

# More Than the Sum of Its Parts: Microbiome Biodiversity as a Driver of Plant Growth and Soil Health

Muhammad Saleem,<sup>1</sup> Jie Hu,<sup>2</sup> and Alexandre Jousset<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, Alabama State University, Montgomery, Alabama 36104, USA; email: msaleem@alasu.edu

<sup>2</sup>Institute of Environmental Biology, Ecology and Biodiversity, Utrecht University, 3584 CH Utrecht, The Netherlands

Annu. Rev. Ecol. Evol. Syst. 2019. 50:145–68

First published as a Review in Advance on July 23, 2019

The *Annual Review of Ecology, Evolution, and Systematics* is online at [ecolsys.annualreviews.org](http://ecolsys.annualreviews.org)

<https://doi.org/10.1146/annurev-ecolsys-110617-062605>

Copyright © 2019 by Annual Reviews.  
All rights reserved

## Keywords

plant–microbe interaction, microbiome, microbial ecology, disease suppression, abiotic stress, biodiversity–ecosystem functioning, soil health, nutrient cycling

## Abstract

Microorganisms drive several processes needed for robust plant growth and health. Harnessing microbial functions is thus key to productive and sustainable food production. Molecular methods have led to a greater understanding of the soil microbiome composition. However, translating species or gene composition into microbiome functionality remains a challenge. Community ecology concepts such as the biodiversity–ecosystem functioning framework may help predict the assembly and function of plant-associated soil microbiomes. Higher diversity can increase the number and resilience of plant-beneficial functions that can be coexpressed and unlock the expression of plant-beneficial traits that are hard to obtain from any species in isolation. We combine well-established community ecology concepts with molecular microbiology into a workable framework that may enable us to predict and enhance soil microbiome functionality to promote robust plant growth in a global change context.

ANNUAL  
REVIEWS **CONNECT**

[www.annualreviews.org](http://www.annualreviews.org)

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

## MICROBES: THE BACKBONE OF SOIL HEALTH AND PLANT PRODUCTIVITY

Microbes are the unseen engines of soil fertility, and plant growth depends on a suite of functions performed by soil- and root-dwelling microorganisms. For instance, bacteria and fungi mineralize soil nutrients, making them available to plants. By secreting sticky polysaccharides, microorganisms glue soil particles together, preventing erosion. They also coregulate plant hormonal balance, helping plants cope with abiotic stressors and protecting them against a range of insect pests, parasites, and pathogens (Berendsen et al. 2012, Fierer 2017). During the last 50 years, agricultural intensification, especially monoculture cropping, has increased crop production by suppressing interactions between plants and microorganisms. It has, for instance, reduced crop dependence on microbes by replacing microbial functions with external inputs of pesticides and fertilizers. Intensive agricultural practices have led to colossal yield increases over the short term. However, such approaches have increased agrochemical pollution, land degradation, and spread of resistant pests. These drawbacks are increasingly offsetting the initial yield gains, calling for more sustainable strategies to support food production. Soil microorganisms may be the backbone of such high-yield, low-input food production systems.

Agricultural soils, and especially rhizosphere soils directly adjacent to and influenced by roots, harbor an exceptionally high microbial biomass and species diversity. Roughly, 1 g of rhizosphere soil contains between  $10^8$  and  $10^{11}$  cultivable cells and approximately  $10^4$  microbial species (for details, see Berendsen et al. 2012). Thanks to its remarkable genetic, ecological, functional, and taxonomic diversity (Saleem et al. 2015, Fierer 2017), the soil microbiome is a vital reservoir of microbial traits that are potentially relevant for plant growth and health. If properly managed, the soil microbiome may enable strong and resilient plant growth while reducing the need for agrochemicals. However, inferring the functionality of a complex multispecies community such as the rhizosphere microbiome can be difficult. To go beyond cataloguing existing species and traits, we need a framework to organize species interactions and connect them to microbiome functions.

We argue that the biodiversity–ecosystem functioning (BEF) framework, first developed for plant and marine communities (Hillebrand & Matthiessen 2009), forms an ideal conceptual toolbox to infer microbiome functionality as an emerging property resulting from species interactions and not solely the presence of a given species or gene (Philippot et al. 2013a, Saleem et al. 2015). Such a structuring framework may support the ongoing shift in the study of plant–microbe interactions away from single species toward whole communities (Berendsen et al. 2018, Li et al. 2019).

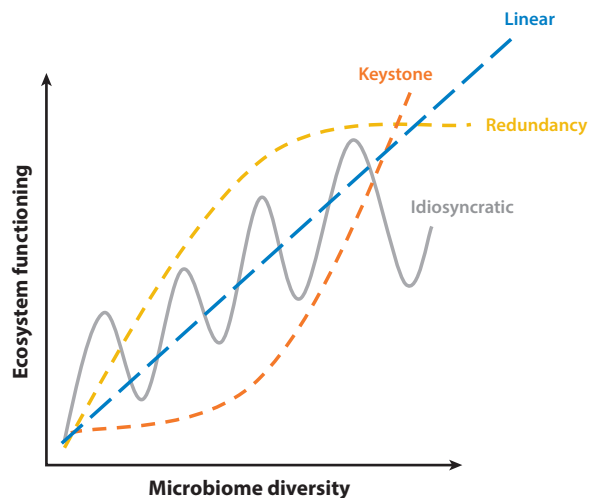
Several decades of research on beneficial plant–microbe interactions have led to a powerful molecular framework encompassing the multiple mechanisms that allow bacteria to enhance plant growth (Lugtenberg & Kamilova 2009). However, microbes are rarely alone with the plant. They face constant interactions with a range of competitors, predators, and parasites, all of which may affect their survival and interactions with plants and the soil matrix. Therefore, microbiologists have progressively sought to place plant–microbe interactions in a broader context of interacting microbial species (Barea et al. 2005, Dubuis et al. 2007). Although more and more molecular mechanisms underlying microbe–microbe interactions are being elucidated, it remains difficult to match these interactions to the complex ecological networks that characterize plant-associated microbiomes (Mendes et al. 2011, Xiong et al. 2017). We argue that bundling these interactions into a community-level framework may bring microbiome research to a predictive level that transcends the descriptive enumeration of present species and traits.

In this review, we use BEF relationships as an overarching framework that combines molecular interactions with community ecology, thereby linking microbiome taxonomic and functional diversity or composition to plant growth and soil health. In doing so, we translate the vast corpus of research established in plant and aquatic ecology into the rhizosphere context. We start by presenting concepts in BEF research, with a focus on microbial communities. We then explore the main mechanisms underlying diversity effects on microbiome function and present an overview of the newest methods used to set up and interpret biodiversity experiments in the context of plant-associated microbial communities, followed by metrics that summarize microbial diversity in a simple way and at the same time have enough explanatory power in regard to community functioning and stability. We explain how these different concepts connect with one another and describe the importance of higher microbiome diversity for plant productivity and climate-change resilience. We describe the different microbiome functions linked to plant nutrition, health, and soil quality, and we discuss the role of microbial biodiversity in the evolution of microbial traits that benefit plants, relevant to long-term agricultural management. We conclude by describing whether and how the different stakeholders involved in food production can enhance microbial biodiversity in a high-output agricultural setting. Finally, we propose a road map to integrate and acknowledge microbial biodiversity services in agricultural policy.

