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Microbially Mediated Plant Functional Traits

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Annu. Rev. Ecol. Evol. Syst. 2011. 42:23–46

First published online as a Review in Advance on August 11, 2011

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi: 10.1146/annurev-ecolsys-102710-145039

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1543-592X/11/1201-0023$20.00

Keywords

mutualism, endophyte, epiphyte, plasticity, context dependence, fitness conflict, ecosystem processes, bacteria, fungi

Abstract

Plants are rife with bacteria and fungi that colonize roots and shoots both externally and internally. By providing novel nutritional and defense pathways and influencing plant biochemical pathways, microbes can fundamentally alter plant phenotypes. Here we review the widespread nature of microbially mediated plant functional traits. We highlight that there is likely fitness conflict between hosts and symbionts and that fitness outcomes can depend on partner genotypes and ecological factors. Microbes may influence ecosystems through their effects on the functional trait values and population dynamics of their plant hosts. These effects may feed back on symbiont evolution by altering transmission rates of symbionts and scale up to ecosystem processes and services. We end by proposing new avenues of research in this emerging field.

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1. INTRODUCTION

Functional trait: a morphological, physiological, or phenological property of an individual plant that is correlated with plant fitness proxies

Scaling: a technique that accounts for covariation among traits, ecophysiology, demography, and the abiotic environment to build predictive ecosystem-level models

Diverse mutualistic bacteria and fungi thrive on plant surfaces and inhabit most plant tissues. Many of these microbes interact with their plant hosts intimately; they can influence plant metabolism and hormonal pathways in addition to providing novel nutritional or biosynthetic capacities. Many phenotypic properties of plants derive not only from the genetic repertoire of the plant itself, but also from the interplay between the plant and its microbial associates. Thus, microbial mutualists can mediate many ecological, evolutionary, and ecosystem processes by altering plant functional traits. These traits influence plants' interactions with competitors, mutualists, herbivores, and pathogens and can play a role in niche breadth, relative abundance, productivity, and nutrient fluxes.

We define a functional trait as a morphological, physiological, or phenological phenotype of a plant measured on an individual that impacts plant fitness through biomass, fecundity, or survival—fitness components that are not considered functional traits per se (Violle et al. 2007). These fitness components, although correlated, can be measured separately from one another. Similarly, functional traits must be measurable and typically influence ecosystem processes (Bernhardt-Romermann et al. 2008, Westoby & Wright 2006), such as the relationship between leaf nitrogen and litter decomposition (Cornwell et al. 2008). A functional trait is microbially mediated if its value is determined, partially or entirely, by the presence or genotype of a microbe or group of microbes. As discussed in Section 2, we lack estimates of the relative contributions of microbes to trait variation for most plant functional traits. Defining microbially mediated plant functional traits at the individual level facilitates the rigorous scaling of the consequences of trait variation to (*a*) plant performance and (*b*) population, community, and ecosystem processes. Scaling requires the measurement of relationships among functional traits, ecophysiological and demographic parameters, and ecosystem fluxes to parameterize models that predict the emergent properties of communities (Díaz & Cabido 2001, Moorcroft et al. 2001). One important trait category is response traits: traits measured across environments that define an organism's response to environmental change (Violle et al. 2007). Abiotic stress tolerance is a response trait that has many examples of microbial mediation (see Section 3.4). Functional traits are often used to capture covariation along key phenotypic axes. For example, the global leaf economics spectrum describes how plant leaves across many species and biomes range from short-lived thin leaves to long-lived, well-defended thick leaves (Wright et al. 2004). The microbial alteration of plant-enemy interactions likely influences a plant's position on the leaf economic spectrum (see Section 3.2).

We focus on emerging examples and restrict discussion of the well-reviewed rhizobia and mycorrhizae symbioses. As discussed in Section 4.1, many definitive tests of mutualism have not been conducted, particularly under natural conditions, and many interactions can vary from parasitism to mutualism depending on ecological context. Thus, although we describe microbes that are potentially mutualists at least some of the time, we urge readers to remain skeptical that the microbial mediation of plant traits is necessarily beneficial for both partners.

We describe the widespread nature of microbially mediated plant functional traits and the exploding interest in plant-associated bacteria and then focus on the molecular mechanisms that microbes use to alter plant traits. Knowledge of the molecular basis of trait mediation is essential for investigators to scale from genes to ecosystems (Whitham et al. 2006). Furthermore, known molecular mechanisms represent convenient genetic or biochemical targets for measuring microbial trait mediation in experimental and natural systems. We discuss the importance of microbially mediated traits in driving the evolution and ecology of plants and ecosystems and highlight ripe avenues of future research.

2. KNOWN MUTUALISTIC MICROBIAL ENDOPHYTES AND EPIPHYTES OF PLANTS

Epiphyte: a microbe that lives on the surface of plant tissue

Endophyte: a microbe that can enter plant tissue

Prokaryotes comprise the greatest number of cells on the planet, with 10^{30} cells containing as much carbon, and an order-of-magnitude more nitrogen and phosphorus, as plants (Whitman et al. 1998). A small fraction of these, 10^{26} cells, are found on leaf surfaces at densities 10^{6-7} cm^{-2} (Lindow & Brandl 2003). In addition to epiphytes on leaf and root surfaces, bacterial endophytes colonize the interiors of root and leaf tissue, stems, xylem vessels, apoplast, seeds, and nodules, often with tissue specificity (Rosenblueth & Martínez-Romero 2006). Current lab-based estimates of endophytic bacterial populations range from 10^7 to 10^{10} cells per gram of tissue (Hardoim et al. 2008); we lack abundance estimates of fungal, archaeal, and viral associates. Although the biomass of plant-associated microbes is small, their effects on ecosystems may be large through their influence on plant functional traits.

Figure 1 shows the genera of endophytic bacteria commonly isolated from plants. The model symbiosis between legumes and rhizobia has been studied since the 1880s, and the beneficial effect of legumes on soil nitrogen was known in ancient times (Sapp 2004); for most microbes, however, an appreciation of their potentially beneficial effects on plants has emerged recently. Using the ISI Web of Knowledge, we estimated the time course of the study of endophytic bacterial genera in relation to plants. Some have been studied since the 1960s, but many genera have become known only in the past decade. The field is currently dominated by a handful of taxa, and research into rhizobia is leveling off (the decline in the genus name *Rhizobium* has resulted from better taxonomic treatment recognizing multiple paraphyletic genera within rhizobia, a generic designation for nodule bacteria).

Root-associated mycorrhizae are found in 80% of terrestrial plants (Bonfante & Anca 2009); they are most commonly either endomycorrhizal (typically Glomeromycota that form arbuscules within plant cells) or ectomycorrhizal (typically Ascomycota or Basidiomycota that do not penetrate cell walls but rather form nets around root cells). The endomycorrhizal form is considered ancestral, and plant evolution shows evidence of many independent associations and losses of mycorrhizal association (Wang & Qiu 2006). Endophytic fungi typically belong to the Ascomycota and Basidiomycota and are ubiquitous in terrestrial plants, although infection frequencies can vary by population (Arnold 2007, Rodriguez et al. 2009, Rudgers et al. 2009). In some instances,

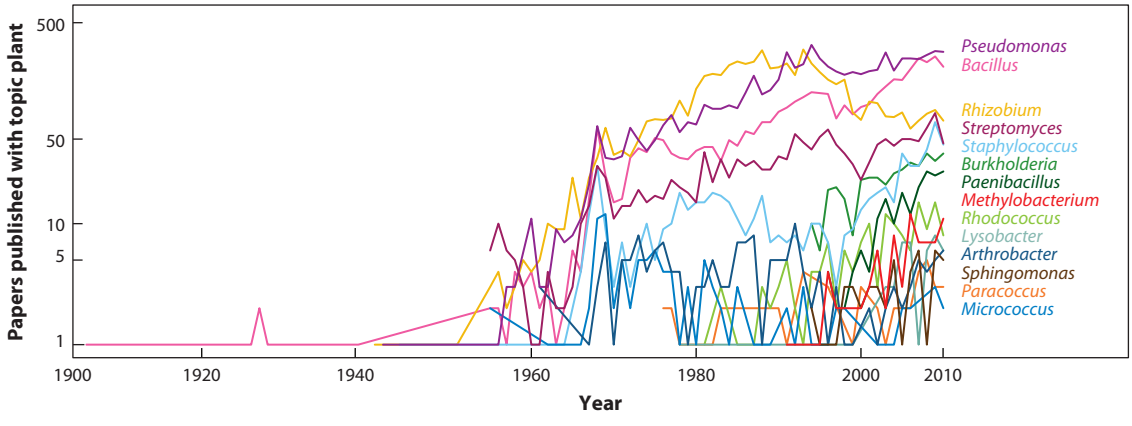

Figure 1

Research effort in terms of yearly publications in different endophytic bacterial genera. Data are from an ISI Web of Science search with "genus" in the title field and "plant" in the topic field.

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such as *Cenococcum geophilum*, the same fungal species can be both a foliar endophyte and a root mycorrhiza (Arnold 2007). Fungi can also colonize the seeds of grasses (Clay & Schardl 2002), conifers (Ganley & Newcombe 2006), and tropical trees (U'Ren et al. 2009).

CAM: crassulacean acid metabolism

Systematic estimates of the proportion of plant-associated microbes that affect plant functional traits and the magnitude of these phenotypic effects are lacking. However, interactions with known molecular basis provide clues that the fraction of important microbes may be large. Of 300 strains cultivated from sugarcane rhizosphere, one-third showed antagonism to the fungal pathogen *Colletotrichum falcatum*. Within the 39 most antagonistic strains, 49% produced indole-3-acetic acid (auxin) and 44% solubilized phosphate (Hassan et al. 2010). In another study focusing on rhizobia, of 13 strains, 38% produced ACC deaminase (Ma et al. 2003), which lowers ethylene levels and can impact enemy resistance (see Section 3.2).

The rhizobia-legume symbiosis provides substantial evidence that microbial symbionts make important contributions to plant phenotypes relative to other sources of variation. For example, an experiment in which 24 alfalfa (*Medicago sativa*) cultivars were inoculated factorially with 11 rhizobium strains demonstrated that the bacterial strain explains as much or more of the phenotypic variation as the plant genotype, with significant interactions between the plant and bacterial genotype. Bacterial strain identity, plant cultivar, and plant-by-bacterial interaction, respectively, explained 24%, 17%, and 47% of the variation in shoot dry weight; 23%, 27%, and 42% of the variation in root dry weight; and 74%, 7%, and 13% of the variation in plant height (Tan & Tan 1986). The larger contribution of the bacterial genotype to plant height as opposed to plant biomass suggests that rhizobia might vary in their alteration of hormones that influence stem elongation.

