

Minireview

Life with compass: diversity and biogeography of magnetotactic bacteria

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Summary

Magnetotactic bacteria (MTB) are unique in their ability to synthesize intracellular nano-sized minerals of magnetite and/or greigite magnetosomes for magnetic orientation. Thus, they provide an excellent model system to investigate mechanisms of biomineralization. MTB play important roles in bulk sedimentary magnetism and have numerous versatile applications in paleoenvironmental reconstructions, and biotechnological and biomedical fields. Significant progress has been made in recent years in describing the composition of MTB communities and distribution through innovative cultivation-dependent and -independent techniques. In this review, the most recent contributions to the field of diversity and biogeography of MTB are summarized and reviewed. Emphasis is on the novel insights into various factors/processes potentially affecting MTB community distribution. An understanding of

the present-day biogeography of MTB, and the ruling parameters of their spatial distribution, will eventually help us predict MTB community shifts with environmental changes and assess their roles in global iron cycling.

Introduction

Iron is the fourth most common element in the Earth's crust and a crucial nutrient for almost all known organisms. The cycling of iron is one of the key processes in the Earth's biogeochemical cycles. A number of organisms synthesize iron minerals and play essential roles in global iron cycling (Westbroek and de Jong, 1983; Winklhofer, 2010). One of the most interesting examples of these types of organisms are the magnetotactic bacteria (MTB), a polyphyletic group of prokaryotes that are ubiquitous in aquatic and sedimentary environments (Bazylinski and Frankel, 2004; Bazylinski *et al.*, 2013). They share a common feature of being able to synthesize magnetosomes, which are intracellular nano-sized iron minerals of magnetite (Fe₃O₄) and/or greigite (Fe₃S₄) (Jogler and Schüller, 2009). Magnetosomes are individually less than 150 nm in size and normally organized into one or multiple chain-like structures within the cell in order to optimize the cellular magnetic dipole moment (Fig. 1). It is widely accepted that magnetosome chain(s) act(s) like a compass needle to facilitate the navigation of MTB using the Earth's magnetic field (Fig. 1).

Because of their remarkable capacity of assimilation of iron, MTB accumulate up to 2–3% iron per cell by dry weight, which is several orders of magnitude higher than iron in non-MTB cells (Heyen and Schüller, 2003). In most aquatic habitats, the numbers of MTB normally range between 10³ and 10⁶ cells ml⁻¹, while in some microhabitats they can even account for a significant proportion (~10–30%) of the microbial biomass (Spring *et al.*, 1993; Flies *et al.*, 2005b; Simmons *et al.*, 2007). There is great geological significance of magnetosomes formed by MTB; spectacular examples are fossil magnetosomes (so-called 'magnetofossils') that may significantly contribute to the bulk magnetization of

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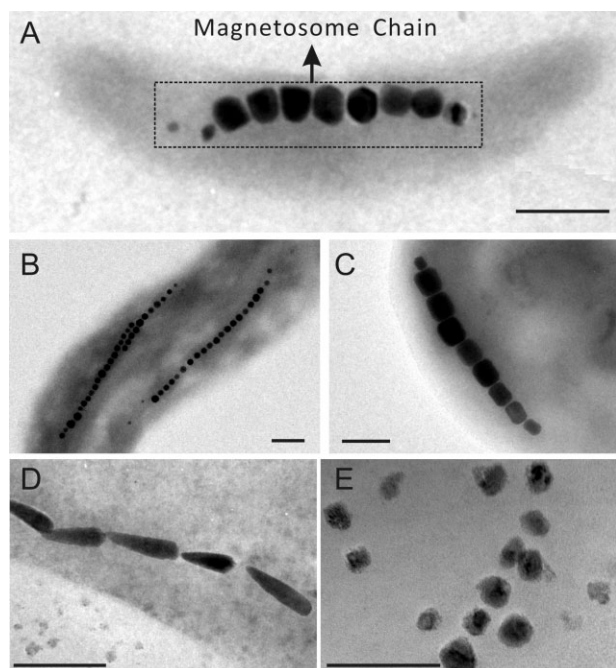


Fig. 1. (A) Transmission electron micrograph of a magnetotactic bacterium with a single magnetosome chain. (B–E) Morphologies of magnetosomes including cuboidal (B), elongated (C), bullet-shaped (D) and irregular (E) crystals. Bars = 200 nm.

sediments (Pan *et al.*, 2005; Kopp and Kirschvink, 2008; Lin *et al.*, 2012a) and act as potential archives of paleomagnetism and paleoenvironmental changes (Mandernack *et al.*, 1999; Kopp *et al.*, 2009; Chang *et al.*, 2012; Kodama *et al.*, 2013). Moreover, the uniform nano sizes and superior magnetic properties of magnetosomes make them potentially applicable in a large number of fields, such as in biotechnological and biomedical applications (Lang *et al.*, 2007; Matsunaga *et al.*, 2007; Faivre and Schüler, 2008; Staniland *et al.*, 2008).

In the past decade, innovative cultivation-dependent approaches and cultivation-independent molecular techniques (such as 16S rRNA gene-based analysis, metagenomic analysis and single cell-based approaches) have become widely applied to probe the diversity and biogeography of MTB. Rather than provide a comprehensive list of all achievements in the field of MTB research that have been reviewed previously in e.g. Bazylinski and Frankel (2004), Schüler (2007), Faivre and Schüler (2008), Bazylinski and colleagues (2013), and Lefèvre and Bazylinski (2013); here, we give an overview of the current understanding of MTB diversity, focusing on novel populations identified in the last 5 years and emphasize novel insights into the distribution and biogeography of MTB. Finally, processes potentially important in the structuring of the biogeography of MTB are discussed.

