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A POTENTIAL SURVIVAL STRATEGY DURING THE LATE HEAVY BOMBARDMENT

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SUMMARY: The Late Heavy Bombardment (LHB) represents a period of time in which an increased number of impactors collided with the Earth. While there were continuous collisions of impactors globally, these would be perceived by populations of life as locally infrequent, as they occurred at different times and locations across the planet. These impactions presented a severe and unpredictable environmental pressure on life, as they could at any moment destroy organisms and their local habitats. However, such an environment could potentially lead to the selection of a particular evolutionary strategy, bet hedging, which is an adaptation to unpredictability itself. Thus, a model for analysing this has been put forward in the form of a system of rings arising from an impact—consisting of the inner primary and outer secondary rings, which demonstrates the dynamic interplay between the external pressure from impact dynamics and life's evolutionary response towards it. The model demonstrates that there is a longer relaxed period where organisms thrive and a short violent period where they must survive three violent events and respond to a potentially different environment. This evolutionary strategy consistently results in a higher number of surviving organisms compared to other evolutionary strategies; thus, it may have played a crucial role in life's endurance through the LHB—an insight relevant to astrobiology.

Key words. Astrobiology – Earth – Minor planets, asteroids: general

1. INTRODUCTION

Impactors have affected the Earth ever since its formation approximately 4.5 billion years ago. Impactors have continued to be infrequent guests, although the frequency and size of these have declined since the event known as the Late Heavy Bombardment (LHB) (Reyes-Ruiz et al. 2012). This event, which may have been due to discrete early, post-accretion, and later planetary instability-driven populations of impactors (Bottke and Norman 2017), began approximately 4 billion years ago. It is usually considered to have ended 3.8 billion years ago, but some evidence indicates that terrestrial impacts did not cease but rather waned gradually until approximately 3 billion years ago (Lowe et al. 2014).

The total mass deposited on the Earth during this event has been estimated to be between 1.8·1020 and 2.2·1020 kg through dynamic modelling (Gomes et al. 2005) and the cratering record of the Earth's moon (Hartmann et al. 2000). This value is in comparison nearly the entire mass of the dwarf planet Ceres—the largest object in the asteroid belt located between the planets Mars and Jupiter.

The LHB has been well-studied, particularly with regard to the many pros and cons of this controversial period of the history of the Earth and the solar

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system. Thus, here, there is not a focus on the many intricate details of the LHB in relation to planetary science. Instead, it is assumed for the sake of discussion that it took place and the relationship that may have existed between this event and life on Earth is discussed.

While the details remain under debate and much remains to be elucidated, an autonomous cell with a high degree of certainty was present on the Earth 3.5 billion years ago in the Archean Eon (Schopf et al. 2007), which is usually dated as spanning between 3.8 and 2.5 billion years ago (Coenraads and Koivula 2007). Yet, the prebiotic processes that produced this microbial life probably did not occur in a single event; instead, the transition from chemistry to biology likely occurred as a gradual series of thresholds of increasing complexity over time (von Hegner 2021). Thus, some lines of evidence point to the emergence of life on the Earth as being between 4.1 and 3.5 billion years ago (Bell et al. 2015) in the Hadean Eon, which usually dates from the end of the Earth's accretion until 3.8 billion years ago (Coenraads and Koivula 2007).

While a relatively modest number of very large impactors were presumably responsible for a large part of the mass deposited during this event, certain models predict ∼90 impactors 50 km or more in diameter all separated by over 1 million years on average (Abramov and Mojzsis 2009), it also seems reasonable to assume that numerous smaller impactors of varying sizes in very large numbers hit the Earth in the same period at different times and locations. Thus, that it was a common occurrence for life overall to experience impactors with sufficiently large diameters or densities to reach the planet's surface and impact, but be small enough to be local impactors, is assumed here.

Thus, an important question arises: did life act in response to this 'heavenly onslaught?' This is a non-trivial question to seek answers to, as life is not a passive entity that is merely moved around. Life responds, not in a Lamarckian sense, but in a Darwinian sense. It responds actively to the stressors it encounters, right from stressors from competition among organisms within or between species or environmental stressors. Thus, where there is life, there is evolution, which leads to adaptations that will affect the possibility of an organism's survival, even in an environment characterised by the LHB.

That large impactors can have significance for life in an astrobiological setting has been explored through the idea that impacts can have such high velocities that matter harbouring life is ejected away from the planet, hypothetically leading to planetary reseeding (Sleep and Zahnle 1998, von Hegner 2021) and/or lithopanspermia (von Hegner 2020). Both planetary reseeding and lithopanspermia do not merely allow the passive transport of life, but evolutionary responses can also take place and affect survival.

Furthermore, for the more modestly sized impactors where the minimum impact velocity a small body has with the Earth is 11.2 km/s (Cordero-Tercero et al. 2016), as this velocity allows it to travel through the atmosphere and make an impact, life remains on the planet in relative proximity to the impact site, and evolutionary responses can be expected as well.

Although there were continuous incoming impactors globally, they were distributed locally at different times and locations on the planet. There are no fixed locations or times that impactors are expected to arrive. This continuous, yet infrequent, incoming of impactors would have provided an erratic environment that presented severe and unpredictable environmental pressures on life.

Certain studies have estimated that the few very large impactors that affected the Earth during the LHB would only have resurfaced less than 25% of the planet's surface. Thus, most of the crust was not melted or thermally metamorphosed to a significant degree (Abramov and Mojzsis 2009). While this did not seem to have been the main issue, and microbial life, such as bacteria and archaea, is tough, incoming impactors could still arrive at any moment and destroy them and their local niche. Thus, it is not obvious how life could build stable ecosystems or endure under such conditions.

However, such a violently unpredictable environment could lead to the selection of a particular evolutionary strategy, bet hedging—an adaptation to unpredictability itself. This could potentially result in an effect that provides numerical values for organisms that are different from those that could be expected from a purely physical angle, i.e., it changes the probability of the continuation of life and thus may have played a crucial role in the endurance of life through this part of life's history.

In the following, a number of realistic constructed scenarios are put forward in order to provide high-level characterisation of the evolutionary processes that can be initiated in response to the effect that the LHB had on life on the Earth, which is relevant to astrobiology.

In this article, Section 2 introduces the evolutionary strategy bet hedging and the variants that are discussed further. Section 3 introduces the primary ring as a consequence of impacts and clarifies the survival rate of the variants. Section 4 introduces the secondary ring and clarifies the ramifications of evolutionary restraints on the variants. Subsection 4.1 highlights the importance of the primary and secondary ring junction. In Section 5, the developed framework is extended into a more realistic scenario by clarifying the importance of infrequent impactors. Finally, Section 6 summarises the results of this investigation as well as its limitations and strengths, and their implications for other worlds.

2. BET HEDGING

The LHB took place over most of the Earth for a narrowly defined period of its history. While impacting has generally been a continuous global event (with continuous incoming of impactors that, over time, hit most major places on the Earth), these were distributed locally over time and place on the planet.

Thus, from the perspective of a given population of microbial life in a particular place and time, these were infrequent impacts. For them, these would most of the time be experienced as something that happened to a 'neighbour population'. However, that most places would be hit were something that was given with some certainty, albeit it was unlikely that the same place would be hit repeatedly. Thus, if life existed before or during the LHB, perhaps distributed over many different locations on the planet, then this must have been experienced as varying environments offering very uncertain conditions for survival.

A number of evolutionary strategies to cope with environmental uncertainty does indeed exist. Thus, there are three evolutionary modes of response to fluctuating terrestrial environments worth mentioning: adaptive tracking, adaptive phenotypic plasticity, and bet hedging (Simons 2011).

Organisms living in changing environments can adapt to new conditions through the mode of adaptive tracking (Rago et al. 2019). Thus, populations that experience environmental change will gradually adapt one or more traits, meaning that the optimal trait values change continuously. Thus, natural selection results in the gradual evolution of more fitting phenotypes and the removal of previously well-adapted forms (Simons 2011). The main issue here, with regards to the LHB, is that traits that are optimal at one time or place can be disadvantageous at another time or place.

It is possible for organisms living in changing environments to achieve an adaptive fit between phenotype and the environment through the modulation of the phenotype in response to direct environmental sensing; that is, through the mode of adaptive phenotypic plasticity (Beaumont et al. 2009). This mode is an effective solution to environmental variance, since it quickly attains the most fitting phenotype for a range of environments (Simons 2011). The main issue here, with regards to the LHB, is that it is adaptive only if there are cues that allow organisms to match the phenotypes to the new environment. It requires that organisms have experienced cues in a similar environment (Reed et al. 2010). A population of organisms cannot predict where and when they will be affected by an impactor, and therefore, a regular life cycle cannot occur.

However, life does indeed have a strategy for a globally predictable but locally unpredictable environment called bet hedging. This is an evolutionary strategy that generates stochastic variation in fitness-related traits, essentially distributing risk among an array of phenotypes, each of which is neither optimal nor a failure across multiple environments (von Hegner 2020). This mode increases the probability that some organisms will possess a phenotype that ensures their initial survival in a changing and unpredictable environment.

This mode is important with regard to the LHB, as conditions of unpredictable environmental variance can provoke the evolution of bet hedging traits, where the long-term or geometric mean fitness is maximised over time, even at the cost of a decrease in the arithmetic mean fitness (Simons 2011). In bet hedging, fitness is treated as a random variable, meaning that the fitness of individual organisms is not known in advance, but it can nevertheless be treated by a probability distribution (Starrfelt and Kokko 2012). Thus, this evolutionary strategy can be viewed as an adaptation to unpredictability itself (Simons 2011).

