

Does the Concept of “Clade Selection” Make Sense?*

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The idea that clades might be units of selection, defended by a number of biologists and philosophers of biology, is critically examined. I argue that only entities which reproduce, i.e. leave offspring, can be units of selection, and that a necessary condition of reproduction is that the offspring entity be able, in principle, to outlive its parental entity. Given that clades are monophyletic by definition, it follows that clades do not reproduce, so it makes no sense to talk about a clade's fitness, so clade selection is impossible. Three possible responses to this argument are examined and found wanting.

1. Introduction. This paper critically examines the idea of *clade selection*, defended by a number of recent authors including G.C. Williams (1992), Sterelny (1996), Stearns (1986), Gould (2001, 2002), Nunney (1999), Gardezi and de Silva (1999), Hurst and McVean (1996), Vermeij (1996) and others. By a clade I mean a monophyletic group of species, i.e. a group comprising an ancestral species, all of its descendent species, and nothing else.¹ The basic idea of clade selection is that a selection process can operate on whole clades, tending to favour those with high ‘clade fitness.’ So the clades that we find in today's biota might be a non-random subset of those that existed in the past, selection having eliminated the unfit ones and

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1. This is the standard cladistic usage of ‘monophyletic,’ which I adopt throughout this paper. There is another (older) usage of the word, associated with ‘evolutionary taxonomists’ such as Mayr (1969) and Simpson (1961), according to which a taxon counts as monophyletic so long as it contains *only* descendents of a single ancestral species, whether or not it contains *all* the descendents (see Sober 1992). The cladistic usage is much more common in contemporary literature.

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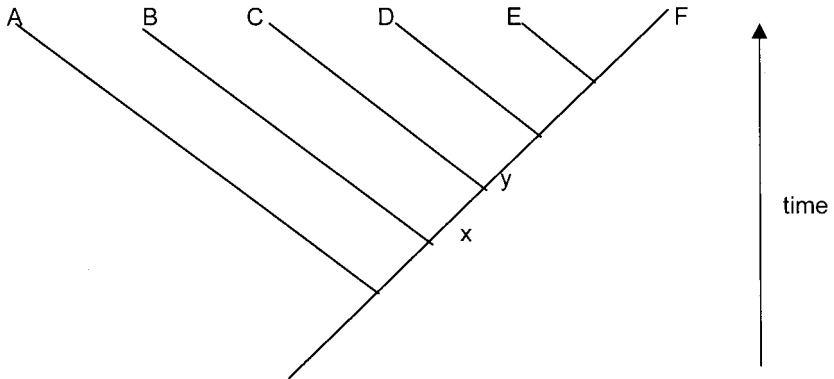


Figure 1

preserved the fit ones. In what follows, I do not speculate about the empirical plausibility of ‘clade selection.’ Rather, I argue that the idea is conceptually flawed. Clades do not have what it takes to be units of selection in the first place.

Before presenting my argument, some conceptual and terminological clarifications are required. Consider the diagram below, which shows the phylogenetic relations between six extant species, marked A to F. The nodes in the interior of the diagram represent speciation events, where ancestral species (not named) split into two. According to standard cladistic conventions, when a lineage splits the ancestral species automatically goes extinct, even if it is phenotypically indistinguishable from one of the daughter species.² Species are therefore temporally bounded entities: a species comes into existence with a speciation event, and goes out of existence when it splits, or when all its members die, whichever happens first. In Figure 1, individual species, persisting through time, are represented by branches of the tree that lie between nodes, such as the branch between nodes x and y.

