Interplanetary transmissions of life in an evolutionary context

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Abstract The theory of lithopanspermia proposes the natural exchange of organisms inside meteorites between solar system bodies. Its focus has been on 3 distinct stages: planetary ejection, interplanetary transit and planetary entry. It is debated whether organisms transported within the ejecta can survive all 3 stages. If the conjecture is granted however, that life can indeed be safely transmitted from one world to another, then it is not only a planetary science question, but a biological question as well. Hence, these stages are only the first 3 factors in the equation. The other factors for a successful lithopanspermia are the quality, quantity and evolutionary strategy of the transmitted organisms in question. Here, the main focus will be on the last factor, the evolutionary strategy. When expanding into new environments, invading organisms often do not survive in the first attempt. It usually takes several attempts through propagule pressure before they obtains a foothold. There is a crucial difference between this terrestrial situation and the one brought about by lithopanspermia. While in the case of invasive species on Earth, species member after member arrives into the new habitat, a species pragmatically only arrives once onto another solar system body. Thus, an all or nothing response will be in effect, the species must survive in the first attempt, which restricts the probability of survival. Furthermore, evolution sets a boundary through the existence of an inverse proportionality between the exchanges of life between two worlds. Thus, there are many different types of habitable environments on a donator world from which an impactor can eject a sample of life. There is, however, only one type of habitable environment on an acceptor world to which this sample of life can be deposited upon entry, thus restricting the probability of survival. However, terrestrial populations do often encounter unpredictable and variable environmental conditions, and this in turn necessitates evolutionary response. Thus, one evolutionary mode in particular, bet hedging, is the evolutionary strategy that best smoothes out this inverse proportionality. This is achieved by generating diversity even among a colony of genetically identical organisms. This variability in individual risk-taking not only increases the probability of survival but also allows organisms to colonize wider ranges of environments. In summary, an analysis to understand conditions relevant to a bacterial colony arriving in a new planetary environment has been introduced, providing a bridge between the theory of bet hedging, invasive range expansion and planetary science.

Keywords: astrobiology, bet hedging, lithopanspermia, Mars.

1. Indledning

Since E. de Montlivault (1821) suggested that meteorites could be carriers of life to Earth, and Hermann Richter (1865) put forward a scientific hypothesis detailing how some meteors rather than fall to the ground as meteorites instead could glancing the Earth's atmosphere at such an angle that they penetrated only part way through, potentially collecting airborne organisms along the way, before bouncing back into space with them, lithopanspermia (rock panspermia), the theory that proposes the natural exchange of organisms between solar system bodies due to asteroidal or cometary impacts [Nicholson, 2009], has grown to become an active field of research.

Scientific research has focused on the following 3 distinct stages: (1) Planetary ejection - organisms need to survive ejection from a planet; (2) Interplanetary transit - organisms need to survive the transmission through space; (3) Planetary entry – organisms needs to survive entry from space onto a planet. These stages represents a multidisciplinary field of research, ranging from studies of ejection rates, dynamical transfer and impact physics, which seeks to clarify whether life can survive each of these stages and what their overall survival chances are being transferred between different solar system bodies.

One of the early objections to lithopanspermia was based on a doubt as to whether material could be exchanged at all between solar system bodies. However, since its proposal, it has become evident that among the over 62000 meteorites found on Earth [The Meteoritical Society, 2020], 142 are Martian in origin [Irving, 2020], thereby eliminating any doubts as to the exchange of material between planets. Most Martian
meteorites have been on Earth long before they were found, though some have been found after falling, such as the Martian Tissint meteorite that arrived in 2011, where it fell in Morocco on July 18 [Brennecke et al., 2014]. That the opposite situation exist, with terrestrial material arriving to Mars, should be clear.

It is estimated that the escape velocity, that is, the minimum velocity required to escape a gravitational field, is 5.03 km/sec for Mars and 11.2 km/sec for Earth [Nicholson, 2009]. Thus, the stages of lithopanspermia would work more easily with planets like Mars. However, Beech et al. (2018) estimated that at least $10^{13}$ kg of material from Earth has been ejected into the inner solar system since the beginning of the Phanerozoic Eon, with an estimated 67% attributed to the Chixculub cratering event. This terrestrial material could potentially reach Mars as well as Venus, provided an impact velocity of 25 km/s, and could potentially reach the moons of Jupiter as well provided the impact velocity exceeds 27 km/s. This estimate was based on documented terrestrial impact craters with diameters larger than 5 km. But it is clear that the un-documented craters could increase the estimate of matter ejected, which the authors deduce from the documented craters as perhaps being on an order of magnitude to $10^{14}$ kg.

However, these travel times given by impacts are, from a biological point of view, frequently long. The majority of Martian meteorites are estimated to have spent from ~0.6 to 15 million years in space. The Martian meteorite Nakhla that fell on June 28 1911 in northern Egypt spent, for example, a transmission time of ~10.75 million years in space [Nyquist et al., 2001], while the Tissint meteorite is estimated to have been ejected between 700,000 and 574 million years ago [Brennecke et al., 2014]. However, shorter travel times have been calculated as being possible, with some meteorites potentially reaching transit trajectories fast enough to allow interplanetary travel lasting months to a few years between Mars and Earth [Melosh, 1988], although it should be noted that major shocks at launch and impact reduces the chance of organism survival.

Since lithopanspermia conjectures that ejected rocks serve as transporters for organisms, and considering that most Martian meteorites are igneous, it is imperative to investigate the presence and persistence of organisms in igneous terrestrial rocks such as basalts and granites. Thus, in one study, microbial communities were recovered from eleven rock samples collected from the walls of deep subsurface tunnels at Rainier Mesa, Nevada Test Site (USA). The numbers of microorganisms from these samples were found to be $~4 \times 10^5$ to $~4 \times 10^7$ total organisms per gram of rock [Haldeman et al., 1994].

Benardini et al. (2003) described the isolation of culturable endolithic Bacillus sp. traces from near-subsurface basalt rocks collected in the Sonoran desert near Tucson, Arizona (USA). The authors reported finding exceedingly low numbers of spores ($~10$ of spores per gram of rock). A related study in contrast obtained numbers of cultivable endolithic Bacillus spores much higher ($5 \times 10^2$ spores out of $~10^5$ cultivable bacteria per gram) from the interior of near-subsurface granite rocks collected in the Sonoran desert. The authors noted that these isolates were closely related to a few Bacillus species that inhabit globally distributed endolithic sites and some extreme environments [Fajardo-Cavazos and Nicholson, 2006].

Thus, there is indeed life existing in globally distributed rocks that can potentially be ejected. But the question then is what their probability of survival is? Many studies have addressed this issue. The issue is not only surviving the launch and landing, but also surviving the transmission itself. Thus, being freely exposed to space means that the transported organisms are subjected to intense radiation, and experience complete desiccation due to being exposed to the vacuum of space, rendering them unable to maintain metabolic functions and doing cellular repair, which leads to degradation of the biological structure of the organisms and hence the cessation of life [Mileikovsky, et al., 2000].

However, bacterial endospores have long been studied with regard to space conditions, since such spores have been recognized as the toughest terrestrial life known, capable of enduring conditions in the dormant state otherwise destructive or lethal to other known life [Nicholson et al., 2000].

Calculations by Mileikowsky et al. (2000) have predicted that a fraction of a Bacillus subtilis spore population ($10^{9}$) would in fact survive cosmic radiation in space for about 1 Ma if protected by 1 m of meteorite material (assuming the rock initially harbors about $10^9$ spores/g) and 25 Ma if protected by 2 to 3 m of meteorite material. Thus, the natural transfer of microorganisms such as D. radiodurans and Bacillus sp. was concluded as not only possible but highly probable in Mars – Earth interplanetary travel. Interestingly, a study of many Martian meteorites indicated that some meteorites never experienced being heated above $~100$ °C during their ejection from Mars and transfer to Earth [Shuster and Weiss 2005], which was one of the survivability criteria set by Mileikowsky et al. (2000).
It is important to mention that the key mechanism behind lithopanspermia is not something from the past, but is still active within the solar system [Beech et al., 2018]. Thus, as mentioned, the Martian Tissint meteorite arrived in 2011, where it fell in Morocco [Brennecka et al., 2014], demonstrating that meteorites continue to be transmitted between solar system bodies to the present day.

