



The microbiomes of deep-sea hydrothermal vents: distributed globally, shaped locally

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Abstract | The discovery of chemosynthetic ecosystems at deep-sea hydrothermal vents in 1977 changed our view of biology. Chemosynthetic bacteria and archaea form the foundation of vent ecosystems by exploiting the chemical disequilibrium between reducing hydrothermal fluids and oxidizing seawater, harnessing this energy to fix inorganic carbon into biomass. Recent research has uncovered fundamental aspects of these microbial communities, including their relationships with underlying geology and hydrothermal geochemistry, interactions with animals via symbiosis and distribution both locally in various habitats within vent fields and globally across hydrothermal systems in diverse settings. Although ‘black smokers’ and symbioses between microorganisms and macrofauna attract much attention owing to their novelty and the insights they provide into life under extreme conditions, habitats such as regions of diffuse flow, subseafloor aquifers and hydrothermal plumes have important roles in the global cycling of elements through hydrothermal systems. Owing to sharp contrasts in physical and chemical conditions between these various habitats and their dynamic, extreme and geographically isolated nature, hydrothermal vents provide a valuable window into the environmental and ecological forces that shape microbial communities and insights into the limits, origins and evolution of microbial life.

Chemosynthesis

The use of chemical energy to fix inorganic carbon into organic carbon for microbial growth.

Microbial mats

Dense, macroscopic communities of microorganisms attached to a solid surface.

Deep-sea hydrothermal vents are regions of the sea floor at which hot, anoxic, chemical-rich water is released into the cold, oxic, deep ocean. Discrete clusters of vent fields exist globally, especially at seafloor-spreading centres not only along mid-ocean ridges but also, as only recently appreciated, in several other geological settings (FIG. 1). Hydrothermal vents are formed when seawater percolates through cracks in the ocean crust into the subsurface. During this process, the water heats up and reacts with hot rocks, enriching it with a variety of chemicals and volatile gases. This buoyant hydrothermal fluid rises and emerges from orifices in the sea floor, rapidly mixing with cold seawater and providing a redox interface at which chemical sources of energy support vent ecosystems. In contrast to most ecosystems, which are fuelled by photosynthesis, vent communities depend on chemosynthesis. Vent microorganisms, including animal symbionts, members of microbial mats and free-living cells, use the energy produced by oxidation of sulfur, hydrogen, methane and iron to fix carbon. In turn, this organic carbon supports dense animal communities largely through symbiotic relationships with bacteria but also via grazing or suspension feeding and subsequent trophic transfer.

The rapid discovery and exploration of vents worldwide over the past few decades¹ (BOX 1) have revealed a range of geologically distinct vent types and associated biological communities, providing new opportunities to understand the relationships between geology, fluid geochemistry, biology and biogeography (BOX 2). In parallel, next-generation sequencing methods have provided new insights into the energy metabolism of uncultured microorganisms², opening windows into how vent-derived energy sources fuel microbial primary production³ and how microorganisms and their animal hosts interact in symbiotic relationships.

This article reviews our current knowledge on the microorganisms that inhabit deep-sea hydrothermal vents. We first survey the different habitats at vents, the dominant microorganisms that inhabit them and the challenges and opportunities for organisms living in such extreme environments. This provides the basis for considering controls on the composition of microbial communities, drawing on the growing data on how microbial taxa are distributed within and between vent sites. The emerging perspective is that geology and geochemistry have important roles in shaping communities both within and between vent fields. Whereas dispersal

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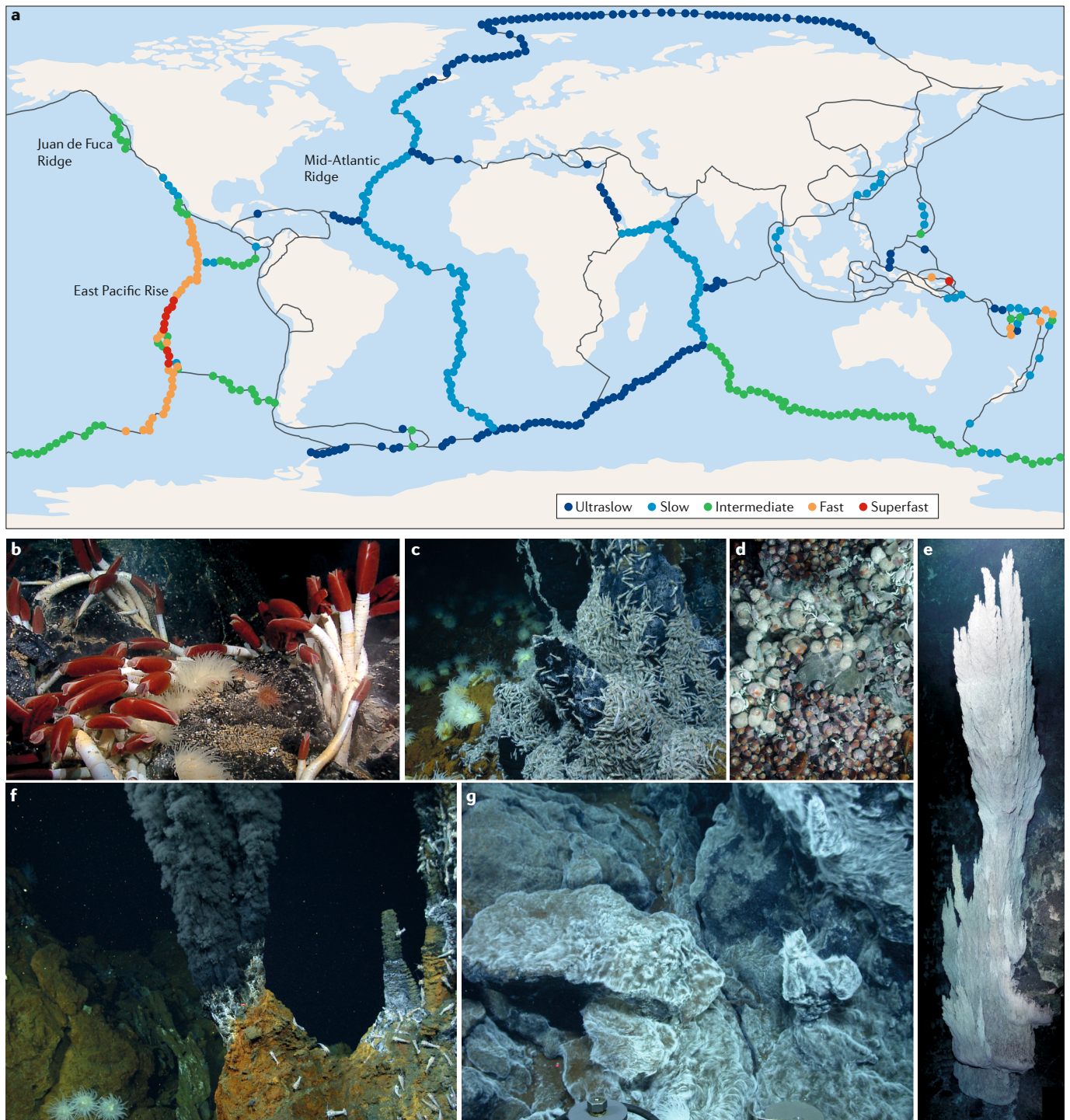
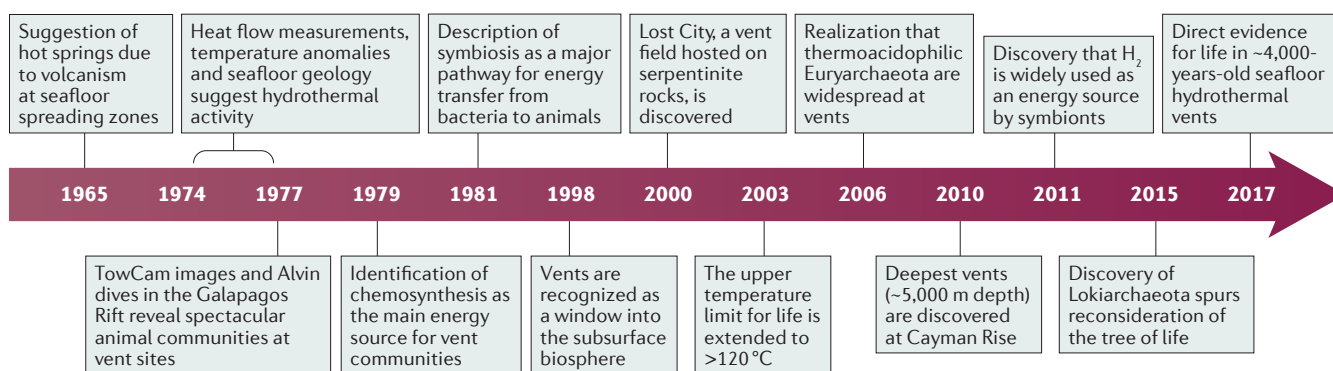