According to strict cladistic usage, stemming from Hennig (1966), the word ‘clade’ refers to a *group* of species that satisfies the criterion of monophyly, e.g. the group comprising D, E, F and their most recent common ancestor. So a single species, i.e. a lineage in the above diagram bounded by two nodes, does not count as a clade, and cannot meaningfully be described as monophyletic or not. Monophyly is a property of collections of species, not single lineages. The situation is complicated because some of Hennig’s followers have tried to apply the concept of monophyly

2. There is of course an important question about what determines when a single lineage has split into two. This is in effect how the traditional ‘species problem’ arises in cladistic guise; see Ridley 1989.

to individual species themselves (usually by arguing that a species is a monophyletic group of *populations*). This often goes hand-in-hand with a broader usage of the word ‘clade,’ according to which a clade is *either* a monophyletic group of species *or* a single species lineage itself. In this paper, I use the words ‘monophyly’ and ‘clade’ in the original cladistic sense (which is still the most common). Clades are therefore supra-specific entities—they are collections of species satisfying the criterion of monophyly. Single species lineages do not count as clades.

2. Reproduction and the Units of Selection. It is widely accepted that natural selection can in principle operate at various different levels of the biological hierarchy. Lewontin (1970) identified three conditions that a population of entities must satisfy for selection to modify its composition. Firstly, the entities should vary with respect to some of their traits; secondly, this variation should correlate with differences in fitness, or expected number of offspring; and thirdly, the traits in question should be heritable, i.e. transmitted from parents to offspring. Where these conditions are satisfied, then over time selection will alter the frequencies of different types of entities in the population. Clearly, a presupposition of Lewontin’s analysis is that the entities in question give rise to other entities of the same type, i.e. reproduce; otherwise it would make no sense to talk about an entity’s expected number of offspring. Other analyses of the abstract structure of Darwinian theory make this presupposition explicit. For example, Maynard Smith (1987) argues that natural selection can act on any entities that exhibit ‘multiplication, variation and heredity’; these requirements are essentially the same as Lewontin’s, once we realize that reproduction is implicit in the concept of fitness.

Which biological entities satisfy the three conditions identified by Lewontin and Maynard Smith? Individual organisms, cells, genes, and species are prime examples. Organisms give rise to other organisms in reproduction; cells give rise to other cells in cell division, genes give rise to other genes in DNA replication, and species to other species in speciation. So the crucial ‘multiplication’ condition is satisfied, thus it makes sense to ascribe fitness to each of the entities in question. If these entities vary in their traits in a way that affects their fitness, and if the traits in question are heritable, then natural selection can act on them—they can be units of selection. Other possible units of selection are demes, populations, and colonies—though in these cases, the notion of reproduction or ‘multiplication’ does not apply quite so naturally.³

3. See Griesemer and Wade 2000 for a recent attempt to apply the notions of reproduction and heritability to demes.

Despite the simplicity and apparent finality of Lewontin's analysis, not all authors conceptualize natural selection in exactly his terms. An alternative analysis, popularized by Hull and Dawkins, holds that *two* types of entity are involved in a selection process: replicators and interactors.⁴ Replicators are entities that "pass on their structure intact" from one generation to another; interactors are entities that "interact as a cohesive whole with their environment," and hence cause replication to be differential. Genes are paradigmatic replicators, while organisms are paradigmatic interactors. According to supporters of the Dawkins/Hull framework, a failure to distinguish between replicators and interactors caused considerable confusion in the early units of selection debate.

Though the replicator/interactor distinction has proved extremely valuable for certain purposes, it does not apply very naturally to selection at supraorganismic levels of the hierarchy, which is my concern here. Attempts have been made to conceptualize species selection and clade selection using the Dawkins/Hull framework, but they are not especially convincing. G.C. Williams (1992) has made one such attempt. He argues that in clade selection, of which species selection is a special case in his view, the replicator is the *gene pool*, and the interactor is the clade itself (or 'phylad' as he sometimes calls it). The utility of this move is not obvious, not least because it is doubtful whether gene pools meet the official criteria for replicator status.⁵ In what follows, my examination of clade selection does not use the replicator/interactor terminology. But nothing hangs essentially on this. My basic argument is that clades do not reproduce, so cannot meaningfully be ascribed fitness, so cannot be units of selection. If this argument is correct, it presumably follows that the gene pools of clades do not replicate. So even if we did conceptualize clade selection in terms of replicators and interactors, this would not escape the force of my argument.⁶

4. Dawkins' analysis contrasted replicators with 'vehicles,' rather than interactors. There are substantive differences between Hull's notion of an interactor and Dawkins' notion of a vehicle. Nonetheless, there are sufficient similarities between the overall approaches of these authors to justify talking about the 'Dawkins/Hull' framework.

