

Review



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Symbiotic magnetic sensing: raising evidence and beyond

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The identity of a magnetic sensor in animals remains enigmatic. Although the use of the geomagnetic field for orientation and navigation in animals across a broad taxonomic range has been well established over the past five decades, the identity of the magnetic-sensing organ and its structure and/or apparatus within such animals remains elusive—'a sense without a receptor'. Recently, we proposed that symbiotic magnetotactic bacteria (MTB) may serve as the underlying mechanism behind a magnetic sense in animals—the symbiotic magnetic-sensing hypothesis'. Since we first presented this hypothesis, both criticism and support have been raised accordingly. Here we address the primary criticisms and discuss the plausibility of such a symbiosis, supported by preliminary findings demonstrating the ubiquity of MTB DNA in general, and specifically in animal samples. We also refer to new supporting findings, and discuss host adaptations that could be driven by such a symbiosis. Finally, we suggest the future research directions required to confirm or refute the possibility of symbiotic magnetic-sensing.

This article is part of the theme issue 'The role of the microbiome in host evolution'.

1. Introduction

Despite lengthy and rigorous research, which has yielded numerous studies supporting the ability of animals to sense the geomagnetic field [1], the identity of the magnetic sensor remains enigmatic [2]. To put this in perspective, it is akin to knowing that organisms can respond to a visual stimulus, but not knowing what the mechanism for photoreception is, and where the light-sensitive structure (i.e. eye) is located. To date, two primary hypotheses have been proposed to explain magnetic sensing in animals [3]. These hypotheses are not necessarily mutually exclusive and are defined as: (i) magnetite-based magnetoreception [4] and (ii) 'radical-pair'-based magnetoreception [5]. The magnetite-based magnetoreception hypothesis suggests that ferromagnetic structures coupled with membrane proteins allow a mechanical moment to transduce a signal of earth's magnetic field [4]. The 'radical-pair' hypothesis suggests that following a short-wavelength excitation, a specific molecule that contains two unpaired electrons, such as the cryptochrome protein, could serve as the sensor for Earth's magnetic field. However, different results, seemingly contradictory, have supported or contradicted each of these two hypothesis [2], leaving the field with no conclusive answer. Recently, we raised the symbiotic magnetic-sensing hypothesis [6], suggesting that symbiotic magnetotactic bacteria (MTB) sensed by the host may serve as the underlying mechanism behind animals' magnetic sense. MTB are a diverse group of prokaryotes which are characterized by having their direction of motility influenced with a magnetic field [7]. Unlike animals, the mechanism behind

their magnetotaxis is well understood, using specialized intracellular organelles called magnetosome (magnetic mineral crystals, each enveloped by a phospholipid bilayer membrane).

One of the strengths of the symbiotic magnetic-sensing hypothesis is that it is supported by findings that both confirm and contradict the magnetite-based magnetoreception hypothesis. The existence of magnetite crystals, similar to those found in MTB magnetosomes, in magnetic-sensing animals, has served as support for the magnetite-based magnetoreception hypothesis [8,9]. However, it has been repeatedly shown that these crystals are found in either the extracellular medium or in macrophages; yet they have not been found within any nerve tissue associated with magnetoreception. These findings conflict with the magnetite-based magnetoreception hypothesis [10,11]; however, they are to be expected according to the symbiotic magnetic-sensing hypothesis [6]. Further, behavioural experiments which have demonstrated that short-wavelength light is required for avian magnetic orientation [12], have been considered as support for the radical-pair hypothesis and oppose the magnetite-based hypothesis. However, in-line with these experiments MTB magnetotaxis is also known to be affected by illumination differences in wavelength [13]. Moreover, short-wavelength light could also take part in perceiving symbiotic MTB (see suggested 'Driving host-sensing mechanisms').

The symbiotic magnetic-sensing hypothesis is particularly plausible given the growing recognition of the varied roles symbiotic bacteria play in their hosts' physiology (e.g. [14,15], as evidenced by this special issue). However, three major criticisms of the hypothesis have thus far emerged: (i) the lack of empirical evidence for the existence of such a symbiosis, (ii) the likelihood of having symbiotic MTB, given that their prevalence in potential host species remains rarely reported, and (iii) the absence of a known mechanism that would allow eukaryotes to sense or communicate with symbiotic MTB. Here, we review and discuss recent evidence of the hypothesis, demonstrate that such a symbiosis is probable, show that MTB DNA is routinely found within animal tissue, and discuss possible host-MTB sensing mechanisms.