In spite of all this, from a biological point of view lithopanspermia may still be considered an extreme situation. It is an active field of research whether the organisms transported within the ejecta can survive all 3 stages, and there are many pros and cons to it. Although the number of different experimental organisms has been relatively limited, new research results continue to arrive, and the current consensus appears to be that organisms can indeed survive all three stages of lithopanspermia [Beech et al., 2018].

That life can survive the transmission to another world and that life has been transmitted to another world are of course two different situations. Thus, we do not yet know if life or biotic material has ever been transmitted between worlds in this solar system. Although the probability of a successful transfer of life between worlds seems modest, and the probability of establishing a viable ecosystem in a new world seems even more modest, the possibility nevertheless seems to exist.

So if the conjecture is granted that life can indeed be transmitted safely from e.g. Earth to Mars or vice versa, then it is not only primarily a planetary science question, but a biological question as well.

Hence, planetary ejection, interplanetary transit and planetary entry, are only the first 3 factors in the equation. After all, the defining characteristic of life is not chemistry or physics, but evolution. Thus, it is important to clarify how this is to be understood in an evolutionary context. Can life per se survive a journey through space? It cannot! Can life per se colonize any environment in which it is deposited? It cannot! Organisms are adapted to their environment. An organism that does well in one environment will do not so well in another. Thus, organisms cannot simply be transmitted to another environment since they will encounter severe environmental stressors there.

Although many studies have investigated the problem of how meteorites can transmit life, and what parameters must apply if they are to survive the journey, systematic and predictive evolutionary theory regarding this matter is still lacking. In this article, I will seek to clarify how the arrival of life on another world can be understood in an evolutionary framework, and what strategy organisms must follow in order to survive the encounter with that world.

2. Discussion

The survival of organisms arriving at another solar system body is more complex than just their survival in the actual transport. Thus, planetary ejection, interplanetary transport, and planetary entry, are just the first 3 factors in the equation for a successful lithopanspermia. The other factors are the quality, quantity, and evolutionary strategy of the transported organisms in question.

Here, there will mainly be focused on the last factor, the evolutionary strategy. This concerns the situation that applies if life successfully reaches another world and how this is to be understood in an evolutionary framework. The many variables involved in lithopanspermia make it uncertain what probability life has in surviving and gaining a foothold on another solar system body. However, uncertainty is in fact a prevalent characteristic of terrestrial environments, and this characteristic in turn necessitates evolutionary response. I will make the following simplifying assumptions in my discussion:

(i) It is assumed that the meteorite manages to bring living organisms to another world.
(ii) It is assumed that the meteorite lands where the transported organisms have a possibility of survival.
(iii) It is assumed that the meteorite carries with it members of the same clonal colony.

Given the general toughness and versatility of bacteria compared to other terrestrial species, and the fact that they are the dominant species on this world, existing in all available niches, their likelihood to be picked up and surviving the journey is the highest, and so I will focus on them. In sections 2.1, 2.2, and 2.3, I will discuss the 3 arrival modes into which lithopanspermia can be divided, which I will call: fractional genetic transfer; fractional componentional drift; and phenotypic continuance. In subsection 2.3.1, I will discuss the
evolutionary framework for the survival of organisms on another world that emerges through 3 overarching evolutionary modes of response to changing environments.

2.1. Fractional genetic transfer

As discussed, research into the possibility of lithopanspermia has focused on 3 distinct stages as the mean to bring living organisms to another solar system body. However, perhaps initially surprising, such entrapped organisms do not necessarily have to survive the journey in order to have an astrobiological significance. The meteorite need not be able to keep them alive. In fact, it only needs to bring its content to the acceptor world, because even if the organisms do not survive the journey, they can still potentially influence any biological evolution that takes place in the environment in which they arrive.

Thus, competent bacterial species can actively take up exogenous DNA, sometimes termed naked DNA fragments, in the surrounding environment and occasionally incorporate it into their chromosomes through homologous recombination, thus changing their own genotype [Mell et al., 2011]. This well-known mechanism called transformation is a primary mode of horizontal gene transfer in bacteria, along with conjugation and transduction [Blokesch, 2016]. Thus, it is in principle possible for a hypothetical Martian bacterial analogue (H MBA) to incorporate a portion of DNA from an arriving terrestrial bacterial genome, or for terrestrial bacteria (TB) to incorporate a portion of DNA from a hypothetical Martian bacterial analogue, see figure 1a.

Thus, from a genetic point of view, one part, the donor, does not have to be alive in order to be a donor. It does not even have to survive as an endospore. All that is required is that the recipient is alive, since natural competence for transformation is entirely controlled by the DNA-absorbing bacterium itself [Blokesch, 2016].

In terrestrial environments, destroyed bacteria are known to be suppliers of the exogenous DNA pool in the environment, where free DNA is thus often abundant; exogenous DNA can in fact persist in the natural habitat for long periods of time and be viewed as representing a record of genes [Moradigaravand and Engelstäder, 2014]. The existence of such pools of DNA can potentially through DNA diffusion spread genes through a bacterial population, enabling a flow of genes without the need for any bacterial migration [Moradigaravand and Engelstäder, 2014].

It seems that most competent bacteria can take up available exogenous DNA from any source, although they take up DNA from their own species much better than DNA from distant bacterial species [Mell et al., 2014]. While the host cells bind double-stranded DNA at their cell surface, they nevertheless transport only single exogenous DNA strands into their cytoplasm [Chen and Dubnau, 2005]. However, it has been demonstrated that competent Bacillus subtilis was capable of incorporating whole-genome DNA, that is, 4215 kb double-stranded DNA from the protoplast lysate of B. subtilis subtilis [Akamatsu and Taguchi, 2001], although this transformation was reported to be different from that incorporated by purified DNA conventionally [Saito and Akamatsu, 2006].

Thus, although the meteorite cannot protect its entrapped organisms in all 3 stages, it may be sufficient to protect the genetic material of the organisms until it arrives. This is quite relevant. While it is not yet known whether organisms can survive the journey between two worlds, it is almost a corollary of the former that such meteorites can carry fragments of life all the way to another world. Indeed, the probability that segments of RNA and DNA endure the journey seems higher than the probability of surviving bacteria.

Of course, RNA and DNA as well as other biotic components can be degraded before arriving at the destination. However, although such free genetic material can often be highly fragmented, terrestrial competent bacteria have evolved active DNA scavenging approaches allowing them to take up exogenous bases and nucleotides where possible [Blokesch, 2016].

This situation is thought provoking. If it is assumed that the bacterium is indeed a universal blueprint for life that exists everywhere where life exists, then it can be imagined that gene fragments from life elsewhere arrive on Earth. Since bacterial life exists virtually in all available niches on Earth, then they will come into contact with this exogenous material. Thus, hypothetical Martian bacterial analogues and terrestrial bacteria could have their cellular material transferred to each other. Such genetic fragments can be of great importance, as they still represent complex information-carrying molecules, meaning that their incorporation can influence the native biological evolution.
Of course, this does not mean that such genes remain permanently in a gene pool. Thus, certain genes can be driven to extinction. But, on the other hand, it can hypothetically provide an advantage, as the recombination of incoming DNA with the native DNA can affect the fitness of bacteria, and become fixed in the gene pool.

![Figure 1](image1.png)

**Figure 1.** The 3 arrival modes which lithopanspermia can be divided into (apart from no effect at all), called (a) fractional genetic transfer, (b) fractional componential drift, and (c) phenotypic continuance. Credits: adapted from Bravo et al, 2018; Zeineldin; Mirumur, 2011, 2014.

### 2.2. Fractional componential drift

As discussed in section 2.1, bacteria do not *ipso facto* have to survive the transmission to another solar system body in order to have an astrobiological significance. Thus, even if there is no native life where the meteorite deposited them, the arriving bacterial components may still matter if it is assumed that it lands on an acceptor world that has conditions suitable for life, see figure 1b.