5. For example, one of Dawkins' criteria was that replicators must pass on any structural changes (mutations) that they incur. Gene pools do not necessarily do this. The 'founder effect' in allopatric speciation is precisely the idea that the gene pool of an incipient species may be *non*-representative of its parental species. So it is quite possible that the gene pool of any species will accumulate genetic changes during the species' lifetime which are *not* passed on to the gene pool of its offspring species.

6. Dawkins explicitly holds that his 'vehicles' must come into existence by reproduction. If I am right that clades cannot reproduce, it follows that they cannot be vehicles in Dawkins' sense.

When an entity reproduces, it gives rise to a numerically distinct entity of the same type. So reproduction automatically involves an increase in the number of entities in question, whatever they are. Griesemer (2000) notes that the notion of “same type” is usually left unanalyzed in discussions of reproduction. This is a valid observation, and something that a fully worked out account of reproduction would surely have to address. Nonetheless, this task will not be attempted here. By “same type,” I simply mean that parent and offspring are both entities *at the same level in the biological hierarchy*, a notion that is reasonably clear. Organisms give rise to other *organisms* when they reproduce; cells give rise to other *cells* when they divide; species give rise to other *species* when they speciate, and so on. However, I do want to insist on one necessary condition for reproduction. An act of reproduction must result in the production of an offspring entity which has an *independent existence* of its parental entity, in the sense that it can continue to exist when its parent dies, at least in principle. This condition is so obvious that it is rarely explicitly stated, and is obviously satisfied by the paradigm cases, but it is important. Sustained evolution would be impossible if offspring were not able to outsurvive their parents, for ancestor-descendent lineages would not exist. Another way to express the ‘independent existence’ condition is to say that if two entities are related as parent and offspring, it must be possible for them to *become* related as ancestor and descendent in the future.⁷

3. Clade Selection and Species Selection. The concept of clade selection emerged from discussions of species selection—a topic much debated in the macroevolutionary literature of the last thirty years. The original formulations of species selection were due to Stanley (1975) and Gould and Eldredge (1977), who argued that certain long-term evolutionary trends might be attributable to selection between species, e.g. the increase in the average body size of species in many mammalian taxa over time. Stanley formulated the basic idea of species selection by direct analogy with standard individual selection. He wrote: “in natural selection types of individuals are favoured that tend to (a) survive to reproduction age and (b) exhibit high fecundity. The two comparable traits of species selection are (a) survival for long periods, which increases chances of speciation, and (b) tendency to speciate at high rates” (1975, 648). If species selection has been an important evolutionary force, then we would expect extant species to have traits that enhance their probabilities of

7. This does not imply, of course, that offspring entities must *always* outlive their parents. The point is simply that the death of the parent entity must not *automatically entail* the death of the offspring entity.

survival/speciation, just as extant organisms have traits that enhance their probabilities of survival/reproduction.

That species selection is a logically possible process is not controversial. However, there is considerable disagreement over its likely empirical importance. Opponents of species selection have argued that the macro-evolutionary trends in question can probably be explained in other ways, e.g. as the side-effect of lower-level forces and processes, including organismic selection (Vrba 1984, 1989). The mere fact that species have experienced differential rates of survival/speciation does not in itself prove that species selection was the cause, any more than differential survival/reproduction of organisms must necessarily be ascribed to organismic selection. For example, the remarkable speciosity of Hawaiian drosophilids is apparently due to the physical environment in Hawaii, which is especially conducive to speciation, rather than to any biological properties of the species themselves (Hoffman and Hecht 1986). But whether or not it has actually occurred, the important point for the moment is that species selection is a coherent idea. Since species beget other species, the notion of species fitness has a clear meaning: a species' fitness is its expected number of offspring species.⁸

