Hypothesis

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The Driving Force of Natural Selection: Maximizing Entropy Production Rates

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Abstract: Although evolutionary theory has yet to fully explain why natural selection occurs, it is crucial to recognize that this phenomenon extends beyond biological systems and is evident in physical systems as well. Specifically, in compliance with the second law of thermodynamics, isolated and closed non-equilibrium systems tend to progress toward states in which entropy increases. When there are multiple pathways for entropy production, such systems will select combinations of pathways that maximize the rate of entropy production from among the available paths. This is known as the fourth law of thermodynamics. Life processes represent one way to achieve increased entropy in nature. Genetic mutations produce organisms with differing rates of entropy production, and when these organisms coexist, they form combinations of pathways with varying rates of entropy production. Nature selects among these possible combinations, selecting those that achieve the fastest rates of entropy production, thereby driving the evolution of life. The process of life's evolution essentially involves exploring and selecting pathways that achieve fast entropy production across different free energy reservoirs through random mutation. As genetic mutations continue and nature persistently selects for faster entropy production rate, information accumulates, further accelerating the rate of entropy production. This physical selection for the pathways that minimize potential or maximize entropy at the fastest possible rate given the constraints, serves as a fundamental driver of the origin and evolution of life.

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Background

Darwinian evolution theory has established the foundation of modern biology, encompassing the fundamental elements of common ancestry, heritable variation, and natural selection[1]. The concept of common ancestry emphasizes that all extant species derive from a shared ancient origin, providing a framework to understand the unity underlying biodiversity and revealing profound evolutionary relationships and kinship among different forms of life[2]. Heritable variation refers to genetic differences present within populations that can be passed on to offspring, serving as the raw material upon which natural selection acts[3,4]. Natural selection, the pivotal mechanism driving evolutionary processes, rests on a fundamental principle: individuals that are more adapted to their environment have a higher probability of survival and reproduction, thus more likely to pass on favorable genetic variations to their descendants[3,4].

Adaptability, commonly referred to as fitness, is defined as the reproductive success of a particular genotype within its given environment[5]. Specifically, fitness measures an individual's capacity to pass its genes to the next generation, encompassing both its survival and reproductive abilities. Individuals with higher fitness are better equipped to survive in specific ecological settings and successfully transmit their genes to offspring. Fitness is a relative concept, contingent upon the specific environmental conditions in which an organism finds itself. Depending on the context, it can include attributes such as keen vision, rapid reflexes, and muscular strength. Notably, Darwinian fitness is a statistical concept, focusing on trends at the population level rather than the fate of

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individual organisms5. In practice, scientists measure fitness by observing changes in gene frequencies over time within populations, indicating that the outcome of natural selection is the alteration of gene frequencies within these populations[5].

However, Darwin's theory of evolution does not explicitly explain why nature performs "selection" or what it is "selecting" from a physical perspective, especially given the view that evolutionary processes lack a predetermined direction. Even within the framework of modern synthesis of evolutionary theory, this question remains unanswered[6,7]. To address these issues, we need to transcend traditional evolutionary frameworks and seek deeper explanations within the realm of physics theory.

Life Activities and the Entropy Increase of Systems

We must first delve into the question of whether nature performs a “selection” solely during biological evolution or whether it universally operates such a “selection” mechanism across all physical processes in nature, namely physical selection[8–11]. If one assumes that nature universally selects all physical processes, then according to Occam’s Razor, these processes should adhere to a unified principle. Otherwise, we would be obliged to hypothesize the existence of two distinct yet non-contradictory natural laws. The First Law of Thermodynamics asserts the conservation of energy over time. However, when external influences are not considered, the Second Law of Thermodynamics introduces a "selection" or directionality to natural processes[8,11–13]. Examples such as the spontaneous diffusion of ink in water, the dissolution of salt, and radioactive decay can be viewed as generalized instances of physical selection[8,11,14,15]. Without the constraints of the Second Thermodynamics Law, a drop of ink in a glass of water could assume numerous statuses, but due to this law, the ink diffuses freely until the water becomes uniformly tinted. This is also the most probable state among all possibilities, indicating that physics selects the state with the highest probability. Similarities can be drawn between the dissolution of salt and radioactive decay. Both are spontaneous processes in the absence of external forces. This signifies a tendency for systems to evolve spontaneously towards states that maximize entropy. Since the Big Bang approximately 13.8 billion years ago, our universe has been evolving in the direction of increasing total entropy, according to the Second Law of Thermodynamics.

