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Evolution by Non-individual Selection Pressures

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Synonyms

Higher-level selection; Supra-individual selection

Definition

The forms of selection that take place above the level of individual organisms, influencing the evolution of traits both within and across groups, populations, or species, thereby affecting their survival, proliferation, and long-term persistence.

Expanding the Scope: Understanding Selection Beyond the Individual Level

Individual selection is the most widely recognized mechanism of evolution, first described by Charles Darwin in his groundbreaking work, "On the Origin of Species" (Darwin, 1860). This theory offers a straightforward and comprehensible account of the development of adaptive traits in living organisms. Its intuitive nature is due, in part, to its similarity with artificial selection, such as breeding practices. As a result, biologists often begin their investigation of an organism's structure or behavior by examining how it maximizes biological fitness in competition with other members of the same population.

This approach is logical because many adaptive traits likely originated through individual selection, which continues to play a crucial role in maintaining these traits in extant species. Traits that do not confer a competitive advantage within a population, or even present a disadvantage, are often quickly eliminated by individual selection, drift, or draft, even if they are beneficial for a population or species as a whole. However, it is important to recognize that individual selection is not the only driving force in the evolution of adaptive traits.

The currently popular concept of multi-level selection acknowledges that selection can occur at various levels of biological organization, from individual genes to entire ecosystems. This framework tries to provide a more comprehensive understanding of the evolution of adaptive traits, integrating individual selection with other mechanisms such as kin selection, group selection, interspecies selection, species selection, and biome-level selection.

Kin Selection and Its Broad Consequences: From Altruism to Spite

Many traits, including parental behavior and numerous (though not all) forms of altruistic behavior aimed at genetic relatives, are well-known products of kin selection, a form of natural selection that focuses on the genetic relationships between individuals within a population. It was first introduced by British evolutionary biologist W.D. Hamilton in the 1960s as an extension of Darwin's individual selection theory (Hamilton, 1964a, b). Kin selection posits that organisms can increase their genetic representation in future generations not only by directly reproducing but also by helping close relatives, who share a significant proportion of their genes, to survive and reproduce.

Hamilton's rule, a central concept of kin selection, is expressed mathematically as rb > c, where r represents the degree of relatedness between the individual providing help and the recipient, b is the benefit gained by the recipient, and c is the cost incurred by the helper. According to Hamilton's rule, a behavior will be favored by kin selection if the benefit to the recipient, weighted by their relatedness, exceeds the cost to the helper.

Kin selection, which operates at a level beyond individual selection, is often used to explain eusociality – the existence of sterile castes in many insect species and even some species of mammals, or the existence of helpers – individuals who temporarily assist their parents in caring for their siblings instead of beginning their own reproduction in some species of birds (Wilson, 1975). Kin selection has also been proposed as an explanation for the existence of menopause in humans and some other species (Shanley et al., 2007; Sherman, 1998).

However, the products of kin selection extend beyond altruistic behaviors and include spite behavior aimed at nonrelatives. Spite behavior decreases the fitness of the victims while typically also having negative impacts on the individual expressing it. An individual can increase its relative direct fitness either by enhancing its own direct fitness or by reducing the direct fitness of other members of the population. In terms of (more important) inclusive fitness, an individual can increase its relative fitness by decreasing the fitness of individuals who are not its genetic relatives. For many species, it is challenging to estimate the relatedness of other population members. However, some species can achieve this, for example, by using olfactory clues. In other species, an individual can achieve the same effect by moving from its native population to a geographically distant population. It has been suggested that the tendency of individuals infected by certain parasites to travel to distant populations is not the result of the manipulative activity of the parasite (aimed at infecting new populations), but the adaptive spite behavior of an infected host aimed at increasing its relative inclusive fitness by infecting unrelated individuals (Rozsa, 1999, 2000).

Menopause as a Product of Kin Selection

Menopause, the permanent cessation of a female's reproductive ability, is a relatively rare phenomenon in the animal kingdom. Most species continue to reproduce throughout their lives, making menopause in humans and a few other species, such as killer whales and pilot whales, an intriguing subject for evolutionary biologists. Kin selection has been proposed as a potential explanation for the existence of menopause in these species (Shanley et al., 2007; Sherman, 1998).