We require similar experiments that measure a suite of plant functional traits on different plant genotypes grown with different microbial strains to partition the effects of variation in host genotype versus symbiont genotype and determine their directions and magnitudes. The legume-rhizobia symbiosis may have inordinately large phenotypic effects relative to other associated microbes because nitrogen fixation supplements the most limiting terrestrial nutrient, but we predict that hormonal effects could be as large.

3. MICROBIAL MEDIATION OF PLANT TRAITS

The main purpose of measuring plant functional traits is to get closer to the mechanistic basis of performance differences between plants as well as their interactions with biotic and abiotic factors. In many cases, microbes could be important components of the proximate mechanisms underlying plant functional traits (see **Figure 2**). Supporting this, we present examples from the literature in relation to a standard set of plant functional traits (Cornelissen et al. 2003). Of 30 functional traits, 14 have known examples of microbial mediation (**Table 1**). These include most leaf traits and all root traits. Five functional traits, including photosynthetic pathways (C3, C4, CAM) and growth forms (herb, vine, shrub, tree), seem unlikely to be under the influence of microbes, although it is intriguing that fungi can influence the degree of the clonality of grasses (Streitwolf-Engel et al. 2001). We lack studies in which the remaining traits are measured in response to microbial manipulation; many of these regard stem characteristics.

There are two distinct ways that microbes mediate plant functional traits: (*a*) by providing novel biochemical capabilities and (*b*) by altering existing plant pathways. Microbes have a greatly expanded metabolic repertoire compared to their plant hosts, synthesizing biologically active chemicals that plants cannot make. Additionally, microbes can alter plant physiological pathways by producing or manipulating phytohormones. Microbes can produce all plant hormones identified to date.

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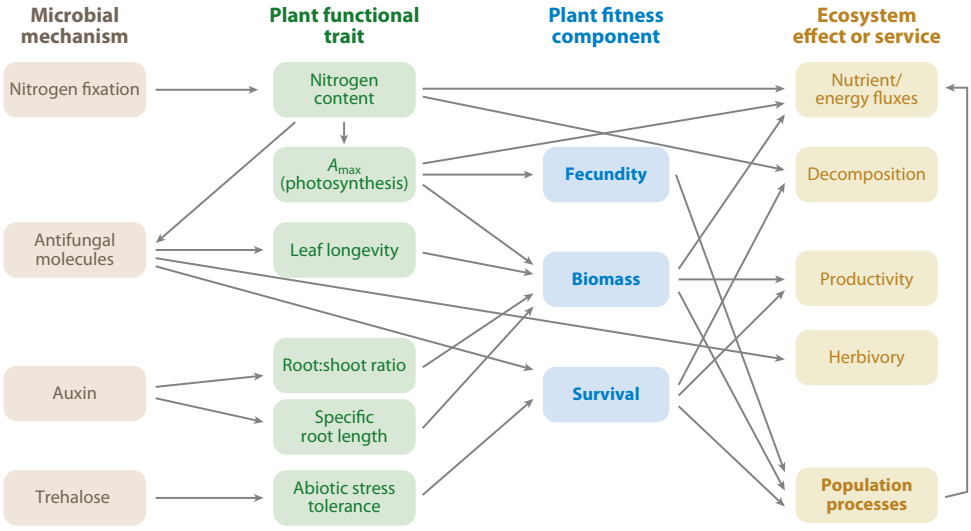

Figure 2

Examples of relationships among microbially mediated mechanisms, plant functional traits, plant fitness components, and ecosystem properties and services. For clarity, not all possible relationships are depicted. There can be interactions between functional traits, such as the maximum photosynthetic rate depending on nitrogen content, and the effects of functional traits on microbial mechanisms, as in a higher nitrogen content enabling the increased production of defense molecules. Functional traits can influence ecosystems directly, such as nitrogen content influencing decomposition and A_{max} altering the fluxes of light, water, and CO_2. Plant defense mediated by microbial antifungal molecules can act through leaf longevity as well as through the direct alteration of plant survival and the ecosystem service herbivory. The microbial mediation of ecosystems can act via functional traits that impact plant fitness, such as microbial auxin production altering the root:shoot ratio and hence biomass, which then changes both plant demography and the ecosystem service productivity. Finally, phytohormones such as auxin can influence multiple functional traits.

Fitness conflict occurs if plant and microbe fitness are maximized at different functional trait values. We note that for novel capabilities, microbes likely bolster plant fitness to values higher than would be possible without the microbe, particularly for nutritional and defensive interactions. The potential for fitness conflicts may be small as both partners' fitness can improve relative to unassociated individuals (Schwartz & Hoeksema 1998). However, microbial pathways require metabolic inputs by the plant host, and microbes may cheat by redirecting plant resources to microbial reproduction. We expect traits impacted by the microbial alteration of plant hormonal pathways to exhibit an even greater fitness conflict. However, because microbes that produce phytohormones can have effects at low abundances, they could consume less plant resources than microbes that require large population sizes to function, such as rhizobia.

In this section we describe how plant functional traits involved in nutrient acquisition, defense, morphology, and abiotic stress tolerance are influenced by microbes. In each case we give examples of novel and altered pathways.

Fitness conflict: occurs when host and microbe fitness are maximized at different values of a trait possessed by one or both partners

3.1. Nutrient Acquisition

Resource availability directly impacts functional traits such as leaf longevity and specific leaf area, leaf nitrogen and phosphorus levels, the root:shoot ratio, and stem density. Microbes mediate

Table 1 Plant functional traits with known microbial mediation[a]

Category	Trait	Plant	Microbe	Reference
Leaf	Specific leaf area	Soybean (*Glycine max*)	Rhizobia (*Bradyrhizobium japonicum*)	Harris et al. 1985
Leaf	Leaf size	Grasses (*Agrostis perennans*, *Poa autumnalis*)	Fungal endophytes (*Clavicipitaceae*)	Davitt et al. 2010
Leaf	Leaf dry-matter content			
Leaf	Leaf nitrogen concentration	*Welfia georgii*	Cyanobacteria	Section 3.1; Bentley & Carpenter 1984
Leaf	Leaf phosphorus concentration		Endomycorrhizae	Section 3.1
Leaf	Physical strength of leaves			
Leaf	Photosynthetic pathway			
Leaf	Leaf frost sensitivity	Alfalfa (*Medicago sativa*)	Rhizobia (*Sinorhizobium meliloti*)	Bertrand et al. 2007
Regenerative	Dispersal mode			
Regenerative	Dispersule shape			
Regenerative	Dispersule size/mass			
Regenerative	Seed mass	Grasses (*Schedonorus phoenix*, *Schedonorus pratensis*)	Fungal endophyte (*Neotyphodium*)	Saari et al. 2010a
Regenerative	Resprouting capacity			
Stem	Specific stem density			
Stem	Twig dry-matter content			
Stem	Twig drying time			
Stem	Bark thickness			
Vegetative	Growth form			
Vegetative	Life-form			
Vegetative	Plant height	Rice (*Oryza sativa*)	Rhizobia (*Rhizobium leguminosarum* bv. *trifolii*)	Perrine-Walker et al. 2007
Vegetative	Clonality	*Prunella vulgaris*	Endomycorrhizae (*Glomus* sp.)	Streitwolf-Engel et al. 2001
Vegetative	Spinescence			
Vegetative	Flammability			
Vegetative	Leaf life span	Cacao (*Theobroma cacao*)	Leaf endophytic fungi	Arnold et al. 2003
Vegetative	Leaf phenology			
Root	Specific root length	Maize (*Zea mays*)	Endomycorrhizae (*Glomus mosseae*)	Kothari et al. 1990
Root	Fine root diameter	Pine (*Pinus taeda*)	Ectomycorrhizae (*Pisolithus tinctorius*, *Cenococcum geophilum*)	Rousseau et al. 1994
Root	Root depth distribution	Clover (*Trifolium subterraneum*)	Rhizobia (*R. leguminosarum* bv. *trifolii*)	Morris & Djordjevic 2006

(*Continued*)

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Table 1 *(Continued)*

Category	Trait	Plant	Microbe	Reference
Root	95% rooting depth	Wheat (*Triticum aestivum*)	Endomycorrhizae (*Glomus fasciculatum*, *Glomus deserticola*)	Ellis et al. 1985
Root	Nutrient uptake strategy		Association with symbiotic microbes	

Row shading indicates level of evidence for microbial influence on each plant functional trait: Pink suggests that microbial influence is implausible, green illustrates that microbes are known to play major roles, light green indicates that some examples of microbial mediation are known, and blue denotes an absence of evidence. Functional traits from Cornelissen et al. (2003).

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plant resource acquisition by (*a*) accessing a form of the nutrient otherwise unavailable to the plant and (*b*) more efficiently gathering resources.

3.1.1. Nitrogen fixation. Nitrogen is required for protein production, particularly Rubisco, and thus determines the maximum photosynthetic rate. Higher nitrogen may also cause plants to invest more into nitrogen-rich defense compounds (see Section 3.2). The ability to fix atmospheric nitrogen is entirely lacking from land plants but is present in at least six bacterial phyla (such as Proteobacteria, which includes both rhizobia and the actinobacterial genus *Frankia*) and several archaeal lineages (Martínez-Romero 2006). Some grasses associate with nitrogen-fixing bacteria (James 2000), but proof of fixed nitrogen being transferred to plants is lacking. Circumstantial evidence that these bacteria are important comes from several studies conducted under aseptic, greenhouse, and field conditions in which nitrogen-fixing bacteria increased yield (reviewed in Bhattacharjee et al. 2008), though mechanisms other than nitrogen transfer could be operating to increase plant productivity.

Leaf epiphytic cyanobacteria have been demonstrated to transfer atmospherically fixed nitrogen to plants—in the case of the palm *Welfia georgii*, it is estimated that 10%–20% of leaf nitrogen is derived from cyanobacteria (Bentley & Carpenter 1984). This phenomenon, however, is not universal and appears to be restricted to tropical forests (Goosem & Lamb 1986). A survey of epiphyll nitrogen fixation across 25 species in Costa Rica documented high variation both within and between species (Bentley 1987); more recent work found that four out of 16 species had nitrogen fixation rates with standard errors that do not overlap zero (Furnkranz et al. 2008). The nitrogenase subunit gene *nifH* sequences associated with these species' leaf surfaces were primarily cyanobacterial (*Nostoc*, *Tolypothrix*, and *Fischerella*), but one species had sequences from *Klebsiella* (Furnkranz et al. 2008). Nitrogen-fixing activity is dependent on leaf moisture and is higher for leaves associated with bryophytes, which could decrease their light-harvesting ability (see Section 3.1.3) (Bentley 1987). Although it is assumed that plants provide carbon as well as habitat to leaf-dwelling microbes, we lack estimates of these costs.

