MICROBIOLOGY AND MOLECULAR BIOLOGY REVIEWS, Dec. 2011, p. 583–609 Vol. 75, No. 4
1092-2172/11/$12.00 doi:10.1128/MMBR.00020-11

Bacterial-Fungal Interactions: Hyphens between Agricultural, Clinical, Environmental, and Food Microbiologists

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INTRODUCTION

Historically, the classical separation of microbiological research between bacteriologists and mycologists has led to the study of bacteria and fungi in axenic settings. This compartmentalization has overlooked the fact that in many environments, bacteria and fungi coexist and interact. Furthermore, these bacterial-fungal interactions (BFIs) often have important ramifications for the biology of the interacting partners. In recent years, research in this area has developed significantly in both breadth and depth. Contemporary studies have revealed that fungi and bacteria often form physically and metabolically interdependent consortia that harbor properties distinct from those of their single components (379). These reports have also highlighted the multiple practical relevancies of these interac-

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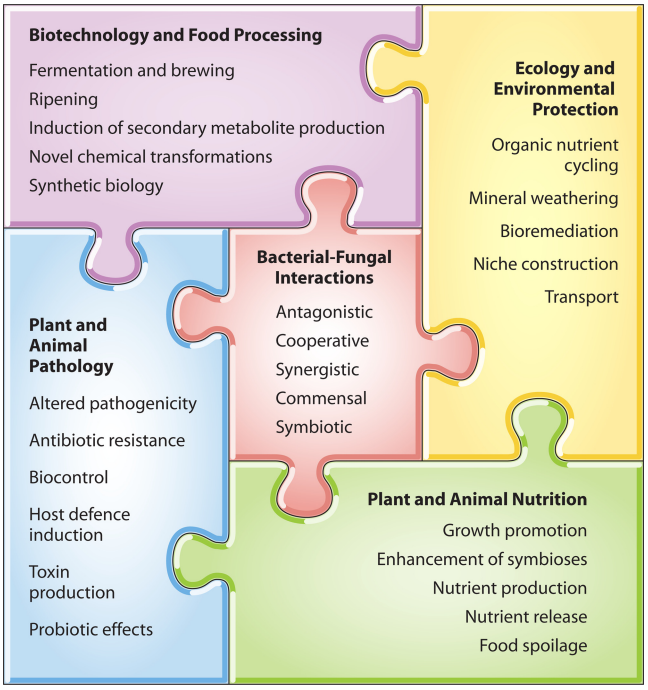

FIG. 1. Relevance of BFIs to different areas of scientific study.

tions (Fig. 1) to an exceptionally diverse variety of fields, including agriculture, forestry, environmental protection, food processing, biotechnology, medicine, and dentistry (119, 120, 200, 397).

In each of the disciplines for which BFIs are important, research has progressed somewhat differently. This is likely a reflection of their distinct contexts but also a reflection of a lack of interactions among researchers working in these different areas. However, many commonalities exist among the BFIs in these different settings, and a greater appreciation of them would help scientists to identify potentially relevant studies outside their normal specialty, a step that is often important when searching for new ideas, hypotheses, methods, or collaborators. Here we attempt to bridge this gap by integrating advances in research from all these fields into a single source. By not focusing exclusively on one area of application, we seek to achieve a novel unifying perspective on BFIs that enables the identification of fundamental themes, mechanisms, and areas of mutual interest. Given the burgeoning research field, it is an ideal time to attempt such an appraisal, as it will soon become impossible to integrate these many facets into a single work.

In this review, we will consider a BFI as a scenario in which the fungus or bacterium has a direct effect on the other microorganism, thus excluding situations of mere physical proximity. We will also exclude situations in which the effect of one partner on the other is mediated solely through a third organism, such as the systemic induction of plant immunity (151). We will occasionally draw upon examples involving oomycetes, which, while not true fungi in a phylogenetic sense, often share similar general morphologies and ecological niches. The BFI theme will be considered at three levels: the diversity of interactions between bacteria and fungi, the effects of bacterial-fungal consortia on other organisms and the environment, and, finally, their use for (or in) biotechnological applications. Thus, our objective is not to discuss in great depth very-well-known model systems but to attempt to give a wider perspective, revealing commonalities and differences that exist in different BFI contexts. Today, humankind faces many practical challenges relevant to BFIs that are important for health, food security, and sustainable ecosystem management. At the same time, technological developments look to be set to transform our ability to address these problems through science. So far, soil, plant, food, and animal bacteriologists and mycologists have neglected each other's research fields; we hope that this review will contribute to closer collaborations between them.

INTERACTIONS BETWEEN FUNGI AND BACTERIA

Associations between bacteria and fungi exist in many different contexts and can be considered from different perspectives (Fig. 2). In this section, we begin by describing the general characteristics of BFIs, reviewing the degrees of intimacy that are exhibited between the two partners in terms of their different physical associations. We then assess the various forms of molecular communication that occur in BFIs, which range from antibiosis and signaling to genetic exchange. Finally, we discuss the consequences that BFIs can have on the development and life cycles of bacteria and fungi. While not exhaustive, our examples have deliberately been drawn from a wide range of different contexts, both to emphasize the diversity of BFIs and to stimulate readers to consider other systems in which parallels to their own field may exist.

Physical Complexes between Bacteria and Fungi

Complexes containing bacteria and fungi are found in many distinct environments, such as the lungs of cystic fibrosis patients (31); the human oral cavity (16); the production of foods such as cheese, wine, tempeh, and sourdough (408); and agricultural and forest environments (119, 402). The physical associations between them can range from seemingly disordered polymicrobial communities to highly specific symbiotic associations of fungal hyphae and bacterial cells. The description of the taxonomic diversity of polymicrobial communities has gained fresh momentum from newly available DNA sequencing technologies that can resolve community structures to a high level. These methods are likely to provide new insights into bacterial and fungal community compositions, their associations, and also their responses to each other and the environment; for example, Rousk et al. recently demonstrated contrasting influences of soil pH on the bacterial and fungal communities (329). Mixed biofilms containing both fungi (filamentous or nonfilamentous) and bacteria can be considered to be a second, more intimate level of bacterial-fungal association. This arrangement differs from mixed communities, as in a biofilm, the microorganisms form structured communities held together by an extracellular matrix of microorganism-derived macromolecules that have physical and physiological properties distinct from those of free-living cells (99). Bacterial-fungal biofilms can exist as mixed complexes of the two, or fungi may provide biotic support for the establishment of a bacterial biofilm (166, 364). Bacterial-fungal contact and ad-

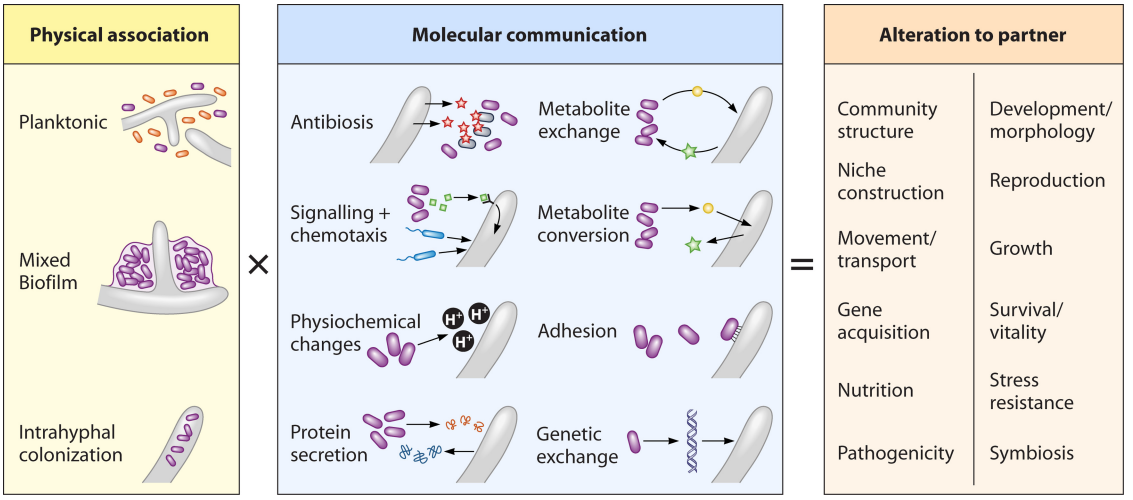

FIG. 2. The BFI equation. The combination of physical associations and molecular interactions between bacteria and fungi can result in a variety of different outcomes for each partner. In turn, these changes may affect the influence of the bacterial-fungal complex on their biotic and abiotic environment.

hesion are likely to be important early events in the process of the formation of mixed bacterial-fungal biofilms. Some specificity may exist in these interactions, depending on the cellular developmental and physiological status; for example, *Pseudomonas aeruginosa* is able to colonize the hyphal but not the yeast form of *Candida albicans*. Bacterial-fungal biofilm structures are an area of considerable interest in a clinical context owing to their prevalence in certain infections (166) and in medical devices such as catheters, prostheses, and mechanical ventilators (18, 309). Microorganisms occupying such structures typically show enhanced resistance to antibiotic therapies; for example, the presence of *C. albicans* has been shown to significantly enhance *Staphylococcus aureus* biofilm formation and its resistance to vancomycin in serum (153, 154). Mixed bacterial-fungal biofilms have also been reported in other contexts, such as mycorrhizal root systems (283, 334) and rice wine production (187), and are implicated in the degradation of historic artifacts such as mural paintings (136, 388).

The most intimate BFIs occur when the two partners establish a symbiosis. These symbioses can be classified as either an ectosymbiotic relationship, in which bacteria remain external to the fungal plasma membrane, or an endosymbiotic relationship, in which bacteria are located inside the fungal cell. A recently described example of the former is the association of certain *Klebsiella* and *Pantoea* species with the fungus gardens of leaf cutter ants (310). Cyanolichens, symbioses formed between fungi (typically ascomycetes, e.g., *Geosiphon pyriformis*) and photosynthetic cyanobacteria (typically belonging to *Nostoc* spp.), are also typically ectosymbiotic (196, 325). However, a clear example of a cyanolichen endosymbiotic relationship can also be found in the symbiosis between *Geosiphon pyriformis* and *Nostoc punctiforme* (196, 199). Nonphotosynthetic endobacteria and ectosymbiotic bacterial partners are also associated with cyanolichens, but their diversity is only beginning to be explored (29, 43, 61, 140, 141, 268, 272, 325, 355). While cyanobacteria are intracellular in the association between *Geosiphon pyriformis* and *Nostoc punctiforme*, they are enclosed in a specialized swollen multinucleate fungal "bladder" that is morphologically distinct from the rest of the hyphae, and within this bladder, the cyanobacteria are surrounded by a host-derived symbiosome membrane (199, 227). This arrangement differs from those of other BFIs involving endobacteria, such as those that occur between *Burkholderia* and *Rhizopus* hyphae (209), *Burkholderia* and *Mortierella elongata* (337), as well as a variety of other endobacteria associated with ecto- and arbuscular mycorrhizal fungi (37, 40, 48, 272, 365). In these pairings, no specialized hyphal structure is present; the bacteria occupy the cytoplasm of hyphae within the fungal mycelium and, in some cases, also fungal spores (227). Indeed, it has been hypothesized that some endobacteria, such as "*Candidatus* Glomeribacter gigasporarum," are obligately dependent on the fungus, as after their isolation from their fungal host, it has not been possible to cultivate them independently in laboratory media (41, 175). A recent report describing over 400 phylogenetically diverse associations of endophytic bacteria with fungi isolated from foliar tissues indicated that such associations may be far more common than was previously appreciated (163).

Bacterial-Fungal Molecular Interactions and Communication

Central to BFIs is the communication or "dialogue" between the bacterium and the fungus, which we outline here to provide a context for a later discussion of the impact of BFIs. Further discussions of these processes, particularly in a clinical context, where *Candida albicans-Pseudomonas aeruginosa* interactions are an intensively studied model system, can be found in several recent reviews (301, 379, 397).

