The role of microbial motility and chemotaxis in symbiosis

Jean-Baptiste Raina[1]*, *Vicente Fernandez*[2], *Bennett Lambert*[2], *Roman Stocker*[2] and *Justin R. Seymour*[1]

Abstract | Many symbiotic relationships rely on the acquisition of microbial partners from the environment. However, the mechanisms by which microbial symbionts find and colonize their hosts are often unknown. We propose that the acquisition of environmental symbionts often necessitates active migration and colonization by the symbionts through motility and chemotaxis. The pivotal role of these behaviours in the onset and maintenance of symbiotic interactions is well established in a small number of model systems but remains largely overlooked for the many symbioses that involve the recruitment of microbial partners from the environment. In this Review, we highlight when, where and how chemotaxis and motility can enable symbiont recruitment and propose that these symbiont behaviours are important across a wide range of hosts and environments.

Chemotaxis
The ability of microorganisms to sense chemical gradients and direct their movement either up the gradient towards the source (attraction) or down the gradient away from the source (repulsion).

Symbiotic interactions are ubiquitous across all ecosystems and have played a profound role in shaping the evolution of life on Earth[1]. The acquisition of microbial symbionts enables host organisms to expand their metabolic capabilities, inhabit otherwise hostile environments and carve new ecological niches, which ultimately promotes species diversity[1,2]. The rise of eukaryotes and their extraordinary expansion[3] have been supported by their capacity to repeatedly harness the metabolic contributions of microbial partners. The very structure of eukaryotic cells contains the relicts of primordial bacterial symbionts — mitochondria and chloroplasts — that are now integrated as organelles[4]. Most currently living taxa rely on symbiotic relationships with microorganisms[1,5], and the perpetuation of these relationships relies on the transmission of symbionts between host generations. Despite the evolutionary and ecological importance of symbiotic partnerships, our understanding of the transmission of microbial symbionts between hosts is limited, and detailed knowledge is restricted to a small number of model systems[6].

As little as 20 years ago, prevailing theory suggested that beneficial symbionts were transmitted only directly to the next generation (vertical transmission), whereas acquisition of symbionts from the environment (horizontal transmission) was considered ineffective[5,7–14]. It is now clear that many mutually beneficial and ecologically important symbiotic relationships in fact rely on the acquisition of microbial partners from the environment, including the partnerships between microbial symbionts and host corals[15], tube worms[16], squid[17], mussels[18], legumes[19], insects[20], protists[21] and phytoplankton[22]. However, for many of these symbioses, the mechanisms by which microbial symbionts find and ultimately colonize their hosts remain unknown.

Given the massive diversity of microorganisms in the environment, the likelihood that specific microbial symbionts are recruited by chance is very low. Furthermore, following initial recruitment, symbionts must frequently undertake complex internal journeys to reach specific cellular compartments or housing organs[6]. We propose that the acquisition of microbial symbionts from the environment can often be achieved through only the involvement of active microbial behaviours. One such behaviour is chemotaxis, that is, the ability to direct active movement towards or away from specific chemical sources. Chemotaxis enables motile microorganisms to locate and colonize a symbiotic partner by homing in on specific signal molecules produced by the host. Whereas the pivotal role of chemotaxis in the onset and maintenance of symbiotic interactions is well established in a few specific model systems[23–27] (FIG. 1) and is key to enable many pathogen infections[28] (BOX 1), the importance of this behaviour has been largely overlooked in most symbiotic partnerships.

The capacity of environmentally acquired symbionts to use chemotaxis and motility can often be inferred from their genomes. Microbial motility and chemotaxis typically go hand-in-hand, as the ability to sense gradients is of limited use when a microorganism has no agency over its position within a chemical field. Genes encoding factors required for chemotaxis and motility are usually lost in vertically transmitted symbionts owing to the lack of selective pressure on

[1]*Climate Change Cluster (C3), University of Technology Sydney, Sydney, Australia.*
[2]*Institute of Environmental Engineering, Department of Civil, Environmental and Geomatic Engineering, ETH Zurich, Zurich, Switzerland.*
**e-mail: Jean-Baptiste.Raina@uts.edu.au*

https://doi.org/10.1038/s41579-019-0182-9

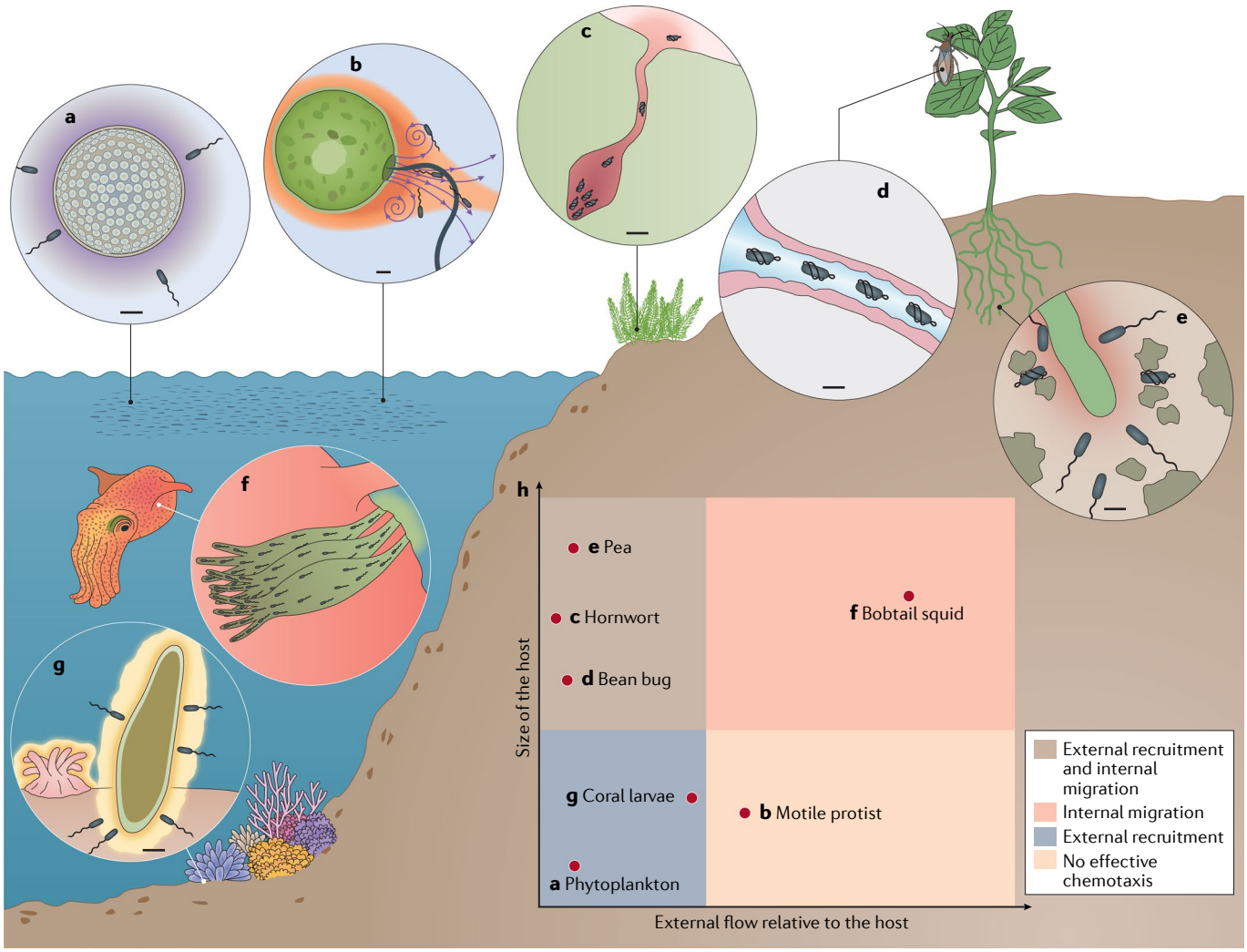

Fig. 1 | **Motility-mediated and chemotaxis-mediated symbioses in different habitats.** Selected examples shown here include external chemotaxis towards phytoplankton cells (part **a**; scale bar: 2 µm); a motile protist preventing the use of chemotaxis as a reliable symbiont recruitment strategy because of its swimming speed (part **b**; scale bar: 2 µm); internal chemotaxis in the hornwort's slime cavities (part **c**; scale bar: 10 µm); internal migration through the symbiont-sorting organ of sap-feeding insects (part **d**; scale bar: 10 µm); external chemotaxis towards plant roots (part **e**; scale bar: 2 µm); internal chemotaxis towards the crypt of the squid's light organs (part **f**; scale bar: 10 µm); and external chemotaxis towards coral larvae or newly settled coral juveniles (part **g** ; scale bar: 20 µm). Utilization of external and internal chemotaxis depends on the size of the host and on the strength of the external flow (part **h**).

these traits[29]. However, the vast majority of sequenced genomes of environmentally acquired symbionts contain the full suite of genes for a functional flagellum and chemotaxis (TABLE 1). This includes symbionts of protists, land plants, microalgae, fishes, insects, gastropods and other invertebrates, suggesting that chemotaxis might be a widespread mechanism in the establishment of symbioses across a wide range of symbiotic partnerships.

In this Review, we discuss the biophysical constraints that govern the recruitment of symbionts. We then identify the two main stages of the host colonization process that can be mediated by microbial chemotaxis, from the initial host–symbiont encounter to the subsequent migration of the symbiont into specific host organs. We illustrate these processes through examples from model systems in which the roles of motility and chemotaxis are already established and then highlight new or previously overlooked examples in which these behaviours could be important for the establishment and maintenance of symbiosis. We conclude that the chemotactic encounter of symbiotic partners is likely to be a pervasive mechanism across hosts and environments and depends on characteristics of the local physical environment, developmental stages of the hosts and rates of host–symbiont encounters.