2. Recent supporting evidence

First critical support for this hypothesis recently arose from the ocean's depth [16]. Consistent with the predictions of the symbiotic magnetic-sensing hypothesis [6], Monteil *et al.* found eukaryotic marine protists (*Symbiontida euglenozoa*) which were covered with MTB. The MTB, along with their magnetosome, were arranged parallel to the motility axis of the eukaryotic cell, optimizing the magnetic moment of the entire host-microbiome holobiont [16]. This study provided the first empirical evidence supporting a symbiotic interaction between MTB and a eukaryote. Moreover, the authors demonstrated that the eukaryotes were able to align with, or sense, the symbiotic MTB, gaining a 'magnetic sense' from the bacteria and using this information for directing the movement of the host protist. Moreover, a recent experiment has shown that when antibiotics are delivered to reed warblers (*Acrocephalus scirpaceus*), a migrating passerine which is known to navigate using the geomagnetic field, the antibiotic treatment caused a loss of directionality—consistent with a bacterial component of a magnetic sense and providing

experimental support for a potential symbiotic relationship with its avian host [17].

3. Magnetotactic bacterial abundance and the polyphyletic nature of the symbiosis

As mentioned above, a common criticism has been that MTB are too rare to be regularly involved in any particular symbiosis. Thus, it is important to emphasize that MTB are not an anecdote of nature, but in fact, MTB are ubiquitous across aquatic and anaerobic environments and have a global distribution [18], occupying aquatic and sedimentary environments, deep-sea sediments and hemi-pelagic environments: inhabiting environments of both neutral pH values to inhabiting extreme environments such as saline-alkaline lakes and even thermals [18]. Moreover, MTB are polyphyletic, currently found in diverse classes and even in different phyla (Proteobacteria, Nitrospirae and Omnitrophica) [18]. Phylogenetic analyses of MTB have suggested that extensive horizontal magnetosome-gene transfer contributed to current MTB diversity [18]. The high occurrence of horizontal gene transfer throughout the phylogeny of magnetosome-possessing bacteria is indicative of symbiotic interactions in the phylogeny of this group [19], specifically, a horizontal transfer of a 'genetic island', such as the magnetosome genes—which also are on a 'genetic island' known as the Magnetosome Island (MAI) [20]. Regarding endosymbiotic bacterial evolution, often it is not necessary that a bacterium evolves *in situ* to be symbiotic, but alternatively, through horizontal gene transfer a characteristic trait of the bacterium is transferred to an existing symbiotic bacterium. For example, the ability for some human populations to digest algae was transferred horizontally from the non-symbiotic marine bacterium *Zobellia galactanivorans* to the human symbiont *Bacteroides plebeius* [21]. The phylogeny of several MTB strains suggests both MAI horizontal gene transfer and a close relationship with several endosymbiotic bacteria (e.g. *Magnetospirillum* [22]), supporting such a scenario. The extensive abundance and taxonomic diversity of MTB suggest that a complete characterization of this polyphyletic group remains largely distant [18,23,24], and more importantly, one cannot exclude symbiosis as a possible trait among MTB taxa. The well-established ecological practice of rarefaction, or the species discovery curve, validates this concept (figure 1). By extrapolating from the temporal pattern of known species descriptions, we can estimate the total number of extant species in a group [25]. We now present an application of this technique on the polyphyletic group of MTB for the first time to our knowledge, about half a century following their first discovery [26,27], and almost four decades since the first public registration of a specific MTB species, *Magnetospirillum magnetotacticum* [28]. A list of all known MTB species was compiled from three NCBI databases (Protein, Gene and Taxonomy), based on the definition of MTB as bacteria that contain magnetosomes (magnetic mineral crystals, each enveloped by a phospholipid bilayer membrane) [7]. Thus, only bacteria that were known to contain magnetosome-related components were included in the dataset. First, the Protein database was queried for magnetosome-related proteins using the search terms 'magnetosome' and 'Mam' [29]. Then the Gene database was searched for magnetosome-related genes using the same search terms [30]. Finally, the Taxonomy database was queried for any organism whose