Although the arriving bacteria have broken down on arrival, their machinery could still remain intact. The meteorite will still carry the genetic systems, metabolic networks and numerous membrane lipids of the bacteria, all structures that are not alive and which will be distributed in the environment. From a prebiotic point of view, such a donation of machinery, fragmented or in a complete state, can be of great importance, as they still represent some of the most complex biostructures in existence. Such a donation may help boost the native chemical evolution.

It is well-known that lipid-like molecules when placed in water have the ability to undergo spontaneous aggregation to form lipid droplets, micelles, vesicles and bilayers even under simple conditions (Safran, 1994). The lipid bilayer is the basic structure for the terrestrial cell membrane. It is the structure and amphipatic nature of the lipids that, through entropy-driven hydrophobic interactions, cause them to spontaneously form sealed compartments under aqueous conditions, capable of resealing if torn [Alberts, 2002]. This spontaneous self-organizing into bipolar membrane sheets does not require complex chemical evolution; instead it depends entirely on physical characteristics of the molecules themselves [Segre et al.,
Importantly here, the most abundant membrane lipid molecules are the phospholipids, and that the bacterial membrane is often formed by one main type of phospholipid [Alberts, 2002].

Thus, even though the arriving bacteria is destroyed and their contents flow into the environment, their components can still potentially subsequently be encapsulated and protected in this new environment. Such amphiphilic molecules presumably existed in abundance in the prebiotic environment on Earth [Segre et al., 2001], becoming available, either from extraterrestrial impacts or through abiogenic synthesis [Pohorille and Deamer, 2009], and may have been abundant in the more watery environment of past Mars as well. Thus, amphiphilic molecules were found in the Murchison meteorite, which spontaneously formed lipid membrane vesicles when placed in water [Deamer and Pashley, 1989].

This is initially merely a passive drift. But these components will be protected for a time in this prebiotic environment, which automatically takes advantage of what is randomly available. The origin of the first fully autonomous cell was probably not a singular event, chemical evolution instead occurred through several stages. Thus, research that reflects the necessary aspects of a cell has put forward 3 models for what appeared first. Thus, a debate between the RNA-first model [Gilbert, 1986], the metabolism-first model [Oparin, 1957], and the lipid-first model [Segre et al., 2001] has been a long-running theme. I will not here discuss the pros and cons of these models, merely mention that no matter how it proceeded, self-replicating genetic systems and metabolic networks must necessarily have been encapsulated within a lipid membrane compartment before the first true autonomous cell could have emerged. Encapsulation is thus inevitably one of the steps in chemical evolution, regardless of what the order must have been.

The arrival of exobiological material and subsequent encapsulation on a new world does not fall directly into these 3 models. Here, instead, it is a form of hybridization between an acceptor world's native lipids and arriving exobiological material from a donator world. Of course, some of these lipids may also come from the numerous membranes the destroyed bacteria themselves brought along. This scenario thus does not ultimately solve the question of the origin of life. It simply shows what interplanetary transmissions in principle can do.

If chemical evolution takes place on any world with the right conditions such as liquid solvent, SPONCH elements and energy sources, then the question is what effect this can have. This situation would hardly occur on Mars, except in hypothetical sub-environments or in its Noachian era where water seemed to have existed in abundance. But for arriving hypothetical Martian bacterial analogues, it could potentially occur on Earth or any world with the right conditions. Whether such membrane-enclosed components will contribute to chemical evolution, accelerate it, initiate it even, or simply continue as fractional componential drift in the environment until broken down is at present speculative. It is merely important to make it clear that this possibility exists.

2.3. Phenotypic continuance

While the scenarios discussed in sections 2.1. and 2.3. are interesting, where it is the genotype and cellular components, or more precisely, fragments of what constitutes these that is addressed, it is perhaps even more interesting to discuss what happens if the organisms arrive alive, what could be called a successful transmission. Here it is in a manner of speaking the phenotype that counts. Once planetary science has done its own, what requirements does evolutionary biology then set for the survival of life? What predictions can an evolutionary framework provide?

It can be argued that the arrival of organisms from one world to the next through the stages of lithopanspermia in principle can be considered invasive biology. Terrestrial invasive biology is traditionally when foreign species invade habitats that are already inhabited. Such an introduction effort can be defined as ‘a composite measure of the number of individuals released into a region to which they are not native’ [Lockwood et al., 2005].

So in this case, interplanetary invasive biology can be considered as a species from one world seeking to gain a foothold in a new world habitat, irrespective of whether there is, or is not, life there already. Species invading other environments or expanding the ecological range into new environments is a natural phenomenon. An equilibrium balance between habitats is always a short-term state, and sooner or later the equilibrium changes and life spreads into other habitats. Thus, the arrival of life from one world to the next with attempts to gain a foothold there is in principle no different.
On a planet, when expanding into new habitats, invading organisms rarely get a foothold in the first attempt. In many cases, these first invading organisms will not survive in the new environment. It usually takes several attempts through a phenomenon called propagule pressure before it gains a foothold.

Propagule pressure is a single consistent correlate of establishment success, and it clarifies that small populations face a greater likelihood than large populations in becoming extinct [Akakaya et al., 1999]. Hence, it follows that large or consistent releases of individuals into one new environment are necessary in order to survive and allow an establishment in the new environment [Lockwood et al., 2005]. However, the fact that the opportunity to settle is low does not mean that it cannot be done. It is still a non-zero possibility.

There is a crucial difference between this terrestrial situation and the situation brought about by lithopanspermia. While for invasive species on a planet like Earth, one member of the species after another enters the new habitat until they gain a foothold through propagule pressure, a species in the practical sense only arrives once onto another solar system body.

The arrival of life into a new world thus represents a low propagule pressure. Even if meteorites arrive with a certain frequency, that frequency will in fact be measured in millions of years between each arrival. But even assuming that, under the most fortunate circumstances, meteorites will arrive within a few years interval, they will still arrive at widely different locations on the acceptor world. So in practice, compared to invasive species between different habitats, in an evolutionary context, it will have the same effect as a single arrival, a propagule singulus.

This is important to mention because, as stated, there exist a direct relationship between success and pressure. Thus, the higher the propagule pressure the higher the possibility of success of the invasion. Therefore, a species from a donator world has to survive and gain a foothold in the acceptor world environment in the first attempt, as it will not be the case that it gradually moves into the new environment in the form of propagule pressure. Instead, a species will be in the same environment at once, it will be exposed to it at once.

This all or nothing response is not specifically due to the arrival of the meteorite. On worlds with atmospheres, the entry proceeds at terminal velocity, that is, the constant maximum velocity reached by an object falling through the atmosphere under the attraction of gravity, which is approximately 50 m/sec for Earth and 300 m/sec for Mars [Nicholson, 2009]. Thus, the forces generated during the delivery of life on an acceptor world such as Mars are in fact relatively modest compared to those prevailing when life was collected on a donator world such as Earth. What is meant here is the severity of the environmental stressors the organisms will encounter in the environment on the new solar system body they arrive at. If these are severe enough, then the arriving life could perish as soon as contact is made.

Of course, there may be billions of bacteria entrapped in the meteorite that have survived the arrival. They will have been protected by the meteorite that brought them there. But the situation will still be different from that of invading organisms on Earth. While terrestrial invasive biology so to speak has a back up supply of organisms to try again and again to gain a foothold, this does not apply to interplanetary invasive biology where the billions of organisms still count as a single attempt to gain a foothold.

2.3.1. Evolutionary modes of response

As discussed in section 2.3. an all or nothing response will apply when life arrives at a new solar system body. To make the situation even more complex, this interplay between planetary science and evolutionary biology shows that there exists an inverse proportionality between the exchanges of life between two worlds. It is based on the fact that there are many different types of habitable environments in a world from which a sample of life can be obtained. However, there is only one type of habitable environment in another world to which this sample of life can be deposited.

Thus, the following rule can be stated: The retrieval of a particular sample of life in a random type of habitable environment on a donator world is inversely proportional to the deposition of a random sample of life in a particular type of habitable environment on an acceptor world. Therefore, the impactor-transporter-bringer mechanism that successfully retrieves, transmits, and deposits life is an invariant.