Global distribution of MTB and their roles in iron cycling

Members of MTB occupy a wide array of ecosystems, including lakes, rivers, ponds, estuaries and salt marshes, lagoons, mangrove swamps, intertidal zones, deep-sea sediments, soils, and even some extreme environments (Fassbinder *et al.*, 1990; Petermann and Bleil, 1993; Flies *et al.*, 2005a; Simmons *et al.*, 2007; Pan *et al.*, 2008; Jogler and Schüler, 2009; Jogler *et al.*, 2009; Wenter *et al.*, 2009; Sobrinho *et al.*, 2011; Lin *et al.*, 2012c; 2013; Martins *et al.*, 2012; Zhang *et al.*, 2012; 2013; Zhou *et al.*, 2012; 2013; Bazylinski and Lefèvre, 2013). So far MTB have been globally detected from Asia, Europe, North and South America, Africa, Australia, and Antarctica (Fig. 2). The water depth at which MTB have been recorded ranges from metre scales to those of deep sea environments (~ 3000 m).

Although additional studies are necessary to understand the distribution of MTB in nature, emerging evidence strongly suggests that MTB occur worldwide in aquatic environments. The majority of studies thus far focus on magnetite-producing MTB communities in lacustrine systems. The annual yield of lacustrine magnetite magnetosomes can be estimated using the following formula: (volume in lakes, ponds and impoundments) \times (average number of MTB cells per mL) \times (average number of magnetite magnetosomes per MTB cell) \times (average number of MTB generations per year) \times (mass of single magnetite magnetosomes). Global lakes, ponds and impoundments are estimated to cover about 4.6 million km² of the Earth's surface (Downing *et al.*, 2006), and we assume that only 50% of this area harbours MTB cells that live in the upper 10 cm of sediment. If we assume that the lower average number of MTB is 10³ cells ml⁻¹, that each MTB cell has 20 magnetosomes, that the generation turnover time of environmental MTB is about 12 h (Moench and Konetzka, 1978) and that the mass of single magnetite magnetosome is 6.48 \times 10⁻¹⁶ g (given the volume of a single magnetosomes is approximately 50 \times 50 \times 50 nm³), the annual yield of magnetite by lacustrine MTB is estimated to be no less than 2 \times 10⁶ kg. This conservative estimate is likely to pronouncedly increase to more than 10⁸ kg of magnetite per year if we consider MTB communities in the world's oceans, although the ecology and distribution of marine MTB are currently poorly understood. In addition, living MTB have been found in soils of a water-rich meadow environment in the southern Bavaria, indicating that MTB may also contribute to the magnetite formation in soils (Fassbinder *et al.*, 1990).

In terms of understanding their ecological functions, the knowledge of to what extent MTB affect local and global