Fig. 1 | Global distribution of hydrothermal-vent systems. **a** | The map shows locations of confirmed and inferred active deep-sea hydrothermal-vent fields (water depths >200 m). Ridge axes are coloured according to spreading rate: ultraslow (dark blue; <20 mm per year), slow (light blue; 20–50 mm per year), intermediate (green; 50–80 mm per year), fast (orange; 80–140 mm per year) and superfast (red; >140 mm per year). **b** | The image shows *Riftia pachyptila* tube worms at a black smoker on the East Pacific Rise; these animals are important models for studying symbiotic relationships. **c** | Swarming *Rimicaris hybisae* shrimp at the Beebe Woods vent, Mid-Cayman Rise, graze on vent microorganisms. **d** | The image shows snails (*Alviniconcha* spp. and *Ifremeria nautilei*) and bythograeid crabs (*Austinograea alayseae*) at the Tu'i Malila vent field, Lau Basin. **e** | The image shows a 10 m-tall carbonate chimney at Lost City in the mid-Atlantic. **f** | The image shows a black smoker and the chimney habitat. **g** | The image shows microbial mats growing on rocks. Part **a** is reproduced from REF.¹⁷¹, CC-BY-4.0. Part **b** is adapted with permission from REF.¹⁷²: Adams, D. K., Arellano, S. M. & Govenar, B., *Oceanography*, **25**, 1, 256–268, <https://doi.org/10.5670/oceanog.2012.24>. Parts **c** and **d** are reproduced with permission from REF.¹⁵⁴, Elsevier. Part **e** is reproduced with permission from REF.¹¹⁹, AAAS. Parts **f** and **g** are courtesy of C. German, Woods Hole Oceanographic Institution, USA.

Box 1 | Milestones and impacts of hydrothermal-vent discovery

In 1977, dense communities of novel and endemic animal species¹⁵⁶ were found thousands of metres below the ocean surface, in complete darkness, where photosynthesis could not possibly be the source of metabolic energy and organic carbon. This discovery of deep-sea hydrothermal-vent ecosystems^{114,157,158} changed our views of biology and ecology in several ways (see the figure). It was the first example of a rich animal ecosystem driven primarily by chemosynthesis. The energetic foundation of these dense communities of bizarre animal species was quickly identified: microorganisms couple the oxidation of reduced inorganic compounds in hydrothermal fluids to the fixation of carbon dioxide into organic carbon, which supports the rest of the food chain. Sulfur was first implicated as an energy source¹⁵⁹, and the implication of hydrogen, methane and iron as energy sources quickly followed¹⁶⁰. A second key biological insight was the mode of energy transfer between trophic levels; symbiosis, in which animals depend on symbiotic chemosynthetic bacteria, is a pervasive mechanism for transferring the geochemical energy from bacteria to animals^{69,161}.

Deep-sea hydrothermal vents also redefined the upper temperature limit for life on Earth¹⁶, yielded new resources for medicine and biotechnology¹⁶² and had an immediate and enduring impact on theories for the origin and evolution of life on Earth and beyond¹⁶³. They are an appealing cradle for the origin of life owing to their chemically reducing conditions, potential for abiotic synthesis of organic carbon, reactive surfaces for polymerization of macromolecules and location beneath the oceans, protected from violent impacts of meteorites and volcanism at the Earth's surface^{164–166}. Recent phylogenetic studies¹⁶⁷ and geological evidence¹⁶⁸ support hydrothermal vents as important habitats for the origin and early evolution of life. The biodiversity at deep-sea hydrothermal vents continues to yield surprises; archaea discovered in deep marine sediments influenced by hydrothermal activity display eukaryotic features, forcing reconsideration of the origin and evolution of eukaryotes and the topology of the tree of life¹⁶⁹.



limitation between vent fields that are separated by vast habitat-free distances shapes the global distribution of vent animals, it remains difficult to evaluate the role of isolation and dispersal limitation in shaping the biogeography of microorganisms owing to relatively sparse sampling across time and space. If anything, accumulating evidence supports the hypothesis that 'everything is everywhere and the environment selects'⁴. Finally, we consider the importance of ecological and biogeochemical interactions at vents and their impact on the broader ocean.

Vent habitats and microorganisms

Deep-sea hydrothermal-vent habitats are defined by physical, chemical and biological characteristics and occur along thermal and chemical gradients between anoxic, hydrothermal fluids and oxic, cold seawater^{3–7}. Mixing between these fluids occurs in various ways and at various scales, generating a diversity of habitats with gradients of temperature and chemistry, which strongly influences the organisms present and their metabolic activities. The main habitats are hydrothermal chimneys, the subsurface surrounding vents, animals at vents and hydrothermal plumes (FIG. 2).

Sampling deep-sea hydrothermal vents is challenging owing to their remote and inaccessible location. Thus, knowledge of these ecosystems is largely limited to snapshots, and their extensive spatial and temporal diversity is poorly studied^{8,9}. Further complicating efforts to synthesize data into understanding are biases and lack of standardization of methods. Finally, many of the organisms identified in vent habitats are uncultured,

which limits our knowledge of their metabolism and physiology⁷. Insights from cultivation continue to be invaluable⁹, but advances are too slow to close the widening gap between sequence-based and physiological or biochemical data.

Despite these challenges, advances in modelling, in situ biogeochemistry and omics approaches have enabled deeper studies of more samples, providing more complete pictures of the biology of deep-sea hydrothermal vents. Although the various habitats within vent fields are physically and ecologically connected (FIG. 2), their microbial communities are distinct^{10,11}, testifying to the importance of distinct environmental conditions and selective forces in each habitat. Biological communities within each habitat of deep-sea hydrothermal vents are shaped by both fluid chemistry and physical characteristics^{12,13}.