3.1.2. Phosphorus and other minerals. Access to soil nutrients can influence many root functional traits. Mycorrhizal fungi are more efficient at nutrient uptake than their plant hosts and can reduce the number of fine roots, the root:shoot ratio, and specific root length (reviewed in Smith et al. 2009). Endomycorrhizae are well known for their phosphorus acquisition ability. The mechanisms of phosphorus uptake include novel plant architecture—hyphae are much thinner than fine roots and access narrow soil pores inaccessible to roots—as well as increased biochemical capacity in the form of hyphal exudates that release immobile soil nutrients. Ericoid mycorrhizae and ectomycorrhizae can produce hydrolytic and oxidative enzymes that release nitrogen from soil

Endomycorrhizae: fungi that form arbuscules (arbuscular mycorrhizae, phosphorus acquiring) or coils (ericoid mycorrhizae, enhanced degradation pathways) within root epidermal cells

Ectomycorrhizae: fungi that ensconce root cells in a net; typically associate with conifers to provide enhanced nitrogen uptake

organic matter; mycorrhizae also provide plants with water, nitrogen, and zinc uptake (Lambers et al. 2008b, Smith et al. 2009). Ectomycorrhizal fungi have been shown to transfer nitrogen to their host plants in boreal forests (Lindahl et al. 2007). In addition, mycorrhizae affect the soil structure, which in turn alters leaf stomatal conductance (see Section 3.4) (Auge 2004).

AHL: *N*-acyl homoserine lactone

3.1.3. Light. Specific leaf area and leaf longevity are functional traits that may depend on the identity and extent of colonization by epiphytic microbes. Photosynthetic and nitrogen-fixing cyanobacteria (in association with lichen, moss, and liverwort epiphytic macroorganisms) can shade leaves in addition to both leaching and exuding nutrients (e.g., Wanek & Portl 2005). We predict that the balance of costs and benefits will affect leaf investment. If younger leaves have higher light-harvesting ability but older leaves are a net nitrogen source due to epiphyte-associated nitrogen-fixing microbes, then light limitation should induce leaf turnover, whereas if nitrogen is limiting, leaves should be retained for longer periods. However, microbes may also influence leaf-turnover decisions; for example, some pathogens are known to prolong leaf life spans by producing cytokinins (Jones & Dangl 2006). Longer-lived leaves have lower rates of colonization by epiphytes (Coley et al. 1993); coupled with the between-species variation discussed in Section 3.1.1, this suggests that plants have mechanisms of controlling epiphyte colonization that are correlated with overall levels of leaf defense.

3.2. Plant Defense

Leaf longevity is a functional trait that depends on the level of tissue defense, and field estimates of these parameters necessarily incorporate the effects of plant enemies. Enemy defense can also directly influence fitness by increasing plant survival. Microbes can directly participate in defense by producing antagonistic molecules inside or on the surfaces of plants (Fravel 1988). They can also prevent the induction of pathogenic genes by interfering with quorum sensing and can compete with pathogens for plant resources. In fact, microbe-microbe competition could lead to the evolution of antagonistic molecules solely for interference competition; in this scenario, host benefits are incidental, and the evolutionary mechanisms to maintain mutualism reviewed in Kiers & Denison (2008) would not be required (see Section 4.2). Additionally, plant-associated microbes can indirectly influence a host's defensive status either by altering the expression of plant defense pathways or by increasing host vigor. For example, nodulated lupins produce more alkaloids than nitrogen-limited plants (Johnson et al. 1987).

3.2.1. Direct mechanisms. Defensive chemicals produced by endophytes are found in plant tissues (e.g., Arnold et al. 2003, Clay & Schardl 2002). Antimicrobials can be produced in plant tissues; e.g., nonanoic acid in seedlings inoculated with the fungus *Trichoderma harzianum* inhibits cacao (*Theobroma cacao*) pathogens (Aneja et al. 2005). Different strains and species of *Bacillus* produce a variety of lipopeptides in rhizospheres, roots, leaves, and fruits; each *Bacillus* strain can produce multiple antibiotics, and there can be synergistic interactions against pathogens (Haas et al. 2000). Because microbial communities may produce a mixture of antipathogen molecules, we predict that more diverse microbial communities will be able to better defend plant hosts.

Plant-associated microbes can protect plants by disrupting the quorum-sensing signal molecules required for virulence in pathogens. Quorum sensing is typically mediated by *N*-acyl homoserine lactones (AHLs). Bacteria that produce AHL-degrading lactonases (e.g., *Bacillus*, *Arthrobacter*, and *Klebsiella*) can interfere with pathogen-pathogen communication and prevent virulence gene expression (Reading & Sperandio 2006). This has been demonstrated

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using transgenics: *Lysobacter enzymogenes* transformed with lactonase genes reduced *Pectobacterium carotovorum* infection on cabbage and cactus relative to its parental strain (Qian et al. 2010).

Some antagonistic molecules may have pleiotropic effects on plants or microbial mutualists. Antimicrobials can act as plant hormones—this may be a mechanism by which plants respond to information about their microbial communities (Phillips et al. 2003). For example, *Azospirillum brasilense* produces phenylacetic acid, related to auxins, which antagonizes plant pathogens (Romero et al. 2003). Microbially produced auxin and other phytohormones can have immediate antibacterial effects (Morshed et al. 2005) as well as impact other physiological processes (see Sections 3.3 and 3.4). Chitinases that protect against fungi can also degrade Nod factor, which is essential for most rhizobia-legume symbioses (Jung et al. 2008). Some *Bradyrhizobium japonicum* produce rhizobitoxine inside soy (*Glycine max*) roots, which protects against the pathogenic fungus *Macrophomina phaseolina*. However, rhizobitoxine also increases the amount of resources hoarded by rhizobia in nodules and reduces plant growth (Ratcliff & Denison 2009). The multifarious effects of microbially produced molecules could result in covariation between plant functional traits and microbial community composition that will be important for scaling (see Section 4.5) and could additionally constrain the evolution of these molecules. The retention of duplicated hormone receptors in plants (e.g., Park et al. 2009) could result from functional divergence in part to circumvent these pleiotropic effects.

Endophytic fungi can reduce leaf and seed herbivory, but they can also affect higher trophic levels (see Section 4.3.2). In grasses, *Neotyphodium* reside in the leaf sheath, and infected plants contain alkaloids, lolitrems, lolines, and peramines that defend against herbivores (Clay & Schardl 2002). Endophyte-produced alkaloids are often concentrated in seeds and can deter seed predators (Knoch et al. 1993). Endophyte mutants with either altered synthesis or altered secretion of inhibitory molecules would be useful to corroborate the microbial origin of such molecules and to estimate their ecological effects.

3.2.2. Indirect mechanisms. The plant immune response involves the recognition of pathogens and the decision to mount a response, typically a hypersensitive response that leads to localized cell death and prevents infection spread (Jones & Dangl 2006). Systemic acquired resistance was first described in response to tobacco mosaic virus (Ross 1961) and has since been described in response to bacteria in the rhizosphere (van Loon et al. 1998). It results in heightened resistance throughout a plant, rather than the localized resistance conferred by many endophytes as discussed above. Salicylic acid, which induces systemic acquired resistance, is produced by *Pseudomonas aeruginosa* in tobacco (*Nicotiana*) rhizospheres (Maurhofer et al. 1998). The fungus *Trichoderma*, widely used in biocontrol, induces both systemic and localized resistance to a variety of plant pathogens (Harman et al. 2004). In barley (*Hordeum vulgare*), the root fungal endophyte *Piriformospora indica* confers disease resistance systemically through the increased activity of glutathione-ascorbate antioxidant systems (Waller et al. 2005). Sometimes host defense is achieved through priming (Conrath et al. 2006). For example, the nonpathogenic Path-1 mutant of *Colletotrichum magna* only induces host defense responses after pathogen exposure, with increased levels of peroxidase and lignin deposition compared with uninfected plants (Redman et al. 2002a). We know little about how plants modulate their induction of defenses when interacting with mutualistic microbes.

3.3. Plant Morphology

Root traits are key functional traits with many examples of microbial alteration (**Table 1**) (Cornelissen et al. 2003). In addition to indirect mediation via nutritional traits (see Section 3.1), microbes can directly influence some aspects of plant architecture. The phytohormone auxin

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influences many of these traits; mutant studies show that *Azospirillum* stimulation of root proliferation results from auxin (Spaepen et al. 2008). Quorum-sensing AHLs can modify root development in *Arabidopsis* (Ortíz-Castro et al. 2008), particularly primary root growth, lateral root formation, and root hair development. Many plant-growth-promoting rhizobacteria are found on root surfaces and typically produce phytohormones or alter ethylene levels with beneficial effects on above-ground biomass (e.g., Ma et al. 2003). Additionally, the plant-growth-promoting rhizobacteria *Phyllobacterium* modifies root architecture in the presence of nitrate.

3.4. Abiotic Stress Tolerance

Tolerance to abiotic stress in the functional trait framework requires that in addition to measuring performance across environments, we also need to measure the functional traits that drive performance variation across environments. However, this decomposition is rarely accomplished. Therefore, although we know that functional traits must vary to cause performance differences, we typically do not know the identity of these traits. Abiotic stress tolerance is crucial in predicting species' ranges (see Sections 4.3 and 4.4) and scaling the response of communities to global change (see Section 4.5). Microbial improvements to plant nutrition (see Section 3.1) may increase their stress tolerance. Microbes can also produce small metabolites that increase salinity tolerance; for example, rhizobia can produce trehalose in nodules (Lopez et al. 2008). The endophytic fungus *Curvularia* enables the grass *Dichanthelium lanuginosum* to tolerate extreme heat on thermal soils in Yellowstone park (Redman et al. 2002b). Phytohormone alteration can impact stress tolerance as well; for example, ACC deaminase produced by *Pseudomonas* and *Gigaspora* can alter the tolerance of heavy metals directly through the manipulation of plant ethylene levels (Gamalero et al. 2010).

Microbes can influence plant water status and response to drought stress in beneficial or detrimental ways. Natural communities of fungal leaf endophytes double the minimum stomatal conductance of cacao (*T. cacao*) seedlings (Arnold & Engelbrecht 2007). In *Arabidopsis thaliana*, stomatal closure occurs as part of the plant defense response to conserved bacterial molecules, but some strains of the pathogen *Pseudomonas syringae* produce coronatine, which causes stomatal reopening (Melotto et al. 2006). In addition, arbuscular mycorrhizal fungi can increase stomatal conductance under normal or drought conditions, with inoculated plants often showing greater drought tolerance (Lambers et al. 2008a); an experiment with a nonmycorrhizal mutant of bean (*Phaseolus vulgaris*) showed that this effect results in equal parts from soil colonization and root colonization by the mycorrhizae (Auge 2004). More work is needed to quantify the prevalence of microbial alteration of stomatal conductance in natural systems.