The "grandmother hypothesis" is a prominent theory that utilizes kin selection to explain menopause. This hypothesis suggests that menopause evolved because it increased the inclusive fitness of older females by allowing them to invest more time and resources in their existing offspring and grandchildren rather than continuing to reproduce. As a woman ages, her reproductive success and the survival of her offspring may decline, while the risks associated with pregnancy and childbirth increase. By ceasing reproduction, older females can redirect their energy toward helping their children and grandchildren, who share a significant proportion of their genes, to survive and reproduce. This assistance can take various forms, such as providing food, care, and protection, or sharing knowledge and experience.

Support for the grandmother hypothesis comes from various sources. Anthropological studies have shown that the presence of grandmothers in hunter-gatherer societies can have a significant positive impact on the survival and reproductive success of their grandchildren (Hawkes et al., 1998). In addition, research on killer whales, one of the few non-human species known to undergo menopause, has found that older, post-reproductive females play crucial leadership roles in their family groups, contributing to the survival and well-being of their relatives (Brent et al., 2015).

Despite the evidence supporting the grandmother hypothesis, other factors may also contribute to the evolution of menopause, such as the accumulation of deleterious mutations in the female germline or the need to avoid mother-daughter reproductive competition. Nevertheless, the kin selection-based explanation provided by the grandmother hypothesis offers a compelling account of how menopause may have evolved as an adaptive strategy for maximizing inclusive fitness in humans and some other species.

Interdemic Selection: An Alternative Perspective on Group Selection Phenomena

Group selection, sometimes also called interdemic selection, is a form of natural selection that operates at the level of groups or populations, rather than individuals, kin, or genetic relatives. This type of selection is encountered in species that form a large number of more or less independent social groups, such as herds, flocks, or bands, and when the survival or reproduction of an individual is closely connected with the survival and success of its social group. The differential survival and reproduction of these groups can drive the evolution of traits that benefit the group as a whole, even if those traits may not necessarily benefit each individual within the group or may even be harmful to the bearer.

Group selection can help explain the evolution of behaviors and traits that promote cooperation and altruism among loosely related or unrelated individuals. In some cases, these behaviors can increase the overall fitness and success of the group, even if they come at a cost to individual members. Examples of group selection include the evolution of cooperative hunting in predators, the formation of social groups for mutual protection against predators, and the emergence of cooperative breeding in certain bird and mammal species.

One specific example of group selection involves the alarm calling behavior in a flock of jackdaws. If a predator appears in the vicinity of the flock, the first jackdaw that notices its presence gives a warning cry, and the whole flock tries to escape or defend itself. From the standpoint of the individual, the issuing of the warning cry and participation in the protection of the flock is disadvantageous behavior. The individual would have a much better chance of survival if it were to selfishly use the information about the presence of the predator for itself alone and, according to the circumstances, either crouch down or inconspicuously move to the other side of the flock and leave some other individual, perhaps its potential competitor, to be eaten. But, instead of this, it warns the rest, gives up its advantage, and exposes itself to the same risk that the predator will attack it as any other member of the flock.

One of the key challenges in demonstrating group selection empirically is the need to show that the benefits of group-level traits outweigh the costs incurred by individuals. The balance between within-group selection, which favors selfish traits, and between-group selection, which favors group-level traits, plays a crucial role in determining the prevalence of group-selected traits in a population.

In determining whether altruistic or selfish individuals predominate in a particular species, several factors play a crucial role. These factors include the population structure of the species, the formation and dissolution of social groups, the degree to which altruistic behavior benefits or harms the individual and the group, and other properties of the specific biological system.

In most cases, individual selection is much stronger than group selection. Consequently, until the 1980s, the prevailing opinion among biologists was that group selection rarely played

a significant role in nature. However, recent analyses of theoretical models have demonstrated that under certain conditions, such as when individual subpopulations frequently emerge and disappear within the larger population, group selection can become an important factor. In some cases, depending on the range of population parameters, group selection can even outweigh individual selection (Alexander & Borgia, 1978; Shanahan, 1998). These findings suggest that a more nuanced understanding of the interplay between individual and group selection is necessary to fully appreciate the complex dynamics that shape the evolution of altruistic and cooperative behaviors within various species.