Chemotaxis and motility in symbionts

Microbial motility comes in a wide range of forms that include swimming, swarming, gliding, twitching and even surfing (FIG. 2). Motile cells achieve chemotaxis by continuously measuring specific chemical concentrations through transmembrane chemoreceptors, which are often arranged into clusters at the cell poles[30,31].

Box 1 | **Using pathogens as examples to study host colonization by symbionts**

Environmentally acquired symbionts and pathogens overlap in their need to find and colonize specific hosts, and they use very similar strategies to do so[101]. The ability of many pathogens to couple chemical sensing and directional swimming is essential during the initial stages of host infection, and pathogens use it to find optimal infection sites and colonize specific niches[102].

A recent analysis revealed that approximately 50% of globally important human and animal pathogens harbour chemotaxis genes, with an average of 17 chemoreceptor genes per genome[28]. Interestingly, the majority of pathogens infecting the respiratory system are non-motile[28,103], whereas chemotaxis genes are prevalent in gastrointestinal pathogens[28]. This pattern might be explained by the spatial complexity of the digestive system, which is characterized by steep chemical and physical gradients forming distinct microenvironments, peristaltic mixing (which moves gut contents) and hostile conditions (such as bile in the duodenum or low pH in the stomach), which may reduce the survival of microorganisms that cannot direct their movement to favourable regions. Chemotactic pathogens (for example, *Vibrio cholerae*, *Helicobacter pylori*, *Salmonella enterica* and *Campylobacter jejuni*)[102,104,105] are also well equipped to approach and penetrate mucous layers[102,104,105], which line all organs of the digestive system, from the oral cavity to the large intestine[103].

In comparison, 90% of plant pathogens harbour chemotaxis genes and encode on average 33 chemoreceptors per genome, almost double the number of human pathogens[28]. Chemotaxis is particularly important for pathogens to locate natural openings or wounds on the plant surface but seems to be less important once pathogens enter the plant, where they can disperse via the vascular system[28]. Similarly, in the marine environment motility and chemotaxis are universal among all identified pathogens of coral[45], fish[106] and many other invertebrates[107].

Motility and chemotaxis of pathogens are well-recognized virulence factors[108], and the importance of these phenotypes during infection has been studied widely through the use of knockout mutants. Given the high likelihood that environmentally acquired symbionts show similar behaviours, we propose that similarly systematic approaches based on the use of chemotaxis-deficient and motility-deficient mutants represent a valuable direction for studying the establishment of symbioses.

This clustering enables bacteria to respond to very small relative changes in specific molecules, as one detection event can affect neighbouring chemoreceptors, amplifying the signal[30]. Information from the chemoreceptors is then transmitted to the cytoplasm and triggers a signalling system that influences the rotation of the flagellar motor(s), which in turn induces changes in swimming direction[30,31]. Although motility and chemotaxis have been mostly studied in a small number of model organisms, such as *Escherichia coli* and *Bacillus subtilis*[31], a basic sensing pathway is conserved across chemotactic bacteria and archaea[30,32,33], with differing complexity between species[30,32] and a subset of proteins that are specific to each domain[33]. In eukaryotes, the diversity of sensing mechanisms is much broader and at times unknown, making a simple overview difficult[34,35].

The physical constraints of life in a microscale world dominated by viscosity limit both sensing and motility[36]. In this environment, most microorganisms swim in a two-step manner (FIG. 2). Microorganisms move through ballistic phases ('runs') interspersed by changes of swimming direction through a reorientation event ('tumble', 'reverse' or 'flick')[36]. Different microorganisms execute their runs and reorientations in different manners. The best studied example is *E. coli*, which interrupts its run by splaying out the flagella from the cell body, leading to a tumble[36]. However, many marine bacteria have only a single flagellum[37], rendering the *E. coli* swimming technique impossible. These bacteria often exhibit 'run-reverse-flick' motility[38], in which runs are followed by a reversal and then a flick of the flagellum that causes the cell to reorient. A simpler implementation is seen in *Rhodobacter sphaeroides*, which uses a 'run-stop' motility in which cells run and then stop rotating their flagella for approximately half a second, during which time Brownian motion reorients them[39] (FIG. 2). Across each of these modes of motility, chemotactic pathways link the sensing of chemical cues to the operation of the flagellar motor, altering the timing of reorientation events on the basis of recent concentration measurements to prolong runs in favourable directions and shorten those in disadvantageous ones, thereby biasing the swimming direction relative to the chemical gradient[36]. The net effect is a migration velocity in the direction of the gradient (chemotactic velocity), often on the order of 10% of the swimming speed[40].

The range of concentration over which chemical sensing is effective is an important, yet often overlooked, component of chemotaxis. The coral symbionts Symbiodiniaceae are capable of chemotaxis towards source concentrations of ~100 pM $NaNO_3$[41]; the gut bacterium *E. coli* moves towards 10 nM amino acids[42]; the rhizosphere bacteria *Azospirillum brasilense* and *Rhizobium leguminosarum* towards 10 nM benzoate[43] and 1 μM xylose[44], respectively; the coral pathogen *Vibrio coralliilyticus* towards 15 μM dimethylsulfoniopropionate (DMSP)[45]; and the phytoplankton-associated bacteria *Silicibacter* spp. and *Pseudoalteromonas haloplanktis* towards concentrations of 200 μM DMSP[46] and 500 μM DMSP[47], respectively. However, it is important to note that these concentrations do not necessarily represent minimum thresholds for chemotaxis, as they are largely derived from capillary assays (Supplementary Table 1). Similarly to natural scenarios, the signal concentration in capillary assay experiments will decrease with distance from the source; therefore, the true microbial threshold for a chemotactic response is likely substantially lower than the source concentration inside the capillary. Nonetheless, the chemotactic thresholds reported here typically correspond to concentrations lower than are known to occur near to or inside relevant hosts[45,48–51], confirming the utility of chemotaxis when microbial partners are close to the hosts.

In addition to navigation via planktonic motility, symbionts often must pass through confined spaces, such as fine pores leading to internal organs[17] or densely packed soil matrices[52]. Under these physical constraints, many bacteria can leverage surface-dependent modes of motility including twitching[53], gliding[54] and swarming[55], which do not necessarily require a flagellum. Although cells generally move slower via surface-dependent motility, they can still effectively follow chemical gradients by adjusting reversal or reorientation frequency[56,57]. Recently, another form of motility to navigate confined spaces was identified in the bacterial symbionts *Aliivibrio fischeri*[58] and *Burkholderia* sp. RPE64 (REF.[58]), whereby cells wrap their flagellum around their body and swim in a corkscrew motion to squeeze through narrow openings (FIG. 2). This unique swimming mode might have a key role in symbiosis by aiding in host colonization[58].

Flagella
Filamentous extracellular appendages that are responsible for the active movement of cells in a liquid environment. Beyond cell motility, flagella are also involved in a range of processes including adhesion, secretion of compounds, virulence and differentiation into biofilms.

Brownian motion
Continuous movement of micrometre-scale particles and organisms in liquid driven by random collisions with water molecules.

Rhizosphere
The zone immediately surrounding the roots of a plant that is enriched in molecules secreted from the root into the soil, providing a key interface for the ecological relationships and chemical exchanges between plants and soil microorganisms.

The biophysics of symbiont chemotaxis

Gradients in the absence of flow. For chemotaxis to be an effective recruitment strategy during the establishment of a symbiotic partnership, there must be a clear and consistent chemical gradient for a symbiont to sense and respond to. Hosts ranging from unicellular algae to sequoia trees, spanning many orders of magnitude in body size, are known to exude chemical

Table 1 | **Presence of motility and chemotaxis genes in genomes of environmentally acquired symbionts**

Common name	Host	Symbiont	Flagellar motility genes	Chemotaxis genes	Refs
Cape gorse	*Aspalathus carnosa*	*Paraburkholderia tuberum*	Yes	Yes	109
Shameplant	*Mimosa pudica*	*Paraburkholderia phymatum*	Yes	Yes	109
Thale cress	*Arabidopsis thaliana*	*Paraburkholderia phytofirmans*	Yes	Yes	109
Kallar grass	*Diplachne fusca*	*Azoarcus* sp. BH72	Yes	Yes	110
Sugar cane	*Saccharum* spp.	*Gluconacetobacter diazotrophicus*	Yes	Yes	111
Rice	*Oryza sativa*	*Azospirillum* sp. B510	Yes	Yes	112
Wheat	*Triticum aestivum*	*Klebsiella pneumoniae* 342[a]	No	No	113
Poplar tree	*Populus deltoides*	*Methylorubrum populi*	Yes	Yes	114
Rapeseed	*Brassica napus*	*Pseudomonas putida*	Yes	Yes	114
Ginseng	*Panax ginseng*	*Pseudomonas stutzeri*	Yes	Yes	115
Poplar tree	*Populus trichocarpa*	*Enterobacter* sp. 638	Yes	Yes	116
Alfalfa	*Medicago sativa*	*Sinorhizobium meliloti*	Yes	Yes	117
Vetch	*Vicia cracca*	*Rhizobium leguminosarum*	Yes	Yes	118
Pea	*Pisum sativum*	*Variovorax paradoxus* S110	Yes	Yes	119
Diatom	*Conticribra weissflogii*	*Marinobacter adhaerens*	Yes	Yes	120
Dinoflagellates	*Pfiesteria piscicida*	*Ruegeria* sp. TM1040	Yes	Yes	121
Flashlight fish	*Anomalops katoptron*	'*Candidatus* Photodesmus katoptron'	Yes	Yes	122
Flashlight fish	*Anomalops katoptron*	'*Candidatus* Photodesmus blepharus'	Yes	Yes	122
Bobtail squid	*Euprymna scolopes*	*Aliivibrio fischeri*	Yes	Yes	123
Zebrafish	*Danio rerio*	*Aeromonas veronii*	Yes	Yes	124
Medicinal leech	*Hirudo medicinalis*				
Northern hatchet shell	*Thyasira gouldii*	*Thyasira gouldii* symbiont phylotype B	Yes	Yes	125
Giant tube worms	*Riftia pachyptila*, *Oasisia alvinae*, *Tevnia jerichonana* and *Ridgeia piscesae*	'*Candidatus* Endoriftia persephone'	Yes	Yes	126
Boneworm	• *Osedax rubiplumus* • *Osedax frankpressi*	• *Osedax* symbiont RS1 • *Osedax* symbiont RS2	Yes	Yes	127
Scaly foot snail	*Chrysomallon squamiferum*	*Chrysomallon* endosymbiont	Yes	Yes	128
Stony coral	*Acropora* spp., *Pocillopora* spp. and *Stylophora pistillata*	*Endozoicomonas* spp.	Yes	Yes	129
Gutless oligochaete worm	*Olavius algarvensis*	γ3 symbiont and δ1 symbiont	Yes	Yes	130
Hydrothermal vent sea snail	*Ifremeria nautilei*	*Thiolapillus brandeum*	Yes	Yes	131
Atlantic awning clam	*Solemya velum*	*Solemya* endosymbiont	Yes	Yes	132
Bean bug	*Riptortus pedestris*	*Burkholderia insecticola* and *Burkholderia* sp. RPE67	Yes	Yes	133,134
Firmicutes	*Bacillus* sp. strain S	*Symbiobacterium thermophilum*	Yes	Yes	135
Mosquito fern	*Azolla* spp.	*Nostoc* spp.	Yes	Yes	136
Human	*Homo sapiens*	*Roseburia hominis*	Yes	Yes	137