However, the existence of life appears to be in contrast with this ubiquitous trend of entropy increase. Lifeforms are capable of drawing matter and energy from their surroundings, constructing and maintaining highly ordered structures, undergoing self-replication, growth, development, and evolution. This process actually reduces the degree of disorder within lifeforms. In response to this paradox, Erwin Schrödinger had put forward the view that “life feeds on negative entropy”[16].This essentially refers to the process of lifeforms continuously exchanging matter and energy with their external environment through metabolic activities, thereby counteracting the entropy increase generated during life activities and maintaining the complexity of their organization and the orderliness of their life processes. The term “negative entropy” is not a reference to a specific form of matter or energy, but rather a figurative representation that emphasizes how lifeforms counteract their inherent entropy increase tendency by orderly absorbing and transforming matter and energy from the external environment to sustain their vital state.

Within lifeforms, although their internal entropy decreases, the overall entropy of the environment increases, which is not contradictory to the Second Law of Thermodynamics but rather grounded in it. A similar phenomenon exists in non-living systems, where the orderliness of a subset of the system increases while the entropy of the rest of the system increases, leading to an overall entropy increase of the entire system[17]. Biological organisms achieve this through their cell membrane system, which separates them from the external environment, enabling an increase in the orderliness within cells and a concurrent increase in entropy outside the cells.

Therefore, we can speculate that the system entropy increase caused by biological activities and the entropy increase resulting from physical process evolution are governed by the same underlying principle, namely, the manifestation of the Second Law of Thermodynamics[8,14,18,19]. This leads us to the answer for the question, "Why does nature make a selection?" Nature, among all possible evolutionary processes, "selects" those that result in an increase in entropy.

The Combinations of Pathways with the Fastest Rates of Entropy Production Under Physical Selection

Amidst the diverse array of entropy production pathways in isolated closed non-equilibrium systems, we ponder: What "selections" does nature make among these pathways? Through the following thought experiment, we seek to unravel this enigma.

Imagine a closed box in a zero-gravity environment. Inside it is a partition that divides it into two spaces. The two separated spaces contain gases of different colors. The partition has two holes of different sizes with switches. When the switches are opened simultaneously, the gases of different colors will exchange through the two holes. Eventually, according to the second law of thermodynamics, there will be a uniform color distribution. In this scenario, more gas exchange will occur through the larger hole, leading to a higher rate of entropy production. This thought experiment demonstrates that the faster pathway among the entropy production alternatives contributes more significantly to the overall entropy production. Echoing this observation, Adrian Hill, in his 1990 study, discovered that the entropy increase rate per unit area is a pivotal factor determining distinct growth morphologies in the crystallization of materials from molten or dissolved states into solid phases[20]. This underscores nature's proclivity to favor evolution modes that efficiently generate entropy during the transition from higher to lower free energy states.

Analogous phenomena abound in nature. Petroleum combustion, battery discharge, and the genesis of typhoons[21] are all instances where processes could potentially proceed along slower pathways of free energy release, yet once the faster pathway is activated, a substantial amount of free energy preferentially flows through this pathway. It is noteworthy that pathways with slower entropy production are not "abandoned" by nature; they still emit free energy, albeit in lesser quantities. Like the smaller hole in the partition, no matter how tiny it is, gases will still exchange.

Entropy maximization is the ultimate destination of all closed and isolated systems, and nature tends to select the combination of pathways that can achieve entropy maximization the fastest. Some physicists refer to this as the fourth law of thermodynamics, which is expressed as "*A system (the universe or any arbitrary out of equilibrium subsystem volume within it) will select the path or assembly of paths out of available paths that minimizes the potential or maximizes the entropy at the fastest possible rate given the constraints*"[8,15,22]. This principle not only addresses the direction of change but also emphasizes the rate of change, serving as a significant complement to the Second Law of Thermodynamics[18]. Previous researchers have linked this physical principle to evolution, suggesting that it underlies the mechanisms driving evolutionary processes[8,15]. Rod Swenson argued that the 4th law of thermodynamics provides a universal physical selection principle that encompasses natural selection, the emergence of life, and cognitive processes[8]. The subsequent reasoning in this paper will be based on this physical principle, and should it prove invalid, the ensuing conclusions would no longer hold.

