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Biology's Dark Matter: From Galaxies to Microbes

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Abstract

Emergent research in metagenomics has unveiled large quantities of previously unknown and unclassified prokaryotic DNA. As these prokaryotes constitute the vast majority of microbial life in environmental samples, some microbiologists and commentators in scientific media have referred to this expansive unknown as 'biological dark matter', translating the rhetorical power of dark matter from the physical to the life sciences. Engaging literatues and approaches from across the philosophy, history, and social studies of science, we explore the cultural significance of the dark matter theory in the physical sciences and examine the implications of its conceptual reworking in biology, through critically engaging the political narratives folded within dark matter's genealogies. 'Dark matter' designates both zones of importance and zones of turbulence, simultaneously emphasizing microbiologists' creativity whilst constructing new ways of relating to microbiota. Such a situation, we propose, also invites theoretical analysis as it calls for a conceptual reconsideration of the gene and its fundamental role within the life sciences.

Keywords
biological dark matter, dark matter, event-body, horizontal gene transfer, metagenomics, myth-history

Introduction

Emergent sequencing techniques in metagenomics have uncovered vast quanitities of 'previously unclassified life' (Raffaetà, 2023: 74), signaling 'new realms for discovery' (Granjou and Phillips, 2019: 399) for microbiology. Whereas traditional genomics is primarily concerned with mapping the genome – the complete genetic material of a single organism, such as the high-profile activities of the Human Genome Project (see

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Reardon, 2019; Richardson and Stevens, 2015) – metagenomics conversely ‘involves sampling the genome sequences of a community of organisms inhabiting a common environment’ (Hugenholtz and Tyson, 2008: 481). Isabelle Stengers (2020: 228) captures the hype of frontierism associated with the development of metagenomics within the scientific community, noting that with the first metagenomic sequencing of a soil sample, ‘once again, there were unknown living things everywhere!’ In the late 20th century, less than 1% of prokaryotic life had been categorized, named, and therefore considered ‘known’ to science (Staley et al., 1997). In that context, when Jo Handelsman et al. (1998: 245) coined the term ‘metagenome’ to describe the ‘collective genomes’ of soil microbiota, they presented ‘the exploration of natural products from previously uncultured soil microorganisms’ as ‘a new frontier of science’. Such enthusiasm often translates into the descriptive use of ‘biological dark matter’, borrowed from the physical sciences of cosmology, astrophysics, and particle physics. The microbial unknown, discursively framed as ‘dark matter’, becomes an unexplored world to be discovered and conquered. This performative construction of an unprecedented frontier is a seductive discourse, found in numerous large-audience books, specialized articles, and ethnographic accounts (Handelsman, 2004, 2007; Handelsman et al., 1998; Helmreich, 2009; Huang et al., 2015; Raffaetà, 2023; Robbins et al., 2016; Zha et al., 2022) as much as in commercial communications (Callaway, 2021, 2022a, 2022b, 2022c; Lin et al., 2023).

Metagenomics is leading to fundamental discoveries in biomedical and environmental fields. Tech giants Google and Meta, for instance, and their respective AlphaFold and ESMFold bioinformatics programs, are shaping technological practice in the endeavour to ‘fill in’ the ‘dark matter of the protein universe’ (Callaway 2022a: 211). These developments employ deep learning algorithms to predict information on the billions of proteins whose structures remain undetermined, a practice positioned at the forefront of scientific knowledge production with the 2024 Nobel Prize in Chemistry being awarded to Demis Hassabis and John Jumper for their work on AlphaFold’s development (Abriata, 2024; Callaway, 2024; see also Jumper et al., 2021). Meta’s ESMFold, for example, scans genetic information gathered from different databases and uses artificial intelligence to hypothesize the 3D protein structure supposedly encoded by the analyzed DNA. Meta describes this work as ‘trawling biological dark matter’ (Callaway, 2022a). They depict their research as ‘decoding metagenomic structures’ (Meta, 2022: n.p.), which entails the analysis of microbes living in soils, oceans, and human bodies as a practice that can ‘help us solve mysteries of evolutionary history, discover proteins that may help cure diseases, clean up the environment, and produce cleaner energy’ (Meta, 2023: n.p.). This ‘mythical’ narrative (Perillán, 2021) illustrates how scientists make sense of, know, and translate biological unknowns. The descriptive use of ‘dark matter’ should not lure readers into thinking that designated microbes are a ‘pure unknown’, invisible to any detection apparatuses. Metagenomics offers genomic sampling at the environmental – rather than organismal – scale, and its techniques offer clues about dark matter’s constitution. The hype, then, is understandable; these practices hold promise for a whole series of challenges in the face of climatic catastrophes and devastating diseases.