[a]*Klebsiella pneumoniae* encodes type IV pili and other adhesion mechanisms[113].

Diffusion
The spread of dissolved compounds from an area of high concentration to an area of lower concentration, driven by random fluctuations. This rate is set by the diffusivity (*D*) of the compound, and the spread of a diffusing cloud progressively slows down as it grows in size.

Viscous boundary layer
The region of fluid in the immediate vicinity of a surface where the effects of viscosity are substantial. Fluid flow decreases with proximity to the surface.

Diffusion boundary layer
A region of fluid near a surface where transport of dissolved compounds is dominated by diffusion rather than advection by flow. The size of this region depends on the diffusivity of the compounds and the viscous boundary layer.

Turbulence
A common type of stochastic, chaotic flow composed of interacting vortices across a range of scales.

compounds into their immediate surroundings[59] that can function as signalling molecules. Diffusion and the hydrodynamic regime of the environment then determine the fate of these signalling molecules and the shape and extent of the chemical field surrounding the host (FIG. 3).

When the local flow is negligible, the distance over which a chemical signal spreads depends on the geometry of the system and the strength of the source. If signalling molecules spread in three dimensions, for example, when the host is a small unicellular planktonic alga, then the concentration of the signal decreases in intensity proportionally to $1/r$ from its maximum value at the source surface, where r is the distance from the centre of the source. This means that a signal will still be at 10% of its maximum at a distance that is 10 times the radius of the source (assuming zero background concentration)[60]. The signal concentration decreases more slowly (linearly) from its maximum if molecules spread in one dimension. This is the case along any internal channels of the host (for example, the excretory ducts of earthworms[61]) or near the external surface of a host that is orders of magnitude larger than its symbionts (for example, the surface of a large plant root[52]).

Influence of flow. Fluid flow relative to the host will transport signalling molecules away and alter the gradients that symbionts can use for chemotaxis. All organisms are surrounded by a region close to their surface where viscous forces quench flow, known as the viscous boundary layer, within which chemical transport is dominated by molecular diffusion[62]. This establishes a diffusion boundary layer, which has a thickness that decreases with increasing ambient fluid velocity. Within this layer, stable chemical gradients form, enabling microorganisms to home in on host surfaces. Smooth (laminar) flows tend to stretch the chemical fields in preferential directions, resulting in their elongation (FIG. 3a,b): signals may be felt from further away in some directions and quenched in others, affecting but not nullifying their role in potentially guiding symbionts. It is commonly thought that when flow becomes turbulent, it completely disrupts chemical gradients[6,63]. However, for turbulence intensities common in natural environments, at the scale of the motility of individual microbial symbionts, and more importantly the typical length scales of the chemical gradients, turbulence often stretches and distorts chemical fields rather than fully erasing chemical gradients[64] (FIG. 3a). Near the surfaces of hosts larger than turbulent eddies, the viscous boundary layer will dampen flow from turbulence, allowing chemical gradients to develop (FIG. 3c). As a result, chemotaxis is possible even in many natural turbulent conditions.

Fluid flow can also affect the efficacy of chemotactic behaviour in symbionts. If the relative flow between the host and symbiont separates the organisms at a rate faster than the swimming speed of the symbiont, then the latter will be unable to reach the host regardless of the direction of swimming. Because purposeful migration through chemotaxis is slower than the swimming speed of the symbiont, it will be inhibited at correspondingly smaller relative flow rates. Interactions within natural environments are often more complex, as the direction of the relative flow near a host depends on the location of the symbiont, and a symbiont may have a short window of opportunity to reach the host as it is swept past. Nonetheless, regions in which the relative flow speed is smaller than the symbiont swimming speed or, more precisely, its chemotactic velocity can provide

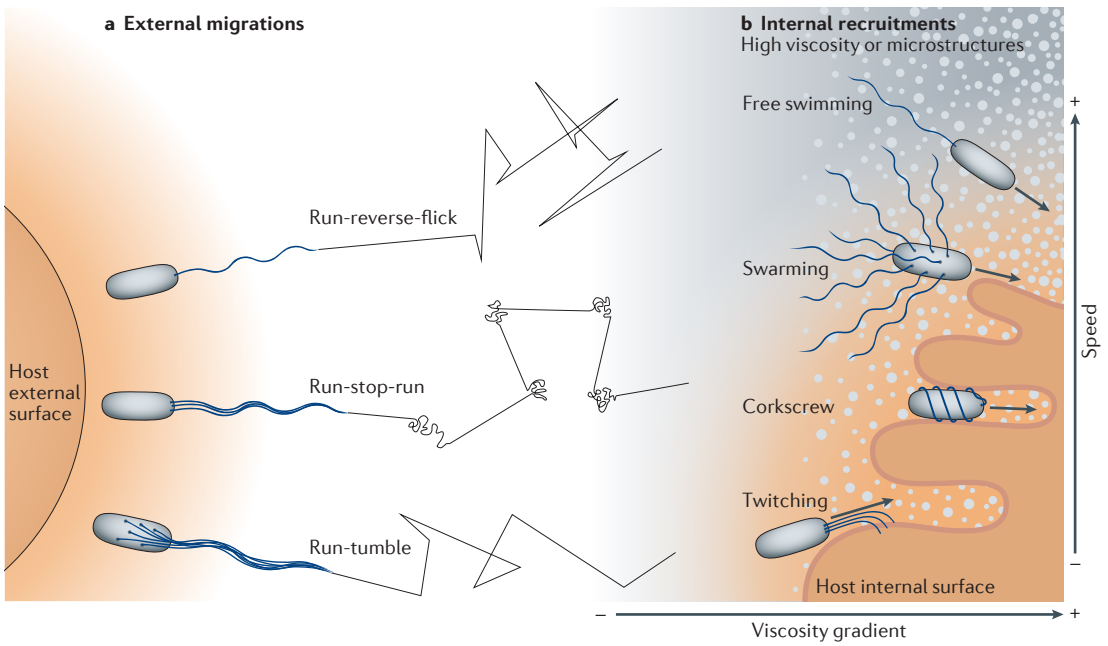

Fig. 2 | **Motility of symbionts.** Chemotactic bacteria can use several different swimming modes during external migration towards a host (part **a**) and internal migration inside a host (part **b**), which typically occurs in mucus-rich, high-viscosity microenvironments.