Interactions via antibiosis. Probably the best-known and most extensively studied category of bacterial-fungal communication is antibiosis, a chemical warfare that is typified by the diffusion of deleterious and often chemically complex molecules from one partner to the other. Research investigating antibiosis has led to the development of numerous important antibiotics to combat microbial infections, the most famous of

which is the beta-lactam antibiotic penicillin, which was developed based on the antibiosis of a *Penicillium* mold contaminating a *Staphylococcus* culture (109). The mechanisms of antibiotic action in BFIs have been of particular interest, especially in the context of the increasing incidence of antibiotic resistance in a clinical setting. A wide variety of mechanisms have been identified, including the inhibition of key cellular functions such as cellular respiration (e.g., hydrogen cyanide and fusaric acid), cell wall synthesis (e.g., penicillin and butyric acid), and transport systems (e.g., β-phenylethanol), while others impair the integrity of cell membranes (e.g., hydrolytic enzymes, cyclic lipopeptides, and polymyxin B). Environments in which antibiotics are present exert a strong selective pressure favoring fungi and bacteria that are either insensitive or that possess effective antibiotic resistance mechanisms. For example, exposure to phenazines and phloroglucinols produced by certain *Pseudomonas* isolates induces the expression of several ABC transporters in the fungal phytopathogen *Botrytis cinerea*, which are thought to prevent the intrahyphal accumulation of antifungal metabolites (348, 349). In addition, a *B. cinerea* laccase was found to be responsible for the production of reactive species that detoxify 2,4-diacetylphloroglucinol (349). Interestingly, isolates of another phytopathogen, *Fusarium oxysporum*, produce fusaric acid in response to 2,4-diacetylphloroglucinol. Fusaric acid was also shown to repress phenazine biosynthesis in *Pseudomonas chlororaphis* PCL 1391 as well as a virulence-associated quorum-sensing system (350, 390). The interaction between the mycorrhizal fungus *Amanita muscaria* and *Streptomyces* sp. strain AcH505 also leads to the suppression of bacterial antibiotic production. In this case, the fungus represses the biosynthesis of the antibiotics WS-5995 B and WS-5995 C by organic acid production (323).

Signaling-based interactions. Other molecules have more subtle effects than antibiotics during BFIs by acting as signaling molecules. Some bacterial metabolites stimulate hyphal growth; for instance, during its interaction with *Amanita muscaria*, *Streptomyces* sp. AcH505 shows an enhanced production of the secondary metabolite auxofuran, which promotes the extension of the fungal mycelium. Unidentified volatile substances produced by some bark beetle-associated bacteria stimulate the growth of their symbiotic fungi (1). Bacterial peptidoglycans have been shown to induce *Candida albicans* hyphal growth, while the presence of the *C. albicans* metabolite farnesol can modulate the expression of virulence genes in *Pseudomonas aeruginosa* by influencing bacterial quorum sensing (82, 83). Interestingly, in the case of the *in vitro C. albicans-P. aeruginosa* BFI, the reverse situation can also occur, in which a bacterial quorum-sensing molecule, 3-oxo-C_{12} homoserine lactone, inhibits yeast filamentation (165). The reciprocal effect of farnesol and 3-oxo-C_{12} homoserine lactone is considered to be due to the presence of a 12-carbon chain within their chemical structures, since other chemically similar molecules with different carbon chain lengths do not cause similar signaling effects (165). Rasmussen et al. (318) showed that *Penicillium* sp. can also produce inhibitors of bacterial quorum sensing. This supports a more general role for quorum-sensing molecules in bacterial-fungal signaling, as does the discovery that another structurally unrelated bacterial quorum-sensing molecule, the 22-amino-acid competence-stimulating peptide of the Gram-positive organism *Streptococcus mutans*, also inhibits the yeast-hypha transition in *C. albicans* (176). As yet, the role of quorum-sensing signaling in nonmedical BFIs is largely unexplored, although quorum-sensing systems are present in many environmental bacteria, and there is some evidence that mycorrhizal fungi can degrade quorum-sensing molecules (387). Interestingly, low concentrations of some antibiotics that do not induce bacterial stress responses can have signaling effects on bacterial biofilm formation and motility (105, 218). This concept has not been extensively studied in the field of BFIs but may be of significant relevance to them, particularly during the early stages of the formation of bacterial-fungal complexes, when antibiotic metabolites may be present in only small quantities.

Interaction via modulation of the physiochemical environment. As well as bacterial-fungal communication that is mediated by a specific molecule and a target/receptor, communication in BFIs may occur via modifications of the physiochemical properties of their environment. A common effect is an alteration of the pH, since although some microorganisms (e.g., streptococci, lactobacilli, and *Candida*) can occupy environments under a broad range of pH conditions, most are susceptible to acidic pHs below 4 (288). Thus, changes in pH can affect microbial community structure by either promoting or inhibiting the growth of acid-sensitive organisms, as demonstrated in the phyllosphere, the human gut, and cheese and wine production (5, 13, 78, 113, 289). On cheese surfaces, for example, yeast lactate metabolism and the production of alkaline metabolites such as ammonia cause deacidification that favors the growth of less-acid-tolerant bacterial strains that are essential for cheese ripening (79). Similarly, the presence of the alkalinizing yeast *Geotrichum candidum* enhances the growth of *Salmonella* on tomato fruit surfaces (395). Coinoculation with *Saccharomyces cerevisiae* was found to significantly improve the viability of *Pseudomonas putida* in grape juice and in a synthetic glucose-rich medium (328). This was attributed to yeast glucose metabolism, the action of which results in a reduced concentration of deleterious gluconic acid produced by bacteria under these nutrient conditions (328). In addition to its effects on microbial growth, environmental pH can also influence other microbial processes; for example, the rate of synthesis of the secondary metabolite aflatoxin by *Aspergillus parasiticus* is higher under acidic growth conditions, while alkaline medium increases the production of penicillin by *Aspergillus nidulans* (59, 302).

Interactions via chemotaxis and cellular contacts. While diffusible molecules play a significant role in many BFIs, migration and physical contact are also important processes in the establishment of BFIs. Chemotaxis (directed movement) of bacteria toward fungi and fungally derived molecules has been demonstrated in several instances; for example, both detrimental and beneficial *Pseudomonas* species exhibit taxis toward fungal mycelial exudates (93, 139). In the case of the chemotactic response of the biocontrol strain *Pseudomonas fluorescens* WCS365, *Fusarium oxysporum* fusaric acid has been identified as an important fungally derived chemotactic signal (95). Cell-cell contact between fungi and bacteria can result in important changes to their physiology and interactions. These interactions may also be modulated by the environment; for example, nutritional conditions have been shown to modulate coadher-

ence between *C. albicans* and oral bacteria (278). The molecular nature of bacterial-fungal contact has been examined in only a few systems, and these studies have, perhaps unsurprisingly, highlighted important roles for membrane proteins. For example, the attachment of *Acinetobacter baumannii* to *C. albicans* (122) is mediated by the bacterial major outer membrane protein OmpA, while the contact-based signaling of *Streptococcus gordonii* toward *C. albicans* is mediated partly via the bacterial cell wall-anchored proteins SspA and SspB (19) and the hyphal wall protein Als3 (369).

Adhesive interactions mediated by polysaccharide for the attachment by *Pseudomonas* bacteria with antifungal activity onto the hyphae of the button mushroom *Agaricus bisporus* have been reported (315). A role for extracellular polysaccharides in the attachment of bacterial species to arbuscular mycorrhizal fungi has also been reported (39), while in the brewing industry, the coflocculation of the fission yeast *Schizosaccharomyces pombe* with the Gram-positive lactic acid bacterium *Pediococcus damnosus* appears to be mediated in part by yeast cell surface mannose and galactose residues, with the latter shielding the former from *P. damnosus* lectin receptors (303). Bacterial lipopolysaccharides are also involved in BFIs. Indeed, *Burkholderia* mutants impaired in poly-D-galactofuranose O-antigen synthesis are not able to establish a successful symbiosis with *Rhizopus* (215). In this case, the bacterial lipopolysaccharide was suggested to promote the evasion of host defense systems, since galactofuranose is a common component of the hyphae of filamentous fungi (215).

Bacterial-fungal contact-based interactions may not be solely adhesive in nature; for example, a lack of O-linked glycans in *C. albicans* confers hypersensitivity to contact-dependent hyphal death caused by *P. aeruginosa* (51). Another interesting example of cell-cell recognition is found in cyanolichens, where an arginase secreted by the fungal partner was recently reported to act as a lectin (97, 392). The binding of this arginase to a polygalactosylated *Nostoc* receptor is paralleled in lichen symbioses formed between algae and fungi and thus may be a key early signaling event in the establishment of lichen symbioses in general (97, 392). A potential role for lectin proteins in BFIs was reported for the truffle fungus *Tuber borchii* (66). The main soluble protein found in its fruiting bodies was shown to bind to exopolysaccharides from truffle-associated *Rhizobium* isolates, suggesting that lectin-mediated interactions may contribute to the selection imposed by the truffle on its associated bacterial community (66).

Trophic interactions. Nutritional interactions between fungi and bacteria are important to many BFIs. Trophic competition between fungi and bacteria is well documented in the plant root environment (rhizosphere), where bacterial competition for nutrients such as carbon (104, 106, 213, 371), nitrogen (239), or iron (104, 213, 214, 402) can be an effective biocontrol mechanism against fungal root pathogens. Examples of bacterial-fungal trophic competition in other environments include competition for carbon substrates during the decomposition of leaves (256); the uptake and release of nutrients by yeast during wine fermentation, which greatly affects growth of malolactic bacteria (5); and competition between the feed additive *S. cerevisiae* CNCM I-1077 and rumen bacteria in an *in vitro* rumen system (71). Protocooperative behavior, which is advantageous but not essential to the two partners involved, is thought to be important for many BFIs and has been of particular interest to scientists investigating the functioning of complex bacterial-fungal communities in the natural environment (177, 391) and in food processing (223, 274).

Some bacteria, such as the phytopathogen *Pseudomonas syringae* B728a, the mushroom pathogen *Pseudomonas tolaasii*, and some collimonads isolated from sand dunes, have been described as being mycophagous; i.e., they are able to acquire all the nutrients that they need for growth from fungi (90, 216, 374, 403). Since nonphotosynthetic endobacteria are completely enclosed within the fungal hypha, they must also obtain their nutrients solely from the fungal cytoplasm. Little is known of the trophic exchanges that occur during these interactions; however, while fungal endobacteria have been observed in dead hyphae (37, 255), they are generally not considered to cause hyphal damage like other mycophagous bacteria. The flow of nutrients in a BFI may not always be directed to the bacterial partner (Fig. 3). Indeed, in cyanolichens, the intrahyphal cyanobacteria probably represent a significant source of carbon and possibly nitrogen for the fungi (80, 197, 198, 356). Some evidence even suggests an enhancement of cyanobacterial photosynthesis when it is engaged in the symbiosis (42). Nitrogen-fixing bacteria have also been isolated from mycorrhizal (including truffle) fungi and in the fungus gardens of leaf cutter ants, further suggesting positive inputs of endobacteria to fungal nutrition (21, 252, 310, 380).

As well as purely trophic interactions, bacteria or fungi can benefit from specific compounds that are produced by the other partner if they cannot produce it themselves or if they can produce it in only growth-limiting quantities. Several mycorrhizal helper bacteria secrete citric and malic acids that are metabolized by *Laccaria bicolor*, promoting its growth (100). The essential micronutrient thiamine (vitamin B_1) has been implicated in the growth promotion exhibited by *Bacillus* sp. strain TB-1 toward the thermophilic yeast *Debaryomyces vanriji* (*Schwanniomyces vanrijiae*) (324) and in the growth-promoting effect of the mycorrhizal helper strain *Pseudomonas fluorescens* BBc6R8 on the ectomycorrhizal fungus *L. bicolor* S238N (93). Conversely, ectomycorrhizal fungi may produce organic acids or sugars, such as trehalose, that can affect the composition and growth of associated bacterial communities (116, 287). In the interaction between *S. cerevisiae* and several *Acinetobacter* species, ethanol secreted by the former was shown to stimulate the growth of the bacterial species and also to act as a signaling molecule, altering cell physiology to increase salt tolerance and, in the case of *A. baumannii*, enhancing *in vitro* pathogenicity toward the nematode *Caenorhabditis elegans* (372).