3.5. Summary

Microbes influence plant traits in a myriad of ways that suggest coevolution between plants and microbes. Only by understanding the molecular nature of these interactions can we predict trait mediation from knowledge of microbial genomes. Fitness conflict can result from different optimal trait values for plant and microbe performance. How this evolutionary process plays out will depend on transmission dynamics and the population- and community-level impacts of trait alteration on fitness, as discussed next.

4. EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE

Microbes, through their influence on plant functional traits, have the potential to dramatically alter plant ecology. Microbes can expand plant niches, with local adaptation and phenotypic

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plasticity being two mechanisms for niche expansion. Competition, herbivory, and pollination mutualisms are central components of plant ecology in which the microbial mediation of functional traits likely plays a major role. Although ecological studies do not always measure the traits that mediate the fitness outcomes of these interactions, measurable fitness differences necessitate variation in underlying functional traits. Quantifying these traits will enable us to scale the effects of microbes to higher levels of biological organization (see Section 4.5). The evolution of microbial trait mediation may occur on ecological timescales, as microbes have large population sizes and short generation times relative to plants. We begin by considering these evolutionary processes.

Plasticity: occurs when the trait value of a genotype depends on the other partner's genotype/trait, other organisms, or the abiotic environment

Context dependence: occurs when the fitness of a genotype or trait value depends on their partner's genotype, other organisms, or the abiotic environment

4.1. Quantifying Relationships Between Functional Traits and Fitness

A fundamental goal in the study of microbial-plant interactions is to discern the magnitude, direction, and prevalence of microbial fitness effects on plants. At a proximate level, molecular-level traits involving plant biochemistry, physiology, and nutrient flows illuminate the mechanistic bases of microbe-driven benefits. However, to ascertain the ultimate effects of infection, one must measure functional traits and fitness components. Because the costs and benefits of infection can vary, measuring fitness components as well as functional traits in inoculation trials is essential. For example, measures of fixed nitrogen by symbiotic rhizobia only accurately reflect microbial effects on host fitness if there are no other benefits or costs of infection; measures of plant growth or seed set with and without infection reflect the net effect of the interaction.

An increasing number of studies show that a microbe that is beneficial in one interaction can become harmful on another host genotype (Klironomos 2003, Parker 1995). Furthermore, mutualisms can shift to parasitism or to abandonment of the interaction (Sachs & Simms 2006). This can happen on the timescale of species differentiation, as shown by a phylogenetic tree of fungi that supports multiple transitions to and from mycorrhizal symbiosis with plants (Hibbett et al. 2000). Shifts can also occur on the timescale that generates variation between rhizobial strains in a local population, demonstrated by the common transitions between symbiotic and nonsymbiotic lifestyles in *Bradyrhizobium* isolated from California native annual legumes (Sachs et al. 2010a). In fact, symbiotic genes can be horizontally transmitted to otherwise nonsymbiotic rhizobia (e.g., Sullivan et al. 1995). Thus, despite the perceived convenience of categorizing microbes into mutualists, commensals, and pathogens, it is important to realize that species interactions are not monolithic.

Plant-microbe interactions, like most species interactions, are context dependent with respect to their costs and benefits (Bronstein 1994). This means that the abiotic environment, the presence of other community members, and the genotypes of the host and symbiont themselves (e.g., genotype-by-genotype interaction) can influence fitness outcomes (Smith & Goodman 1999). Tests of sympatric versus allopatric partner genotype interactions can provide evidence for adaptation between hosts and symbionts. In *Amphicarpaea bracteata*, plants grew better with *Bradyrhizobium* from their native sites, but bacterial fitness was not measured (Parker 1995). In contrast, for three species of pine (*Pinus*) inoculated with strains of false truffle (*Rhizopogon*), only the fungus showed adaptation to hosts from its home sites (Hoeksema & Thompson 2007). Genotype-by-genotype interaction is present at the species level in plant-mycorrhizal interactions for growth increases (Klironomos 2003) and pathogen protection (Sikes et al. 2009) as well as within species (reviewed in Hoeksema et al. 2010). The effect of genotypic interactions may depend on the environment in which they interact, such as different combinations of *Medicago truncatula–Sinorhizobium medicae*, whose performance depends on the nitrate level they experience (Heath et al. 2010). The presence of other microbes in the community may also play a role;

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a meta-analysis showed that growth benefits from mycorrhizal fungi are greater in the presence of other soil microbes (Hoeksema et al. 2010).

Transmission mode: how a microbe is spread between host individuals—vertically from parent to offspring or horizontally between potentially unrelated hosts

Evolutionary theory predicts that symbioses will evolve to be more mutually beneficial as environmental quality decreases (Schwartz & Hoeksema 1998). This is supported by the finding that mycorrhizae from fertilized soil are less beneficial for their hosts (Johnson 1993). However, abiotic stress can disrupt symbioses and lead to reduced dependence on microbial partners, such as salt-tolerant species of *Acacia* that benefit less from rhizobia than sensitive relatives (Thrall et al. 2008).

Currently, most work focuses on fitness outcomes for plants; more research is needed on microbial fitness. One of the few meta-analyses of plant-microbe interactions with fitness proxies for both partners found positive legume-rhizobia fitness covariance in the presence of multistrain interactions (M.L. Friesen, manuscript in preparation). An important area for future research is the incorporation of host genotype, symbiont genotype, and environmental context into studies of local adaptation in species interactions or studies of abiotic tolerance (Nuismer & Gandon 2008). These studies will allow researchers to distill the relative importance of partner genotypes versus environmental context to functional trait values and fitness outcomes for both partners.

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4.2. Evolutionary Pressures Shaping Trait-Mediating Microbes

Microbially mediated plant functional traits are unique in that their evolution depends not only on their effects on host plant fitness, but also on the fitness of the causal microbe. Potential fitness conflict over functional trait values in principle can lead to suboptimal trait values for both partners. Two major ecological processes influence the degree of host-symbiont conflict: (*a*) transmission, including mode, host abundance, and host diversity, and (*b*) symbiont regulation via partner choice, sanctions, and rewards. Much of the evolutionary theory regarding the selective conditions that promote or act against beneficial symbiont traits comes from the study of parasite evolution. Models of optimal virulence predict how host fitness benefits evolve owing to microbial evolution (Sachs et al. 2004). One gap in these models is that they typically do not consider the intermediate functional traits that impact fitness, so they are difficult to apply directly to empirical systems.

Microbes can be transmitted horizontally or vertically, with each transmission mode leading to different trajectories of microbial evolution. Horizontal transmission leads to infection between unrelated hosts, so host survival or reproduction might have minimal impact on the microbe's fitness, and they may evolve to be harmful (e.g., Sachs et al. 2010a). Plant hosts infected with horizontally transmitted symbionts must evolve control mechanisms to selectively maintain beneficial infections (Bever et al. 2009, Kiers & Denison 2008, Kiers et al. 2003, Sachs et al. 2010b). Conversely, vertically transmitted infections are passed from parent to offspring, and microbe fitness can be directly tied to the continued survival and reproduction of the host; this results in vertically transmitted microbes providing increased host benefit (Sachs et al. 2004). Fungal endophytes of grasses partly accord with virulence theory—the horizontally transmitted species are often harmful, whereas the vertically transmitted taxa are mostly beneficial to invasive grasses (Clay & Schardl 2002) but not necessarily to native grasses (see Section 4.3.2). Horizontally transmitted species are predicted to maximize their transmission when uninfected hosts are available nearby in the population. Consistent with this prediction, the frequency of horizontally transmitted endophytes is often positively correlated with host density, whereas vertically transmitted endophytes do not exhibit such a correlation (Rudgers et al. 2009). In rare cases, selection on transmission could lead to fitness alignment between partners; microbes such as nectar yeasts should

evolve higher transmission rates, which could also increase their host's fitness through increased pollinator visitation (see Section 4.3.3).

Despite the potential evolutionary benefits, there appears to be a paucity of vertically transmitted microbes in plants, including only a handful of fungal (Clay & Schardl 2002) and bacterial (e.g., López-López et al. 2010, Ran et al. 2010) lineages. Because most plant-associated microbes are transmitted horizontally, control mechanisms may be key in preventing plant symbionts from undergoing evolutionary shifts from mutualism to parasitism (Kiers & Denison 2008, Sachs et al. 2004). These processes have only been studied in rhizobia and mycorrhizae. Legumes can choose more beneficial rhizobial strains to initiate root nodule formation (Heath & Tiffin 2009), and once nodules are formed, plants can sanction poorly performing nodules and allocate more resources to beneficial strains (Kiers et al. 2003, Sachs et al. 2010b). Nodules with greater biomass allocation typically contain greater numbers of rhizobia (but see Sachs et al. 2010a), indicating that sanctions can be an effective evolutionary mechanism for promoting cooperative behavior in microbes. Plants can also preferentially allocate photosynthate to more beneficial mycorrhizae (Bever et al. 2009), although the evolutionary effect on limiting cheating in diverse fungal communities will depend on the strength of selection and the spatial structure of fungal lineages. There is accumulating circumstantial evidence that plants can selectively allow certain microbes to become endophytic, but the mechanisms are not well understood (Hardoim et al. 2008). We reiterate Kiers & Denison's (2008) prediction that choice and sanction mechanisms operate in many microbial associations and urge investigators to conduct additional experiments measuring plants' abilities to select microbes with beneficial impacts on functional traits by performing mixed inoculations with strains of varying effects.

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4.3. Microbes Alter Plant Niches

Microbes, through their impact on plant functional traits, alter the distribution and abundance of plant species, i.e., their niche. Mutualists may be capable of expanding a species' realized niche; conversely, mutualist dependency could contract a partner's niche if the mutualist is either dispersal limited or constrained by other environmental factors. Some plants are unable to colonize novel habitats because they lack compatible symbionts, such as the failed introduction of *Pinus patula* to Zambia (Richardson et al. 1994). When the appropriate ectomycorrhizae was cointroduced in live soil, their host plant flourished, and many species of *Pinus* are now invasive. Additional examples of niche expansion are microbes that enhance abiotic stress tolerance (see Section 3.4), including heat (Redman et al. 2002b), salinity (e.g., Rodriguez et al. 2008), and heavy metal tolerance (e.g., Adriaensen et al. 2005).

4.3.1. Competition. By altering how plants acquire resources, microbes can enhance or decrease species coexistence. Overall plant species diversity was lower after 4 years when a seed-borne fungal endophyte was present, although total productivity did not change (Clay & Holah 1999). Mycorrhizal fungi increase competition at the community level, as demonstrated by a biomass–species richness relationship that saturates sooner in the presence of these symbionts than in their absence (Klironomos et al. 2000). Mycorrhizal species have different effects on plant competition as measured by biomass, nitrogen content, and phosphorus content, with the dominant plant species switching in the presence of different symbionts (van der Heijden et al. 2003). However, rhizobial inoculation can increase community diversity by enabling legumes to persist without reducing the biomass of grass competitors (van der Heijden et al. 2006). This implies that symbioses with specialized effects can promote niche separation and thus positively impact plant diversity.