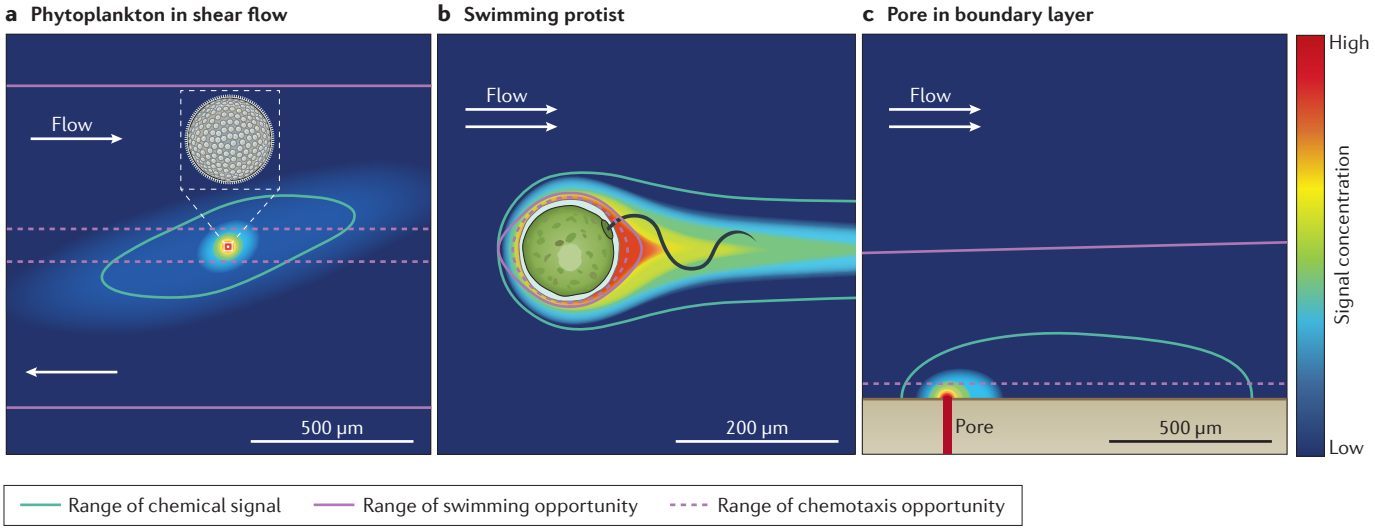

Fig. 3 | **The opportunity for chemotaxis depending on host size.** In each representative case of host–symbiont interactions, the colour gradients depict the dispersing dissolved compounds released by the host. A contour (green) at 10% of the host surface concentration shows the deformation by flow and provides a rough approximation of the range of the signal for symbionts. Regions near the host with relative flow below symbiont swimming speed (100 µm per second) and chemotactic migration speed (10 µm per second; see Supplementary Box 1) are also shown. Both chemical signal and effective motility are required for chemotaxis. For small hosts (part **a**; for example, phytoplankton), chemical signals exuded from the host surface create a chemical field that is 3D from the perspective of the symbiont. These small hosts move with speed that is similar to or slower than the symbionts but may be subject to environmental shear flows (shown). These host are also too small to accommodate internal symbiont migrations. All these criteria also apply to intermediate hosts (part **b**; for example, motile protists), except that the host can move considerably faster than the symbiont and thus creates a flow field that limits any opportunity for chemotaxis. The example shows a protist of 100 µm diameter swimming at 1 mm per second. Internal migration of the symbionts is possible for large hosts (part **c**; for example, towards and through a pore at the surface of invertebrates), and chemicals are typically exuded from a specific region of the host surface. The viscous boundary layer near the host surface creates a region where symbiont chemotaxis is feasible.

estimates for where chemotaxis is potentially effective (FIG. 3) if the typical flow around the host is known.

Influence of host movement. For successful chemotactic interactions, symbionts must be able to move along the chemical gradient they have sensed (see below). The same flow that alters chemical fields can also inhibit the motility of symbionts by transporting them past the potential host. Some hosts, such as microscopic eukaryotes, live at a scale smaller than that of the smallest eddies generated by turbulence (the Kolmogorov scale, often 10–100 mm in the ocean[65]). At these scales, both the host and its microbial symbionts are embedded in the local flow, and displacement between them occurs only as the result of motility and small-scale gradients in flow velocity (FIG. 3a). As a consequence, conditions are more favourable for chemotaxis if the host is not motile. For larger hosts, such as most animals, the same viscous boundary layer surrounding the host's external surface that favours the formation of chemical gradients generates a region in which the relative movement between the symbiotic partners owing to flow is quenched such that symbionts have increased opportunities to swim and thus navigate the chemical gradient towards their host (FIG. 3c).

By altering the local flow field, a host can shape or overwhelm the motility and chemotaxis of its symbionts. Motile protists can generate ciliary flows on the order of 100 µm per second in their immediate vicinity[65], which is faster than the swimming speed of many marine bacteria, in principle preventing bacteria from chemotaxing to them. However, there is evidence that these flows may help bacteria track phytoplankton by exerting forces that continuously reorient them towards the phytoplankton[65,66]. Larval hosts, such as the bobtail squid, actively rely on flows they generate through cilia motion to collect and concentrate their symbionts onto specific loctions[63]. Within benthic habitats, corals use cilia to generate flows as fast as 1.5 mm per second on their external surface[67], whereas marine sponges create feeding currents as fast as 220 mm per second[68]. These flows speeds are substantially higher than swimming speeds of microbial symbionts and therefore likely shape host–symbiont recruitment. Strong fluid flows such as those produced by squid, corals or sponges also imply strong velocity gradients (shear) near the host surface, which can trap motile bacteria near the host surface by forcing them to align with the direction of flow[69] and thereby increasing their probability of encountering the host's surface[70].

Chemotaxis to increase recruitment

External chemotaxis in the environment. When hosts and symbionts are of similar body size, chemotaxis towards the host's external surface can mediate the initial encounter of the symbionts with the host and their retention[46,71–74]. This is aided by the hydrodynamic regime of the host, characterized typically by small to medium

Shear flows
A type of flow in which the fluid moves in parallel directions but with changing magnitude. Shear flow exists in regions with gradients in velocity, such as the region between a surface with no flow and a constant external flow parallel to the surface.

Feeding currents
Fluid motion generated by an organism to increase prey encounter. These currents can be generated through beating cilia (in protists), mouth appendages (in copepods) or specialized ciliated cells (in sponges).

effects of flow. This is often the case for small hosts, during the early life stages of large hosts or in quiescent environments, such as soil. These external migrations of microorganisms towards host surfaces are selective, despite the diverse pool of microorganisms present in the environment.

The role of chemotaxis in selectively increasing the encounter rates of similarly sized symbionts and hosts can be illustrated by the interactions between phytoplankton and bacteria, for which the small size and planktonic nature of both organisms make random encounters unreliable. For a phytoplankton cell with a radius of 20 µm in an environment with 1,000 potential symbionts per millilitre, 1 motile symbiont randomly (that is, in the absence of chemotaxis) encounters the host on average every 73 minutes (this time increases to 115 days if the symbiont is not motile; see Supplementary Box 1). If the host generates a chemical gradient, chemotactic symbionts will be attracted from a far larger distance. The actual distance in natural environments is not known and depends on the amount of chemoattractant exuded[22]. If we consider a gradient that extends to 10 times the host radius (that is, 200 µm in this example), then one chemotactic symbiont would encounter the host every 7 minutes. This chemical gradient would substantially increase the concentration of chemotactic symbionts near the phytoplankton cell, as they would be attracted to the source of the gradient. By contrast, motile but non-chemotactic as well as non-motile bacteria would remain at background levels near the host. Many aquatic bacteria are highly chemotactic towards specific compounds exuded by eukaryotic and bacterial phytoplankton, such as DMSP, amino acids, acrylate, *N*-acetylglucosamine, glucose, galactose, citrate, fumarate and glycolate[22], and the importance of chemotaxis in the onset of phytoplankton–bacteria symbioses has been confirmed using non-motile and non-chemotactic mutants[74,75].

Beyond interactions between microorganisms, there is evidence for the potential role of chemotaxis in encounters between symbionts and the early life stages of larger hosts. For example, some macroalgae release DMSP to recruit specific bacteria through chemotaxis; in turn, the bacteria produce morphogenic substances that control the growth and cellular differentiation of the algae[72]. Coral endosymbiotic algae from the Symbiodiniaceae family colonize their hosts primarily during larval stages[76] and are chemotactic towards coral extracts, more specifically towards *N*-acetylglucosamine-binding lectins[41]. Chemosynthetic bacterial symbionts of multiple species of tubeworms from hydrothermal vents, including the iconic *Riftia pachyptila*, colonize the skin of larvae after settlement, before proliferating internally within a dedicated organ[16].

External chemotaxis in soil. The porous structure, variable water content and absence of fluid flow that characterize soil environments also present conditions under which hosts can recruit symbionts across large distances through chemotaxis. The rhizosphere, which is the region of soil immediately surrounding plant roots that is enriched in excreted molecules, harbours very active microbial communities[77]. One of the largest plant families on Earth, Fabaceae (legumes), is ubiquitously associated with nitrogen-fixing bacteria, referred to as rhizobia[52]. These host–symbiont systems have evolved complex chemical signalling that enables specific rhizobia to colonize the roots, ultimately resulting in the development of nodules populated by the symbionts[78]. Within this interaction, rhizobia exhibit strong chemotaxis to specific root exudates, including carbohydrates, phenolic compounds, sugar alcohols and organic acids[79], which increases their cell density in the rhizosphere and facilitates subsequent nodule initiation[80]. Chemotaxis also seems to mediate many other plant root symbioses. For example, seedlings of *Arabidopsis thaliana* that are infected by the pathogen *Pseudomonas syringae* secrete malic acid, which attracts the beneficial bacteria *B. subtilis* in a dose-dependent manner[81,82], ultimately leading to the exclusion of the pathogen and mitigation of infection[82]. Chemotaxis-driven recruitment also occurs in marine sediments surrounding seagrass roots[83], where specific amino acids, such as serine, threonine and glycine, and other uncharacterized organic compounds promote root colonization[83].

Symbiont chemotaxis in microbial communities. Although the vast majority of microbial symbionts identified to date associate with eukaryotes, there is growing evidence that symbiotic interactions between prokaryotes are also prevalent[84]. Microorganisms that form close aggregations can profit from tight metabolic coupling, and the use of motility and chemotaxis can help overcome encounter rate limitations and short chemical diffusion distances caused by the small size of both partners. Chemotaxis often mediates the establishment and maintenance of highly structured microbial consortia in many habitats. For example, filamentous nitrogen-fixing cyanobacteria *Anabaena* spp. excrete specific signalling molecules at the junction of its heterocysts — the thick-walled cells that fix nitrogen — selectively attracting *Pseudomonas* spp., which in turn increase nitrogen fixation rates[73]. Sulfate-reducing *Desulfonema* spp. use gliding motility to colonize the mucous sheaths covering *Thioploca* spp., another filamentous bacterial taxon living at the interface of sulfide-rich sediments, allowing complete sulfate reduction and reoxidation among these organisms[71]. Other examples of symbioses between microorganisms support the importance of chemotaxis and motility, specifically the complex spatial arrangement of dental plaque, which involves the specific positioning of nine microbial taxa in consortia measuring hundreds of micrometres in size[85] or the candidate phyla CPR and DPANN, which represent a substantial fraction of the bacterial and archaeal diversity on Earth and are predicted to be motile (through flagella or type IV pili) and to live as episymbionts of other microorganisms[86].

