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Trends in Microbiology

Review

Intermicrobial Hitchhiking: How Nonmotile Microbes Leverage Communal Motility

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Motility allows many microbes to traverse their environment to find nutrient sources or escape unfavorable environments. However, some microbes are nonmotile and are restricted to their immediate conditions. Intriguingly, sporadic reports have demonstrated that many nonmotile microbes can utilize the motility machinery of other microbes in their vicinity. This form of transportation, called hitchhiking, has been observed with both prokaryotic and eukaryotic microbes. Importantly, many hitchhiking microbes are pathogenic to humans or plants. Here, we discuss reports of intermicrobial hitchhiking to generate a comprehensive view of hitchhiking mechanisms and how such interactions may influence human and plant health. We hypothesize that microbial hitchhiking is ubiquitous in nature and may become the subject of an independent subfield of research in microbiology.

Highlights

Sporadic reports demonstrate that some nonmotile microbes utilize trans-species hitchhiking to traverse their environment.

Hitchhiking has been observed with eukaryotic and prokaryotic microbes.

Four general hitchhiking mechanisms have been elucidated thus far: mechanical pushing by motile cells, direct attachment to cell bodies, direct attachment to bacterial flagella, and internal transport by cells.

Several immotile human and plant pathogens hitchhike motile microbes that are natively found in their vicinity.

In some instances, hitchhiking is implicated in infectivity mechanisms of microbial pathogens.

Motility Behaviors of Motile and Nonmotile Microbes

Cell motility is responsible for a variety of complex and fascinating behaviors that are crucial for survival. Many free-living motile microbes utilize motility machinery to traverse their environment to find optimal conditions. For microbial pathogens, this same process is often utilized to invade host tissues [1,2]. To combat such invading microbes, some types of immune cells also employ motility to chase and destroy these pathogens [3,4]. Cells utilize different machineries for motility depending on the specific organism and environment. In liquid environments, cells can propel themselves through **swimming** (see Glossary) motility via rotating or beating extracellular filamentous appendages called flagella and cilia [5,6]. On surfaces, cells can move by utilizing other motile behaviors such as **crawling**, **gliding**, **sliding**, **swarming**, or **twitching** [5,6]. Many of these behaviors depend on a process called chemotaxis which allows the cell to sense its chemical environment and control its movement toward favorable molecules such as nutrients or away from deleterious compounds [2–4,7].

Although these forms of motility are present in diverse organisms, some microbes are nonmotile and lack any such machinery or are nonmotile under certain conditions. However, emerging research has identified a unique form of dispersal used by many microbes – hitchhiking on motile microbes. Hitchhiking allows otherwise nonmotile microbes to traverse their environment by effectively using the motility machinery of the motile partner. Remarkably, hitchhiking behavior has been revealed in both prokaryotic and eukaryotic microbes, and four general mechanisms have been elucidated: mechanical pushing by motile cells, direct attachment to cell bodies, direct attachment to bacterial flagella, and internal transport by cells. Here, we discuss reports of intermicrobial hitchhiking mechanisms that occur across taxonomic kingdoms and consider their potential impacts on human and plant health. However, it should be noted that microbes can also be transported by small animals [8–10], large animals [11,12], abiotic waste materials [13,14], and weather perturbations [15]. Additionally, phage particles can be transported by motile bacteria, but those findings [16] will not be discussed here.

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Reports of Microbial Hitchhiking

Hitchhiking among Bacteria

Transport via hitchhiking occurs among bacteria found in the soil [17–19], on plant tissues [17–19], on abiotic surfaces [18,20], and in human tissues [20–22]. Hitchhiking is advantageous to nonmotile microbes that would otherwise occupy a single location and can also be favorable to the motile partner. For example, the soil-dwelling motile bacterium *Paenibacillus vortex* is noted for its 'hyper-swarming' behavior. *P. vortex* can swarm on hard surfaces, whereas most other bacteria are nonmotile under such conditions. To aid in its migration, *P. vortex* is able to carry antibiotic-resistant nonmotile bacterial 'cargo' at the leading edge of the swarm (Figure 1A, Key Figure) [23]. As the cargo degrades antibiotics to nonlethal substances, the trailing *P. vortex* swarm can then occupy the previously toxic niche. *P. vortex* can effectively carry many nonmotile bacteria as cargo (nonmotile strains of *Escherichia coli, Klebsiella pneumoniae,* and *Enterobacter aerogenes*) and this cotransport can be advantageous as long as the cargo possesses the antibiotic resistance necessary for survival in the new niche [23].