It is a strategy well-suited to survival in uncertain circumstances, as would have been the case during the LHB. While the other evolutionary modes may also have been at play, it must be expected that bet hedging occurred under these circumstances, providing more survivors overall, making it a truly ancient strategy.

Bet hedging traditionally occurs in two forms: diversified and conservative (Seger and Brockmann 1987). In the diversified bet hedging strategy, a genotype produces two phenotypes, each of which is most fit for a given environment that shifts unpredictably. For example, a variant can be fit in a wet environment while the other is fit in a dry environment. In the conservative bet hedging strategy, an organism is persistently sub-optimal in two changing environments. Thus, it has traded thriving in an environment for long-term survival.

In the following, the focus will be on the diversified bet hedging strategy in the form of two variants: $V_{\text{Intervallum}}$ and V_{Robustus}.

$V_{\text{Intervallum}}$ is the variant that does best in the environment that an organism lives in, i.e., in the environmental interval between two impacts.

V_{Robustus} is the variant that, in comparison to the other, does best in the face of sudden pressure and heat shock that occurs with each impact.

In the following, only adaptive tracking (hereinafter referred to as mode 1) and bet hedging (hereinafter referred to as mode 2) will be discussed further and used as opposing examples, as adaptive phenotypic plasticity, as will be seen, cannot achieve cues in the given situations.

3. THE PRIMARY RING

In the following, a model is established that illustrates the difference between the two modes. The model consists of the primary ring placed on a flat surface. The primary ring consists of five rings, almost like rings in a tree trunk, in which the impactor strikes in the inner ring—the centre. For the sake of simplicity, no distinction is made here between direct and oblique impacts. To simplify the situation further, a large population of microbial organisms will be considered to be evenly distributed throughout, and all organisms will be assumed to be from the same clonal population, as it is then only necessary to consider variants evenly distributed here.

Today, microbial life exists in virtually all available habitats on the Earth. However, at this early stage in the history of Earth, life may have either been widespread or a limited phenomenon. Since the purpose is to show the inter-relationship between the modes, no matter how large the numbers are, and since traces of life from that time are limited and debated, it will be assumed here that each ring initially contains $N = 5 \cdot 10^6$ organisms. This quantitative assessment would be a low number today, and possibly too high for then, but for the sake of the calculation, this will be assumed here.

3.1. Survivors after impact: Mode 1

The first stage of the interaction between impact dynamics and the evolutionary response is the landing of the impactor and the effect of this on the life present.

Thus, in ring 1 (the centre of impact), 100% of the $1 \cdot 10^6$ organisms perish. In ring 2, 80% of the $1 \cdot 10^6$ organisms perish; thus, 200,000 organisms survive the impact blast. For rings 3, 4 and 5, the survival rate decreases correspondingly by 60%, 40% and 20% (Table 1).

Thus, $n = 2 \cdot 10^6$ organisms out of $N = 5 \cdot 10^6$ organisms survive the impact blast T_1 (Table 1).

In this model, the impactor is in some sense an invariant, as although the incoming impactors may have different diameters, densities, and velocities, it is still the case that the organisms in the centre of the impact blast perish, while those in the adjacent rings might survive. The quantitative assessment with 100%, 80%, 60%, 40%, and 20% of organisms perishing with each consecutive ring is based on that the effect of the impact blast decreases for each consecutive ring.

Only local impactors are considered; the minimum impact velocity a small body has with the Earth is 11.2 km/s and the maximum is 72.8 km/s (Cordero-Tercero et al. 2016), which is sufficient to travel through the atmosphere and make an impact. Global planet-sterilising impactors are not considered here as this would make the present discussion redundant, and because if life existed at the time, then it evidently survived. Thus, only local impactors hitting land or shallow waters are considered, where the impactors have different diameters, densities, and velocities but the same result, thus allowing life to survive in the adjacent rings of impact.

3.2. Survivors after impact: Mode 2

For mode 2, the first phase of the interaction between impact dynamics and the evolutionary response is the impactor's landing and the effect of this on the life present.

In bet hedging, two variants exist simultaneously, but usually not in the same proportion (Seger and Brockmann 1987). Thus, there can, for instance, be 48% of V_{Robustus}, which is a specialist in that it can cope with the pressure and heat shock from the impact blast better than the other variant, and 52% of $V_{\text{Intervallum}}$, which is a specialist that copes with the same environment as the organism in the first mode.

The mutual survival ratio between the variants is assumed to be that 3/4 of the population of V_{Robustus} survives the effect of the impact compared to 1/4 of $V_{\text{Intervallum}}$. The conversion factor for the relationship between the variants is given as follows:

$$\frac{V_{\text{Robustus}}}{V_{\text{Intervallum}}} = 0.25 \tag{1}$$

Thus, in ring 1, 100% will perish among the 48%, i.e., 100% among 480,000 organisms due to the impact blast, while 100% will perish among the 52%, i.e., 100% among 520,000 organisms due to the impact blast. In ring 2, 20% will perish among the 48%, i.e., 20% among 480,000 organisms; thus, 384,000 organisms will survive the impact blast, while 80% will perish among the 52%, i.e., 80% among 520,000 organisms, and thus, 104,000 organisms will survive the impact blast. For the next rings 3, 4 and 5, the survival rate will decrease correspondingly by 15%, 10%, 5%, and 60%, 40%, 20% (Table 2).

Thus, $n = 2.72 \cdot 10^6$ organisms out of $N = 5 \cdot 10^6$ organisms survive the impact blast T_1 (Table 2).

For mode 1, there are many survivors overall when the rings are counted collectively. However, if a new impact of the same strength follows a relatively short time after in the same location, then it will again apply that 80% of the organisms present in ring 2 perish, i.e., 40,000 organisms out of the surviving 200,000 organisms will survive. This is because the surviving organisms survived by random chance, not because the most robust ones were selected. It is a clonal population with similar organisms, so even though there may be longer distances between the organisms this time around (since their survival was random chance), the same proportion will be retained.

Thus, in ring 1, the centre of impact, there will be no organisms to be eliminated this time. In ring 2, 80% of the $2 \cdot 10^5$ organisms will perish, i.e., 40,000 organisms will survive the impact blast. For the next rings 3, 4 and 5, 60%, 40% and 20% of the organisms will perish, while 160,000, 360,000 and 640,000 organisms will survive the impact blast.

Thus, $n = 1.2 \cdot 10^6$ organisms out of $n = 2 \cdot 10^6$ organisms will survive the next impact blast T_2.

Thus, in ring 5, the ring with the most survivors, it will take $T_n = 31$ impacts to reduce the 1 million organisms to a mere $n =\sim$1,000 organisms. For mode 2, it will again apply to the surviving organisms that 20% of the V_{Robustus} organisms present in ring 2 will perish, i.e., 307,200 organisms out of the 384,000 or-

Table 1: Values for mode 1.

Primary ring	**Ring 1**	**Ring 2**	**Ring 3**	**Ring 4**	**Ring 5**	**Total number**
Initial number of organisms	1,000,000	1,000,000	1,000,000	1,000,000	1,000,000	5,000,000
Survivors after impact	0	200,000	400,000	600,000	800,000	2,000,000
Organisms being transported	0	160,000	240,000	240,000	160,000	800,000
Secondary ring	**Ring 6**	**Ring 7**	**Ring 8**	**Ring 9**	**Ring 10**	
Survivors after landing	128,000	144,000	96,000	32,000	0	400,000
Fitting environments	50%	38%	25%	16%	0	

ganisms will survive, while it will again be the case that 80% of the $V_{\text{Intervallum}}$ organisms present in ring 2 will perish, i.e., 20,800 organisms out of the surviving 104,000 organisms will survive.

Thus, in ring 1, the centre of impact, no organisms will be eliminated this time. In ring 2, 20% of organisms will perish among the 48%, i.e., 20% among 384,000 organisms, or 307,200 organisms will survive the impact blast, while 80% of organisms will perish among the 52%, i.e., 80% among 104,000 organisms, or 20,800 organisms will survive the impact blast.

For the next rings 3, 4 and 5, 15%, 10% and 5% will perish among the 48%, while 60%, 40% and 20% among the 52% will survive the impact blast.

Thus, $n = 2.1 \cdot 10^6$ organisms out of $n = 2.72 \cdot 10^6$ organisms will survive the impact blast T_2.

Thus, in ring 5, the ring with the most survivors, it will take $T_n = 28$ impacts to reduce the 520,000 $V_{\text{Intervallum}}$ organisms to a mere ∼1,000 organisms, while it will take $T_n = 120$ impacts to reduce the 480,000 V_{Robustus} organisms to ∼1,000 organisms, a significant difference.

Thus, in subsequent rapid impacts, the organisms in the first mode will gradually perish, while the benefit quickly goes to the next mode. This will not affect the bet hedging strategy however, as a unique aspect of bet hedging is that even after the point where only V_{Robustus} is left after several impacts, i.e., it acts as a bottlenecking effect, where only a modest number of organisms from a larger population survive each time the impactor hits, the remaining V_{Robustus} will continue to be able to produce both variants in the population, regardless of which of the two variants from the clonal population survives.