Protist–bacteria symbiosis. Movement of the host can substantially reduce the importance of chemotaxis by microbial symbionts in initiating interactions. This is the case when the host is small enough that its chemical signals spread in three dimensions at microbial scales but large enough that its motility considerably exceeds that of its symbionts. For example, high swimming

Pili
Thin filamentous appendages made out of extracellular protein fibres that are involved in various microbial behaviours, including attachment, twitching motility and virulence.

Mucus
Viscous aqueous secretion typically produced by specialized cells that has a role in the protection against infectious agents. Mucus coats the gastrointestinal, respiratory and urogenital tracts of most animals, as well as the external surfaces of marine organisms.

speeds (~1 mm per second) will substantially distort the gradients of solutes released by small protists (~0.1 mm diameter) (FIG. 3b). Because of the small size of the host, these speeds also indicate that chemotactic symbionts would have only a very brief window of time to migrate to the host surface. By contrast, for similarly small hosts that move more slowly than their symbionts, chemotaxis can still mediate symbiont recruitment. For example, amoeba recruit two strains of *Burkholderia* spp. through chemotaxis, potentially using proline-rich peptides as signalling molecules[87], and subsequently, these bacteria help their host to forage on other microorganisms.

Despite the physics-based hurdles that can reduce the role of chemotaxis in establishing protist–bacteria symbioses, chemotaxis can still have a role for such symbionts, at times in unexpected ways. Protist–bacteria interactions occur in almost every ecosystem, but they have been best studied in the gut of wood-feeding termites[88]. Some protists in this environment are entirely covered by thousands of bacterial ectosymbionts from the Spirochaetes and Synergistetes phyla, which propel the otherwise non-motile protists, enabling them to navigate the highly structured termite gut and encounter cellulose degradation products to sustain their growth[89]. Other ectosymbionts are not directly involved in protist movement but function instead as chemotactic sensors and enable their host to direct its swimming towards specific compounds, such as sodium acetate[90]. In this case, the bacterial symbionts, which typically cover the entire surface of the protist, have no role in the host motility, but when they are removed through antibiotic treatment, the host loses its capacity to exploit chemical gradients[90].

Chemotaxis to colonize host organs

Finding larger hosts. When hosts are orders of magnitude larger than their symbionts, they can have more active roles in the initial encounter with symbionts through mechanisms such as active water pumping, feeding or swimming. These host-driven flows typically overwhelm the motility of the symbionts, apparently removing the utility of chemotaxis for recruitment of symbionts from the environment. However, even within these scenarios, chemotactic behaviour by the symbionts can be effective after the symbionts are brought close to the host (FIG. 3c). When within hundreds of micrometres from the host surface, symbiont motility becomes effective owing to reductions in the relative fluid motion (exceptions to this include some hosts, such as corals, that create strong flows directly adjacent to their surfaces through cilia[67]). This provides an opportunity for symbionts to use chemotaxis to target specific regions or openings on the host surface (for example, squid pores[25]).

Finding niches inside the host. After the initial encounter between large hosts and their symbionts, symbionts often migrate inside the host to reach specific housing organs[6,25,91,92]. Internal migrations are characterized by their high selectivity, with host-mediated step-wise eliminations and checkpoints to exclude nonspecific microorganisms, as well as active behaviour of the symbionts[6,25,91,92]. Long internal channels with gradients that guide chemotactic symbionts provide a barrier that selects for symbionts and directs them to the right location (for example, hornwort slime cavities[91] or squid ducts[17]). Chemotactic motile symbionts will pass through a channel of 1 mm in length at a rate that is 10 times higher than motile but non-chemotactic cells and 20,000 times higher than non-motile cells (see Supplementary Box 1). The selectivity increases with channel length (55 times the enrichment of chemotactic motile cells compared with motile non-chemotactic cells for a 10 mm channel). Coupled with additional elimination mechanisms by the host, this suggests that symbiont chemotaxis can contribute substantially to the selectivity that occurs within large hosts.

Sap-feeding insects harbour orally acquired *Burkholderia* spp. bacteria, which populate specialized sacs or crypts in the posterior region of the insects' midgut[93]. A constricted region lined with mucus and located in the middle of the gut functions as a symbiont-sorting organ, blocking food fluid and non-symbiotic microorganisms but enabling *Burkholderia* spp. to pass through[94]. Experiments with bacterial mutants have demonstrated that symbiont motility is required to pass this organ[94] and successfully colonize the crypts[92]. Yet, the observation that other motile bacteria (*Pseudomonas putida*, *E. coli* and *B. subtilis*) are blocked at the sorting organ indicated that motility is necessary but not sufficient[94]. The crossing mechanism possibly rests in an alternative, recently described swimming mode of *Burkholderia* sp. RPE64 (REF. [58]). (and other bacteria[95]), which in high-viscosity environments glides in a corkscrew-like motion with its flagella wrapped around its body, a mechanism that appears well-suited to cross the mucus-rich sorting organ[58]. Similar internal migrations through narrow ducts have been reported in earthworms, leading to the colonization of the excretory organ during host embryogenesis by specific *Verminephrobacter* spp.[61,96].

The symbiosis between *A. fischeri* and the Hawaiian bobtail squid (*Euprymna scolopes*) is a well-described model system of symbiosis in which the host animal uses the light produced by the bacteria on its ventral side as camouflage against predators during nocturnal foraging[17]. In the few hours following hatching of squid juveniles, *A. fischeri* is selectively taken up from the pelagic environment through a physical selection process[17]. Cilia present on specialized appendages of the squid sweep bacteria into the vicinity of the squid's light organ, where they accumulate in host-secreted mucus[63]. *A. fischeri* cells embedded in this mucous matrix actively migrate towards the pores of the light organ, using chemotaxis to follow a chitin gradient through ducts and antechambers before finally reaching the crypts of the light organ[25]. Similarly to *Burkholderia* spp., *A. fischeri* can swim in a corkscrew-like motion and might use this form of motility during the internal migration process[58]. Following successful crypt colonization, *A. fischeri* cells lose motility, the specialized ciliated appendages of the squid undergo apoptosis, and bacterial recruitment ceases[17]. Other squid and cuttlefish species are also colonized by bacterial symbionts, which populate specific glands of the reproductive organ of sexually

mature females and might have a role in the protection of squid embryos against pathogens[97]. These symbiotic consortia are composed of bacterial genera known for their motility and chemotaxis, including *Roseobacter*, *Pseudoalteromonas*, *Vibrio* and *Shewanella*[98], suggesting that chemotaxis-enabled internal organ colonization similar to that of *A. fischeri* might be prevalent among many marine symbioses.

In terrestrial environments, the most common cyanobacterial symbiont of plants are the nitrogen-fixing *Nostoc* spp.[99]. These cyanobacteria are typically not motile[91]; however, their plant hosts secrete hormogonium-inducing factors, stimulating the symbionts to produce hormogonia, which are specialized appendages on their cell surface that enable the bacteria to glide and chemotax towards specific points of entry on the plant surface, including roots, stems, leaves or shoots. Plant-derived chemical signals then guide *Nostoc* spp. internally to symbiotic cavities[99], where host signals inhibit further hormogonia formation, resulting in a loss of motility, and stimulate cell differentiation into nitrogen-fixing symbionts[91].

Conclusions

Although several symbioses show that chemotaxis and motility are not the only mechanisms involved in the recruitment of symbionts from the environment — as illustrated, for example, by the use of adhesins by some non-motile symbionts and the lack of any apparent motility in methanotrophic consortia of sulfate-reducing bacteria and methane-producing archaea in marine sediments[100] — the examples presented in this Review suggest that, similarly to pathogens, many environmentally acquired symbionts use motility and chemotaxis to colonize their hosts. We base this conclusion on several well-documented cases, as well as widespread evidence for the presence of motility and chemotaxis genes in the genomes of many horizontally transmitted symbionts (TABLE 1). In addition, biophysical conditions favourable for the use of chemotaxis and motility by symbionts to colonize their host are present in many systems. The prevalence of these conditions strongly suggests that the examples provided here represent only a small sample of those occurring in the environment, inviting one to consider these behaviours in future studies and to test their role in symbiont recruitment through the use of chemotaxis and motility-deficient mutants.

Our goal here was not only to provide a synthesis of current knowledge on the role of motility and chemotaxis across a broad range of symbiotic partnerships but also to identify general principles for when and where these behaviours are likely to be important. By considering the size and morphology of the hosts and symbionts and the biophysical nature of their habitat, in particular, the role of fluid flow and symbiont motility, we propose that many environmentally acquired symbionts can use chemotaxis for either recruitment from the external environment (often the case when hosts and symbionts are small and when external fluid flow relative to the host is weak) or internal migration towards specific host regions or organs (often the case when the host is large). As the ubiquity and ecological importance of symbioses continue to emerge, understanding the establishment and acquisition of symbionts will provide a better appreciation of the factors governing the occurrence of important symbioses.