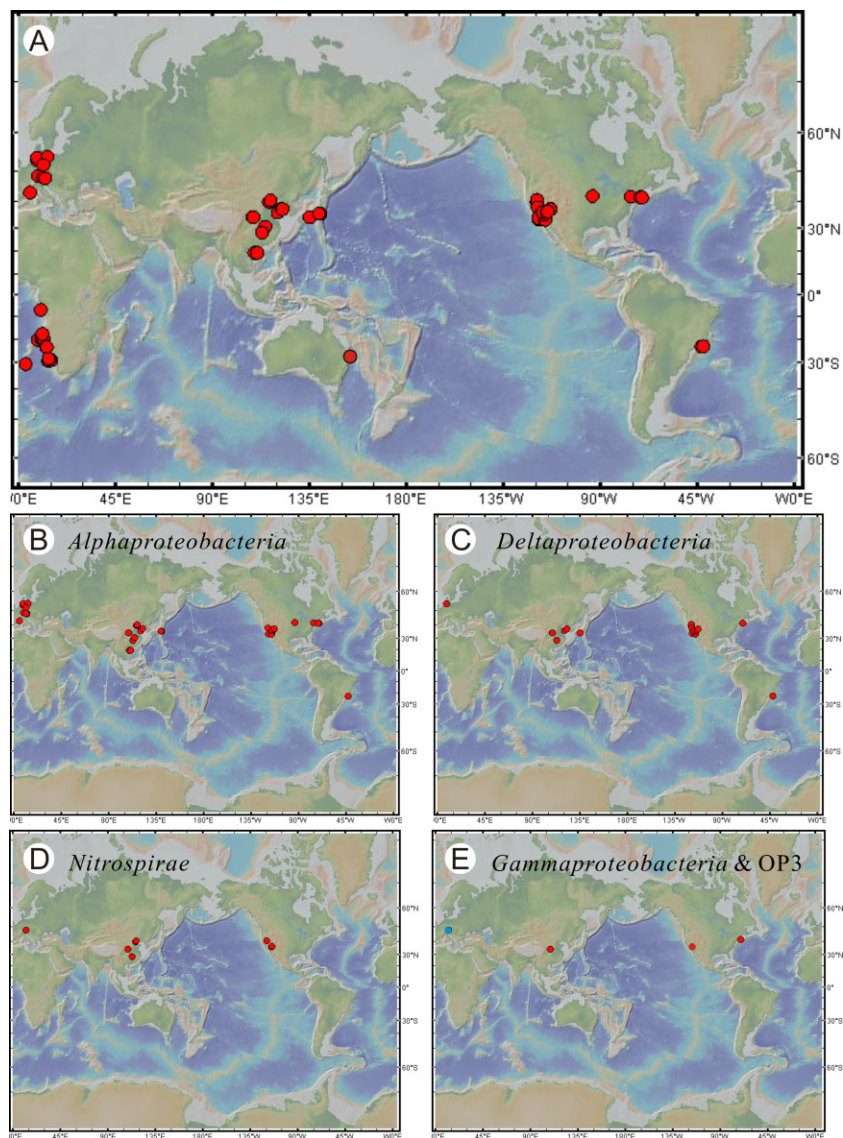


Fig. 2. (A) Global distribution of representative locations studied with respect to the occurrence of MTB. (B–E) Distribution of MTB populations belonging to the *Alphaproteobacteria* (B), *Deltaproteobacteria* (C), phylum *Nitrospirae* (D), and the *Gammaproteobacteria* and candidate division OP3 (E). Red circles in (E) refer to locations where *Gammaproteobacteria* MTB have been found, while the blue circle refers to the site where MTB within the candidate division OP3 are detected. Detailed information is described in Supplementary Table S2. The maps were generated using the GeoMapApp version 2 (<http://www.geomapapp.org/>).

iron cycling would be very useful. Although this represents an area in which there is a paucity of understanding, the earlier estimate strongly suggests that MTB communities play important roles in present-day global iron cycling and the deposition of iron formation through geological history (Fig. 3). Ferrous and ferric ions could be actively taken up by MTB cells in natural environments and accumulate within the cell during the formation of intracellular magnetite or greigite magnetosomes, the biochemical/chemical pathways of which are still not fully understood (Schüler, 2008). When MTB die, parts of, or entire magnetofossils could be dissolved thereby releasing ferrous and ferric ions back to environmental iron cycling (Fig. 3), while other magnetofossils may be deposited into sediments eventually leading to mineral iron formation. On the other hand, some MTB cells can be ingested by their predators, e.g. protozoa (Martins *et al.*, 2007), which

causes the iron from MTB to enter into the food chain (Fig. 3). More research involving the distribution and ecology of MTB in nature, especially in marine habitats, will help us better understand the conditions under which and to what extent MTB affect the biogeochemical cycle of iron.

Diversity of MTB

Thanks to their active magnetotactic behaviour, environmental MTB can be magnetically extracted and at least partially purified from water or sediment samples relatively easily. The identification of novel MTB populations has mostly relied on both cultivation-based approaches and 16S rRNA gene-targeting analyses, such as clone library sequencing, fluorescence *in situ* hybridization (FISH), restriction fragment length polymorphism and denaturing

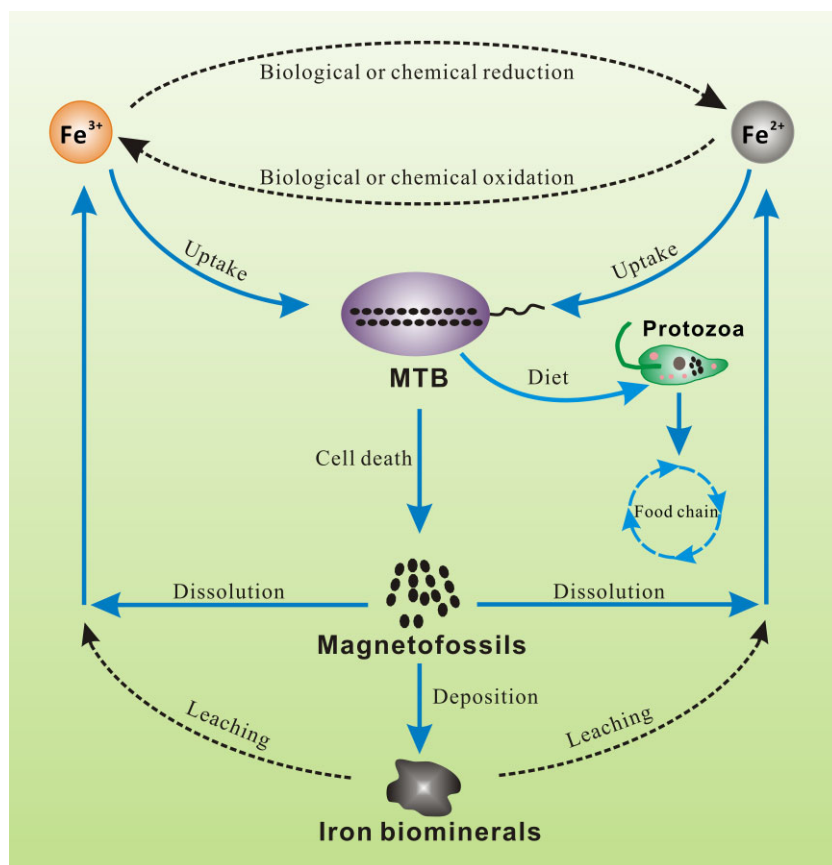


Fig. 3. Schematic illustration of MTB-mediated iron cycling. Environmental ferrous or ferric ions are transported into MTB cells during magnetosomes synthesis. When the bacteria died, some fossil magnetosomes (magnetofossils) could be dissolved and release ferrous and ferric ions into environment, while others may be deposited into sediments and form iron biominerals. In addition, MTB populations could be ingested by protozoa, and the iron from bacterial magnetosomes thus enters into the food chain.

gradient gel electrophoresis. Recently, newly developed metagenomics (Jogler and Schöler, 2009; Jogler *et al.*, 2009; Lin *et al.*, 2011) and approaches of single-cell separation in combination with whole genome sequencing (Arakaki *et al.*, 2010; Jogler *et al.*, 2011; Kolinko *et al.*, 2012; 2013) have also provided powerful and effective ways to investigate the diversity and metabolic information on environmental MTB.