Negative frequency-dependent performance in response to microbes was recently measured in tropical trees, with species performing best with heterospecifics' microbes (Mangan et al. 2010). However, every soil inoculum gave higher overall growth than the sterilized control, suggesting that these negative feedbacks could result from differences in the benefit of soil mutualists present. Mutualisms can result in negative frequency dependence—if the most beneficial partner of one host species has the highest growth rate on another host, the two species can coexist (Bever 2002). A plant may amplify a microbial rhizosphere community that either negatively or positively affects its own, its progeny's, or its competitor's fitness, and mutualistic microbes play an important role in the outcomes of these interactions (Bever et al. 2009).

In some cases competition occurs via allelopathy toward the symbionts of a competitor. This phenomenon highlights the importance of microbial symbionts in plant performance. For example, invasive garlic mustard (*Alliaria petiolata*) inhibits mycorrhizal colonization of competitors (Wolfe et al. 2008). Similarly, 13 of 20 tested annuals inhibit nitrogen-fixing rhizobia and nitrifying bacteria in plant exudate tests; four of these species reduce nodulation when grown together with two different bean (*P. vulgaris*) species (Rice 1964). In one instance, this antagonism arose from a symbiont, with a fungal endophyte killing competitors' mycorrhizal fungi (Antunes et al. 2008).

4.3.2. Herbivory. There is abundant evidence for microbes altering herbivory levels, but these alterations are neither universal nor always in the direction most beneficial for the plant. In a field study of aphid (*Acyrthosiphon pisum*) herbivory of soy (*G. max*), natural rhizobia were found to provide herbivore protection relative to a commercial inoculum strain of rhizobium and to nitrogen fertilization (Dean et al. 2009). Although endophytic fungi are typically described as defensive mutualists, this field has a severe taxonomic bias; a meta-analysis shows that endophyte defense occurs primarily for two well-studied invasive grasses and that overall there is no significant defense by tree fungal endophytes (Saikkonen et al. 2010). Recent studies of native grasses find strikingly different effects of endophytes on herbivores, namely that herbivore population sizes are increased by fungal endophytes, with reduced parasitoid abundance and increased herbivore species richness (e.g., Jani et al. 2010). Similar effects have been found for vertebrate herbivores, with voles fed endophyte-infected grass suffering less predation by weasels than those fed uninfected grass despite no difference in body size (Saari et al. 2010b). Faeth (2009) suggested that vertically transmitted fungi may increase herbivory of their hosts because herbivory can promote earlier plant reproduction, increasing the transmission rate of the endophyte as they can be spontaneously lost during plant development (Afkhami & Rudgers 2008). This study found that *Neotyphodium* infection caused *Festuca arizonica* to flower earlier, allocate more to reproduction in the first two years, and have higher herbivore loads (Faeth 2009). A potential explanation could be that native grass–endophyte associations have coevolved with herbivores, leading to overall higher tolerance of herbivores to defensive chemicals and a shift in endophyte traits that are under selection via increased transmission from protection to decreased loss from host lineages.

4.3.3. Pollination. Through their impact on plant traits, microbes can alter plant relationships with beneficial insects as well as harmful ones. Pollinator visitation rates significantly increase with mycorrhizal colonization, as shown in inoculation experiments (Gange & Smith 2005) as well as a three-year field study in which mycorrhizae were removed (Cahill et al. 2008). The removal experiment found significant shifts in pollinator community composition and differences between plant species in their responses (Cahill et al. 2008). The inoculation experiment measured plant traits and found that the traits mediating increased pollinator visitation differed between the three species tested (Gange & Smith 2005). Yeasts that inhabit floral nectaries of *Helleborus* and *Aquilegia* can alter the sugar composition and raise the flower temperature of *Helleborus foetidus* (Herrera

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& Pozo 2010). In this case the microbe's transmission is coupled with pollinator visitation and gamete transmission of the plant, potentially aligning host and symbiont fitness, and nectar yeasts may prove to be mutualists.

4.4. Microbially Mediated Adaptive Plasticity and Local Adaptation

When microbes alter functional traits that influence plant fitness in a context-dependent way, the plant's ability to regulate the identity or number of microbial partners could itself be a fitness-altering trait. Adaptive phenotypic plasticity occurs when an individual expresses trait values in the direction of the optimal value for a given environment (Schlichting & Pigliucci 1998). The best-understood system showing evidence of adaptive plasticity is the legume-rhizobia symbiosis. Legumes are plastic in rhizobial partner number and investment, depending on the nitrogen environment in the soil: They decrease root nodule number and investment in nitrogen-fixing rhizobia with increasing soil nitrate availability (Heath et al. 2010, Streeter 1985). This plasticity is adaptive, as shown by a study of supernodulating mutants that constitutively express high numbers of nodules and consequently produce fewer offspring than wild type under high-nitrogen conditions (Song et al. 1995). Domesticated crop legumes show that there is genetic variation in plasticity; selection in the high-nitrogen context of modern agriculture appears to have reduced modern crops' ability to exercise adaptive plasticity via partner choice and sanctions (Kiers et al. 2007).

The breadth of a species' fundamental niche is often a collection of more specialized niches at the population or individual level (Bolnick et al. 2003). Variation in microbial partners could influence functional traits that determine where an individual can grow. For example, some mycorrhizal fungi provide the most benefit to their hosts when grown under temperature regimes similar to their site of origin (Antunes et al. 2011). Other examples of local adaptation via symbionts are fungi that confer stress tolerance or enhanced nutrient uptake in particular habitats (Johnson et al. 2010, Rodriguez et al. 2008). In grasses, infection with fungal endophytes varies between individuals, and vertically transmitted symbionts are lost at some rate (Afkhami & Rudgers 2008). If these endophytes are only beneficial under some ecological circumstances, variation in transmission could be a form of cross-generational adaptive plasticity.

For traits such as phosphorous acquisition, heat tolerance, and drought tolerance, adaptation can occur through the evolution of either the microbial symbiont or the host plant. For example, whereas many grass lineages have evolved genetically based salt tolerance, others depend on a fungal endophyte (Rodriguez et al. 2008). We can learn about the ecological and evolutionary conditions favoring a plant's evolution of the fundamental niche versus adoption of interactions that expand the realized niche by examining clades in which both microbial trait mediation and plant trait evolution occur. The capacity for local adaptation in hosts and microbes depends on the balance between gene flow and selection across environmental heterogeneity. We require experiments that test hosts and symbionts for local adaptation and estimate migration and genetic variation in each partner to determine if there are general patterns.

4.5. Plant Microbial Trait Mediation Influences Ecosystem Processes and Services

Plants are central players in terrestrial ecosystem processes, mediating fluxes of energy and nutrients between biotic and abiotic components of Earth systems (Díaz & Cabido 1997, Whitham et al. 2006). Trait-based approaches enable models to scale up from individuals to ecosystems by quantifying the relationships among plant functional traits, fitness, and ecosystem fluxes

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(**Figure 2**) (de Bello et al. 2010, Díaz & Cabido 2001, Violle et al. 2007). A major component of this integration is connecting population processes (e.g., demography) to ecosystem processes by modeling how trait distributions and species' abundances change over time through variation in plant fitness. The context dependence of fitness outcomes (see Section 4.1) will likely yield nonlinear dynamics with important impacts on scaling (Medvigy et al. 2010).

We argue in previous sections that many plant functional traits can be altered by microbes (**Table 1** and **Figure 2**). Moreover, because the majority of known plant endophytes and epiphytes are horizontally transmitted, there is potential fitness conflict between partners. Antagonistic coevolution between plants and microbes over optimal functional trait values may be an example of an evolutionary process altering ecosystem function. We first describe connections between microbes and ecosystem functions and then describe how models that scale from individuals to ecosystems could incorporate microbial effects on traits. We close with urgently needed experiments to determine the extent of microbial involvement in ecosystem processes.

4.5.1. Ecosystem processes and services. Ecosystem services are defined as processes of particular importance to humans. A recent meta-analysis reports significant relationships between plant functional traits and many ecosystem services (de Bello et al. 2010). Of the 27 services considered, several are likely linked to the microbially mediated traits discussed in previous sections: fodder productivity and primary production (Section 3.1), evapotranspiration (Section 3.4), herbivory (Section 3.2), carbon sequestration, soil formation, decomposition, and nutrient mineralization.

Productivity is primarily influenced by the availability of limiting resources and plant traits related to resource acquisition and resource use efficiency (Lambers et al. 2008b). Nitrogen and phosphorus uptake (see Section 3.1) are two major microbially mediated functional traits associated with ecosystem productivity as well as nutrient cycling and soil processes. The presence of nitrogen fixers in a community increases biomass and soil-available nitrogen (e.g., Liao et al. 2008, Loreau & Hector 2001, Vitousek & Walker 1989). For example, the estimated amount of nitrogen input into the ecosystem by invasive *Myrica faya* in Hawaii is over threefold the combined input from native nitrogen fixers and rainfall (Vitousek & Walker 1989). Increased phosphorus uptake by arbuscular mycorrhizal fungi can similarly increase ecosystem productivity, with more diverse microbial communities providing greater benefits (Klironomos et al. 2000, van der Heijden et al. 1988). In some ecosystems water is limiting, and microbial effects on water uptake and stomatal conductance could have implications for productivity as well as the fundamental ecosystem process of water cycling. Finally, microbes that alter plant allocation, e.g., above- versus belowground and plant-branching patterns (see Section 3.3), could influence patterns of light limitation, size-dependent growth, forest size distributions, and, by extension, standing biomass.

Decomposition and soil formation are highly dependent on microbes. Some leaf litter fungi that act as decomposers are also found as endophytes and/or epiphytes (Osono 2006). Mycorrhizae may influence ecosystem processes indirectly through litter feedbacks and effects on soil biota (Langley & Hungate 2003, Rillig 2004). Aboveground microbial mutualists can also influence belowground nutrient dynamics. In tall fescue (*Lolium arundinaceum*), infection by endophytic fungi that confer herbivory resistance and stress tolerance causes slower litter decomposition and also alters soil biota (Lemons et al. 2005).