Therefore, the above scenarios show prima facie that although mode 2 has the most survivors after impacts, mode 1 has many survivors as well. It could, thus, be said that since microbial life reproduces quickly, and assuming there are good conditions for life in the rings after impact, they will quickly build up their numbers again. Therefore, the first mode can be expected to continue to function, either by building up the same number of organisms again and thus surviving, or by having time to build up so many organisms that it takes more impacts than calculated in the example before the population disappears.

However, if impactors collide with greater frequency than the organisms are able to respond to in terms of increasing their numbers to the same level again, and hit in ring 1 each time, then the organisms in the original primary ring will eventually be eliminated completely. In fact, it will be more likely that the next impactor hits another ring, e.g., hits ring 5 instead of ring 1, which drastically reduces the total number of organisms compared to the previous calculation example (more on this in Section 5).

Thus, while the LHB was a persistent event, it is not the case that consecutive impactors hit exactly the same limited location on the Earth with high frequency; thus, organisms should have had some time to rebuild their numbers.

However, it must also be considered that the environment after each impact blast can damage and degrade the environmental conditions in which the organisms lived, i.e., access to nutrients and energy source. Moreover, the environment in the rings may have been fragmented, with some of the fragments molten. It may have taken some time for the environment to recover, meaning that life could not reproduce as quickly as under more ideal circumstances.

Thus, many variables are at stake and, depending on how many impacts occurred consecutively and which rings were affected, this decrease and increase in organism numbers (if viewed purely from a physical science or numerical point of view) could mean that some organisms potentially endured until the impacting subsided; thus, the first mode is expected to have continued to operate.

However, this is not how biology works. If infrequent impacts like this continue to occur, then this will, in fact, provoke an evolutionary response where the first mode could be expected to eventually switch to the second mode. Thus, the continuous infrequent impacts may have led to bet hedging occurring in the population of the first mode. In fact, the second mode must have originated from a dwindling population in the first mode that had experienced several impacts.

Table 2: Values for mode 2.

Primary ring	**Ring 1**	**Ring 2**	**Ring 3**	**Ring 4**	**Ring 5**	**Total number**
Initial number of V_{Robustus} organisms	480,000	480,000	480,000	480,000	480,000	
Initial number of $V_{\text{Intervallum}}$ organisms	520,000	520,000	520,000	520,000	520,000	5,000,000
V_{Robustus} survivors after impact	0	384	408	432	456	
$V_{\text{Intervallum}}$ survivors after impact	0	104,000	208,000	312,000	416,000	2,720,000
V_{Robustus} organisms being transported	0	307,200	244,800	172,800	91,200	
$V_{\text{Intervallum}}$ organisms being transported	0	83,200	124,800	124,800	83,200	1,232,000
Secondary ring	**Ring 6**	**Ring 7**	**Ring 8**	**Ring 9**	**Ring 10**	
V_{Robustus} survivors after landing	86,640	155,520	208,080	245,760	0	
$V_{\text{Intervallum}}$ survivors after landing	66,560	174,880	49,920	16,640	0	904,000
Fitting environments	75%	56%	38%	23%		

It could also be said that in this situation, instead, an optimum fit in the environment between the arrival of each impactor would be selected, so that the organisms in mode 1 would be good at withstanding pressure and heat shock just like V_{Robustus} in mode 2. Indeed, if it was continuous impacts that came at regular intervals, almost like a seasonal change, then bet hedging would not have evolved here. Then it would be predictable when they occurred, and the organisms would have time to build up their numbers each time and would benefit by being optimally adapted to their environment.

Thus, in a predictable environment, it would be beneficial to be optimally adapted and have reproductive success. Impactors arrived regularly, many organisms survived, and they could build up their numbers sufficiently to ensure overall population survival upon the arrival of the next impactor. Evolution is a short-term tinkerer and will, in these circumstances, indeed select for the variant that does well in the environment between the arrival of each impactor.

However, the issue is that these are infrequently arriving impactors that cause an unpredictable environment. During the LHB, impactors arrived continuously, affecting most areas of the Earth. That they would come was almost certain, but exactly when and where was unpredictable. There may have been a long period of time between each impact, or there may have been a short time; there were no cues for populations regarding this. Thus, even if the first mode could eventually produce the same tough organism V_{Robustus} that bet hedging uses as its one variant, a bet hedging strategy would still be the safest use of resources. First, investing only in being robust does not protect the population against a direct hit, as organisms cannot survive such a direct impact. Secondly, producing only robust organisms will not help the population, as the changing unpredictable environment is precisely not favourable for a particular optimum organism.

V_{Robustus} is best in the face of sudden and unpredictable, yet expected, pressure and heat shock that occurs with each impact but does poorly in the environment that exists between each blast. Conversely, $V_{\text{Intervallum}}$ is best in the environment they live in, i.e., in the environmental interval between two impacts but does poorly with regard to surviving the effects of the blast.

Thus, a strategy could have evolved whereby the selection was made for both the variant that does well in the environment between the blasts, and for the variant that does well during the blast. Therefore, rather than short-term success - the arithmetic mean fitness, long-term survival - the geometric mean fitness, are selected, i.e., bet hedging, because resources are otherwise wasted.

It also applies to mode 2 that even though microbial life reproduces quickly, assuming there are good conditions for life in the rings after impact (so that the organisms can quickly build up their numbers again), if impactors occur consecutively and with greater frequency than those that allow organisms to recover their numbers again, hitting the same or different rings, then these organisms will eventually be eliminated. It is true, however, that there are more survivors in this second mode than in the first mode, and the organisms thus can recover their numbers to the original level faster and endure for longer in this mode. However, even then, bet hedgers can still in the original primary ring gradually disappear in this way.

However, these impacts continued through the LHB with many variables regarding frequency, location, which rings were hit, how fast organism numbers recovered, and others. Therefore, through these many changes, life may have endured through this mode until the impactors subsided again, or it may have been eliminated. However, in this constructed scenario, this only applies if the primary ring is the only one considered. The primary ring is only one part of the overall picture; thus, a realistic constructed scenario includes other parts as well, that is, the impact blast ejects organisms into the secondary ring.

4. THE SECONDARY RING

In the following, the outer secondary ring, consisting of five rings after the inner primary ring, is discussed. Thus, there are 10 rings in total. It is implicitly assumed that all environments were life-friendly in the secondary ring, but with environmental stressors different from each other. Since the purpose of this extended model is to illustrate the inter-relationships and differences between the modes, regardless of how large the numbers are, it is still assumed here that each ring initially contains $N = 1 \cdot 10^6$ organisms.

Organisms being transported: Mode 1

As discussed in the section on the primary ring, in the first phase, the organisms in each ring (as a result of the impact blast) perished in a series: 100%, 80%, 60%, 40%, and 20%, for each consecutive ring outward from the blast. This left a survival of 0%, 20%, 40%, 60%, and 80% for each ring outward from the blast. In the second phase of the interaction between impact dynamics and the evolutionary response, some organisms were ejected into the secondary ring as a result of the impact blast.

Thus, in ring 1 in the primary ring, 100% of the organisms perished, i.e., no living organisms were launched into the secondary ring. In ring 2 in the primary ring, 80% of the $2 \cdot 10^5$ organisms, i.e., 160,000 organisms, were launched into the secondary ring. For the next rings 3, 4 and 5, the organisms were similarly launched with proportions of 60%, 40% and 20%, respectively (Table 1).

Therefore, $n = 1.2 \cdot 10^6$ organisms remained in the primary ring, while $n = 8 \cdot 10^5$ organisms were launched into the secondary ring, all of which would have occurred within a matter of minutes (Table 1).

Thus, when the impact in the primary ring launches organisms into the secondary ring, fewer organisms remain in the primary ring. This means that repeated rapid impacts can reduce their number in the primary ring faster than discussed in the previous section, making their likelihood of survival less secure. The model is, in a sense, an invariant, because although the incoming impactors may have different diameters, densities, and speeds, the result is still that some organisms are launched into the secondary ring.

Survivors after landing

The third stage of the interaction between impact dynamics and the evolutionary response is the landing of organisms in a new environment. The material ejected from an impact crater follows ballistic trajectories, that is, ejecta are launched from their launch position with some initial velocity, following a nearly parabolic trajectory above the world's surface, then fall back to the surface (Melosh 1989).

The innermost ejecta, such as those in rings 1 and 2, are launched first and travel fastest, following the steepest trajectories, thus falling far away from the crater rim. This means that, at greater distances from the crater rim, as the range increases, such as in rings 9 and 10, the ejecta strike with progressively larger velocity. Ejecta originating farther from the centre, such as in rings 4 and 5, are launched later and travel more slowly, falling nearer to the crater rim. This means that material falling near the crater rim, such as in rings 6 and 7, strikes with a low velocity because it travels only a short distance.

As discussed in the primary ring section, the organisms in each ring, as a result of the impact blast, perished at proportions of 100%, 80%, 60%, 40%, and 20% for each consecutive ring outward from the blast. As the ejecta follow a nearly parabolic trajectory, when it starts to fall back to the surface, it strikes with the same velocity as when it was launched from the blast. Thus, in the secondary ring, organisms perish in a reverse sequence, similar to that in the primary ring.

Thus, matter from ring 1 lands in ring 10, there will not land organisms there, as these were eliminated in ring 1. Matter alongside 160,000 organisms from ring 2 will land in ring 9, and 80% of the arrived organisms will not survive the landing. Thus, 32,000 surviving organisms will be deposited there. For the next rings 3, 4 and 5, the survival proportion will similarly be 60%, 40% and 20%, respectively (Table 1).