Key Figure

An Illustrated Overview of Microbial Hitchhiking Reports

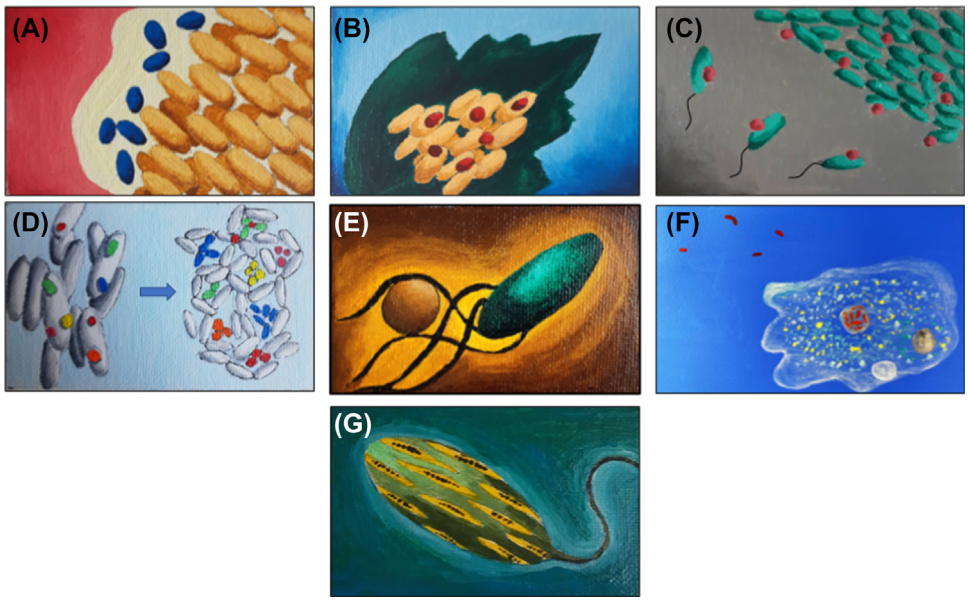

Figure 1. (A) *Paenibacillus vortex* and *Acinetobacter baylyi* (orange cells) can push immotile bacteria at the colony's leading edge (blue cells). *P. vortex* can push antibiotic-resistant cells (blue cells) at the colony's front, and these cells hydrolyze antibiotics (red background) to nonlethal substances (white background). (B) *P. vortex* (orange cells) can serve as a raft for the phytopathogen *Xanthomonas perforans* (red cells) for transport across plant leaves. (C) Staphylococci (pink cells) can attach to the cell body of motile bacteria (teal cells) and form communal biofilms with the motile partners. (D) *Capnocytophaga gingivalis* (gray cells) can transport various immotile microbes (multicolored cells) to establish communal biofilms with specific spatial features (right). (E) The immotile spores of the bacterium *Streptomyces* and the fungus *Aspergillus* (brown cell) are transported by swarming bacteria (blue cell) via direct attachment to flagella. (F) *Legionella pneumophila* (red cells) are aquatic bacteria that are free-living or infect amoebae (white cell). (G) Immotile Deltaproteobacteria (yellow cells) that possess ferromagnetic particles (black dots) can adhere to the surface of some protists (green organism) to create a microbial consortium that is capable of magnetotaxis.

Glossary

Crawling: a form of cell motility that occurs on surfaces through the extension and retraction of filaments located at the leading edge of the cell. For eukaryotes, these filaments are composed of the protein actin. For bacteria, this movement involves type IV pili and is specifically called 'twitching motility' (see later).

