1. Thesis statement

Clade is a level of selection.

2. Background

It is true that the majority of scientists agree that selective mechanisms of nature play an important role in shaping the diversity of life on the earth. However, there has been ongoing debate on the level of selection, i.e. the level of the biological hierarchy at which natural selection occurs. This concern about the level of selection is crucial because a trait could hold different effects on different levels. At the genetic level, selection of the Y chromosome may favor the reproduction of more male offspring. But at the individual level, biased sex ratio may result in many male not getting the chance to mate. Without specifying a level or levels of selection, it is meaningless to say selection occurred.

Some biological hierarchies, such as genes and organisms, have been proposed as potential levels of selection. Clade refers to the taxonomic group of organisms that are monophyletic. In other words, a clade is composed of a common ancestor and all of its descendants. In this paper, I aim to argue that clade can be a level of selection.

3. Main argument

(1) Evolution by natural selection (ENS) generally should fulfill the four criterias: population, variation, fitness, and heritability (§§3.1). (2) Clade selection (CS) meets those criterias in its own way (§§3.2).

3.1. Evolution by natural selection (ENS)

ENS requires both selection (§§3.1.1) and response to selection (§§3.1.2). If there is no selection, the composition of life on earth is random. If there is no response to selection, the selection will not be cumulative to cause evolution. Here are the general criterias of ENS.

3.1.1 Selection: population, variation

Selection could, technically, be operated on one unit, for a short time. But as long as the only unit dies, the story ends. When there is only one unit under selection, the unit can thrive without any evolution. The thriving unit then contains many sub-units, which contradicts with "there is only one unit under selection". In order for selection to produce evolution, there must be multiple units that may potentially be selected. Those many units form a population of units, and selection acts on a population.

If there is no variation within a population, there is no selective pressure. Individuals in the population can thrive without any evolution. To generate evolution from selection, there must be selective pressures and thus there must be variation on traits that can affect the fitness of the individuals.

ENS requires a population and variation between the individuals for selection to happen. The individuals are the interactors, or, the units of selection. And the biological hierarchy of the units of selection is referred to as the level of selection. Selection occurs when different units at the same level of selection compete with others based on their varied interaction with the environment.

3.1.2 Response to selection: fitness, heritability

In general, fitness is the outcome of natural selection, reflecting on the extent an interactor is likely to survive in the environment. Since interactors that are more likely to survive are more likely to reproduce, and the only way for some interactors to be recorded is by reproduction, many evolutionary biologists define fitness as the measure of offsprings of an interactor. The differential reproduction of one generation records the consequence of selection on the current generation, and determines a basis for the next generation's composition.

Heritability, or parent-offspring connection is necessary during reproduction. Traits that increase the fitness of parents are inherited by their offsprings. Otherwise, evolution will not occur since the response of selection is limited within the time period of one generation.

ENS requires differential fitness and heritability of traits for the response of selection to be recorded. The media of recording the response of selection is referred to as replicators, or, the units of inheritance. Replicators do not need to be the same nor at the same level as interactors. Response to selection is recorded when fitness-affecting traits can affect further selection.

3.2 Clade selection (CS)

CS does not align with the usual ENS format, CS can support a process as a form of ENS. At the clade level, the ENS requirements of selection (§§3.2.1) and response to selection (§§3.2.2) are fulfilled.

3.2.1 Selection: balance

Due to the rank-free characteristics of clades, it may be hard to see that clades have a population-individual structure. Scientists could, technically, regard clades as interactors of the population of clades. However, the interactor model does not apply very naturally to selection at supraoganismic levels of the hierarchy (Okasha, p.742) because of the complexity of scaling.

The derive of selection at the clade level is better explained by the balance between speciation (clade growth) and extinction (clade death). The aim of natural selection is to maintain equilibrium on earth, and the balance between speciation and extinction is the process of natural selection that maintains the equilibrium. There are many clades to be potentially selected to undergo speciation and extinction, which corresponds to "there must be multiple units that may potentially be selected".

The selective pressure comes from the variation of clade-level traits that can affect the fitness of the clade, for example, sex ratio and geographical distribution (Doolittle, p.277). Clades with larger geographical distribution are more likely to survive.

Different clades at the level of clade compete with others based on their varied interaction with the environment, so CS can lead to selection of ENS.

3.2.2 Response to selection: differential persistence

It is true that there is no reproductive mechanism for clades (p.279). Since a clade comprises an ancestor and all its descendants, it cannot have descendants that are not part of it (p.280). The replicator model does not apply to CS, also because of the complexity of scaling.

The response to selection at the clade level is better explained by differential persistence. The aim of response to selection is to operate further selection based on the current consequence of selection, and this can be done by differential persistence. Clades that have high fitness are more likely to undergo further selection, As long as a clade is not extinct, it will continuously undergo selection. Since clades can record the result of selection without reproduction, clades do not need to reproduce.

CS is heritable. First, all organisms in a clade derive from the same common ancestor. Descendants inherit some traits from the ancestor by genetic material transmission, so there is something inherited that is shared within a clade. Second, the clade-level traits that can affect fitness (§§3.2.1) can be differentially persisted by descendants depending on their evolutionary pathways. For example, the clade of ducks has a long evolutionary history of flying. Therefore, it is more likely for the future generations of ducks to maintain wing structure than the generations of dogs to develop wings.

Fitness-affecting traits are recorded for further selection by differential persistence, so CS can record the response of selection of ENS.

4. Objection

A possible objection is that CS cannot produce engineering adaptation and thus it is not interesting (Okasha, p.746). CS can only explain the extinction of losers, rather than the engineering adaptation of the survivors. If a level of selection cannot produce engineering adaptation, it is not interesting.

5. Reply

CS can produce engineering adaptation. CS is powerful on filtering out clades that have low fitness, but this does not mean it cannot lead to engineering adaptations among the survivors. First, the main difference between the product of selection and engineering adaptation is whether it is a complex trait built up by the accumulation of multiple simpler parts over time. If a

subclade survives in an extinction event and has the chance to move into a vacant niche, this counts as a one step in the accumulation. This step in their evolutionary pathway is recorded and can further undergo natural selection. After the subclade repeated the process over time, the accumulation of steps can lead to engineering adaptation (Doolittle, p.289). Second, CS can serve as a layer of multi-level selection. It is commonly believed by evolutionary biologists that species selection produces engineering adaptations. But species do not build engineering adaptation from nothing, instead, they evolved their engineering adaptation by accumulating small changes on their evolutionary pathway from the state of their ancestor. This proves that CS is cumulative and can produce engineering adaptations. Furthermore, if the species speciate, the descendant species will inherit the engineering adaptation of their ancestor, and they may further build engineering adaptation on the top of that.

Even if CS cannot produce engineering adaptation, CS is still interesting for providing a framework for evolutionary biologists to look at the evolutionary pathways of organisms. Also, as I mentioned in the previous paragraph, CS can produce engineering adaptation and engineering adaptations of species is better explained linearly at the clade level.

Reference

- Doolittle, W. 2017. Making the Most of Clade Selection. Philosophy of Science, 84(2), 275-295. doi:10.1086/690719
- Okasha, S. 2003. Does the Concept of "Clade Selection" Make Sense? Philosophy of Science, 70(4), 739-751. doi:10.1086/378862