Published online: 28 March 2019

1. Margulis, L. *Symbiosis in Cell Evolution: Life and Its Environment on the Early Earth* (W. H. Freeman, 1981).
2. Ochman, H. & Moran, N. A. Genes lost and genes found: evolution of bacterial pathogenesis and symbiosis. *Science* **292**, 1096–1099 (2001).
3. Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B. & Worm, B. How many species are there on earth and in the ocean? *PLOS Biol.* **9**, e1001127 (2011).
4. Eme, L., Spang, A., Lombard, J., Stairs, C. W. & Ettema, T. J. G. Archaea and the origin of eukaryotes. *Nat. Rev. Microbiol.* **15**, 711 (2017).
5. Boucher, D. H., James, S. & Keeler, K. H. The ecology of mutualism. *Annu. Rev. Ecol. Syst.* **13**, 315–347 (1982).
6. Bright, M. & Bulgheresi, S. A complex journey: transmission of microbial symbionts. *Nat. Rev. Microbiol.* **8**, 218 (2010).
This is an important description of the journey undertaken by horizontally and vertically transmitted symbionts, from their initial contact with their host to their final residence.
7. Bennett, G. M. & Moran, N. A. Heritable symbiosis: the advantages and perils of an evolutionary rabbit hole. *Proc. Natl Acad. Sci. USA* **112**, 10169–10176 (2015).
8. Bull, J. J., Molineux, I. J. & Rice, W. R. Selection of benevolence in a host-parasite system. *Evolution* **45**, 875–882 (1991).
9. Doebeli, M. & Knowlton, N. The evolution of interspecific mutualisms. *Proc. Natl Acad. Sci. USA USA* **95**, 8676–8680 (1998).
10. Douglas, A. E. Host benefit and the evolution of specialization in symbiosis. *Heredity* **81**, 599 (1998).
11. Ewald, P. W. Transmission modes and evolution of the parasitism-mutualism continuum. *Ann. NY Acad. Sci.* **503**, 295–306 (1987).
12. Hartmann, A. C., Baird, A. H., Knowlton, N. & Huang, D. The paradox of environmental symbiont acquisition in obligate mutualisms. *Curr. Biol.* **27**, 3711–3716 (2017).
13. Herre, E. A., Knowlton, N., Mueller, U. G. & Rehner, S. A. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol. Evol.* **14**, 49–53 (1999).
14. Wilkinson, D. M. & Sherratt, T. N. Horizontally acquired mutualisms, an unsolved problem in ecology? *Oikos* **92**, 377–384 (2001).
15. Knowlton, N. & Rohwer, F. Multispecies microbial mutualisms on coral reefs: the host as a habitat. *Am. Nat.* **162**, S51–S62 (2003).
16. Nussbaumer, A. D., Fisher, C. R. & Bright, M. Horizontal endosymbiont transmission in hydrothermal vent tubeworms. *Nature* **441**, 345 (2006).
17. Nyholm, S. V. & McFall-Ngai, M. The winnowing: establishing the squid–vibrio symbiosis. *Nat. Rev. Microbiol.* **2**, 632 (2004).
This is a classic overview of the establishment of the squid–*Vibrio* spp. symbiosis.
18. Fontanez, K. M. & Cavanaugh, C. M. Evidence for horizontal transmission from multilocus phylogeny of deep-sea mussel (Mytilidae) symbionts. *Environ. Microbiol.* **16**, 3608–3621 (2014).
19. Oldroyd, G. E. D. Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. *Nat. Rev. Microbiol.* **11**, 252 (2013).
This is an excellent overview of the complex signalling occurring between plants and their symbionts.
20. Kikuchi, Y., Hosokawa, T. & Fukatsu, T. Insect-microbe mutualism without vertical transmission: a stinkbug acquires a beneficial gut symbiont from the environment every generation. *Appl. Environ. Microbiol.* **73**, 4308–4316 (2007).
21. Decelle, J. et al. An original mode of symbiosis in open ocean plankton. *Proc. Natl Acad. Sci. USA* **109**, 18000–18005 (2012).
22. Seymour, J. R., Amin, S. A., Raina, J.-B. & Stocker, R. Zooming in on the phycosphere: the ecological interface for phytoplankton–bacteria relationships. *Nat. Microbiol.* **2**, 17065 (2017).
23. Böhm, M., Hurek, T. & Reinhold-Hurek, B. Twitching motility is essential for endophytic rice colonization by the N_2-fixing endophyte *Azoarcus* sp. strain BH72. *Mol. Plant Microbe Interact.* **20**, 526–533 (2007).
24. Geng, H. & Belas, R. Molecular mechanisms underlying roseobacter–phytoplankton symbioses. *Curr. Opin. Biotechnol.* **21**, 332–338 (2010).
25. Mandel, M. J. et al. Squid-derived chitin oligosaccharides are a chemotactic signal during colonization by *Vibrio fischeri*. *Appl. Environ. Microbiol.* **78**, 4620–4626 (2012).
26. Munoz Aguilar, J. M. et al. Chemotaxis of *Rhizobium leguminosarum* biovar *phaseoli* towards flavonoid Inducers of the symbiotic nodulation genes. *Microbiology* **134**, 2741–2746 (1988).
27. Robidart, J. C. et al. Metabolic versatility of the *Riftia pachyptila* endosymbiont revealed through metagenomics. *Environ. Microbiol.* **10**, 727–737 (2008).
28. Matilla, M. A. & Krell, T. The effect of bacterial chemotaxis on host infection and pathogenicity. *FEMS Microbiol. Rev.* **42**, fux052 (2018).
This is a recent review focusing on the prevalence of chemotaxis in human, animal and plant pathogens.
29. Moran, N. A., McCutcheon, J. P. & Nakabachi, A. Genomics and evolution of heritable bacterial symbionts. *Annu. Rev. Genet.* **42**, 165–190 (2008).
30. Porter, S. L., Wadhams, G. H. & Armitage, J. P. Signal processing in complex chemotaxis pathways. *Nat. Rev. Microbiol.* **9**, 153 (2011).
31. Wadhams, G. H. & Armitage, J. P. Making sense of it all: bacterial chemotaxis. *Nat. Rev. Mol. Cell Biol.* **5**, 1024 (2004).
This is a comprehensive and clearly written review covering the genetic systems involved in bacterial chemotaxis.
32. Bi, S. & Sourjik, V. Stimulus sensing and signal processing in bacterial chemotaxis. *Curr. Opin. Microbiol.* **45**, 22–29 (2018).

