution is capable of. In particular, it shows that via the incremental evolution of developmental, ecological, or reproductive organisations natural selection is sufficient to produce significant features of intelligent problem solving (Watson and Szathmari 2016, 155).

Third, if acceptance of CS leads to liberation of the concept of adaptation from even the most nuanced definitions of reproduction (Godfrey-Smith 2015), then what Maynard

Smith considered the “main task of any evolutionary theory ... to explain *adaptive complexity*, [that is] the same set of facts which Paley used as evidence for a Creator” would be usefully broadened. In particular the question of whether or not our biosphere has evolved homeostatic mechanisms (Doolittle 2014) could be properly phrased in evolutionary terms, and brought in out of the cold of anthropic and theological speculation.

References

- Amundson, Ron. 1996. “Historical Development of the Concept of Adaptation.” In *Adaptation*, ed. Michael R. Rose and George V. Lauder, 11-53. San Diego: Academic Press.
- Arnold, Anthony J., and Kurt Fristrup. 1982. “The Theory of Evolution by Natural Selection: A Hierarchical Expansion.” *Paleobiology* 8: 113-129.
- Arnold Stevan J, 2014. “Phenotypic evolution: the ongoing synthesis” *The American Naturalist* 183(6): 729-746
- Bedau, Mark. 1991. “Can Biological Teleology be Naturalized?” *Journal of Philosophy* 88(11): 647-655.
- Bouchard, Frederic. 2008. “Causal Processes, Fitness and the Differential Persistence of Lineages.” *Philosophy of Science* 75: 560-570.
- Bouchard, Frederic. 2011. “Darwinism Without Populations: A More Inclusive Understanding of the “Survival of the Fittest”.” *Studies in History and Philosophy of Biological and Biomedical Sciences* 42: 106-114.
- Bouchard, Frederic. 2014. “Ecosystem Evolution is about Variation and Persistence, not Populations and Reproduction.” *Biological Theory* 9: 382-391.
- Chopra, Aditya and Charles H. Lineweaver. 2016. “The Case for a Gaian Bottleneck: The Biology of Habitability.” *Astrobiology* 16: 7-22.
- Damuth, John. 1985. “Selection Among “Species”: A Formulation in Terms of Natural Functional Units.” *Evolution* 39: 1132-1146.
- Damuth, John, and Lorraine Heisler. 1988. “Alternative Formulations of Multilevel Selection.” *Biology and Philosophy* 3: 407-430.
- Dawkins, Richard. 1976. *The Selfish Gene*. Oxford: Oxford University Press.
- Dawkins, Richard. 2010. “Universal Darwinism.” In *The Nature of Life*, ed. M.A. Bedau and C.E. Cleland, 360-373. Cambridge: Cambridge University Press.

Depew, David J., and Bruce H. Weber. 2011. "The Fate of Darwinism: Evolution After the Modern Synthesis." *Biological Theory* 6: 89-102.

Doolittle, W. Ford. 2014. "Natural Selection for Survival Alone, and the Possibility of Gaia." *Biology and Philosophy* 29: 415-423.

Dussault, Antoine C., and Frédéric Bouchard. 2016. A persistence enhancing propensity account of ecological function to explain ecosystem evolution. *Synthese* DOI: 10.1007/s11229-016-1065-5.

Dykhuizen, Daniel E., and Daniel L. Hartl. 1983. "Selection in Chemostats." *Microbiological Reviews* 47: 150-168.

Elena, Santiago F., and Richard E. Lenski. 2003. "Evolution Experiments with Microorganisms: The Dynamics and Genetic Basis of Adaptation." *Nature Reviews Genetics* 4: 457-469.

Finnegan, Seth, Noel A. Heim, Shanan E. Peters, and Woodward W. Fischer. 2012. "Climate Change and the Selective Signature of the Late Ordovician Mass Extinction." *Proceedings of the National Academy of Sciences USA* 109: 6829-6834.