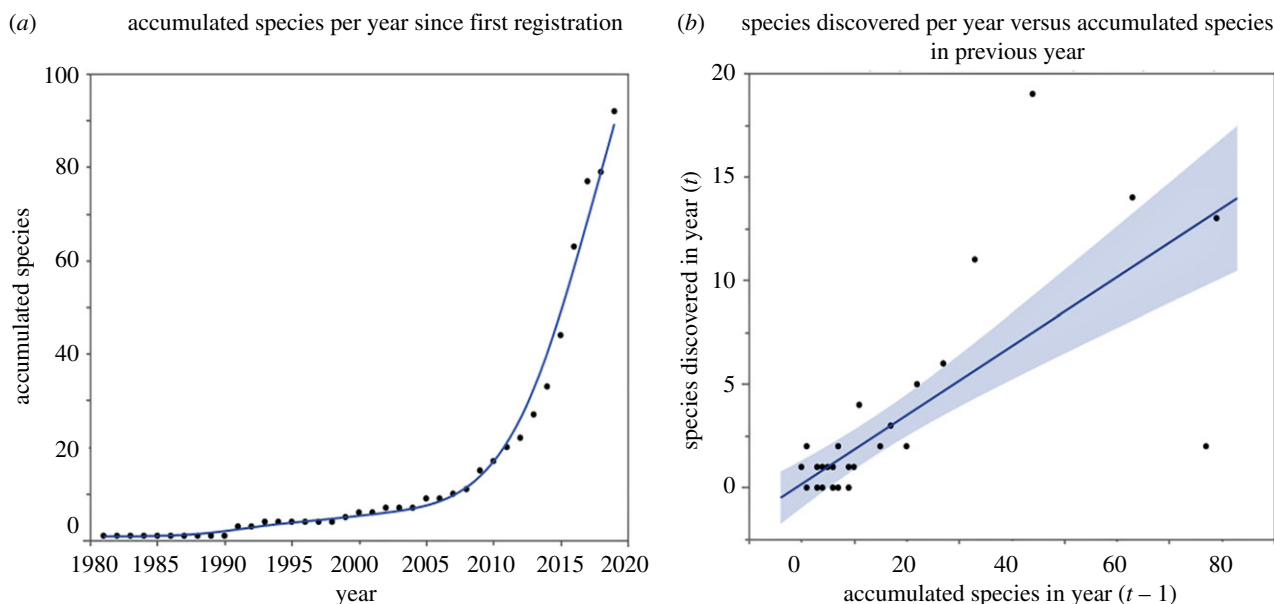


Figure 1. (a) Number of registered MTB species per year since first registration; an increase in discovery rate in the last decade is evident (line indicates a fitted smoothed spline with lambda of 0.05). (b) Regression of the number of discoveries per year in relation to the accumulated number of species in the previous year (shaded area indicates 95% confidence interval of the regression). A significant positive linear correlation indicates that much of the MTB diversity remains undiscovered [$Y = 0.1668 + 0.1663 * N(t - 1)$, $R^2 = 0.569$]. (Online version in colour.)

name contained ‘magnet’ [31] and could be subsequently validated as MTB in the corresponding publication. The taxonomic rank of each relevant organism was checked in the Taxonomy database, and only validated species were included. The search yielded 92 MTB species discovered over 39 years. This includes well-characterized species and species which were described from environmental samples or from other culture-independent criteria (see the electronic supplementary material, table S1). The method described in [25] was applied to the dataset to estimate how close the currently described assemblage of MTB species is to encompassing the entire diversity, and possibly to attain a point estimate of the extent of this diversity. As shown in figure 1a, the rate of new species description (illustrated by the slope) is rapidly increasing. A considerable increase in detection rate is evident in the last 10 years (figure 1a), corresponding to the growing use of environmental sampling and metagenomic techniques. Figure 1b displays a significantly positive linear correlation between the number of new species discovered annually and the accumulated number of species detected in all previous years ($R^2 = 0.57$; $F_{1,37} = 48.75$, $p < 0.0001$). These trends clearly indicate that the extant, described MTB diversity is far from completion, making a point estimate of the number of species impossible.

4. Prevalence of magnetotactic bacteria among metagenomic surveys

While symbiotic MTB have been found to inhabit bivalves [32], a key criticism raised regarding the symbiotic magnetic-sensing hypothesis has been that there is no clear evidence of MTB residing in animal tissues. This is an important consideration, because according to the hypothesis one should thus expect to find MTB present in an organism with a magnetite-based magnetic sense, and more specifically, associated with the particular tissue and/or cells serving as the receptor. Along these same lines, if MTB were found within animal tissue, are they providing a physiological benefit to the host

(e.g. magnetoreception) or are they inadvertently present as a result of environmental contamination (e.g. from food, exposure to sediment/soil)? Advances in microbial diversity surveys, notably enabled by metagenomic techniques and next-generation DNA sequencing, provide an excellent means by which to investigate these questions. Furthermore, the tremendous volume of metagenomic datasets being published have, unintentionally, *already* generated a wealth of information that can be used to *infer* the patterns of MTB distribution. Below we examined a particular database of metagenomic surveys, called MGRAST [33], for the presence of MTB.