What about clade selection? Do clades engage in reproduction too? Proponents of clade selection believe that they do. Williams (1992) explicitly describes cladogenesis as reproduction for clades (52). Similarly, van Valen (1988) argues that supraspecific taxa can beget other supraspecific taxa, hence be subject to selection; for example, he talks about the probability that "one family gives rise to another" (59). (Though van Valen does not actually use the term 'clade selection'; more on this point later.) Sterelny (1996) apparently concurs. He argues that clades have 'adaptations,' and he insists that adaptations must be *heritable* characters, so they can be honed by cumulative selection. He rules out some alleged clade adaptations on the grounds that the characters in question are unlikely to be heritable. (An identical argument is made by Vermeij (1996) in his discussion of 'clade adaptations.')

Heritable means transmitted from parents to offspring, so Sterelny and Vermeij presumably think that clades can beget other clades. If this were right, then clade selection would constitute a natural generalization of species selection, as indeed Williams explicitly holds. Williams writes: "there is no reason why species selection

8. Some authors define species fitness slightly differently, as the difference between speciation rate and extinction rate, by analogy with the Malthusian parameter in population biology (e.g. Vrba 1984). An analogous definition of organismic fitness is used by Michod (1999). My argument below—that there is no coherent notion of clade fitness comparable to the notion of species fitness—applies equally, whichever definition of species fitness we prefer.

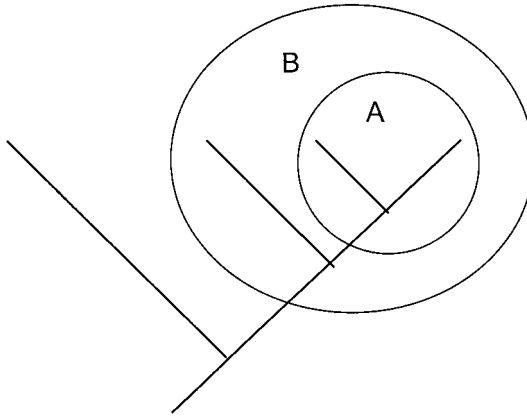


Figure 2

should be recognized as a special process different from any other kind of clade selection . . . selection can take place among clades of higher than the species level” (1992, 125). Similarly, Nunney (1999) says that species selection “can be subsumed under the more general category of clade selection” (247).

However, there is a complication here. For clades are by definition monophyletic, and as a matter of logic, monophyletic clades cannot stand in ancestor-descendent relations with one another: if all higher taxa are required to be monophyletic, then ancestral higher taxa do not exist (Nelson and Platnick 1984). A taxon which contains all the descendents of its members as proper parts cannot be ancestral to any other such taxon. To see this point, consider the cladogram in Figure 2. If we ask what the ancestor of the highlighted clade A is, then the answer can only be a *species*, not another clade. Clade A is of course a *part* of the larger clade B, but it is not the *descendent* of B. Nor is A is the *offspring* of B. For as I have stressed, the parent-offspring relation must be able to become the ancestor-descendent relation—offspring must be able to outlive their parents. But clade A cannot outlive clade B. The only way a monophyletic clade can cease to exist is if all of its constituent species go extinct, which implies that all the sub-clades which are parts of it must cease to exist too. If clade B ceases to exist, then clade A must do so too. So B is clearly not the parent of A.