33. Szurmant, H. & Ordal, G. W. Diversity in chemotaxis mechanisms among the bacteria and archaea. *Microbiol. Mol. Biol. Rev.* **68**, 301–319 (2004).
34. Van Haastert, P. J. M. & Devreotes, P. N. Chemotaxis: signalling the way forward. *Nat. Rev. Mol. Cell Biol.* **5**, 626 (2004).
35. Swaney, K. F., Huang, C.-H. & Devreotes, P. N. Eukaryotic chemotaxis: a network of signaling pathways controls motility, directional sensing, and polarity. *Annu. Rev. Biophys.* **39**, 265–289 (2010).
36. Berg, H. C. *Random Walks in Biology* (Princeton Univ. Press, 1993).
This is an intuitive reference on the mathematics and biophysics of bacterial motility and chemotaxis.
37. Leifson, E., Cosenza, B. J., Murchelano, R. & Cleverdon, R. C. Motile marine bacteria. I. Techniques, ecology, and general characteristics. *J. Bacteriol.* **87**, 652–666 (1964).
38. Xie, L., Altindal, T., Chattopadhyay, S. & Wu, X.-L. Bacterial flagellum as a propeller and as a rudder for efficient chemotaxis. *Proc. Natl Acad. Sci. USA* **108**, 2246–2251 (2011).
39. Packer, H. L., Lawther, H. & Armitage, J. P. The *Rhodobacter sphaeroides* flagellar motor is a variable-speed rotor. *FEBS Lett.* **409**, 37–40 (1997).
40. Son, K., Menolascina, F. & Stocker, R. Speed-dependent chemotactic precision in marine bacteria. *Proc. Natl Acad. Sci. USA* **113**, 8624–8629 (2016).
41. Takeuchi, R. et al. Establishment of a model for chemoattraction of Symbiodinium and characterization of chemotactic compounds in *Acropora tenuis*. *Fish. Sci.* **83**, 479–487 (2017).
42. Sourjik, V. Receptor clustering and signal processing in *E. coli* chemotaxis. *Trends Microbiol.* **12**, 569–576 (2004).
43. Lopez-de-Victoria, G. & Lovell, C. R. Chemotaxis of *Azospirillum* species to aromatic compounds. *Appl. Environ. Microbiol.* **59**, 2951–2955 (1993).
44. Bowra, B. J. & Dilworth, M. J. Motility and chemotaxis towards sugars in *Rhizobium leguminosarum*. *Microbiology* **126**, 231–235 (1981).
45. Garren, M. et al. A bacterial pathogen uses dimethylsulfoniopropionate as a cue to target heat-stressed corals. *ISME J.* **8**, 999 (2013).
46. Miller, T. R., Hnilicka, K., Dziedzic, A., Desplats, P. & Belas, R. Chemotaxis of *Silicibacter* sp. strain TM1040 toward dinoflagellate products. *Appl. Environ. Microbiol.* **70**, 4692–4701 (2004).
47. Seymour, J. R., Simó, R., Ahmed, T. & Stocker, R. Chemoattraction to dimethylsulfoniopropionate throughout the marine microbial food web. *Science* **329**, 342–345 (2010).
48. Adibi, S. A. & Mercer, D. W. Protein digestion in human intestine as reflected in luminal, mucosal, and plasma amino acid concentrations after meals. *J. Clin. Invest.* **52**, 1586–1594 (1973).
49. Caruana, A. M. N. & Malin, G. The variability in DMSP content and DMSP lyase activity in marine dinoflagellates. *Prog. Oceanogr.* **120**, 410–424 (2014).
50. Jaeger, C. H., Lindow, S. E., Miller, W., Clark, E. & Firestone, M. K. Mapping of sugar and amino acid availability in soil around roots with bacterial sensors of sucrose and tryptophan. *Appl. Environ. Microbiol.* **65**, 2685–2690 (1999).
51. Szmant, A. M., Ferrer, L. M. & FitzGerald, L. M. Nitrogen excretion and O:N ratios in reef corals: evidence for conservation of nitrogen. *Mar. Biol.* **104**, 119–127 (1990).
52. Gage, D. J. Infection and invasion of roots by symbiotic, nitrogen-fixing rhizobia during nodulation of temperate legumes. *Microbiol. Mol. Biol. Rev.* **68**, 280–300 (2004).
53. Mattick, J. S. Type IV pili and twitching motility. *Annu. Rev. Microbiol.* **56**, 289–314 (2002).
54. Nan, B. & Zusman, D. R. Novel mechanisms power bacterial gliding motility. *Mol. Microbiol.* **101**, 186–193 (2016).
55. Kearns, D. B. A field guide to bacterial swarming motility. *Nat. Rev. Microbiol.* **8**, 634 (2010).
56. Kearns, D. B. & Shimkets, L. J. Chemotaxis in a gliding bacterium. *Proc. Natl Acad. Sci. USA* **95**, 11957–11962 (1998).
57. Oliveira, N. M., Foster, K. R. & Durham, W. M. Single-cell twitching chemotaxis in developing biofilms. *Proc. Natl Acad. Sci. USA* **113**, 6532–6537 (2016).
58. Kinosita, Y., Kikuchi, Y., Mikami, N., Nakane, D. & Nishizaka, T. Unforeseen swimming and gliding mode of an insect gut symbiont. *Burkholderia* sp. RPE64, with wrapping of the flagella around its cell body. *ISME J.* **12**, 838–848 (2018).
This paper provides a description of the recently discovered corkscrew motility mode in insect and squid symbionts.
59. Bakus, G. J., Targett, N. M. & Schulte, B. Chemical ecology of marine organisms: an overview. *J. Chem. Ecol.* **12**, 951–987 (1986).
60. Crank, J. *The Mathematics of Diffusion* (Clarendon Press, 1975).
61. Dulla, G. F. J., Go, R. A., Stahl, D. A. & Davidson, S. K. *Verminephrobacter eiseniae* type IV pili and flagella are required to colonize earthworm nephridia. *ISME J.* **6**, 1166 (2011).
62. Mann, K. H. & Lazier, J. R. *Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans* (John Wiley & Sons, 2013).
This oceanography text includes an important chapter on small-scale turbulence and the physics of boundary layers.
63. Nyholm, S. V., Stabb, E. V., Ruby, E. G. & McFall-Ngai, M. J. Establishment of an animal–bacterial association: recruiting symbiotic vibrios from the environment. *Proc. Natl Acad. Sci. USA* **97**, 10231–10235 (2000).
64. Taylor, J. R. & Stocker, R. Trade-offs of chemotactic foraging in turbulent water. *Science* **338**, 675–679 (2012).
This is a modelling study that illustrates how turbulent fluid motion gives rise to small-scale heterogeneity and chemical gradients.
65. Guasto, J. S., Rusconi, R. & Stocker, R. Fluid mechanics of planktonic microorganisms. *Annu. Rev. Fluid Mech.* **44**, 373–400 (2012).
66. Locsei, J. T. & Pedley, T. J. Bacterial tracking of motile algae assisted by algal cell's vorticity field. *Microb. Ecol.* **58**, 63–74 (2009).
67. Shapiro, O. H. et al. Vortical ciliary flows actively enhance mass transport in reef corals. *Proc. Natl Acad. Sci. USA* **111**, 13391–13396 (2014).
68. Vogel, S. Current-induced flow through living sponges in nature. *Proc. Natl Acad. Sci. USA* **74**, 2069–2071 (1977).
69. Rusconi, R., Guasto, J. S. & Stocker, R. Bacterial transport suppressed by fluid shear. *Nat. Physics* **10**, 212 (2014).
This is a study that highlights some of the unexpected dynamics that arise when bacteria are subjected to fluid flows near surfaces.
70. Lecuyer, S. et al. Shear stress increases the residence time of adhesion of *Pseudomonas aeruginosa*. *Biophys. J.* **100**, 341–350 (2011).
71. Fukui, M., Teske, A., Aβmus, B., Muyzer, G. & Widdel, F. Physiology, phylogenetic relationships, and ecology of filamentous sulfate-reducing bacteria (genus Desulfonema). *Arch. Microbiol.* **172**, 193–203 (1999).
72. Kessler, R. W., Weiss, A., Kuegler, S., Hermes, C. & Wichard, T. Macroalgal–bacterial interactions: role of dimethylsulfoniopropionate in microbial gardening by *Ulva* (Chlorophyta). *Mol. Ecol.* **27**, 1808–1819 (2018).
73. Paerl, H. W. & Gallucci, K. K. Role of chemotaxis in establishing a specific nitrogen-fixing cyanobacterial-bacterial association. *Science* **227**, 647–649 (1985).
74. Sonnenschein, E. C., Abebew Syit, D., Grossart, H.-P. & Ullrich, M. S. Chemotaxis of Marinobacter adhaerens and its impact on attachment to the Diatom Thalassiosira weissflogii. *Appl. Environ. Microbiol.* **78**, 6900–6907 (2012).
75. Miller, T. R. & Belas, R. Motility is involved in *Silicibacter* sp. TM1040 interaction with dinoflagellates. *Environ. Microbiol.* **8**, 1648–1659 (2006).
76. Yamashita, H., Suzuki, G., Kai, S., Hayashibara, T. & Koike, K. Establishment of coral–algal symbiosis requires attraction and selection. *PLOS ONE* **9**, e97003 (2014).
77. Scharf, B. E., Hynes, M. F. & Alexandre, G. M. Chemotaxis signaling systems in model beneficial plant–bacteria associations. *Plant Mol. Biol.* **90**, 549–559 (2016).
78. Jones, K. M., Kobayashi, H., Davies, B. W., Taga, M. E. & Walker, G. C. How rhizobial symbionts invade plants: the *Sinorhizobium–Medicago* model. *Nat. Rev. Microbiol.* **5**, 619 (2007).
79. Gaworzewska, E. T. & Carlile, M. J. Positive chemotaxis of *Rhizobium leguminosarum* and other bacteria towards root exudates from legumes and other plants. *Microbiology* **128**, 1179–1188 (1982).
80. Caetano-Anollés, G., Wrobel-Boerner, E. & Bauer, W. D. Growth and movement of spot inoculated *Rhizobium meliloti* on the root surface of Alfalfa. *Plant Physiol.* **98**, 1181–1189 (1992).
81. Massalha, H., Korenblum, E., Malitsky, S., Shapiro, O. H. & Aharoni, A. Live imaging of root–bacteria interactions in a microfluidics setup. *Proc. Natl Acad. Sci. USA* **114**, 4549–4554 (2017).
This is a recent study imaging root–bacterial interactions at previously unattainable spatiotemporal resolutions.
82. Rudrappa, T., Czymmek, K. J., Paré, P. W. & Bais, H. P. Root-secreted malic acid recruits beneficial soil bacteria. *Plant Physiol.* **148**, 1547–1556 (2008).
83. Wood, D. C. & Hayasaka, S. S. Chemotaxis of rhizoplane bacteria to amino acids comprising eelgrass (*Zostera marina* L.) root exudate. *J. Exp. Marine Biol. Ecol.* **50**, 153–161 (1981).
84. Overmann, J. & Schubert, K. Phototrophic consortia: model systems for symbiotic interrelations between prokaryotes. *Arch. Microbiol.* **177**, 201–208 (2002).
85. Mark Welch, J. L., Rossetti, B. J., Rieken, C. W., Dewhirst, F. E. & Borisy, G. G. Biogeography of a human oral microbiome at the micron scale. *Proc. Natl Acad. Sci. USA* **113**, E791–E800 (2016).
86. Castelle, C. J. et al. Biosynthetic capacity, metabolic variety and unusual biology in the CPR and DPANN radiations. *Nat. Rev. Microbiol.* **16**, 629–645 (2018).
87. Shu, L., Zhang, B., Queller, D. C. & Strassmann, J. E. Burkholderia bacteria use chemotaxis to find social amoeba Dictyostelium discoideum hosts. *ISME J.* **12**, 1977–1993 (2018).
88. Gast, R. J., Sanders, R. W. & Caron, D. A. Ecological strategies of protists and their symbiotic relationships with prokaryotic microbes. *Trends Microbiol.* **17**, 563–569 (2009).
89. Ohkuma, M. Symbioses of flagellates and prokaryotes in the gut of lower termites. *Trends Microbiol.* **16**, 345–352 (2008).
90. Dyer, B. D. & Khalsa, O. Surface bacteria of *Streblomastix strix* are sensory symbionts. *Biosystems* **31**, 169–180 (1993).
91. Adams, D. G. & Duggan, P. S. Cyanobacteria–bryophyte symbioses. *J. Exp. Bot.* **59**, 1047–1058 (2008).
92. Lee, J. B. et al. Bacterial cell motility of *Burkholderia* gut symbiont is required to colonize the insect gut. *FEBS Lett.* **589**, 2784–2790 (2015).
93. Kikuchi, Y., Hosokawa, T. & Fukatsu, T. An ancient but promiscuous host–symbiont association between *Burkholderia* gut symbionts and their heteropteran hosts. *ISME J.* **5**, 446 (2010).
94. Ohbayashi, T. et al. Insect's intestinal organ for symbiont sorting. *Proc. Natl Acad. Sci. USA* **112**, E5179–E5188 (2015).
This study provides a fascinating example of an overlooked mechanism enabling symbiont selection.
95. Kühn, M. J., Schmidt, F. K., Eckhardt, B. & Thormann, K. M. Bacteria exploit a polymorphic instability of the flagellar filament to escape from traps. *Proc. Natl Acad. Sci. USA* **114**, 6340–6345 (2017).
96. Davidson, S. K. & Stahl, D. A. Selective recruitment of bacteria during embryogenesis of an earthworm. *ISME J.* **2**, 510 (2008).
97. Kaufman, M. R., Ikeda, Y., Patton, C., van Dykhuizen, G. & Epel, D. Bacterial symbionts colonize the accessory nidamental gland of the squid *Loligo opalescens* via horizontal transmission. *Biol. Bull.* **194**, 36–43 (1998).
98. Barbieri, E. et al. Phylogenetic characterization of epibiotic bacteria in the accessory nidamental gland and egg capsules of the squid *Loligo pealei* (Cephalopoda: Loliginidae). *Environ. Microbiol.* **3**, 151–167 (2001).
99. Nilsson, M., Rasmussen, U. & Bergman, B. Cyanobacterial chemotaxis to extracts of host and nonhost plants. *FEMS Microbiol. Ecol.* **55**, 382–390 (2006).
100. Orphan, V. J., House, C. H., Hinrichs, K.-U., McKeegan, K. D. & DeLong, E. F. Methane-consuming Archaea revealed by directly coupled isotopic and phylogenetic analysis. *Science* **293**, 484–487 (2001).
101. Hentschel, U., Steinert, M. & Hacker, J. Common molecular mechanisms of symbiosis and pathogenesis. *Trends Microbiol.* **8**, 226–231 (2000).
102. Chaban, B., Hughes, H. V. & Beeby, M. The flagellum in bacterial pathogens: for motility and a whole lot more. *Semin. Cell Dev. Biol.* **46**, 91–103 (2015).
103. Butler, S. M. & Camilli, A. Going against the grain: chemotaxis and infection in *Vibrio cholerae*. *Nat. Rev. Microbiol.* **3**, 611 (2005).
104. Allweiss, B., Dostal, J., Carey, K. E., Edwards, T. F. & Freter, R. The role of chemotaxis in the ecology of bacterial pathogens of mucosal surfaces. *Nature* **266**, 448 (1977).