Interactions via cooperative metabolism. An interesting extension to the concept of the utilization of specific metabolites from one BFI partner to aid the general growth requirements of the other is that of metabolite conversion. In this scenario, metabolite exchange in the BFI results in the formation or degradation of a molecule that neither partner can produce alone. In the case of several complex food products that require BFIs for their production, like wine and cheese, each partner contributes to the synthesis and organoleptic qualities of the final end product. For example, in cheese ripening, the interaction between *Kluyveromyces lactis* and *Brevibacterium linens* results in an altered profile of aromatic volatile sulfur compounds, which is believed to be due to the supply of an

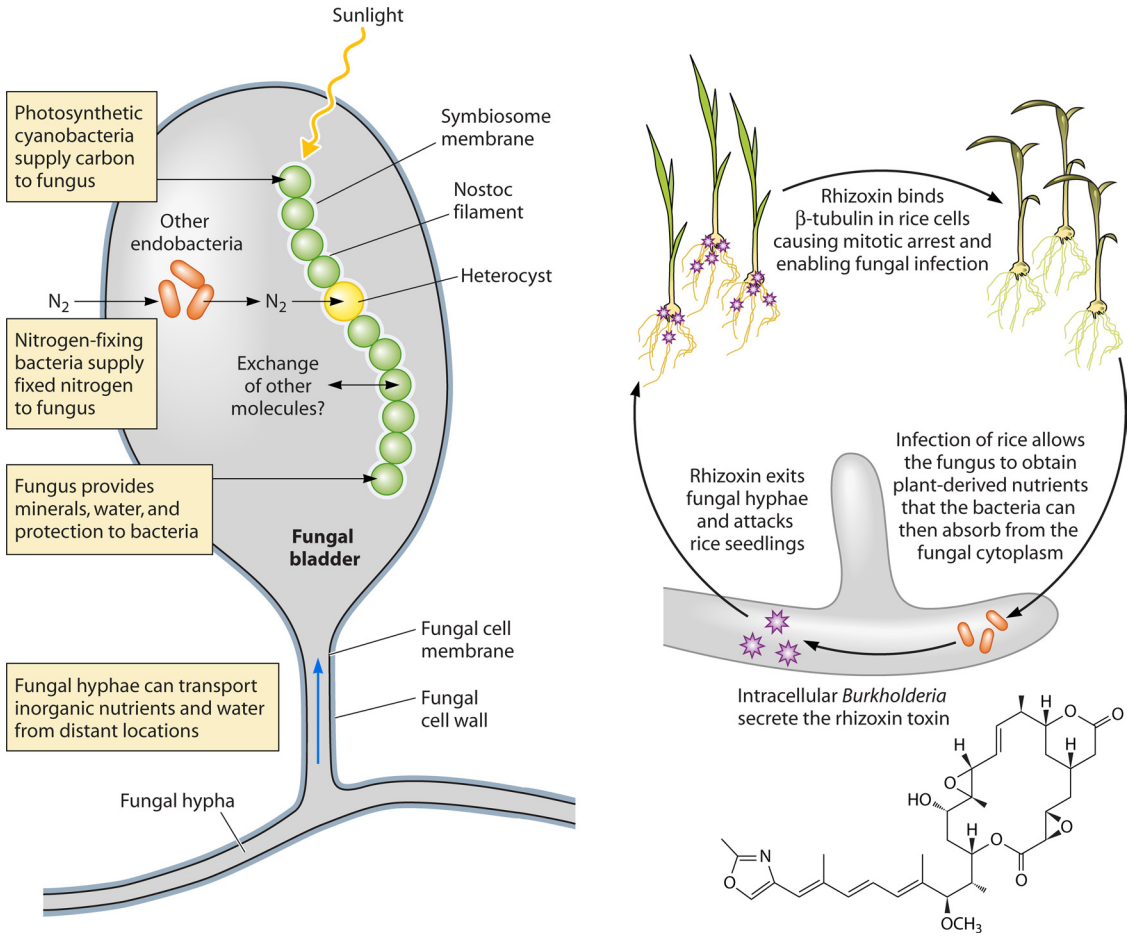

FIG. 3. Role of autotrophic versus heterotrophic endobacteria in promoting fungal nutrition. (Left) Cartoon illustrating the nutritional relationship between *Nostoc* cyanobacteria and the lichenous fungus *Geosiphon pyriforme* during their BFI. Fungal cell structures such as vacuoles, nuclei, lipid bodies, and mitochondria are omitted for clarity. Carbon fixation occurs in photosynthetic cyanobacterial cells, while *Nostoc* heterocysts are able to fix atmospheric nitrogen (197, 198). Bacteria benefit from micronutrients supplied by the fungus, such as phosphate (356). Other nonphotosynthetic endobacteria living within the bladder may also supply fixed nitrogen to the fungus (355). (Right) Cartoon illustrating the role of *Burkholderia rhizoxinica* in the nutrition of *Rhizopus microcarpus*. In contrast to the cyanolichen example, the bacterium is not a primary producer of organic carbon or nitrogen for the fungus (208). However, the bacterial biosynthesis of the toxin rhizoxin is crucial for fungal pathogenicity toward rice seedlings and therefore to the fungal exploitation of plant-derived carbon and nitrogen (298). *R. microcarpus* also requires *B. rhizoxinica* for vegetative reproduction (299).

important precursor molecule, methanethiol, by the bacterium to the yeast (10). Another example of such anabolism is the synthesis of melanin pigments during the *Klebsiella aerogenes-Cryptococcus neoformans* BFI (114, 115). *C. neoformans* is able to use homogentisic acid produced by *K. aerogenes* as a precursor for the synthesis of melanin pigments that enhance the virulence of the fungus and afford it protection against UV and other environmental stresses (114, 115). A less beneficial conversion of a bacterial metabolite occurs upon coculturing of *P. aeruginosa* and *C. albicans*, since a pyocyanin precursor produced by the former is converted to a toxic red pigment within the fungus (131, 257). Cooperation to achieve novel catabolic reactions is also known in some instances; for example, mixed bacterial-fungal consortia are able to biodegrade and mineralize high-molecular-weight polycyclic aromatic hydrocarbons (49, 203). The degradation of fungal self-inhibitory molecules by bacteria was hypothesized to play an important role in the growth-promoting effects of bacteria on certain fungi, including the metabolism of toxic polyphenols secreted by the ectomycorrhizal fungus *Paxillus involutus* (100) and the induction of mushroom formation in *Agaricus bisporus* by *Pseudomonas putida* (314). Conversely, fungi or bacteria may benefit from the production of toxins by their BFI partner. A particularly interesting example of this is found with *Rhizopus*, a phytopathogenic fungus that causes rice seedling blight (298). Rhizoxin, the antimitotic toxin responsible for the initiation of the disease, was shown to be synthesized not by the fungus but by *Burkholderia rhizoxinica* and *Burkholderia endofungorum*, bacteria that live within the fungal hyphae (297, 298).

Interactions via protein secretion and gene transfer. In addition to the transfer of nutritive metabolites, antibiotics, and signaling molecules, the exchange of other biomolecules between bacteria and fungi can also occur. Many bacteria rely on secretion systems to translocate molecules, such as proteins and DNA, into neighboring cells and the extracellular milieu (46). In Gram-negative bacteria, these secretion systems can

range from simple transporters to multicomponent protein complexes and have been classified into six categories (type I secretion system [T1SS] to T6SS). T1SS and T2SS substrates, such as lipases, proteases, and beta-glucanases, are implicated in the antifungal activities of several different bacterial species (11, 38, 172, 229, 330, 374) and in some cases may function synergistically with bacterial secondary metabolites (110). Other secretion systems, such as the T3SS and T4SS, are responsible for the direct delivery of bacterial proteins or DNA into the host cytoplasm and have been widely studied in the context of bacterial virulence toward higher eukaryotes (7, 129, 312). The heterologous expression of T3SS effector proteins from a range of plant- and animal-pathogenic bacteria in *S. cerevisiae* has been used successfully to identify their potential cellular functions (368). Surprisingly, evidence for the translocation of T3SS effectors into the fungal cytoplasm does not exist; however, two recent studies employing T3SS mutants suggested that these systems may play a role in BFIs (87, 206). Cusano et al. (87) demonstrated that a disruption of the T3SS of *Pseudomonas fluorescens* BBc6R8 abolished its mycorrhizal helper effect, although whether the plant of the fungus was the T3SS target is unknown. Lackner et al. (206) found that the disruption of a T3SS gene cluster in the endobacterium *Burkholderia rhizoxinica* resulted in a reduced intrahyphal survival of the bacterium and a failure to elicit the sporulation of the *Rhizopus microsporus* host.

Scientists have employed the T4SS of bacteria to transform fungi with foreign DNA for over 2 decades. This was first achieved by using *Escherichia coli* to transform *S. cerevisiae* (158, 279) but is becoming more widely adopted as a method of fungal transformation, since *Agrobacterium tumefaciens*, a natural plant genetic engineer, is capable of transforming both *S. cerevisiae* (55) and a range of filamentous fungi (92, 188, 294). Interestingly, evidence for natural horizontal gene transfer between bacteria and fungi is also mounting as more genome sequences become available (56, 107, 322, 343, 401, 403). Mallet et al. (232) found that among all putative lateral gene transfers in *Aspergillus fumigatus*, the main proportion (40%) were of bacterial origin. Another recent study identified 713 genes of probable prokaryotic origin in fungal genomes, putatively involved in amino acid isomerization, arsenate detoxification, and peptidoglycan synthesis (237). One might speculate that these genes were acquired from bacteria that were previously part of a BFI with the fungi in question and that may have fulfilled the same functional role as that of the horizontally acquired fungal gene.

Consequences of Bacterial-Fungal Interactions for Participating Organisms

The successful establishment of an association between bacteria and fungi has profound consequences for both organisms. In this section, we describe the main outcomes of BFIs in relation to changes in the bacterial and fungal partners' physiology, life cycles, and survival.

Effects on fungal development. Extracellular bacteria can affect fungal development and spore production, to the benefit or the detriment of the fungus. Bacteria stimulate spore germination in several fungi, including the plant-pathogenic oomycete *Phytophthora alni* (68), the saprophytic cheese-associated fungus *Penicillium roqueforti* (152), several bark beetle fungal symbionts (1), and the arbuscular mycorrhizal fungus *Glomus intraradices* Sy167 (161, 162). Interestingly, antibiotic treatment to "cure" *Rhizopus* of the *Burkholderia* endobacteria living within its hyphae results in a fungus that no longer produces reproductive sporangia or spores (299). This is believed to be a mechanism that ensures the presence of bacteria within fungal spores during vegetative reproduction, guaranteeing the vertical transmission of the bacteria (299), and thus is likely to have been essential for spreading the symbiosis globally (205). As such, it promotes a permanent association with the fungus, which is distinct from the cyclical associations seen for cyanolichens (227). Another notable effect on fungal development is seen in the life cycle of the edible button mushroom *Agaricus bisporus*. The commercial production of mushrooms occurs via the initial colonization of mushroom compost by the fungal mycelium followed by casing with a layer of a peat/limestone mix that stimulates fruiting body initiation (280). The presence of bacteria, notably *Pseudomonas putida*, in this casing layer is highly beneficial for the induction of mushroom production by *A. bisporus* (103, 157, 316). Pseudomonads are also strongly associated with the fruiting bodies of the ascomycete truffle fungus *Tuber borchii* and the oyster mushroom *Pleurotus ostreatus* and may play a role in their development (73, 75, 338, 339). A stimulatory effect on *Pleurotus* mushroom formation caused by *Bradyrhizobium* has also been observed (307). Effects of bacteria on fungal growth, measured by biomass, hyphal branching patterns, elongation, morphology, and density, have been documented in a number of settings, including mushroom formation (316), *in vitro* studies of mycorrhizal fungi (94, 230), rice wine fermentation (187), and clinically relevant BFIs (165, 189, 282). The mycorrhizal helper strain *Streptomyces* sp. AcH505 was shown to have a pronounced effect on the organization of the cytoskeleton of the ectomycorrhizal fungus *Amanita muscaria* (351). The same strain also produces auxofuran, a metabolite that contributes to its growth-promoting effect, the synthesis of which is promoted in bacterial-fungal cocultures and at acidic pH values that typify the growth conditions of ectomycorrhizal fungi (323).

