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REVIEW

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Thinking outside Earth's box—how might heredity and evolution differ on other worlds?

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Abstract

Scholars and the public conceive of extraterrestrial life through the lens of "life as we know it" on Earth. However, assumptions based on centuries of study around heredity and evolution on Earth may not apply to life truly independent forms of life, and some perspectives accepted or ruled out in the nineteenth century may need to be re-evaluated for life outside of Earth. In honor of the 200th birthday of Mendel, and to provide raw material for the creativity of storytellers, filmmakers, and the public, this thought experiment essay revisits a handful of classic concepts and approaches, as well as some unusual forms of life on Earth, to posit whether different types of genetics and evolution may exist in truly independent extraterrestrial forms. While fundamental evolutionary processes like natural selection and genetic drift are likely to still apply at least similarly in independent life forms, inheritance may be quite radically different from that envisioned by Mendel and others since.

Keywords: Mendel, Darwin, Lamarck, Natural selection, Genetic drift, Inheritance of acquired characters, Outreach

Background

Two of the most fundamental questions in all of biology are whether life exists on other worlds and what form such life may take. While a simple explanation for life on other worlds may involve some variant of "panspermia" (e.g., see Kawaguchi 2019), wherein extraterrestrial life is not fully independent of life on our planet, more intriguing prospects exist wherein extraterrestrial life is truly independent. Because we have only observed life on our planet, all of which shares common ancestry, imagining unrelated extraterrestrial life forms and how they may differ from those on Earth poses a challenge.

Much of the field of astrobiology focuses on the potential detection of life on other worlds and what the physical and chemical nature of that life may be. The evolutionary aspects of astrobiology often focus on the "origin of life" and/ or possible relationships to life on Earth. Less attention has been paid to how heredity and evolution may operate on such extraterrestrial life. While some classical evolutionary biologists have weighed in on astrobiology at times (e.g., Simpson 1964; Mayr 1993), our understanding of inheritance and evolution in hypothetical extraterrestrial life necessarily remains severely constrained by what we have observed on Earth limiting what we can imagine elsewhere. While I am not an astrobiologist, I have encountered questions repeatedly about genetics and evolution in life on other worlds outside of academic contexts via outreach talks and work with storytellers and filmmakers (Loverd et al. 2018; Noor 2018).

If and when we finally encounter extraterrestrial life, we may have to view aspects of it with a perspective similar to the one with which nineteenth century naturalists explored life on Earth: scholars speculating with a (nearly) blank slate about the nature of inheritance and how evolution occurs. Correspondingly, and in honor of just passing through the 200th anniversary of Mendel's birth, I propose a brief thought experiment here where I reconsider some foundational basic concepts in heredity and evolution in the context of hypothetical extraterrestrial life. Some of these concepts include Mendel's laws, Lamarck's inheritance of acquired characters, Darwin's theories of natural selection and common ancestry, and

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the Wright-Fisher concept of genetic drift. I also outline a bit of the diversity we see in life on Earth and approaches taken to studying it that are sometimes not considered outside of evolutionary biologists with regard to these principles. My intention is that this thought experiment would be useful for astrobiologists who may not have formal training in genetics and evolution or for storytellers and filmmakers to stimulate their creativity.

Main text

Heredity

Heritability

Before going into the foundational historic concepts, one must first consider related issues around heritability, transmission fidelity, and mode of inheritance. The concept that at least some biochemical characteristics are passed on from parents to offspring is at the very essence of the word "heredity" and has been appreciated for millennia by animal and crop breeders (e.g., see Poczai and Santiago-Blay 2021) as well as the general public through parent–offspring resemblance (e.g., Zimmer 2018).