Gliding: a form of microbial motility that occurs on surfaces and does not depend on propulsive structures. Although this form of motility is still only partially understood it is proposed that gliding is accomplished by the contraction and relaxation of cell walls via specialized transmembrane proteins. Other gliding bacteria are thought to propel themselves through forces generated by the secretion of polysaccharides.

Sliding: a passive form of bacterial motility that relies on forces generated from an expanding colony.

Swarming: a form of bacterial motility that occurs on surfaces through the rotation of flagella. Swarmer cells possess multiple flagella which continuously rotate to propel the cell forward.

Swimming: a form of cell motility that occurs in liquid environments through the rotation or beating of flagella or cilia.

Twitching: a form of bacterial motility that occurs on surfaces and within biofilms through the extension and retraction of type IV pili.

It is still unclear how the cargo is transported by *P. vortex*. While there is some indication that the cargo may interact with *P. vortex* flagella, the cargo may also be mechanically pushed by the *P. vortex* at the leading edge of the swarm. Indeed, a recent study has found that, in the presence of crawling *Acinetobacter baylyi*, hitchhiking *E. coli* cells are always found at the leading edge of the growing *A. baylyi* colony [24]. The presence of *E. coli* at the colony boundary creates instabilities in the region that ultimately result in the formation of macroscopically visible flower-like patterns of the *E. coli* cells. Comigration experiments and computational modeling of these patterns suggest that *E. coli* is kept at the leading edge by pushing and bumping forces generated by the *A. baylyi* cells (Figure 1A) [24]. Nevertheless, the presence of similar migration patterns among these diverse bacteria suggests that hitchhiking bacterial migration at the colony leading edge may be a common occurrence in nature.

In addition to carrying antibiotic-resistant cargo, *P. vortex* can also carry the phytopathogenic bacterium *Xanthomonas perforans* [17]. Unlike *P. vortex, X. perforans* is nonmotile on hard surfaces. Remarkably, *X. perforans* is able to attract leaf-dwelling *P. vortex* to its immediate location on the leaves through the secretion of airborne volatile compounds. The *P.* vortex then disperses *X. perforans* across the leaf, potentially helping it to infect plant tissues [17]. Scanning electron microscopy images show that swarming *P. vortex* cells form multilayered 'rafts' and that the *X. perforans* cells are localized on top of these rafts, indicating that the nonmotile cells may 'surf' on them for dispersal (Figure 1B) [17]. However, it is unclear if the *X. perforans* cells preferentially attach to a specific location or feature on the *P. vortex* cells, such as flagella or the cell wall.

P. vortex is not the only bacterium that serves as a raft for riding hitchhikers. In a similar fashion, *Capnocytophaga gingivalis*, which is an opportunistic pathogen found in the human oral microbiome, can disperse several nonmotile bacteria commonly associated with periodontal diseases [22]. *C. gingivalis* forms multilayered colonies that glide on top of one another. Microscopic examination of living bacterial communities demonstrates that several species of nonmotile bacteria (*Porphyromonas endodontalis, Prevotella oris, Parvimonas micra, Actinomyces* sp. *Taxon-169, Fusobacterium nucleatum, Streptococcus sanguinis,* and *Veillonella parvula*) attach directly to the *C. gingivalis* cell body and continuously circulate from one cell pole to the other during transport (Figure 1C) [22]. The observed attachment and circulation pattern are due to the presence of polysaccharide-binding protein, SprB, on the *C. gingivalis* cell surface. This protein interacts with the cell wall of the hitchhiking bacteria. Collectively, these interactions allow substantial transport of the hitchhikers and facilitate specific spatial organizations of the microbial communities that establish over time [22].

Hitchhiking by nonmotile opportunistic pathogens has also been reported in some staphylococcal species (*Staphylococcus aureus* and *Staphylococcus epidermidis*) [20]. These bacteria are able to adhere directly to the cell bodies of swimming bacteria (*Pseudomonas aeruginosa* and *Escherichia coli*) for transport and are subsequently associated with biofilms made by their mobile partners (Figure 1D) [20]. This interaction allows *S. aureus* and *S. epidermidis* to colonize niches that are otherwise inaccessible to them.