In other words, this rule states that organisms are adapted to the specific environment in which they live. The asteroidal or cometary impactor can land anywhere on a donator world and eject organisms. However, as such organisms are adapted to the specific environment from which they are ejected, it is not irrelevant
where on an acceptor world the meteorite deposit them upon landing. The meteorite has to deposit them in a similar specific environment in order for them to survive. Thus, the impactor-transporter-bringer is to be considered a constant $k$ as long as it can successfully retrieve, transmit, and deposit organisms on another world.

**Figure 2.** Rock transmissions between two Earth-like planets in a solar system given by a triangle. The tip of the arrow shows impact and ejection (the rock is not to scale) in an Antarctic-like environment, while the vertical end of the arrow shows several possible impact sites for the same rock, such as ocean, Sahara, forest, etc. Credit: adapted from NASA.

From a purely physical point of view, the situation is the same. An impactor hits a single point on a solar system body and sends material up. An impactor hits a single point on another solar system body and deposits material. This would be a line with a single point at each end. Thus, it could be inferred that if multiple environments are potentially life-friendly, then it should be irrelevant which of them life is retrieved from and deposited on.

But planetary ejection and planetary entry are only 2 factors in the equation. Another factor is the evolutionary strategy of the transported organisms in question. Thus, for the evolutionary strategy of the transported organisms, the situation is not the same.

If we take Earth and Mars as an example. Earth is a life-friendly planet, while present day Mars overall is not, though it is assumed to have sub-environments where life could live. Thus, hypothetical Martian bacterial (or archaeal) analogues transported to and deposited on Earth could, from a planetary science perspective, be more likely to survive than the opposite scenario. Indeed, we could simplify the situation and look at a transmission of life between two planets with Earth-like conditions, as seen in Figure 2, which should presumably make it easier for life to gain a foothold.

However, from an evolutionary perspective, this is not valid. While it is correct that terrestrial life would have to be placed in sub-environments on Mars in order to survive at all, this does not guarantee success. Organisms are adapted to their environment; even extremophiles are adapted to the environment in which they live.

Thus, from a biological point of view, the situation is different from the physical one, given more by a triangle than a line. For example, we could take two environments on Earth, the Sahara and Antarctica. Both of these environments are harsh, yet contain several life forms. But if organisms were taken from a Sahara-like environment, and deposited in an Antarctic-like environment, then their chances of survival will be low, and this despite both environments are potentially life-friendly. Thus, although one might be tempted to assume that extremophiles will be better suited to colonize other worlds, this is not valid according to the above.

Thus, there will be variation between two environments, even if they from an initial estimate appear as similar environments. So even hypothetical Martian bacterial analogues, which upon arrival on Earth are
more likely to be deposited in a place where there is already life than in the reverse scenario, will not necessarily be adapted to the environment.

It is possible that bacteria can only survive the journey in the form of, for example, desiccation tolerant life or bacterial endospores. The latter has long been considered the most durable form of known terrestrial life, capable of withstanding severe environmental stressors in the dormant state [Horneck et al., 2008]. For these, the difference between the environments will not be that high. But endospores do not do much in themselves; they're basically a nearly indestructible shell. Shall they have a biological significance, i.e. a life cycle with growth, metabolism and reproduction, they must necessarily become active bacteria again on the acceptor world, and thus face the environment.

Thus, with both an inverse proportionality and an all or nothing response between changing environments, it seems that the possibility of a successful lithopanspermia where a bacterial colony arrives in a potentially habitable environment on a new solar system body and automatically survives and adapts to it, is up against great challenges.

However, terrestrial populations often encounter unpredictable and variable environmental conditions, and surviving under such fluctuating conditions thus poses evolutionary challenges [Martín et al., 2019]. A number of evolutionary strategies have emerged in order to cope with such environmental uncertainty. Thus, there are overall 3 evolutionary modes of response - besides extinction of course - to fluctuating terrestrial environments: adaptive tracking, adaptive phenotypic plasticity and bet hedging [Simons, 2011], see figure 1c. These 3 modes do not give the same probability of survival for the same environment. So the question is how these evolutionary modes will come into play in an interplanetary transmission between two different environments. This will be addressed in the following.

**Adaptive tracking**

Organisms in changing environments experience selective pressures, and can adapt to such new environmental conditions through adaptive tracking [Rago et al., 2019]. Thus, populations that experience environmental change will gradually adapt into one or more traits. This means that optimal trait values change continuously and that natural selection results in the gradual evolution of more fitting phenotypes, thus removing suboptimal forms that hitherto were well adapted to the environment [Simons, 2011]. This evolutionary mode of response thus requires that the necessary genetic variance as well as mutational variance for fitness with respect to changing environments exists [Simons, 2011].

This is perhaps the most well-known mode. Any organism is adapted to its environment. When organisms spread to new environments, they become adapted as they spread, where they over time eventually can become a new species.

However, the transmission of terrestrial bacteria to a sub-environment on Mars or hypothetical Martian bacterial analogues to Earth will not benefit from this mode, as it will not be able to prepare the organisms for the journey itself, or for the initial encounter with the new environment. In this situation, the meeting between two environments is abrupt and extreme. There is no possibility of propagule pressure or time for the organisms to gradually adapt to the new environment. They must survive in the first attempt.

The main issue here is that environmental variance may lead to variable selection, meaning that traits that are optimal at one time or place are disadvantageous at another. Organisms have been adapted to a specific environment among many in the donator world, but here they arrive to an environment on the acceptor world that can be any random environment. Thus, there is an inverse proportionality here as discussed in section 2.3. However, the probability of survival can be high if the organisms happen to be adapted to the environment they arrive at on the acceptor world. But what is the probability of that?

To model this situation, the binomial distribution formula can be used where the probability of obtaining exactly k successes in n trials can be calculated. Thus, the following simplified situation can be set up. A bacterial colony encounters 10 different environments on an acceptor world. If each environment is either similar or non-similar to the colony's native environment, what is the probability of encountering exactly 1 environment similar to the native environment on the donator world? Plugging in the numerical values:

\[ n = 10 \]
\( k = 1 \)
\( n - k = 9 \) = number of failures
\( n - k = p = 0.5 \) = probability of encountering a similar environment
\( 1 - p = q = 0.5 \) = probability of encountering a non-similar environment,
we get the probability that the colony encounters 1 environment, and also does not encounter a specific set of 9 environments, is:

\[
P_{\text{specific 1 environment}} = (0.5)^1 \cdot (0.5)^9 \quad (1)
\]

However, it is necessary to update this based on how many ways it is possible to divide a group into sets of 1 and 9, which is obtained by the binomial coefficient. Thus, the final probability is:

\[
P(\text{match out of 10 environments}) = \binom{10}{1} \cdot (0.5)^1 \cdot (0.5)^9 \quad (2)
\]

\( \approx 0.0098 \approx 1\% \).

Thus, it is possible for the bacterial colony to survive the encounter with a new solar system body through this evolutionary mode, but the probability is not encouraging, especially since only ten environments are a generous assumption (remember, we have restricted ourselves to only talking about environments where the possibility of life is present and such worlds will in principle have many different environments). The probability that the organisms are not adapted to the specific environment they arrive in is much higher than the opposite case.

If a random environment allows the possibility of life at all, then it would be possible to adapt to it. But adaptive tracking requires a period of time to take place. Upon the arrival of organisms from a donator world to an acceptor world, their invasion of the environment will not take place during a long period of time with the possibility of adaptation and multiple attempts, it will be virtually instantaneous. Even terrestrial extremophiles adapted to a cold, arid desert environment can face serious challenges if transported to a sub-environment on Mars. As soon as there is a hole through to the meteorite where the organisms have lived protected, the organisms will be in contact with the new environment and the reaction will be virtually instantaneous. Their survival will be an all or nothing response.

Upon arrival, the meteorite will likely be further shattered and it and its cargo will effectively be distributed into the acceptor worlds crust, water, ice etc. But even though the incoming colony is thus divided over a larger area, collectively, it is still an all or nothing response that applies, since the arriving organisms as a clonal colony is similar.