In this article, we analyze the discursive function of dark matter in biology, and the reasons for its conceptual translation from the physical sciences. Following Donna Haraway’s (1996: 137) observation that ‘nothing comes without its world’, we critically examine the dynamics of transferring a concept across scientific vernaculars, disciplines, methodologies, and traditions. We show that the concept of dark matter comes with a lexicon that constructs a zone of importance for promoting scientific activity: mobilizing the allure of exploration at the frontiers of modern science (see Bush, 1945), and testifying to a culture of scientific valorization specific to 'modern' societies, as described by Bruno Latour (2012). Designating an 'unknown region' in a discipline not only calls for its exploration as an emergent frontier but also indicates a zone of importance; such a powerful trope serves as a signpost for social scientists interested in what interests other 'hard scientists'. In this article, we take seriously the feeling of importance that emanates from the use of dark matter in biology, which is shaped by the epistemic turbulence it produces. Microbiological discoveries indeed seem to call for a reconsideration of the theoretical scope of the gene and its central position in the life sciences. Such shifts echo parallel advances in epigenetics – whose analysis is largely beyond the scope of this article – that address non-coding DNA that constitutes most of a genome's matter, what gene-centric molecular biologists would refer to as 'junk DNA' or even 'genomic dark matter' (Carey, 2015; Guan and Lazar, 2019). Molecular biological examination into the wider context of the gene as part of chromatin bodies – constituted of non-coding proteins and DNA-containing chromosomes – for example, is contributing to another substantial revision of the gene as biology's central dogma (see Keller, 2014; Lappé and Landecker, 2015; Meloni, 2019).

Dark matter was conceptualized to answer specific problems in the physical sciences, but through its repurposing in other academic languages (like literature, molecular biology, microbiology, or political science) it has come to designate an object or abstraction that has a major structural role in each field and yet remains intangible or invisible. We want to show that 'dark matter' cannot simply be reduced to 'an important and yet invisible thing'. Therefore, our article begins with a brief conceptual history of dark matter in cosmology, which helps to clarify the issues involved when translating dark matter from the physical to life sciences. With metagenomics, we explore the emergence of another form of unknowability in biology, and the reasons for its description as dark matter. Through discussing the microbiological complexities of horizontal gene transfer (HGT), which is commonly used to characterize the biological unknown, we follow intense debate among microbiologists in how to respond to the epistemological challenges HGT poses to fundamental concepts.

Addressing Alfred North Whitehead's philosophy, Didier Debaise (2004: 16) outlines ways to interrogate the 'novelty' of a thinker or a theory: a question of 'what kind of shock it has produced, what sort of irreversibility it has introduced in a particular domain'. If dark matter has been theorized through a slow process rather than a shock (see de Swart et al., 2017), it has introduced an irreversibility in cosmology, astrophysics, and particle physics. In a way, every model, proposition, and hypothesis concerning the ways of the universe cannot neglect dark matter, whether searching for its presence or proving its absence. Indeed, as underlined by Ashley Yeager (2021: 186) in her biography of astronomer Vera Rubin, despite doubts about dark matter's existence, 'with so many instruments and so many professional careers invested in this new particle physics venture', Rubin said, 'that's a faucet that will be hard to shut off'.

Empirically, we were drawn to question why, and how, 'biological dark matter' gathered importance and descriptive power. Its use entails a marketing move to attract funds by mobilizing the colonial trope of the frontier, which has proven effective in similar contexts – as highlighted by critical scholarship on science in outer space (e.g. Salazar and Gorman, 2023) or oceans (e.g. Liboiron, 2021). We highlight the differences and problems that come with ‘dark matter’ applied in galactic and microbial contexts. We argue that the *irreversibility* mentioned above constitutes a guiding line around which to organize, categorize, and contrast these differences. We show that what the concept designates when translated into the life sciences – a sheer amount of unclassified and metamorphic prokaryotic life – doesn’t perform the same function of irreversibility. Rather, it elucidates a great inventiveness in the ways to name, and relate to, microbial worlds. What has been retained in translation, principally, is an invitation to explore the unknown. Following the criterion of irreversibility, we speculatively ask what kind of entity indeed plays this role in the life sciences, and propose the concept of ‘the gene’ itself.

Dark Matter Myth-Histories

Without a prefix or qualifier, the term ‘dark matter’ usually conjures up imaginaries of the universe’s physical, spatial, and temporal constitution. If astronomy began as ‘a quest for light’ to understand Earth’s place within the cosmos, contemporary practices simultaneously undertake ‘a quest for darkness’; the invention of tools and techniques of galactic observation, modelling, and prediction brought with it the realization that something was missing (Freeman and McNamara, 2006). It took considerable time, contestation, and reworking for dark matter to become an established object of scientific inquiry with paradigmatic status (de Swart et al., 2017; Sanders, 2010). As noted by Jaco de Swart et al. (2017: 6), ‘simply asking “what was the evidence for missing matter?” misses the point: we need to understand why certain observations were eventually conceived as “evidence” of anything in the first place’.

Origin stories of dark matter can be understood as iterations of scientific ‘myth-history’: ‘a chimeric genre that bridges distinct narrative modes’ (Perillán, 2021: 11). For Perillán (2021: 12), myth-histories are employed by scientists as a ‘rough scaffolding’ that filters out ‘unwanted historical details’ and infuses ‘narratives with mythological tropes’ to ultimately ‘deliver value, coherence, and inspiration to their communities’. Rather than open a Pandora’s box of historiographical debate, our intention is not to debunk the validity of these myth-histories but rather heed Perillán’s (2021: 13) call for a constructive interdisciplinary common ground that seeks ‘to examine how myth-histories are constructed, deployed, and metabolized within scientific communities, and, more-broadly, in society’. As we will come to discuss in the case of galactic dark matter (Prescod-Weinstein, 2020, 2021a), it is crucial to understand how ‘the same cohesive and convergent forces that these narratives bring to a scientific community can also erect barriers to inclusivity, which leave women, people of color, and those with divergent ideas feeling like they don’t belong’ (Perillán, 2021: 12).