## **BIODIVERSITY-ECOSYSTEM FUNCTIONING RELATIONSHIPS IN THE MICROBIAL WORLD**

In the context of the worldwide loss of biodiversity linked to human activities, more and more scientists have explored the relationships between biodiversity and ecosystem functioning. Perhaps the most prominent examples in this field are grassland experiments that have addressed whether species loss negatively affects productivity, stability, and the provisioning of ecosystem services (i.e., desired functions such as biomass production, carbon sequestration, or the support of pollinators) (Hector & Bagchi 2007, Reich et al. 2012). These experiments have consistently demonstrated that biodiversity increases ecosystem services and buffers against perturbations such as climatic extremes. Such effects arise from the complementary use of existing resources as well as interactions between coexisting species in a community.

More recently, biodiversity research has been extended to microbial communities, demonstrating that microorganisms follow the same conceptual rules as higher organisms, albeit with different underlying molecular mechanisms. Microorganisms compete for resources, exchange nutrients, or antagonize one another (Krause et al. 2014a). As a consequence, BEF response curves reported in microbial microcosms show striking similarities to those observed in grasslands or aquatic ecosystems (**Figure 1**) (Bell et al. 2005, Saleem et al. 2016a, Jousset et al. 2017). In our meta-analysis of studies experimentally manipulating microbial diversity, dating from 2000 to 2017, we show that in 80% of the studies species richness was positively associated with one or more microbially derived services (**Figure 2**). This positive relationship could be explained by complementarity/synergy, redundancy, or selection effects (**Figure 2b**). In contrast, in around 20% of the studies, higher diversity reduced microbial community function, mostly as a consequence of a high prevalence of antagonistic interactions among the present species (**Figure 2**). Overall, on the basis of this meta-analysis, we suggest that microbial diversity may drive several functions essential to plant growth, such as nutrient cycling, pathogen suppression, and/or the production of phytohormones. Moreover, microbially derived services may be context dependent (Jousset et al. 2011a). Therefore, understanding the mechanisms underlying microbial community function and how they are affected by environmental conditions is essential in order to better harness microbiome functionality.



**Figure 1**

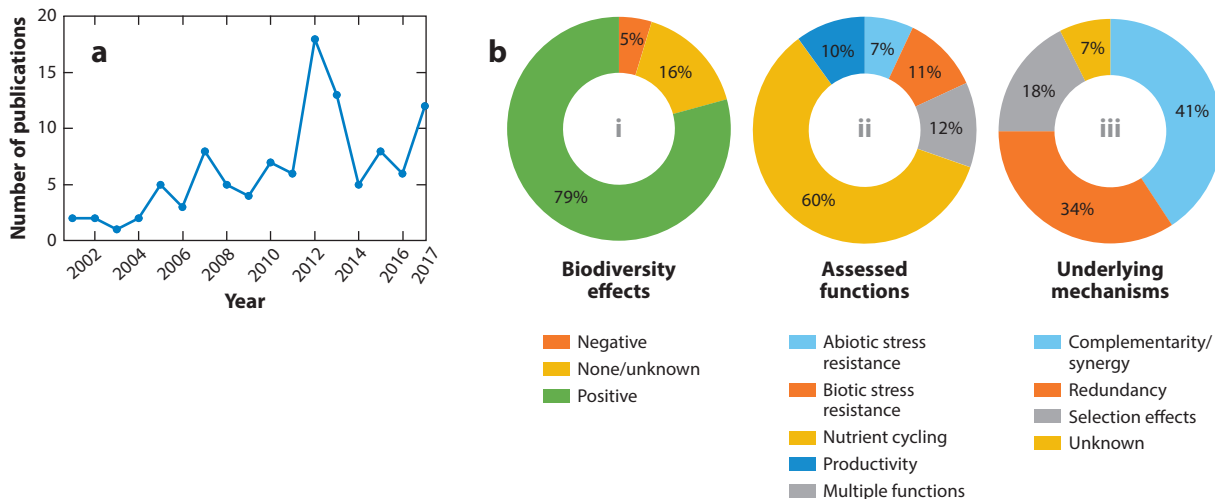
Microbiome biodiversity and ecosystem functioning. Four scenarios of biodiversity–ecosystem functioning relationships: linear (*blue*, ecosystem functioning increases with increasing microbiome biodiversity due to niche differentiation); keystone (*orange*, keystone species have effects on ecosystem functioning that are disproportionate to their abundance); redundancy (*yellow*, at higher diversity, ecosystem functioning is saturated due to niche overlap); and idiosyncratic (*gray*, biodiversity–ecosystem functioning relationships depend on environmental conditions and often fluctuate). Figure adapted from Scherer-Lorenzen (2005).

## MECHANISMS AND CONCEPTS UNDERLYING BIODIVERSITY EFFECTS ON MICROBIOME FUNCTION

Soil- and root-associated microorganisms form complex networks of interacting species, and interspecific interactions determine to a large extent the expression of plant-beneficial traits (Dubuis et al. 2007). We can interpret these complex interactions as a function of microbial biodiversity by using ecological concepts that have already been validated in plant and microbial communities. In the following subsections, we summarize some concepts that together form a useful set of guidelines to assess and understand the role of higher microbiome diversity in plant growth and soil health.

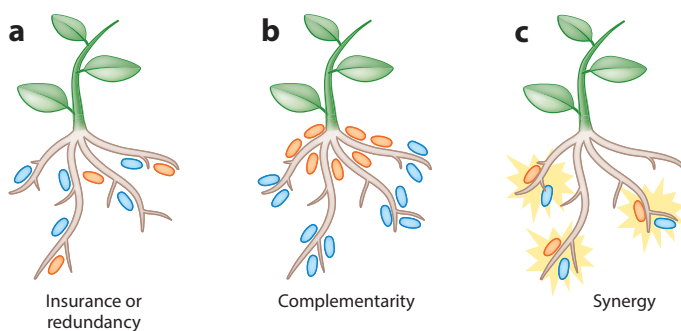
### Functional Redundancy: The Portfolio or Insurance Effect

The portfolio or insurance effect is a metaphor inspired by the financial world. Similar to investors diversifying their assets as a bet-hedging strategy, multispecies communities may prevent substantial alterations in their average function against perturbations. In the context of the rhizosphere, the stabilizing effect of biodiversity may emerge as a consequence of functional redundancy, when different species can perform a specific function but vary in their niche or sensitivity to environmental stressors (Schindler et al. 2015). As an example, if microbial species in a community differ in their ability to withstand water deficiency, even if an extreme drought event perturbs the community, a subset of the present species is likely to survive and deliver a given function (**Figure 3a**). In contrast, a single species in isolation may show a more fluctuating functionality, ranging from full functionality (when the conditions are optimal) to complete loss of function when adverse conditions inhibit this species. Insurance effects have been linked to microbial community resistance to the stresses induced by heavy metals (Koechler et al. 2015) or salts (Awasthi et al. 2014). We expect that insurance effects can stabilize microbiome function in the soil environment where