Forber, Patrick. 2013. "Debating the Power and Scope of Natural Selection." In *The Philosophy of Biology: a Companion for Educators*, ed. K. Kampourakis, 145-160. Berlin: Springer Science.

Fullmer, Matthew S., Shannon M. Soucy and J. Peter Gogarten. 2015. The Pan-genome as a Shared Genomic Resource: Mutual Cheating, Cooperation and the Black Queen Hypothesis. *Frontiers in Microbiology* 6: 278.

Ghiselin, Michael. 1974. "A Radical Solution to the Species Problem." *Systematic Biology* 23: 536-544.

Godfrey-Smith, Peter. 2009. *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.

Godfrey-Smith, Peter. 2012. "Darwinism and Cultural Change." *Philosophical Transactions of the Royal Society B* 367: 2160-2170.

Godfrey-Smith, Peter. 2015. *Philosophy of Biology*. Princeton: Princeton University Press.

Gould, Stephen J. 1983. "The Hardening of the Modern Synthesis." In *Dimensions of Darwinism*, ed. M. Grene, 71-93. Cambridge: Cambridge University Press.

Gould, Stephen J., and Elizabeth A. Lloyd. 1999. "Individuality and Adaptation Across Levels of Selection: How Shall We Name and Generalize the Unit of Darwinism?" *Proceedings of the National Academy of Sciences USA* 96(21): 1190-11909.

Gould, Stephen J. 2002. *The Structure of Evolutionary Theory*. Cambridge, MA: Harvard University Press.

Grantham, Todd A. 1995. "Hierarchical Approaches to Macroevolution: Recent Work on Species Selection and the "Effect Hypothesis." *Annual Review of Ecology and Systematics* 26: 301-321.

Haber, Matthew H., and Andrew Hamilton. 2005. "Coherence, Consistency, and Cohesion: Clade Selection in Okasha and Beyond." *Philosophy of Science* 72: 1026-1040.

Hamilton, Andrew, and Matthew H. Haber. 2006. "Clades are Reproducers." *Biological Theory* 1: 381-391.

Hardin, Garrett. 1960. "The Competitive Exclusion Principle." *Science* 131(3409): 1292-1297.

Hoehn, Kenneth B., Paul G. Harnik, and V. Louise Roth. 2016. "A Framework for Detecting Natural Selection on Traits Above the Species Level." *Methods in Ecology and Evolution* 7: 331-339.

Hull, David L. 1976. "Are Species Really Individuals?" *Systematic Biology* 25: 174-191.

Hull, David L. 1980. "Individuality and Selection." *Annual Review of Ecology and Systematics* 11: 311-332.

Hunt, Gene, Melanie J. Hopkins, and Scott Lidgard. 2015. "Simple Versus Complex Models of Trait Evolution and Stasis as a Response to Environmental Change." *Proceedings of the National Academy of Sciences USA* 112(16): 4885-4890.

Jablonski, David. 1986. "Background and Mass Extinctions: The Alternation of Macroevolutionary Regimes." *Science* 231: 129-133.

Jablonski, David. 2001. "Lessons From the Past: Evolutionary Impacts of Mass Extinctions." *Proceedings of the National Academy of Sciences USA* 98: 5393-5398.

Jablonski, David. 2007. "Scale and Hierarchy in Macroevolution." *Paleontology* 50: 87-109.

Jablonski, David. 2008. "Species Selection: Theory and Data." *Annual Review of Ecology, Evolution, and Systematics* 39: 501-524.

Jankovic, Srdja, and Milan M. Cirkovic. 2016. "Evolvability is Evolved Ability: The Coding Concept as the Arch-Unit of Natural Selection." *Origins of Life and Evolution of Biospheres* 46: 67-79.

Kirschner, Marc, and John Gerhart. 1998. "Evolvability." *Proceedings of the National Academy of Sciences USA* 95: 8420-8427.