This means that Williams’ idea that cladogenesis constitutes ‘reproduction for clades’ is incorrect. Reproduction means one entity giving rise to another entity of the same type, but clades cannot do this. In cladogenesis, the entity that splits is a species lineage. Presuming it splits into two (which is most usual), and given the standard cladistic convention that a

species automatically goes extinct when it speciates, the result is a new clade containing three species—the original one (now extinct), and two new ones. But the new clade is not the *offspring* of any of the clades to which the original species belonged, but rather a part of them. Williams' argument that there is no special reason to focus on species in a theory of higher-level selection is therefore misleading. There is such a reason: species give rise to offspring species, hence form ancestor-descendent lineages, but clades do not give rise to offspring clades.⁹ The notion of clade fitness, as expected number of offspring clades, therefore does not make sense. Monophyletic clades are not the sorts of entity to which fitness can be meaningfully ascribed. When van Valen talks about the probability of one family giving rise to another, his suggestion only makes sense from a non-cladistic point of view.¹⁰

4. Three Possible Responses. How might defenders of clade selection respond? One possible response would be to concede that clades do not reproduce, but argue that differential extinction of clades might nonetheless be an important evolutionary mechanism on its own. Different clades might have different probabilities of going extinct depending on their 'clade traits.' So even though clades cannot transmit these traits to their offspring (for they have none), selection could operate by eliminating those clades whose traits reduce their probability of survival. This is true enough, and has no doubt happened many times in the history of life on earth, transforming the biota—e.g. when the various dinosaur clades went extinct. But selection on entities that do not reproduce their kind is not very interesting, and will not lead to complex adaptations. All sorts of entities are subject to selection in this weak sense. A collection of atoms may have different probabilities of radioactive decay, a collection of buildings may have different probabilities of being demolished, and so-on. Natural selection is only an interesting idea when applied to entities that reproduce (Dawkins 1982). Moreover, clade selection in this weak sense is clearly not a more general version of species selection. It is precisely because species *do* leave offspring species that species selection is a potentially interesting evolutionary mechanism.

9. The claim that clades cannot reproduce has previously been made by Niles Eldredge (1985, 2003). However, Eldredge does not provide an argument for this claim, and does not dwell on it at length; he apparently regards it as obviously true. Thanks to an anonymous referee for pointing this out to me.

10. I do not mean to suggest that van Valen himself is unaware of this. He himself does not use the label 'clade selection' and in any case rejects cladism, for reasons given in his 'Why not to be a cladist' (1978). Abandoning the requirement that higher taxa be monophyletic is certainly a way of making sense of the idea of 'higher taxon' selection, but this is not *clade* selection, for clades are monophyletic by definition.

It is of course true that natural selection often operates on differences in survival (viability selection), rather than on differences in reproduction (fecundity selection). But in ordinary cases of viability selection, the entities which survive the selection then go on to reproduce, and transmit their survival-enhancing traits to their offspring. So my claim is *not* that interesting cases of natural selection must be cases of fecundity selection rather than viability selection; that is certainly not true. Rather, my claim is that natural selection, whether it operates on differences in survival or on differences in reproduction, is only interesting when applied to entities that do *in fact* reproduce. Differential survival of organisms and species is interesting, because organisms and species reproduce their kind. Differential survival of clades is not, because clades do not reproduce their kind. So while differential clade survival may well have been a transforming factor in biotic evolution, from the viewpoint of a theory of *selection* it is not an interesting phenomenon. It cannot lead to clade adaptations, since adaptation requires cumulative selection, hence reproduction.

A second possible response is to concede that clade fitness in the sense of expected number of offspring clades does not make sense, but replace it with another notion. Why not let clade fitness refer to the probability that a clade comes to have other sub-clades as parts, rather than as offspring? And by heritability, we could mean resemblance between a larger clades and its sub-clades, rather than its offspring clades. Clade selection in this sense could help explain the differences in bushiness between clades. Fittest clades are the ones whose particular traits confer on them a higher probability of becoming bushy.

One might object that re-defining clade fitness in this way means that clade selection ceases to be a genuinely Darwinian process. This objection is not conclusive, for some variation is presumably tolerable in the range of processes that count as ‘genuinely Darwinian’; not all bona fide selection processes need be isomorphic in every respect. But in any case, there is another objection to the suggested re-definition of clade fitness, which is conclusive.

Consider the clades marked A and B in Figure 3, 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 sub-clades 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.