The Accelerating Effect of Life Activities on Entropy Production

Let us revisit the iconic thought experiment in physics—Maxwell's demon, initially conceptualized by the physicist James Clerk Maxwell in 1871 [23]. This hypothetical entity aimed to explore the limits and potential exceptions of the second law of thermodynamics. Maxwell's demon envisioned an intelligent being that, theoretically, could violate the second law by allowing only fast-moving (hot) molecules to pass from one gas container to another, while retaining slow-moving (cold) molecules. This process would theoretically accumulate hot molecules in one container. This creates a temperature gradient that could drive a heat engine. It poses a challenge to the second law of thermodynamics.

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Subsequent research uncovered the underlying mechanisms of Maxwell's demon. Advances in information theory revealed that the demon's acquisition and processing of molecular information actually consume energy, leading to additional entropy production, thus upholding the universal validity of the second law. Specifically, Landauer's principle underscores the energetic cost of information erasure, bridging the apparent gap in the system's total entropy and ensuring that the universe's entropy tends to increase[24,25].

Consider two containers filled with gas, each at a different temperature, separated by a small door controlled by a demon. The demon can observe the velocity of each gas molecule and has the ability to open and close the door while consuming energy. The demon selectively identifies high-velocity molecules and allows them to move from one container to the other, while retaining low-velocity molecules in their original container. However, the demon imposes a "toll" on the high-velocity molecules passing through the door by storing a portion of their energy within itself. The toll collected from each high-velocity molecule must exceed the energy consumed in identifying the molecule and opening the door. Theoretically, as long as the energy difference between the two containers is greater than the energy required for identification and door operation, the system can continue to function until the energy difference becomes insufficient to cover the demon's operational costs. Since this process does not violate the Second Law of Thermodynamics, it results in an overall increase in the over entropy of the two containers. If the demon can accumulate the toll and use this energy to replicate itself, new demons will be produced.

ATP synthase, found in the membranes of bacterial cells or mitochondrial membranes of eukaryotic cells, functions similarly to the demon described in thought experiments. ATP synthase plays a critical role in cellular energy production[26,27]. Located in the cell membrane, it participates in chemiosmosis. When protons ($H+$) flow from areas of high concentration (outside the membrane) to areas of low concentration (inside the membrane), ATP synthase harnesses this energy to catalyze the formation of ATP (adenosine triphosphate) from ADP (adenosine diphosphate) and inorganic phosphate (Pi)[26,27]. ATP serves as the primary energy carrier in cells[26,27]. Thus, organisms rely on ATP synthase embedded in their membranes to convert energy and maintain their ordered state. Cells use this converted energy for self-replication, including the replication of ATP synthase itself. Similar to the demon in the thought experiment, the ability of ATP synthase to recognize protons stems from its protein conformation, which is encoded by DNA.

Further, imagine if there were two gates between the containers: one always open and the other controlled by the demon. Could the demon still collect a "toll"? Food spoilage offers a relevant analogy. Among various degradation processes, microbial decay is often the most rapid and efficient, accelerating free energy release and transformation through metabolic activities. Similarly, in this hypothetical experiment, even if the demon's entropy production rate is lower than that of hot molecules freely passing through the open gate, the coexistence of both pathways results in a higher overall entropy production rate. Therefore, the demon can still collect a "toll" by efficiently converting and transferring energy, thus accelerating the system's entropy production.

Sustainable Entropy Production Acceleration through Genetic Mutations and Natural Selection

The origins of life on Earth may be traced back to the physical selection pressures arising from the release of accumulated energy sources such as solar, geothermal, or chemical energies in the early Earth environment. The presence of early life forms likely accelerated the pathways through which the Earth dissipated its stored free energy, thereby contributing to an overall increase in the planet's entropy[28]. This aligns with the views of Ilya Prigogine, who argued that self-organizing phenomena can only occur in non-equilibrium systems where there is an exchange of matter and energy with the environment and where complex nonlinear coherent effects arise within the system[29]. He termed the ordered states formed under these conditions as dissipative structures[29].