**Figure 2**

Meta-analysis of microbial biodiversity–ecosystem functioning (BEF) studies from 2000 to 2017. (a) Microbial BEF studies published between 2000 and 2017 that investigated or tried to link microbial diversity and composition with ecosystem functions. (b) A qualitative analysis of (i) biodiversity effects, (ii) assessed functions, and (iii) underlying mechanisms, as reported in BEF studies. Subpanel *i* shows negative, no (or unknown), and positive effects of biodiversity on microbially derived services. The nature of the services examined, shown in subpanel *ii*, includes abiotic and biotic stress resistance, multiple functions, nutrient cycling, and productivity. “Abiotic stress resistance” includes studies on contaminant biodegradation and plant abiotic stress alleviation as a function of higher microbial biodiversity. “Biotic stress resistance” includes studies that reported pathogen suppression, plant protection, and antipathogen metabolite production as a function of higher microbial biodiversity. “Multiple functions” includes studies that attempted to link several functions such as nutrient cycling, productivity, stress tolerance, trophic-level stability, and other ecosystem properties with microbial diversity and community composition. “Nutrient cycling” includes studies that investigated turnover of substrate resources, nutrients and their different forms, enzyme activities, and in some cases nutrient consumption and biomass production, as a function of higher microbial biodiversity. “Productivity” includes studies that investigated the impact of microbial biodiversity on microbial abundance and plant biomass production. Subpanel *iii* describes the proportion of studies that predicted ecological mechanisms underlying microbial BEF relationships.



**Figure 3**

Effects of biodiversity on the success and function of plant-associated microbiomes. (a) Insurance. If a perturbation eliminates one strain, the other will survive and take over plant growth promotion. (b) Complementarity. Different strains may use different niches, such as various parts of the root system or different resources. Together they will reach a higher population density than any single strain on its own. (c) Synergy. Different strains stimulate one another by, for instance, providing one another with required resources, ensuring strong plant growth.

temperature, water, and nutrient availability frequently vary. Insurance effects are likely to be very important in soil, where they might be reinforced by a vast pool of dormant microbial cells that become active under optimal conditions (Locey et al. 2017).

### Complementarity Effects

We define complementarity as the ability of different species to each utilize a different subset of the available niches, with the consequence that a multispecies assemblage will exploit a larger part of the environment than any species in isolation (**Figure 3b**). As a result, a combination of different species may not only coexist but also outperform any of them grown in isolation. Several scenarios have been proposed to explain complementarity effects; here, we discuss how the main ones apply to microbiome functioning.

The root causes of complementarity effects are physiological limitations: One cell cannot carry and express all the possible traits needed for life in the rhizosphere. Consequently, each microbial species shows a given level of niche specialization. A single species cannot use all of the resources or tolerate the conditions present in the whole rhizosphere environment in its entirety. Therefore, if different species use a subniche of the whole environment, they may complement one another and together reach a higher level of functioning. Complementarity effects typically drive positive diversity effects on ecosystem services (Gamfeldt et al. 2013, Saleem & Moe 2014). In the rhizosphere environment, the niche of a given microbial species can be determined by, for instance, the type and amount of root exudates, which change locally and with plant development (Chaparro et al. 2014). In the following subsections, we define three kinds of complementarity effects that are directly relevant in the context of microbe–microbe interactions in the rhizosphere. These three effects are conceptually similar but refer to distinct processes related to resource differentiation, spatial dynamics, and temporal dynamics.

**Resource use complementarity.** On a local scale, co-occurring species are in direct competition for limiting resources such as root exudates or soil organic matter (Saleem et al. 2015). The rhizosphere environment is associated with high chemical diversity, with carbon available as a blend of plant-derived compounds such as carbohydrates, organic acids, and amino acids. One species is unlikely to be able to use this broad set of resources, creating the potential for complementarity among species. For instance, if competing species in a local community can each use a different set of resources (Tang & Zhou 2011), together they may be able to use the available resources in a more complete way and thereby reach higher productivity and metabolic activity as a community than any of the species alone. In the context of the rhizosphere, resource complementarity can boost the function of root-associated beneficial microbial communities. As complementary, multispecies communities can consume more resources, they will reach a higher density, increasing their effect on plants (Hu et al. 2016, 2017). Furthermore, they will leave few vacant niches for pathogens, thereby improving plant protection (Ji & Wilson 2002, Wei et al. 2016).

**Spatial complementarity.** Spatial complementarity is another important mechanism that promotes the coexistence of organisms. Space itself is a limiting resource, and if competing organisms can distribute themselves across all of the available physical environments, competition may be reduced. For instance, spatial complementarity among tree crowns enhances productivity in forests (Williams et al. 2017). In the context of the rhizosphere, microbes may colonize different parts of the root system depending on root age and on phenotypic, architectural, and biochemical traits (Achouak et al. 2004; Saleem et al. 2016b, 2018) (**Figure 3b**). As a result, the whole root system will support a higher diversity of microbes than any one part of the root system, which can provide multiple functions to plants.

**Temporal complementarity.** Some microbial species specialize in colonization of roots during early plant growth stages, while others are more competitive at later stages (Chaparro et al. 2014). This palette of preferences may lead to a turnover in rhizosphere- and root-associated microbial species. The dominance of different species at various points in time, called asynchrony, is crucial to maintaining plant community function in grassland ecosystems (Hautier et al. 2018). We expect that it may also influence the relationship between the biodiversity of the available species pool and the functioning of the rhizosphere microbiome throughout the growing season. In a situation of low asynchrony, all microbes from the available species pool are specialized on one single plant growth stage such as seedling emergence. In this case, all species will compete against one another during the first growth phase, potentially killing one another. Furthermore, few or no species will be able to efficiently colonize the roots in later growth stages, leaving the plant without mutualists. Although few data are available to evaluate the importance of asynchrony, recent research has shown a temporal match between root exudation patterns and the species present, suggesting a given level of temporal complementarity due to changes in niche preferences (Chaparro et al. 2014), although the effects on functions relevant to plants are unknown.

### Jack-of-All-Trades Effect

Different species may excel at some functions, but not all. In the context of the rhizosphere, a given species might, for instance, fix nitrogen, inhibit pathogens, or mobilize phosphorus. However, due to inherent trade-offs, one species likely cannot fulfill all functions simultaneously (Carlson & Taffs 2010). In the so-called jack-of-all-trades effect, the mixing of different species that each excel at a specific function can result in a higher overall level of multifunctionality, such that the whole community expresses multiple traits simultaneously, than would be the case for any species by itself. This averaging effect requires species coexistence but does not imply that the different species interact with one another. However, the jack-of-all-trades effect also has drawbacks. In particular, because a community contains both high- and low-performing species, each individual function carried out by a community will be averaged to an intermediate level (van der Plas et al. 2016). This effect might be offset when the metabolic costs of carrying out multiple functions are high, and mixtures of specialists may outperform generalists, for instance, by efficiently carrying out all the metabolic steps that constitute complex metabolic pathways (Tsoi et al. 2018).