The dark matter hypothesis is intricately linked to Newtonian gravity, as examined in astronomer Robert H. Sanders’ myth-history *The Dark Matter Problem: A Historical Perspective* (2010). Mathematician Urbain Le Verrier’s prediction that his 1845 observations of irregularities in Uranus’ orbit could be explained by the existence of an unseen celestial body – later proven by the visual identification of Neptune – is a victorious myth-history routinely mobilized to defend Newtonian models and the search for invisible matter that explains cosmological irregularities (Elbaz, 2022). Indeed, these myth-histories construct a historical progress narrative that allows scientific consensus to form, shaping both scientific research agendas and their understanding in public discourse (Perillán, 2021). For instance, theoretical physicists Jonathan Feng and Mark Trodden (2010: 40) draw parallels between the 19th century search for the 'dark world' of Neptune and 'a similar drama – in which astronomers observe anomalous cosmic motions, deduce the presence of new matter, and go out to hunt for it'. The rhetorical power of myth-history recasts the contemporary search for, and theoretical speculation upon, dark matter as a 'heroic tale' that imagines successive generations of scientists as causally linked, standing on the shoulders of giants (Perillán, 2021). When told this way by scientists, finding answers to 'the dark matter problem' is not only a conceivable feat but one imbued with historical importance, drama, and public support.

Common accounts of dark matter's myth-history usually begin in the early 20th century with astronomer Fritz Zwicky's observations of the Coma galaxy cluster. Zwicky 'made the first systematic kinematic study of a cluster of galaxies and pointed out that in order to gravitationally bind the cluster the actual mass had to be several hundred times larger than the observed mass in stars' (Sanders, 2010: 2). In principle, the observed movement of the entire cluster *should* be concordant with the mass of each individual galaxy, or there was not enough observable mass to account for the cluster's movement. Something was missing to allow the laws of Newtonian physics to remain true: invisible, massive material that would explain glitches in the mass to luminosity ratio. Zwicky called this invisible actor 'dark obscuring matter' ['*dunkle materie*'], marking the phrase's origin: 'dark obscuring matter has been discovered to be sparsely distributed throughout the whole of the visible universe showing cloudy concentrations in various points with particular preference for the central regions of the large clusters of galaxies' (Zwicky, 1953: 7).

Zwicky's work rose to prominence in the mid-20th century when the dark matter concept began to gain traction. Scientists began to hypothesize that the instability of galaxy systems – the reason why galaxies maintained a fairly constant rotational velocity further away from the observational masses at the galaxy's core – could be 'explained by assuming the presence of extra mass that cannot be seen or detected by other means as yet' (Neyman et al., 1961: 533). There was a lingering feeling, however, that it was 'perhaps distasteful for astronomers and cosmologists to think that their theories are based on observations of less than 1% of the matter that is really there!' (p. 553). It was the work of Vera Rubin who confirmed the existence of dark matter for most of the astronomical community, using optical telescopes to plot the movement of galaxies (Rubin, 1996; Rubin et al., 1980; Yeager, 2021). Although Rubin herself even conceded that dark matter may not exist, such a recognition would demand the complete rewriting of Newtonian gravitational equations, and for most astronomers and cosmologists 'such a modification is more traumatic than to accept the existence of matter which does not radiate' (Rubin, 1988: 443; see also Einasto, 2010; Sanders and McGaugh, 2002).

'Beginning with Zwicky, dark matter has been postulated to accommodate the disparity between the observations of large astronomical systems and the predictions of Newtonian dynamics' (Sanders, 2010: 132). Rather than explaining these disparities with unobserved matter, physicist Mordehai Milgrom (2002) postulated that models used to predict the behavior of celestial bodies were inaccurate, proposing a modification to Newtonian dynamics (‘MOND’) as an alternative to dark matter to explain galactic mass discrepancies. Yet despite alternative hypotheses, dark matter remains an undefeated paradigm as it elegantly solves a large range of different problems across several disciplines. It is ‘remarkably simple: one just needs an additional cold collisionless component that interacts only through gravity’ to ‘achieve a similar level of agreement with observational data over such a large range of spatial and temporal scales’ (Einasto, 2010: 14). In this sense, dark matter acts as a coherence operator for the fields that mobilize it at the confluence of three disciplines: astrophysics, cosmology, and particle physics. There are two reasons for this: firstly, because it allows Newtonian gravitational equations to be maintained, and secondly, because it represents a colossal endeavor to fill the ‘voids’ in the universe.

Recent estimates suggest that the universe is composed of 25% dark matter, 70% dark energy,[1] and only 5% known matter.[2] These proportions designate dark matter as an enormous remainder, a form of science’s unfinished business. One of the fundamental components of the universe remains unknown. That statement is sufficient to deepen the romantic narrative of research as a quest in which the adjective ‘dark’ is fundamental, as it so easily re-enacts the score of knowledge as light to illuminate the unknown. Some scientists within the dark matter community have addressed the semantic legacy of this appellation. Chanda Prescod-Weinstein (2021b: 158), who forwards a critical reading of dark matter in her scholarship, argues that: ‘dark matter is a terrible name: we can see matter that is dark. We can see dark hair, for example, when light scatters off it into our eyes. A better name would be invisible matter, transparent matter, or clear matter.’ In her monograph *The Disordered Cosmos*, she adds that ‘a Black feminist physicist working in the 1960s would never have used this language’ (Prescod-Weinstein, 2021a: 21), further drawing attention to the colonial overtones equating ‘darkness’ with a new frontier to be capitalized upon and appropriated (see Browne, 2015; Winant, 2015). Some critical theorists have mobilized ‘dark matter’ to highlight the unacknowledged labor of Black people that has been systematically erased from history (e.g. Thomas, 2000; cf. Prescod-Weinstein, 2021a). This use nevertheless entails a potential danger according to Prescod-Weinstein (2021a: 117, emphasis in original), who argues:

> If you feel the urge to compare Black people to dark matter, *resist*. There’s a lot of dark matter passing through you right now. The density of dark matter is 1 proton mass per cubic centimeter, so a few per coffee cup. There are not a lot of Black people of any size passing through you, promise. [. . .] Why is dark matter passing through you? Because unlike Black people, it doesn’t interact with other matter normally. There’s also this: if Black people are so invisible, how come the police are so good at shooting and beating our friends and family? [. . .] Black people are extremely visible – what’s not visible is our humanity. That’s not because of how we are built; that’s because of how white supremacy structures our social relations.

Although it remains unknown, contentious and – with contemporary tools of investigation – unprovable, dark matter is approached using a variety of direct and indirect criteria. The most consensual list of criteria includes ‘weakly interactive massive particles’, or WIMPs, yet there are a range of non-WIMP candidates to explain dark matter, such as axion-like particles (Prescod-Weinstein, 2021b; Roszkowski et al., 2018). As noted, dark matter lies at the crossroads of cosmology, astrophysics, and particle physics, and therefore the concept is a site of multidisciplinary exchange. Even if particle physics were to find a new particle – WIMP or other – outside the Standard Model of elementary particles, it would still have to be proven that it could play the role of dark matter in cosmological and astrophysical hypotheses (Bertone, 2010). Ongoing experiments seek to capture the signal of interaction between an atomic nucleus and a dark matter particle through either direct or indirect detection (Roszkowski et al., 2018). The conditions for effectively detecting WIMPs are extremely demanding, despite ongoing large-scale and high-profile efforts like those at the Conseil Européen pour la Recherche Nucléaire (CERN). Underground detectors like the Large Hadron Collider are used to reduce noise in modes of detection 'at the limits' through treatments of 'noise reduction' to produce evidence of specific particulate interaction (see Stengers, 2006).

Whether in cosmology, particle physics, or astrophysics, contemporary dark matter research is ultimately ill-described by the metaphor of knowledge as light heroically advancing over the dark unknown. Rather, detection is more a question of producing conditions of sufficient darkness for a specific particle to emerge. It's not light that scientists need, but opacity, sorting, and sensors. Scientists don't advance upon the unknown, they walk through it. The aim of these research projects is probably better described by the creation of significant interactions. Whether it's collisions in particle accelerators or the detection 'through elastic scatterings of DM ["dark matter"] particles off nuclei' in underground detectors (Roszkowski et al., 2018), the aim is always to produce and/or record significant interactions. We stress here the importance of *interactivity* as a way of knowing dark matter, as this is an important node of comparison in which dark matter is translated from the physical to biological sciences.

The Microbiological Unknown

Dark matter's rhetorical power is now finding new meaning in microbiology. The term is used as an informal descriptor, shorthand for unclassified genetic material or prokaryotic life. Its use dates to Yann Marcy et al.'s paper in the *Proceedings of the National Academy of Sciences* (2007: 11889), claiming:

> We have only scratched the surface of this microbial world. It has been estimated that <1% of bacterial species have been axenically cultured, and fewer than half of the recognized bacterial phyla include cultivated representatives. This can be viewed as biology's 'dark matter' problem: just as astronomers can only indirectly infer the existence of a large amount of as-yet-undetected mass in the universe, microbiologists can only estimate microbial diversity by using techniques such as [. . .] metagenomic gene inventories.

Metagenomics has transformed microbiology, traditionally dependent on the availability of laboratory-grown pure cultures that inaccurately represent real-world microbial diversity, as most microbes cannot be cultivated in laboratory conditions (see Lewis et al., 2021; Tyson and Banfield, 2005). For microbiologists, 'these uncultured microbes are the "dark matter" of the microbiological world and play important roles in natural ecosystems and the human microbiome' (Huang et al., 2015: 15), despite their ecological function, genomic cartography, or taxonomic specificity eluding most scientific knowledge. The microorganisms concerned are predominantly prokaryotes – unicellular organisms without a nucleus like bacteria and archaea – which commonly depend on specific environmental conditions, nutrients, and interactions with other species and thus are difficult to isolate in laboratories. Metagenomic samples can be taken directly from 'field' environments, like soil, feces, or water, and thus grant a closer perspective on microbial life in its own process. As noted by Ana Delgado (2021: 14), 'metagenome analysis amplifies the scope of what can be seen', essentially allowing researchers to extract more information from smaller samples and to reduce their reliance on laboratory conditions.