David Sloan Wilson and E. O. Wilson (2007) have argued for a revival of the group selection concept, proposing that multi-level selection, which includes group selection, can provide a more comprehensive framework for understanding the evolution of cooperative and altruistic behaviors. They emphasize that while within-group selection often favors selfish individuals, between-group selection can favor groups with more cooperative members, leading to the persistence of group-level traits in a population.

Despite its potential explanatory power, group selection remains a controversial topic for many scientists. In response to this ongoing debate, evolutionary biologists have increasingly adopted the term "interdemic selection" to describe this process. This terminology shift helps sidestep the contentious label of "group selection" and addresses concerns from those who may have been taught that group selection is not a valid concept. By using the term "interdemic selection," researchers can continue to explore the important role that selection between groups plays in the evolution of cooperative and altruistic behaviors, while avoiding unnecessary controversy.

Religion as a Product of Group Selection

Religion has been a pervasive and enduring aspect of human societies throughout history. It serves to connect individuals, establish shared moral codes, and provide a framework for understanding the world and our place within it. The prevalence and persistence of religious beliefs and practices have led some researchers to suggest that religion may be a product of group selection, an evolutionary process that shapes traits beneficial to the collective success of a group rather than the individual (Wilson, 2002).

Group selection posits that traits that enhance the cohesion, cooperation, and overall success of a group can evolve, even if they are not directly beneficial to individual members (Wilson, 2002). Religion appears to promote many behaviors that can increase group cohesion and cooperation. Shared religious beliefs and practices can create a sense of unity, strengthen social bonds, and foster trust among group members (Graham & Haidt, 2010). Moreover, many religious doctrines prescribe altruistic behaviors and discourage selfishness, which can improve the collective well-being of the group (Sosis & Alcorta, 2003).

Religion can also contribute to the success of a group in competition with other groups. Religious rituals can enhance group identity and foster loyalty, which may be critical during conflicts with other groups (Atran & Hendrich, 2010). Additionally, religious beliefs can provide a basis for justifying territorial expansion, resource acquisition, or even violence against perceived enemies. Furthermore, religion can offer solace and meaning in times of crisis, helping to maintain group morale and cohesion.

Empirical evidence supporting the role of group selection in the evolution of religion comes from various sources. Cross-cultural studies have shown that societies with more demanding and costly religious rituals tend to be more cooperative and cohesive (Sosis & Alcorta, 2003). Experimental research has also demonstrated that priming participants with religious concepts can increase prosocial behavior and cooperation in economic games (Norenzayan & Shariff, 2008).

Despite this evidence, the idea that religion is a product of group selection remains controversial. Critics argue that religious beliefs and behaviors can also be explained by individual-level selection, as they may enhance personal reputation, social status, or psychological well-being (Boyer, 2001; Henrich, 2009). Additionally, some researchers suggest that religion may be a byproduct of other cognitive processes, such as

the human tendency to attribute agency and intention to natural phenomena (Guthrie, 1993).

Interspecific Selection: The Role of Interspecies Competition in Evolution

Interspecific selection is a type of selection that arises from the competition between different species, typically but not only, when they compete for the same resources. This form of selection can lead to the elimination of species that are less efficient in acquiring common resources or have a lower ability to withstand the effects of common predators or parasites. Interspecific competition can shape the distribution and coexistence of species within an ecosystem, as well as drive the evolution of traits that are advantageous in competitive scenarios.

Conditions in different parts of a species' geographic range can vary substantially, leading to different outcomes of interspecific competition in different regions. For example, a common parasite might be absent in certain parts of the range, or a limiting resource may be abundant enough that it no longer constrains the reproduction of one or both competing species. As a result, different species may prevail in interspecific competition in different parts of their range, and under some conditions, both competing species with identical niches can coexist in the same place for extended periods (Hardin, 1960).