Fundamental to such heredity of traits are that a biochemical basis to inheritance exists and that the parents contribute these genetic instructions stably. However, even these basic assumptions need not be true in extraterrestrial life, and sometimes are not completely true even among species on Earth. Parent–offspring resemblance may have a large shared-environmental basis, or perhaps something more active wherein offspring learn and "mimic" traits of their parents. Language use in humans is highly shared by parents and offspring yet has no biochemical inheritance, and research on song in various bird species have has shown strong learned components (for review, see e.g., Mooney 2020). Such resemblance need not be limited to behaviors—e.g., *Biston betularia* caterpillars develop to resemble the branches on which they grow based on visual cues (Noor et al. 2008).

Extraterrestrial life may well also bear traits that are heavily environmentally determined or perhaps even mimetic, so repeating classic-style reciprocal transplant (e.g., Clausen et al. 1940) or other studies to clarify biochemically mediated inheritance will be critical. While exploring how hypotheses may be tested is beyond the scope of the present review, this particular example has historical precedents. Imagine variation among alien plant-like forms in which those forms found at higher altitudes are short and those at low altitudes are tall. Classic reciprocal transplant experiments involve introducing organisms from each of 2 environments into the other and are used to test whether a genetic component existed to observed differences between populations found in different places/ environments. If size is hereditary and encoded biochemically, then moving alien plant seeds from high altitude to low altitude should result in short plants (perhaps after an extra generation to account for early-life effects). In contrast, if the trait is largely environmental or mimetic, the transplanted plants or their offspring should resemble the local tall ones. Such experiments were pioneered a century ago (Turesson 1922; Clausen et al. 1940) and continue to be useful today (Johnson et al. 2022) but may have similar usefulness in some astrobiology contexts.

Fidelity, genetic code, and inheritance

We know that the biochemical instructions associated with heredity on Earth are generally stable, but not perfectly so. Focusing on uniparental inheritance, mutation necessarily reduces parent–offspring resemblance at the genetic level. In life on Earth, replication fidelity is quite high, with some of the most extreme mutation rates reaching only as high as 10^{-3} of misincorporated nucleotides per round of replication in RNA viruses (e.g., Villa et al. 2021). Given that mutations reduce fidelity and often lead to fitness consequences, there necessarily has to be an upper limit on mutation rates: e.g., a genome-wide mutation rate of 10% per nucleotide per round of replication presumably would not allow even the most basic form of Earth's life to persist. However, any upper limit to mutation rate would be partially constrained by Earth's near-universal use of the 3-nucleotide standard genetic code for translation of RNA to amino acids. Most changes in the first-position, all changes in the second-position, and some changes in the third-position of this RNA code alter the amino acid incorporated into the resultant protein. Correspondingly, life-on-Earth's instruction system raises three potential targets for any amino acid change, and 1–3 of 3 mutational changes would have an effect and be potentially "not tolerated".

One could imagine an alternative code (whether relating RNA to amino acids or other kinds of instructions to products) may have greater redundancy built into it, or fewer mutational targets, and thereby be more tolerant to changes than Earth's most abundant system. Parent–offspring genetic resemblance may even become more qualitative, similar to how we observe physical similarity between parents and offspring in multicellular organisms. The specifics could impact the efficacy of processes like natural selection—for example, if the connection between genotype and phenotype was reduced, natural selection would become less efficient, a point to which I return later. But more fundamentally, the "fidelity" of specific hereditary information units in a hypothetical extraterrestrial species may be quite a bit lower than seen on Earth, to the extent that we may struggle to even identify the hereditary function of the instructions.

Additionally, we focus on inheritance as being from one or two parent progenitors from whom we inherit genetic material. One could imagine having more than 2 genetic parents. One possibility may be parasexual reproduction akin to bacterial conjugation, wherein some genetic material is passed directly into individuals. Such a process could potentially accelerate the pace of adaptation across populations since reproduction is not required: individuals that grab good gene variants immediately improve themselves, thereby producing more offspring. One might even imagine large genetic "pools" from multiple parents that are absorbed into immature individuals. If particular gene variants are advantageous and help their bearers reproduce, those variants may become overrepresented in the pool based on the higher reproduction of the bearers. While mutations are often detrimental, most strongly bad mutations are recessive and appear to result from loss-of-function (Lewontin 1974, Simmons and Crow 1977, Kacser and Burns 1981, Houle et al.1997, Lynch et al. 1998, Eyre-Walker and Keightley 2007), so acquiring extra copies may sometimes provide benefits without much risk of strong negative effects (Raynes and Sniegowski 2014). Evidence that this hypothesis of masking bad effects by acquiring multiple copies may sometimes apply comes from the abundance of polyploidy (e.g., Van de Peer et al. 2017), which is especially common in plants and some other taxa.