Effects on fungal pathogenicity. Associations with bacteria can have a considerable influence on the pathogenicity of fungi; for example, the presence of bacteria associated with a strain of *Fusarium oxysporum* appears to be important for allowing it to adopt invasive\pathogenic growth (253). Indeed, effects of bacteria on fungal life cycles often influence fungal pathogenicity. An early observation of a negative effect on fungal pathogenicity is the inhibition of the spore germination of the phytopathogen *Botrytis cinerea* by an antagonistic bacterial community on *Chrysanthemum* leaves (44). Another study examining the interaction of *B. cinerea* with soil bacteria provided evidence that the bacterial degradation of oxalic acid produced by the fungus can reduce *B. cinerea* pathogenicity (347). In a clinical setting, various bacterial small molecules have been shown to affect the morphological transition of fungi from the yeast form to the filamentous form, which is critical in the context of fungal pathogenicity. These include short-chain fatty acids from lactic acid bacteria (282) and mutanobactin A from *Streptococcus mutans* (182), which inhibit this transition in *C. albicans*. Bacterial effects on fungal biofilm formation

have also been documented; for example, a recent study indicated that diffusible molecules from *P. aeruginosa* suppress *Aspergillus fumigatus* biofilm formation *in vitro*, which may explain why the fungus causes only low mortality in the lungs of cystic fibrosis patients in which *P. aeruginosa* is a common inhabitant (262).

Effects on bacterial and fungal physiology. Observation of the effects of fungi on bacterial development is difficult due to the small size and single-cell nature of prokaryotes. However, if we consider bacterial-fungal biofilms, it is clear that fungi can promote distinct differences in bacterial development by contributing to a distinctive ecological niche, within which bacteria exhibit physiological differences, such as resistance to antibiotics, stress, and an altered expression of virulence genes, compared to free-living bacteria (153, 154, 306). There is also body of literature that points to the influence of fungi on bacterial community structure at both the taxonomic and functional levels, notably in the mycorrhizosphere and pathorhizosphere (119, 332, 370) but also in other contexts, such as cheese and wine production (2, 58, 173, 261, 386). However, it is a significant challenge to make the link between cell-cell communication in BFIs and community-level organization.

The effects of fungal interactions on bacterial physiology (and vice versa) can be assessed by using global techniques such as proteomics and transcriptomics, which may reveal changes that are undetectable by other means. Indeed, various studies have used "omics" techniques to probe the changes that occur during BFIs at the subcellular level (25, 94, 167, 231, 235, 259, 281, 352); for example, a recent study of the arbuscular mycorrhizal fungus *Gigaspora margarita* using combined proteomic and lipid metabolite profiling revealed that the presence of endobacteria had a significant impact on fungal physiology (331). Targeted approaches assessing the proteomic or transcriptomic responses of one BFI partner to molecules produced by the other also allow the testing of specific hypotheses relating to BFIs, such as responses to antibiotics (245, 246). However, many mechanistic investigations of BFIs are performed in controlled microcosms with a very limited number of interacting microorganisms, whereas natural interactions often involve a complex community of microorganisms whose combined properties may be unpredictable. A good illustration of this was reported by de Boer et al. (91), who observed that the consortia of soil bacteria reduce the expansion of pathogenic fungi, whereas the individual species had no effect on the growth of the fungi. New sequencing technologies are now beginning to allow us to address more complex microbial communities but have yet to be applied to bacterial-fungal consortia.

Effects on survival, dispersal, and colonization. Fungi and bacteria also play important roles in promoting the survival of their interacting partners. This effect can be reciprocal; for example, *P. fluorescens* BBc6R8 promotes the viability of the mycorrhizal fungus *Laccaria bicolor* under unfavorable growth conditions in soil (54), while the fungus can also promote the survival of the bacterium (93). Filamentous fungi can also provide a vector for bacteria by transporting them to new locations where they may access new niches or substrates, as was observed for the degradation of polycyclic aromatic hydrocarbon pollutants (202). This may have relevance in other contexts as well; for example, it has been postulated that the association of *Staphylococcus aureus* with *Candida* hyphae provides a mechanism for the bacterial invasion of otherwise inaccessible tissues, such as epithelial layers (306). BFIs may also favor the colonization of surfaces that are otherwise inaccessible to some microorganisms. *C. albicans* was shown to strongly enhance biofilm formation by *Staphylococcus aureus* in an *in vitro* polystyrene-serum system, with the bacteria associating with the fungal hyphae rather than the plastic substrate as part of a polymicrobial biofilm (154). Similar effects may be important for the colonization of medical devices by a range of microbes (99).

Evidence for heritable changes. The evolutionary consequences of BFIs are generally poorly understood, although in certain circumstances, such as intrahyphal bacteria or horizontal gene transfer between bacteria and fungi, a clear heritable component to the interaction can be discerned. The first complete genome sequence of an intrahyphal bacterium, the rhizoxin-producing bacterium *Burkholderia rhizoxinica* (207), has revealed a genome size reduction compared to the genome sizes of other *Burkholderia* bacteria, a characteristic that is common in the genomes of many bacteria that have adapted to obligate or symbiotic associations with eukaryotes (258), although this reduction is less extreme than those of some bacterial symbionts of insects, and those authors suggested that *B. rhizoxinica* has a "genome in transition" to adaptation to the intrahyphal niche (208). The *B. rhizoxinica* genome also suggests some metabolic adaptation to an intrahyphal existence by the bacterium and possesses a surprisingly large number of genes that are predicted to be involved in the biosynthesis of nonribosomal peptides (208). As more intrahyphal bacterial genomes become available, such as that of "*Candidatus* Glomeribacter gigasporarum" (175), it will be interesting to see if there are common features that are indicative of strains that can live within fungi. On the fungal side of the symbiosis, recent studies of *Rhizopus microsporus* β-tubulin sequences indicate that its resistance to the endobacterial rhizoxin toxin is likely to predate the establishment of the symbiosis, since other Zygomycota that do not harbor the endobacterium are also rhizoxin resistant (344). Two studies suggested that the horizontal gene transfer of bacterial genes into *Saccharomyces* may contribute significantly to its metabolic potential. In *S. cerevisiae* and *Saccharomyces bayanus*, an alphaproteobacterium is thought to have been the source of a gene encoding a sulfatase, which catalyzes the hydrolysis of sulfate esters (150). Those authors and Gojkovic et al. (135) also identified a second gene in *S. cerevisiae*, encoding a dihydroorotate dehydrogenase involved in *de novo* pyrimidine biosynthesis, which is likely to have been acquired from the *Lactobacillales*. Interestingly, the ancestral eukaryotic gene, which encodes a mitochondrial rather than a cytoplasmic form of the enzyme, has been lost in *S. cerevisiae*. Analysis of the role of dihydroorotate dehydrogenases in *Saccharomyces kluyveri* (which possesses both forms of the enzyme) suggests that only the prokaryotic form functions in the absence of oxygen, suggesting that this innovation may have contributed to the adaptation of *S. cerevisiae* to anaerobic growth (135).

Complexity in life cycles. As well as studying evolutionary questions, it is also important to appreciate the temporal aspect of BFIs over shorter time periods, since interactions may occur transiently or have different outcomes depending upon

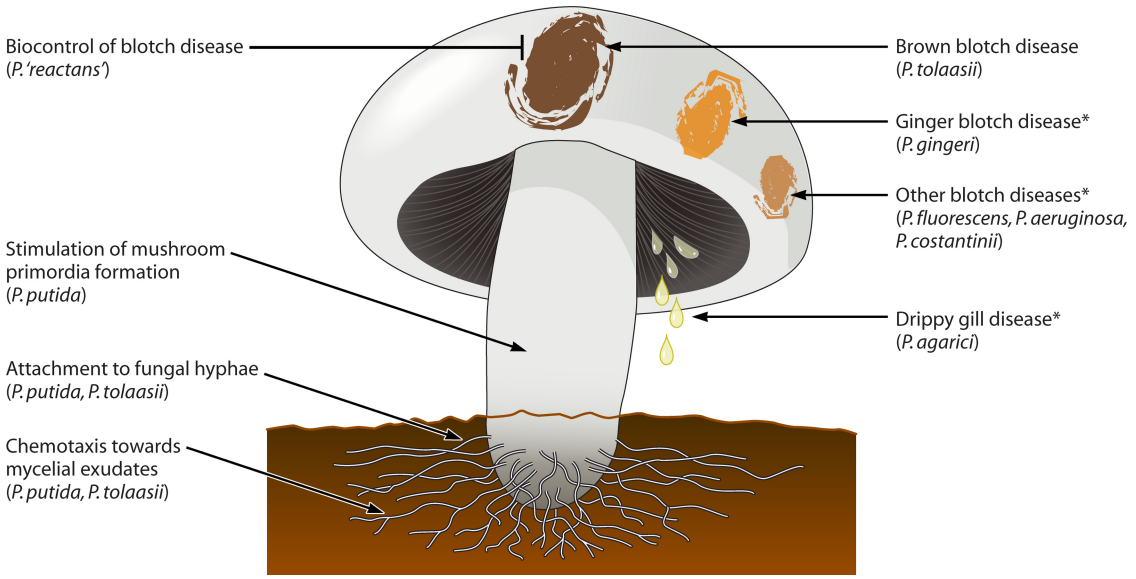

FIG. 4. Interactions of pseudomonads with *Agaricus bisporus* lead to both positive and negative outcomes for the fungus, depending on the bacterial isolate and the developmental stage of the fungus. The toxin tolaasin is the primary factor responsible for brown blotch disease caused by *P. tolaasii*; other contributing factors are a secreted protease, lipase, and exopolysaccharide. *, mechanism unknown.

the physiological or developmental stages in which the two partners meet. A good example of this is seen for the biology of mushroom production by *Agaricus bisporus* (Fig. 4), which, as described above, is partly dependent on the presence of *Pseudomonas putida* in the casing layer (103). However, pseudomonads also cause disease on mushrooms, resulting in symptoms such as brown blotch, ginger blotch, and drippy gill (381, 383, 407). It appears that the tolaasin toxin used by *P. tolaasii* to cause brown blotch symptoms is either not expressed or ineffective against hyphae during their initial colonization of the mushroom bed, since mushroom beds are initially symptomless (317). Furthermore, other pseudomonads and the products of their metabolism have been shown to antagonize the pathogenicity of *P. tolaasii* (270, 373). Thus, within a single genus, we can see growth- or development-promoting, deleterious, and biocontrol activities of bacteria toward fungi, highlighting the complexity and specificity of the interactions that can exist in BFIs through time. This also illustrates the notion of a dynamic relationship between bacteria and fungi, with the potential for both beneficial and detrimental effects depending on the environment and phenology of the organisms. Identification of the key mechanistic determinants for these different behaviors, both genetic and environmental, therefore represents the first step in controlling or manipulating them.

IMPACT ON OTHER ORGANISMS AND THE ENVIRONMENT

The impact of BFIs on the nutrition and health of the host organisms is often significant, as both plants and animals host consortia of bacteria and fungi in a variety of niches (Fig. 5). In the soil environment, BFIs play a role in processes such as mineralization and the degradation of toxic compounds. In this section, we describe the relevance of BFIs in these different contexts, highlighting common or contrasting themes.

Influence on Host Nutrition

Effects on plants. Plants photosynthesize to obtain the carbon that they require, but the other nutrients that are essential for their growth and development must be obtained from the soil. In terrestrial ecosystems, the root systems of most plant species interact with mycorrhizal fungi to form symbiotic structures called mycorrhizas (178, 241). Mycorrhiza formation enhances root access to water and poorly available mineral nutrients in the soil, while heterotrophic fungi benefit from plant carbohydrates exuded by roots. Under natural conditions, mycorrhizas are surrounded by a wide diversity of bacterial communities that interact with the symbiosis at physical, metabolic, and functional levels, forming a multitrophic mycorrhizal complex (118). Individual strains have been isolated from these and other soil bacterial communities that behave as mycorrhiza helper bacteria (124), since they promote mycorrhiza establishment or functionality (23, 119, 180). Additive or synergistic effects on plant growth and nutrition between helper or mycorrhiza-associated bacteria and mycorrhizal fungi are now well documented. The nature of the nutritional benefit provided by a BFI for plants has also been demonstrated in some instances. A *Bacillus subtilis* helper strain with a phosphate-solubilizing ability significantly increased the biomass and nitrogen and phosphorus accumulation in onion tissues when inoculated with the mycorrhizal fungus *Glomus intraradices* in a soil with low phosphorus bioavailability (382). In another study, Requena et al. (321) identified *Rhizobium* strains that were able to enhance the *Anthyllis cytisoides-G. intraradices* symbiosis and improve the plant nitrogen status. Therefore, it is clear that mycorrhiza-associated bacteria and mycorrhizal fungi can positively interact to promote a sustainable nutrient supply to plants.