Interspecific selection resulting from interspecific competition is, in principle, a form of stability-based sorting, rather than a true selection process. In this context, less adapted species go extinct earlier, while better-adapted species survive longer. However, these better-adapted species do not necessarily transmit their adaptations to daughter species. Because the process of outcompeting less adapted species occurs rapidly on an evolutionary timescale, complex adaptations are unlikely to evolve solely through interspecific selection. Instead, preadaptations – traits that have evolved in response to other selection pressures – and spandrels, traits that have evolved without the involvement of any form of selection, play a crucial role in interspecific selection

(Toman & Flegr, 2017). These preexisting traits can provide a competitive advantage in certain scenarios, enabling a species to outcompete others in specific contexts.

However, if two competing species have only partially overlapping niches and geographic ranges, the weaker species may not be completely eradicated. Instead, it may modify its niche or survive in specific, limited habitats where the competing species is absent, allowing for potential evolutionary changes to accumulate over time through intraspecies selection.

As was already explained, intraspecific selection, particularly individual selection, plays a unique role in constructing complex adaptive traits. Interspecies selection has also a specific and important role in determining organism properties. Its primary significance lies in "niche pruning," which forces organisms to specialize and select life strategies tailored to their specific properties. Without interspecies competition, organisms would likely be generalists with less well-adapted organs and life functions. Individual organs of such species would probably not be as well adapted to the environment as those of contemporary, mostly highly specialized species. If the survival of a member of a certain species depends on its speed, the evolution of its locomotive organs will occur much more rapidly for this species (and will advance much further) than if its survival were determined by a broader spectrum of its traits.

The concepts of interspecies competition and intraspecies competition are occasionally conflated in specific contexts. The idea of a vacant niche, which gained popularity especially in the 1980s, illustrates this confusion. A niche is defined only by the ecological requirements of the organism that occupies it, making the concept of a vacant (empty) niche inherently contradictory. However, the concept of a vacant niche is so intuitive that it still persists (and probably continues to persist) in expert literature. Many field researchers have observed a surplus of unutilized resources in nature, suggesting that the environment could support a far greater number of species than currently exist. Numerous species of herbivorous insects feed on only one species of plant,

while many plants remain unutilized by insects. This observation has led some biologists to argue that the existence of unutilized resources contradicts Darwin's theory of evolution, as it implies a lack of substantial competition to drive biological evolution.

The existence of vacant niches and unutilized resources may indicate less intense interspecies competition but is unrelated to the presence or absence of intraspecies competition. In environments with many unutilized resources and potential niches, individual species still occupy their niches, where fierce competition within a single species is common. Competition can take various forms, such as competing for shelter, reproductive success, or resistance to predator pressure. Even in seemingly idyllic conditions with abundant resources, intraspecies selection can still be expected. If organisms faced no limitations, their populations would grow exponentially rather than remaining stable.

Target Parameters of Interspecific Selection: The Turbidostat-Chemostat Discontinuum Theory

Both intraspecific and interspecific competitions involve different species competing for various traits (parameters). In principle, these parameters can influence only two basic aspects of any system: the maximum rate and maximum efficiency of operation. In the case of living systems, these aspects are the maximum rate of reproduction (the number of offspring per unit of time) and the maximum efficiency of reproduction (the number of offspring per unit of consumed limiting resource). The actual rate and actual efficiency of the reproduction will depend on the actual condition and availability of resources and can be subjected to physiological and ethological regulation – optimization and trade-offs. In the following text, the rate and efficiency of reproduction always mean the maximum rate and maximum efficiency of reproduction. Which of these basic parameters will be the subject of competition between two species depends on the type of negative feedback regulating the population size to which the species is exposed (turbidostat type or chemostat type).

Despite the varying rates of reproduction and death of organisms, the long-term population sizes of individual species remain constant. This stability can only be ensured by the existence of negative feedback regulating the population size and compensating for random effects of varying reproduction and death intensities (Flegr, 1997). In principle, there can only be two types of negative feedback, and technical laboratory models exist for both types. The first type, "top-down regulation," can be modeled in the laboratory using continuous cultivation systems of the turbidostat type. In this system, an increase in population size leads to an increase in the death rate of its members. This occurs, for example, in populations where the size of the prey or host population is regulated by the activity of predators or parasites.