As stated, this mode can, over time, allow the organisms to adapt to this new environment. But the issue here is that they do not have that time, because adaptive tracking precisely requires time to adapt to a new environment. There is an unavoidable time lag in adaptation behind shifts in optimal trait values [Simons, 2011]. If the rate of environmental alteration is sufficiently slow, as might be the case in the native environment, the mean phenotype will remain close to the optimum such that a fitness depression can be avoided [Lynch and Lande, 1993]. But if the environmental alteration is too sudden, or the new environment is alien, as is the case here, the organisms will be overwhelmed. Even if the organisms survived the initial encounter, then due to this time lag in adaptation, they will go to extinction since there is no time for such adaptation to the environment, even for organisms such as bacteria with their fast mutation and natural selection rates.

Of course, these bacteria may have survived the journey in the form of endospores or microbial cysts. This type of protection can also protect them when the meteorite is shattered. But the fact remains that if they are to have a life cycle on the acceptor world, then they have to emerge from these, and thus face the new environment.

This evolutionary mode, in this situation with a shift to an alien environment, seems most suitable before planetary launch, since it may have evolved organisms that can survive the journey. It can also appear to be suitable for colonizing the new environment after surviving the encounter with the new environment.
However, one further limitation of this evolutionary strategy under fluctuating selection exists. Thus, heritability itself is environment-dependent, and it has been shown that negative correlations exist between the two parameters heritability and the strength of natural selection [Wilson et al., 2006], meaning that responses to natural selection will in fact be constrained and phenotypic stasis favored when environmental shifts are too harsh. Thus, it goes that environmental variance reduces heritabilities under strongly unfavorable conditions, which certainly is the case here with the shift to an acceptor world with its potentially different environmental conditions.

Thus, all in all, the most well-known evolutionary mode provides little opportunity to gain a foothold on another solar system body.

Adaptive phenotypic plasticity

This evolutionary mode makes it possible for individuals to achieve an adaptive fit between phenotype and environment through the modulation of phenotype in response to direct environmental sensing [Beaumont et al., 2009]. It is thus an effective solution to environmental variance, since it instantly attains the most fitting phenotype for a range of conceivable environments [Simons, 2011]. Adaptive phenotypic plasticity is thus superior to the previous mode for a wide range of environmental conditions [Rago et al., 2019].

The initial situation is the same as in the previous section. As soon as there is a hole through to the meteorite, the organisms will be in abrupt and extreme contact with the new environment. There is no possibility of propagule pressure in the new environment. They must survive in the first attempt.

This mode appears to give organisms from a donator world a higher chance than the previous mode in surviving the initial encounter with the new environment on an acceptor world due to the fact, that it is not so limited by the either-or-situation with traits that are advantageous at one time but disadvantageous at another, but instead has a range of phenotypes expressed over a range of environments.

However, the evolution of adaptive phenotypic plasticity does have a serious limitation in that it requires the phenotype-fitness association to be predictable across the native environments. Organisms utilizing this evolutionary strategy produce only optimum fitness phenotypes by responding appropriately to environmental cues [Reed et al., 2010]. Thus, it is an effective strategy only under the range of native environments previously encountered by the arriving bacterial colony.

Obviously, as a remark only, since impacts can occur at such large intervals of time, none of which follow a predictable sequence, and can occur at any point on a world, they are, from an evolutionary point of view, an unpredictable event (though they from a physical point of view are not). There are thus no cues available for this event.

Thus, adaptive phenotypic plasticity is adaptive only if there are reliable cues that allow the arriving organisms to match the phenotypes to the acceptor world’s environment. However, it is only if the arriving organisms through this mode have achieved cues about a similar environment on the donator world that they will easily survive the initial encounter. The issue here is that the arriving organisms have evolved to diverse, but still restricted predictable environments on the donator world, and here arrives in an environment on an acceptor world that can be any random environment.

Furthermore, it has been shown that when the correlation between cue and optimum is weakened and environmental variability is high, strong plasticity diminishes population size, so that it faces much greater extinction probability [Reed et al., 2010]. Both the journey and the encounter with the new world are obviously an extreme situation, so even if it should happen that individual organisms survived this, then their continued survival through this mode itself will be further reduced.

Thus, there is an inverse proportionality here as discussed in section 2.3. And although the bacterial colony possess a range of phenotypes expressed over a range of environments, phenotypic plasticity is pragmatically in the same situation as adaptive tracking, and thus their probability of arriving at an appropriate environment, and survive, is again given by equation 2, with $P = 0.0098$ or 1 %. Thus, as for adaptive tracking, adaptive phenotypic plasticity is constrained. This evolutionary mode in this situation with the shift to an alien environment would be most suitable before planetary launch. So all in all, this evolutionary mode, albeit possessing greater range, nevertheless provides little opportunity to gain a foothold on another solar system body.
**Bet hedging**

In this evolutionary mode of response bet hedging traits can evolve under conditions of unpredictable environmental variance, where long-run, or expected geometric-mean fitness is maximized over time, even at the cost of a decrease in the arithmetic mean [Simon, 2011]. Fitness is here treated as a random variable, where the fitness of individual organisms is not known in advance, but where the fitness 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].

The initial situation is again the same as in the previous sections. As soon as there is a hole through to the meteorite, the organisms will be in abrupt and extreme contact with the new environment. There is no possibility of propagule pressure in the new environment, so this meeting represents an all or nothing response. They must survive in the first attempt.

This arrival at another solar system body can clearly be viewed as unpredictable natural selection. Since bet hedging is an evolutionary strategy that generates stochastic variation in fitness-related traits among terrestrial bacteria or hypothetical Martian bacterial analogues, in essence distributing risk among an array of phenotypes, each one neither optimal nor a failure across multiple environments, then this strategy increases the probability that some of these arriving bacteria express a phenotype that will ensure their immediate survival in this new unpredictable world.

The inverse proportionality as discussed in Section 2.3 still exists. But bet hedging is the evolutionary strategy that seems best to smooth out this inverse proportionality between any point on a donator world versus one point on an acceptor world, since this mode of response can ensure survival under the broad array of environmental situations wherein adaptive tracking and adaptive phenotypic plasticity are restricted.

In the previous sections, the adaptive trait or the environmental cue of the bacterial colony had to match the new environment in order to survive. But here the situation is different. Bet hedging does not require a 1:1 match. It has a wider range over environments. Thus, it should not be asked what the probability is regarding this modes effectiveness on exactly 1 out of 10 environments on an acceptor world. Instead the correct wording will be that if an evolutionary mode is effective say 75% of the time in shifting environments on a donator world, what is the probability that the mode will be effective on say exactly 6 out of 10 environments on an acceptor world? Plugging in the numerical values:

\[
\begin{align*}
n &= 10 \\
k &= 6 \\
n - k &= 4 \\
p &= 0.75 = \text{probability of effectiveness} \\
q &= 0.25 = \text{probability of ineffectiveness},
\end{align*}
\]

we get the probability that it works on a specific set of 6 environments, and also doesn't work on a specific set of 4 environments, is:

\[
P_{\text{specific 6 environment}} = (0.75)^6 \cdot (0.25)^4
\]

However, as before, it is necessary to update this based on how many ways it is possible to divide a group into sets of 4 and 6, which is obtained by the binomial coefficient. Thus, the final probability is:

\[
P(\text{effectiveness on 10 environments}) = \binom{10}{6} \cdot (0.75)^6 \cdot (0.25)^4
\]

\[
\approx 0.1459 \approx 14.6\%.
\]

As can be seen, it is not a high probability (given the specific assumptions) demonstrating that it is a drastic process not only to be transferred to another solar system body, but also to survive there. This 75% effectiveness is based on the fact that the bacterial colony consists of different phenotypes, with different possibilities, in contrast to the first mode, where the same number of bacteria were similar. The 4 environments may have environmental stressors that are simply too far from what bet hedging evolved to
deal with, or are too severe for all life. But the interrelationships between the probabilities of the different modes remain relatively similar, with bet hedging yielding the highest probability.

Of course, it should be made clear that the organisms the meteorite brings have not developed their bet hedging strategy with a transmission to a new world in mind. Instead, this assumes that the meteorite brings with it organisms that have obtained bet hedging on the donator world. To illustrate how bet hedging strategies can evolve on a donator world, I will use a simple model that follows a methodology originally advanced by Seger and Brockmann (1987), and then discuss its application when meeting an acceptor world. Hence, a bet hedging strategy can evolve by assuming that, for example, the native environment of the donator world can be either warm or cold during a generation, where a bacterial colony can encounter warm and cold periods of time with equal frequency.