The MGRAST database is a high-throughput pipeline constructed to annotate and analyse random metagenomic surveys of microbial communities [33]. MGRAST thus provides the ability to compare and contrast functional taxonomic assignments of bacteria across studies and sampled environments through its automated and controlled curation service. At the time of analysis (26 June 2018), there were 2159 projects publicly available in MGRAST, comprising 53 775 individual metagenomic samples. We accessed these data using a series of application programming interface tools, developed to retrieve data from MGRAST via an R (package *matR*) or python environment [34]. For each metagenome sample, we retrieved both the sample metadata and counts of known MTB species. The counts were normalized by the total sequencing depth of the sample multiplied by 10 000, and can thus be interpreted as ‘number of MTB per 10 000 DNA sequences’. We consider these count data to be a rough approximation of relative abundance, but acknowledge that numerous other factors (e.g. different DNA extraction methods, amplification procedures, treatment conditions) can substantially affect these values [35]. The 21 MTB species retrieved were based on cross-referencing taxonomic assignments made by MGRAST by default with the SEED database [36] with known MTB species described previously [24,37–39].

Of the 53 775 metagenomes analysed, 24 038 (44.7%) did not contain any evidence of MTB (normalized counts = 0).

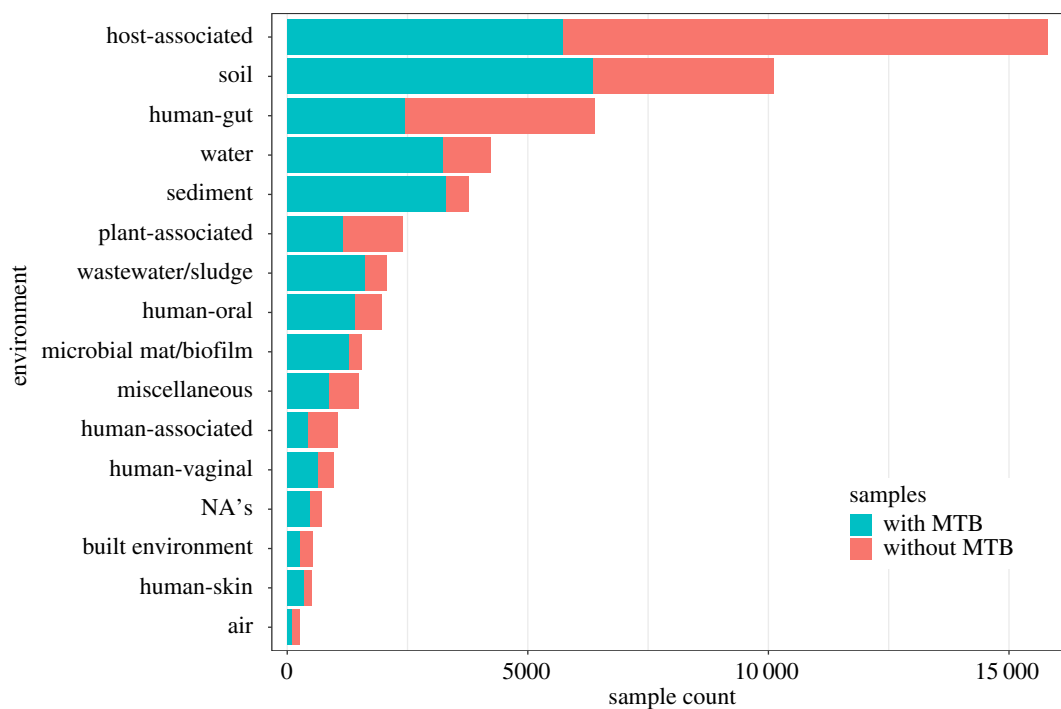


Figure 2. Summary of the environmental types for the 53 775 samples publicly accessible in the MGRAST database, of which 29 737 samples contained magnetotactic bacteria (MTB). The environmental types are as defined in the MGRAST database which has implemented the use of minimum information about any (X) sequence (miXs) developed by the Genomic Standards Consortium (GSC). Refer to the GSC for more specific descriptions of the types (<http://gensc.org/>). The environments 'host-', 'plant-' and 'human-' associated refer to samples originating directly from organismal tissues, surfaces, fluids or waste products, although human-associated samples are further broken down into additional types (i.e. vaginal, oral, skin and gut). NA, not applicable: these samples contained no identifying metadata associated with sample origin in the MGRAST database. (Online version in colour.)