The second type of negative feedback, "bottom-up regulation," is modeled using continuous cultivation systems of the chemostat type. In these systems, if the population size increases, the resources are consumed more rapidly, leading to a decrease in reproduction rate and an eventual decrease in population size (Flegr, 1997). In nature, this occurs, for example, in populations of predators (parasites) regulated by the availability of prey (hosts).

In intraspecies competition, the type of negative feedback determines which parameters of the organism will be crucial for success and, therefore, the subject of natural selection, i.e., which mutations will spread in the population and species. Theoretical analysis (Flegr, 1997) suggests that the maximum rate of reproduction is the critical parameter in turbidostat-type systems, whereas the critical parameter in chemostat-type systems is the maximum efficiency of utilizing a limiting resource. As a result, mutants with a higher maximum rate of reproduction spread and become fixed in populations exposed to turbidostatic regulation and therefore turbidostatic selection, and the corresponding species shift along the r-K continuum toward an r-strategy (Pianka, 1970, 1972). Conversely, if a population is exposed to chemostatic regulation and therefore to chemostatic selection, mutations increasing the efficiency of reproduction become fixed, and the

species shifts toward a K-strategy. The fate of a mutation that increases the rate while decreasing the efficiency of reproduction (or vice versa) depends on whether the corresponding population is exposed to turbidostatic or chemostatic selection.

In the case of interspecific competition between two species, the outcome of the competition depends on the type of negative feedback applied to both species. If both species are exposed to regulation by the same factor, such as turbidostatic regulation through the same parasite or the same predator, the species with a higher growth rate will prevail. Similarly, if both species are exposed to chemostatic regulation and their population growth is limited by a shortage of the same nutrient, the species with greater efficiency in utilizing that nutrient will win, and the other species will be locally or even globally displaced. In practice, it is common for each competing species to be regulated differently, such as by a shortage of different nutrients or parasites, or even one species being limited by a specific nutrient (chemostatically) and the other being affected by a particular parasite. In this case, both species can coexist long-term or even permanently in ecological terms within the same territory.

Results of numeric modeling indicate that stable coexistence of two species is possible even when both rely on the same nutrient and are exposed to the same parasite/predator. This situation can occur when one species has a higher maximum rate of reproduction and is therefore, in the same environment, exposed to chemostatic regulation, while the other has a higher efficiency of reproduction and is thus exposed to turbidostatic regulation. This coexistence appears to contradict the competitive exclusion principle (Gauze, 1934; Hardin, 1960), which states that two species competing for the same resources cannot coexist indefinitely. However, it does not truly conflict with this principle, as the mode of population regulation is part of the ecological niche definition (Elton, 1927) for a given species. Although both species have the same resource requirements and are exposed to the same parasite, the existence of differences in maximum rate and efficiency of resource utilization exposes

them to different types of population size regulation, giving them distinct niches and enabling long-term coexistence.

This coexistence is stable in ecological timeframes but not in evolutionary timeframes. Sooner or later, the species exposed to selection for a higher reproduction rate will accumulate mutations that allow it to escape turbidostatic regulation and become subject to chemostatic regulation, or the species exposed to selection for higher reproduction efficiency will accumulate mutations that enable the opposite – a transition from chemostatic to turbidostatic selection. Both species will then converge in their niches, and the species with the higher maximum growth rate will displace the species with a lower rate of reproduction (which is under turbidostatic regulation), or the species with higher reproduction efficiency will displace the species with lower efficiency (which is under chemostatic regulation).

Persist or Perish: The Crucial Role of Species Selection in Evolution

Species selection is a unique evolutionary mechanism that is often confused with interspecific selection. The criterion for success in species selection is not direct fitness or inclusive fitness, but rather the resistance of a species to extinction and its capacity for speciation (Lieberman & Vrba, 2005; Vrba, 1984). This process can result in the evolutionary success of a clade, even if certain traits may be maladaptive in other forms of selection. For instance, the loss of wings in some insect clades might increase the probability of speciation, despite being disadvantageous in most other selection scenarios.