Pre-mendelian ideas on inheritance

Turning to biparental inheritance, pre-Mendelian ideas did not assume stable particulate factors (now called "alleles") being passed on from parents to offspring. One early concept was that of "blending inheritance", wherein offspring traits are intermediate to parents' traits, almost like the blending of two colors of paint. Indeed, the multilocus nature of many traits approximates this effect in species on Earth even though the underlying basis involves generally stable alleles at individual loci. However, conceivably, an extraterrestrial species may have a different system that is closer to this original blending concept. The challenge with blending inheritance is that it typically leads to a loss of hereditary variation over time (e.g., Jenkin 1867), which would then make natural selection on any new beneficial variation very difficult since new variation would quickly blend away and be lost. On the other hand, extraterrestrial species may not have the same capacity to retain variation that Earth-bound species do, so this blending inheritance concept may still apply.

A potential solution to the problem of lost variation was popularized by French zoologist Jean-Baptiste Lamarck: the inheritance of acquired characters. Essentially, this concept proposes that the experiences and behaviors of parents can become encoded in the germline in such a way as to affect the traits or behaviors of the offspring (Lamarck 1809). Although attributed to him, this concept predates Lamarck, but Lamarck proposed that it was a source of almost unlimited new variation (Burkhardt 2013). While stable particulate inheritance is now broadly accepted as the norm on Earth, a small amount of renewed interest in the inheritance of acquired characters has resurfaced from some limited observations of transgenerational epigenetic inheritance (Gissis and Jablonka 2011), crudely mimicking this concept. Briefly, "marks" on DNA that affect how much a gene produces its protein products are sometimes placed based on an individual's exposure, and in rare occasions, such marks can even make it into the germline and affect traits in subsequent generations. While the evidence to date suggests that such transgenerational epigenetic inheritance is likely quite limited in its application to species on Earth (Heard and Martienssen 2014, Charlesworth et al.2017), again, extraterrestrial species may indeed have their genetic instructions directly modified through their experience in some manner. One could imagine a simple mechanism that could work in some terrestrial species via copy-number increases of genes expressed at high rates in specific conditions being introduced into the genome, germline, and offspring via reverse transcription and integration into a genome (similar to Sui and Peng 2021). Extraterrestrial species may have more complex means of achieving the inheritance of acquired characters, particularly if the molecular basis of their genetic instructions is readily malleable.

Mendel's laws

Mendel assumed particulate, stable factors underpinned inheritance and proposed three laws that frame our modern thinking of inheritance. His law of segregation proposes that the pair of alleles possessed by a parent at one gene separate, and only one (at random) is included in each of their resultant gametes. The assumption then is that each offspring inherits one of these alleles from each parent. The law of dominance posits that traits are controlled by a pair of underlying factors (alleles) and that, if heterozygous for different variants, the effect of one will mask the effect of the other. Finally, his law of independent assortment notes "the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks" (translated from Mendel. 1866, Stenseth et al. 2022).