Prior to the emergence of life, the quantity of large molecules on Earth was likely very limited. Early life on Earth may have originated from autocatalytic chemical networks composed of a few compounds[2]. Due to the effect of the second law of thermodynamics, the original pools of energy were unstable and were subject to various perturbations. Under these disturbances, compounds within the chemical networks could form different combinations. Some of these combinations released free energy efficiently, others less so, while some may have possessed information storage capabilities. Such information storage might have arisen from certain specific compounds whose presence facilitated the more stable and efficient reorganization of the chemical network. When seasonal changes or other perturbations depleted or rendered unusable the free energy available in an original pool for the chemical network, the network would disintegrate driven by the second law of thermodynamics. However, when free energy is available again, chemical networks with information storage capabilities would be reconstituted randomly on a preferential basis.

This is similar to the hypercycle model proposed by Manfred Eigen, where the system can self-direct its overall replication and provide catalytic support for the next cycle[30]. Information carriers not only contain the information needed for their own replication but also the information required to generate specific mediators (often enzymes) that facilitate the activation of the next information carrier. A hypercatalytic cycle consists of multiple intertwined catalytic cycles, requiring two essential functions: each cycle must be able to self-replicate, and the product of one cycle must support the next[30]. Biologists Tracey Lincoln and Gerald Joyce discovered a similar system involving two ribozyme molecules that could sustain each other's replication[31]. These molecules could replicate themselves without the help of surrounding proteins or other biological structures. More interestingly, these molecules sometimes mutate, allowing for Darwinian evolution where more adaptive structures are more likely to survive. Although this is not sufficient to constitute a cell, it does demonstrate a critical step in the transition from chemistry to life.

Once physical and chemical self-organizing processes produced replicable material structures, replication could proceed repeatedly, establishing mechanisms for the transmission of genetic information[10]. At this point, natural selection comes into play, continually optimizing the rate of entropy production. Whether a system can replicate itself and transmit information may be the key distinction between natural selection and physical selection. For example, entropy production by setting a forest ablaze is not sustainable over different seasons and involves randomness. In contrast, natural selection favors organisms such as animals and microorganisms that consistently and stably release the free energy stored in forests, achieving a sustainable increase in the rate of entropy production. In other words, natural selection can be regarded as a special case of the physical selection, since it involves the selection of replicating systems[8,10].

Natural selection fundamentally involves the selection of replicating systems, which translates into a selection for the number of offspring. To support this argument, we propose the following scenario: consider two minimal viable units from Species A and Species B, both capable of increasing the overall entropy of their environment at the same rate. Additionally, both entities possess an equal amount of surplus energy beyond what is required for basic survival and reproduction. If Species A uses all its surplus energy solely for its own survival, it will not be able to increase its offspring count. Conversely, Species B divides its surplus energy, using part for its own survival and the remainder for offspring reproduction, thus necessitating some investment in the increased number of offspring. In a scenario without Natural selection, during the first generation of reproduction, selective forces would be ineffective because both species contribute equally to the rate of entropy production in the environment. However, by the second generation, the population of Species B would surpass that of Species A. Given that the minimal viable units of both species contribute equally to the rate of entropy production, the collective contribution of Species B to the entropy production of the environment would exceed that of Species A. Assuming no competitive interactions between the two species, after multiple generations of reproduction, the population of Species B would far outnumber that of Species A. This description presents an idealized scenario; in reality, Natural selection tends to favor even partial sacrifices of parental fitness to increase the number of offspring[32,33].

In most cases, the interests of parents and offspring are highly aligned, thus evolution does not excessively sacrifice parental well-being to increase offspring numbers[34]. Instead, organisms enhance offspring production through efficient energy utilization methods, such as the streamlined body shapes of animals, optimized movement for different body sizes, and the closing of stomata in plants at night[35]. The constructal law states that for a flow system to persist over time, it must evolve in such a way as to provide easier access to its currents[35]. On the surface, the pursuit of rapid rate of entropy production by natural selection seems at odds with the conservation of energy use by organisms; however, both ultimately aim at the same goal: maximizing the entropy production through increased offspring numbers. Natural selection molds organisms into channels for rapid and efficient energy flow and reproductive machines[36].

The second law of thermodynamics also affects the replication of genetic information, leading to errors that produce organisms contributing differently to the rate of environmental entropy production, providing raw material for natural selection[4,37]. While most genetic mutations reduce individual fitness, if the genetic mutation base is large enough, some mutations might unexpectedly increase fitness, significantly increasing offspring numbers and survival in competition, thus favoring certain species. Subsequently, influenced by the second law of thermodynamics, errors occur again in the replication of genetic information, allowing natural selection to act anew. This cycle repeats, iterating continuously, eventually evolving the diverse and varied life forms we see today. These replicating systems called organisms appear designed for future survival and reproduction but have merely retained ancestral replication errors that allowed their ancestors to survive and propagate. Natural selection achieves sustainable increases in the rate of entropy production and information through selection of genetic variation, a sustainability achieved through long-term and continuous physical selection.