### Selection Effect

Individuals in a given community may not function similarly, and a subset of species may be responsible for delivering core functions to plants. The selection effect suggests that dominant species with particular traits can overperform specific functions in a community (Yachi & Loreau 1999, Yang et al. 2017), which can affect community functioning in either a positive or a negative way, depending on whether the traits associated with competitiveness are correlated with the expression of the function of interest. For instance, in microbial communities, the selection effect on microbial biomass production can be negative when the dominant species are toxic, slow-growing species that dominate by killing their competitors (Jiang et al. 2008, Saleem et al. 2017).

### Synergies and Cross Talk

Coexisting microorganisms can facilitate one another, thereby contributing to greater performance of multispecies communities (**Figure 3c**). For instance, one species may produce waste products that are used as resources by another, co-occurring species. This effect, called syntrophy, enables organisms lacking the ability to produce key nutrients to survive while saving the cost associated with particular metabolic capabilities (Seth & Taga 2014). Syntrophy is common in soil

microbes (Kim & Levy 2008, Jiang et al. 2018), as illustrated by the high occurrence and fitness advantages of auxotrophic strains that are unable to synthesize certain essential organic compounds such as amino acids. Facilitation may also occur when one species produces compounds that protect other species against natural enemies, or when different species trade public goods, such as siderophores or biofilm matrix (Driscoll et al. 2011).

Interactions among species may affect their functionality even in the absence of competition. One example is the impact of interspecific microbial communication on the expression of traits linked to plant growth and health. In a multispecies community, each species is constantly interacting and communicating with co-occurring organisms. The best-described case of communication is quorum sensing, in which microorganisms produce chemical signals allowing them to estimate the density of kin around them. However, interspecific cross talk is even more diverse and probably influences community function. Species can sense cues from other species and react by up- or downregulating specific traits (Dubuis & Haas 2007, Tyc et al. 2015). Microbial communication can also activate silent gene clusters that are not expressed in isolation (Netzker et al. 2015). Such interactions can result in biodiversity effects on trait expression. For instance, *Pseudomonas* spp. can react to the presence of competitors by upregulating antibiotics production, leading to greater potential for multispecies communities to suppress pathogens compared with the respective species in isolation (Jousset et al. 2014). Stimulation of secondary metabolite production in competitors shows conserved phylogenetic patterns, providing potential links between phylogenetic diversity and microbiome function (Tyc et al. 2014). In addition, the activity of each microbial group may increase plant fitness as well as the functioning of other microbes, thereby improving exudation (carbon and nutrient supply) and promoting beneficial interactions.

### Antagonism

Microbial species may also interact by producing compounds that inhibit competitors (Hibbing et al. 2010, Coyte et al. 2015). Antagonistic interactions may shape community-level functions; thus, we classify them conceptually as reverse facilitation. While this high level of antagonism may stabilize the community (Coyte et al. 2015) and contribute to functions such as pathogen suppression at higher biodiversity (Hu et al. 2016), increased antagonistic interactions may, in extreme cases, lead to a negative BEF relationship, as illustrated by the collapse of microbial communities at high diversity (Becker et al. 2012, Mehrabi et al. 2016) or by the dominance of poorly functioning but highly antagonistic species in a community (Jiang et al. 2008, Saleem et al. 2017).

## HOW TO INVESTIGATE THE BIODIVERSITY-ECOSYSTEM FUNCTIONING RELATIONSHIP IN THE MICROBIAL WORLD

Several methodological frameworks have been developed to assess the relationship between microbial biodiversity and community-level function. Each method has advantages and drawbacks and can be combined with different statistical and interpretation frameworks (**Table 1**).

### Observational Studies

Classically, there have been survey-type studies measuring biodiversity and linking it to ecosystem functioning (Delgado-Baquerizo et al. 2016). Thanks to improvements in high-throughput DNA sequencing, we can now easily survey, sample, and extract environmental DNA and obtain information about diversity (Shoemaker et al. 2017). Because of complex covarying factors and potentially spurious correlations, however, it is hard to pinpoint the causal mechanisms linking microbial biodiversity to ecosystem functioning by use of observational studies alone (**Table 1**). Therefore, we need to design experiments to find the causal links.



**Table 1 Methods of studying BEF relationships in the microbial world**

| Approaches to the study of BEF relationships | Description   | Examples   | Advantages   | Disadvantages   | Reference(s)                                  |
|--|---|--|--|---|---|
| Observational studies                        | Comparative/correlational studies and sample surveys    | Use of environmental DNA sequence information and association of such information with measurements of functions among samples | Observational results show BEF relationships, and samples are relatively easy to obtain from different environments.   | Impossible to distinguish cause and effect or to attribute the causal mechanisms underlying relationships   | Delgado-Baquerizo et al. (2016)               |
| Experimental studies                         | Synthetic communities                                   | Use of microcosms combining different microorganisms   | Experiments manipulate community diversity for investigations of BEF relationships. Experimental results reveal the mechanisms underlying BEF relationships. | Environmental factors, especially abiotic factors, need to be controlled carefully, and large numbers of studies should be conducted to minimize the effects from environmental variations. | Wei et al. (2015)<br>Hu et al. (2016)         |
|  | Removal experiments                                     | Use of a series of soil dilutions, microorganism filtering, or soil fumigation to remove certain groups from natural systems   |  |   | Griffiths et al. (2001)<br>Wagg et al. (2014) |
| Modeling studies                             | Deletion of soil microbial and faunal functional groups | Effects on plant growth of manipulating the composition of the microbial and faunal community                                  | Models can cope with irregular events, identify trends, and predict scenarios.   | Any model is a simplification of reality and, thus, has limitations that may lead to improper generalizations.  | Hunt & Wall (2002)                            |
|  | Interaction based                                       | Lotka–Volterra model, rock–paper–scissor model, co-occurrence network  |  |   | Brophy et al. (2017)                          |

Abbreviation: BEF, biodiversity–ecosystem functioning.

## Experimental Studies

Manipulations of biodiversity are excellent complements to observational studies because they enable testing of specific hypotheses about underlying mechanisms. Microbial diversity can be manipulated both in the field and in laboratory studies, generating more or less controlled biodiversity gradients that can be linked to functions such as biomass production, nutrient cycling, and biotic and abiotic stress resistance (e.g., Weisser et al. 2017). In the microbial world, we can investigate BEF relationships in microcosms by using macroecological experimental designs and approaches.

**Synthetic communities.** The artificial design of beneficial microbial consortia has recently received significant attention (Wei et al. 2015, Hu et al. 2016, Saleem et al. 2017). Through the

assembly of species mixtures with defined genetic properties, synthetic communities have great potential to disentangle the potential mechanisms underlying BEF relationships. We can draw these communities from a specific species pool on the basis of phylogenetic, evolutionary, and functional criteria (Jousset et al. 2013, Singh et al. 2015). Several hypotheses can be tested in a very detailed way so as to assess, for instance, the importance of functional redundancy, facilitation, or antagonism for microbiome function (Becker et al. 2012; Saleem et al. 2013, 2017). Furthermore, we can mechanistically partition the relative effect size of species interactions such as complementarity and selection effects on microbially driven processes (Connolly et al. 2013) such as plant growth promotion (Saleem et al. 2017). Studies on synthetic communities have assembled and tested at most 72 species (**Table 1**) (e.g., Bell et al. 2005). This number is several orders of magnitude below the actual microbial diversity in the rhizosphere, so complementary approaches to develop complex communities similar to natural ones are needed.