Thus, in total, $n = 4 \cdot 10^5$ surviving organisms will be deposited there (Table 1).

Fitting environments

The fourth stage of the interaction between impact dynamics and the evolutionary response is life's response to stressors in the new environment.

Descend with modification, that is, Darwinian evolution, fundamentally concerns adaptation to changing local environments. Thus, although from a purely physical science point of view, it might seem irrelevant where the organisms end up, as those that survived impact, transportation, and landing have arrived, this is not the case.

This is because organisms generally move into new environments slowly, i.e., through the boundary areas between environments, while the organisms, through reproduction, variation, and selection—the key mechanisms of Darwinian evolution—gradually become adapted to new environments. An immediate shift between different environments cannot generally take place, as illustrated by propagule pressure, where it usually takes several trials before organisms establish themselves (Lockwood et al. 2005). Thus, organisms cannot just be placed in a different environment, as they are adapted to their local environment.

Thus, there is an inverse proportionality at stake in rapid shifts between environments. The more different a new environment is from an organism's native environment, the more maladapted that organism is to the new environment, and the worse the organism's ability is to survive the initial encounter with that environment (von Hegner 2020). The inverse proportionality poses a serious challenge if the impact is so powerful that life can be transferred between two solar system bodies, even if both of these worlds are considered to be life-friendly (von Hegner 2020). Here, it poses a less serious challenge since we are looking only at local impacts where life remains on the planet. However, even though the distance that life is launched by such an impact is limited, it is still in effect, as the adjacent environments can still be different from each other; the farther away the environments are, the more different they can potentially be.

This is more profound for multicellular life, and microbial life, such as bacteria, can overcome this faster than multicellular life due to their general 'toughness', versatility, and rapid evolvability. For microbial life, the initial survival at the encounter with a new and different environment is often more due to confronting the environment at the right time. However, the organisms do not emigrate to the new environments, and they do not have the influence to meet a new environment at a certain time; they are simply launched into it. Thus, an inverse proportionality will still be in effect for them and must therefore be included.

This is important here. If the impact is not too violent, the organisms will be launched into environments that are potentially not so different from their own, as environments mostly gradually separate from each other, where the intermediate layers only gradually become different. However, if the impact is very violent, then the organisms can be launched far away, and the environment they land in can potentially be very different.

Thus, there is an inverse survival proportionality between how powerful the impact is and the adaptation the organisms have. The declining survival rate is not due here, in contrast to the scenario in the primary ring, to how powerful the direct impact is, but rather to how far away the impact can launch the organisms. Thus, it is the impactor blast that determines how much the inverse survival proportionality tips to one side. It is like a see-saw standing horizontally, where each of the seats represents two environments that are as similar as possible. When impact pushes down on one, then the other rises into the air, i.e., the environments are becoming more diverse.

Thus, in the primary ring, the stronger the impact blast, the fewer organisms survive and the closer they move into the various adjacent rings, i.e., survival increases the further away the organisms are from the impact centre. However, in the secondary ring, the stronger the impact blast, the further away the organisms are launched, and the less they are adapted to the environment that they land in; thus, the less likely they are to survive their initial encounter with new environmental stressors. The two scenarios are, thus, reversed from each other. The primary ring represents an increasing survivability outward, while the secondary ring represents an increasing survivability inward.

Estimating survival is not easy. It has been stated previously that the environments potentially become more diverse the further one moves outwards in the system. Thus, it is assumed here, for the sake of calculation, that the environment in each ring is different from that of the adjacent ring and that the differences in the five types of environments become more marked for each ring moving outward.

Thus, the environment in ring 2 can potentially be very different to that in ring 9. Thus, ring 2 may, for example, be a highly saline environment, while ring 9 could be a low-saline environment, which could greatly reduce the organism's chance of survival. In fact, a high saline-adapted organism could burst open upon placement in a low-saline environment. Conversely, adjacent environments, such as those in rings 5 and 6, could potentially be very similar. Therefore, the probability of being adapted to the next adjacent environment, and thus being able to survive there, decreases for each new ring. However, it is not a given that they are different; just that there is a probability involved.

Following the procedure that has been used so far, it is tempting to suggest that 80% of the 32,000 surviving organisms from ring 2 will die shortly after being deposited in ring 9; 60% of the 96,000 arriving surviving organisms from ring 3 will die shortly after being deposited in ring 8, and so on.

However, organisms are adapted to their environment, and since they are members of a clonal population, they have the same response to an environment. Therefore, rather than there being a proportion of organisms that survives regardless of the environment that they encounter, it is more accurate to estimate which environments they may encounter, and thus, survive in.

Thus, the differences in the environments increase the further one moves outward in the rings. The organisms survive if they land in an environment that fits suits them but perish if they land in one of the other environments.[1] There is always one environment available for the organisms in each outward ring that is suitable for them to live in. However, the number of environments in which they cannot live

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[1] In reality, organisms can not only live optimally in an environment, but also for a time live sub-optimally in an environment that is different but not so different they cannot survive the initial deposition. However, this also applies to each variant of bet hedging. Each variant can thrive optimally in an environment, and sub-optimally in a slightly different environment. So the fact that organisms in mode 1 do it does not give them an advantage as mode 2 also does it. Thus, for simplicity, it will be considered as if each organism must meet an environment similar to their native one.

increases for each ring, thereby diminishing the likelihood of their survival. The additional environments represent the uncertainty involved here, as we cannot be sure what the environment is. This situation is also the reason why adaptive phenotypic plasticity has not been discussed here, as it is not possible to obtain cues about the environments in which the organisms could have been launched into, and thus, it is the same situation as mode 1.

Thus, there are two possible environments in ring 6: one that is similar, and one that is different to the native environment of the organisms. The goal is to determine the probability of an organism encountering exactly one environment similar to its native environment, as follows:

$$n = 2,$$

$$k = 1,$$

$$\begin{aligned} n - k &= 1 \\ &= \text{number of failures,} \end{aligned}$$

$$\begin{aligned} n - k = p &= 0.5 \\ &= \text{probability of encountering} \\ &\quad \text{a similar environment,} \end{aligned}$$

$$\begin{aligned} 1 - p = q &= 0.5 \\ &= \text{probability of encountering} \\ &\quad \text{a different environment.} \end{aligned}$$

The probability that the organism encounters one environment and also does not encounter a specific set of environments is calculated as follows:

$$P_{\text{specific 1 environment}} = (0.5)^1 \cdot (0.5)^1. \qquad (2)$$

However, it is necessary to update this based on the number of ways it is possible to divide a group into sets of 1 and 1, which is obtained by the binomial coefficient. Thus, the final probability is as follows:

$$P \text{ (match out of two environments)} = \binom{2}{1} \cdot (0.5)^1 \cdot (0.5)^1 = 0.5. \qquad (3)$$

Thus, the probability of landing in an environment where they can live is 50% for the organisms from ring 5. Similarly, there are three possible environments in ring 7: one where the organisms can live, and two where they cannot live, where the final probability is as follows:

$$P \text{ (match out of three environments)} = \binom{3}{1} \cdot (0.5)^1 \cdot (0.5)^2 = 0.38. \qquad (4)$$

Thus, the probability of landing in an environment in which they can live is 38% for the organisms from ring 4. Similarly, there are four possible environments in ring 8: one where they can live and three where they cannot live, and five possible environments in ring 9; one where they can live, and four where they cannot live (Table 1).

Therefore, there are two serious challenges to life here. First, as discussed, the primary ring can be gradually depleted if rapid impacts both eliminate organisms within it and launch other organisms into the secondary ring. However, it can be said, that the fact that the organisms are eliminated from the primary ring does not mean that the organisms in the secondary ring are also eliminated, since, once they are ejected there, subsequent impacts are irrelevant. Thus, mode 1 does it reasonably well.

However, secondly, although the above occurs in a completely predictable way, organism numbers are reduced mechanically, and launched mechanically; the situation in the secondary ring is only partially mechanical. Thus, whether organisms survive in an alien environment depends on the environmental stressors and evolutionary mechanisms at play. Therefore, the organisms being launched into environments where they cannot survive is a matter of probability, not certainty. Thus, the LHB posed a serious challenge to life in this way. However, evolution could cause mode 1 to evolve into mode 2.

Organisms being transported: Mode 2

As discussed in the primary ring section, for the first phase, the V_{Robustus} organisms in each ring as a result of the impact blast perished with a proportion of 100%, 20%, 15%, 10%, and 5% for each consecutive ring outward from the blast, leaving survival at 0%, 80%, 85%, 90%, and 95% for each consecutive ring outward from the blast. Furthermore, the $V_{\text{Intervallum}}$ organisms in each ring as a result of impact blast perished with a proportion of 100%, 80%, 60%, 40%, and 20% for each consecutive ring outward from the blast, leaving survival at 0%, 20%, 40%, 60%, and 80% for each consecutive ring outward from the blast. In the second phase of the interaction between the impact dynamics and the evolutionary response, some organisms were launched into the secondary ring as a result of the impact blast.

Thus, organisms from ring 1 will not land in the secondary ring, as they are eliminated by the impact. In ring 2, from the primary ring, 80% of the surviving 384,000 V_{Robustus} organisms, i.e., 307,200 organisms, and 80% of the surviving 104,000 $V_{\text{Intervallum}}$ organisms, i.e., 83,200 organisms, will be launched into the secondary ring. Thus, a total of 390,400 organisms will be launched into the secondary ring. For the next rings 3, 4 and 5, the organisms are similarly launched at a proportion of 60%, 40% and 20%, respectively (Table 2).