4.5.2. The quantitative ecosystem scaling approach. Quantitative scaling analysis can link ecophysiological flux measurements on small units of vegetation to whole ecosystems. For example, big-leaf models scale photosynthesis from the leaf to the region (De Pury & Farquhar 1997). Leaf-level photosynthesis is influenced by the maximum photosynthetic rate, A_{max}, and stomatal conductance, which interact with CO_2 concentration and leaf temperature. A more sophisticated

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scaling approach integrates over these functional trait values combined with variation in the environments that leaves experience to calculate regional values of production and can drastically improve regional estimates of ecosystem production (Medvigy et al. 2010). These improved predictions arise from the nonlinear response of ecophysiological processes to environmental factors; nonlinearity interacts with variation to alter regional processes in relation to the simple expectations based on mean trait and environmental values (De Pury & Farquhar 1997, Moorcroft et al. 2001). The ecosystem demography model further incorporates plant demography (Moorcroft et al. 2001).

We predict that the microbial mediation of leaf traits will be found to strongly influence ecosystem production and evapotranspiration, key processes in understanding the role of the biosphere in global climate change. Leaf endophytes are ubiquitous, particularly in tropical forests, and both the frequency and the degree of infection vary substantially (Arnold 2007). Forest structure and leaf age may influence infection (reviewed in Saikkonen 2007), potentially creating covariation between these factors that must be understood when accounting for nonlinearities in ecosystem scaling (De Pury & Farquhar 1997, Moorcroft et al. 2001).

There are three potential sources of covariation between plant leaf functional traits and microbial infection patterns. First, leaves low in the canopy experience higher infection rates because of higher stomatal opening, wetter surfaces, and higher transmission rates via dripping or splashing water (Underwood et al. 2007). These forest microenvironments are also associated with shade-leaf phenotypes that differ in foliar nitrogen concentration, are thicker, and have lower maximum photosynthetic rates than sun leaves (Lambers et al. 2008a)—this can create covariation between microbial trait mediation, background leaf functional trait values, and leaf environments. Second, older leaves have longer exposure times for microbial infection to occur. As leaf phenology often corresponds to seasonal cycles, microbial trait mediation could play a strong role in seasonal changes in plant functional traits that covary with seasonal environmental changes (see Chambers et al. 2007). Additionally, endophyte composition could vary seasonally, as found in oaks (Faeth & Hammon 1997). Third, host plants with higher relative abundances may experience increased microbial transmission rates. Evolutionary theory predicts that higher transmission rates may increase fitness conflict and select for less beneficial/more pathogenic microbes (see Section 4.2). This would reinforce negative frequency-dependent selection and enhance species diversity (see Section 4.3.1).

Ecosystem scaling models are powerful quantitative tools to connect microbial functional trait meditation, coevolution, and ecosystem processes. We suggest exciting future investigations that quantify microbial impacts on leaf functional traits, including ecophysiological parameters, in the field. A large network of eddy covariance flux towers directly measures ecosystem processes in plant canopies around the world; these provide excellent canopy access in addition to detailed data. Photosynthetic light and temperature response curves should be measured on age-matched leaves with varying evidence of infection over many species across environmental gradients. Genomic analysis would reveal the identities of associated epiphytes and endophytes. This ground data can be coupled with the growing body of remote sensing data for tropical forests (Chambers et al. 2007). Techniques for estimating epiphyte colonization from remote sensing data are being developed, relying on the altered leaf spectral properties of epiphytes (Toomey et al. 2009). These data can be used to parameterize models, such as the ecosystem demography model, that include plant and microbial species to predict ecosystem fluxes, which can then be tested against flux tower data. In addition to these crucial observational studies, we propose that newly emerged leaves be isolated and inoculated with conspecific and heterospecific microbial communities to determine whether the same frequency-dependent patterns found for soil microbes are true for leaf associates.

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SUMMARY POINTS

1. Microbes can influence almost all plant functional traits, but most of these traits are not measured in inoculation studies.
2. Microbial influence on trait variation can be as large as the effects of the plant genotype.
3. Plant-associated microbial communities are diverse and potentially under selection by their host plant, but few taxa have received research effort.
4. Ecological context can alter fitness outcomes related to microbially mediated plant traits.
5. By affecting microbial transmission patterns, host abundance and the ability to exert partner choice and sanctions can influence microbial evolution when there is fitness conflict over functional trait values.
6. Microbes can fundamentally alter plant niches, both the range of abiotic conditions tolerated and interactions with other species.
7. Microbes likely impact ecosystem processes and services through their influence on plant ecophysiological traits and plant population dynamics.

FUTURE ISSUES

1. All plant biologists should consider the impacts that microbes and the traits they influence may have on plant performance and function. We recommend that tissue samples be kept from field and greenhouse experiments for future microbial identification.
2. Surveys of taxonomic and functional diversity are needed to document the distribution and abundance of plant-associated microbes across tissues, ecosystems, and time. High-throughput sequencing technology will facilitate surveys of taxonomic loci as well as loci implicated in impacting plant phenotypes (e.g., nitrogen fixation and phytohormone pathway genes).
3. Inoculation experiments, preferably in the field, are required to estimate the direction and magnitude of microbes' effects on plant functional traits. Microbes mutated in specific pathways will be useful in linking microbial genes to ecosystem processes. Mixed inoculations will elucidate the roles of partner choice and sanctions in structuring plant microbiomes.
4. The relationship between plant functional traits and microbial fitness needs to be quantified simultaneously with plant fitness to determine which traits exhibit host-symbiont fitness conflict. If little conflict is found, the mechanisms aligning partner fitness need to be sought.
5. More studies of local adaptation and dissection of its molecular basis are needed to determine if there are general principles governing when adaptation occurs via genetic changes in the host versus the symbiont.
6. Using the functional trait framework, it will be possible to scale up the effects of microbes on plant functional traits to ecosystem processes. Such studies need to quantify covariation in microbial communities and traits in field surveys and demonstrate microbial effects with field experiments. Nitrogen-fixing tropical leaf epiphytes are an understudied system requiring these experiments.

7. The link between microbially mediated plant defenses, the reduction of natural enemies, and ecosystem processes such as nutrient cycling and productivity remains underexplored. Experiments monitoring ecosystem responses that manipulate both enemy loads and infection with microbes that mediate plant traits are needed. We predict that plants at different positions on the leaf economics spectrum will have different microbial communities associated with them and that in some cases these microbes mediate leaf turnover traits. If microbially mediated defense is less costly than genetically based defense, species relying on microbes may have relative fitness advantages.
8. Certain traits need to be screened for microbial mediation—one notable category of traits for which we completely lack studies involves stem traits such as wood density. For traits that are not influenced, what are the evolutionary and molecular mechanisms preventing microbial involvement?

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ACKNOWLEDGMENTS

We thank R.F. Denison, S.R. Saleska, and an anonymous reviewer for critical comments that improved this article. M.L.F. is supported by NSF DBI-0820846. S.C.S. is supported by NASA NNX09AI33G. S.S.P is supported by a UCD Dissertation Year Fellowship and an NSF Graduate Research Fellowship. E.M. acknowledges funding from PAPIIT IN200709 from UNAM and thanks Julio Martinez for technical support.

LITERATURE CITED

Adriaensen K, Vrålstad T, Noben JP, Vangronsveld J, Colpaert JV. 2005. Copper-adapted *Suillus luteus*, a symbiotic solution for pines colonizing Cu mine spoils. *Appl. Environ. Microbiol.* 71:7279–84

Afkhami ME, Rudgers JA. 2008. Symbiosis lost: imperfect vertical transmission of fungal endophytes in grasses. *Am. Nat.* 172:405–16

Aneja M, Gianfagna T, Hebbar P. 2005. *Trichoderma harzianum* produces nonanoic acid, an inhibitor of spore germination and mycelial growth of two cacao pathogens. *Physiol. Mol. Plant Pathol.* 67:304–7

Antunes P, Klironomos J, Miller J, Carvalho L, Newman J. 2008. Even after death the endophytic fungus of *Schedonorus phoenix* reduces the arbuscular mycorrhizas of other plants. *Funct. Ecol.* 22:912–18

Antunes PM, Koch AM, Morton JB, Rillig MC, Klironomos JN. 2011. Evidence for functional divergence in arbuscular mycorrhizal fungi from contrasting climatic origins. *New Phytol.* 189:507–14

Arnold AE. 2007. Understanding the diversity of foliar endophytic fungi: progress, challenges, and frontiers. *Fungal Biol. Rev.* 21:51–66

Arnold AE, Engelbrecht BMJ. 2007. Fungal endophytes nearly double minimum leaf conductance in seedlings of a neotropical tree species. *J. Trop. Ecol.* 23:369–72

Arnold AE, Mejía LC, Kyllo D, Rojas EI, Maynard Z, et al. 2003. Fungal endophytes limit pathogen damage in a tropical tree. *Proc. Natl. Acad. Sci. USA* 100:15649–54

Auge R. 2004. Arbuscular mycorrhizae and soil/plant water relations. *Can. J. Soil Sci.* 84:373–81

Bentley BL. 1987. Nitrogen fixation by epiphylls in a tropical rainforest. *Ann. Mo. Bot. Gard.* 74:234–41

Bentley BL, Carpenter EJ. 1984. Direct transfer of newly-fixed nitrogen from free-living epiphyllous microorganisms to their host plant. *Oecologia* 63:52–56

Bernhardt-Romermann M, Romermann C, Nuske R, Parth A, Klotz S, et al. 2008. On the identification of the most suitable traits for plant functional trait analyses. *Oikos* 117:1533–41

Bertrand A, Prévost D, Bigras FJ, Castonguay Y. 2007. Elevated atmospheric CO_2 and strain of rhizobium alter freezing tolerance and cold-induced molecular changes in alfalfa (*Medicago sativa*). *Ann. Bot.* 99:275–84

Bever JD. 2002. Negative feedback within a mutualism: host-specific growth of mycorrhizal fungi reduces plant benefit. *Proc. R. Soc. Lond. Ser. B* 269:2595–601

Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecol. Lett.* 12:13–21

Bhattacharjee RB, Singh A, Mukhopadhyay SN. 2008. Use of nitrogen-fixing bacteria as biofertiliser for non-legumes: prospects and challenges. *Appl. Microbiol. Biotechnol.* 80(2):199–209

Bolnick D, Svanbäck R, Fordyce J, Yang L, Davis J, et al. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161:1–28

Bonfante P, Anca I. 2009. Plants, mycorrhizal fungi, and bacteria: a network of interactions. *Annu. Rev. Microbiol.* 63:363–83

Bronstein J. 1994. Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* 9:214–17

Cahill JF, Elle E, Smith GR, Shore BH. 2008. Disruption of a belowground mutualism alters interactions between plants and their floral visitors. *Ecology* 89:1791–801

Chambers J, Asner G, Morton D, Anderson L, Saatchi S, et al. 2007. Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. *Trends Ecol. Evol.* 22:414–23

Clay K, Holah J. 1999. Fungal endophyte symbiosis and plant diversity in successional fields. *Science* 285:1742–45