Through these approaches, MTB identified thus far are phylogenetically associated with the *Alphaproteobacteria*, *Deltaproteobacteria*, *Gammaproteobacteria* classes of the *Proteobacteria* phylum, the *Nitrospirae* phylum and the candidate division OP3 (Fig. 4 and Table S1). Magnetite-producing members are affiliated with all known taxa of MTB, while greigite-producing MTB have only been found in the *Deltaproteobacteria* (Abreu *et al.*, 2011) and perhaps the *Gammaproteobacteria* (Simmons *et al.*, 2004). MTB that are able to simultaneously biomineralize both magnetite and greigite magnetosomes are thus far exclusively detected within the *Deltaproteobacteria* (Lefèvre *et al.*, 2011d; Wang *et al.*, 2013) (Fig. 4).

Although MTB of the *Alphaproteobacteria* represent the dominant populations of MTB in many environments in nature, recent studies have shown that those of other taxa

are much more diverse than previously thought (Table S1). For example, MTB in the phylum *Nitrospirae* were for many years thought as comprising only one uncultivated species, the large rod '*Candidatus Magnetobacterium bavaricum*' (Spring *et al.*, 1993). However, a number of MTB from this phylum have recently been recovered from Germany (Flies *et al.*, 2005a; Kolinko *et al.*, 2013), China (Lin *et al.*, 2011; 2012a) and the USA (Lefèvre *et al.*, 2010; 2011a), which suggests that the *Nitrospirae* MTB consist of multiple evolutionary groups (Fig. 4 and Table S1).

Our understanding of the diversity of the *Deltaproteobacteria* and *Gammaproteobacteria* MTB has been advanced as well. Novel MTB affiliated with the *Deltaproteobacteria* have been identified and/or isolated, including iron sulphide-producing multicellular magnetotactic prokaryotes (MMPs) from the North Sea in Central Europe (Wenter *et al.*, 2009), magnetite-producing MMPs from the Yellow Sea in East Asia (Zhou *et al.*, 2011; 2012) and three alkaliphilic vibrioid strains from highly alkaline environments in North America (Lefèvre *et al.*, 2011b) (Table S1). Of note, a number of MTB populations from USA were found to represent two novel groups of sulphate-reducing bacteria in the *Deltaproteobacteria* (Lefèvre *et al.*, 2011d). Of these MTB, one greigite-