Table 1. The absolute fitness values for 4 different genotypes.

|                     | \( A_{\text{cold}} \) | \( A_{\text{warm}} \) | \( A_{\text{con}} \) | \( A_{\text{div}} \) |
|---------------------|------------------------|------------------------|------------------------|------------------------|
| Cold, \( P_{\text{cold}} = 1/2 \) | 1                      | 0.560                  | 0.765                  | 0.745                  |
| Warm, \( P_{\text{warm}} = 1/2 \) | 0.540                  | 1                      | 0.765                  | 0.815                  |
| Arithmetic mean fitness \( \delta \) | 0.770                  | 0.780                  | 0.765                  | 0.776                  |
| Geometric mean fitness \( \Omega \) | 0.735                  | 0.748                  | 0.765                  | 0.775                  |

It holds that none of the bacterial genotypes can change their development depending on the native environment they live in, and since it is a bacterial colony asexual inheritance are in effect. The reproductive success of each bacterial genotype in each period listed in table 1 is equivalent to the absolute fitness of an individual bacterium [Seger and Brockmann, 1987; Starrfelt and Kokko, 2012].

These have been procured through the following assumptions. For the bacteria interpretation, a constant of 100 means that a bacteria of genotype \( A_{\text{cold}} \) will produce 100 descendents of the same genotype in a cold period (in reality, it would be 128 due to the constancy of bacterial doubling, which for simplicity is assumed here as 100), equivalent to 1, and 54 descendents in a warm period of equal duration as the cold period, equivalent to 0.540. Furthermore, we have that a bacteria of genotype \( A_{\text{warm}} \) will produce 100 descendents of the same genotype in a warm period, equivalent to 1, and 56 descendents in a cold period of equal duration, equivalent to 0.560. In this model, the fitness of for instance bacteria \( A_{\text{warm}} \) is given by its fitness achieved in cold and warm periods, where the probability of a period being cold is \( P = 1/2 \) [Seger and Brockmann, 1987; Starrfelt and Kokko, 2012].

Now consider the situation that in the native environment where the population was initially fixed for \( A_{\text{cold}} \), a mutant \( A_{\text{warm}} \) has just emerged. Thus, comparing the two specialists \( A_{\text{cold}} \) and \( A_{\text{warm}} \), their arithmetic mean fitness is given by:

\[
\delta_{\text{cold}} = P(\text{cold period}) \times (0.540) + P(\text{warm period}) \times (1) = 0.770, \tag{5}
\]

and

\[
\delta_{\text{warm}} = P(\text{warm period}) \times (0.560) + P(\text{cold period}) \times (1) = 0.780. \tag{6}
\]

The geometric mean fitness, for the two specialists are given by:

\[
\Omega_{\text{cold}} = (0.540 \times 1)^{P(\text{cold period year})} = 0.735, \tag{7}
\]

and

\[
\Omega_{\text{warm}} = (1 \times 0.560)^{P(\text{warm period})} = 0.748. \tag{8}
\]

In this methodology there is temporal variability in the native environment, whereas there is no spatial variability [Seger and Brockmann, 1987]. This means that all bacterial individuals experience either a warm or a cold period, which means that since \( A_{\text{warm}} \) has the highest geometric mean fitness, it will eventually prevail, that is, increase to fixation.

Thus, if \( A_{\text{warm}} \) arrives on an acceptor world in our lithopanspermia scenario, it could indeed survive if it encounters an environment that is either cold or warm (it is assumed, that the temperatures are within the
limits for sustainable bacterial life), or one that can vary between cold and warm, and thus match its native environment. Here it is a specialist whose situation is virtually similar to the situation in adaptive tracking. Of course, the same is true for \( A_{\text{cold}} \). It is also a specialist whose situation is virtually similar to that of adaptive tracking.

Once again, consider that on the donator world, \( A_{\text{warm}} \) is fixed, and \( A_{\text{con}} \), the conservative bet hedger emerge as yet another mutant. This is a consistent but low risk phenotype within a genotype [Liu et al., 2019]. Thus, this one is a generalist, that here is assumed to have a fitness of 0.765.

Bacteria have historically been viewed as clonal populations of identical prokaryotes, the result of symmetrical cell division producing cells genetically identical, with their phenotypes merely reflecting the genetic constitution [Casadesus and Low, 2013]. However, this view is not valid. Besides the fact that, for example, \textit{Bacillus subtilis} undergo spor formation [Errington, 2003], and \textit{Caulobacter} undergo asymmetric cell division [Kirkpatrick and Viollier, 2012], which are bacterial development where the genome sequence remains unchanged, there are also phenotypically distinct bacteria [Casadesus and Low, 2013]. Various mechanisms are involved in bet hedging strategies in bacteria, such as phase variation [van der Woude et al., 2004], contingency loci [Moxon et al., 2006], and epigenetically inherited bistability [Veening et al., 2008].

\( A_{\text{con}} \) does well regardless of the native environmental conditions, it is equally unremarkable in both periods, and is typically less fit than either of the \( A_{\text{cold}} \) or \( A_{\text{warm}} \) specialists on average. Because it is costly in the short term, this bet hedging adaptation appears compared to the other ones to be detrimental, because it is sacrificing short-term performance. However, \( A_{\text{con}} \) has higher geometric mean fitness than \( A_{\text{warm}} \) because its fitness does not vary and thus eventually prevail, that is, increases to fixation [Seger and Brockmann, 1987; Starrfelt and Kokko, 2012]. Thus, although \( A_{\text{con}} \) is characterized by lower arithmetic mean fitness, it will still replace both a bacterial population of \( A_{\text{cold}} \) and a bacterial population of \( A_{\text{warm}} \) because the individual geometric fitness of these are lower than \( A_{\text{con}} \). One period out of two, each specialist suffers the cost of being maladapted to the environment, while \( A_{\text{con}} \) fitness does not vary and it will go on in every period.

Thus, in our lithopanspermia scenario, if the population has gone to fixation in the native environment of the donator world, then only \( A_{\text{con}} \) will arrive with the meteorite to the new environment on the acceptor world. Since its success is the result of giving up high success in any period and avoiding very low success in any period in its native environment, then it will, regardless of whether it encounters a cold or warm environment, be able to handle the initial brunt from the new environment. The conservative generalist \( A_{\text{con}} \), with its reduced genotypic variance, will thus do reasonably well regardless of the acceptor world’s environmental conditions, since \( A_{\text{con}} \) is a consistently low risk phenotype within a genotype.

If the arriving population has not yet gone to fixation, then both \( A_{\text{cold}}, A_{\text{warm}} \) and \( A_{\text{con}} \) individuals will be able to arrive to the new environment. They will all now experience the full brunt from the acceptor world’s environment. \( A_{\text{cold}} \) and \( A_{\text{warm}} \) specialists will now each suffer the cost of being maladapted, they will essentially be in the situation of adaptive tracking, while \( A_{\text{con}} \) fitness does not vary and it will go on.

If \( A_{\text{cold}} \) and \( A_{\text{warm}} \) individuals survived the initial encounter at all, then they will still be able to survive for a while, yet neither \( A_{\text{cold}} \) nor \( A_{\text{warm}} \) would continue surviving against \( A_{\text{con}} \) because the geometric fitness of each individual is lower. So eventually \( A_{\text{con}} \) will go to fixation and outcompete \( A_{\text{cold}} \) and \( A_{\text{warm}} \). Thus, \( A_{\text{con}} \) is the biological equivalent of a jack of all trades and master of none, but it is precisely this quality that allows it to displace a mixture of masters such as \( A_{\text{cold}} \) and \( A_{\text{warm}} \) under temporal environmental variation. And it is precisely this quality that gives it an advantage over the specialists open the arrival on a new world, regardless of whether it comes to a cold or warm environment.

And finally, with \( A_{\text{con}} \) fixed in the native environment, consider the emergence of the diversified bet hedger \( A_{\text{div}} \), yet another mutant. The diversified bet hedging strategy reduces the correlation of reproductive success between bacterial individuals sharing the same allele, thus accomplishing a reduction in the genotypic variance. Thus, \( A_{\text{div}} \) individuals picked at random will not all display the same reproductive success within a period, some individuals will have developed into \( A_{\text{cold}} \) bacteria, while other individuals will have developed into \( A_{\text{warm}} \) bacteria [Seger and Brockmann, 1987; Starrfelt and Kokko, 2012].