In the studies discussed thus far, the hitchhikers were metabolically active bacteria. However, nonmotile bacterial spores from streptomycetes are also capable of hitchhiking on motile bacteria [19]. Spores from several *Streptomyces* species (*Streptomyces coelicolor*, *Streptomyces tendae*, *Streptomyces griseus*, and *Streptomyces scabies*) are able to attach directly to the flagella of swarming soil bacteria (*Bacillus subtilis* and *Pseudomonas fluorescens)* and are translocated to plant tissues where they can germinate (Figure 1E). Dispersal can occur over long distances

(at least 10 cm). The interaction between flagella and spores is facilitated by two spore coat proteins, RdlA and RdlB, that compose the spore coat rodlet layer [19,25].

Comigration of Bacteria and Fungi

Analogous to the transportation of *Streptomyces* spores, the nonmotile conidia (fungal spores) from some *Aspergillus* and *Penicillium* species also hitchhike on swarming soil-dwelling bacteria via direct attachment to flagella (Figure 1E) [18]. While several motile bacteria have been tested for their capacity to transport the fungal spores, *P. vortex* is the most efficient, and it can disperse the spores across large distances (up to 30 cm). The flagellar interaction with the spores is abrogated by perturbations to the protein coat, which also possesses a rodlet layer. In exchange for spore dispersal, the swarming *P. vortex* is able to cross air gaps due to 'bridges' formed by elongated fungal hyphae, and can thus occupy new niches [18].

Indeed, several studies have found that various species of fungi and bacteria comigrate across so-called 'fungal highways' that span air gaps [26–28]. In these instances, bacteria use their intrinsic motility to cross the mycelia bridges. To date, transport of fungal spores by these species has not been reported. However, there is evidence that bacterial migration may be facilitated by first actively attaching to the tip of emerging fungal hyphae using a type III secretion system. They are then translocated along with the growing hyphae [27,28]. Collectively these studies suggest that fungi and bacteria may act alternatively as transporter and hitchhiker at various stages of their comigration.

Bacterial Transport by Protozoans

There have been reports of bacterial hitchhiking with protozoans that occur by internalization or direct attachment to the surface of the organism. The former mechanism is illustrated by the interaction of the pathogenic bacterium *Legionella pneumophila* with its amoebae hosts [21]. Motile *L. pneumophila* is found in aquatic environments, either in a free-living state or residing inside aquatic amoebae (e.g., *Acanthamoeba* and *Naegleria*), within which the bacteria replicate. Although infected amoebae present 'sickly' phenotypes, microscopic examination shows that they remain motile and carry the internalized *L. pneumophila* (Figure 1F) [21].

Hitchhiking mechanisms with protista can also be symbiotic, as seen with the interaction between aquatic Deltaproteobacteria and Excavata (Symbiontida and Euglenozoa) [29]. The Deltaproteobacteria are capable of synthesizing intracellular ferrimagnetic nanoparticles, which are utilized by magnetotactic bacteria – bacteria that can sense magnetic fields and move in response to them [30]. However, the Deltaproteobacteria are nonmotile. Although the bacteria do not possess their own motility system, they attach themselves to the surface of the protist so that the linear ferrimagnetic particles are aligned to its motility axis, effectively making the protist magnetotactic (Figure 1G) [29]. This may allow the resulting consortium of organisms to move toward niches with favorable redox and chemical environments while the bacteria also are protected from protozoan predators.

Drawing Insights and Parallels among Hitchhiking Mechanisms

In the instances of microbe–microbe transport discussed here, many motile partners are chemotactic, including: *P. vortex* [31], *A. baylyi* [32], *P. aeruginosa* [33], *E. coli* [34], *B. subtilis* [35], *P. fluorescens* [36], *Acanthamoeba* species [37], and *Naegleria* species [38]. These microbes sense favorable conditions and move towards them, bringing their hitchhiking guests along. Hitchhiking to such motile partners may effectively allow the nonmotile microbes to utilize the chemotaxis machinery of their host to reach their preferred microenvironment. A clear example of this is the *Streptomyces* spores that are produced on the soil surface but germinate and thrive near nutrient-rich plant roots that attract their transporters [19,39].