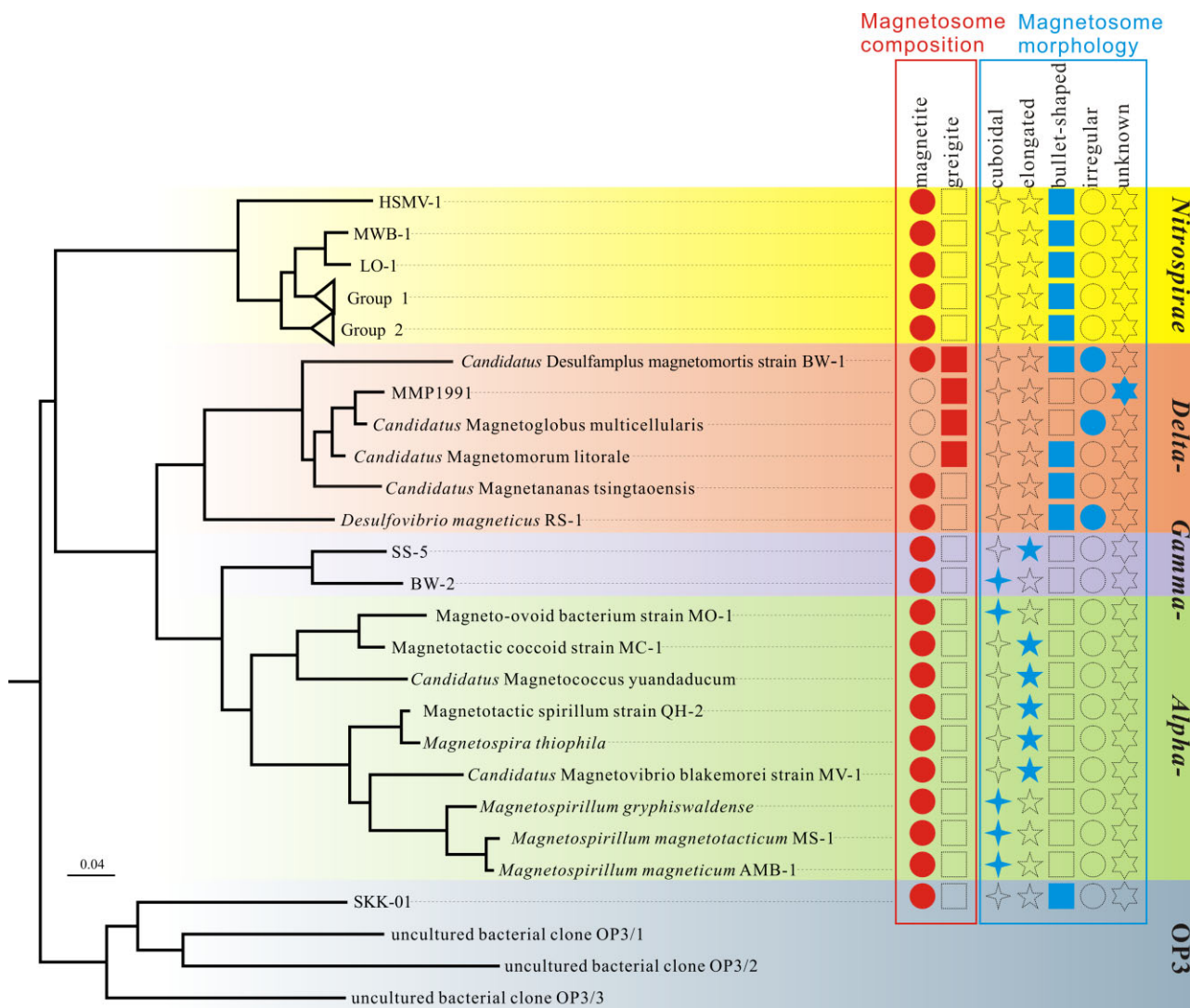


Fig. 4. Maximum-likelihood phylogeny of nearly full-length 16S rRNA gene sequences representing different groups of representative MTB. This tree shows that all currently known MTB are affiliated within the *Alphaproteobacteria*, *Deltaproteobacteria*, *Gammaproteobacteria*, phylum *Nitrospirae* and the candidate division OP3. Information of magnetosome composition and morphology is shown for each MTB strain or group. MTB sequences and their magnetosomes information are from literature (DeLong *et al.*, 1993; Abreu *et al.*, 2007; Lefèvre *et al.*, 2009; 2010; 2011a,b,d; 2012; Nakazawa *et al.*, 2009; Wenter *et al.*, 2009; Zhu *et al.*, 2010; Kolinko *et al.*, 2012; Lin *et al.*, 2012a; Zhou *et al.*, 2012).

producing strain, known as ‘*Candidatus Desulfamplus magnetomortis*’ strain BW-1, was successfully cultivated in the lab and found to form greigite and/or magnetite magnetosomes depending on cultivating conditions (Lefèvre *et al.*, 2011d). Recently, a high diversity of *Deltaproteobacteria* MTB, including one that simultaneously produces magnetite and greigite magnetosomes, was characterized in a single freshwater niche in China (Wang *et al.*, 2013) (Table S1). The first evidence for *Gammaproteobacteria* MTB was obtained from a coastal salt pond in the USA (Simmons *et al.*, 2004). Two rod-shaped magnetite-producing strains were recently isolated and were identified as belonging to the orders

Chromatiales and *Thiotricales*, respectively, in the *Gammaproteobacteria* (Lefèvre *et al.*, 2012) (Table S1). In addition, two populations of *Gammaproteobacteria* MTB were detected in a freshwater niche in China that coexist with MTB belonging to the *Alphaproteobacteria* and *Deltaproteobacteria* (Wang *et al.*, 2013).

It has been shown that MTB are not restricted to the phyla *Proteobacteria* and *Nitrospirae*. A large melon-shaped MTB (designated SKK-01) with low abundance was discovered in sediments of Lake Chiemsee, Germany (Kolinko *et al.*, 2012). Cells of SKK-01 contain iron-oxide bullet-shaped magnetosomes organized in multiple bundles of chains. Micromanipulation of

individual cells followed by single-cell genomic and FISH analyses has assigned SKK-01 to the candidate division OP3 belonging to the *Planctomycetes-Verrucomicrobia-Chlamydiae* superphylum (Kolinko *et al.*, 2012).

There is an interesting and possibly evolutionary important correlation between the composition and morphology of magnetic magnetosome mineral and specific phylogenetic groups of MTB. MTB of the more deeply branching phylogenetic groups that contain MTB of the *Nitrospirae* and strain SKK-01 of the candidate division OP3 are only known to biomineralize bullet-shaped magnetite crystals that display a great deal of morphological variation (Hanzlik *et al.*, 1996; Li *et al.*, 2010; Jogler *et al.*, 2011; Lefèvre *et al.*, 2011c; Lin *et al.*, 2011; 2012a; Kolinko *et al.*, 2012) (Fig. 4). This is also true of MTB of the deeply diverging class of the *Proteobacteria*, the *Deltaproteobacteria* (Lefèvre *et al.*, 2011c), although some species biomineralize greigite magnetosomes in addition to those containing bullet-shaped crystals of magnetite. MTB of the later diverging classes of the *Proteobacteria*, the *Alphaproteobacteria* and *Gamma-proteobacteria*, biomineralize consistent, well-defined cuboctahedral, and elongated prismatic crystals of magnetite (Fig. 4) (Devouard *et al.*, 1998; Lefèvre *et al.*, 2012). Based on this phylogenetic information, it has thus been hypothesized that bullet-shaped magnetite crystals were the more ancient type of magnetic mineral crystals biomineralized within magnetosomes (Lefèvre *et al.*, 2013a).

Magnetosome formation by MTB species in the *Alphaproteobacteria* is under strictly genetic control through a genomic magnetosome island (MAI) that encodes a group of proteins involving in magnetosome membrane biogenesis, magnetosome membrane chain arrangement and magnetosome biomineralization (Schüler, 2008; Murat *et al.*, 2010; Komeili, 2012). Following comparative genomic analyses have revealed that MAI also exists in genomes of MTB belonging to the *Deltaproteobacteria* and *Nitrospirae*, which strongly indicate that this structure is horizontally transferred (Nakazawa *et al.*, 2009; Abreu *et al.*, 2011; Jogler *et al.*, 2011; Lefèvre *et al.*, 2013b). Although several core magnetosome genes are identified in all characterized MTB (Nakazawa *et al.*, 2009; Lefèvre *et al.*, 2013b), the gene content and organization of MAIs differ in distinct MTB groups, which may account for the diversity of composition, morphology and arrangement of magnetosomes. For example, the formation of bullet-shaped magnetosomes in the *Deltaproteobacteria* MTB is hypothesized to be due to the deficiency of particular magnetosome genes (Nakazawa *et al.*, 2009) or the existence of several specific *mad* genes currently only found to be present in those MTB that synthesis bullet-shaped magnetosomes (Lefèvre *et al.*, 2013b).