Leroi, Armand M. 2000. "The Scale Independence of Evolution." *Evolution and Development* 2: 67-77.

Lewontin, Richard C. 1970. "The Units of Selection." *Annual Review of Ecology and Systematics* 1: 1-18.

Lieberman, Bruce S., and Elisabeth S. Vrba. 2005. "Stephen Jay in Species Selection: 30 Years of Insight." *Paleobiology* 31(2): 113-121.

Longrich, Nichola R., Bhart-Anjan S. Bhullar, and Jacques A. Gauthier. 2012. "Mass Extinction of Lizards and Snakes at the Cretaceous-Paleogene Boundary." *Proceedings of the National Academy of Sciences USA* 109: 21396-21401.

Mayhew, Peter J. 2007. "Why Are There So Many Insect Species? Perspectives From Fossils and Phylogenies." *Biological Reviews* 82(3): 425-454.

Maynard Smith, John. 1969. "The Status of 'Neo-Darwinism'." In *Towards a Theoretical Biology*, ed. C.H. Waddington, 82-90. Edinburgh: Edinburgh University Press.

Maynard Smith, John. 1988. *Did Darwin Get it Right?* Chapman and Hall.

Maynard Smith, John, and Eors Szathmary. 1995. *The Major Transitions in Evolution*. Oxford: Oxford University Press.

McInerney, James O., Davide Pisani, Eric Baptiste, and Mary J. O'Connell. 2011. "The Public Goods Hypothesis for the Evolution of Life on Earth." *Biology Direct* 6: 41.

McKinney, Michael L. 1997. "Extinction Vulnerability and Selectivity: Combining Ecological and Paleontological View." *Annual Review of Ecology and Systematics* 28: 495-516.

McShea, Daniel W., and Robert N. Brandon. 2010. *Biology's First Law*. Chicago: University of Chicago Press.

Morris JJ, Lenski R, Zinser ER. (2012) The Black Queen hypothesis: evolution of dependencies through adaptive gene loss. *MBio* 3: e00036-12.

Notley-McRobb, Lucinda, and Tom Ferenci. 2000. "Experimental Analysis of Molecular Events During Mutational Periodic Selections in Bacterial Evolution." *Genetics* 156: 1493-1501.

- Okasha, Samir. 2001. "Why Won't the Group Selection Controversy Go Away?" *British Journal for the Philosophy of Science* 52: 25-50.
- Okasha, Samir. 2003. "Does the Concept of "Clade Selection" Make Sense?" *Philosophy of Science* 70: 739-751.
- Okasha, Samir. 2005. "Multilevel selection and the major transitions in evolution." *Philosophy of Science* 72(5): 1013-1025.
- Okasha, Samir. 2006. *Evolution and the Levels of Selection*. Oxford: Oxford University Press.
- Okasha, Samir. 2011. "Biological Ontology and Hierarchical Organization: A Defense of Rank Freedom." In *The Major Transitions in Evolution Revisited*, ed. B. Calcott and K. Sterelny, 53-64. Cambridge, MA: MIT Press.
- Okasha, Samir. 2014. "Emergent Group Traits, Reproduction, and Levels of Selection (open peer commentary on Smaldino PE, 2014. The cultural evolution of emergent-level traits)." *Behavioral and Brain Sciences* 37: 243-295.
- Pepper, John W. 2003. "The Evolution of Evolvability in Genetic Linkage Patterns." *Biosystems* 69: 115-126.
- Pigliucci, Massimo. 2008a. "The Proper Role of Population Genetics in Modern Evolutionary Theory." *Biological Theory* 3(4): 316-324.
- Pigliucci, Massimo. 2008b. "Is Evolvability Evolvable?" *Nature Reviews Genetics* 9: 75-82.
- Rabosky, Daniel L. 2015. "Reproductive Isolation and the Causes of Speciation Rate Variation in Nature." *Biological Journal of the Linnean Society* (Dec. 2015, online early, DOI: 10.1111/bij.12703).
- Rabosky, Daniel L., and Amy R. McCune. 2009. "Reinventing Species Selection With Molecular Phylogenies." *Trends in Ecology and Evolution* 25: 68-74.
- Rao, Veena, and Vidyanand Nanjundiah. 2011. "J.B.S. Haldane, Ernst Mayr and the Beanbag Genetics Dispute." *Journal of the History of Biology* 44: 233-281.
- Raup, David M. 1991. *Extinction: Bad Genes or Bad Luck?* New York: Norton.
- Rieppel, Olivier. 2008. "Do Clades Cladogenerate?" *Biological Theory* 3: 375-379.
- Smith, Dena M., and Jonathan D. Marcot. 2015. "The Fossil Record and Macroevolutionary History of the Beetles." *Proceedings of the Royal Society of London B* 282: 2015060.