Opportunities and challenges. Fluid chemistry and physical characteristics present both opportunities and lethal challenges to hydrothermal-vent organisms. High temperature sets a hard limit on life owing to the biochemical constraints of membranes, proteins and nucleic acids¹⁴. The highest temperature at which microbial growth has been observed is 122 °C, a record set by deep-sea hydrothermal-vent archaea including *Methanopyrus kandleri*¹⁵ and strain 121, which is most closely related to *Pyrodicticum*¹⁶. Some hyperthermophiles use flagella to move towards heat sources, to avoid lethally high temperature and to adhere to chimney surfaces¹⁷. Temperature has a central role in determining 'who is where' along the thermal gradient between

Box 2 | Diversity and biogeography of deep-sea hydrothermal vents

Since their initial discovery over 40 years ago, deep-sea hydrothermal vents have now been found in a variety of settings around the world (FIG. 1). These vents are diverse in terms of their large-scale geological setting (mid-ocean ridges, back-arc spreading centres, hotspot volcanoes and seamounts), the host rock (for example, basalt versus ultramafic rock, such as peridotite) and the rate of seafloor spreading at which tectonic plates diverge (ultraslow to fast). These factors shape the chemical and physical aspects of microbial habitats^{7,9,18,170} (see the table, which presents a simplified summary of the relationships between these characteristics). The geological setting can be further modified by sediment cover⁵².

In turn, this newly recognized variety of geological settings for deep-sea hydrothermal vents has expanded our understanding of the range of different physical and geochemical conditions that support biological communities and the relationships between geochemistry and microbiology^{7,25}. Whereas sulfur oxidation is prevalent and often a dominant electron donor in basalt-hosted systems at fast-spreading ridges, hydrogen gas and methane are abundant constituents of hydrothermal fluids and key electron sources for microbial metabolism at ultramafic systems at slow and ultraslow spreading ridges.

Spreading rate	Host rock	Setting	Fluid chemistry
Fast to superfast	Mafic (high MgO and FeO and Si >45%)	Mid-ocean ridge-spreading centres	H ₂ S rich
Slow to ultraslow	Mafic and ultramafic (high MgO and FeO and Si <45%)	Mid-ocean ridge-spreading centres and ocean core complexes	H ₂ and CH ₄ rich (for ultramafic)
Various	Felsic, dacitic or andesitic (Si >65%)	Volcanic arcs at convergent plate boundaries	Low pH, H ₂ and CH ₄ , and metal rich

hot fluids and cold seawater because microorganisms are adapted to specific temperature ranges and have thermal-growth optima (FIG. 3), although they have strategies to survive fluctuating temperatures¹⁸. Pressure also presents challenges¹⁹ but is not a primary stressor at the depth of most deep-sea vents on mid-ocean ridges^{20,21}. Microorganisms inhabiting the deepest known hydrothermal vents at the Mid-Cayman Rise at nearly 5,000 m water depth must be adapted to high pressure, but the presence of species that are also found at shallower vents suggests that these pressure adaptations are encoded at fine taxonomic scales²².

Hydrothermal geochemistry also strongly influences the composition and metabolism of microbial communities along mixing gradients (FIG. 3); fluids emerging from vents carry reduced chemical species (for example, hydrogen sulfide, Fe²⁺, hydrogen gas and methane) that are electron sources for chemolithoautotrophic growth. The free energy available from each metabolic reaction can be estimated from the concentration of reactants and products and is a function of the chemical composition of the hydrothermal fluid, which depends on the geology of the local rock^{6,23–25} (BOX 2); the degree of mixing and dilution with seawater; and biotic and abiotic chemical reactions that modify water chemistry along the water flow path^{26,27}. Although there are still relatively few comparisons of such predictions to empirical data, such estimates of free energy generally match well with the abundance of metabolic pathways observed through metagenomic and metatranscriptomic methods^{3,12,22,28}. However, the biomass of microorganisms that are capable of each type of metabolism does not necessarily correlate well with observed concentrations

of substrates for energy metabolism at a given point in space and time owing to consumption of chemicals by microorganisms, limiting reactants and/or nutrients and kinetic limitations¹³.

Pathways for carbon fixation are also distributed according to geochemistry and temperature²⁹. The energy-efficient yet oxygen-sensitive reductive tricarboxylic acid cycle (rTCA), which runs the TCA cycle in reverse by substituting three key enzymes, often predominates at 20–90 °C, where oxygen levels are sufficiently low (yet potentially high enough to support microaerobic growth with oxygen as an electron acceptor). The TCA cycle can be run in reverse via bidirectional enzymes (as opposed to specific rTCA cycle enzymes), and the directionality (heterotrophic versus autotrophic) likely depends on environmental conditions³⁰. The energetically costly yet oxygen-tolerant Calvin–Benson–Bassham cycle predominates at temperatures <20 °C. Above 90 °C, most growing microorganisms are hyperthermophilic archaea that perform methanogenesis or sulfate reduction using the Wood–Ljungdahl pathway and the dicarboxylate–4-hydroxybutyrate pathway for carbon fixation, respectively²⁹.

Vent fluids range from acidic to highly alkaline, not only demanding capacity for pH homeostasis but also shaping the availability of dissolved inorganic carbon (concentrations are higher at lower pH), which is required in excess for the rapid chemoautotrophic growth exhibited by bacteria–animal consortia such as the giant tubeworm *Riftia pachyptila*³¹. Hot, acidic fluids often hold sufficient carbon dioxide, which is obtained directly by animals³¹, whereas carbon dioxide may be limiting in cold, neutral or basic fluids³², thus requiring mechanisms for carbon uptake and concentration³³. Hydrothermal fluids also contain several toxic compounds, such as heavy metals (copper, cadmium and lead) and hydrogen sulfide, that require specific adaptations^{6,9}.

Owing to rapid cooling and dynamic chemistry, the temporal and spatial window in which microorganisms can exploit their preferred physical and chemical niches may be narrow. This situation is particularly challenging for free-living organisms that are carried along in fluids in the subsurface, diffuse flow and in rising plumes^{12,13,28}. Some organisms maintain their position in the thermochemical gradient by attaching to surfaces as biofilms^{9,18} or finding refuge within animal hosts, although even here temperature and chemistry fluctuate substantially³⁴. Adaptations to such dynamic conditions include motility and metabolic versatility, which provide the ability to find preferred environments and to use multiple electron acceptors, such as oxygen, nitrate and sulfur^{18,35}.

Hydrothermal chimneys. At areas of hot, focused venting, hydrothermal fluids (up to at least 407 °C (REF.³⁶) and perhaps near 500 °C (REF.³⁷) mix with seawater (2–4 °C) over short spatial scales of just a few centimetres⁶. Minerals precipitate and often deposit structures such as chimneys. The temperature and chemistry of these vent fluids and mineral deposits depend on the temperature and geology of the local rock, duration of water–rock reactions and degree of subsequent mixing with cooler

Chemolithoautotrophic growth

The growth of bacteria or archaea using an inorganic, chemical source of energy (for example, reduced forms of iron, sulfur, hydrogen and ammonia) to fix inorganic carbon into organic carbon.

Reductive tricarboxylic acid cycle

(rTCA). A metabolic pathway for carbon fixation in which two molecules of carbon dioxide are converted into acetyl coenzyme A; it uses most of the same enzymes as the oxidative tricarboxylic acid cycle but runs it in reverse by using three alternative enzymes: fumarate reductase, 2-oxoglutarate synthase and ATP citrate lyase.