Various hypotheses have been proposed to explain the mechanistic basis for the bacterial mycorrhiza-helper effect

FIG. 5. Coexistence and impact of bacteria and fungi in contrasting microbial ecosystems. Bacterial and fungal communities occupy overlapping niches in soil or when associated with plants and humans or other animals. Disturbing the communities that occupy these niches, for example, by the introduction or removal of key members, may alter the balance that exists between them. This can cause changes to the influences of bacteria and fungi on their niche, with consequences for the functioning of the ecosystem. BFIs may also result in novel effects in niches that do not occur in their absence.

(119), some of which may be mediated through the host, such as the suppression of plant defense responses (212). Interestingly, it appears that there may be some overlap between strains that can suppress fungal diseases of plants and strains that can act as helper bacteria; for example, recently, Pivato et al. (311) revealed that *Pseudomonas fluorescens* C7R12, which can reduce wilt caused by *Fusarium*, can also behave as a helper strain by specifically promoting the symbiosis between the legume *Medicago truncatula* and *Glomus mosseae*. In contrast, Lehr et al. (212) observed that the helper strain *Streptomyces* sp. AcH505 facilitates the colonization of plant roots by the phytopathogen *Heterobasidion abietinum*. Nevertheless, others have demonstrated that the mycorrhizal helper effect is not a general phenomenon among all soil bacteria (15, 186). An understanding of the basis of mycorrhizal helper bacteria specificity will aid the selection of the best strains for application in crop plants to enhance mycorrhization and may provide insight into BFIs beyond those found in the context of mycorrhizas.

Effects on humans and other animals. In some ways, the digestive tracts of humans and other animals can be considered analogous to the zone surrounding plant root systems. Digestive tracts are ecosystems containing diverse polymicrobial microbiota that exhibit complex physical, chemical, and functional interrelationships, and their contents can be considered "external" to the body, since they have not been internalized by a membrane system (361). Human gut microbial communities are thought to play a major role in health and disease, but an exhaustive analysis of their composition and diversity has only recently become feasible with the advent of new DNA se-

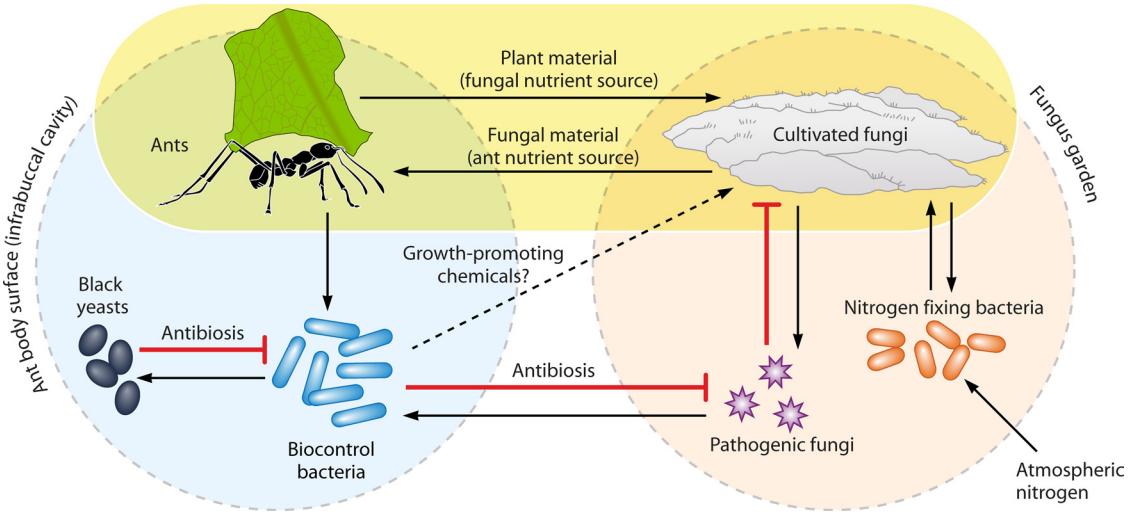

FIG. 6. Role of BFIs in ant-fungus mutualism. Nutrient flows and inhibitory interactions between organisms are indicated by arrows and blocked arrowheads, respectively. Major inputs of carbon (plant biomass) and nitrogen (plant biomass and nitrogen-fixing bacteria) provide the raw materials to support the web of interactions and are indicated with bold arrows. Ants transfer pathogenic *Escovopsis* fungi to their infrabuccal pocket during sanitization of the fungus garden.

quencing technologies (273, 313). To date, the scientific community has focused on the rich bacterial communities (101) colonizing the digestive tract, whereas the diversity of fungi inhabiting the human gut is very poorly documented (340, 354). While the level of fungal diversity in the human gut is almost certainly much lower than the level of bacterial diversity, a culture-independent rRNA oligonucleotide fingerprinting approach for the murine intestine suggested that an abundant and diverse fungal microbiota is likely to be present (358).

Fungi may play unique functional roles in the gut that are complementary to those ascribed to bacteria, such as nutrient release and exchange (375). However, the extent to which the fungi and bacteria interact in the human gut is largely undetermined. More is known about BFIs in the digestive tracts of ruminant mammals, where bacteria are believed to play a major role because of their metabolic diversity, while ruminal fungi, although less numerous, are able to weaken and degrade the more recalcitrant plant tissues thanks to the wide range of polysaccharide-hydrolyzing enzymes that they secrete. However, the precise role and overall contribution of each fungal and bacterial group to the *in vivo* degradation and fermentation of plant cell wall materials are still hypothetical (111). Interactions between ruminal fungi and bacteria have been studied largely *in vitro*, sometimes in artificial rumen ecosystems (30, 36, 179, 211, 242). These interactions range from synergism to antagonism, depending on the microbial composition and the type of plant substrate. Hydrogen-utilizing bacteria such as methanogens were reported to improve the efficacy of ruminal fungi for cellulose degradation (30, 242). In contrast, some rumen cellulolytic bacteria were observed to inhibit the ability of ruminal fungi to degrade cellulose (36). Further *in vivo* studies of the bacterial-fungal interactions in the rumen will be necessary to clarify their real impact on animal nutrition and will open new perspectives in the worrying context of increasing greenhouse gas production, to which the contribution of livestock is significant.

To improve animal performance and health, yeasts such as *Saccharomyces cerevisiae* have been used widely in recent years as probiotic additives in the diets of ruminant mammals and horses (102). *In vivo* investigations have demonstrated that ruminant diets supplemented with *S. cerevisiae* increase cellulolytic bacterial densities as well as the rate of straw degradation in the rumen (70, 275). When supplied to young ruminants switching over from a milky diet to solid feed, yeast probiotics could thus be of value in stabilizing the rumen microbial ecosystem (70). Recently, live *S. cerevisiae* cells coincubated with three different rumen bacterial species were found to reduce bacterial proteinase activities compared to the activities in bacterial monocultures (71). *In vivo*, such an effect could be harnessed to reduce the proteolysis of rapidly degradable dietary proteins in the rumen and consequently to avoid the accumulation of ammonia. Bacteria, yeast, and also protozoa may also have beneficial effects in the rumen due to their ability to degrade mycotoxins produced by members of the fungal genera *Fusarium*, *Penicillium*, and *Aspergillus* present in ingested fodder (277, 384).

A clear beneficial role for BFIs in host nutrition is found in the mutualism between "fungus-gardening" (attine) ants and their fungal associates, which is thought to have existed for an estimated 45 to 65 million years (263). Fungus-growing ants are dependent on their fungal associates, since the cultivars serve as the sole food source for the ant larvae and queen; however, their fungus gardens may come under attack from members of the ascomycete genus *Escovopsis* (85). The ants keep their gardens free of microbial pathogens thanks in part to host-beneficial BFIs (Fig. 6). Attine ants support populations of actinomycete bacteria (usually *Streptomyces* or *Pseudonocardia* species) by means of cuticular crypts fed by exocrine glands (84). The bacteria produce antibiotics that antagonize the parasitic *Escovopsis* populations; for example,

Trachymyrmex ants rear symbiotic antibiotic-producing bacteria in an infrabuccal pocket into which they transfer parasitic *Escovopsis* spores and hyphae, aiding in the sanitization of their fungal gardens (221). Recent studies have identified several antibiotics produced by bacteria associated with attine ants, such as the cyclic depsipeptide dentigerumycin and the polyenes mycangimycin and candicidin (149, 285, 286), that selectively target *Escovopsis* but not the fungal garden (24). A similar strategy of using a bacterium-derived antibiotic to control an antagonistic fungus is also utilized by the southern Pine beetle, *Dendroctonus frontalis* (357). The beetle is able to selectively suppress *Ophiostoma minus*, a competitor fungus of its beneficial symbiotic fungus *Entomocorticium* sp., using the polyene peroxide mycangimycin that is produced by the actinomycete bacteria that it carries in a specialized storage compartment (357).

Another fungus associated with attine ants is *Phialophora*, a genus of ascomycete black yeasts. *Phialophora* cells grow on the ants' cuticle and appear to be localized to sites where mutualistic bacteria reside (220). The basis for this localization is unknown, but the yeasts appear to obtain nutrients from the bacteria and have a negative effect on their growth, consequently reducing their antibiotic effect on *Escovopsis* (219). Bacteria also provide other benefits to fungi and attine ants beyond pathogen control. A recent study reported the presence of symbiotic nitrogen-fixing bacteria within the fungus gardens of several ant species (310). The presence of these bacteria is important due to the low nitrogen input available from plant leaves (310). Bacterial nitrogen fixation, thought to be performed mainly by members of the genus *Klebsiella*, is likely to be of substantial nutritional benefit to both the fungi and, consequently, their ant gardeners. Interestingly, the fungal cultivars of *Apterostigma* ants grow faster under the influence of *Streptomyces* culture filtrates, suggesting that the bacterium may produce fungal growth-promoting compounds, although their identities are unknown (85).

Roles in Host Health and Disease

Effects on plants. The efforts of ants to control the parasitic fungi that attack their fungal gardens are paralleled by the attempts made by humans to control fungal diseases of plant crops. It has been recognized for a long time that many bacteria living in the root environment are able to promote plant health and growth (226) and that in some cases this is a consequence of their antagonistic impact on fungal pathogens in the soil (400). There is a large body of literature describing the use of rhizosphere bacterial isolates as potential "biocontrol" agents targeting a variety of soilborne fungal pathogens, indicating the potential of biocontrol bacteria to complement or even replace the application of chemical fungicides (147, 399, 402). Indeed, several commercial biocontrol agents targeting pre- and postharvest fungal diseases are available (34). However, despite meeting with a high degree of success in controlled environments, the widespread use of biocontrol bacterial strains is challenging, since each crop protection strategy is to some extent unique due to differences in cultivars, soil chemistries, and environmental conditions (147). Moreover, the usefulness of particular strains is not always predictable, mainly because of the variable abilities of the biocontrol bacteria to compete with resident rhizobacteria during root colonization, although they are often more efficient in disturbed natural ecosystems (77, 398). In some instances, attempts have been made to use combinations of bacterial and fungal biocontrol agents to afford plants better protection from disease (142, 228, 234). Whether interactions between the biocontrol agents has affected the outcome of these tests has generally not been investigated, except in the case of *P. fluorescens* CHA0 and *Trichoderma atroviride*, which appear to have enhanced the expression of key biocontrol factors in each other's presence (228).