The remaining samples (55.3%) contained normalized counts ranging from 0.000179 to 7480 (see the electronic supplementary datafile). The samples containing the highest amounts of MTB were generally from wastewater treatment plants, including studies specifically enriching for *Magnetospirillum* sp. Of the 21 MTB species queried, *Magnetospirillum gryphiswaldense* was the most common (26.5% of all MTB counts). Of the samples containing MTB, most of them were from either soil (21.4%), host-associated (19.3%), sediment (11.1%) or water (10.9%) environments (figure 2).

Because MTB ubiquitously inhabit aquatic and anaerobic environments [18], it is not surprising that a large fraction of MTB was found in these generally anaerobic samples. In the next stage, we focused exclusively on the host-associated environments and further excluded any reference to human-derived samples. The remaining 4803 metagenomic samples contained MTB and were derived from organism-associated environments (e.g. gut, skin, faecal). Although at present the metadata labelling associated with each project in MGRAST is inconsistent and often lacks scientific names of taxa, the complete dataset is available (electronic supplementary material, table S2) and five examples are shown in figure 3*a–e*. Interestingly, penguin and loggerhead sea turtle (*Caretta caretta*) metagenomes are composed of similar MTB, notably the regular occurrence of *Candidatus Magnetobacterium bavaricum* (figure 3*a,b*). On the other hand, the two mammalian species shown (brown bats *Myotis* sp. and Atlantic right whales) have a similar MTB assemblage—dominated by the genera *Magnetospirillum* and *Magnetococcus*—which is drastically different from that of the reptile and bird. Furthermore, this general pattern of *Magnetospirillum* and *Magnetococcus* presence remains even when compared with all human-derived samples (figure 3*e*). These preliminary findings suggest two

things: (i) MTB are present in the microbiomes of many animals, and (ii) the MTB profiles in different species may recapitulate phylogeny, or in other words, similar animal species may have more similar MTB assemblages. Although the latter needs future investigation using controlled empirical studies, both are consistent with the prediction of the symbiotic magnetic-sensing hypothesis—MTB are part of the microbiome. It still remains possible that much of the MTB observed in figure 3 are strictly a result of environmental contamination, as many samples are of gut and/or faecal origin. However, the similarity in MTB profiles between animals of the same class suggest otherwise, requiring additional data in the future to verify these findings. Nonetheless, future research needs to be performed to examine these patterns more closely.

5. Driving host-sensing mechanisms

Another open question raised from this hypothesis is: how does the host align along the magnetic field presented by its symbionts? Does the host sense the MTB's orientation through a mechanical, e.g. mechanoreceptor? Do the host and MTB communicate physiologically? and: what is the evolutionary genetic background that facilitates such a symbiosis? It has been well established that the microbiome can impact or regulate host behaviour, such as altering host anxiety level, stress and appetite via the microbiota–gut–brain axis [40,41]. Magnetoreception is widespread throughout the animal kingdom—with evidence in such diverse groups as planarians [42], molluscs, insects, fishes, amphibians, mammals, birds, reptiles and others [43]. The list of magnetoreceptive species is growing and obviously polyphyletic, yet there appears to be no common ecological thread. Thus, it remains possible that