Calvin–Benson–Bassham cycle

A carbon fixation pathway in which carbon dioxide is converted into glyceraldehyde-3-phosphate using the key enzyme Rubisco.

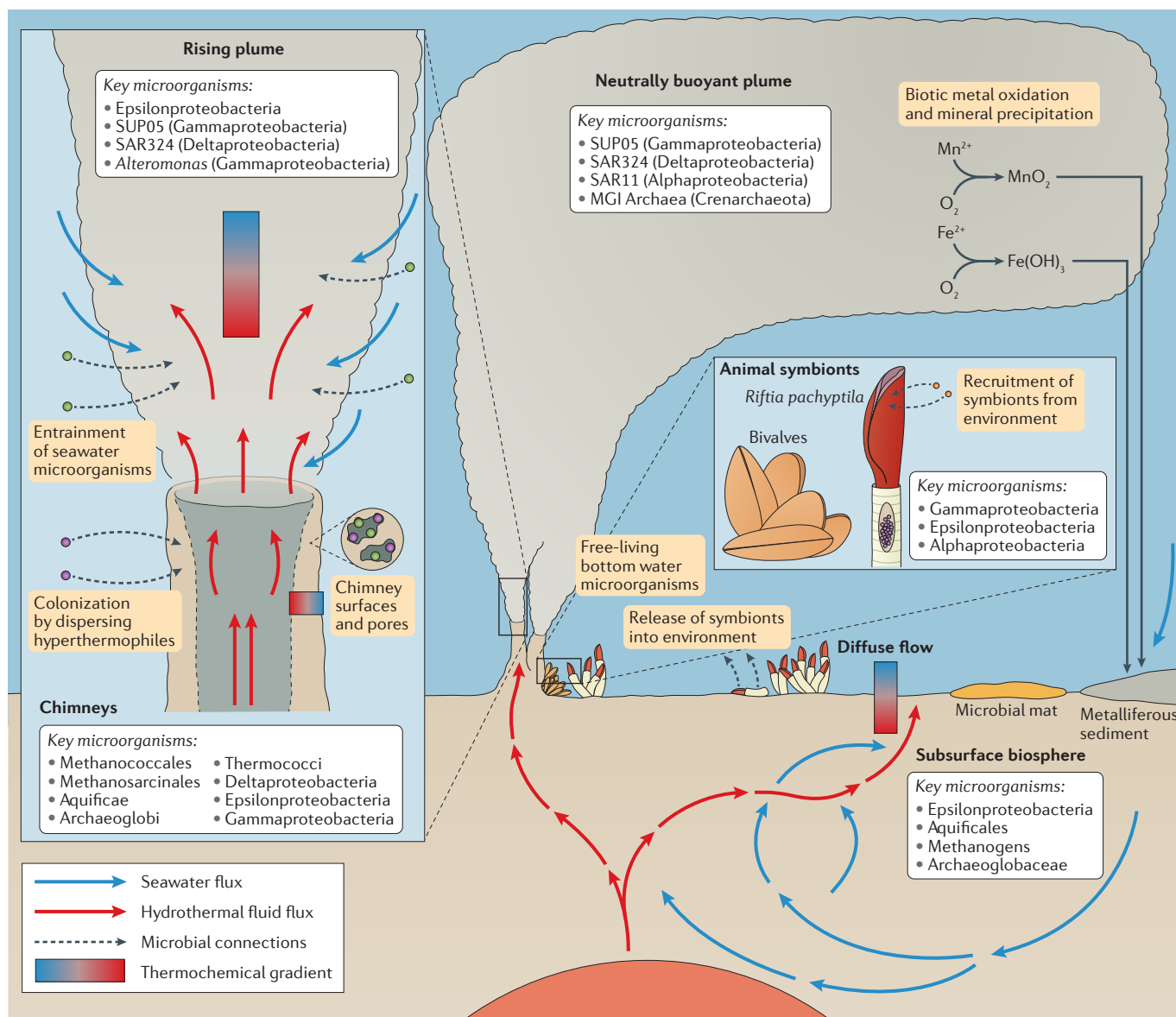


Fig. 2 | Microbial habitats at deep-sea hydrothermal vents. The main habitats at hydrothermal vents are chimneys, the surrounding subsurface, animals and rising plumes. Hydrothermal fluids move between habitats and mix with cold seawater. Key microorganisms for each habitat represent abundant taxa observed across multiple vent fields by various cultivation-independent approaches. The red–blue rectangle indicates a thermochemical gradient between anoxic, chemically reducing, hot hydrothermal fluids and oxic, cold seawater and is detailed further in FIG. 3. Note that this illustration is generalized, not comprehensive, and it does not represent any particular vent field.

fluids in the subsurface. This results in a variety of vent types and fluids (black smokers, white smokers and alkaline and carbonate vents), mineral deposits (sulfides and carbonates) and vent structures (for example, chimneys, beehives, flanges and mounds)⁷. Thermophiles and hyperthermophiles thrive on the surfaces and within pore spaces of these mineral deposits³⁸ (FIG. 2). Hot fluids lack oxygen, and thus the energy metabolisms of organisms in the near-vent environment are typically anaerobic and lithoautotrophic. However, fluid mixing and thus the transition to microaerobic and aerobic processes occur over short spatial scales³⁹.

The steep thermal and chemical gradients at active hydrothermal chimneys create a diversity of niches^{5,25}.

Dominant organisms include thermophiles and hyperthermophiles from Methanococcales, Methanosarcinales, Aquificae, Archaeoglobi, Thermococci, Deltaproteobacteria, Epsilonproteobacteria and Gammaproteobacteria^{7,22,25,40,41} (FIG. 2). Ultramafic-hosted chimneys harbour anaerobic methanotrophic archaea³² and hydrogen-gas-oxidizing Betaproteobacteria and Clostridiales⁴². Microbial colonization of freshly formed hydrothermal structures such as chimneys remains poorly understood but presumably involves hyperthermophiles that can disperse in cold seawater⁴³. This scenario is supported by observations that hyperthermophiles are present in cold plumes⁴⁴ and that endemic vent taxa can be found in ambient seawater⁴⁵.

Wood–Ljungdahl pathway
A metabolic pathway for carbon fixation in which two molecules of carbon dioxide are converted into acetyl coenzyme A by the key enzyme carbon monoxide dehydrogenase–acetyl coenzyme A synthase.