Compared to the extensive literature describing the effect of biocontrol strains on soilborne phytopathogenic fungi, much less is known about the effect of their application on resident nonphytopathogenic fungi. Interestingly, a study of biocontrol inoculation of bacteria to combat the effect of phytopathogenic *Rhizoctonia solani* on lettuce found that the bacterial treatments had only small short-term effects on endophytic fungi and resident rhizobacteria (342). Another study reported that the application of biocontrol strains to protect lettuce from *R. solani* reduced the disturbance to the indigenous bacterial and fungal communities caused when the phytopathogen alone was present (3). Small but detectable effects of the antibiotic-producing biocontrol strain *P. fluorescens* CHA0 on fungi resident in the cucumber rhizosphere have been reported, but in this case, no target phytopathogen was included, so the effect of the biocontrol interaction on resident fungi is unknown (133). Uncontrolled side effects on symbiotic mycorrhizal fungi may partly explain the inconsistent results of some large-scale biocontrol field experiments (398). However, biocontrol strains will not necessarily be antagonistic toward mycorrhizal fungi; for example, Barea et al. (22) found that the biocontrol strain *Pseudomonas fluorescens* F113, which produces the antifungal metabolite 2,4-diacetylphloroglucinol, did not exhibit antibiosis toward the mycorrhizal fungus *Glomus mosseae* and actually promoted root colonization by the fungal hyphae. The antifungal specificity of biocontrol could therefore be one criterion for the selection and evaluation of biocontrol strains in the future. An interesting illustration of the importance of the context in which an antifungal metabolite acts is seen with rhizoxin. A gene cluster similar to that of *B. rhizoxinica* that is responsible for the biosynthesis of several rhizoxin analogs has been identified in the plant-associated biocontrol strain *P. fluorescens* Pf-5 (52, 225). However, while Pf-5 rhizoxin analogs can cause effects on rice seedling root morphology that are similar to those seen with rice seedling blight, in a biocontrol context, Pf-5 probably uses rhizoxin to attack fungal hyphae rather than to promote fungal growth in the manner seen for the *Rhizopus-Burkholderia* BFI (225). The need for establishing the "fungus specificity" of mycorrhizal helper bacteria has also been recognized, since some strains have been shown to promote mycorrhiza formation by a few fungal species and to inhibit other mycorrhizal fungi (124).

Bacteria and fungi can both elicit defense responses that protect plants, via the mechanisms of induced systemic resistance and systemic acquired resistance, against subsequent pathogen attack (151). Since these effects are mediated by the plant, we will not consider them further here. Plants are usually occupied by endophytic bacteria and fungi, some of which have been isolated and tested *in vitro* and in field tests with the view

to exploit them for the biocontrol of pathogens (9, 17, 20, 35, 238, 247). Results from these studies indicate the potential for antibiotic-mediated or other BFIs among naturally occurring endophytes *in planta*, but a demonstration of direct BFIs in this setting is very difficult due to potential indirect plant-mediated effects. As discussed above, under natural conditions, plant roots benefit from the presence of mycorrhizal fungi; however, mycorrhizal fungi not only improve plant nutrition but also can protect plant roots against fungal disease. This results from direct effects of the mycorrhizal fungus on the plant but also from indirect effects of the mycorrhizal symbiosis on the surrounding bacterial communities. Indeed, *in vitro* antagonism against phytopathogenic fungi by mycorrhiza-associated bacteria has been frequently reported (12, 74, 217, 230), and there is evidence for the enrichment of bacterial communities with a high antagonistic potential toward fungal pathogens by mycorrhizal and other fungi (88, 117). Further experiments will be necessary to determine whether these observations result exclusively from fungally induced selection on the bacterial community from the soil reservoir.

As well as the plant-beneficial bacterial-fungal relationships, one should not forget that some plant-detrimental BFIs also take place. Associated bacteria were shown to enhance the pathogenicity of the foliar fungal pathogen *Stagonospora nodorum* when infecting wheat, even though the bacteria themselves were nonpathogenic toward the host (96). Synergistic interactions between *Pectobacterium atrosepticum* (*Erwinia carotovora* subsp. *atroseptica*) and the foliar pathogen *Septoria tritici* on wheat have also been reported (276). In the rhizosphere, different functions can coexist, with *Pseudomonas* bacteria increasing or decreasing the plant pathogenesis of the soilborne fungus *Gaeumannomyces* (335). The antimitotic toxin rhizoxin is an important component in the pathogenicity of the rice seedling blight pathogen *Rhizopus microsporus*; however, the synthesis of rhizoxin is performed not by the fungus but by *Burkholderia* bacteria living within its hyphae (298, 341).

Effects on humans and other animals. Humans and other animals are naturally colonized by fungi and bacteria that occupy an array of niches, including the skin, the oral cavity, and the respiratory, digestive, and genital tracts (125). In healthy individuals, these microorganisms are commensal and in some cases even beneficial to human health. Pathogenic fungi and bacteria do, however, represent a serious threat to the health of individuals, especially those who are immunocompromised, since many pathogens are opportunistic rather than obligate. There are many instances where bacteria and fungi have been found together in infections of human burn wounds and keratitis (144, 146, 160, 233, 300). However, clinical therapies that have been developed to target either fungal or bacterial infections have generally failed to consider that fungi and bacteria often coinfect, forming mixed communities that have virulence and resistance properties significantly different from those of the single-species communities (366, 397). An understanding of the functioning of BFIs in human health is therefore an emerging and important challenge for medical researchers, particularly given the development of strains that are resistant to drug therapies (127, 243, 290, 292).

The lungs of immunocompromised individuals are also frequently cocolonized by bacteria, notably *Pseudomonas aeruginosa*, and fungi such as *Candida albicans* and *Aspergillus fumigatus*. Coinfection by these pathogens is considered to worsen lung function relative to infection by each pathogen alone (265, 301). Most studies of clinical BFIs to date have focused on *Candida albicans* (366, 397), a yeast which is common in the buccal, dermal, and intestinal human microbiota but which can also cause a large number of infections (308). Gupta et al. (146) revealed a significant *in vivo* inhibition of *C. albicans* growth in the presence of *P. aeruginosa* in burn wounds, which are highly susceptible to bacterial and fungal superinfections. A similar detrimental effect of *P. aeruginosa* on *C. albicans* has been demonstrated *in vitro*, specifically toward the virulent filamentous form of the fungus (164). *P. aeruginosa* can also grow at the expense of dermatophyte fungi associated with skin and nail infections (112). Contrastingly, *Escherichia coli* and *Staphylococcus aureus* can both behave as synergistic *C. albicans* copathogens, increasing mortality rates in animal models of polymicrobial peritonitis (62, 63, 194). All these examples clearly illustrate the need for a combination of clinical studies and *in vitro* experimentation to understand how BFIs impact human health.

The oral cavity is another site at which the potential for BFIs exists in humans. A recent study of 20 healthy individuals revealed a variety of culturable and nonculturable fungi to be present in this setting (130). *In vitro* studies suggested that oral bacteria may modulate the ability of the yeast *Candida albicans* to form biofilm structures (168, 291), while a mixed *C. albicans-E. coli* biofilm was found to possess enhanced resistance to an oral antiseptic. Thus, a fuller understanding of these interactions may lead to improved dental health. BFIs also contribute to the increasing number of nosocomial (hospital-acquired) infections; for example, Curvale-Fauchet et al. (86) reported that a high proportion of hospital intravascular catheters were simultaneously colonized by the pathogenic lipophilic yeast *Malassezia* and bacteria, including staphylococci. These mixed biofilms, which have also been evidenced with *C. albicans* (195, 289), can be more resistant to antibiotic treatments; for example, the presence of *Staphylococcus epidermidis* was shown to delay the diffusion of antifungal drugs in mixed *Candida-Staphylococcus* biofilms (6). Bacterial-fungal associations with potentially detrimental impacts on human health may also occur in moldy houses (170). In these damp environments, actinobacteria frequently cohabit with fungal genera associated with moisture damage, such as *Stachybotrys* and *Aspergillus*. Research evaluating the impact of such BFIs in cell lines indicates a significant potential for synergistic effects between these bacteria and fungi on cytotoxicity and mammalian inflammatory responses (170, 267, 304, 305). While mixed bacterial-fungal communities have been shown to have detrimental effects on human health, to our knowledge, there have been no reports describing the roles of intrahyphal bacteria in fungal infections of humans. Several clinical zygomycete isolates harboring intrahyphal *Burkholderia* bacteria that produce the rhizoxin toxin have been identified, but the presence of these bacteria is not universal in clinical zygomycoses (171, 295). In contrast to the important role of these bacteria in rice seedling blight, there is currently no evidence that intrahyphal *Burkholderia* promotes infections of humans by *Rhizopus*. Compared to parental strains, bacterium-cured *R. microsporus* organisms are equally destructive toward cell cultures and show

no difference in virulence in animal models (171). Deleterious effects of the bacteria may, however, exist later during infection, while from the perspective of the bacteria, the fungus may provide better access to a niche that they can later exploit if released from hyphae (126, 171).

Despite the many examples of detrimental BFIs, these relationships can also have beneficial effects on animal and human health. Researchers have demonstrated that chytridiomycosis, a serious disease affecting amphibian populations worldwide which is caused by the chytrid pathogenic fungus *Batrachochytrium dendrobatidis*, can be successfully tackled in frogs and salamanders by exploiting antifungal-producing bacteria that naturally live on their skin (53, 155, 156). In the marine environment, a similar scenario was revealed for the shrimp *Palaemon macrodactylus* (132). The production of the metabolite 2,3-indolinedione by a surface-associated *Alteromonas* strain was shown to protect shrimp embryos from attack by the oomycete pathogen *Lagenidium callinectes* (132). In the insect world, the European beewolf wasp cultivates *Streptomyces* in antennal glands and uses the bacterium to protect its larvae from fungal infestation, again probably due to antibiotic production (185, 204).

BFI-based interventions are also of great interest in the context of mammalian health. "Probiotic" bacteria and yeasts have been used extensively within the livestock industry because of beneficial impacts on host defenses and as alternatives to the use of antibiotics in promoting animal health (123). The addition of the probiotic *Saccharomyces cerevisiae* CNCM I-1077 led to the elimination of Shiga toxin-producing *Escherichia coli* in rumen fluid (69), while in poultry, mannanoligosaccharides derived from *S. cerevisiae* were shown to promote the colonization of beneficial bacteria and reduce colonization by pathogenic strains (32). In human health, there is evidence for a probiotic BFI effect with the use of *Saccharomyces boulardii* to combat antibiotic-associated diarrhea caused by the loss of indigenous microbes after antibiotic therapy and subsequent colonization by pathogens, notably *Clostridium difficile* (411). The effect of *S. boulardii* has been attributed to a variety of mechanisms (411), including some direct BFI effects: the degradation of *C. difficile* toxins by yeast protease activity (64, 65) and an alteration of *E. coli* lipopolysaccharide by a yeast phosphatase (57). Reduced bacterial adherence and colonization of intestinal epithelial cells as well as reduced expression of virulence factors were also reported for colon inflammation caused by *Citrobacter rodentium* in the presence of *S. boulardii* (409). The question of gut fungi in microbial immune homeostasis is a novel avenue for studies in this area and can now be addressed with the advent of modern techniques to profile microbes associated with the human body. Further studies will be necessary to evaluate whether BFIs within this context may be of benefit or harm to human and animal health.

Roles in Biochemical Cycles and the Environment

Terrestrial and aquatic ecosystems. Fungi and bacteria play central roles in terrestrial ecosystems, where they participate in numerous biochemical cycles. Lignocellulolytic substrates, such as wood, that constitute very abundant but very recalcitrant organic compounds and play a central role in the carbon cycle are considered to be degraded mainly by fungi under aerobic conditions (45, 76, 138, 193). This is despite the ubiquitous presence of bacteria on these substrates that may negatively or positively interact with the fungal degraders (389). Previous studies have shown that competitive interactions between fungi and bacteria can be important during the fungal degradation of recalcitrant organic matter (89), but this does not appear to be universally true. Wood decay by the white rot fungus *Heterobasidion annosum* was shown to be inhibited or promoted by bacteria found in association with it, depending on the relative timing of the fungal and bacterial inoculations, suggesting a more complex ecological relationship (266). *Phanerochaete chrysosporium*, another white rot fungus, was also reported to live in close association with several bacterial species, even in *in vitro* cultures from which bacteria had been thought to be eliminated (360). Whether this coexistence is obligate and whether the fungus-associated bacteria actively participate in the degradation of lignocellulolytic substrates still remain to be determined. Certainly, bacteria can cause changes in wood chemistry, permeability, and structure, which may favor subsequent succession by fungi (76). Bacteria may also provide nutritional benefits to wood-degrading fungi, for example, by nitrogen fixation *in situ* or in the surrounding soil that the fungal hyphae can transport to the site of wood degradation (4, 76, 359). Bacteria may also assist in the fungal degradation of preserved woods through the sequestration or detoxification of preserving agents (76, 174, 396). In the context of wood preservation and industrial wood transformation, more studies are needed to understand better how bacteria interact with wood-degrading fungi and the practical implications of these BFIs. This will aid in the development of novel preservation strategies targeting not only wood-decaying fungi but also their associated helper bacterial communities and may improve wood transformation processes by exploiting the cooperative effect of fungi and bacteria in the breakdown of the lignocellulose complex.