The diversified bet hedging strategy’s fitness values are calculated by assuming that the cold period specialist is produced with a probability 0.42. Thus, the \( A_{\text{div}} \) genotype develops the phenotype of cold period
specialists 42 percent of the time and 58 percent of the time the \( A_{\text{div}} \) genotype develops the phenotype of warm period specialists. Thus, the values are given by:

\[
\text{Fitness}_{\text{cold}} = (0.42 \times 1 + 0.58 \times 0.560) = 0.7448, \\
\text{Fitness}_{\text{warm}} = (0.42 \times 0.540 + 0.58 \times 1) = 0.815. 
\]

The arithmetic mean fitness of \( A_{\text{div}} \) in the native environment is given by:

\[
\delta_{\text{div}} = P(\text{cold period}) \times (0.42 \times 1 + 0.58 \times 0.560) + P(\text{warm period}) \times (0.42 \times 0.540 + 0.58 \times 1) 
\]

\[
= 0.776, 
\]

and the geometric mean fitness of \( A_{\text{div}} \) in the native environment is given by:

\[
\Omega_{\text{div}} = (0.42 \times 1 + 0.58 \times 0.560)^{P(\text{cold period})} \times (0.42 \times 0.540 + 0.58 \times 1)^{P(\text{warm period})} 
\]

\[
= 0.775. 
\]

Thus, the \( A_{\text{div}} \) genotype obtains a higher geometric mean fitness than the 3 previous genotypes, and even drives \( A_{\text{con}} \) to extinction.

So if we look again at our lithopanspermia scenario, then it follows that if the arriving bacterial colony has not yet gone to fixation on the donator world, then both \( A_{\text{cold}}, A_{\text{warm}}, A_{\text{con}} \) and \( A_{\text{div}} \) individuals will be able to arrive on the acceptor world. They will all now experience the full brunt from the new environment. \( A_{\text{cold}} \) and \( A_{\text{warm}} \) will now each suffer the cost of being maladapted. \( A_{\text{con}} \) fitness does not vary and it will go on, while \( A_{\text{div}} \) will continue to produce both cold period and warm period specialists with a fixed probability.

The phenotype of \( A_{\text{div}} \) offspring develops independently of both the progenitor cell and the new environment on the acceptor world. These individuals can thus be viewed as 'flipping' a coin to determine which phenotype to develop into [Starrfelt and Kokko, 2012].

\( A_{\text{cold}} \) and \( A_{\text{warm}} \) individuals will still be able to survive for a while, yet neither \( A_{\text{cold}} \) nor \( A_{\text{warm}} \) would continue surviving against \( A_{\text{con}} \) and \( A_{\text{div}} \), because the geometric fitness of each individual is lower. If this took place in the colony’s native environment, then \( A_{\text{div}} \) would eventually outcompete \( A_{\text{con}} \) and go for fixation, because one or the other of its phenotypes will be highly successful, and there is in fact never a period where the genotype generally does poorly. Indeed, if the population had gone into fixation with \( A_{\text{div}} \) upon arrival into the new world, then it would continue to produce both cold period and warm period specialists and thus be able to cope with the initial brunt from the new environment, regardless of whether it is a cold or warm environment, as it can produce specialists for both a cold or warm environment at the same time.

It could be said that the acceptor world environment, unlike the arriving organisms donator world environment, does not experience a shift between cold and warm, thus representing a new interesting situation for bet hedging. The advantage of \( A_{\text{div}} \) is that it is evolved in an environment that changes periodically between cold and warm. However, if the environment on the new solar system body remains either cold or warm, then it will suffer the total cost of continuously producing many individuals, e.g. warm adapted individuals who are being maladapted in the cold environment, while \( A_{\text{con}} \) fitness does not vary and will do reasonably well regardless of circumstances, and thus continue to go on.

However, although \( A_{\text{con}} \) is a genuine bet hedger, it has not evolved optimum traits and is thus competitively inferior. Thus, although \( A_{\text{div}} \) produces both cold period and warm period specialists and suffers the cost of some of these being maladapted, the thing is that it still produces specialists with optimal traits. Thus, it will still outcompete \( A_{\text{con}} \), especially as it may be the case that in a world without changing environments, the environment may eventually prove too harsh for \( A_{\text{con}} \), and that by producing high-fitness individuals, \( A_{\text{div}} \) will still be able to remain in the new environment.
As reviewed, $A_{\text{cold}}$ could indeed survive if it arrives in an environment that matches its native environment. Here it is a specialist whose situation closely matches the situation in adaptive tracking. But as seen, the probability of this happening is not high. If there are ten different environments on the acceptor world, then the probability that it encounters its own environment was just $P = 0.0098$ or 1%.

But it could be said that if $A_{\text{cold}}$ arrives in the environment for $A_{\text{warm}}$, which is not its own optimal environment, then it will still be able to produce 54 descendents in a warm period, rather than the 100 descendents in a cold period. Thus, it will suffer the cost of being maladapted overall, but some individuals will be able to survive anyway. It may go to extinction eventually, but it can survive the initial encounter and subsequent encounter for a time, thus defying the above probability. The same would of course be the case for $A_{\text{warm}}$.

But the issue here is that the model discussed is too simple. In that model, there was a probability of $P = \frac{1}{2}$ to encounter the right environment, where either $A_{\text{cold}}$ or $A_{\text{warm}}$ could be optimally fit, which is a very generous assumption. In reality, there will be more than just two changing environmental stressors a and b in a given environment. This can be seen during, for example, bacterial infection [Casadesus and Low, 2013]. The immune system obviously mounts more than just two environmental stressors against the invading pathogens. But despite the immune systems many responses, it is well-known that certain bacteria can utilize phenotypic switching in order to survive in the body much longer than bacteria that do not use that strategy.

Thus, a given bet hedger would have to deal with, for example, four environmental stressors a, b, c and d, all in interplay. Here, c and d could be specific nutrients, specific pH, wet, dry environments, etc. It could for example be the case that $a \neq b$, which in a applies to $c > d$, and which in b applies to $c < d$, where the mutual relationships between $c$ and $d$ in both a and b vary from year to year.

Here the situation is more complex. In their native environment, $A_{\text{cold}}$ and $A_{\text{warm}}$ have evolved fitness with respect to the exact relations of $a \neq b$. But that $A_{\text{cold}}$ or $A_{\text{warm}}$ should encounter an environment on the acceptor world with all the parameters present in the right relations appears to have a lower probability than $P = \frac{1}{2}$. Thus, they would find it more difficult to gain a foothold on the new world.

However, even in this more complex situation, the situation would still proceed the same way regarding bet hedging. In the donator world environment, $A_{\text{con}}$ or $A_{\text{div}}$ would through bet hedging evolve fitness with regard to all four environmental stressors. And whether they have reached fixation or not when they arrive on the new world, $A_{\text{con}}$ or $A_{\text{div}}$ would be able to survive and thrive when they encounter an environment where all four environmental stressors a, b, c and d are in interplay. This is why bet hedging offers a greater possibility for life’s survival when transmitted to another solar system body.

There may have been billions of bacteria with the meteorite, bacteria that had evolved to behave as if they sensed a stressful environment. This encounter with the new environment may have been so extreme, but still fortunate enough that a few bacteria have survived the encounter. Once the environmental shock is over and this small number of individuals has survived, they will then be able to proliferate and rebuild a new clonal colony of bacteria, which of course, is why bet hedging is in place to begin with.

For this new growing population of bacteria, specific environmental cues may now be available, which means that it is possible to evolve an expression of an optimal bacterial phenotype over a range of new environments, rather than merely maintaining an array of bacterial phenotypes, each one neither optimal nor a failure across new environments. Over time, adaptive tracking can become possible so that species formation will occur, so that this initially genotypically similar, but phenotypically diverse, population of bacteria will give rise to a diversity of organisms with optimal trait values in their new world. While propagule pressure didn't matter when they arrived on the acceptor world, it may matter now. The population of bacteria will be located at the site where the meteorite deposited them, and as they or their evolved descendents begin to expand their range, population pressure will come into effect again.