Biomineralization of greigite magnetosomes appears to have originated in the *Deltaproteobacteria*, the only group known to contain greigite-producing MTB (Abreu *et al.*, 2011; Lefèvre *et al.*, 2011d) and, interestingly, not the most deeply branching groups that contain MTB. '*Candidatus* Desulfamplus magnetomortis' strain BW-1, the only greigite-producing magnetotactic bacterium currently in pure culture, biomineralizes both greigite and magnetite, and contains two sets of magnetosome genes, one presumably responsible for magnetite biomineralization and the other for greigite biomineralization (Lefèvre *et al.*, 2011d). Both sets of genes have nine magnetosome genes in common, although they are not identical. Because of the similarities between both sets of magnetosome genes, the second set putatively involved in greigite biomineralization may have originated from gene duplication and/or subsequent mutation or other genetic changes that appears to have only occurred in the *Deltaproteobacteria*.

Biogeography of MTB

Spatial variation

Microbes were previously thought to be randomly distributed over space and that similarities between microbial communities were independent of geographic distances and environmental gradients between sites because of their great metabolism capacity, large population numbers, long evolutionary history, short generation times and high dispersal capabilities; this being the so-called 'everything is everywhere' concept (Baas Becking, 1934; Finlay, 2002; Fontaneto, 2011). If this was true, all kinds of MTB populations should be cosmopolitan and would lack local, regional or global biogeographic patterns.

Building on more than three decades of effort to determine the diversity of MTB in various ecosystems, we have reached a point where comparisons can be made between different environments to identify distribution patterns of MTB. Some specific well-known species of MTB, such as '*Candidatus* Magnetobacterium bavaricum'-like bacteria and the MMPs that have conspicuous morphologies and are easily distinguished from other MTB and non-MTB, have shown clear biogeographic distributions. So far, all known '*Candidatus* Magnetobacterium bavaricum'-like MTB appear to be restricted to freshwater or low-salinity ecosystems (Lefèvre *et al.*, 2010; 2011a; Jogler *et al.*, 2011; Lin *et al.*, 2011; 2012a), while MMPs have been exclusively found in saline environments (Martins *et al.*, 2009; Wenter *et al.*, 2009; Zhou *et al.*, 2012). In addition, recent studies using molecular techniques have revealed biogeographic patterns in MTB communities at local and continental scales (Lin and Pan, 2010; Lin *et al.*, 2012c; 2013). In order to address the global distribution patterns of MTB, here, we conducted a

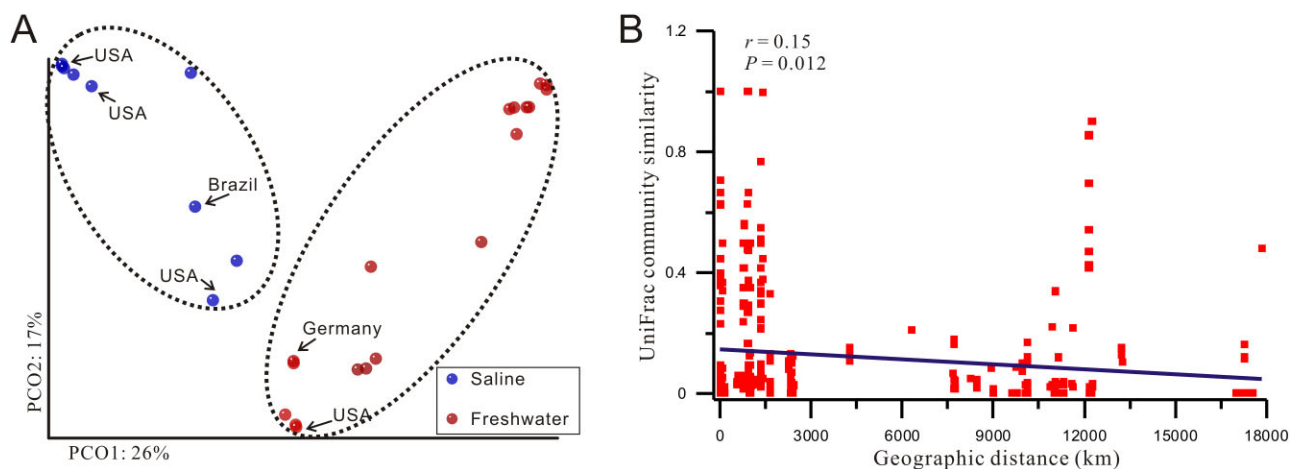


Fig. 5. (A) Cluster of representative MTB communities ($n = 27$) from China (Lin *et al.*, 2012c; 2013), USA (Simmons *et al.*, 2004; 2006; Lin *et al.*, 2013), Germany (Lake Chiemsee) (Spring *et al.*, 1992; 1993; Kolinko *et al.*, 2012; 2013) and Brazil (Itaipu lagoon) (Spring *et al.*, 1998) using principal coordinates plots of the unweighted UniFrac distance matrix that considers the phylogenetic distance between taxa and reflects the occurrence of distinct microbial lineages among different communities (Lozupone and Knight, 2005). The unlabelled samples are those from China. (B) Relationship between MTB community similarity and the geographic distance between sampling sites. Sequence data manipulations and statistics were performed using the QIIME (Caporaso *et al.*, 2010). Because some MTB sequences span different regions of the 16S rRNA gene, operational taxonomic units were picked through a closed-reference process against the Greengenes reference database (McDonald *et al.*, 2012) based on 97% sequence similarity. Details about sample locations can be found in Supplementary Table S2.