BFIs also contribute to cycling on inorganic nutrients. In nutrient-poor soils such as those of forests, inorganic mineral ions derived from rocks by weathering are a key source of important tree nutrients, and both mycorrhiza-associated bacteria and mycorrhizal fungi are known to contribute to mineral weathering (385). Evidence now suggests that these microorganisms cooperate in nutrient mobilization from soil minerals (386); for example, using a budget analysis, Koele et al. (201) recently quantified the respective impacts of two ectomycorrhizal fungal strains (*Laccaria bicolor* and *Scleroderma citrinum*) and two mycorrhizosphere bacterial strains (*Burkholderia glathei* and *Collimonas* sp.) on the weathering of a phyllosilicate. The level of weathering tended to be highest for all the bacterial-fungal coinoculation treatments, supporting the hypothesis that bacterial-fungal cooperation may contribute to the cycling of inorganic nutrients in forest ecosystems and, therefore, to forest sustainability in nutrient-poor soils. The coinoculation of a phosphate-solubilizing strain of *Penicillium ostreatus* and a nitrogen-fixing strain of *Bradyrhizobium elkanii* significantly increases the quantity of phosphorus released from rock phosphate (177). Cyanolichen BFIs have also been shown to enhance the release of essential elements from minerals in the soil (192, 362). In agricultural soils, there is now an increasing need for sustainable ecofriendly fertilization strategies. Efforts should be made now to develop new bio-

technological processes based on the coinoculation of bacterial-fungal consortia with weathering abilities to enable the efficient utilization of natural phosphate rocks as alternative phosphate fertilizers. To date, the roles and importance of bacterial-fungal consortia in environmental nutrient cycling have been largely overlooked. Qualitative and quantitative analysis of the contribution of these consortia to different key biogeochemical cycles (e.g., nitrogen, iron, sulfur, carbon, and phosphorus) may provide important insights into these processes that could aid in the development of ecofriendly technologies with beneficial plant and human impacts.

Despite evidence that fungi can colonize even extreme aquatic environments such as deep-sea hydrothermal vents (210), the presence and distribution of fungi in aquatic environments are poorly documented, while the co-occurrence of fungi and bacteria is even more poorly appreciated. In aquatic environments, bacteria and fungi dominate the decomposition of aquatic plant residues and live in close proximity to each other. However, only a few studies have addressed the role of BFIs during the decomposition process, and these have described mostly antagonistic relationships between fungi and bacteria (145, 251, 256, 406). Interestingly, Mille-Lindblom et al. (250) found indications of a trade-off between the fungal growth rate and the tolerance of fungi toward antagonistic and competing bacterial communities. After the cocultivation of six different fungal strains isolated from aquatic plants with a complex natural bacterial community originating from aquatic plant litter, those authors observed that the fungal strains that grew best in the absence of bacteria were most severely affected by the presence of bacteria; in contrast, those that were less inhibited in cocultures with bacteria had lower maximal growth rates in the absence of bacteria. The authors of that study hypothesized that different fungi may allocate resources differentially between their growth and mechanisms to tolerate resident microbes. Given that plant decomposition by fungi occurs in a heterogenous and nonsterile environment, clearly, account must be taken of BFIs when one tries to understand or improve such processes.

Threat of bacterial-fungal interactions to cultural heritage. The conservation of cultural heritage, such as cave rock art, archaeological sites, historic buildings, and books, is a major challenge worldwide. Whatever the material (e.g., stone, ceramics, metals, window glasses, paintings, mortars, and adobes) and the location (indoors or outdoors) of the heritage to preserve, surfaces are often colonized by complex microbial communities. The number of studies reporting an inventory of the bacterial and fungal diversity colonizing these surfaces has increased substantially in recent years thanks to advances in molecular techniques that now allow the analysis of nonculturable microbial communities (27, 136, 249, 293). These microbial communities are often organized into biofilms that may be aggressive, producing pigments and/or mineral-weathering agents that deteriorate the colonized surfaces (169, 264, 333). These microbial communities may also threaten the health of visitors in indoor environments due to the release of bacterial and fungal toxins (293).

Many studies are under way to identify strategies for the control or elimination of deleterious biofilms associated with cultural heritage. In the view of what is already known for other environments and surfaces containing mixed bacterial-fungal communities, such as medical devices and soil minerals, such studies should consider the potential importance of BFIs occurring inside these biofilms. Bacterial antibiotics are thought to play a role in preventing the fungal colonization of cave paintings (183). Furthermore, a study of the cave of Dona Trinidad in Spain pointed to the potential of nutritional complementation between fungi and bacteria under nutrient-poor conditions; bacteria may benefit from phosphate and organic nutrients exuded by fungi whose growth can be limited by ammonium availability (378). The role of human interventions in such environments is also important (28, 378). As has been described for the human gut, antimicrobials applied to artifacts disturb the indigenous microbiota, providing an open niche for resistant microorganisms to colonize. In environments such as rock surfaces, resistant strains may also benefit significantly from the cell lysis of sensitive microbes, which can provide an additional source of nutrients to them. BFIs may influence the success of these disinfection procedures, as seems to have occurred in the prehistoric Lascaux cave. In 2001, 38 years after its closure to visitors, a bacterial-fungal invasion (*Fusarium solani* associated with *Ralstonia* sp. and *Pseudomonas fluorescens*) occurred in the cave (27). The first biocidal treatments resulted in an unexpected prompt development of the *F. solani* colonies despite the known *in vitro* efficiency of benzalkonium chloride against *Fusarium solani*. It has been hypothesized that the bacteria protected the associated *F. solani* that was embedded in the same biofilm against the biocidal treatment (27, 28). Moreover, *Pseudomonas* may also have been able to degrade the antifungal molecule (26).

APPLICATIONS OF BACTERIAL-FUNGAL INTERACTIONS

Food Processing

Fermentation and brewing. Mixed bacterial-fungal communities play a key role in determining the taste, quality, and safety of a wide range of foods (367). The complex interactions between filamentous fungi, yeast, and bacteria that lead to wine production begin in the vineyard, on the surfaces of ripening grape berries (224, 320), and continue throughout the fermentation process until packaging (108). The biotransformation of pressed grape juice into wine results from a primary alcoholic fermentation performed by *Saccharomyces cerevisiae* that is frequently followed by a secondary so-called "malolactic fermentation." Deacidification by this conversion of L-malic acid to L-lactic acid occurs either spontaneously, owing to the activity of bacteria naturally present in musts and wine, or after the inoculation of commercially available bacterial strains (184). Achieving appropriate malolactic conversion is critical for wine quality, as it contributes significantly to establishing the desired organoleptic parameters as well as wine microbiological properties and, thus, stability. The lactic acid bacterial species *Oenococcus oeni* has become the dominant "starter" species among those used for triggering malolactic fermentation (376). An important parameter can be the timing of the addition of the lactic acid bacterium at the end of the primary fermentation, as it must tolerate an environment that now contains yeast-derived ethanol and other toxic metabolites, such as sulfur dioxide, as well as having a low nutrient avail-

ability and a low pH (184). Interestingly, the coinoculation of yeast and a malolactic fermentor in the production of Chardonnay was shown to reduce fermentation times while producing wines that were broadly comparable to those produced through more typical two-phase inoculations (184). Dual bacterial-fungal starter cultures may also improve organoleptic properties in some instances (410). Relationships ranging from competition to inhibition to mutualism between yeast and bacteria during winemaking have been reported; for example, studies have established that yeast nitrogen metabolism can have significant and various effects on malolactic fermentation (143, 319). Further descriptions of these relationships can be found in reviews by Fleet (108) and Alexandre et al. (5). A fuller understanding of the ecology and biochemistry of this microbial ecosystem will undoubtedly have significant benefits for the wine industry and may also provide insights into the cometabolism of BFIs in other contexts.

A variety of other food products are formed due to the actions of mixed bacterial-fungal cultures (367, 408). The fermented soy product tempeh is produced by the action of *Rhizopus oligosporus*, which inhibits contamination by other microorganisms, including many bacteria (148). Lactic acid bacteria also contribute to the tempeh fermentation process and can similarly inhibit the growth of potentially harmful pathogenic bacteria (14). Not all *Lactobacillus* species are capable of coculture with *Rhizopus*, and the rate of fungal growth can be reduced by the bacterium, an effect which also seems to be dependent on the starting inoculum of bacteria (148). A detailed analysis of BFIs in sourdough between lactic acid bacteria and yeasts pointed strongly to key trophic relationships such as the lack of competition for preferred nitrogen sources and even the stabilization of the population of lactobacilli due to yeast-derived amino acids and peptides (134). In some cases, multiple fungi and bacteria may be involved in food production. Soy sauce fermentation involves an initial inoculation with koji (*Aspergillus oryzae* or *A. soyae*) to break down complex oligosaccharides and proteins in soybeans, followed by the transfer of the koji to brine, where it is further fermented by a mixture of bacteria (*Tetragenococcus halophilus* and lactic acid bacteria such as *Lactobacillus delbrueckii*) and yeasts (*Zygosaccharomyces rouxii* and *Candida* sp.), which are metabolically adapted for the osmotic and pH conditions of the brine (60). Similarly, a range of different yeasts and *Acetobacter* sp. are needed to form the fermented sweetened tea kombucha (244).

Cheese ripening. Like wine production, cheese manufacture involves complex microbial ecosystems where BFIs play a central role, and rich mixed communities are often present (2). In bacterial smear surface-ripened cheeses such as German "Limburger," French "Munster," and Italian "Taleggio," molds and yeast such as *Debaryomyces hansenii* and *Geotrichum candidum* initially dominate the cheese surface because they are acid and salt tolerant (79). They utilize lactate and thus deacidify the cheese surface, enabling the establishment of less-acid-tolerant bacterial communities, which play a significant role in the quality and safety of the final product (79). To understand the BFIs that occur during ripening, Bonaiti et al. (47) developed a microbial Livarot cheese model by selecting microbial associations contributing to cheese aroma. They succeeded in simplifying an ecosystem of 83 microbial strains from a commercial Livarot cheese to a subecosystem composed of nine species that had a strong similarity to that of the commercial cheese. In this model ecosystem, yeast appeared to play a key role in bacterial colonization and bacterial diversity; for example, the growth of some bacterial species, such as *Leucobacter* sp. or *Brevibacterium aurantiacum*, significantly relied on the presence of the yeast *Geotrichum candidum* (261). An understanding of the specificity of the BFIs that occur on the yeast surface will help industries that commercialize ripening microbial cultures to select the most adapted bacterial strains. Indeed, it was shown that despite massive early inoculations, commercial inocula do not always colonize the cheese surface due to the rapid development of adventitious microbiota originating from the cheese production environment (260). Unraveling the ecology of the multispecies cheese ecosystem may have benefits for food safety as well. Control of the development of the human pathogen *Listeria monocytogenes* in cheese is difficult due to the favorable growth conditions and its ubiquity. However, some smear-ripening bacterial communities have strong antilisterial activities (236) that might be harnessed to restrict or prevent the development of human pathogens such as *L. monocytogenes* during cheese ripening.

Food spoilage. While BFIs are exploited for the production of certain foods, fungi and bacteria are also key food spoilage organisms; however, few studies have examined whether BFIs contribute to food spoilage, perhaps due to an emphasis on diagnostics/systematics and shelf life prediction within the food industry (327). Some studies have examined the potential of fungi to assist colonization by human-pathogenic bacteria; for example, spoilage fungi on tomatoes can promote *Salmonella* colonization, an effect which is believed to be due to their effect on pH (393, 394). The presence of rhizonin toxins produced by endobacteria inhabiting *Rhizopus microsporus* is a critical cause of food spoilage due to their hepatotoxicity (296). Similarly, rhizoxin-producing endobacteria present a potential threat in food processing since *R. microsporus* is used during the fermentative production of tempeh (209, 296, 326). Bacteria can also cause spoilage on mushroom tissues, although the effect is largely on mushroom yield and cosmetic appeal to the consumer rather than on human health (374). There has been some interest in the role of bacteria, notably lactic acid bacteria, as biopreservatives of food and animal feed (128, 336, 346). Increasing our knowledge of the antifungal activities of beneficial food-associated bacteria and also their ecology, notably their relationships with beneficial and spoilage fungi within food and animal feed, will help industries to select either strains with a wide range of applications or, conversely, strains that are well adapted to specific environments and applications.