There is another situation that needs to be addressed. The overall goal for arriving bacteria is to survive the encounter with the new environment. But thereafter it will be the case, that this new solar system body can either be empty of other life forms or it can contain native life forms already. The environmental stressors can thus be both the environment itself or competing species, yet this phenotypic strategy is still convenient for the success of population expansions, regarding both the environment itself or competing species. Thus, populations possessing increased variability in individual risk-taking are capable of colonizing wider ranges of territories [Martín et al., 2019].
For hypothetical Martian bacterial analogues arriving on Earth during and after the Archean Eon, encountering native life forms will clearly be the case. Thus, terrestrial bacteria exist virtually in all available niches on Earth. So arriving bacterial analogues will both have to survive the encounter with the new environment, and, assuming this life is life as we know it, and thus share traits with them, compete with these. Thus, they must either compete with already existing species or create a viable ecosystem in a new world. For the latter, it is important to make clear that while a world can be inhabitable for life, this does not necessarily mean that there is life on that world [von Hegner, 2019].

There is a possibility that, despite this mode, the arriving organisms do not survive the initial encounter. P ≈ 0.1459 or 14.6% was calculated for success. The model parameters are very general and can of course be varied. The 4 environments where success did not occur denote environmental stressors that are simply too different or severe for any way of life as we know it. Thus, there are still restrictions for this mode in an interplanetary context. Life has its limits. But bet hedging is still the evolutionary strategy that best smooths out this inverse proportionality between any point on a donator world versus one point on an acceptor world.

3. Conclusion

Astrobiology, as the name implies, requires a framework from both astronomy and biology. Planetary science is only one part of the equation; the second part is evolutionary biology. Thus, while planetary ejection, interplanetary transit, and planetary entry are essential to the transmission of life between solar system bodies, the quality, quantity, and evolutionary strategy of the organisms is essential for the survival and foothold of life on a new world. A successful lithopanspermia requires a successful evolutionary strategy.

Lithopanspermia experiments demonstrate that not all organisms can survive the journey. But evolutionary theory also predicts that although organisms survive the journey, it does not mean that they can survive the encounter with the new world as well. Thus, evolution set a serious boundary through the fact that there is an inverse proportionality between the two points on the donator and acceptor world, that lithopanspermia necessarily interacts between.

However, although evolution sets this boundary through adapting organisms to a specific environment, evolution has nevertheless evolved space for stochastic phenotypic switching, a loop hole so to speak. This provides an adaptive solution to life when facing uncertainty by generating diversity even among a colony of genetically identical organisms, allowing them to increase their robustness against environmental variation, that is, increase the organism's probability of survival when facing environmental shocks. Thus, phenotypic quality matters.

Bet hedging strategy has been suggested to be among the earliest evolutionary solutions to life in fluctuating environments on Earth [Beaumont et al. 2009], and it could thus represent the most fundamental strategy to ensure life’s survival on a new world. In fact, bet hedging may also contribute to their survival on the actual transport between two solar system bodies. Thus, preadaptation is a common strategy in which a minority in a bacterial population utilizes stochastic phenotypic switching in order to obtain a dormant metabolic state, which allows them to achieve slower bacterial growth but increased robustness against environmental shocks [Ogura et al., 2017].

The successful transmission of life can be understood in an evolutionary framework by realizing that although the transmission of life from one world to another is an extreme form of population expansion, it is, however, fundamentally still a population expansion. If life can be transported to an environment in another world, then this belongs to an ecological setting, and although this is not a traditional setting, so will bet hedging theory that has been applied in many other traditional ecological settings, still be applicable to face this situation with an all or nothing response, where among the organisms involved there must at least be one who can live immediately in this environment.

Thus, given that meteorite transfers between worlds exist and that evolution is the guiding principle of life, it could be extrapolated such that organism’s invading and colonizing neighboring worlds are a naturally occurring astrobiological phenomenon in a solar system. It can thus be the way of life to secure its existence by spreading the risk of existing over to several worlds; by exploring all available niches in a solar system.

Bet hedging may in fact have already played a role in experiments relevant to astrobiology, without this being realized. Numerous experimental organisms have been subjected to simulated Mars-like conditions, as
well as to simulated and true space conditions. Here, among other things, the percentage of surviving organisms was measured according to how long they were exposed to these conditions, according to the intensity of these conditions, etc. (for review, see for instance de Vera et al., 2019). In experiments where the relation between time and intensity were considered, the percentage of survivors should be relatively similar in repeated experiments among genetically identical organisms of the same species. In cases where a seemingly random survival over repeated similar experiments occurs, this may be attributed to a purely statistical chance; some organisms simply survive by chance. However, from a bet hedging standpoint, this latter case need not be attributed to statistical chance. This random survival of individual members may mean that the organisms involved have already evolved bet hedging strategies. Thus, a seemingly random survival is not so random anyway, and future experiments should look into it.

Of course, this situation requires that bet hedging have evolved in the population transmitted and deposited by the meteorite. The asteroidal or cometary impactor may not necessarily transmit organisms that have this strategy. However, bet hedging is widespread among bacteria, and bacteria are the dominant life form on Earth, existing in virtually all niches. But still, $A_{con}$ and $A_{div}$ may not have evolved to the parameters they encounter in the new world. Even with bet hedging, the new environment can be very far from the environment where a bet hedging strategy was evolved. Thus, $A_{con}$ and $A_{div}$ do not of course represent universal types that can live everywhere. They can survive a wider range of environments than specialists and thus the probability of their survival is higher.

But they are still evolved in a particular environment where a number of parameters existed and which must exist if they are to survive in a new environment. So the inverse proportionality still exists. It demonstrates that although organisms invading and colonizing neighboring worlds may be a naturally occurring astrobiological phenomenon in a solar system, successful transmission of life to another world does not have a high probability.

I have treated this as a one-way scenario. But it could also be treated as a two-way scenario. Thus, life may have been transported to another world, and descendants of that life may since have been transported back to the first world, and since life has evolved in different environments in the intervening time, such life will not necessarily be the same.

If life has indeed been transported back and forth over multiple rounds between e.g. Earth and Mars, then from a biological perspective, these planets are considered two ecosystems interacting with each other; they are a simplistic dual biosphere. Mars may have been habitable during its Noachian era, [Worth et al., 2013], and life may have existed there in the past. Indeed, it may even exist in the present in the form of an analogue to the terrestrial *Halorubrum lacusprofundi*. This is a microorganism that is both a halophile and a psychrophilic organism, and is thus in principle capable of living in Martian brines where it can survive under Martian surface temperatures [Reid et al., 2006].

As discussed, we could simplify the discussion and easily imagine a solar system where there are two or more Earth-like planets. It is now known that there exist many solar systems in the galaxy, and that a solar system with two worlds suitable for life exist, is not far stretched. Here, the effect of such reciprocal genetic exchange of altered gene pools could be profound. Such worlds should therefore not be considered as isolated worlds, but instead as ecological niches where life can be exchanged. True, in such a general ecosystem, it will not be easy to say whether life occurred on either or only one of them to begin with.

Indeed, if components produced by chemical evolution can move back and forth between two worlds, as seen in the section on fractional componentional drift, indeed, chemical evolution happening on two worlds, then from an evolutionary point of view it is better to perceive the origin of life as occurring in a dual world system rather than a one world system.

In summary, I have introduced an analysis to understand conditions happening in a colony that is expanding into a new planetary environment. The analysis provides a bridge between the theory of bet hedging, invasive range expansion and planetary science. Of course, as with all scientific models, bet hedging rests on a number of assumptions. Thus, the concept of geometric mean fitness relies on assumptions such as nonoverlapping generations and externally fixed population sizes [Liu et al., 2019], which are themselves open to research and thus possible modification. However, the results of the analysis highlight the demands and restrictions between population diversity and the environmental variations encountered during range expansion into a new planetary environment.
More work is needed. Applying evolutionary theory to the interplanetary exchange of life is a novel attempt. But the generality of this framework makes it a valuable starting point for analyzes and modeling of ecological scenarios regarding transmissions of life or biocomponents between worlds in a solar system.

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