Clay K, Schardl C. 2002. Evolutionary origins and ecological consequences of endophyte symbiosis with grasses. *Am. Nat.* 160:99–127

Coley P, Kursar T, Machado J. 1993. Colonization of tropical rain forest leaves by epiphylls: effects of site and host plant leaf lifetime. *Ecology* 74:619–23

Conrath U, Beckers G, Flors V, García-Agustín P, Jakab G, et al. 2006. Priming: getting ready for battle. *Mol. Plant Microbe Interact.* 19:1062–71

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51:335–80

Cornwell WK, Cornelissen JH, Amatangelo K, Dorrepaal E, Eviner VT, et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* 11:1065–71

Davitt AJ, Stansberry M, Rudgers JA. 2010. Do the costs and benefits of fungal endophyte symbiosis vary with light availability? *New Phytol.* 188:824–34

Dean J, Mescher M, De Moraes C. 2009. Plant–rhizobia mutualism influences aphid abundance on soybean. *Plant Soil* 323:187–96

de Bello F, Lavorel S, Díaz S, Harrington R, Cornelissen JHC, et al. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers. Conserv.* 19:2873–93

De Pury D, Farquhar G. 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant Cell Environ.* 20:537–57

Díaz S, Cabido M. 1997. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8:463–74

Díaz S, Cabido M. 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16:646–55

Ellis JR, Larsen HJ, Boosalis MG. 1985. Drought resistance of wheat plants inoculated with vesicular-arbuscular mycorrhizae. *Plant Soil* 86:369–78

Faeth SH. 2009. Asexual fungal symbionts alter reproductive allocation and herbivory over time in their native perennial grass hosts. *Am. Nat.* 173:554–65

Faeth SH, Hammon KE. 1997. Fungal endophytes in oak trees: long-term patterns of abundance and associations with leafminers. *Ecology* 78:810–19

Fravel DR. 1988. Role of antibiosis in the biocontrol of plant diseases. *Annu. Rev. Phytopathol.* 26:75–91

Furnkranz M, Wanek W, Richter A, Abell G, Rasche F, Sessitsch A. 2008. Nitrogen fixation by phyllosphere bacteria associated with higher plants and their colonizing epiphytes of a tropical lowland rainforest of Costa Rica. *ISME J.* 2:561–70

Gamalero E, Berta G, Massa N, Glick BR, Lingua G. 2010. Interactions between *Pseudomonas putida* UW4 and *Gigaspora rosea* BEG9 and their consequences for the growth of cucumber under salt-stress conditions. *J. Appl. Microbiol.* 108:236–45

Gange AC, Smith AK. 2005. Arbuscular mycorrhizal fungi influence visitation rates of pollinating insects. *Ecol. Entomol.* 30:600–6

Annu. Rev. Ecol. Evol. Syst. 2011.42:23-46. Downloaded from www.annualreviews.org
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Ganley RJ, Newcombe G. 2006. Fungal endophytes in seeds and needles of *Pinus monticola*. *Mycol. Res.* 110:318–27

Goosem S, Lamb D. 1986. Measurements of phyllosphere nitrogen fixation in a tropical and two sub-tropical rain forests. *J. Trop. Ecol.* 2:373–76

Haas D, Blumer C, Keel C. 2000. Biocontrol ability of fluorescent pseudomonads genetically dissected: importance of positive feedback regulation. *Curr. Opin. Biotechnol.* 11:290–97

Hardoim PR, van Overbeek LS, Elsas JD. 2008. Properties of bacterial endophytes and their proposed role in plant growth. *Trends Microbiol.* 16:463–71

Harman GE, Howell CR, Viterbo A, Chet I, Lorito M. 2004. Trichoderma species: opportunistic, avirulent plant symbionts. *Nat. Rev. Microbiol.* 2:43–56

Harris D, Pacovsky RS, Paul EA. 1985. Carbon economy of soybean-*Rhizobium*-Glomus associations. *New Phytol.* 101:427–40

Hassan MN, Afghan S, Hafeez FY. 2010. Suppression of red rot caused by *Colletotrichum falcatum* on sugarcane plants using plant growth-promoting rhizobacteria. *BioControl* 55:531–42

Heath KD, Stock AJ, Stinchcombe JR. 2010. Mutualism variation in the nodulation response to nitrate. *J. Evol. Biol.* 23:2494–500

Heath KD, Tiffin P. 2009. Stabilizing mechanisms in a legume-rhizobium mutualism. *Evolution* 63:652–62

Herrera CM, Pozo MI. 2010. Nectar yeasts warm the flowers of a winter-blooming plant. *Proc. R. Soc. B* 277:1827–34

Hibbett DS, Gilbert LB, Donoghue MJ. 2000. Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. *Nature* 407:506–8

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, et al. 2010. A meta-analysis of context dependency in plant response to inoculation with mycorrhizal fungi. *Ecol. Lett.* 13:394–407

Hoeksema JD, Thompson JN. 2007. Geographic structure in a widespread plant–mycorrhizal interaction: pines and false truffles. *J. Evol. Biol.* 20:1148–63

James E. 2000. Nitrogen fixation in endophytic and associative symbiosis. *Field Crops Res.* 65:197–209

Jani A, Faeth S, Gardner D. 2010. Asexual endophytes and associated alkaloids alter arthropod community structure and increase herbivore abundances on a native grass. *Ecol. Lett.* 13:106–17

Johnson NC. 1993. Can fertilization of soil select less mutualistic mycorrhizae? *Ecol. Appl.* 3:749–57

Johnson NC, Wilson GWT, Bowker MA, Wilson JA, Miller RM. 2010. Resource limitation is a driver of local adaptation in mycorrhizal symbioses. *Proc. Natl. Acad. Sci. USA* 107:2093–98

Johnson ND, Liu B, Bentley BL. 1987. The effects of nitrogen fixation, soil nitrate, and defoliation on the growth, alkaloids, and nitrogen levels of *Lupinus succulentus* (Fabaceae). *Oecologia* 74:425–31

Jones JD, Dangl JL. 2006. The plant immune system. *Nature* 444:323–29

Jung WJ, Mabood F, Souleimanov A, Park RD, Smith DL. 2008. Chitinases produced by *Paenibacillus illinoisensis* and *Bacillus thuringiensis* subsp. *pakistani* degrade Nod factor from *Bradyrhizobium japonicum*. *Microbiol. Res.* 163:345–49

Kiers ET, Denison RF. 2008. Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. *Annu. Rev. Ecol. Evol. Syst.* 39:215–36

Kiers ET, Hutton MG, Denison RF. 2007. Human selection and the relaxation of legume defences against ineffective rhizobia. *Proc. R. Soc. B* 274:3119–26

Kiers ET, Rousseau RA, West SA, Denison RF. 2003. Host sanctions and the legume–rhizobium mutualism. *Nature* 425:78–81

Klironomos J. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology* 84:2292–301

Klironomos JN, McCune J, Hart M, Neville J. 2000. The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecol. Lett.* 3:137–41

Knoch T, Faeth S, Arnott D. 1993. Endophytic fungi alter foraging and dispersal by desert seed-harvesting ants. *Oecologia* 95:470–73

Kothari S, Marschner H, George E. 1990. Effect of VA mycorrhizal fungi and rhizosphere microorganisms on root and shoot morphology, growth and water relations in maize. *New Phytol.* 116:303–11

Lambers H, Chapin F, Pons T. 2008a. *Plant Physiological Ecology*. New York: Springer-Verlag

Annu. Rev. Ecol. Evol. Syst. 2011.42:23-46. Downloaded from www.annualreviews.org
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Lambers H, Raven JA, Shaver GR, Smith SE. 2008b. Plant nutrient-acquisition strategies change with soil age. *Trends Ecol. Evol.* 23:95–103

Langley JA, Hungate B. 2003. Mycorrhizal controls on belowground litter quality. *Ecology* 84:2302–12

Lemons A, Clay K, Rudgers JA. 2005. Connecting plant-microbial interactions above and belowground: a fungal endophyte affects decomposition. *Oecologia* 145:595–604

Liao C, Peng R, Luo Y, Zhou X, Wu X, et al. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol.* 177:706–14

Lindahl BD, Ihrmark K, Boberg J, Trumbore SE, Högberg P, et al. 2007. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. *New Phytol.* 173:611–20

Lindow SE, Brandl MT. 2003. Microbiology of the phyllosphere. *Appl. Environ. Microbiol.* 69:1875–83

Lopez M, Tejera NA, Iribarne C, Lluch C, Herrera-Cervera JA. 2008. Trehalose and trehalase in root nodules of *Medicago truncatula* and *Phaseolus vulgaris* in response to salt stress. *Physiol. Plant.* 134:575–82

López-López A, Rogel MA, Ormeño-Orrillo E, Martínez-Romero J, Martínez-Romero E. 2010. *Phaseolus vulgaris* seed-borne endophytic community with novel bacterial species such as *Rhizobium endophyticum* sp. *nov*. *Syst. Appl. Microbiol.* 33:322–27

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76

Ma W, Sebestianova SB, Sebestian J, Burd GI, Guinel FC, Glick BR. 2003. Prevalence of 1-aminocyclopropane-1-carboxylate deaminase in *Rhizobium* spp. *Antonie van Leeuwenhoek* 83:285–91

Mangan SA, Herre EA, Bever JD. 2010. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant-soil feedback. *Ecology* 91:2594–603

Martínez-Romero E. 2006. Dinitrogen-fixing prokaryotes. In *The Prokaryotes*, ed. M Dworkin, S Falkow, E Rosenberg, KH Schleifer, E Stackebrandt, pp. 793–817. New York: Springer

Maurhofer M, Reimmann C, Schmidli-Sacherer P, Heeb S, Haas D, Défago G. 1998. Salicylic acid biosynthetic genes expressed in *Pseudomonas fluorescens* strain P3 improve the induction of systemic resistance in tobacco against tobacco necrosis virus. *Phytopathology* 88:678–84

Medvigy D, Wofsy SC, Munger JW, Moorcroft PR. 2010. Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability. *Proc. Natl. Acad. Sci. USA* 107:8275–80

Melotto M, Underwood W, Koczan J, Nomura K, He S. 2006. Plant stomata function in innate immunity against bacterial invasion. *Cell* 126:969–80

Moorcroft P, Hurtt G, Pacala S. 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecol. Monogr.* 71:557–86

Morris A, Djordjevic M. 2006. The *Rhizobium leguminosarum* biovar *trifolii* ANU794 induces novel developmental responses on the subterranean clover cultivar Woogenellup. *Mol. Plant Microbe Interact.* 19:471–79

Morshed MH, Hossain MS, Ibrahim M, Shafique MZ, Helali MOH, et al. 2005. Bacteria killing kinetics of the four plant hormones. *Pak. J. Biol. Sci.* 8:1025–29