It is quite possible that several important traits in modern organisms, such as sexuality (Stanley, 1979), emerged due to species selection. However, the formation of complex adaptive traits can only be attributed to intraspecific selection, mainly individual selection, as it is the only known mechanism for gradually optimizing complex adaptive traits through the accumulation of minor changes resulting from mutations.

A primary limitation of species selection compared to individual selection is the smaller number of competing units and the limited time available for the stepwise evolution of more complex traits. In individual selection, a vast number of individuals compete simultaneously, whereas the number of species coexisting in a specific territory at any given moment is significantly lower. Additionally, the lifespan of an individual is much shorter than the duration of a species' existence, enabling intraspecies individual selection to accumulate numerous advantageous changes over time, ultimately leading to the development of complex adaptive traits.

In contrast, the average lifespan of a species is roughly several million years. This means that even considering the entire duration of life on Earth, there may not be enough "generations" of successive species for the stepwise evolution of more complex traits. This disparity in the number of competing units and available time hampers species selection's capacity to generate intricate adaptive features as efficiently as individual selection.

Despite these limitations, species selection has certain advantages over other forms of selection. The principal advantage is that it ultimately determines the fate of a trait. A trait that is advantageous for an individual will eventually disappear from nature if it leads to the extinction of the species bearing that trait. Human intelligence is advantageous from the standpoint of individual selection, but if humans cause their own extinction, such as in an atomic war, less intelligent species like sloths will prevail in larger time scales.

Species selection also has advantages over group selection. Firstly, it is resistant to the invasion of an alternative form of the trait. Traits advantageous for a group but disadvantageous for individuals may eventually disappear, as individuals without the trait will invade the population and predominate through individual selection. However, traits advantageous for a species and disadvantageous for individuals are less likely to disappear, as reproductive isolation prevents the invasion of traits from one species to another.

Both interspecies and species selection are believed to play a significant role in the evolution of a distinct class of traits. These traits are expressed at the level of a species or population, rather than at the individual level. Typical examples of such traits include population density, population variability, dispersal capacity, and population fragmentation, among others. For a long time, it was widely but erroneously believed that only this class of traits was subject to species and interspecies evolution. However, it is now recognized that species and interspecies selection can also influence traits beyond this specific category, affecting a broader range of evolutionary processes.

Selection on the Level of Ecological Communities: Biomes and Beyond

Definition: Biome-level selection, also referred to as community-level selection, is the competition for survival, adaptability, and invasiveness among different biomes (ecological communities) within a specific, potentially shared, environment.

Natural selection, a fundamental process driving evolution, is most commonly discussed in the context of individuals, populations, and species. However, it is possible that selection could occur at even higher levels, such as entire ecological communities or biomes, and potentially even at a cosmic scale, with entire biospheres of various planets competing.

Biomes, such as tropical forests or deserts, and "mini-biomes", like freshwater ponds or mountain wetlands, are unique ecological units characterized by a community of multiple species that have adapted to live together in a specific physical abiotic environment. Selection at the biome level refers to the interactions and dynamics of entire ecological communities occurring in particular locations, rather than focusing solely on individual species or traits. The outcome of competition and selection between biomes is primarily influenced by the abiotic conditions prevailing in a given location. The dominance of a particular biome in a given area is determined by these conditions and the local history, which is

influenced by both deterministic and random events.

Nonetheless, the results of competition between biomes is influenced by the biological species that compose each biome, which can affect the spread, retreat, and stability of not only their own biome but also potential competing biomes. Some species can alter their habitat (the environment where an organism or a community of organisms lives) in such a way that it becomes unsuitable for species of competing biomes. Other species can interact directly with species of competing biomes, eliminating them through predation, for example. If such predation affects a key species or group of key species of a given biome, it can lead to the destruction of the entire biome. Experiences with numerous invasive species demonstrate that even the introduction of a single species (e.g., the introduction of the zebra mussel in North American waterways) can completely disrupt the functioning of an apparently stable biome, leading to its temporary or often permanent replacement by another biome.