Rather than the world of the Petri dish, visions for new knowledge and scientific exploration at the microbial scale are now prospecting the unknown worlds of 'biological dark matter'. Early metagenomic sampling and analysis granted a novel gene-oriented gaze upon microbial bodies and matter; spaces of human familiarity such as soil, water, or skin were found to be bursting with a seemingly infinite number of alien genes. The taxidermic identity of most of these genes was unknown due to their absence from laboratory cultures. For Jo Handelsman (2004: 669), this realization 'forced microbiologists to question their belief that the microbial world had been conquered' and to acknowledge 'the extent of our ignorance about the range of metabolic and organismal diversity'. The myth-histories deployed by microbiologists here are not dissimilar to those told by cosmologists half a decade earlier: a great unknown had been unleashed that held with it deep secrets about the universe. Metagenomics has thus been likened to a paradigm-altering 'reinvention of the microscope' in that it 'provides a new way of examining the microbial world that not only will transform modern microbiology but has the potential to revolutionize understanding of the entire living world' (Handelsman, 2007: 2).

Metagenomics provides access to new worlds through novel perspectives of what biologist Robert J. Robbins et al. (2016: 2) call the 'genomoscope': 'it is essentially Humboldt in a new biosphere: wherever the genomoscope is pointed, new discoveries swarm into view'. Yet when translated from the physical to life sciences, the notion of unknowability in relation to dark matter is not consistent. In biology, 'unknown to science' concerns the non-assignability of genes and proteins to any known species: it's a *taxonomic* unknown, a clearly visible and encounterable entity, but unclassifiable 'matter'. This illustrates the diminished meaning of 'knowledge' in the context of biological dark matter. The question that arises then is: if, as discussed above, dark matter is a concept that acts as a coherence operator for the understanding of current cosmology at the confluence of astrophysics and particle physics, why do biologists find it useful? We want to emphasize that the concept intervenes in biology in a uniquely performative mode; it is not its possible descriptive capacity that is borrowed, but the kind of scene it sets. If 'nothing comes without its world' (Haraway, 1996; Puig de la Bellacasa, 2012), then what comes with dark matter, when reworked into the biological lexicon, is a narrative world rather than an accurate analogy between galaxies and microbes.

Dark matter simultaneously highlights the incompleteness of science and stimulates the desire for greater knowledge. The myth-histories of galactic dark matter – along with the broader cultures that shaped them – prompt microbiologists to requalify their subject of study. The rhetorical power of this 'quest' narrative not only designates biological dark matter of similar intellectual importance but imbues it with parallel drama. What is at stake in this transfer is the equivalence of the *terra incognita* of science. Whether in galaxies or in soils, the same gesture of discovery is staged, and in so doing, dark matter loses the special status it had for the field of cosmological research, to ultimately designate only that which 'is mostly present but not known'. It seems significant to us that 'dark matter' is rarely used in technical microbiological debates concerning the activity of unclassified organisms. Dark matter is a rhetorical concept used as a tool for presenting, educating, or recounting scientific research, yet it is of little constructive help when it comes to discussing what produces the unknown in microbiology, namely the weird biologies of prokaryotes, as discussed below.

Metamorphic Living Beings

Donna Haraway (2006: 112), in her reading of Lynn Margulis and Sagan (2002), notes that microbiota 'pass genes back and forth all the time and do not resolve into well-bounded species, giving the taxonomist either an ecstatic moment or a headache'. In designating prokaryotic organisms (constituting, in particular, microbiota), biological dark matter produces effects similar to those described by Haraway, on the threshold of ecstasy and agony. Prokaryotes, notably, abide by different biological rules than eukaryotes. The differences between these are so important that they have been coined as constituting a 'quantum leap' in scientific understanding of microbial life (Robbins et al., 2016). Prokaryotes are epistemic tricksters within classical biology, as they challenge a list of common central concepts such as movement, reproduction, heredity, species, and evolution (Robbins et al., 2016). In coming to terms with prokaryotes through metagenomics, this 'quantum leap' produces both amazement and the feeling of paramount unknowability, hence the dark matter appellation. We can already sense that this is not the same kind of unknown as the physical sciences; rather than a coherence operator, it carries destabilizing potential calling for scientific inventiveness. One of the reasons for this destabilizing power lies in the ability of prokaryotes to exchange genes between individuals, a phenomenon commonly termed 'horizontal gene transfer' or HGT. Genes are not transferred 'vertically' between parent and offspring – as is the case with most eukaryotes – but genetic exchanges are 'horizontal' between different individuals, sometimes of different species, over the course of a lifetime. What genetically constitutes an individual can consequently change several times during a single lifetime, therefore complicating vertical lines of heredity.

As Stefan Helmreich (2009: 17) notes, prokaryotes are 'difficult to place because of their habit of exchanging genes laterally, confounding linear genealogies. They remind us that aliens[3] often mess up lineages and confuse the unfolding of chronology itself.' In phylogenetics, the disruptive power of HGT poses fundamental questions to classical ideas about, and representations of, 'the evolutionary tree' (Gogarten and Townsend, 2005; Kurland et al., 2003; Philippe and Douady, 2003). Are foundational concepts like the organism still relevant if we take both HGT and the microbial scale seriously? This question recalls controversies in astrophysics regarding the theoretical reach of Newtonian equations, and speaks to larger debates among biologists surrounding concepts of the individual, the species, and their taxonomic delimitation (Gilbert et al., 2012; Helmreich, 2003; McFall-Ngai et al., 2013; Robbins et al., 2016).