non-exhaustive compilation of MTB community datasets ($n = 27$) from Asia (China), Europe (Germany), North America (USA) and South America (Brazil) (see legend of Fig. 5 for details). Although the lack of environmental metadata for several datasets prevents in-depth quantitative analyses, our results have clearly revealed that MTB communities from different habitats cluster by salinity (freshwater or saline) along principal coordinate 1 (Fig. 5A). This result indicates that MTB represent biogeographic patterns at the global level as well.

Martins and colleagues (2009), and Sobrinho and colleagues (2011) noted that the abundance and distribution of the greigite-producing MMP, '*Candidatus Magnetoglobus multicellularis*', are largely affected by water salinity and the ratio of iron and bioavailable sulphur concentrations. Lin and colleagues (2012c; 2013) and the present analysis (Fig. 5A) have revealed that salinity influences the overall phylogenetic diversity of MTB communities across global different ecosystems, i.e. MTB communities from freshwater environments are more phylogenetically similar than those from saline environments. In fact, previous studies have shown that MTB from the two types of environments normally form separate lineages in the phylogenetic tree, which suggests a potential evolutionary separation between saline and freshwater MTB lineages (Spring *et al.*, 1998; Zhang *et al.*, 2010b). These results from MTB are consistent with the observation that salinity is one of the major drivers of global distribution in bacterial diversity (Lozupone and Knight, 2007). Although the mechanisms of salinity-

dependent distribution of MTB are not fully understood, the gradients in osmotic pressure and ionic concentration across salinities could be important factors affecting the biogeography of MTB (Lin *et al.*, 2012c). For example, recent genomic analysis showed adaptation of *Magnetospira* sp. QH-2 to marine habitats, i.e. it possesses genes coding for Na^+ transporters, Na^+ -dependent NADH-quinone oxidoreductase, Na^+ -motive force-driven flagellar motors and osmoprotectant synthesis that are absent from genomes of the freshwater *Magnetospirillum* strains (Ji *et al.*, 2013).

The most unique property of MTB, compared with other bacteria, is their capability to interact with the Earth's magnetic field. Previous studies have suggested that the strength of the Earth's magnetic field may influence the morphologies and sizes of magnetosome crystals in MTB, e.g. some MTB in regions of lower geomagnetic field strength appear to contain larger magnetosome crystals (Frankel *et al.*, 1981; Farina *et al.*, 1994; Spring *et al.*, 1998). Recently, variations in the strength of magnetic field have been experimentally found to affect the magnetotactic swimming velocity or cell metabolism of some MTB populations (Wang *et al.*, 2008; Pan *et al.*, 2009; Lin *et al.*, 2012a). By analysing MTB community structures from different ecosystems in East Asia and North America, it is first noted that the β -diversity (variation in community composition) of dominant MTB populations shows a surprising degree in response to differences in the strength of the Earth's magnetic field in the Northern Hemisphere (Lin *et al.*, 2013). Although the

correlation between biogeography of MTB and the strength of the geomagnetic field is supported by a substantial amount of data, it is still a testable hypothesis that requires additional studies, especially those from areas of high latitude and the southern hemisphere.

Additional environmental factors that could have significant potential effects on MTB biogeography include temperature (Lin *et al.*, 2012b; 2013), redox potential (Simmons *et al.*, 2006; Zhang *et al.*, 2010a; Lin *et al.*, 2013), light (Shapiro *et al.*, 2011), the presence and concentration of sulphur compounds (Postec *et al.*, 2012) and nitrate (Lin and Pan, 2010), and the concentration of total iron (Lin *et al.*, 2013).

Processes that structure MTB biogeography

A central goal of studies of microbial biogeography is to understand the mechanisms that generate and maintain MTB distribution and community composition. Several processes have been assumed to sustain and control biogeography of microbes. The classical niche-based model assumes that the abundance and community composition of microbes are largely determined by environmental parameters (Martiny *et al.*, 2006). For example, a recent study has suggested that the global ocean contains a shared microbial seed bank and that the biogeography of marine microorganisms reflect shifts of rare or dominant taxa depending on environmental conditions (Gibbons *et al.*, 2013). On the other hand, the neutral theory assumes that all species are ecologically equivalent and that community variation arises solely from the spatial process (Hubbell, 2001; Fontaneto, 2011). The

latest studies, however, suggest that these two processes may not be mutually exclusive but jointly control microbial communities (Hanson *et al.*, 2012).

For biogeographic analysis of MTB, the niche-based process is much easier to measure than the spatial process. For example, variations of MTB communities are normally explained by changes of local environmental factors as stated earlier (Fig. 6). In addition, recent genomic analysis provides new insights into the molecular adaptation of MTB to ecological niches. For example, TonB protein and TonB-dependent iron transporters widely spread among bacteria and nitrogen fixation have been considered as common features of MTB. However, the intertidal strain *Magnetospira* sp. QH-2 possesses neither TonB/TonB-dependent iron transporters nor the nitrogen fixation pathway (Ji *et al.*, 2013). Mechanisms leading to such environmental specification are still unknown and need further studies.