Nonetheless, even on Earth, exceptions have been known to these laws for over a century (e.g., Castle 1903), and the exceptions have sometimes helped us understand the mechanistic basis for why these laws normally apply (Wolf et al. 2022). The law of segregation probably holds the most consistently, but even with respect to that principle, inheritance need not be from two parents nor in equal amounts from each parent. Cases of inheritance from more than two parents are less common on Earth but certainly possible via mechanisms like bacterial transformation as described earlier. But unequal contributions from two parents is not so unusual even on Earth: for example, mitochondrial genomes are typically inherited from mothers alone (with some exceptions, see Breton and Stewart 2015), and haplodiploid insect species have sons descending only from their mothers but daughters descending from both parents. Further, many examples of "meiotic drive" are documented wherein one of two alleles is passed on far more than the other from carriers (for review, see e.g., Bravo Nunez et al. 2018). Even if we are to assume that extraterrestrial species possess inheritance via somewhat immutable factors inherited from two parents, we can only imagine that far more extreme deviations than those described above could exist, particularly if the extraterrestrial species have different mechanistic underpinnings to such inheritance.

The other 2 of Mendel's laws have so many exceptions on Earth that these exceptions are not worth covering in detail, particularly the law of independent assortment: some scholars have described them more as "guidelines" than laws. However, we might speculate extreme versions of or deviations from the law of dominance. One might imagine an extraterrestrial species wherein a complete genome is "silenced" upon its inheritance, making all contributions from a particular parent effectively recessive. Parent-of-origin effects on which alleles are expressed in individuals are well known even on Earth, with some cases involving most of a parent's genome being partially silenced in at least some tissues (de la Filia et al. 2021). Taken to the extreme in a hypothetical extraterrestrial species, whole genome copies are transmitted and may become manifest in a future generation, perhaps under specific conditions. The other extreme, a case of "no dominance ever" seems biochemically unlikely at first glance. Dominance on Earth sometimes results in part from the pace of activity from multiple enzymes acting together, where a substantial reduction in activity by 1 enzyme would often not affect the catalytic speed (Kacser and Burns 1981). Since this conclusion is largely based on somewhat general properties of catalyzed chemical reactions, which likely would be general features of life, it could often hold even outside the confines of our planet. However, genetic dominance can and is achieved through other means even on Earth, so we cannot rule this possibility out.

Evolution

Darwinian concepts

Two contemporaries of Mendel's, Charles Darwin (1859) and Alfred Russell Wallace (1889), proposed (with some subtle differences: Kutschera 2003; Smith and Beccaloni 2009) the most famous mechanism for generating the diversity of life we see on Earth today: natural selection. The beauty of natural selection is the simplicity of the three tenets that make it almost a mathematical inevitability: variation, heredity, and effects on survival or reproduction. If a trait has multiple forms (say, tall and short), if the instructions for those distinct forms are passed on from parents to offspring with fidelity (e.g., "short" is more likely to beget "short" than "tall", and vice versa), and if those forms have different effects on survival or reproduction (e.g., "short" has more offspring on average), then natural selection must follow. The outcome of natural selection is typically that the favored form will spread through subsequent generations, though other forces may counteract it, a point to which I shall return shortly.

This simplicity allows for easier extrapolation to extraterrestrial forms of life, specifically by exploring the tenets. Absence of any effect of variation on survival or reproduction obviates natural selection. Similarly, absence of variation also eliminates the possibility of natural selection occurring. However, the complete absence of any variation in any trait appears somewhat unrealistic: it would imply that fidelity of reproduction is universally perfect. This point leads to the second tenet: heredity. One can have variation without any biochemical basis to its heredity if all variation is environmentally induced, such as the example given earlier of language. Natural selection does not yield changes in succeeding generations to traits lacking heritability. Similarly, a low connection between phenotype and genotype (or "low heritability") will reduce the efficacy of natural selection. But a more intriguing case is when multiple factors contribute to a trait but with strong, complex interactions (epistasis) between them. Natural selection is typically envisioned as operating on additive traits, where alleles at many individual genes have simple "greater" vs. "lesser" effects on the phenotype. But certain forms of interactions among alleles at different genes (e.g., systematic negative epistatic interactions) can reduce the efficiency of natural selection (Wright 1931; Hansen 2013; Barton 2017). Nonetheless, despite these examples of extreme cases wherein natural selection may be somewhat less efficient, the simplicity and likely near-universality of the three conditions suggests that natural selection would very likely apply to any extraterrestrial life encountered, even if perhaps slightly less efficiently.