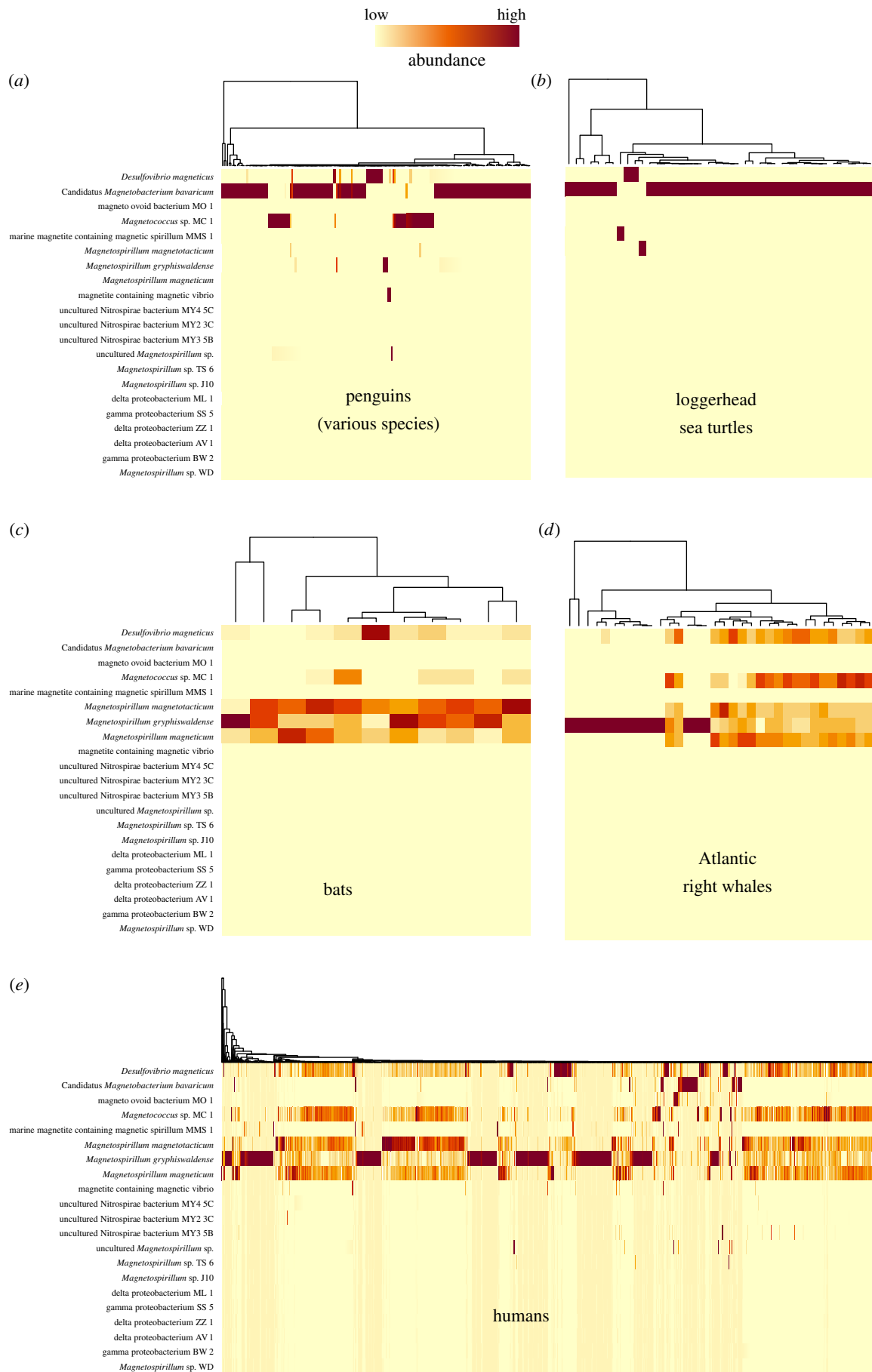


Figure 3. Heatmaps of the normalized MTB counts in samples derived from (a) penguin species ($n = 186$), (b) loggerhead sea turtles (*Caretta caretta*; $n = 42$), (c) bats (*Myotis* sp.; $n = 11$), (d) Atlantic right whales (*Eubalaena glacialis*; $n = 34$), and (e) all human-derived samples ($n = 5295$). The human-derived samples include all human-associated, human-gut, human-skin, human-oral and human-vaginal environmental types. The 21 potential MTB taxa annotated by MGRAST are shown as rows and individual samples as columns. Hierarchical clustering above each panel shows Euclidean-based distance similarities among samples for the 21 MTB taxa. Darker shades (from bright grey to black) indicate increasing abundance. Species were chosen for visualization purposes, see the electronic supplementary material, table S2 for the complete dataset. (Online version in colour.)