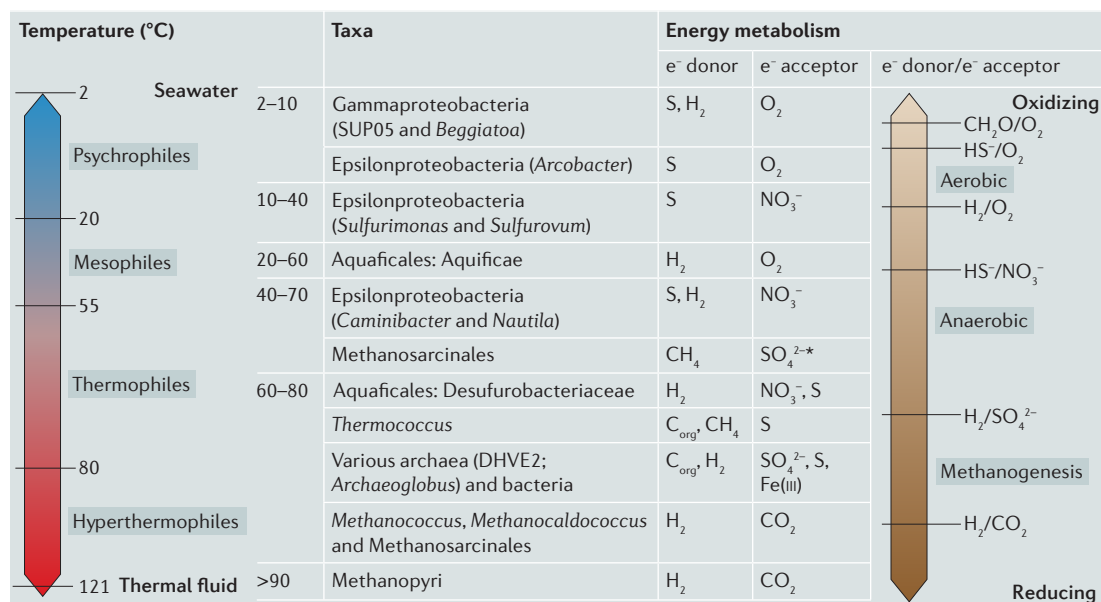


Fig. 3 | **Generalized characteristics of vents.** The figure presents a simplified view of how temperature and quantitatively dominant taxa and metabolisms vary across the chemical and thermal gradient from hydrothermal fluids to seawater. These characteristics are generalized for all vent habitats (see FIG. 2) and do not represent any particular vent location. Temperature zones on the left panel are coarse and encompass a wide range of taxa, whereas the thermal-growth ranges for particular families and genera are shown in the middle panel. See Nakagawa and Takai¹⁷³ and Sievert and Vetriani⁹ for details on particular species. *Sulfate reduction is carried out by syntrophic partners.

Dicarboxylate–4-hydroxybutyrate pathway

A recently described carbon fixation pathway in archaea in which a molecule of bicarbonate (HCO₃⁻) is fixed onto acetyl coenzyme A via a combination of enzymes from the reductive tricarboxylic acid cycle and the 4-hydroxybutyrate part of the 3-hydroxypropionate–4-hydroxybutyrate cycle.

Black smokers

Hydrothermal vents that eject plumes of black suspended particles, chiefly iron sulfide minerals.

White smokers

Hydrothermal vents that eject plumes of white suspended mineral particles composed mainly of calcium, barium and silica.

Ultramafic

Relating to igneous rocks that have a very low silica content and very high content of magnesium and iron.

Denitrifying

A type of process in which nitrate is used as an electron acceptor for energy metabolism and is reduced to di-nitrogen gas (denitrification).

Although hyperthermophiles such as *Thermococcus* spp. require high temperatures for growth, they can survive for months in cold conditions and then quickly respond when the temperature increases¹⁷.

Subseafloor and diffuse flow. Mixing of hydrothermal fluids and seawater also occurs below the sea floor, over much larger distances, as seawater circulates through the ocean crust on the flanks of the mid-ocean ridge system⁴⁶ (FIG. 2). This subsurface water constitutes the largest aquifer system on Earth. Porous subseafloor basalts and chemical and thermal gradients between the hydrothermal fields on spreading centres and the cool ocean crust on ridge flanks (hundreds of kilometres away) provide vast habitats, nutrients and energy sources for microorganisms^{10,47,48}. The recognition that these subseafloor communities are biologically diverse, metabolically active and important for deep-ocean biogeochemistry was a major advance^{10,49–53}.

Subsurface habitats near active hydrothermal vents host regions of hot, anoxic hydrothermal fluids that mix to varying extents with cold, oxic seawater, producing different thermal and metabolic zones⁵⁴ (FIG. 2). The associated microbial communities are highly productive and diverse⁵⁵ and can be accessed via diffuse flow⁴⁷. Dominant groups in diffuse flow and subsurface fluids include Epsilon proteobacteria and Aquificales, which use mainly sulfur and hydrogen gas as electron donors and elemental sulfur and nitrate as electron acceptors for lithotrophic growth^{5,9,13,22,54,56,57}, as well as methanogens and heterotrophs^{7,22}. Anaerobic oxidation of methane is favourable in ultramafic habitats^{22,24} and hydrothermal sediments⁷. Members of the Archaeoglobaceae, which are sulfur reducers that can use hydrogen gas and/or

organic carbon⁵⁸, are among the most abundant archaea in diffuse flow²².

Warm subsurface fluids (from near ambient temperature up to ~100 °C) re-emerge from the sea floor at diffuse-flow vents, which provide windows into the subseafloor biosphere^{47,59}. Further, as these diffuse flows mix with oxygenated bottom water, they provide habitats for aerobic and denitrifying chemolithoautotrophic organisms, including dense microbial mats⁴⁷ and animal symbionts. Microbial mats and mineral flocs in the subsurface or at the sea floor are composed of Methanococcales, Gamma proteobacteria and Epsilon proteobacteria, especially filamentous sulfur-oxidizing bacteria such as *Beggiatoa* and *Arcobacter*^{60–64}, or Zetaproteobacteria in Fe(II)-rich fluids⁶⁵. The relative importance of diffuse versus high-temperature flow varies from field to field, but diffuse flow may account for the majority of heat flux⁴⁷.

Symbioses with animals

Vent animals, mainly tubeworms, shrimp, crabs, bivalves and snails, are excluded from high-temperature zones because they are unable to tolerate sustained temperatures above 55 °C (REF. 66,67); they thrive in lower temperature habitats either on the periphery of high-temperature zones or in diffuse flow. Many vent animals depend on chemosynthetic symbiotic bacteria as a source of energy and organic carbon, which is produced by the bacterial coupling of vent-derived electron donors with seawater-derived electron acceptors via lithoautotrophic metabolism⁶⁸. Thus, these animals must deal with a trade-off between obtaining reducing chemicals (mainly sulfide, hydrogen gas and methane) from hydrothermal fluids for their chemosynthetic symbionts while facing physiological challenges ranging from

thermal stress to low-oxygen levels and high levels of toxic sulfide and heavy metals⁶⁹. The microbial symbionts benefit from a relatively stable habitat at the interface of electron donors and acceptors for energy metabolism and, in return, provide organic carbon to their animal hosts⁷⁰. Symbiont physiology can be somewhat flexible in order to adapt to the local environment⁷¹.

Symbiotic bacteria are selected not only by the physical and chemical characteristics of the vent environment but also by their animal hosts, which themselves have adaptations to their symbionts and the environment⁷² and display strong biogeography^{1,73}. Across their various hosts, symbionts occupy different animal tissues ranging from specialized organs such as the trophosome of tubeworms, gills of bivalves and oesophageal glands of gastropods to the external surfaces of shrimp, crabs and mollusks⁶⁸. Endosymbionts are typically Gammaproteobacteria and use either sulfur or methane as energy sources, but in some cases, they are Alphaproteobacteria or Epsilonproteobacteria^{74,75}. Symbionts can also use hydrogen gas as an energy source, and the common occurrence of hydrogenase genes suggests that this capability is widespread among hydrothermal-vent symbionts^{76,77}. Endosymbionts can switch between different carbon fixation pathways^{77,78} and even between autotrophy and heterotrophy⁷⁹. This mixotrophy may be an adaptation to changing conditions and/or a free-living life stage and may help explain why symbionts appear to be abundant in the environment⁸⁰.