Smocovitis, Vassiliki B. 1992. "Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology." *Journal of the History of Biology* 25: 1-65.

Sober, Elliott. 1992. "Screening-off and the Units of Selection." *Philosophy of Science* 59: 142-152.

Stanley, Steven M. 1979. *Macroevolution: Pattern and Process*. W.H. Freeman.

Sterelny, Kim. 2001. *The Evolution of Agency and Other Essays*. Cambridge: Cambridge University Press.

Toprak, Erdal, Adrian Veres, Jean-Baptiste Michel, Remy Chait, Daniel L. Hartl, and Roy Kishony. 2011. "Evolutionary Paths to Antibiotic Resistance under Dynamically Sustained Drug Stress." *Nature Genetics* 44: 101-105.

Tyrrell, Toby. 2013. *On Gaia: A Critical Investigation of the Relationship Between Life and Earth*. Princeton: Princeton University Press.

Van Valen, Leigh. 1989. "Three paradigms of evolution." *Evolutionary Theory* 9: 1-17.

Van Valen, Leigh. 1994. "Concepts and the Nature of Selection by Extinction: Is Generalization Possible?" In *The Mass Extinction Debates: How Science Works in a Crisis*, ed. W. Glen, 200-216. Stanford: Stanford University Press.

Vetsigian, Kalin, Carl Woese, and Nigel Goldenfeld. 2006. "Collective Evolution and the Genetic Code." *Proceedings of the National Academy of Sciences USA* 103(28): 10696-10701.

Vrba, Elisabeth S. 1983. "Macroevolutionary Trends: New Perspectives on the Roles of Adaptation and Incidental Effect." *Science* 221: 387-389.

Vrba, Elisabeth S., and Niles Eldredge. 1984. "Individuals, Hierarchies and Processes: Towards a More Complete Evolutionary Theory." *Paleobiology* 10: 146-171.

Vrba, Elisabeth S., and Stephen J. Gould. 1986. "The Hierarchical Expansion of Sorting and Selection: Sorting and Selection Cannot be Equated." *Paleobiology* 12: 217-228.

Wagner, Gunter P., and Lee Altenberg. 1996. "Complex Adaptations and the Evolution of Evolvability." *Evolution* 50: 967-976.

Wagner, Peter J., and George F. Estabrook. 2014. "Trait-based Diversification Shifts Reflect Differential Extinction Among Fossil Taxa." *Proceedings of the National Academy of Sciences USA* 111: 16419-16424.

Watson, Richard A., and Eors Szathmary. 2016. "How Can Evolution Learn?" *Trends in Ecology and Evolution* 31: 147-157.

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Williams, George C. 1966. *Adaptation and Natural Selection*. Princeton: Princeton University Press.

Zhaxybayeva, Olga, and J. Peter Gogarten. 2004. "Cladogenesis, Coalescence and the Evolution of the Three Domains of Life". *Trends in Genetics* 20: 182-187.