105. Bordas, M. A., Balebona, M. C., Rodriguez-Maroto, J. M., Borrego, J. J. & Moriñigo, M. A. Chemotaxis of pathogenic *Vibrio* strains towards mucus surfaces of gilt-head sea bream (*Sparus aurata* L.). *Appl. Environ. Microbiol.* **64**, 1573–1575 (1998).
106. Austin, B. & Austin, D. A. *Bacterial Fish Pathogens* (Springer, 2012).
107. Austin, B. & Zhang, X. H. *Vibrio harveyi*: a significant pathogen of marine vertebrates and invertebrates. *Lett. Appl. Microbiol.* **43**, 119–124 (2006).
108. Josenhans, C. & Suerbaum, S. The role of motility as a virulence factor in bacteria. *Int. J. Med. Microbiol.* **291**, 605–614 (2002).
109. Angus, A. A. et al. Plant-associated symbiotic *Burkholderia* species lack hallmark strategies required in mammalian pathogenesis. *PLOS ONE* **9**, e83779 (2014).
110. Krause, A. et al. Complete genome of the mutualistic, N_2-fixing grass endophyte *Azoarcus* sp. strain BH72. *Nat. Biotechnol.* **24**, 1384 (2006).
111. Bertalan, M. et al. Complete genome sequence of the sugarcane nitrogen-fixing endophyte *Gluconacetobacter diazotrophicus* Pal5. *BMC Genomics* **10**, 450 (2009).
112. Kaneko, T. et al. Complete genomic structure of the cultivated rice endophyte *Azospirillum* sp. B510. *DNA Res.* **17**, 37–50 (2010).
113. Fouts, D. E. et al. Complete genome sequence of the N_2-fixing broad host range endophyte *Klebsiella pneumoniae* 342 and virulence predictions verified in mice. *PLOS Genet.* **4**, e1000141 (2008).
114. Mitter, B. et al. Comparative genome analysis of Burkholderia phytofirmans PsJN reveals a wide spectrum of endophytic lifestyles based on interaction strategies with host plants. *Front. Plant Sci.* **4**, 120 (2013).
115. Yan, Y. et al. Nitrogen fixation island and rhizosphere competence traits in the genome of root-associated Pseudomonas stutzeri A1501. *Proc. Natl Acad. Sci. USA* **105**, 7564–7569 (2008).
116. Taghavi, S. et al. Genome sequence of the plant growth promoting endophytic bacterium *Enterobacter* sp. 638. *PLOS Genet.* **6**, e1000943 (2010).
117. Sourjik, V. et al. Mapping of 41 chemotaxis, flagellar and motility genes to a single region of the *Sinorhizobium meliloti* chromosome. *Gene* **223**, 283–290 (1998).
118. Crossman, L. C. et al. A common genomic framework for a diverse assembly of plasmids in the symbiotic nitrogen fixing bacteria. *PLOS ONE* **3**, e2567 (2008).
119. Han, J.-I. et al. Complete genome sequence of the metabolically versatile plant growth-promoting endophyte *Variovorax paradoxus* S110. *J. Bacteriol.* **193**, 1183–1190 (2011).
120. Gärdes, A. et al. Complete genome sequence of *Marinobacter adhaerens* type strain (HP15), a diatom-interacting marine microorganism. *Stand. Genomic Sci.* **3**, 97–107 (2010).
121. Moran, M. A. et al. Ecological genomics of marine roseobacters. *Appl. Environ. Microbiol.* **73**, 4559–4569 (2007).
122. Hendry, T. A., de Wet, J. R., Dougan, K. E. & Dunlap, P. V. Genome evolution in the obligate but environmentally active luminous symbionts of flashlight Fish. *Genome Biol. Evol.* **8**, 2203–2213 (2016).
123. Ruby, E. G. et al. Complete genome sequence of *Vibrio fischeri*: a symbiotic bacterium with pathogenic congeners. *Proc. Natl Acad. Sci. USA* **102**, 3004–3009 (2005).
124. Stephens, W. Z. et al. Identification of population bottlenecks and colonization factors during assembly of bacterial communities within the Zebrafish intestine. *mBio* **6**, e01163–15 (2015).
125. McCuaig, B., Pena-Castillo, L. & Dufour, S. C. Metagenomic analysis suggests broad metabolic potential in extracellular symbionts of the bivalve Thyasira cf. gouldi. Preprint at *bioRxiv* https://www.biorxiv.org/content/10.1101/330373v1 (2018).
126. Perez, M. & Juniper, S. K. Insights into symbiont population structure among three vestimentiferan tubeworm host species at eastern pacific spreading centers. *Appl. Environ. Microbiol.* **82**, 5197–5205 (2016).
127. Goffredi, S. K. et al. Genomic versatility and functional variation between two dominant heterotrophic symbionts of deep-sea *Osedax* worms. *ISME J.* **8**, 908 (2013).
128. Nakagawa, S. et al. Allying with armored snails: the complete genome of gammaproteobacterial endosymbiont. *ISME J.* **8**, 40 (2013).
129. Neave, M. J., Michell, C. T., Apprill, A. & Voolstra, C. R. Endozoicomonas genomes reveal functional adaptation and plasticity in bacterial strains symbiotically associated with diverse marine hosts. *Sci. Rep.* **7**, 40579 (2017).
130. Woyke, T. et al. Symbiosis insights through metagenomic analysis of a microbial consortium. *Nature* **443**, 950 (2006).
131. Nunoura, T. et al. Physiological and genomic features of a novel sulfur-oxidizing gammaproteobacterium belonging to a previously uncultivated symbiotic lineage isolated from a hydrothermal vent. *PLOS ONE* **9**, e104959 (2014).
132. Dmytrenko, O. et al. The genome of the intracellular bacterium of the coastal bivalve. *Solemya velum*: a blueprint for thriving in and out of symbiosis. *BMC Genomics* **15**, 924 (2014).
133. Shibata, T. F. et al. Complete genome sequence of Burkholderia sp. strain RPE64, bacterial symbiont of the bean bug Riptortus pedestris. *Genome Announc.* **1**, e00441–13 (2013).
134. Takeshita, K. et al. Whole-genome sequence of Burkholderia sp. strain RPE67, a bacterial gut symbiont of the Bean Bug Riptortus pedestris. *Genome Announc.* **2**, e00556–14 (2014).
135. Ueda, K. et al. Genome sequence of *Symbiobacterium thermophilum*, an uncultivable bacterium that depends on microbial commensalism. *Nucleic Acids Res.* **32**, 4937–4944 (2004).
136. Warshan, D. et al. Genomic changes associated with the evolutionary transitions of *Nostoc* to a plant symbiont. *Mol. Biol. Evol.* **35**, 1160–1175 (2018).
137. Patterson, A. M. et al. Human gut symbiont Roseburia hominis promotes and regulates innate immunity. *Front. Immunol.* **8**, 1166 (2017).

Acknowledgements
This research was funded in part by the Gordon and Betty Moore Foundation Marine Microbiology Initiative, through grant GBMF3801 to J.R.S. and R.S. and an Investigator Award (GBMF3783) to R.S., as well as through an Australian Research Council grant (DP180100838) to J.R.S. and J.-B.R., an Australian Research Council Fellowship (DE160100636) to J.-B.R. and a grant from the Simons Foundation (542395) to R.S. as part of the Principles of Microbial Ecosystems (PriME) Collaborative.

Author contributions
V.F., B.L. and J.-B.R. researched data for the article. V.F. carried out the theoretical component of this work. All authors contributed substantially to discussion of the content, wrote the article and reviewed and edited the manuscript before submission.

Competing interests
The authors declare no competing interests.

Publisher's note
Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Reviewer information
Nature Reviews Microbiology thanks Y. Kikuchi, M. Mandel and the other anonymous reviewer(s) for their contribution to the peer review of this work.

Supplementary information
Supplementary information is available for this paper at https://doi.org/10.1038/s41579-019-0182-9.