Animals are highly selective of their lineages of endosymbionts^{68,81}. When multiple lineages are present within one host, they may use different energy sources⁸², and these lineages can change with geography and geochemistry⁸³. Even within a single animal genus, there are systematically varying host-symbiont associations, with symbionts being shaped by both environmental chemistry and host phylogeny⁸⁴. Reciprocally, symbionts may mediate how their animal hosts interact with their environments^{75,84}. Endosymbiosis appears to have evolved convergently multiple times⁷⁴.

Although chemosynthesis-based transfer of energy from endosymbiotic bacteria to animals was the first and most spectacular example of symbiotic relationships, subsequent discoveries revealed diverse symbiotic relationships and functions⁸⁵. Bacteria colonizing external animal surfaces (epibionts) are cultivated and harvested by their hosts as sources of carbon and energy^{86,87}. Epibionts on the foot of gastropods are also involved in deposition of mineralized scales, presumably as a protective armor⁸⁸. In other cases, symbionts may produce natural products to protect their hosts from parasites⁸⁹.

Hydrothermal plumes. Hot hydrothermal fluids mix with seawater, forming hydrothermal plumes, which rise up to hundreds of metres off the sea floor and disperse thousands of kilometres off the ridge axis. Plumes provide a habitat for lithotrophs^{90–92} that have key roles in determining the fate and impact of hydrothermal inputs into the oceans^{11,93,94}. Although hydrothermal fluids are highly diluted in plumes (~1:10,000), concentrations of reduced chemicals remain sufficient to support the considerable lithotrophic growth that may have substantial

impacts on broader deep-sea microbial communities and biogeochemistry²⁸. Plumes also function as vectors for dispersing vent microorganisms and animal larvae throughout the deep oceans⁹⁵.

Hydrothermal plumes undergo rapid cooling and geochemical changes during the turbulent mixing between hydrothermal fluids and seawater, making for a dynamic habitat^{11,28} (FIG. 2). The distribution and source of microbial communities within plumes, especially the rising portion, were long elusive owing to sampling challenges that were resolved by recent technological advances⁹⁶. Plumes are composed primarily of organisms derived from the water column, such as SUP05 (Gammaproteobacteria), SAR324 (Deltaproteobacteria), SAR11 (Alphaproteobacteria) and Marine Group I archaea^{97–99}. Sea floor and/or subsurface organisms such as Epsilonproteobacteria can be present in plumes^{98,99} but are quickly diluted owing to the massive entrainment of background seawater²⁸. Microorganisms spend just a few hours in the rising portion of the plume; thus, the vast majority of growth takes place in the horizontally dispersing, neutrally buoyant (nonrising) plume, and depletion of electron donors for lithotrophy leads to a spatio-temporal succession over the course of weeks and across tens of kilometres^{28,100}. Voluminous ‘megaplumes’ resulting from seafloor eruptions are an exception to the above principles, as they contain abundant microorganisms from seafloor and subseafloor habitats^{6,44,101}.

Connections between vent habitats. Vent habitats are physically connected to each other, with transfer of water, chemicals and organisms between them, enabling migration between habitats (FIG. 2). Indeed, some taxonomic groups occur in multiple habitats; mussel symbionts are closely related to free-living populations (including the SUP05 group)⁷⁴. Direct release of heavy loads of endosymbiotic bacteria from dead animals into the surrounding environment can enrich free-living populations with endosymbionts that are available to colonize new hosts¹⁰². However, closer examination often reveals that close relatives in different habitats are distinct species or strains with traits that reflect their different niches, as exemplified by the presence of distinct *Thermococcus* strains on chimneys versus diffuse flow¹⁰³. Although physiological and highly resolved genetic data are not yet sufficient to draw universal conclusions, results to date indicate that high similarity in organisms between different habitats within a vent field is often due to evolutionary linkages rather than direct migration between habitats. Phylogenetic studies suggest that symbiosis has evolved multiple times in multiple bacterial lineages⁷⁴.

Biogeography of vent communities

Local scales (within a single vent field). Different vents within the same vent field often have different microbial communities^{13,104–107}. The rich body of data now available provides a foundation to determine factors that shape the composition of these microbial communities. As described above, temperature is an important determinant of the distribution of organisms at vents. For example, many members of the Epsilonproteobacteria and Aquificales use the same electron donors (hydrogen gas and different

Mineral flocs

Flocculent materials sometimes emitted from hydrothermal vents, composed of fine mineral particles and often microbial biomass.

Trophosome

An internal organ in tubeworms used to host chemosynthetic symbiotic bacteria.

Autotrophy

The growth of an organism through the fixation of inorganic carbon into organic carbon.

Heterotrophy

A mode of organism growth in which exogenous organic carbon functions as the source of carbon.

Allopatric speciation

The evolutionary divergence of a population into distinct species due to geographic separation.

Thermohaline conveyor

The global circulation of water in the oceans, driven by density gradients due to differences in the temperature and salinity of water masses.

forms of sulfur) and acceptors (nitrate and oxygen), but they are adapted to different temperatures⁹ (FIG. 3).

Variation in fluid chemistry, which defines the energy available to lithotrophs, has emerged as another key control. It varies according not only to the chemistry of nascent hydrothermal fluids but also to the physical aspects such as fluid flow rate and residence time, degree of mixing, the chemical form and bioavailability of chemical compounds¹⁰⁸ and the physical forms of vents^{13,109}. For example, within Axial Seamount, diffuse-flow microbial communities at individual vent sites are both taxonomically and functionally distinct from one another owing to local seafloor geochemical and physical characteristics¹³. On one hand, in this and other diverse hydrothermal-vent ecosystems, the availability of hydrogen gas, an energy-rich electron donor for microbial metabolism, has a key role in structuring microbial communities^{22,24,41,42,110,111}. On the other hand, hydrogen sulfide, which is abundantly used as an electron donor, is not usually limiting, and thus, variation in its concentration may not often limit the abundance of sulfur-oxidizing microorganisms³.

At finer taxonomic scales, niches are partitioned on the basis of the concentration of substrates for energy metabolism. The distribution of sulfur oxidizing Epsilonproteobacteria, *Sulfurovum* and *Sulfurimonas*, is determined by the concentrations of sulfur and oxygen¹¹². Members of the SUP05 group of Gammaproteobacteria occupy yet another niche at even lower oxygen and sulfur levels. Two groups of Aquificales differ in their tolerance of oxygen¹³. Thus, variation in temperature and the concentration of electron donors and acceptors are likely responsible for the diversity of bacterial families, genera, species and genotypes within species²². This likely explains, in part, the functional redundancy observed within plume communities, which receive microorganisms from multiple habitats¹². By analogy to environmental drivers that shape the diversity of photosynthetic organisms such as *Prochlorococcus*¹¹³, we can expect that deeper lineages share adaptations to physical and chemical conditions (for example, in temperature optima and central energy metabolism), whereas viral predation and grazing pressure promote diversity at finer scales. However, temperature may also differentiate closely related organisms, as suggested for SUP05 (REF.¹³). Finally, as in other ecosystems, the degree of environmental variability likely influences the richness of vent microbial communities¹¹².