Since hitchhikers can utilize the motility machinery of other microbes, the question arises whether some nonmotile bacteria have 'chosen' not to evolve their own motility machinery and instead evolve hitchhiking mechanisms. Although there is no evidence for this specific idea yet, there are reports of microbes that may have lost their motility machinery because it is metabolically costly and no longer necessary [40,41]. For instance, the spores of some fungi, called zoospores, as well as spores of the bacterium *Actinoplanes missouriensis*, are flagellated and chemotactic to enable dispersal [42–44]. But upon germination, the organisms no longer express motility proteins as they are not needed for survival [42–44]. Additionally, bioinformatics studies of the Methylophilaceae family of bacteria reveal that ancestors of these microbes were motile and chemotactic but as they evolved to occupy a new niche, those genes became inactive [45].

Microbial hitchhiking occurs by four general mechanisms. Remarkably, the hyperswarmer *P. vortex* seemingly employs three of them: potential pushing of antibiotic-resistant cargo [23], cell body interaction with *X. perforans* [17] (in the form of rafts), and attachment of spores to *P. vortex* flagella [18]. Many other swarming bacteria were tested for their ability to move resistant cargo and fungal spores, but *P. vortex* was by far the most efficient transporter in all cases [18,23]. The apparent low-specificity of cargo for *P. vortex* could be a result of its unique swarming method; *P. vortex* swarms consist of multiple layers of tightly packed cells that move with stable connections to their neighbors [31]. Therefore, a multitude of cargo can become ensnared by this moving barrier and carried in the direction of the swarm. *P. vortex* can also move micro-beads of vastly different sizes (1–20 μm) without covalent attachment, which further supports the idea of nonspecific cargo transport [31].

However, it is also possible that some microbes have evolved to specifically hitchhike onto *P. vortex* because it is motile on hard surfaces where most other bacteria are immobilized. This certainly appears to be the case for *X. perforans* [17]. The volatile compounds emitted by *X. perforans* can even induce swarming in laboratory-cultivated *P. vortex* strains that had seemingly lost swarming capabilities [17]. Additionally, some fungal conidia possess unidentified coat proteins that facilitate transport by *P. vortex*, suggesting that some coat proteins may have evolved for this function [18].

Low-specificity cargo carrying is also demonstrated by the following examples: swimming *P. aeruginosa* can transport polystyrene beads [20], *C. gingivalis* can transport numerous nonmotile bacteria [22] , and certain Gram-positive and Gram-negative bacteria can transport *Streptomyces* spores [19]. But is there an evolutionary advantage for a motile organism to participate in low-specificity hitchhiking? Many studies have shown that organisms within diverse microbiomes receive advantages from their neighbors, such as: sensing of environmental chemicals, metabolic symbiosis of adjacent microbes, communal sharing of excreted molecules, and communal antibiotic resistance [46–49]. Therefore, low-specificity hitchhiking may assist in the formation of a highly diverse microbiome, which may provide a direct benefit for the motile partner. Indeed, the hitchhiking study with *C. gingivalis* directly illustrates that coincubation with nonmotile bacteria eventually leads to the establishment of communal biofilms. The resulting communities possess specific spatial organizations that, in turn, benefit the entire consortium [22,49].

There are obvious parallels between the transport of bacterial *Streptomyces* spores and fungal spores from *Aspergillus fumigatus*, *Aspergillus niger*, and *Penicillium*. Both spore types attach directly to the flagella of motile bacteria via spore coat proteins. In the *Streptomyces* system, these proteins have been identified as the rodlins (RdlA and RdlB) that produce the outermost surface layer of the spores, called the rodlet layer. Although the fungal spore coat component(s)

involved in transport were not identified, an analogous rodlet layer is also present on *Aspergillus* and *Penicillium* spores [50,51]. Together, these data suggest that prokaryotic and eukaryotic rodlet layers may have convergently evolved as a mechanism for spore dispersal. Transport of fungal spores is also beneficial for the motile partner, in this case *P. vortex*, as the fungus provides 'fungal highways' of hyphae that allow the bacteria to cross air gaps [18,26,27]. Although streptomycetes are bacterial, they form filamentous colonies with hyphae that are structurally similar to fungal hyphae [52]. Therefore, streptomycetes may also be able to provide 'bacterial highways' of hyphae to their motile carriers but such an occurrence has not been reported.