Initially posed as a technical problem in microbiology, prokaryotic HGT is an event of academic intrigue not only for biologists, but also for those interested in the ways scientists understand living organisms (Brives, 2022; Helmreich, 2009; Paxson, 2008; Raffaetà, 2023; Robbins et al., 2016; Zimmer, 2019). We believe that part of the attraction of this phenomenon for theorists and social scientific scholars of science stems from the fact that prokaryotes inspired and gave substance to the rhizomatic model celebrated by philosophers Gilles Deleuze and Félix Guattari in their critique of the arborescent scheme. Horizontal gene transfer uproots the arborescent model of evolution, that of a hierarchical, vertical genealogy. The rhizome, they say, is an 'anti-genealogy':

> Evolutionary patterns are no longer based solely on arborescent descent models, moving from the least differentiated to the most differentiated, but on a rhizome operating immediately in the heterogeneous, jumping from one already differentiated line to another. [. . .] Transversal communications between differentiated lines blur family trees. (Deleuze and Guattari, 1980: 17–18)

If HGT is indeed anti-genealogical, it poses problems for microbiologists trying to reconstruct microbial evolutionary history (phylogeneticists) or to clarify the groups to which prokaryotes are supposed to belong (taxonomists). The HGT phenomenon is therefore an event that obliges microbiologists to answer for their concepts, which are being put at risk. As a result, scientists are deploying a great deal of creativity in the creation of new concepts – or the transformation of old ones – to account for horizontal genetic transfers and their implications.

For instance, some speak of a *pan-genome* today to describe the set of genes belonging to multiple forms of bacteria: 'the set of all genes present in the genomes of a group of organisms' (Lapierre and Gogarten, 2009: 107; see also McInerney et al., 2017). As the genome of one individual varies during its life course, it will not be identical to that of another, even though it belongs to the same 'species'. Using bacteria's pan-genome as the starting point of analyses has had creative consequences for microbiology. As recounted by James McInerney et al. (2017: 1–2): 'interestingly, exploring the pattern of gene presence and absence in a sample of 573 genomes and then extrapolating to a larger number of genomes, the entire bacterial pangenome has been estimated to be infinite in size' (see also Tettelin et al., 2005). Lapierre and Gogarten (2009: 109) refer to this as a 'constant rain of genetic material on genomes from a cloud of frequently transferred genes'. This 'constant rain' refers to the 'public goods' hypothesis, in which 'the majority of genes in the biosphere are not strongly attached to any group of organisms' (McInerney et al., 2017: 5), therefore constituting biological dark matter as a kind of public stock for prokaryotes to interact with.

Nevertheless, all genetic exchanges may not be of the same value or have the same impact on the organisms. Microbiologists qualitatively distinguish transfers in identifying the different parts of the genome affected by HGT. In this regard, some researchers devised a new partition, splitting the genome into a *hard core* 'composed of genes that are never transferred', a *soft core* 'with genes rarely transferred', and *shell genes* 'where all the genes susceptible to HGTs belong and for convenience's sake all genes that do not contain enough information to be classified as core genes' (Philippe and Douady, 2003:

502). The evolutionary unit would become, in this context, the *core genome*, allowing for the maintenance of an arborescent shape in representations of evolution – although its branches would be connected by a dense network of vines intertwining with adjacent trees.

As HGT shows, biological dark matter describes a specific set of entities, unknown because of their deeply metamorphic nature, and thus unclassifiable under traditional models. Rather than the tree of life, novel practices that bring new light to microbial worlds recast this biological ensemble as the *slime* of life (Helmreich, 2009). The slipperiness of prokaryotic life, as recounted by Stefan Helmreich, allows microbes to evade bio-capitalist appropriation:

> Slime is a sign of that which slips away from containment and calibration, and which must be managed to make anything like biocapital circulate. Without stable boundaries – and without ends in the instrumental sense – slime, like the figure of the alien, exceeds and disturbs representation [. . .] slime-exuding, gene-trafficking microbes erase their own species being. (2009: 129–30)

The moniker of biological dark matter invites investment for economic exploration to capitalize upon and commodify it. Yet prokaryotic life characterized as slime is an unknown that doesn't require relentless exploration but an inventiveness and scientific creativity in concepts to be able to account for it. These creations testify to microbiology's entry into the field of biology, but they also point to a fundamental phenomenon concerning the place accorded to the concept of 'gene' itself. In this respect, HGTs are part of a history of problems concerning what we could call the gene's monopoly on the legitimate definition of life.

DNA's monopoly over biological thought was expressed according to its 'central dogma', here criticized by Evelyn Fox Keller (2000: 54) as that which:

> established DNA as the molecule that not only holds the secrets of life but also executes its cryptic instructions – it was, in short, the 'Master Molecule.' In the colloquial paraphrase of the 'central dogma' formulated by Francis Crick in 1957, 'DNA makes RNA, RNA makes protein, and proteins make us.' [. . .] We think of the cell's DNA as the genetic program, the *lingua prima*, or, perhaps best of all, the book of life.

The 'book of life' metaphor has been complicated by several investigations into genetic variation and the link between genotype and phenotype (Keller, 1995; Sonigo and Kupiec, 2000; Sonigo and Stenger, 2003), but also in embryology (Gilbert et al., 2012), epigenetics (Landecker, 2011) and today in metagenomics (Raffaetà, 2023). Although heterogeneous, what all these critiques share is the decentralization of DNA in its role as a 'master molecule'. In each case, genes – defined as a particular locus on the DNA that 'code' for a phenotypical character – are no longer the sole causal agent. They are systematically associated with others – from the same DNA or from DNA of different species – or reinserted into the larger apparatus of the cell, the organism, and a larger biochemical environment (in the case of epigenetics), in which they inscribe their actions and from which they can no longer be abstracted.