Therefore, $1.49 \cdot 10^6$ organisms remain in the primary ring, while $1.23 \cdot 10^6$ organisms are launched into the secondary ring, all of which happens within 1-2 min (Table 2).

Survivors after landing

The third stage of the interaction between impact dynamics and the evolutionary response is the landing of organisms in a new environment. As mentioned, the material ejected from an impact crater follows ballistic trajectories, that is, ejecta are launched from their launch position with an initial velocity, following a nearly parabolic trajectory above the planet's surface, then fall back to the surface (Melosh 1989).

The innermost ejecta, such as those in rings 1 and 2, are launched first and travel the fastest, following the steepest trajectories and falling far from the crater rim. This means that at greater distances from the crater rim, as the range increases, such as at rings 9 and 10, the ejecta strike with progressively larger velocities. Ejecta originating from further from the centre, such as in rings 4 and 5, are launched later and move more slowly, falling nearer the crater rim. This means that material falling near the crater rim, such as in rings 6 and 7, strikes with a low velocity because it travels only a short distance.

As discussed in the primary ring section, the V_{Robustus} organisms in each ring as a result of the impact blast perished at proportions of 100%, 20%, 15%, 10%, and 5% for each ring outward from the blast. It was also found that the $V_{\text{Intervallum}}$ organisms in each ring as a result of the impact blast perished at proportions of 100%, 80%, 60%, 40%, and 20% for each ring outward from the blast.

The ejecta follow a nearly parabolic trajectory, and when they start to fall back to the surface, they will strike with the same velocity as when they were launched with the blast. Thus, in the secondary ring, they will perish in a reverse sequence, similar to that in the primary ring. A physical detail here is that when the ejecta start to fall downwards, the potential differences in mass between the variants will be irrelevant, as the acceleration of gravity is the same for both, due to moving along locally straight paths in the same curvature of spacetime caused by the mass of the Earth. For simplicity, it is here ignored that they are subject to the frictional force, and air resistance.

Thus, there is the same mutual survival rate at landing between $V_{\text{Intervallum}}$ and V_{Robustus} as at impact in the primary ring. The surviving V_{Robustus} organisms can still withstand pressure and heat shock better than the surviving $V_{\text{Intervallum}}$ organisms can, which is the same advantage given by bet hedging.

Thus, matter from ring 1 from the primary ring will land in ring 10 in the secondary ring, there will not land-living organisms there, as these were eliminated in ring 1. Matter with 390,400 organisms from ring 2 of the primary ring will land in ring 9 of the secondary ring. Overall, 20% of the 307,200 V_{Robustus} organisms will not survive the landing, i.e., 245,760 organisms will survive and be deposited there, while 80% of the 83,200 $V_{\text{Intervallum}}$ organisms will not survive the landing, i.e., 16,640 organisms will survive and be deposited there. For the next rings 3, 4 and 5, the survival proportion will similarly be 15%, 10%, 5%, and 60%, 40%, 20%, respectively (Table 2).

Thus, overall, $n = 9.04 \cdot 10^5$ surviving organisms will be deposited (Table 2).

Fitting environments

The fourth stage of the interaction between the impact dynamics and the evolutionary response is life's response to stressors in the new environment.

Mode 2 has so far displayed two advantages over mode 1, which could be calculated mechanically as a result of impact dynamics and increased robustness as a proportion of organisms. V_{Robustus} provides a significant advantage in the primary ring by allowing more organisms to survive the effect of the impact blast, and in the secondary ring, by allowing more organisms to survive the landing. However, the concept that bat hedging provides benefits of landing in potentially very different environments is more complex because being able to withstand the effects of an impact blast and landing does not prima facie make V_{Robustus} more suitable than $V_{\text{Intervallum}}$ for survival in a new environment.

Thus, following the approach that has been used so far, it might be tempting to say that 20% of the 245,760 arriving survivors of V_{Robustus} organisms from ring 2 will not survive; that 80% of the 16,640 arriving survivors of $V_{\text{Intervallum}}$ organisms will not survive in ring 9; that 15% among the 208,080 arriving survivors of V_{Robustus} organisms from ring 3 will not survive; that 60% among the 49,920 arriving survivors of $V_{\text{Intervallum}}$ organisms will not survive in ring 8; and so on.

However, organisms are adapted to their environment, and an inverse proportionality between environments and survival exists. The more different a given environment is to the environment that the transported organisms originated from, the less adapted they are to the new environment and the lower their chance of survival. Therefore, rather than there being a proportion of organisms that survives no matter what environment they encounter, it is more accurate to estimate which environments they may encounter, and thus, survive in.

For the calculations in mode 1, it is difficult to determine the probability of environmental variation for mode 2. However, as before, it is assumed here for the sake of calculation that the environment in each ring is different from that in the adjacent ring and that the differences between the five types of environments become more marked with each consecutive ring moving outwards. Therefore, the probability of being adapted to the next adjacent environment, and thus being able to survive there, decreases for each new ring. The differences in the environments increase the further one moves outwards in the rings. However, it is not a given that they are different; just that there is a probability involved.

This scenario does not directly depend on the mechanics of impact blast. While it is possible to calculate how far matter will be launched, if one knows the impact velocity and trajectory of the impactor, it is not as easy to estimate what kind of environment it will be launched into. The impact blast determines the rings that the organisms are launched into, but the evolutionary strategy determines the survival rate of the organisms.

Bet hedging can indeed provide a third advantage in that although only organisms with a single genotype from the same clonal population arrive; two phenotypes arrive rather than one for new environments, which increases the possibility of surviving in several different environments, thereby increasing the possibility of at least one phenotype surviving. A trivial example is that if the organisms are launched into an environment that is still hot after a previous impact, then the initial benefit will go to the pressure and heat shock robust variant.

However, bet hedging provides a more non-trivial opportunity for increased survival. Thus, there could seem to be three environments at stake for bet hedging.

$V_{\text{Intervallum}}$ can handle two environments. It does this by being able to live optimally in one, which corresponds to 1, while it can live sub-optimally in the other, which corresponds to 0.5.

V_{Robustus} can handle two environments. It does this by being able to live optimally in one, which corresponds to 1, while it can live sub-optimally in the other, which corresponds to 0.5.

Thus, by adding these values together, it can be considered that there are three environments that they can live in. However, the variants come from the same clonal population, live together in the same environment, and overlap each other before being launched into another ring.

Thus, $V_{\text{Intervallum}}$ can live sub-optimally in the V_{Robustus} environment, while V_{Robustus} can live sub-optimally in the $V_{\text{Intervallum}}$ environment. The optimal environment of one variant is, thus, the sub-optimal environment of the other. Since the variants overlap and change position when one environment changes to another, it is instead, mathematically speaking, 1.5 environments that the organisms in mode 2 can live in together (as opposed to mode 1, where the environment that the organisms can live in is 1).

This increased ecological range can be mathematically processed by adding an external term, r, to the binomial distribution, so that a bet hedging fraction of 3/2 is multiplied with the situation in mode 1 to model the correct situation in mode 2. Thus, the procedure for mode 2 is the same as that for mode 1, with the exception that rather than the ecological range being $r = 1$, implicitly assumed for that scenario without stating it, it is $r = 1.5$ for this scenario. Thus, there are for the otherwise two different environments that can be encountered in ring 6 the following numerical values:

$$n = 2,$$

$$k = 1,$$

$$\begin{aligned} n - k &= 1 \\ &= \text{number of failures,} \end{aligned}$$

$$\begin{aligned} n - k = p &= 0.5 \\ &= \text{probability of encountering} \\ &\quad\ \text{a similar environment,} \end{aligned}$$

$$\begin{aligned} 1 - p = q &= 0.5 \\ &= \text{probability of encountering} \\ &\quad\ \text{a different environment,} \end{aligned}$$

$$\begin{aligned} r &= 1.5 \\ &= \text{ecological range or capability of} \\ &\quad\ \text{handling more than one environment.} \end{aligned}$$

In this case, the final probability is:

$$P(\text{survival match in two environments}) = \left(\binom{2}{1} \cdot (0.5)^1 \cdot (0.5)^1\right) \cdot (1.5) = 0.75. \tag{5}$$

Thus, the probability of survival in the environment in which they land is 75% for the organisms from ring 5. Similarly, it applies that there is, for the otherwise three different environments that can be encountered in ring 7, the following final probability:

$$P(\text{survival match in three environments}) = \left(\binom{3}{1} \cdot (0.5)^1 \cdot (0.5)^2\right) \cdot (1.5) = 0.56. \tag{6}$$

Thus, the probability of landing in an environment in which they can live is 56% for the organisms from ring 4. Similarly, there are four different environments that can be encountered in ring 8, and five in ring 9 (Table 2).

These differences between mode 1 and mode 2 for each ring do not immediately appear large, but more survivors arrived in mode 2. Thus, bet hedging also offers a third advantage when arriving in a new and potentially very different environment, in that no matter which of the variants arrives, it will be able to relate either optimally or sub-optimally to that environment and will be able to live there either way and produce both variants themselves. This means that mode 2 can potentially handle more environments than mode 1.