**Species removal.** Another way to approach biodiversity gradients is to remove species from the total pool by using different constraints, thereby generating a gradient of biodiversity that is relatively close to natural conditions (**Table 1**). For instance, a series of dilution or fumigation steps will remove rare species (Hol et al. 2010). Alternatively, size fractionation may allow examination of the importance of trophic structure for soil function (Wagg et al. 2014). None of these approaches is fully neutral; for instance, fumigation selects for spore-forming species. Furthermore, these approaches do not allow the researcher to control which species will be removed, complicating the interpretation of the results. Nonetheless, these results can provide valuable insights into the causal mechanisms underlying BEF relationships.

### Modeling Studies

Mathematical modeling provides an additional way of generating and testing hypotheses about microbial diversity and can be particularly powerful when combined with experimental approaches (Gravel et al. 2011). By exploring a broad range of conditions, models enable the assessment of general patterns that would be impossible to address experimentally. While to date few models have focused on species interactions in the rhizosphere, other research has demonstrated the usefulness of models for assessing BEF relationships in microbial communities. For instance, trait-based models predict interactions between competing microorganisms on the basis of their metabolic and plant-beneficial capabilities (Freilich et al. 2011, Krause et al. 2014a), and trophic interaction-based models predict the dynamics of co-occurring species under a range of environmental conditions, such as nutrient availability or temperature (Fussmann et al. 2014, Brophy et al. 2017). Models also can predict how changes in species interactions will affect community performance and stability.

## MICROBIOME BIODIVERSITY INDICES

Advances in sequencing technologies have made it possible to obtain detailed catalogs of root- and rhizosphere-colonizing microbial species and functional genes. We present some of the most common indices used to summarize community taxonomic and functional characteristics and explain their relevance for a better understanding of microbiome assembly and function.

### Richness

Richness is the simplest index and accounts for the number of species (or any other operational taxonomic unit). This index is a convenient and widely used predictor of community function and is functionally meaningful when all species have additive effects on ecosystem function

(Bell et al. 2009)—that is, each new species addition will increase (or decrease) the function of interest. However, in real communities, the relationship between richness and community function tends to saturate at some level of richness (Connolly et al. 2013). Other indices accounting for species abundance and functionality may, therefore, offer better explanatory power (Hillebrand & Matthiessen 2009).

## Evenness

Evenness indices seek to describe biodiversity as the probability that each species will interact with others, regardless of their identity and number. Therefore, the most widely used evenness indices, such as the Shannon, Simpson, and Gini diversity indices, reflect species' relative abundances rather than simply their presence or absence. In an uneven community dominated by a few species, any given organism is likely to interact with its kin. In contrast, in a species-rich, even community, an organism will most likely interact with other species. Evenness can predict community function (Wittebolle et al. 2009) and reflects a basic assumption: If interactions between organisms belonging to different species are more positive (in term of growth or trait expression) than interactions within the same species, higher evenness will result in greater community function. The value of evenness as a predictor is independent of the underlying mechanisms. The type of intra- and interspecific interactions can be driven by, for instance, resource complementarity, facilitation, or chemical cross talk between species.

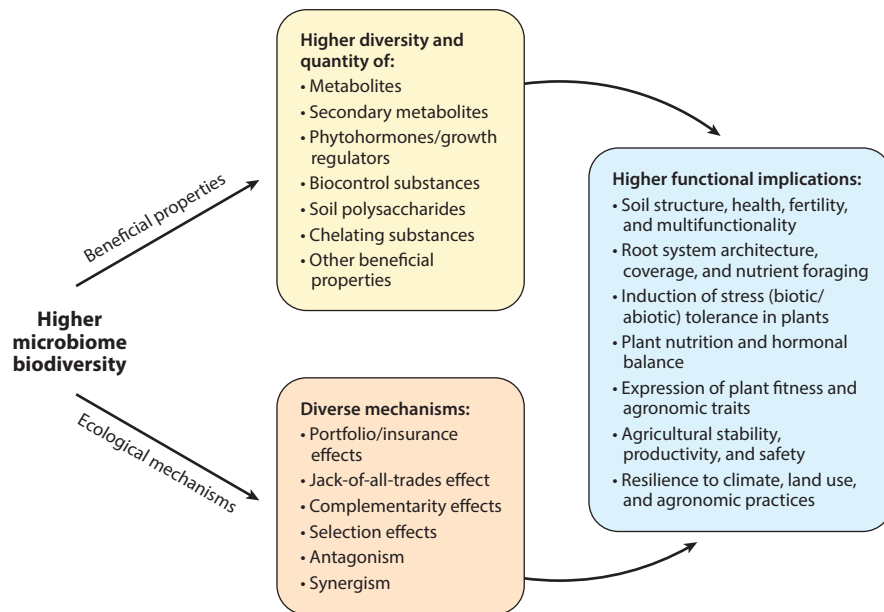
## Functional and Phylogenetic Indices

Accounting for functional differences sometimes provides a stronger prediction of community function than the number of species. Phylogeny can be used as a convenient index of functionality when niche differentiation between species correlates with their phylogenetic distance (Steinbauer et al. 2016). Despite being good predictors of community function, regardless of species number, phylogenetic and functional dissimilarity indices rely on the average distance between species in relatedness and function, respectively. In microorganisms, the assumption that physiological differentiation correlates with phylogenetic distance holds up to a point. However, the high level of horizontal gene transfer may blur phylogenetic signals in several bacterial traits linked to primary and secondary metabolism (Jousset et al. 2011a, Krause et al. 2014b).

Network approaches to quantify biodiversity have recently become popular. These methods focus on interactions among species rather than on their single contributions. We can express resource competition patterns by using bipartite networks, in which a single matrix is used to map the relationships between species (in this case, different bacteria) and their resources (carbon sources derived from root exudates). Such networks can provide a better prediction of community function than any classical biodiversity index (Wei et al. 2015). Co-occurrence networks may also provide hints about niche differences among species. To date, their use has been mainly descriptive, but in the future their use may increase in predictive models (Faust & Raes 2012). Future biodiversity indices will likely combine trait- and species-abundance matrices. Traits may be retrieved either by classical cultivation-dependent methods or by inference of the metabolic potential on the basis of the genomic data of the reference strains (Freilich et al. 2010, 2011).