Another major insight from Darwin and Wallace's thinking was the interpretation that all life on Earth is related through shared common ancestry. While we may encounter vastly different species on Earth like *E. coli* and ring-billed seagulls, they share a common ancestor and have evolved into their modern forms over billions of years. When extraterrestrial life is found, we will have an opportunity to assess further just how universal such common ancestry may be. If life on Earth was seeded through a process like panspermia, we may find our own distant cousins on other worlds seeded with microbes or materials from comets or other vectors, further extending Darwin's ideas to the cosmos. At the other extreme, a world may be discovered wherein independent, distinct forms of life arose more than once. Identifying truly independent forms of life, particularly ones that arose in a single environment, would allow researchers to better explore the questions of whether "fundamental" properties of life may exist and whether specific conditions are especially likely to generate new life. I do not cover these possibilities here since astrobiology researchers have explored these hypotheses more thoroughly and more eloquently than I am able to contribute.

Post-darwin: random genetic drift

Natural selection drove many of the observed trait differences between populations or species, but random chance events can overpower natural selection especially in small populations. For instance, a favorable allele found in only one individual who dies prematurely for reasons unrelated to their genetic makeup would never spread. Further, existing variation in many inherited traits may simply have negligibly small effects on survival or reproduction, so much so that natural selection becomes almost irrelevant. This premise leads to the opportunity for stochastic change over time: reproduction essentially generates samples from a population's gene pool each generation. Such random samples (especially if small in number) from a population will on average become increasingly unrepresentative of the original population each generation, and these chance deviations are often lumped under the umbrella of "random genetic drift". Darwin himself acknowledged the role of random chance events in evolution (Darwin 1872), and it was elaborated by Hagedoorn and Hagedoorn and Hagedoorn-VorstheuvelLaBrand (1921), but the main popularizers of the concept were Sewall Wright (1931) and Ronald Fisher (1922), though they disagreed on its importance (Provine 1986).

Of all the concepts discussed, this one is perhaps the most "absolute" in that it would certainly apply to extraterrestrial life bearing any level of heredity in the same manner as it does to life on Earth. Genetic drift is essentially the consequence of statistical sampling error applied to hereditary variation. Neither the nature of inheritance nor the form of the organism would eliminate it. If population sizes are consistently very large, its effect would be mitigated, but this property is also true for life on Earth. Genetic drift could be eliminated if every living organism always produces exactly the same number of offspring, and nothing ever prevents this survival and reproduction from happening (ie, no random chance events ever occur to kill one), but this seems a rather contrived scenario that, at best, would have very limited application. In general, genetic drift would likely be an evolutionary force affecting any form of life with heredity, sometimes even overpowering natural selection in small populations.

Conclusions

I have briefly covered a few foundational basic concepts in genetics and evolution here and discussed each in the context of their potential application to hypothetical extraterrestrial species. In a sense, our explorations of extraterrestrial species is a chance to "reset" and explore the foreign world through a partial nineteenth century lens. We cannot rule out some concepts that have been largely dismissed here on Earth, such as Lamarck's inheritance of acquired characters, nor can we assume Mendel's laws apply even to an approximate degree. Much of this uncertainty ties to the high potential for a completely different material basis for inheritance. Inheritance may not involve nucleic acids like DNA or RNA, and may have vastly different properties of change, transmission, and connection to traits. However, evolutionary principles such as natural selection and genetic drift are more likely to apply in the same way they do on Earth given they have fundamental mathematical properties not as constrained by the mode of inheritance.

If and when such extraterrestrial life is found, we shall have the opportunity to test some aspects of this thought experiment. At that time, biologists and others will have the excitement of potentially discovering entirely new modes of inheritance and possibly some new evolutionary forces not yet conceived. Nonetheless, even if many aspects are entirely different, we will continue to stand on the shoulders of the classical work conducted in the preceding centuries.

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