Early descriptions of vent fauna interpreted differences in biological communities between vents as different successional stages¹¹⁴. Indeed, succession and other temporal effects have been shown to function alongside geochemical and physical forces in shaping microbial-community composition¹⁸. Destruction of extant communities and formation of new fields lead to colonization and ecological succession⁶. Microbial communities on rock surfaces change over time, for example, as basalts are altered^{50,115} and when venting ceases^{100,116}. However, the year-to-year temporal consistency observed in diffuse flows of Axial Seamount¹³ suggests that vent microbial communities can stabilize on intermediate timescales.

Global-scale biogeography. Deep-sea hydrothermal-vent provinces around the world have strikingly different fauna^{1,73}. This large-scale biogeography of animals is due, in part, to limited dispersal of larvae, resulting in isolated populations and allopatric speciation. The composition of microbial communities also varies across large scales between vent fields, especially between vents of different types and ridge-spreading rates^{6,18,40}. The substantial distances (~100 km) and differences between microbial populations and communities of different vent fields and the apparent endemism of some vent taxa^{9,35,106} have been taken as evidence that geographic isolation and limited dispersal also shape microbial populations and communities at vents¹¹⁷. Indeed, extensive evidence supports the existence of biogeographic patterns of microorganisms, and these patterns are thought to be governed by the same processes (selection, drift, dispersal and mutation) that shape the biogeography of larger organisms¹¹⁸. However, the relative importance of these factors in shaping microbial biogeography, both in general and specifically at deep-sea hydrothermal vents, remains unclear.

Available evidence suggests a strong role for the selection in shaping microbial biogeography at deep-sea vents. As in vents within the same site, physical and geochemical characteristics drive differences between microbial communities across vent sites^{8,22,27,32,41,110,119}. The role of geochemistry in shaping microbial communities is particularly noticeable when comparing sites with different host rock geology. Sulfur oxidation and hydrogen oxidation are prevalent in nearly all hydrothermal systems, but sulfur oxidation is generally more important at basalt-hosted systems. Methanogenesis and oxidation of hydrogen gas and methane are often more prevalent at ultramafic systems owing to the availability of carbon dioxide³² and the production of hydrogen gas and methane during hydrothermal reactions with rocks such as peridotite^{6,18,111,120,121}. Mineralogy also has a direct role in shaping chimney communities¹²¹. Finally, variation in water column seawater chemistry (for example, pH) in different settings and along the thermohaline conveyor also affects microbially mediated biogeochemical reactions^{122,123} and thus may influence microbial-community composition.

Few studies have attempted to directly quantify the relative importance of environmental selection versus geographic distance in shaping microbial biogeography at vents. At both the levels of whole microbial-community composition and within species, patterns of biogeography have been found to correlate more strongly with geographic distance than with environmental factors^{106,117,124,125}. However, given the challenge of exhaustively measuring and testing all environmental factors that could contribute, the role of selective forces is often underestimated¹¹⁸.

The case for geographic isolation and limited dispersal having a primary role in shaping microbial communities is weakened by several recent findings. First, microorganisms thought to be endemic to vents are present in ambient deep seawater, suggesting the presence of a 'seed bank' of microorganisms that are transported between distant vent sites via thermohaline circulation⁴⁵.

Second, closely related organisms have been found at vents across ocean basins^{12,13} and even in different ocean basins²². A critical question regarding the close relationships of these organisms from distant vents as well as those found at whale falls⁷, at other nonvent environments¹¹ and in background seawater⁴⁵ is whether they reflect current ecological connectivity (for example, migration of organisms between sites) or merely shared evolutionary ancestry; even organisms that share >99% sequence identity of 16S rRNA genes may have a common ancestor millions of years in the past¹²⁶. Questions regarding the viability and functional equivalence of purported vent microorganisms in the open ocean also remain open¹²⁷.

Disentangling the relative strengths of the different forces shaping microbial biogeography at vents will require deeper sampling, quantitative methods that are rooted in ecological theory and the use of genetic markers that are more sensitive¹²⁸ and more suitable for detecting the neutral genetical variation associated with drift than are 16S rRNA genes¹⁸. We should also keep in mind that different organisms display different biogeographic patterns and may have different dispersal capabilities and drivers of biogeography¹²⁵. If evidence emerging from multiple independent approaches continues to converge on the conclusion that geographic distance is not a primary determinant of microbial-community assembly at deep-sea hydrothermal vents, it would be consistent with results from other microbial ecosystems indicating that selection has a stronger influence than dispersal limitation¹¹⁸. The strong environmental gradients between deep-sea hydrothermal vents and their geographic separation at various scales provide valuable opportunities for studying microbial biogeography and how it compares with that of animals.

Wider interactions

Metabolic and ecological interactions. The microbial portion of the food web at deep-sea hydrothermal vents remains poorly characterized, but the framework for how carbon and nutrients flow and how microorganisms fit into the broader food web is now apparent¹²⁹ (FIG. 4). Lithoautotrophs fix inorganic carbon into biomass, which can then be released through cell death and/or viral lysis or transferred directly into the food web via protists, zooplankton and filter-feeding or mineral-grazing invertebrates^{7,86}. This biomass may also contribute to the pool of dissolved organic matter, thus fuelling heterotrophic bacterial production¹³⁰. Animals also harvest organic carbon from their symbionts and take up and release partially oxidized sulfur compounds such as thiosulfate and polysulfides, which can be used by other microorganisms and/or animals¹³¹.

The enrichment of viruses in deep-sea hydrothermal vents^{132,133} compared with surrounding seawater suggests that viruses exert a strong influence on microbial vent communities and biogeochemical cycles, similar to their role in the broader oceans^{134,135}. The limited data available suggest that temperate, lysogenic phages are favoured in diffuse flow, where they may enhance host fitness and mediate horizontal gene transfer¹³⁶. In hydrothermal plumes, viruses have been found to carry genes

for oxidation of elemental sulfur, suggesting a direct role in the biogeochemistry and horizontal transfer of genes that are central to energy metabolism¹³⁷. Evidence for viral participation in a wide variety of different pathways through such auxiliary metabolic genes¹³⁵ has also been shown in hydrothermal sediments¹³⁸.

The broader impact of vent microbiology on biogeochemistry. Deep-sea hydrothermal ecosystems have an impact on the broader oceans that reaches far beyond the regions immediately surrounding vent fields. Hydrothermal fluids contain elements such as iron and manganese at concentrations up to a million times that of background seawater. In vent fields around the world, this 'tap' is always on; thus, vents are a substantial source of oceanic iron and manganese^{139,140}. These elements can be dispersed on an ocean-basin scale¹⁴¹, aided by microbial production of organic chelators including siderophores that solubilize metals^{94,142} (FIG. 4). Microorganisms can also influence the fate of hydrothermal elements by catalysing the formation of particulate iron and manganese minerals through enzymatic oxidation or cell surface catalysis^{93,143} (FIG. 4). These chemically reactive minerals participate in scavenging reactions that are a substantial sink for biologically critical elements such as phosphorous^{144,145}. Because a volume of water equal to that of the entire ocean cycles through hydrothermal plumes on timescales (2.4×10^5 years) comparable to residence times of critical micronutrients such as phosphorus and vanadium, plumes and their associated microorganisms and biogenic minerals function as chemical filters for the global oceans¹⁴⁶. Similarly, microbial biogeochemistry in the igneous subsurface, where there are large fluid fluxes, substantially affects marine biogeochemical cycles^{51,147}.