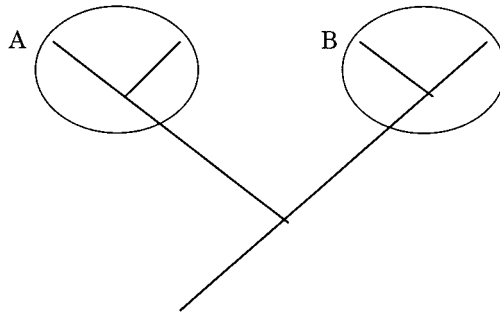


Figure 3

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. Quite apart from the fact that this is a strained notion of ‘fitness,’ clade selection in this sense explains nothing that is not already explained by species selection.

A third (related) response also argues for a redefinition of clade fitness. Why not define the fitness of a clade as the average fitness of its constituent species? Defining the fitness of a higher level entity as the average fitness of its lower level constituents is not unknown in models of higher level selection. In the literature on group selection (rather than species selection), a group’s fitness is usually defined as the average fitness of its constituent organisms. Indeed, many authors have called attention to the important distinction between group fitness in the sense of average organismic fitness, and group fitness in the sense of expected number of offspring groups (Damuth and Heisler 1988, Arnold and Fristrup 1982, Okasha 2001, 2003). Clearly this distinction can be generalized to any higher-level selection theory. Let us call selection theories that define higher-level fitness the first way ‘HLS1,’ and those that define higher-level fitness the second way ‘HLS2.’ The suggestion, therefore, is that we should treat clade selection as HLS1 rather than HLS2, to avoid the problem that clades do not leave offspring clades.

Two points about this move deserve mention. Firstly, understood this way, clade selection would certainly not constitute a generalization of species selection, as its proponents intend it to be. For species selection is a HLS2 theory. As has often been pointed out, in species selection theory a species’ fitness is defined as its expected number of offspring species, *not* as the average fitness of its constituent organisms. (It is for this reason that species selection and (most versions of) group selection are not isomorphic.) A species with high fitness is one which has a high probability of surviving/speciating, not one whose constituent organisms are especially

well adapted.¹¹ So if clade selection were defined as average species fitness, the resulting theory would be of a different logical *type* from species selection theory. This would not vindicate the view that species selection is a special case of the more general phenomenon of clade selection.

Secondly, it is hard to see what the *point* of a HLS1 theory of clade selection would be. The point of a group selection theory which defines group fitness as average organismic fitness is to model situations where the fitness of an organism depends on the composition of its group. In the paradigm example, organisms are either selfish or altruistic, and their fitness depends in part on the proportion of altruists in their group. If there were no group level effects on organismic fitness, then there would be no need for a group selection theory of this sort: there would be nothing for it to explain. Changes in the frequencies of different types of organisms would be predictable *without* taking group structure into account, i.e. by individual level selection. In the clade case, it is not likely that there are clade level effects on species fitness, in the way that there are often group level effects on individual fitness. Why should the fitness of any species, i.e. its probability of surviving/speciating, depend on which other species are in its clade? Such a dependence is of course possible. For example, if a given species goes extinct, this could increase the fitness of a sister species with which it competes for resources. But given that con-cladistic species are not necessarily sympatric, systematic clade-level effects on species fitness are not likely.

If this is correct, then a HLS1 theory of clade selection, though conceptually possible, is unlikely to have useful empirical application. If average species fitness is greater in clade A than clade B, then clade A is more likely to become bushy than clade B. But as with the second response considered above, this falls entirely within the purview of *species* selection. If clade A does in fact become bushier than B, this can be explained by A's constituent species having higher species fitness than B's. Nothing is gained by defining clade fitness as average species fitness and then attributing the difference in bushiness to clade selection. In the absence of systematic clade level effects on species fitness, this is to artificially multiply levels of selection for no reason.

I conclude that clade selection is at worst conceptually incoherent, and at best simply collapses into species selection. Evolutionists should therefore abandon the concept.

11. Though high average organismic fitness may of course *contribute* to high species fitness, by reducing the species' probability of extinction. The point is that species fitness is not *defined* as average organismic fitness.

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