Potential Impacts on Human Health

Bacterial hitchhiking has been observed with opportunistic pathogens that impose health risks to humans with compromised immune systems. Hitchhiking staphylococcal species (*S. aureus* and *S. epidermidis*) and *A. fumigatus* spores are notably pervasive opportunistic pathogens. These microbes are commonly found on household surfaces and medical supplies [53,54]. While it is unknown if or how hitchhiking capabilities may affect pathogenicity, it may allow these microbes to spread and survive longer on abiotic surfaces via increased access to nutrients. This would especially impose difficulties in medical settings where staphylococcal infections are commonly acquired [54]. More speculations could lead one to propose that hitchhiking by these microbes may be involved in invasion of host tissues. This could feasibly occur by hitchhiking of these pathogenic organisms onto microbes found in the hosts' native microbiome or onto motile cells of the host (such as macrophages and neutrophils). Although there is no evidence to support such conjectures yet, it is well established that motility is essential for the infection mechanisms of diverse pathogens [1,2,55,56].

Recent research has demonstrated that combined infections by *A. fumigatus* and *P. aeruginosa* are common in the lung tissues of cystic fibrosis patients [57]. *A. fumigatus* infections occur by inhalation of nonmotile spores, which are ubiquitous in the air. Motile *P. aeruginosa* is prevalent in moist environments and can be inhaled as aerosolized water droplets. Infection by these organisms is synergistic; coinfection increases the severity of infections of both microbes [57]. As *A. fumigatus* spores can be transported by *P. vortex* via flagellar adherence, it is possible that they may also utilize *P. aeruginosa* for transport. *P. aeruginosa* is capable of transporting staphylococci and polystyrene beads, suggesting low cargo specificity [20]. As discussed, *A. fumigatus* has been shown to produce 'fungal highways' that can assist in bacterial migration [18]. Therefore, *A. fumigatus* spores may be transported by *P. aeruginosa* and, in turn, germinated *A. fumigatus* colonies could provide *P. aeruginosa* migration assistance through the formation of fungal highways. Could such hypothesized cotransport of both organisms contribute to the observed synergy of coinfections in lung tissues? Although such interactions have not been reported to date, several *in vitro* studies have demonstrated that these microbes can stimulate each other's growth [57–61].

Studies with the opportunistic oral pathogen *C. gingivalis* demonstrate that hitchhiking is involved in the formation of communal biofilms with nonmotile bacteria. In this case, the nonmotile bacteria are also opportunistic pathogens that are often found in the human oral microbiome. In *C. gingivalis* infections, the bacterium is present in plaques in the host oral cavity that result in destruction of tooth-supporting structures. These plaques do not just consist of *C. gingivalis* but also other pathogenic bacteria, including nonmotile bacteria that hitchhike on *C. gingivalis* (*P. endodontalis*, *Prevotella oris*, *Parvimonas micra*, *Actinomyces* sp. *Taxon-169*, *F. nucleatum*, *S. sanguinis*, and *V. parvula*) [22,49]. As adherence of the nonmotile bacteria to *C. gingivalis* is necessary for the formation of plaque-like biofilms *in vitro*, it is very likely that hitchhiking is directly

involved in the formation and organization of plaques and the pathogenicity of these nonmotile bacteria [22]. Interestingly, the motile oral pathogen *Treponema denticola* is also able to attach to nonmotile oral bacteria through a sheath protein, but transport of the nonmotile microbes by this pathogen has not been reported [62].