## SIGNIFICANCE OF GREATER MICROBIOME DIVERSITY FOR SOIL FERTILITY AND PLANT GROWTH

Similar to other ecosystems, rhizosphere microbiome biodiversity may strongly affect functions associated with plant vigor. Theoretical models, experimental studies, and field surveys mostly



**Figure 4**

Benefits of higher microbiome diversity, ranging from microbial properties to soil and plant health.

point to an increase in microbiome functioning such as nutrient mineralization or disease suppression at high microbial diversity (Singh et al. 2014, Wood et al. 2015, Slade et al. 2017). In particular, species-rich ecological communities may deliver more than one function simultaneously, a phenomenon named ecosystem multifunctionality (Wagg et al. 2014, Delgado-Baquerizo et al. 2016). Given the large number of plant-beneficial functions performed by the rhizosphere microbiome, the ability to express them efficiently and simultaneously is essential to ensure plant growth. A single species is unlikely to perform multiple desired functions, and indeed, most bacteria cluster into functional groups harboring a subset of the known plant-beneficial traits, such as disease suppression or growth promotion (Agaras et al. 2015). Therefore, higher microbiome biodiversity could lead to higher diversity of microbial processes and effects on soil properties that are important to support soil health and plant productivity (**Figure 4**).

Most microbial biodiversity studies have focused on individual functions (**Figure 2**) that saturate at relatively low species-richness or trophic levels (Bell et al. 2005, Saleem et al. 2012). Because microbes perform multiple functions, it is very likely that diversity effects could be even stronger and more significant when several rhizosphere functions are considered. In contrast, in some cases, trade-offs among various functions may reduce the potential of species-rich ecosystems to deliver a higher level of multifunctionality compared with the highest-performing monocultures (Zavaleta et al. 2010, Gamfeldt et al. 2013). Such trade-offs might be expected in diverse rhizosphere microbial communities where functions and life history strategies change under various environmental conditions. Therefore, it is important to understand community-level trade-offs among vital microbial functions, such as nutrient cycling, nitrogen fixation, and synthesis of public goods or phytohormones, to exploit microbial biodiversity for rhizosphere multifunctionality. In the following subsections, we summarize existing knowledge of how microbial diversity may be linked to a range of soil attributes and functions relevant to the improvement of plant growth and soil fertility.

## Soil Structure

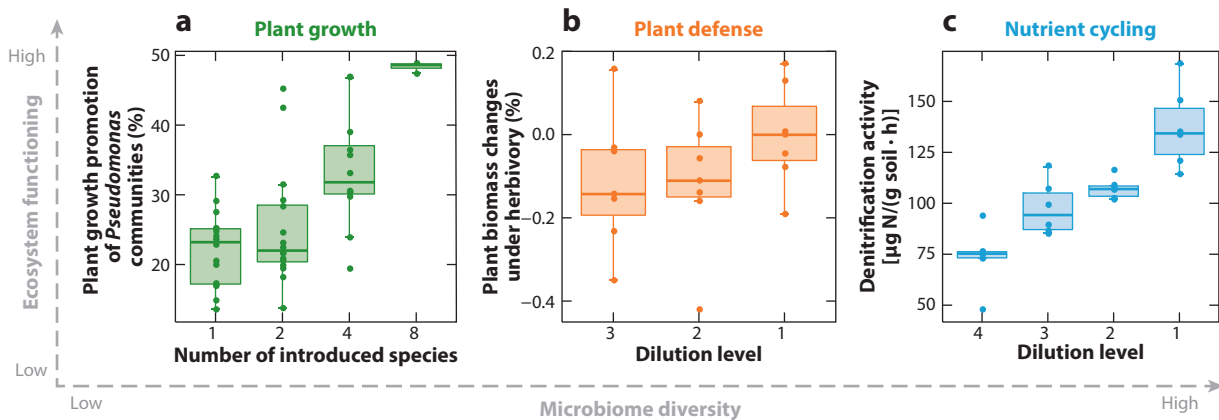
Soil structure is determined largely by the aggregation of soil particles, and it has a strong effect on several soil properties. For example, well-aggregated soil improves erosion resistance, nutrient sequestration, and water transport, thereby supporting plant growth and productivity (Bronick & Lal 2005). Microorganisms may affect soil structure in two main ways. First, microbes can convert labile organic compounds into extracellular polymers that aggregate soil particles (Degens & Sparling 1995). Second, microbial interactions with plant roots and other soil organisms such as mycorrhizal fungi enhance soil aggregation and structure (Rillig et al. 2015). Some recent evidence suggests that soil structure, microbial biomass, and microbial diversity mostly correlate with one another irrespective of soil type and climatic conditions (Rabbi et al. 2016), suggesting that higher microbial biodiversity may increase soil aggregation. The importance of synergetic interspecific interactions for extracellular polysaccharide formation in soil bacteria also indicates that microbial biodiversity may promote soil aggregation (Ren et al. 2015). Soil microbial communities composed of functionally diverse species may produce more heterogeneous polymers responsible for soil aggregation than any of the species alone. Our recent data (M. Saleem, unpublished data) suggest that an increase in microbial species richness increases soil polysaccharide contents and soil aggregation. We predict that microbiome diversity may serve as a tool to improve the formation of soil micro- and macroaggregates.

## Modulation of Phytohormone Levels and Plant Nutrition

Several plant-associated microbes can produce or degrade plant hormones. Thus, they have the potential to shift plant hormonal balance, thereby altering plant physiology and resource allocation (Saleem et al. 2007, Ravanbakhsh et al. 2017). These changes can affect plant performance in various directions, promoting, for instance, biomass production or stress resistance. Changes in microbial diversity will alter this hormonal modulation by microbes. For instance, loss of rare microbial species can shift plant resource allocation from defense to growth, leading to higher plant biomass but also a high vulnerability to pests (Hol et al. 2010). Rhizosphere microbial community composition is linked to several plant fitness traits such as flowering phenology (Wagner et al. 2014), confirming that alteration of plant hormonal balance by associated microorganisms may have far-reaching consequences for plant life history.

Similarly, microbial diversity may enhance plant nutrition. Experiments with synthetic communities have revealed a positive impact of microbial biodiversity on plant growth (Weidner et al. 2015). In a recent study, increasing species richness in the rhizosphere enhanced microbial activity and plant biomass, probably as a result of resource partitioning among the species present and the higher number of functions performed by a multispecies community (Singh et al. 2015). Interestingly, inoculation of plants with diverse bacterial species expressing only a single plant-beneficial trait (nitrogen fixation) did not increase plant growth, supporting the hypothesis that diverse microbial traits are needed to increase plant biomass (Singh et al. 2015). Such diversity effects on microbiome function can occur even at a fine phylogenetic scale: Despite containing closely related species sharing several traits, multispecies mixtures of fluorescent pseudomonads, a common group of rhizosphere dwellers, provided more functions linked to plant nutrition, hormonal balance, and pathogen suppression than any single species in isolation (Hu et al. 2016, 2017). Furthermore, the impact of bacterial diversity on plant biomass (**Figure 5a**) and nutrition (essential nutrients) increased with increasing production of plant-beneficial traits such as phytohormones, siderophores, and plant nutrient assimilation (Hu et al. 2017).