In many cases, a particular biome is inherently unstable and will automatically transition into another biome over time. Biomes then inevitably progress through various successional stages, culminating in a climax stage. In some instances, such development is cyclical, and the cyclical alternation of fundamentally different ecological stages ensures the long-term stability of a given biome (or rather meta-biome) and its resistance to replacement by another biome.

The evolution of biomes is often linked to the evolution of the species that compose them. However, this connection may not be tight; a species or group of species that play a crucial role in the functioning of a particular biome may be replaced in the macroevolutionary timeframe by other species that can begin to perform the same function within the biome. An example of such a change can be observed in the evolution of coral reefs. Early reefs were primarily constructed by rugose and tabulate corals, which thrived during the Paleozoic Era. In contrast, modern reefs are predominantly dominated by scleractinian corals, which emerged during the Mesozoic Era and continue to play a vital role in shaping present-day reef ecosystems.

The main mechanism driving the competition and evolution of biomes is not analogous to selection (competition of variants of biomes for higher speed or efficiency of reproduction – spreading), but rather stability-based sorting, the competition for the slowest rate of disappearance. This is because biomes exhibit very low heritability. Species that make up a specific biome do not create an analogy of propagules in which they are passed on together to subsequent generations, as genes of the same organism do. Instead, in a typical case, a biome is created de novo on new territory as individual species that make it up arrive. If a particular biome in a specific location forms an excellent combination of species, there is no guarantee that this combination of species will be inherited by the biome that forms in another location. Systems without heritability can be subject to sorting in terms of stability, but they cannot undergo natural selection. The evolution of biomes occurring in long-term timeframes is, therefore, only a very rough analogy to the evolution occurring at the level of individuals and species.

Selection at the Planetary Level: The Gaia Hypothesis and Implications for Earth's Biosphere

The Gaia hypothesis, proposed by Lovelock and further developed by Lovelock and Margulis, presents an intriguing perspective on selection above the species level, extending to the entire planet (Lovelock, 1983; Lovelock & Margulis, 1974). In its strong variant, the hypothesis suggests that Earth's biosphere functions as a single, enormous super-organism. This super-organism, named Gaia, is proposed to have various regulatory mechanisms that maintain optimal conditions for life, such as surface temperature and atmospheric chemical composition. A weak version of the Gaia hypothesis proposes that geological and biological cycles are tightly interconnected on Earth, with living organisms significantly influencing geological and geochemical processes.

Accumulated evidence over the past 40 years supports this weaker variant, demonstrating the profound interplay between life and Earth's properties.

From an evolutionary biology standpoint, the formation of global homeostatic mechanisms supporting life appears highly improbable. Gaia, as a hypothetical super-organism, lacks competition in our region of the universe, and without competition, selection cannot occur. However, selection is not the only mechanism that can create a complex system capable of maintaining long-term equilibrium. The same goal can be achieved through universally acting *stability-based sorting* processes, which can influence Gaia's evolution at the level of individual internal homeostatic systems as well as interplanetary levels.

The long-term stability of various systems on Earth, such as specific biomes, can be attributed to the fact that systems and subsystems are more likely to be encountered in stable states, sustained by negative feedback mechanisms, than in transient unstable states. Therefore, it is not surprising that we find various ecological systems maintained in a stable state over long periods, thanks to the existence of diverse feedback loops, despite being continuously exposed to steady or fluctuating external influences. Among the former are the gradual increase in the intensity of radiation from our star, the Sun, and among the latter are random catastrophes of abiotic or biotic origin. Systems without the necessary negative feedbacks have disappeared or transformed into other, more stable systems.

At the planetary level, stability-based sorting may also occur. It is likely that we will more frequently encounter planets with a biosphere maintained in a stable state by systems of negative feedbacks than planets without such a system. However, it is also possible that the mere presence of life, particularly the existence of intelligent life that has the potential to destroy the entire biosphere or even the entire planet, introduces instability to planetary systems, making planets without life (or higher forms of life) even more common.

The profound version of the Gaia hypothesis, while fascinating, may bear potentially hazardous implications. It is perhaps more prudent, and unfortunately, likely closer to reality, to perceive Earth's biosphere as a chaotic and sensitive system, vulnerable to irreversible damage from human interference, rather than as a purposefully arranged organism capable of neutralizing our various impacts on its structure.