Biological dark matter and the manifold metamorphoses of HGTs similarly decenter this molecular mastery. Far from representing an ‘essential core’ from which one could virtually reproduce the whole organism, they jump from one organism to another, integrating into foreign DNA or detaching from it in unforeseeable ways. If the biological sciences thought it had found in DNA its essential particle – the equivalent of the atom to the physical sciences – its status is under scrutiny by the problems posed by these genetic transfers. With the results of metagenomic sequencing, it is no longer possible to simply ask which gene codes for a particular phenotypic trait. Rather, one must consider how genes participate, together with other elements, in the advent of a particular event.

A Proposition: The ‘Event-Body’

Prokaryotes are tricky for taxonomists, as genetic exchanges blur ontological lines drawn around organisms. Prokaryotic bodies are difficult to conceive of in isolation, just as many of them are impossible to grow in isolated laboratory cultures. It seems to us that, here, a ‘thought of relationship’ (Debaise, 2004) could help theorize prokaryotic bodies otherwise, in an alternative vernacular. We follow the proposition of sociologist and philosopher Gabriel Tarde, who claims that Western philosophy has been structured by, and obsessed with, the verb ‘to be’ [‘*être*’]. While, for Tarde (1893: 43), ‘it can be said that, if it had been based on the verb “to have” [*avoir*], many sterile debates and much trampling of the mind on the spot would have been avoided’. Applying Tarde’s proposition to biological dark matter, we define what a prokaryote is *in relation*. We therefore would no longer consider horizontal gene transfers abnormal, alien, or headache-inducive. HGT loses its exceptional ontological status if instead of asking ‘what cell is this?’, we ask, ‘from what set of possessions does the cell emerge?’

Tarde’s conceptual framing helps us to think with prokaryotic life, engaging microbial bodies as what we call ‘event-bodies’. Microbial event-bodies emerge at a certain moment, in response to, and in interaction with, their environments. Out of a sea of genetic exchange, something appears, that, at a given moment, holds and then receives the name ‘organism’. The terms are reversed; we start from a set of fluctuating relationships and arrive, as a result, at the definition of a stable organism. Living prokaryotic bodies are no longer fixed entities but slimy, rhizomatic events. The prokaryotic organism is therefore defined as *what is happening*, not *what is*. Thinking with the verb ‘to have’ – rather than ‘to be’ – invites the acknowledgement of ‘precarity’ faced by prokaryotes, understood through the work of Anna Tsing (2015), who conceptualizes precarity as an openness toward potential connections. Through defining an organism as an event, rather than a finite entity, the organism remains open to be caught up in other constitutive events.

In this sense, the microbial body constitutes its consistency through a churning series of organizations and disorganizations: through metabolic interaction, transience, and change. Biological organization appears in this sense as an event in time. It relates to recent research around gut microbiota and the problems concerning the possibility of their isolation from human bodies to be cultured and conserved. As Alexis Zimmer (2019: 146) asks with regard to HGT, ‘what happens to *a* bacterium once it has been removed from its environment? Can we say that the bacterium will remain *the same*, regardless of the collective life they led?' The 'event-body' we propose here takes the problem in reverse. In metagenomic worlds, there is no longer a body to which something happens; at the microbial scale, there are events, adventures, and modifications to which a body happens.

Conclusion

Horizontal genetic transfer illustrates the major differences that mark dark matter research in the physical and life sciences. For research in particle physics, cosmology and astrophysics, it challenges scientists to produce 'significant interactions' that testify to the existence of a particle that can play the role of dark matter. For biology – and in our case, microbiology – the problems raised by prokaryotes call for the prevention of interactions. It is precisely because what is referred to as biological dark matter is *highly* interactive that it is given the status of the unknown, repurposing the rhetorical power of dark matter's myth-history in the life sciences. Success – in this process-oriented narrative – is found in the abstraction of stabilized taxa and species names from the flow of genetic exchanges.

If the stakes are so different between scientific practices, then what is translated into biology has much more to do with dark matter's narrative register than its descriptive capacity: a register based on a partition of the universe into known and unknown parts, and even if the term dark matter has been criticized (see Prescod-Weinstein, 2021a), what it designates mathematically – 25% unknown matter, 70% mysterious energy and only 5% known matter – never ceases to exalt the modern refrain exhorting the sciences to push ahead with knowledge production, conceived as a continent to be unveiled by a pioneering front. In this sense, dark matter is not only indispensable to the edifice of astrophysics but also a beacon of hope for *moderns* – in the Latourian sense – in search of an emergent frontier (Bush, 1945), or the construction of what Chanda Prescod-Weinstein (2021a), drawing on Alan Gross (2018), calls the 'scientific sublime' of dark matter. The irresistible thing about the dark matter concept is that it unlocks new regions in which the modernization front can flourish:

> The modern ideal type is the one who is heading – who was heading – from that past to that future by way of a 'modernization front' whose advance could not be stopped. It was thanks to such a pioneering front, such a Frontier, that one could allow oneself to qualify as 'irrational' everything that had to be torn away, and as 'rational' everything toward which it was necessary to move in order to progress. Thus the Moderns were those who were freeing themselves of attachments to the past in order to advance toward freedom. In short, who were heading from darkness into light – into Enlightenment. (Latour, 2013: 8–9)