The net effect of biodiversity on plant growth may depend on the available microbial species pool and soil chemical characteristics. Using the dilution to extinction approach, Hol et al. (2015a)



**Figure 5**

Impact of higher microbial biodiversity on (a) plant growth, (b) plant defense, and (c) nitrogen cycling. Biodiversity gradients in panels b and c were established by serial dilutions of natural communities and in panel a through the addition of synthetic communities (probiotics). Numbers greater than one refer to higher levels of dilution and, thus, reduced microbial diversity. (a) Each point represents a different *Pseudomonas* community (monocultures were duplicates, eight-genotype communities were quadruplicates, and the rest were triplicates). Higher bacterial species diversity increased plant growth. Plant growth promotion was determined as the change in the percentage of plant-shoot dry weight of bacterial versus control treatments. (b) The plants showed relatively higher biomass in the low-dilution treatments under insect herbivory, probably as a result of greater production of the defense compound glucosinolate. (c) Species removal from a natural community leads to a reduction in denitrification by the soil microbiome. Panel a adapted from Hu et al. (2017). Panel b adapted from Hol et al. (2010). Panel c adapted from Calderón et al. (2017).

reported that a decrease in microbial diversity could have positive, negative, or neutral effects on plant growth, depending on soil type and the original microbial species pool. The presence of some rare microbial species was associated especially strongly with the accumulation in leaves of glucosinolates, a class of secondary metabolites with insecticide activity. Therefore, increasing microbial diversity may rewire plant physiology in a way that promotes plant resistance to herbivory (Figure 5b) (Hol et al. 2010).

### Pathogen Suppression in the Rhizosphere

The rhizosphere microbiome is the first line of defense protecting plants against soilborne pathogens. In some soils, often referred to as disease-suppressive soils, plants remain healthy even without the application of pesticides. Some of the best-studied examples of effective disease suppression include the take-all fungus (*Gaeumannomyces graminis* var. *tritici*), *Rhizoctonia* in wheat and sugar beet, and *Fusarium* spp. root rot and wilt in various crops (Raaijmakers & Mazzola 2016, Schlatter et al. 2017). Several microorganisms belonging to microbial groups such as *Pseudomonas*, *Bacillus*, *Lysobacter*, and *Trichoderma* are known to suppress soilborne diseases (Schlatter et al. 2017).

However, we argue that in several cases the interplay among species, rather than the performance of individual ones, determines disease suppression by the soil and rhizosphere microbiomes. For instance, invasion of soil by pathogens is negatively correlated with the level of microbial diversity (Wei et al. 2015, Yang et al. 2016). Van Elsas et al. (2012) demonstrated that invasion with the human opportunistic pathogen *Escherichia coli* O157:H7 decreases across two types of diversity gradients (consortia of culturable bacteria and dilution of natural soil microbial communities) in the soil environment. It is very likely that species-rich communities do not allow the pathogen to colonize because of greater resource utilization and competition (van Elsas et al. 2012). Such

negative biodiversity–invasibility effects also occur within genera: The high richness of *Pseudomonas* spp. leads to an increased suppression of pathogen invasion by *Pseudomonas putida* and *Serratia liquefaciens* (Jousset et al. 2011b, Eisenhauer et al. 2013).

Similar mechanisms apply to plant pathogens, which have to establish within the indigenous community in order to infect the plants (Wei et al. 2015). In the rhizosphere, multispecies bacterial communities showing high functional diversity prevent infection by *Ralstonia solanacearum* by consuming most plant-derived resources (Wei et al. 2015). In a similar study in tomato, Irikiin et al. (2006) showed that plants inoculated with a mixture of 15 bacterial strains are better protected than those inoculated with a single strain. These authors suggested that efficient resource exploitation in the rhizosphere by diverse microbial species enhances pathogen and disease suppression (Irikiin et al. 2006).

The relationship between microbial diversity and pathogen suppression is highly context dependent and may fluctuate on the basis of various environmental factors, such as resource availability (Yang et al. 2017, 2018) and the potential of native or introduced communities to exclude pathogens through efficient resource preemption (Messiha et al. 2009). For instance, even if efficient resource exploitation by diverse microbial communities suppresses pathogen invasion, pathogens might invade during pulses of high resource supply (Yang et al. 2017, 2018).

Higher species richness may enhance the production of antibiotics and community-wide antagonistic interaction, which in turn can be helpful in pathogen suppression. For instance, species-rich bacterial communities produce more diffusible and volatile bioactive molecules, thereby showing stronger antifungal activity against the phytopathogen *Fusarium oxysporum* than species-poor communities (Jousset et al. 2014, Hol et al. 2015b). Antagonism or facilitation within the resident community is also a determinant of pathogen invasion; facilitative communities become very vulnerable to invasion by the bacterial wilt agent *Ralstonia solanacearum* (Li et al. 2019). Overall, rhizosphere microbiome diversity appears to increase resistance to pathogen invasion, resistance that may rapidly be lost when soil degradation erodes microbial diversity.

## Insect Pest Suppression

Pests cause yield reductions of up to 20% worldwide. Soil microbes produce a variety of secondary metabolites that can suppress weeds and insects. According to recent studies of the stimulatory effect of biodiversity on secondary metabolism (Jousset et al. 2014), microbiome biodiversity may enhance pest suppression, and research findings may inform microbiome management to reduce pest damage (Pineda et al. 2017). For instance, microbiome-treated *Arabidopsis thaliana* plants inhibit larval feeding compared with untreated control plants (Badri et al. 2013). In another study, a mixture of the insect-parasitic fungus *Beauveria bassiana* and the antifungal bacterium *Bacillus subtilis* provided protection against both *Fusarium* wilt disease and fruit borer herbivory in tomato plants (Prabhukarthikeyan et al. 2014). Plants treated with mixtures of these two organisms show higher levels of defense-related enzymes such as polyphenol oxidase, lipoxygenase, and peroxidase compared with plants inoculated with one species only, indicating that, in addition to its direct effects on pathogens, biodiversity may be essential to keep plant defenses active. Given that plants are colonized simultaneously by both pathogenic and beneficial bacteria, Saleem et al. (2017) investigated the impact of monocultures and mixtures of three bacterial species (*Pseudomonas syringae* DC3000 and *Xanthomonas campestris*, both pathogens, and *Bacillus cereus*, which is beneficial to plants) on plant growth. Higher species richness increases seed production in the host plants under insect attack (Saleem et al. 2017), thus suggesting a diversity effect on plant performance under insect attack.

## Induction of Abiotic Stress Tolerance in Plants

Plants face multiple abiotic stressors, such as drought and temperature extremes, salinity, UV radiation, and environmental pollution. All of these stressors compromise food security by reducing yields and may hamper food safety if pollutants enter crops. Rhizosphere microbiota play an essential role in protecting plants against stressors, and recent studies have demonstrated the induction of stress tolerance in plants as a function of microbial biodiversity. In a microbiome study, plants grown in soils supporting a highly diverse microbiome produced more biomass under water stress, thus suggesting that microbiome biodiversity has a greater impact on plant performance under drought conditions (Zolla et al. 2013). Thijs et al. (2014) developed a synthetic microbial consortium containing plant-beneficial bacterial species resistant to the abiotic stressors 2,4-dinitrotoluene (2,4-DNT), drought, cold, and/or nutrient starvation. After 9 days of inoculation, the consortium doubled the root length of plants in 2,4-DNT-contaminated soil (Thijs et al. 2014). Likewise, inoculation of lupines with a mixture of metal-resistant rhizobacteria (*Bradyrhizobium* sp., *Pseudomonas* sp., and *Ochrobactrum cytisi*) increases plant biomass and reduced metal accumulation in shoots and roots, suggesting that microbial diversity has a plant-protective effect (Dary et al. 2010). Furthermore, in a study of the effects of synthetic communities of one, two, or five bacterial species on growth parameters of grapevine rootstocks under drought stress, diverse mixtures promoted plant growth when the plants experienced drought stress, whereas monocultures induced better plant growth than mixtures in the control (nondrought) conditions (Rolli et al. 2015). This finding emphasizes the role of microbial diversity but indicates that phenotypic shifts induced by microbes can be either beneficial or deleterious, depending on the environmental conditions.