Nuismer S, Gandon S. 2008. Moving beyond common-garden and transplant designs: insight into the causes of local adaptation in species interactions. *Am. Nat.* 171:658–68

Ortíz-Castro R, Martínez-Trujillo M, López-Bucio J. 2008. *N*-acyl-L-homoserine lactones: A class of bacterial quorum-sensing signals alter post-embryonic root development in *Arabidopsis thaliana*. *Plant Cell Environ.* 31:1497–509

Osono T. 2006. Role of phyllosphere fungi of forest trees in the development of decomposer fungal communities and decomposition processes of leaf litter. *Can. J. Microbiol.* 52:701–16

Park SY, Fung P, Nishimura N, Jensen DR, Fujii H, et al. 2009. Abscisic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. *Science* 324:1068–71

Parker MA. 1995. Plant fitness variation caused by different mutualist genotypes. *Ecology* 76:1525–35

Perrine-Walker FM, Gartner E, Hocart CH, Becker A, Rolfe BG. 2007. *Rhizobium*-initiated rice growth inhibition caused by nitric oxide accumulation. *Mol. Plant Microbe Interact.* 20:283–92

Phillips DA, Ferris H, Cook DR, Strong DR. 2003. Molecular control points in rhizosphere food webs. *Ecology* 84:816–26

Qian G-L, Fan J-Q, Chen D-F, Kang Y-J, Han B, et al. 2010. Reducing *Pectobacterium* virulence by expression of an *N*-acyl homoserine lactonase gene P_{lpp}-*aiiA* in *Lysobacter enzymogenes* strain OH11. *Biol. Control* 52:17–23

Annu. Rev. Ecol. Evol. Syst. 2011.42:23-46. Downloaded from www.annualreviews.org
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Ran L, Larsson J, Vigil-Stenman T, Nylander JA, Ininbergs K, et al. 2010. Genome erosion in a nitrogen-fixing vertically transmitted endosymbiotic multicellular cyanobacterium. *PLoS ONE* 5:e11486

Ratcliff WC, Denison RF. 2009. Rhizobitoxine producers gain more poly-3-hydroxybutyrate in symbiosis than do competing rhizobia, but reduce plant growth. *ISME J.* 3:870–72

Reading NC, Sperandio V. 2006. Quorum sensing: the many languages of bacteria. *FEMS Microbiol. Lett.* 254:1–11

Redman RS, Roossinck MJ, Maher S, Andrews QC, Schneider WL, Rodriguez RJ. 2002a. Field performance of cucurbit and tomato plants colonized with a nonpathogenic, mutualistic mutant (path-1) of *Colletotrichum magna*. *Symbiosis* 32:55–70

Redman RS, Sheehan KB, Stout RG, Rodriguez RJ, Henson JM. 2002b. Thermotolerance generated by plant/fungal symbiosis. *Science* 298:1581

Rice EL. 1964. Inhibition of nitrogen-fixing and nitrifying bacteria by seed plants I. *Ecology* 45:824–37

Richardson D, Williams P, Hobbs R. 1994. Pine invasions in the Southern Hemisphere: determinants of spread and invadability. *J. Biogeogr.* 21:511–27

Rillig M. 2004. Arbuscular mycorrhizae and terrestrial ecosystem processes. *Ecol. Lett.* 7:740–54

Rodriguez RJ, Henson J, Van Volkenburgh E, Hoy M, Wright L, et al. 2008. Stress tolerance in plants via habitat-adapted symbiosis. *ISME J.* 2:404–16

Rodriguez RJ, White JF Jr, Arnold AE, Redman RS. 2009. Fungal endophytes: diversity and functional roles. *New Phytol.* 182:314–30

Romero AM, Correa OS, Moccia S, Rivas JG. 2003. Effect of *Azospirillum*-mediated plant growth promotion on the development of bacterial diseases on fresh-market and cherry tomato. *J. Appl. Microbiol.* 95:832–38

Rosenblueth M, Martínez-Romero E. 2006. Bacterial endophytes and their interactions with hosts. *Mol. Plant Microbe Interact.* 19:827–37

Ross AF. 1961. Systemic acquired resistance induced by localized virus infections in plants. *Virology* 14:340–58

Rousseau J, Sylvia D, Fox A. 1994. Contribution of ectomycorrhiza to the potential nutrient-absorbing surface of pine. *New Phytol.* 128:639–44

Rudgers J, Afkhami M, Rua M, Davitt A, Hammer S, Huguet V. 2009. A fungus among us: broad patterns of endophyte distribution in the grasses. *Ecology* 90:1531–39

Saari S, Helander M, Faeth SH, Saikkonen K. 2010a. The effects of endophytes on seed production and seed predation of tall fescue and meadow fescue. *Microb. Ecol.* 60:928–34

Saari S, Sundell J, Huitu O, Helander M, Ketoja E, et al. 2010b. Fungal-mediated multitrophic interactions: Do grass endophytes in diet protect voles from predators? *PLoS ONE* 5:e9845

Sachs JL, Ehinger MO, Simms EL. 2010a. Origins of cheating and loss of symbiosis in wild *Bradyrhizobium*. *J. Evol. Biol.* 23:1075–89

Sachs JL, Mueller UG, Wilcox TP, Bull JJ. 2004. The evolution of cooperation. *Q. Rev. Biol.* 79:135–60

Sachs JL, Russell JE, Lii YE, Black KC, Lopez G, Patil AS. 2010b. Host control over infection and proliferation of a cheater symbiont. *J. Evol. Biol.* 23:1919–27

Sachs JL, Simms EL. 2006. Pathways to mutualism breakdown. *Trends Ecol. Evol.* 21:585–92

Saikkonen K. 2007. Forest structure and fungal endophytes. *Fungal Biol. Rev.* 21:67–74

Saikkonen K, Saari S, Helander M. 2010. Defensive mutualism between plants and endophytic fungi? *Fungal Divers.* 41:101–13

Sapp J. 2004. The dynamics of symbiosis: an historical overview. *Can. J. Bot.* 82:1046–56

Schlichting CD, Pigliucci M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sunderland, MA: Sinauer

Schwartz MW, Hoeksema JD. 1998. Specialization and resource trade: biological markets as a model of mutualisms. *Ecology* 79:1029–38

Sikes BA, Cottenie K, Klironomos JN. 2009. Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. *J. Ecol.* 97:1274–80

Smith FA, Grace EJ, Smith SE. 2009. More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. *New Phytol.* 182:347–58

Smith KP, Goodman RM. 1999. Host variation for interactions with beneficial plant-associated microbes. *Annu. Rev. Phytopathol.* 37:473–91

Song L, Carroll BJ, Gresshoff PM, Herridge DF. 1995. Field assessment of supernodulating genotypes of soybean for yield, N_2 fixation and benefit to subsequent crops. *Soil Biol. Biochem.* 27:563–69

Annu. Rev. Ecol. Evol. Syst. 2011.42:23-46. Downloaded from www.annualreviews.org
by University of California - Riverside on 10/14/14. For personal use only.

Spaepen S, Dobbelaere S, Croonenborghs A, Vanderleyden J. 2008. Effects of *Azospirillum brasilense* indole-3-acetic acid production on inoculated wheat plants. *Plant Soil* 312:15–23

Streeter JG. 1985. Nitrate inhibition of legume nodule growth and activity I. Long term studies with a continuous supply of nitrate. *Plant Phys.* 77(2):321–24

Streitwolf-Engel R, van der Heijden MGA, Wiemken A, Sanders IR. 2001. The ecological significance of arbuscular mycorrhizal fungal effects on clonal reproduction in plants. *Ecology* 82:2846–59

Sullivan JT, Patrick HN, Lowther WL, Scott DB, Ronson CW. 1995. Nodulating strains of *Rhizobium loti* arise through chromosomal symbiotic gene transfer in the environment. *Proc. Natl. Acad. Sci. USA* 92:8985–89

Tan G, Tan W. 1986. Interaction between alfalfa cultivars and *Rhizobium* strains for nitrogen fixation. *Theor. Appl. Genet.* 71:724–29

Thrall P, Bever J, Slattery J. 2008. Rhizobial mediation of *Acacia* adaptation to soil salinity: evidence of underlying trade-offs and tests of expected patterns. *J. Ecol.* 96:746–55

Toomey M, Roberts D, Nelson B. 2009. The influence of epiphylls on remote sensing of humid forests. *Remote Sens. Environ.* 113:1787–98

Underwood W, Melotto M, He SY. 2007. Role of plant stomata in bacterial invasion. *Cell. Microbiol.* 9:1621–29

U'Ren JM, Dalling JW, Gallery RE, Maddison DR, Davis EC, et al. 2009. Diversity and evolutionary origins of fungi associated with seeds of a neotropical pioneer tree: a case study for analysing fungal environmental samples. *Mycol. Res.* 113:432–49

van der Heijden MGA, Klironomos J, Ursic M, Moutoglis P, Streitwolf-Engel R, et al. 1988. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Geol. Soc. Am. Bull.* 100:912–27

van der Heijden MGA, Bakker R, Verwaal J, Scheublin TR, Rutten M, et al. 2006. Symbiotic bacteria as a determinant of plant community structure and plant productivity in dune grassland. *FEMS Microbiol. Ecol.* 56:178–87

van der Heijden MGA, Wiemken A, Sanders IR. 2003. Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plants. *New Phytol.* 157:569–78

van Loon LC, Bakker PA, Pieterse CM. 1998. Systemic resistance induced by rhizosphere bacteria. *Annu. Rev. Phytopathol.* 36:453–83

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, et al. 2007. Let the concept of trait be functional! *Oikos* 116:882–92

Vitousek P, Walker L. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecol. Monogr.* 59:247–65

Waller F, Achatz B, Baltruschat H, Fodor J, Becker K, et al. 2005. The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proc. Natl. Acad. Sci. USA* 102:13386–91

Wanek W, Portl K. 2005. Phyllosphere nitrogen relations: reciprocal transfer of nitrogen between epiphyllous liverworts and host plants in the understorey of a lowland tropical wet forest in Costa Rica. *New Phytol.* 166:577–88

Wang B, Qiu YL. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* 16:299–363

Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. *Trends Ecol. Evol.* 21:261–68

Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* 7:510–23

Whitman WB, Coleman DC, Wiebe WJ. 1998. Prokaryotes: the unseen majority. *Proc. Natl. Acad. Sci. USA* 95:6578–83

Wolfe BE, Rodgers VL, Stinson KA, Pringle A. 2008. The invasive plant *Alliaria petiolata* (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range. *J. Ecol.* 96:777–83

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–27

Annu. Rev. Ecol. Evol. Syst. 2011.42:23-46. Downloaded from www.annualreviews.org
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Annual Review of Ecology, Evolution, and Systematics

Volume 42, 2011

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