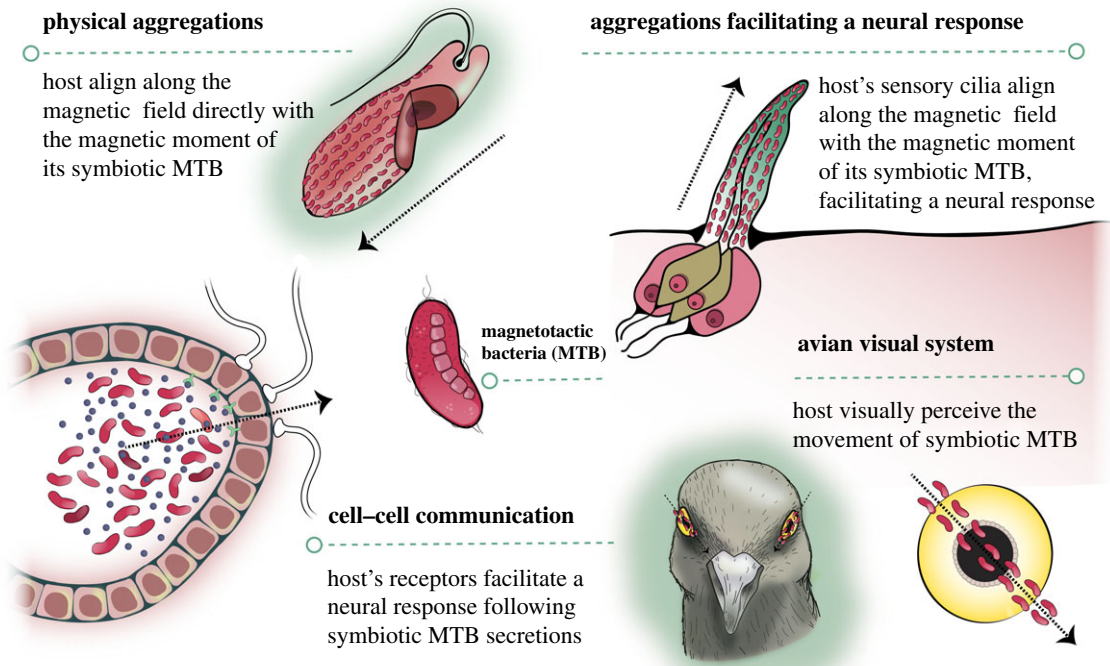


Figure 4. Visual abstract illustrating the suggested host sensing mechanisms, see detailed text below (artwork by Aya Mark). (Online version in colour.)

different mechanisms of magnetoreception may have evolved. If symbiotic magnetic-sensing is the underlying mechanism in at least some of these species, we would expect different hosts to evolve different adaptations, constrained by the host's ecology, senses and size; below we speculate and suggest some possible sensing mechanisms (see figure 4 for a visual abstract).

(a) Physical aggregations

In very small eukaryotic organisms, e.g. protists, MTB could provide the permanent magnetic moment necessary for aligning the host with the geomagnetic field. In such a symbiosis, the host may evolve specific metabolites to facilitate such symbiosis and maintain the MTB; see [16].

(b) Aggregations facilitating a neural response

In larger organisms, physical aggregations within specific organs, including designated sensory cilia or hairs, could communicate the magnetic field direction to the host, promoting the production of specific metabolites and evolution of specific dendrites in the host.

(c) Cell-cell communication

One possible mechanism for MTB to operate as a sensor is cell-cell communication. It has been well established that microorganisms can signal, in a one- or two-way fashion with their host [40]. Quorum sensing (QS) was termed initially to describe cell-cell communication within the same, or different, microbial communities. However, the term was later expanded to include the interaction between bacteria and other species, such as with their host [44]. QS is based on chemical secretion, where a molecule is produced and secreted by the bacterium and received by the host. These molecules are usually hormones or other small molecules such as nitric oxide. Critically, this signalling will lead to gene regulation in the receiving cell, with a potential effect on the host's overall behaviour. For example, the role of the microbiome in several aspects of human

behaviour, including depression and anxiety [45], via the microbiota-gut-brain axis. The mechanism of this axis includes the transformation of information, via a series of molecules and ions, from the microbiota, via the gut tissue and neurons all the way to the brain. Despite decades of research and gathering knowledge, it is unclear whether magnetotaxis involves gene regulation within MTB. But if it does, it is likely to involve QS/secretion of molecules that can be sensed by other MTB and the host. MTB are typically characterized by having some of the highest numbers of signalling proteins among bacteria [46]. Maintaining such a capacity is costly and indicates the importance of communication for these bacteria. Thus, we suggest that another possible mechanism by which the host could sense the symbiotic MTB is through cell-cell communication as illustrated in figure 4.