Bioremediation of Pollutants

The microbial degradation of polycyclic aromatic hydrocarbons (PAHs) has significant potential for use in bioremediation (67, 181). PAHs are a large group of toxic environmental contaminants originating for fossil fuels and also made as a result of the incomplete combustion of various carbon-containing fuels. Most PAHs are hydrophobic and so bind to soils and sediments, thus reducing their bioavailability; they also accumulate in food chains. Due to the failure to isolate a single

microorganism capable of growing on and mineralizing PAHs with five and or more benzene rings and the ubiquitous coexistence of bacteria and fungi in the environment, some authors have investigated the degradation efficacy of mixed bacterial-fungal cocultures. Boonchan et al. (49) compared the degradations of pyrene, benzo[*a*]pyrene, and dibenz[*a*,*h*]anthracene in monocultures of *Penicillium janthinellum* and *Stenotrophomonas maltophilia* and in cocultures of the two. *Penicillium janthinellum* by itself could partially degrade pyrene and benzo[*a*]pyrene but did not use either of them as a carbon source. *Stenotrophomonas maltophilia* by itself could use pyrene as a carbon source and cometabolize benzo[*a*]pyrene. Bacterial-fungal cocultures grew on pyrene, benzo[*a*]pyrene, and dibenz[*a*,*h*]anthracene and significantly improved the benzo[*a*]pyrene mineralization. Moreover, they significantly reduced the mutagenicity of contaminated soils with benzo[*a*]pyrene or dibenz[*a*,*h*]anthracene (49). Similarly, a *Penicillium* sp. culture and three bacterial strains originating from a hydrocarbon-contaminated soil were shown to have a synergistic effect on the removal of polluting phenanthrene when coinoculated into contaminated soil (72). Bacterial-fungal cocultures have also been found to have an enhanced ability to decolorize waste azo dyes that cause environmental pollution (137), while a mixed bacterial-fungal biofilm of *Penicillium frequentans* and *Bacillus mycoides* demonstrated a greater ability to degrade polyethylene than either partner alone (363). Similar effects of bacterial-fungal cocultures on polycaprolactone degradation have also been reported (33). These results highlight the fact that bacteria and fungi can cooperatively or synergistically mineralize soil pollutants. These results open interesting practical applications for the complete bioremediation of PAH-contaminated sites, and in view of these results, one should consider microbial interactions as well as the individual potential of isolates for pollutant degradation to improve the PAH bioremediation process.

Naturally occurring BFIs also play a key role in bioremediation in contaminated soil ecosystems. Heinonsalo et al. (159) observed decreased levels of mineral oil (nonpolar hydrocarbons) in petroleum hydrocarbon-contaminated soil colonized by pine roots and mycorrhizal fungi naturally associated with soil bacterial communities. *P. fluorescens* isolates that possess *xylE* and *xylMA*, plasmid-borne genes that are involved in the degradation of monoaromatics, have been found to naturally form biofilms around the hyphae of ectomycorrhizal fungi symbiotically associated with Scots pine seedlings, providing strong evidence for a bacterium-assisted breakdown of monoaromatic compounds in petroleum-contaminated soil colonized by ectomycorrhizal fungi (334). Air and a lack of moisture create barriers to the mobility of pollutant-degrading bacteria in the soil, which prevent them from spreading and delay the breakdown of pollutants. The potential of hydrophilic fungal hyphae to serve as vectors for the dispersion of several pollutant-degrading bacteria was first demonstrated by Kohlmeier et al. (202). Hyphae of the oomycete *Pythium ultimum* were subsequently also shown to facilitate the movement of the phenanthrene-degrading strain *Pseudomonas putida* PpG7 in soil (121, 404). The use of bacteria that are able to move across this "fungal highway" could help speed up the remediation of contaminated land (202). To fully exploit this potential, further research is needed to address whether all bacteria are able to use such fungal vectors and whether all fungi are able to route bacteria and to assess what impact fungal and bacterial cell walls have on this process.

Natural Product Discovery and Synthetic Biology

Humans are increasingly using BFIs, or harnessing knowledge garnered from them, for many novel applications. For instance, basic research on BFIs continues to be of importance to the development of novel agents against pathogens. This is exemplified by the discovery of the fungal defensin peptide plectasin from *Pseudoplectania nigrella* (345). Plectasin targets lipid II, a key component in bacterial cell wall biosynthesis, and thus provides a promising lead for a new antibiotic therapy in the face of the increased incidence of multiple-antibiotic-resistant bacteria in hospitals (269, 345). As well as the identification of secondary metabolites, recent findings suggest that BFIs can also be used to activate putative fungal secondary metabolite gene clusters that are not expressed under other culture conditions (50). Schroeckh et al. (353) demonstrated that the specific BFI between *Aspergillus nidulans* and *Streptomyces hygroscopicus* ATCC 29253 induces the expression of a fungal gene cluster responsible for the biosynthesis of several polyketide metabolites, including orsellinic acid and lecanoric acid, the latter being a typical lichen metabolite, in a contact-dependent manner. Similarly, the biosynthesis of the chlorinated benzophenone antibiotic pestalone by the marine fungus *Pestalotia* was triggered when the fungus was cocultivated with the marine alphaproteobacterium CNJ-328 (81). Strain CNJ-328 was also used to induce the synthesis of novel diterpenoids from the marine fungus *Libertella* sp. (284). Several other studies have supplemented fungal cultures with bacteria and bacterial supernatants to induce or enhance the production of fungal natural products, illustrating potential industrial applications for BFIs in this context (98, 248). An example of the fungal stimulation of a bacterial product can be seen in the enhancement of nisin (a food preservative) biosynthesis by *Lactococcus lactis* upon cocultivation with yeast that is able to metabolize inhibitory lactic acid that is produced during the fermentation (222). An understanding of neutral BFIs may also be of benefit in some circumstances; for example, the selection of vitamin-producing bacterial strains that can be cocultured with *Rhizopus* was suggested as a method for the provision of vitamin B_{12} in tempeh production (190, 405).

A more reductive approach to harnessing BFIs involves the transfer of specific genes provided by one partner to the other. This may have benefits in allowing a more controlled expression of the heterologous trait, providing a more straightforward means of obtaining the same result, or allowing the expression of a trait where a "real" BFI is either undesirable or unachievable. Such approaches have been pioneered in yeast thanks to the availability of amenable genetic and cultivation techniques. In one case, an *S. cerevisiae* strain was engineered to produce a levanase from *Bacillus subtilis* that increased its ability to produce bioethanol from waste plant biomass (240). The enzyme allows the yeast to use novel carbon sources which otherwise need to be released by a separate pretreatment of the input plant material (240). In wine production, *S. cerevisiae* and *Schizosaccharomyces pombe* have been engineered to express the malolactic gene from *Lactococcus lactis* in order to

Characteristic	Parallel	
Tolerance to antibiotic treatment	Human polymicrobial infections (141)	Cave painting biofilms (22)
Removal of inhibitors/toxins	Probiotics in the digestive tract (56)	Degradation of wood preservatives (371)
Suppression of fungal pathogen	Disinfection of ant fungus gardens (136)	Biocontrol of crop diseases (374)
Enhanced release of nutrients	Ruminal digestion (223)	Mycorrhizal helper effect (357)
Mobilization of bacteria to new niches	Invasion of human tissues (283)	Transport of PAH degrading bacteria in soil (188)
Metabolic cooperation	Cyanolichen symbiosis (183)	Food production (39)

FIG. 7. Examples of some parallels among BFIs in different settings (22, 39, 56, 136, 141, 183, 188, 223, 283, 357, 371, 374).

enable them to perform both the alcoholic and malolactic fermentation stages without the need for malolactic bacteria (8). *E. coli* strains have been engineered with a combination of genes from *S. cerevisiae* and from other bacterial strains to convert dihydroxyacetone phosphate into 1,3-propanediol, which can be used as building blocks for industrial polymers (271). Bringing together subelements (e.g., protein domains) from bacterial and fungal systems into a single unit also has the potential for many novel applications; for example, protein domain sequences from a fungal nonribosomal peptide synthetase have been used to modify a similar gene in *Bacillus subtilis*, resulting in the production of novel secondary metabolites (377). In another example, a hybrid protein containing a fungal (*Trichoderma viride* HK-75) cellulose binding domain from an exoglucanase I enzyme fused to a bacterial (*Bacillus subtilis* BSE616) endo-beta-1,4-glucanase has improved binding and hydrolytic activities toward microcrystalline cellulose (191). Such hybrid constructions have been investigated with the purpose of producing artificial cellulosomes with enhanced abilities to biodegrade complex plant cell wall components (254). Clearly, the explosion in the amount of genome data from both the bacterial and fungal kingdoms is opening up tremendous possibilities for innovations in synthetic biology that may draw inspiration from our knowledge of BFIs.

CONCLUDING REMARKS

Everywhere, including in unexpected places and environments, bacteria and fungi have been found to live side by side and interact, and clear parallels can be drawn between some of these diverse BFIs (Fig. 7). The range of mechanisms for both antagonism and cooperation exhibited during BFIs is undoubtedly a reflection of the continuous interplay between bacteria and fungi that has occurred over the course of their evolutionary histories. It is likely that many more BFIs exist, particularly in natural environments such as the ocean, that are relatively understudied from a microbiological perspective. We are beginning to appreciate the range of effects that BFIs bring about, but there are many interesting aspects of BFIs that warrant further investigation and that will benefit from technological advances made in recent years. While many examples of bacterial-fungal communities are known, in many instances, our knowledge of the factors contributing to their initial formation (particularly, complex communities such as those in the mycorrhizosphere) and subsequent stability/homeostasis is scant. The availability of high-throughput metagenomic methodologies and data analysis techniques will enable researchers to robustly address questions such as the specificity that exists in bacterial-fungal community interactions and the changes in functionality that occur as mixed bacterial-fungal communities develop, although these sequencing-based approaches can be fully exploited only with complementary information gathered through other means, such as metabolite profiling and isotopic labeling. The ability to perform culture-independent microbial identification may also reveal previously unrecognized bacterial-fungal consortia if researchers take care to perform simultaneous prokaryotic and eukaryotic identification from environmental DNA samples.

The study of BFIs has led to the discovery of a great number of natural products and tools to transform fungi, but there is currently a dearth of data pertaining to non-antibiotic-mediated cell-cell communication between fungi and bacteria at the molecular level. A deeper appreciation of BFI signaling at the cellular level may lead to novel therapeutic targets for combating single- and mixed-microbial infections and conversely may also allow the enhancement of beneficial BFIs. From a biotechnology perspective, knowledge of the metabolic relationships during BFIs has significant potential for exploitation in numerous fields but has not received much attention beyond food technology research. The metabolic effect of bacterial-fungal communities on their environment will also be of great interest in the context of climate change, bioremediation, and searches for novel antimicrobials and drug therapies. Fungal endobacteria may represent an excellent approach for producing easy-to-apply "stabilized" BFIs in which modified bacteria reside within fungal hyphae, but currently, our understanding of the global ecology, evolution, trophic relationships, and functioning of these and other BFIs remains in its infancy, hampering the development of such applications. Research addressing these issues will have major implications for our view of bacterial and fungal biology and ecology.

ACKNOWLEDGMENTS

We thank Jean Garbaye for providing helpful suggestions for the manuscript.

We also gratefully acknowledge the financial backing provided by INRA to P. Burlinson and the support that has been given towards research on bacterial-fungal interactions in the Tree-Microbe Interactions Department by both INRA and the Lorraine Region for over 10 years.

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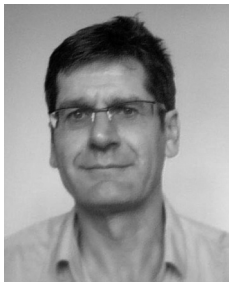

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