There are still serious challenges to survival. First, the primary ring can eventually be depleted if rapid impacts both eliminate organisms and launch other organisms into the secondary ring. However, as mentioned, it will require a significant number of impacts to eliminate V_{Robustus} in the primary ring, posing a lesser challenge for mode 2 than mode 1. However, the number of organisms will be reduced in a completely predictable way by repeated consecutive impacts, even for V_{Robustus}. Despite this, it could be said the organisms being eliminated from the primary ring does not mean the organisms in the secondary ring are eliminated, since once they are placed there, subsequent impacts are irrelevant.

However, the second challenge is the arrival of organisms to the appropriate environments, which is more a contingent than a deterministic event. Thus, while the above happens in a completely predictable way, organisms are reduced and launched mechanically, and the situation in the secondary ring is only partially mechanical, so whether organisms survive in an alien environment depends on the environmental stressors and evolutionary mechanisms at play. However, as discussed, mode 2 provides greater possibilities for handling several different environments at once. Thus, bet hedging is the best strategy in this situation. However, there is still a possibility that life can be launched into environments where it cannot survive. It is not a given that life survives, and the LHB still posed a serious challenge to life in this way.

Yet, the number of survivors after impact, transport, and landing is higher in mode 2, which can handle a wider range of environments. Thus, the number of organisms may have decreased overall during the LHB in both modes, but in mode 2, they may have endured in sufficient numbers for sufficient time until the impacting subsided again.

4.1. The primary and secondary ring junction

Organisms are adapted to their environment, and an inverse proportionality between environment and survival exists. The more different a given environment is to that which the transported organisms originated from, the less adapted they are to the new environment, and the lower their chance of survival. The survival rate of the organisms is almost nonexistent in rings 1 and 10, while it is low in rings 2 and 9, but for very different reasons: the first is due to the sudden matter and energy delivery forced upon the organisms by the impact blast, whereas the second is due to the ecological constraints forced upon the organisms by evolution.

However, the primary and secondary rings converge inward from these rings, achieving an increasing survival rate towards the junction between the primary and secondary rings, with the primary ring representing an increasing outward survivability and the secondary ring representing a decreasing outward survivability. In ring 5, the numbers equalise, i.e., the two variants achieve their greatest similarity in terms of the highest number of survivors of each variant. In ring 6, not as many organisms are transported in comparison with the other rings, yet the prediction of the number of survivors is generally highest here. Thus, the inverse proportionality decreases when the primary and secondary rings go against rings 5 and 6, almost like a see-saw coming into horizontal equilibrium.

So far, diversified bet hedging has been discussed. However, another strategy called conservative bet hedging exists (Seger and Brockmann 1987). This strategy is characterised by maintaining the same sub-optimal phenotype in both types of changing environments that it may experience. It is, thus, not specialised for any of the given environments but is sub-optimal in comparison to an organism with optimal fitness in each environment.

The conservative bet hedger is, thus, a ‘Jack of all trades, but master of none’, while both the diversified bet hedgers are each ‘master of their trade’, i.e., of their particular environment. Thus, it does not thrive in any of the environments and does poorly in comparison to both variants of diversified bet hedging. However, it still manages to survive in the changing environments by exchanging optimum fitness in any environment for long-term survival. Thus, the conservative bet hedger is, in some ways, the reverse of diversified bet hedging. They represent, for the purposes of the LHB, a reverse situation of each other in terms of both advantages and disadvantages.

It will not withstand pressure and heat shock in the primary ring very well compared to the variants of diversified bet hedging; even $V_{\text{Intervallum}}$ may survive impact, launch, and landing better. Thus, conservative bet hedging will do poorly in comparison to both variants of diversified bet hedging in this regard, but it may do better in another regard. This is because organisms in both strategies have no control over which environments they are launched into. Organisms will generally move into new environments slowly, existing in the border areas, while they gradually adapt to the environment. An immediate switch between environments cannot generally take place as organisms are adapted to their local environment. The organisms can, at launch, end up in environments to which they are not adapted.

Thus, rather than a proportion of organisms surviving regardless of the environment that they encounter, it is, as previously mentioned, more accurate to estimate which environments they may encounter, and thus, survive in.

The variants of the diversified bet hedging strategy perform better than the conservative bet hedger regarding the highest possible number of organisms coping with the blast in the primary ring and surviving the launch and landing in new environments best. However, interestingly enough, in this specific situation, this also makes the conservative bet hedger manage the secondary ring better.

In this volatile environment, the fact that both variants are highly specialised is an issue in itself. Thus, ending up in a different unpredictable environment will not be an advantage, as neither is an optimal fit. However, it is here that the conservative bet hedger has its greatest strength in this very specific situation; while fragile in terms of the effect of impact blast, it is, in some sense, an extremotolerant organism in terms of coping with being deposited in a new alien environment. It has a greater environmental range by not being optimum specialised and thus has a better chance of surviving the encounter with more new environments in the secondary ring than the variants. They can better potentially ‘smooth out’ the inverse proportionality, i.e., smooth out the differences in the environments they are deposited into after landing.

Thus, while this strategy does not have a high survival rate in the primary ring, it may have a high survival rate in the secondary ring. In the interval between impacts, both variants will be produced, i.e., resources are being spent on an organism that is not optimal. However, the conservative bet hedger does not use extra resources regardless of the environment. If it survives the deposition, then it remains suboptimal, focusing on long-term survival rather than short-term well-being. Overall, the variants will still provide the best chances of survival, leading to the most survivors. However, in terms of resources used, the conservative bet hedger in this situation will be less costly.

It may also indeed be the ‘master of its trade’ in the junction between the primary and secondary rings. The survival rate is greatest in ring 5 in the primary ring and in ring 6 in the secondary ring due to the impact blast having the lowest effect on ring 5, while ring 6 is most likely to have environmental similarity to ring 5. Thus, the connection between these two rings is where there is the greatest benefit to organisms. Therefore, since it possesses a larger range, it may have a greater survival rate in this ring than the variants have.

However, as there will mainly be survivors here, this benefit is of limited value, since continuous impacts are unlikely to hit ring 1 each time (as is discussed in Section 5). Some could randomly survive in modest numbers in the inner rings and thus be launched into the outer rings, but this will not concern many organisms, thus limiting this benefit.

Thus, whether that strategy will emerge rather than the diversified strategy is up for discussion, as diversified bet hedging performs better overall than conservative bet hedging. However, it will provide a chance for survival and thus may evolve.

5. INFREQUENT IMPACTORS

In the previous sections, how many impacts it would take to reduce the number of organisms was calculated. These were ‘clean’ examples, based on the fact that no matter where an impactor hits, it will be the centre of the impact blast. The model, therefore, took this as its starting point, which was defined here as ring 1, and the effect on the primary and secondary rings was analysed. However, while subsequent impacts hitting the same centre again are possible, this has low probability. In fact, there is a higher probability that the next impactor hits another ring, e.g., ring 5, rather than ring 1, because when the next single impactor arrives, there are five possible rings it can hit in the primary ring, which is a more realistic constructed scenario than the previous one. Thus, the probability of any one of them being hit is as follows:

$$P = \frac{1}{5} = 0.20. \tag{7}$$

Thus, in this situation, life will be eliminated first in ring 1 and subsequently in ring 5, which drastically reduces the total number of organisms compared to the previous calculated examples. This puts some restrictions on bet hedging, it is not a wonder strategy, as even organisms producing endospores—the hardiest terrestrial structure known, will not be able to cope with a direct impact; therefore, only some of the organisms in the changing adjacent rings will survive through this strategy. Furthermore, as discussed, the primary ring is only one part of what is transpiring. The more realistic constructed scenario includes the secondary ring as well. Thus, when the next single impactor arrives, there are, in fact, 10 possible rings that it can hit. The probability of any one of them being hit is as follows:

$$P = \frac{1}{10} = 0.10. \tag{8}$$

If subsequent impacts hit different rings in the primary ring, then the next group of surviving organisms is sent even further away in a different number in other rings in the secondary ring than their counterparts were at the previous impact. In fact, this affects not only the rings in the primary ring but also those in the secondary ring, as if an impact hits one of the rings here, it becomes a primary ring, while new rings are formed and added to it.

In this more realistic scenario, there will be a system of rings that partially overlaps other systems of rings that even overlap other systems of rings, where organisms are both reduced in number and launched into each other, or into previously uninhabited environments, as a system of rings over large parts of the planet. There are many primary and secondary rings; new primary rings occur frequently, both when impacts hit new areas or when they hit existing rings, as when an impact hits one side of a ring system of both primary and secondary rings, new rings appear on the other side. Thus, it is a very dynamic system, rather than the more mechanical one that was put forward earlier. It is a dynamic interaction between the physical science of impacts and the biological science of adaptation.

There is an infrequent shuffling and reshuffling of organisms, a decrease and increase of organism numbers in the rings due to infrequent impacts, and the survival rate is more ‘muddy’ than that given in the calculations due to the absence of this same sequence of impacts. However, this situation is exactly what could be expected to provoke the emergence of bet hedging, which not only provides a higher number of survivors in this situation but also better ensures that there are survivors at all.

Vast connected ring systems may have existed with a metapopulation of organisms that emerged from a single original ring system. This can have a number of sub-scenarios, as organisms experience biotic stressors from competition with each other, traditionally called the Red Queen hypothesis (Van Valen 1973), and experience abiotic stressors from the surrounding environment, traditionally called the Court Jester hypothesis (Barnosky 2001).