(d) Avian visual system

Avian magnetoreception has been repeatedly associated with both the visual system [47,48] and the trigeminal nerve [49]. Thus, we have suggested that one mechanism which may bridge these seemingly contradictory results is that symbiotic MTB reside within the lacrimal glands, which are neurologically associated with the trigeminal nerve, and are secreted into the host's eyes. The MTB movement is then perceived by the host [6]. Here we elaborate on this suggested mechanism and clarify its feasibility with respect to optical physics. One possible mechanism is that if MTB move along the eye, their movement may be perceived by the host. If in both eyes, which are located on the sides of the head, the same angle is perceived, then the host is moving in perfect alignment with the magnetic north-south axis. The angle will also indicate the magnetic inclination angle, as MTB move along the field. Three characteristics of avian (or more generally, reptilian) visual systems make this mechanism feasible (i): very short-wavelength spectral sensitivity (λ) [50], (ii) a low ratio between the axial length (f) and the corneal diameter (d) [51], these attributes directly affect the diffraction (see equation below), and

(iii) the large number of cones per area within the retina which increases resolution (analogous to a high pixel number in a digital camera) [52]. Various factors could further aid bacterial movement detectability: the use of polarized light, asymmetric movement along a specific axis, or movement close to the retina within the eye (similar to ‘muscae volitantes’—eye floaters seen by humans). Movement within the eye close to the retina will cause the bacterium to project a shadow on the retina at least as big as the bacterium itself (near field optics). But even when considering the most conservative approach of movement along the cornea, in such a case, the ability of an optical system such as the eye to resolve detail would be limited by diffraction.

The diffraction equation [53]:

$$\text{diffraction} = \frac{1.22 * \lambda f}{d},$$

where λ is the wavelength, f equals the axial length and d the corneal diameter and 1.22 is the factor of the diffraction spot diameter. Using this equation, we can rule out diffraction as the limiting factor preventing birds from detecting bacterial movement along their cornea, as even in low light (using full corneal diameter) avian visual system diffraction should be as low as approximately 900 nm, markedly shorter than many MTB species (see the electronic supplementary material, table S3). As vision is a perceptual rather than merely physical attribute, only behavioural and/or neurological tests can verify whether avian species detect MTB movement through their visual system. However, as even humans can perceive rather small objects moving across their eyeballs, it would not be incorrect to make such an assumption. If such a mechanism has evolved it will select for the host to maintain short-wavelength vision, low f -ratio (axial length/corneal diameter) and maybe more sophisticated mechanisms such as polarized light sensitivity.

6. Discussion

In this manuscript we emphasize the ubiquity of MTB, the large proportion of uncharacterized species, and the high occurrence of MTB DNA in different samples, and specifically, in different animal samples. Taken together with evidence of horizontal transfer of the MAI and the close relationship with various symbiotic MTB, it is probable that additional examples of symbiotic bacteria that possess a magnetosome could be identified [16,32]. From an evolutionary perspective several questions are thus posed: (i) do hosts create an environment

that would maintain MAI genes in their symbiotic MTB? (ii) for how long has this relationship existed and from how many independent origins? and (iii) have hosts evolved mechanisms to coordinate their magnetic orientation with that of their symbiotic MTB? Providing magnetic information to the host will further drive host evolution—allowing hosts to orient, in search of food, mates, or habitat, or confer other unknown benefits. With new accumulating evidence we know that one group of eukaryotes does exactly this—move along the magnetic field using symbiotic MTB [16]. Furthermore, antibiotics were recently shown to affect orientation in a migrating passerine, adding more support to the hypothesis [17]. We emphasize that despite the accumulating evidence, there is currently no conclusive support for the symbiotic magnetic-sensing hypothesis in metazoans. Because this proposed mechanism remains in its infancy and is at least partly speculative, we encourage future research in this area to further confirm or refute elements of a symbiotic mechanism of magnetoreception. One key area will be behavioural experiments following Koch’s postulates. A second key area will be to harness the power of next-generation sequencing approaches to applications in microbial diversity studies. These datasets will aid in determining the prevalence of MTB taxa across animals, and more specifically, within which tissues MTB may reside. Nevertheless, widespread surveys of MTB distribution are necessary for identifying and characterizing other systems that may be impacted by this unique feature of interacting with magnetic fields. Even if a symbiotic magnetic sense is indeed widespread, a further challenge lies in unravelling the mechanism by which the host and MTB communicate, i.e. how does a host, such as birds sense the bacterial reaction to changes in the ambient magnetic field? All in all, the symbiotic magnetic-sensing hypothesis is a hypothesis worth considering.

Data accessibility. All data is available in the electronic supplementary material, tables S1 and S2.

Authors’ contributions. Y.V. and E.N. designed the paper, R.F. designed and conceived the DNA database analysis, Y.W. conceived the MTB species discovery curve, all authors wrote the paper and commented on various versions of the manuscript.

Competing interests. We declare we have no competing interests.

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