Interactions with ecosystems surrounding deep-sea vents also extend to trophic interactions and exports of microorganisms and larvae⁹⁵. Microbial growth in hydrothermal plumes occurs tens of kilometres away from the vent source, and these lithotrophy-enriched communities are likely transported for at least hundreds of kilometres²⁸. Given the availability of electron donors for lithotrophy in marine particles^{148,149}, oxygen minimum zones and oil spills and that microbial communities found in these habitats have similarities to hydrothermal plumes¹¹, there may be interactions between vent and nonvent communities²⁸.

Conclusions

Since the startling discovery of deep-sea hydrothermal vents four decades ago, their microbiology has been a frontier for fruitful exploration, discovery and research. These ventures have transformed our views of ecology and the origin and evolution of life and have yielded valuable products for biotechnology. Combined microbiological and geochemical studies have revealed the energy sources that fuel these chemosynthetic ecosystems and the microbial players and pathways that harness them. Although these microorganisms are distributed globally in the same geography and spatial isolation that strongly impact animal communities, growing evidence suggests that microbiomes of deep-sea hydrothermal

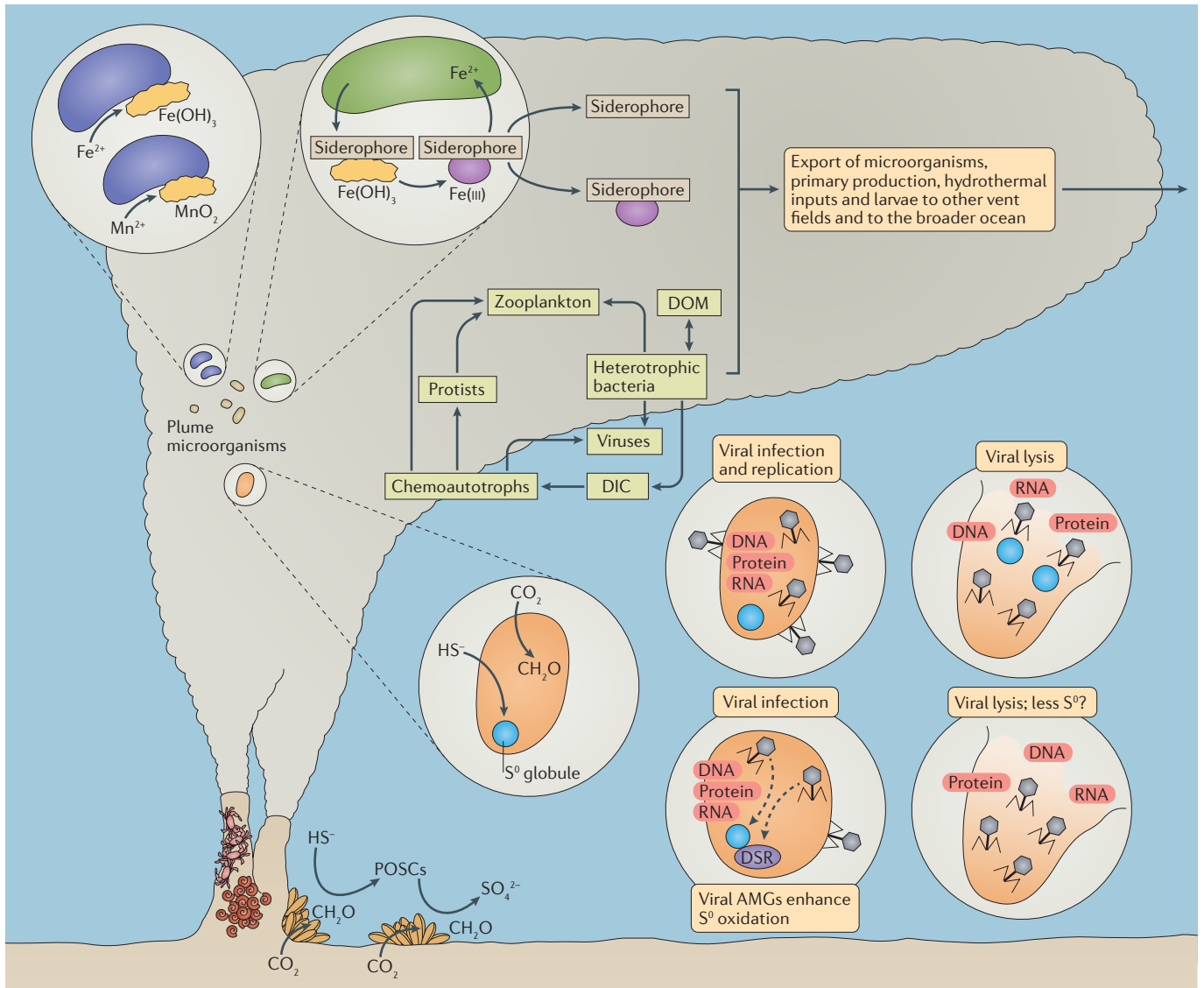


Fig. 4 | Ecological and biogeochemical interactions at deep-sea hydrothermal vents from a microbial perspective. Primary production by chemolithoautotrophy occurs in free-living planktonic microorganisms, microbial mats (not shown) and symbionts of animals, which can release and utilize partially oxidized sulfur compounds (POSCs). Iron and manganese-oxidizing microorganisms catalyse the precipitation of iron and manganese oxide minerals, which may sink and contribute to metalliferous sediments, whereas siderophore-producing microorganisms may solubilize and enhance the mobility of hydrothermal metals such as iron. AMGs, auxiliary metabolic genes; DIC, dissolved inorganic carbon; DOM, dissolved organic matter; DSR, dissimilatory sulfite reductase. The summary of trophic interactions is based on information in Bennett et al.¹³⁰.

vents are largely shaped by local geochemical, physical and geological conditions. More quantitative studies that incorporate ecological theory and leverage high-resolution genetic data are required to determine the relative importance of environmental selection versus dispersal limitation in structuring hydrothermal-vent microbial communities.

Deep-sea hydrothermal vents are difficult to sample and study, but technological innovations are enabling a new wave of experiments and monitoring. The integration of different approaches, including culture-dependent and culture-independent tools, geochemical rate measurements¹⁴⁷ and molecular methods, provides great promise⁹. As in the research of other microbiomes,

the gap between rapidly accumulating sequences of macromolecules (DNA, RNA and protein) and knowledge about physiological, ecological and biogeochemical functions continues to widen and to inhibit scientific progress². Thus, high-throughput methods to link sequence to function will be critical. Modelling provides a path to synthesizing diverse data streams and testing our understanding of vent ecosystems. Modelling has long been used for the study of energetics of vent ecosystems and has demonstrated its value as a theoretical and quantitative framework for understanding microbial-geochemical interactions and as a window into inaccessible environments. Thanks to the advent of models that quantitatively integrate microbial biogeochemistry

with the growing volume of genetic data^{28,150–152}, exciting opportunities abound.

We are only just beginning to understand the intricate relationships between different hydrothermal-vent organisms, their interactions with the chemical and physical environment and the links and impacts of vent ecosystems on the broader system of Earth. However, it is clear that hydrothermal-vent biomes have a role in global biogeochemistry and have much to teach us as

we seek to uncover the principles of microbial ecology and look towards potentially habitable worlds beyond our own. These spectacular ecosystems are now threatened by human activities¹⁵³ such as deep-sea mining; thus, research and exploration of deep-sea hydrothermal vents take on new urgency in light of the need for science-driven conservation and restoration^{1,154,155}.

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