If this is the first impact, then there may not be native organisms in the rings that the arriving organisms are launched into. However, with subsequent impacts, this changes. First of all, matter that impacts the other rings can cause destruction, thus eliminating some of the previously arrived organisms and making overall survival harder. Second, by impact, the organisms can be launched into rings where there may be previously arrived organisms that have had time to gain a foothold and evolve. Some organisms also remain in each ring, while others are launched away. These organisms can thus compete against the newly arrived organisms, making survival even harder.

There may also have been vast interconnected ring systems that arose as a result of many independent ring systems joining together. This is because although life may have emerged only once on the Earth, bet hedging may occur independently repeatedly; this can also have a number of sub-scenarios. First, matter that impacts the other rings can cause destruction, thus eliminating some of the organisms that already existed in these rings. This may be the reason why bet hedging occurs among surviving organisms in the rings. Second, if these independent ring systems join together, there will be organisms from different independent clonal populations in them, which, in the time since the origin of life, have evolved into different organisms. Thus, they will compete against the newly arrived organisms from other independent ring systems, i.e., a potential competition for both who survives best in the interval between impacts and who applies the most robust survival strategy. Thus, a competition for the best bet hedging strategy can take place, which means that the strategy itself evolves.

While it could initially be said that rather than a bet hedging strategy evolving, there could instead be an optimum fit selected for in the environment between the arrival of each impactor, the situation is more unpredictable and changeable than that which has been discussed so far. These are globally continuous impactors, but for life, this is experienced as locally infrequent impactors. It is an unpredictable environment in the form of arriving impactors that do not impact the same place, and there are no cues for the population regarding this. Not only does bet hedging pragmatically yield the most survivors, but, in such an environment, it must theoretically be expected to occur.

In Section 3, selecting for an optimum fit in the environment between the arrival of each impactor was suggested, so that the organisms in mode 1 are able to withstand pressure and heat shock, such as V_{Robustus} in mode 2, which would be the case as it has less cost. Indeed, having a population that maintains the existence of organisms that are sub-optimal has a greater cost than if the entire population was an optimum fit. As mentioned, $V_{\text{Intervallum}}$ is the variant that does best in the environment that they live in, i.e., in the environmental interval between two impacts, while V_{Robustus} is the variant that, in relation to the other variant, does best in the face of the sudden and unpredictable, yet expected, pressure and heat shock that occurs with each impact. The second variant has the advantage in the environment that they live in, and in this environment, organisms such as $V_{\text{Intervallum}}$ would, in other circumstances, outcompete organisms such as V_{Robustus}, as they have less cost in terms of not having to maintain robustness. They may also reproduce faster, better utilise environmental resources, and have other better qualities.

Maintaining this increased robustness of the population in an environment where it is not needed, and where $V_{\text{Intervallum}}$ has less cost and possibly does better, will therefore be costly. However, if impacts eliminate most of the population of fit organisms in a ring system, then the cost is quite large. Indeed, if the entire population is eliminated it is, of course, the ultimate cost. Thus, when impacts happen, V_{Robustus} will ensure the most survivors and, indeed, may be the only survivors in many cases. Thus, both variants are high cost, but in the environment between each impact, one variant is less costly than the other.This is the unique feature of bet hedging; the cost seems large in the short term, the decrease in the arithmetic mean fitness, where it maintains sub-optimal organisms in the population, but the cost is low in the long term, the maximized geometric mean fitness, as it ensures the most survivors in the long run in an unpredictable and changeable environment. Therefore, given these special circumstances due to the LHB, this strategy is the safer bet.

Furthermore, if one invests only in being robust, then they will only have sub-optimal success in their local environment. V_{Robustus} may do poorly in the environment between each impact, and it may reproduce more slowly, process available resources more inefficiently, or require many resources to maintain its robustness. They will survive but not take full advantage of their environment and adaptive potential in the environment, even though they have a greater chance of surviving an impactor. Thus, through natural selection, it will not be maintained in the population.

Conversely, if they invest in being like $V_{\text{Intervallum}}$, then they will have optimum success in their local environment, e.g., be fast-reproducing or require fewer resources to maintain themselves. Then, they would be selected for as evolution is a short-term tinkerer, and short-term tinkering it would indeed be, as this would be wasted if hit by an impactor. However, if their resources are divided between V_{Robustus} and $V_{\text{Intervallum}}$, then the strategy can pay off over the longer term, as opposed to betting on only one of the two strategies.

This is another benefit of bet hedging during the LHB; if, for example, a series of impacts briefly occurred in quick succession in the same location, thus decreasing the number of organisms until there were only a few members of V_{Robustus} left, and the series of impacts then changed to being infrequent again, this would not have as significant an effect as might first be thought. This is because even if only one V_{Robustus} variant survived, it would continue to produce both variants, and thus, $V_{\text{Intervallum}}$ would reappear. A mixed population would pay off in this situation.

When discussing that increased robustness in one of the variants could have led to long-term survival through the LHB, it will be relevant to look into robustness. Increased robustness can be defined as the ability of a particular organism to withstand environmental stressors that other organisms encountering the same environment cannot, such as pressure, heat, salinity, and desiccation. Thus, there are different types of robustness; it is not a physical invariant, but changes depending on local environments and changing organisms.

Going into more detail on the purely biochemical mechanisms that can make a microbial organism more robust than other microbial organisms is out of scope for this paper. However, it is relevant to briefly cover robustness stemming from different mechanisms—to cover how increased robustness occurs by evolutionary responses, i.e., that there are different strategies for robustness.

Thus, a mechanism that could be applied is that for some organisms a physiological response may occur when they have experienced a sublethal injury (Lou and Yousef 1996). Thus, stress hardening could occur, which allows organisms to better withstand the stressor that caused the injury. This is a short-lived process that disappears when the stressor disappears and requires resources to maintain. However, it also has the added benefit of being able to lead to cross-protection (Johnson 2003), such that the organism can withstand other stressors, rather than just the particular one that stress hardening was a response to.

Another mechanism that can apply to surviving organisms, both those that are not launched away and those that are, comes from the fact that they will have experienced a brief pressure and heat shock. It is possible for organisms experiencing a stressful event to achieve an increased resistance to a subsequent stressful event of the same kind (Gayán et al. 2016, Lenz et al. 2018) given the fact that a physiological state is conferred upon them. Thus, while they may not survive in the centre of the impact, the number of survivors in the subsequent rings could potentially increase, because they may have achieved enhanced resistance towards the effect of the next impact blast.

A type of organism that is relevant to consider when discussing survival in extreme environments is an extremophile, which can aid our understanding of how life could cope with such environments. Thus, one could opinionate that bet hedging could produce two variants: $V_{\text{Intervallum}}$ in the form of a mesophile, and V_{Robustus} in the form of an extremophile. While it could be hypothesised that bet hedging can indeed produce both mesophiles and extremophiles in the same clonal population, it is, however, the case that extremophiles are as highly adapted to their local environment as $V_{\text{Intervallum}}$. Thus, in the specific situation discussed here with impactors, they offer no greater chances than mesophiles. First, even they cannot survive direct hits by impactors, and second, they are not only tolerant of extreme environments but require them to live. To be launched away from their local environment and deposited in another provides the same issues for them as for mesophiles. In fact, it can be a major issue for them, as many species cannot tolerate being moved to other environments.

Another evolutionary response and mechanism that may apply concerns the bacterial endospore—the hardest structure known in terrestrial organisms (Nicholson et al. 2000). These are formed when the environment is not favourable for organisms, and they wait for a more suitable environment to emerge. A bet hedging population could also be hypothesised to be able to produce both active organisms and endospores simultaneously. Unusually here, endospores are formed in an environment that is suitable for active organisms, i.e., they are formed even though all available cues show that the environment is not yet approaching unfavourable conditions for the organisms, and there is, therefore, no reason to await a more suitable environment. Thus, one variant lies dormant while another is active, which indeed is a bet hedging strategy. While an endospore cannot cope with a direct impact, it would be able to survive in large numbers the subsequent scenarios of being launched and landing in other environments. However, it is not certain that it could cope with the environment in which it is placed when it becomes necessary to become active again.

Another evolutionary response that could apply when discussing extreme environments concerns extremotolerant organisms that could aid with understanding how life can cope with such environments. Thus, bet hedging could be hypothesised to lead to two variants in the same clonal population: $V_{\text{Intervallum}}$ and V_{Robustus}, in the form of an extremotolerant organism. Of course, an organism need not be defined as being extremotolerant in order to be more robust in an environment relative to another organism. However, here it is relevant, as it is the same genotype that produces two different phenotypes, and the two variants are established as opposites of each other in terms of extremotolerance. Thus, that some of the organisms can better cope with pressure and heat shock while others in the same population cannot is indeed a bet hedging strategy.

The previous discussion focused on mechanisms that lead to robustness and the evolutionary responses that could lead to these mechanisms, but what about the evolutionary strategy itself? An optimum fitness for organisms will not be beneficial in this situation; however, crucially, bet hedging does not aim for optimum fitness for individual organisms. It instead aims for an optimum strategy for a population of organisms. While bet hedging is not necessarily the only strategy that existed among life during the LHB, it is also the case that there was not necessarily only one bet hedging strategy. If initially independent ring systems eventually merged (as mentioned previously in this section), then in these there would have been organisms from different independent clonal populations that had evolved into different organisms. This means that organisms can compete against newly arrived organisms from other independent ring systems, i.e., a potential competition of who both best survives in the interval between impacts and who best survives the effect of the impact. Thus, different clonal populations that meet will compete against each other to evolve the best bet hedging strategy, meaning that the strategy itself evolves.