Besides the niche-based process, a study using a variation partitioning approach has revealed that the spatial process also structure the biogeographic patterns of MTB across a large spatial scale (Lin *et al.*, 2013). Although the niche-based process plays an important role, the contribution of the spatial process to the biogeography of MTB cannot be neglected (Fig. 6). Our analysis on available global MTB community data sets conducted in this study also finds a significant correlation of the variation of MTB communities and the geographic distance between sampling sites ($P < 0.05$, Fig. 5B). This distance–decay relationship indicates that the spatial process may shape the global biogeography of MTB as well. We note several relatively high community similarities (UniFrac similarity

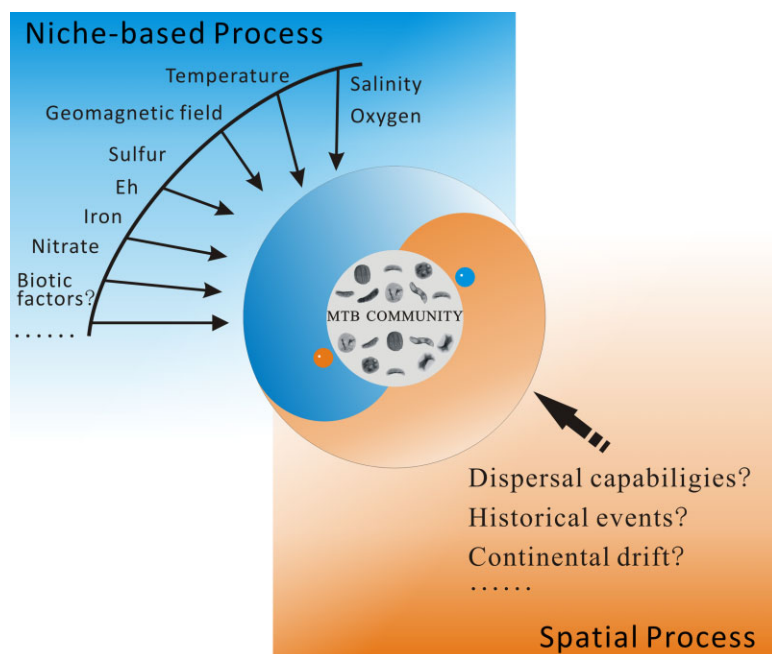


Fig. 6. Conceptual model denoting influences of niche-based and spatial processes on MTB community structure. The Taiji symbol represents that (i) both niche-based process and spatial process jointly control biogeography of MTB community and (ii) their relative contributions to MTB biogeography may vary under different conditions, like across distinct spatial scales.

> 0.5) around a geographic distance of 12 000 km in Fig. 5B, which are between MTB communities from California, USA, and Hainan province, China with similar salinity. This result, together with the result from Fig. 5A, suggests that both environment and geographic distance could affect MTB global distribution, and the biogeography of MTB is perhaps more influenced by environmental factors (such as salinity) than geographic distance. Taken together, these observations strongly suggest that the biogeography of MTB is likely controlled by the same processes affecting macroorganisms (animals and plants), i.e. the niche-based process and the spatial process interact to control their communities in nature (Fig. 6). Further studies are required to quantitatively assess the relative contributions of these processes to the global biogeography of MTB.

Concluding remarks and future perspectives

We show in this review clearly that our understanding of diversity and biogeography of MTB has been greatly advanced. MTB represent a valuable model group for addressing some ecological questions in microbial biogeography because of their global distribution, moderate diversity and active magnetotactic behaviours. A deeper characterization of MTB through cultivation-based approaches and advanced cultivation-independent techniques (such as 'omics'-based analyses and single cell-based approach) will allow for future studies of their diversity and biogeography.

Only a small proportion of the community variation of MTB has been explained by characterized factors (Lin *et al.*, 2013), which is likely due to the relatively small amount of data on MTB and the lack of additional important environmental information. Surveys of MTB conducted to date largely focus on mid-low latitudes in the Northern Hemisphere, while the diversity and biogeography of MTB in the Southern Hemisphere as well as high-latitude zones are still poorly characterized (Fig. 2). Standard protocols should be established in MTB diversity analyses that could make results from different labs comparable. Meanwhile, the key factors that influence the microbial biogeography of MTB should be quantitatively determined.

Bacterial populations are dynamic in nature, with their abundance and community structure changing over time. Although a few studies on the temporal variation of particular MTB, such as '*Candidatus Magnetoglobus multicellularis*' (Martins *et al.*, 2012) and several dominant populations in a coastal brackish pond (Simmons *et al.*, 2007), have been reported, our knowledge on the variation of MTB communities over time is still very limited. It is thus of great importance for future studies to consider the temporal variation of overall MTB communities in nature.

In a geological context, single-domain magnetofossils preserved in sediments are not only ideal carriers of magnetization for paleomagnetism but also potential biomarkers for retrieving paleoenvironmental information (Kopp *et al.*, 2007; 2009; Roberts *et al.*, 2011; Chang *et al.*, 2012; Larrasoana *et al.*, 2012; Kodama *et al.*, 2013). A better understanding of the present-day biogeography of MTB and its correlation with specific environments will pave the way for reconstructions of past environmental change that will eventually help us predict and assess how MTB communities shift with climate changes. Thus, probing fossil magnetosomes in periods of intensive paleoclimatic changes and geomagnetic field events (e.g. polarity reversals and excursions) will be of particular interest in future investigations.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. MTB strains and populations that have been characterized in the last 5 years (2009–2013).

Table S2. Details of the representative locations where MTB have been detected.