Translated into the life sciences, dark matter retains only a narrative impetus and its denominative confusions: biological *dark matter* being indeed no less *dark* than its cosmic counterpart, nor even *matter*, or at least not in the physical sense of the term, as it refers to living organisms. Nor does biology borrow modes of restructuring the discipline through dark matter. And although frontierism didn't wait for dark matter to be operative in biology, this conceptual recycling provides microbiology with a significant strengthening of that narrative, granting the discipline depictions of an unknown horizon left to be explored. This time, however, the mystery is taxonomic; it concerns possible encounters and multiple discoveries, and no longer an elementary component – a particle – that would account for a desired entity. In this sense, metagenomic sequencing techniques grant microbiology the proportions and numbers of a pioneering science: 99% of uncultured genes in a few grams of soil (Schloss and Handelsman, 2003), 5×10^5 prokaryotic cells/ml for 'the continental shelf and the upper 200 m of the open ocean' or '10^3–10^4 cells/cm^2 as prokaryotes density on the skin of humans' (Whitman et al., 1998: 6578, 6580). All these statements are performative and prescriptive – they do not only describe an ecology, but also create new *terra incognita* to be explored, described, and conquered. In this context, 'dark matter' becomes a definitional operation that isolates local ecologies and sets them on a different stage where they become a standardized mystery in front of a standardized humanity.

The performative use of proportions plays an important role in dark matter's narrative power. It establishes a pre-given totality of knowability as an implicit goal to achieve. Associated with the use of 'matter' to qualify living organisms, such discourse implies there has always been a unique, fixed, and stable prokaryotic unknown, only veiled by a lack of knowledge. Yet microbiology is dealing with highly metamorphic communities, and this 'biological dark matter' is in fact plural, transient, and unpredictable. When found, it might be different from that being searched for. The high interactivity of prokaryotes underlined by microbiologists probably designates what kind of exploration is required. Far from an 'already constituted matter' waiting to be discovered, microbes foster research more attuned to their *weird* and unconquerable behavior (Hendrickx, 2022; Turnbull, 2021; Turnbull et al., 2022). As proposed by philosopher Kim Hendrickx (2022: 4), keeping biology *weird* might help us understanding what is at stake: 'a commitment to science, and a way of living on Earth that is not destined to prevail over any designated "darkness" but geared to encounter the possibility of freedom within life itself'. What is designated by 'biological dark matter' thus calls not for a relentless exploration but rather obliges those working and living with microbial worlds, by its very characteristics, to constantly invent new verbs, new modes of action or relationships, and to be able, at the same time, to account for it and to live with it. We are not tasking microbiologists with this labor but rather celebrating their creativity in finding new ways of accounting for prokaryotic life and the unknown. Our intentions in this article were not simply to critique biological dark matter from a historical perspective, but also to celebrate the zone of importance 'dark matter' is used to designate within scientific practice – a zone of importance we humbly tried to inhabit with our 'event-body' proposition.

In the end, we are drawn to ask: what does biological dark matter do to microbiology? Does it operate the same kind of irreversibility as physical dark matter in its field of research? Novel insights into prokaryotic worlds point toward a necessity to requalify the gene and its relation to DNA. Somehow, the genetic central dogma which was presented as crystal clear when enunciated as a linear equation has been – and continues to be – weakened, and the role of DNA loses its centrality in biology. The gene is slowly being detached from DNA, acquiring other entities in its definition: the 'epi-', the 'meta-', 'transforming the genome from an executive suite of directorial instructions to an exquisitely sensitive and reactive system' (Keller, 2015). As we focused on metagenomics, it has exceeded the scope of this paper to consider emergent practices in epigenetics that bring attention to the regulatory function of non-coding DNA, previously overlooked as 'genomic dark matter' or 'junk DNA' (see Carey, 2015; Meloni, 2019). However, despite constant complexification concerning DNA, the gene itself, for its part, remains central to biology. All the propositions concern ways to add or associate new elements, never to completely abandon it. Such an operation would certainly be very costly as so much in biology depends on the gene; to borrow Vera Rubin's phrase, it's a faucet that will be hard to shut off in the life sciences. Insight into the prokaryotic unknown therefore seems to declare the conceptual inevitability of the gene. As new discoveries 'swarm into view' (Robbins et al., 2016: 2) and genetics is being complexified accordingly, the relevance of thinking with the gene in biology remains. In that sense, far from playing the same irreversibility function as in physics, biological dark matter rather highlights how genes themselves play that role in biology. We can weigh the importance of an idea by asking: what would happen if we were to think without it? We saw that in cosmology, thinking without dark matter would require the mammoth endeavor of reconsidering Newtonian gravitational equations. What, then, would biology look like if we were to think without the gene?

We do not call for such an erasure. In this article, rather, we tried to follow and describe the consequences of a conceptual translation from the physical to the life sciences. It appeared that dark matter doesn't directly operate with the same irreversibility in biology. Nevertheless, it draws contours around a zone of importance and turbulence, a scientific region where something comes to matter for the researchers, forcing them, at the same time, to reconsider their conceptual approaches in the intellectual endeavor to make sense of weird life.

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Notes

1. Dark energy is another problem in astrophysics related to that of dark matter. Dark energy does not refer to invisible matter but the energy responsible for accelerating the expansion of the universe.
2. Percentages shown are rounded.
3. Helmreich uses the term ‘alien’ in relation to the weirdness of ocean microbes in *Alien Ocean*.

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