However, despite this, it is still possible that each variant ultimately, depending on the severity and length of the impacts, is a losing strategy for the full time span of the LHB. However, the losing strategy may, in fact, be what caused organisms to endure until the impacting subsided. Thus, here, a paradox in game theory could come into play. Parrondo's paradox is a strikingly counter-intuitive phenomenon in which two independently losing games or strategies, when alternating between them in a specific order, can become a winning strategy (Abbott and Harmer 1999). The two variants are constantly accompanying each other in a population, as they can each produce the other and may thus be considered pairs of gambling games: A and B. Thus, even though each variant is a losing strategy, they could, when combined, lead to a winning strategy.

6. DISCUSSION AND CONCLUSIONS

In this paper, a realistic constructed scenario that may have occurred during the LHB is presented. It is based on the premise that, while globally continuous impacts occurred, these were experienced by life as locally infrequent impactors. Thus, there was variation in the frequency of impacts, where many sometimes arrived over certain areas and sometimes only a few arrived.

It was unpredictable, from an evolutionary point of view, when the next impact would arrive (albeit not from a physical point of view). However, the mechanism remained the same, which was predictable. Thus, the impact blast washed over organisms, leaving some survivors, and the impact blast launched some of these into new environments. There was a longer period with a relaxed nourishing environment where the organisms thrived, and there was a short period where the organisms must survive three violent events as well as survive in a new, potentially different, environment.

The adaptive response of the surviving life could not predict when these shifts would occur; there were no cues available, unlike with regular seasonal change, but life may have responded to the nature of both of these. Thus, although the timing of the shift between the two environments could not be predicted, a proper adaptive response, bet hedging, could nevertheless occur.

This scenario is partially maintained by the external pressure from impact dynamics, which have been well-described in terms of physical science, and partially maintained by an evolutionary response, which has been well-described in terms of evolutionary theory. Thus, organisms can react towards even such 'celestial stressors' and maintain an adaptive response to them. It is a response that could enable life to get through even such a violent period of the world's history.

It is not claimed here that this scenario took place, although under these conditions one might expect it to, but simply that the possibility of bet hedging could have been present under these conditions during this time of the solar system's history and could explain how life survived through it. It may have only occurred among a few populations.

The scenario is, to some extent, idealised. In reality, it would be more 'messy' than the calculations show here. In this model, the impactor has been treated as an invariant, which means that although the incoming impactors may have had different diameters, densities, and velocities, it is still the case that the organisms in the centre of the impact blast perish, while those in the adjacent rings can survive in the sequence discussed. Thus, the system of rings with the primary and secondary rings will, in this model, occur each time by impact on land. This is why the physical size of each ring and its distance from the previous ring to the next ring has not been discussed, as the physical effect of ring formation remains the same every time, such as the rings that emerge when a stone is thrown into a pond. However, impactors with different diameters, densities, and velocities can have a biological effect.

Thus, the assumption that each ring has 1 million organisms may change. The stronger the impacts, the wider each ring can be, and thus, there can be more organisms in them. It also applies that each subsequent ring grows, which means that there are more organisms in each ring. Thus, the effect of an impact can indeed be a variant. However, the high-level characterisation of the relationship between each mode to a good approximation will follow what is presented here, even though the calculations become more complex in these more realistic scenarios. Thus, mode 2 consistently had a higher number of survivors, and the higher number of surviving organisms may prove to have been critical for life to endure throughout the LHB.

One issue is how long it takes for bet hedging to occur. How many impacts would it take for life to adopt this strategy, and how many impactors were there in reality? Would this strategy have been able to emerge at such impacts before life was eliminated completely (albeit impactors in fact may have helped to spread life around the planet if it was not already diversified)? Did life thrive on this strategy during the LHB, or did it only endure such that when the bombardment reached the critical point then subsided, there may have been only a few habitats with organisms left that could now start using other strategies?

Another issue is the nature of the Earth's surface at that time. Some studies estimate that less than 25% of the Earth's surface would have been resurfaced due to very large impactors (Abramov and Mojzsis 2009), meaning that this would not have posed a particularly big issue. Thus, the Earth's environment may have been relatively stable, and different types of environments may have existed, although they may have been less inhomogeneous than today and still posed serious challenges to life compared to the present day. However, if life did indeed exist then, there must also have been habitats for it to exist in.

While even local impactors have a tremendous impact, whether the set model is most applicable on land surfaces and shallow waters and not underground or in the deep ocean and thus has only impacted life existing in these environments can be discussed. This also brings up the issue of how widespread life may have been; was it still a local phenomenon, or was it already a global phenomenon?

The scenarios reviewed are based on the simplest model, where there was an even distribution of organisms in the rings from the same population. Thus, microbial organisms, such as bacteria and archaea, are clonal, and a single organism can give rise to a colony, so that a group of organisms from the same colony can be considered to exist at a point that spreads outwards. However, even then, there could have been an uneven distribution of organisms from the same clonal population. There could have been many different organisms from different populations existing amidst each other. This could give different results in terms of survival rate, although the relationship between the two modes ultimately remains the same. However, in effect, it does not matter if there were different clonal populations that used bet hedging in the rings where impacts occurred. As mentioned, each population would have been able to use their version of bet hedging, and this could have led to competition between different bet hedging strategies.

This adaptive response to an external pressure from 'celestial stressors' need not only be limited to incoming impactors and will, thus, be even more relevant to astrobiology. Therefore, while similar scenarios could potentially also occur on other worlds in the galaxy and beyond, for example, LHB-like conditions around Eta Corvi, an F-type main-sequence star, may take place (Lisse et al. 2012), it does not only have to be impactors that initiate this evolutionary response.

There may exist worlds where the atmospheric conditions are such that there will infrequently be acid rainfall over local areas, for example. Life can handle a world's atmosphere, which is not the issue. Acid rain is an atmospheric condition, but it is, for life, not seasonal enough to give cues; it occurs infrequently in different locations and at different times in local areas, posing serious environmental stress. Such a scenario could be hypothesised to provoke the evolution of a bet hedging strategy for the long-term survival of organisms, not by being launched away by an impactor, but through variants that can withstand these conditions by lying dormant.

There may be many planets or moons, like the moons Europa and Enceladus, in the Galaxy and beyond that possess a liquid ocean protected by a thick ice cap. Such worlds can experience periodic, but for life unpredictable, cracks in their ice cap. Here, water sprays out in the form of plumes, and increased radiation enters the ocean, both potentially resulting in severe consequences for hypothetical life living near these cracks. Such a scenario could be hypothesised to provoke a bet hedging strategy to varying degrees to ensure the local long-term survival of life.

There may also be worlds with a star that sends infrequent fluxes of radiation through the protective magnetic field or ice cap of the world. Continuous radiation from a star is something that life can handle as it is not sufficient to sterilise the world per se, but infrequently, there could be a sudden increase in radiation that poses serious 'celestial stress' for hypothetical life in that world. Such a scenario could provoke a bet hedging strategy to varying degrees to ensure the long-term survival of organisms.

This was not necessarily the only existing strategy during the LHB. Although impacting (from a planetary science perspective) was a long-lasting event, (from a biological perspective) there may have been long periods of time between the impacts. As external pressure declined, life would have eventually been able to move away from this strategy. When external pressure increased again, life would eventually be able to adopt this strategy once more. Thus, there may have been many periods where the bet hedging strategy was not applied and evolved away from again. Adaptations must be used, otherwise, there is a tendency that they will be selected away from again. Thus, evolution can go both ways; acquired traits can disappear or occur again. Together, there may have been many periods where impactors arrived with great frequency, spreading unpredictably over time and location, but with such great frequency that bet hedging may have evolved as an evolutionary response.

This strategy may have been used as long as life existed and impactors arrived. Therefore, bet hedging may have arisen and disappeared again over several rounds in these early stages of the Earth's and life's history. A continuous, albeit infrequent, arrival of impactors would select more strongly for this strategy. Thus, life could indeed have acted against this 'heavenly onslaught' and may have come out as the victor.

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ПОТЕНЦИЈАЛНА СТРАТЕГИЈА ПРЕЖИВЉАВАЊА У ПЕРИОДУ КАСНОГ ТЕШКОГ БОМБАРДОВАЊА

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Оригинални научни рад

Период касног тешког бомбардовања (КТБ) је време када је број удара у Земљу био учесталији него иначе. Иако су судари били стални гледано глобално, они би од стране популација живих бића били опажени као локално ретки, јер су се догодили у различита времена и на локацијама широм планете. Ови удари представљају тешки и непредвидиви еколошки притисак на живот, јер су у било којем тренутку могли да униште организме и њихова локална станишта. Међутим, такво окружење би потенцијално могло довести до селекције одређене еволуционе стратегије која смањује генералну прилагођеност а повећава прилагођеност на стресне услове, и која одговара самој непредвидивости. Модел за анализирање оваквог сценарија представљен је у облику система прстенова који настају од удара - састоји се од унутрашњег примарног и спољашњег секундарног прстена, што демонстрира динамичку интеракцију између спољашњег притиска од динамике удара и еволуцијског одговора живота према њему. Модел показује да постоји дужи опуштени период у ком организми напредују и кратак насилан период у ком морају преживети три насилна догађаја и реаговати на потенцијално другачију средину. Ова еволуцијска стратегија конзистентно резултира већим бројем преживелих организама у поређењу са осталим еволуцијским стратегијама; стога, могла је играти кључну улогу у издржљивости живота кроз КТБ - увид релевантан за астробиологију.