Conclusion

The expansive range of evolutionary selection, spanning from kin to group, interspecific, clade, species, biome, and potentially even planetary levels, illuminates the multilayered complexity of life's evolutionary processes.

Kin selection, a concept introduced by W.D. Hamilton, demonstrates the essential role of genetic relationships in steering behaviors that augment inclusive fitness. Examples of altruistic behaviors, eusociality, and even spiteful tendencies underscore the profound influence of genetic relatedness in guiding evolution. Without a doubt, kin selection emerges as a potent force that can drive incredible adaptations, transcending the conventional notion of individual fitness.

Group selection, or interdemic selection, layers an additional degree of complexity onto the evolutionary tableau. This form of selection operates at the group or population level, where the success of a group can impact the evolutionary trajectory of its constituent members. It provides potential explanations for the evolution of behaviors fostering cooperation and altruism among loosely related or unrelated individuals. Despite recurring debates surrounding its validity, group selection offers compelling explanations for numerous phenomena related to altruistic and cooperative behaviors in genetically unrelated individuals.

In the context of interspecific selection, competitive interactions between distinct species create an evolutionary landscape with significant implications for biodiversity. This form of selection arises from instances where species compete for similar resources. This competition can lead to the elimination of less competent species, or those with diminished resistance to shared predators or parasites. One main outcome of interspecies

competition is niche pruning, which narrows the ecological specialization of individual species. Another result could be the extinction of one of the competing species, either within the entire area or just a portion of it.

Species selection, in turn, elucidates how traits related to resistance to extinction and capacity for speciation can take precedence, thus shifting the focus from individual fitness to species and higher taxa survival and expansion. Contrary to what the name might suggest, in this type of selection, it's not the individual species competing for a higher frequency of speciation and lower frequency of extinction, but rather the individual clades, the distinct branches of the phylogenetic tree. Furthermore, both selection and, arguably more so, stability-based sorting fuel the process of species selection. Species selection provides us with a theoretical framework for studying evolutionary trends and other macro-evolutionary processes that occur over extended geological timescales.

When considering biome evolution, the primary driver is competition based on stability, rather than selection. Biomes are subject to stability-based sorting due to their low heritability, and as a result, competition between biomes can infrequently give rise to more complex adaptations. However, this competition underpins many macroecological phenomena and powers numerous ecological processes, deserving greater attention in explaining ecological events.

Lastly, the Gaia hypothesis brings in a planetary perspective on selection, suggesting the potential for Earth's biosphere to function as a unified super-organism capable of long-term equilibration in the face of fluctuations caused by random external influences. While the existence of global homeostatic mechanisms supporting life might seem improbable, numerous Earthly processes incorporate negative feedback mechanisms, ensuring their long-term stability. As with selection among biomes, the driving force here is not selection, but stability-based sorting.

This exploration of selection across various scales – from kin to group, interspecific, clade, species, biome, and planetary – highlights the complex, multifaceted nature of life's evolutionary processes. Every level provides unique contexts, mechanisms, and implications for selection, painting a rich picture of the intricate interplay between organisms and their environments.

The contemporary concept of multilevel selection doesn't present a comprehensive model capable of fully describing or explaining evolutionary processes. Instead, it stands as an intellectual compromise, facilitating discourse among proponents of inter-allelic, individual, and group selection without conflict. This concept proposes that selection operates simultaneously at all levels, suggesting a cessation of disagreements. This cornerstone idea is undoubtedly accurate. However, in many instances, it's essential to ascertain the specific level where selection is in operation. Moreover, it is frequently crucial to distinguish between the levels where selection drives evolution and where stability-based sorting takes precedence.

Cross-References

- ▶ Altruistic Behavior
- ▶ Gaia
- ▶ Group Selection
- ▶ Inclusive Fitness Theory
- ▶ Interdemic Selection
- ▶ Kin Selection
- ▶ Menopause
- ▶ Religion
- ▶ Species Selection
- ▶ Spite Behavior
- ▶ Stability-Based Sorting

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