Not all hitchhiking pathogens are normally found in the human body – the aquatic bacterium *L. pneumophila* is the causative agent of legionellosis in humans, also known as Legionnaire's disease. *L. pneumophila* infects humans when contaminated aerosolized water droplets are inhaled [63]. Once in the lung tissue, the bacterium infects amoeboid macrophage cells, a cell type of the immune system that is extremely motile [64]. Interestingly, the *L. pneumophila* infection mechanisms are remarkably similar for both of their hosts: amoebae protist and mammalian macrophages [65]. Continuous replication of the bacteria occurs inside the living macrophage until the macrophage bursts, thereby releasing the free bacteria in the lung tissue. Live microscopy experiments demonstrate that *L. pneumophila*-infected macrophages remain motile immediately after infection under *in vitro* conditions [66]. It is unknown if motility is affected at later time points, but infected macrophages can survive at least 14 h postinfection [67]. Therefore, it is possible that internal transport by macrophages may exacerbate infections by releasing *L. pneumophila* to new locations within the host.

Potential Impacts on Plant Health

Plants also possess associated microbiomes. The microbes can be beneficial or harmful to the plant tissues they are associated with. Studies have shown that colonization of plant roots by *Streptomyces* colonies protects the plant from potential phytopathogens [39,68,69]. This protection comes from antibiotics that are produced by germinated *Streptomyces* to ward off microbial competitors [39]. In addition to *Streptomyces* spores, the spores of *Aspergillus niger* also hitchhike onto motile soil bacteria, and this fungus is a plant pathogen [70]. Like streptomycetes, the germinated fungal spores thrive near plant tissues. However, the fungus does not protect plants but is responsible for many plant rot diseases, including those of crop plants. Hitchhiking microbial spores may thus confer both positive and negative effects on plant health.

The bacterium *X. perforans* is a plant pathogen that causes blight of several crop plants [71]. The bacterium enters plant leaves through open stomata or wounds, and replicates using host nutrients. Although it is motile in moist environments, it cannot move on hard surfaces such as dry plant leaves. Instead, it seemingly uses the motility machinery of *P. vortex* for dispersal on plant surfaces, presumably to find openings on the plant leaves for infection. The fact that *X. perforans* has evolved volatile compounds to attract *P. vortex* indicates that hitchhiking on *P. vortex* is of particular importance to the survival of *X. perforans*, likely due to the support rendered by the former to the latter's pathogenicity.

Concluding Remarks

Microbial hitchhiking has been observed in diverse prokaryotes and eukaryotes, suggesting that such interactions are ubiquitous in nature. Remarkably, all reports of microbe–microbe hitchhiking, with the exception of *L. pneumophila*'s transport by amoebae, were made within the last decade. As methods for studying multiplex biological systems advance, it is likely that emerging research will elucidate the pervasiveness of microbial hitchhiking in natural settings. In most reported instances, the molecular components and physiological interactions that underlie hitchhiking are unclear. We predict that intermicrobial hitchhiking will develop into an independent subfield in microbiology and such ambiguities will be elaborated. Collectively, these insights may help to identify infection mechanisms for pathogens and underscore the importance of examining microbes in the context of their native microbiomes (see Outstanding Questions).

Outstanding Questions

How pervasive is microbial hitchhiking in nature?

Have some immotile microbes evolved hitchhiking mechanisms instead of motility machinery?

What advantages are there for motile organisms to act as 'taxis' for hitchhikers?

What are the molecular components that underlie observed hitchhiking interactions?

How does hitchhiking contribute to the survival of the nonmotile partner?

Is intermicrobial hitchhiking important for the establishment and survival of microbiomes?

Does hitchhiking contribute to the infectivity or pathogenicity of nonmotile pathogens?

Do *Aspergillus* spores utilize the spore rodlet layer for hitchhiking?

Can streptomycetes form 'bacterial highways' that serve a similar function to 'fungal highways'?

Are *A. fumigatus* spores dispersed by *P. aeruginosa*, the common copathogens of cystic fibrosis patients?

Does the oral pathogen *T. denticola* participate in hitchhiking interactions?

Is the pathogen *L. pneumophila* internally transported by macrophage cells?

Does the presence of *P. vortex* contribute to the pathogenicity of *X. perforans*?

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