Genetic inheritance and variation essentially involve information replication and variation, with variation being the source of new information. With the advent of human society, information replication no longer relies solely on producing offspring, and new information creation is not confined to genetic mutation alone. Information can be transmitted both orally and in writing. Moreover, human beings are capable of leveraging existing knowledge to generate new knowledge. Knowledge becomes a tool guiding energy flow, and the more energy acquired, the larger the human population grows. From hunter-gatherer societies to agricultural societies, and then to industrial societies, the energy harnessed and utilized by humans has grown exponentially. Therefore, the evolution of human societies may also be a manifestation of the fourth law of thermodynamics[8,9,38,39].

Nature Accelerates Entropy Production by Exploring All Possible Pathway Combinations

Nature tends to select pathways that maximize entropy at the fastest possible rate. However, this does not imply that evolution has a fixed directionality. In fact, the distribution of free energy in nature is uneven, with free energy pools varying in size and the amount of usable free energy they contain. Consequently, the rate of entropy production is heavily influenced by the specifics of these free energy pools. In environments where free energy supply is relatively scarce, unable to support the survival and reproduction of large organisms, such conditions favor the evolution of smaller species, much like how a pond cannot sustain whales. In these settings, smaller organisms can utilize limited resources more efficiently, ensuring their survival and reproduction, and thereby accelerating the rate of entropy production within the free energy pool over a short period. Conversely, in free energy rich environments, nature indeed selects larger organisms to explore the limits of the rate entropy production along single pathways. However, these larger organisms do not entirely deplete all available free energy; instead, their carcasses, excreta, and sweat still contain residual free energy. To utilize this free energy, saprotrophic and parasitic microorganisms evolve, playing a crucial role in free energy release within ecosystems. Energy is passed down like a baton relay, from larger organisms to smaller ones, until the gradient of free energy difference reaches the limits of what life can transfer. When the free energy in large pools is insufficient to support megafauna, these organisms are naturally phased out, as evidenced by the extinction of dinosaurs. Moreover, social

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organisms may evolve within large free energy pools, accelerating entropy production through cooperation among individuals. Different species fulfill distinct roles within ecosystems, with nature selective pressures generally aimed at minimizing the energy gradient between upstream and downstream components in the shortest time possible[40].

The long-term experimental evolution project conducted by Richard Lenski's team indirectly illustrates this point[41]. Typically, E. coli metabolizes glucose but does not feed on citrate in aerobic conditions. However, when citrate was added to the culture medium, Lenski and his collaborators observed that, around the 31,000th generation, certain bacteria in one of the flasks had evolved the ability to metabolize citrate, not just glucose[41]. This means that the two substances present in the medium (glucose and citrate) created an energy gradient, with E. coli initially only releasing energy from glucose. After many generations, they gained the capability to release energy from citrate. While this phenomenon superficially indicates that E. coli acquired the ability to metabolize citrate, fundamentally, it reflects the ubiquitous pursuit of natural selection to minimize energy gradient in the shortest possible time[36,42,43].

Nature drives the evolution of organisms through random mutations[4], capable of exploring and utilizing all possible pathways to accelerate entropy production whenever exploitable free energy gradient exists. Regardless of the magnitude, stability, and continuity of free energy supplies, nature explores and exploits every possible pathway to speed up the rates of entropy production, which is a manifestation of the 4th law[8,15].

Conclusions

Since the Big Bang approximately 13.8 billion years ago, our universe has been evolving toward a state of maximum entropy. Nature tends to select combinations of pathways that maximizes the entropy at the fastest possible rate given the constraints, aiming to reach a state of maximum entropy as quickly as possible. Under this selective pressure, early life emerged and significantly accelerated the rate of entropy production on Earth. As natural selection continued to favor higher rates of entropy production, life forms evolved, further hastening the planet's entropic production rate. The origin and evolution of life represent nature's effort to quickly attain a state of maximum entropy, rather than being mere insignificant accidents in the primitive environment. The process of cosmic entropy increase resembles a stone rolling down a mountain, gathering speed as it descends, ever accelerating.

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