## BIODIVERSITY AND EVOLUTION OF PLANT-BENEFICIAL TRAITS IN MICROORGANISMS

Biodiversity is an important driver of evolution, and microbial diversity may play a significant role in maintaining plant-microbe mutualisms. Mutualistic interactions between plants and rhizosphere microorganisms are evolutionarily unstable because the plant has few ways to enforce microbial cooperation (Kiers & Denison 2008). We propose that biodiversity may be an important driver of the evolution of microbial traits in the rhizosphere. For instance, biodiversity fosters the evolution of new bacterial phenotypes by increasing the benefit of innovations that enable species to escape competition (Jousset et al. 2016). Highly diverse communities could, therefore, evolve even more new species that together could exploit plant-derived resources more efficiently (Jousset et al. 2016) and potentially provide more services. Some studies suggest that multispecies interactions may drive the evolution of more beneficial interactions over time (Lawrence et al. 2012, Fiegna et al. 2015) as a result of public good sharing and division of labor among species (Dragoš et al. 2018). Biodiversity may also affect the evolution of plant-beneficial traits. Competition between related bacterial species promotes the evolution of both niche complementarity and production of antibiotics (Kinkel et al. 2014), two characteristics that may increase pathogen suppression by root-associated communities (Hu et al. 2016). However, it is possible that biodiversity can, in some cases, cause a decline in plant-microbe mutualism. For instance, phylogenetically diverse communities are less able to control social cheaters in experimental *Pseudomonas* spp. assemblages (Jousset et al. 2013). Because these mutants lack the ability to produce antibiotics or enzymes linked to nutrient mineralization and disease suppression, we expect that phylogenetically diverse communities may be very good plant mutualists on ecological timescales but that the benefits to plants may decline over evolutionary timescales (Jousset et al. 2013).



Nevertheless, we suggest that species diversity may also provide the opportunity for microbes to adopt various life history strategies (e.g., growth, stress resistance). Diversification increases, for instance, the resistance of biofilms to stress by generating mixed communities of novel mutants with distinct phenotypes (Boles et al. 2004). Given that bacteria also form biofilms on plant roots, we expect that diversification will generate insurance effects that buffer microbiome function under stress.

## **MICROBIAL BIODIVERSITY AND AGRICULTURE RESILIENCE TO GLOBAL CHANGE**

Agricultural production faces multiple threats, ranging from increasing climatic extremes to soil pollution. Soil microbes are essential to help crops cope with such stresses, yet agricultural intensification and agrochemical application exert significant pressure on various key microbial functional groups, such as nutrient cyclers, disease suppressors, and plant growth promoters, which are essential to increase and sustain crop yields. Indeed, some recent studies have reported adverse effects of agronomic practices and climatic factors on microbial communities, functional groups, and microbially driven functions (Hussain et al. 2009, Hartmann et al. 2015, Lupatini et al. 2017). Thus, there is growing interest in enhancing agricultural yields by increasing microbial biodiversity (Bender et al. 2016).

Soil microbial diversity is linked to multiple functions of agroecosystems underlying plant yield, soil fertility, and environmental quality (Wagg et al. 2014). Much of microbial diversity has long been considered functionally redundant, yet recent BEF studies have repeatedly described the negative effects of microbial diversity loss on ecosystem functions such as microbial biomass, nutrient cycling, plant growth, pathogen suppression, and pollutant degradation. For example, Delgado-Baquerizo et al. (2016) showed that a reduction in bacterial biodiversity decreases microbial biomass, respiration, and biodegradation of contaminants. Their results indicate a lack of functional redundancy in microbial communities. Loss of microbial diversity also negatively affects nitrogen cycling (Philippot et al. 2013b), indicating that species loss may compromise soil fertility.

In contrast, some studies suggest that higher microbial biodiversity could prove harmful for plants. For example, loss of microbial diversity by serial dilution alters the composition of microbial communities and negatively affects denitrification (**Figure 5c**); lower denitrification with lower diversity could benefit plants if it increases nitrogen availability (Calderón et al. 2017).

Nevertheless, following the BEF framework, we advocate that microbial biodiversity resources, if managed and preserved to develop multifunctional and stress-resistant microbiomes, could increase the resilience of agroecosystems to anthropogenic perturbations. Highly diverse communities containing microbes harboring a broad range of life history strategies could ensure that more species will survive stressors. Thus, species-rich ecosystems may recover faster from, and be more resistant to, climate and land-use change.

## **HOW CAN WE INCREASE MICROBIAL DIVERSITY IN THE AGROECOSYSTEM?**

With some exceptions, contemporary agronomic practices, such as conventional tillage, pesticides, chemical fertilizers, monoculture cropping, conventional irrigation, intensive cropping, and lack of organic amendments, are considered to reduce microbial diversity and beneficial interactions and functions in the agroecosystem. Interest in restoring soil fertility by improving microbiome composition is increasing (Bender et al. 2016). Recent research suggests that innovative farming

practices such as organic amendments, crop rotation, crop diversity, and probiotics increase microbiome diversity (taxonomic, phylogenetic richness) and spatial heterogeneity, in addition to increasing the abundance of microbial taxa involved in pest and soil disease suppression and nutrient cycling (Ling et al. 2016, Lupatini et al. 2017). Tiemann et al. (2015) showed that a cropping diversity gradient develops unique soil microbial communities that are linked to multiple soil functions such as microbial activity, organic carbon storage, total nitrogen content, and soil aggregation. A recent meta-analysis suggested that organic systems demonstrate 32% to 84% higher soil microbial biomass (carbon, nitrogen, total phospholipid fatty acids) and enzyme (dehydrogenase, urease, protease) activities compared with conventional systems. Crop rotation, intercropping with legumes, and organic inputs are associated with higher microbial biodiversity in agricultural soils (McDaniel et al. 2014, Lori et al. 2017). Apart from these management practices, application of biological control agents and probiotics may also increase microbial biodiversity in the soil. For instance, treatment of soil with biofertilizers containing key plant-beneficial species such as monocultures of *Bacillus* and mixtures of *Trichoderma* and *Pseudomonas* spp. increases microbial functional diversity, ultimately increasing plant stress tolerance (Hu et al. 2016, Fu et al. 2017, Pang et al. 2017, Xiong et al. 2017). Moreover, manipulation of the soil system by adding microbial probiotics, organic amendments, and/or biochar has been suggested to increase microbial diversity, nutrient cycling, and below- and aboveground plant performance (Pang et al. 2017, Zhang et al. 2017, Meng et al. 2019).

## **INTEGRATING MICROBIAL BIODIVERSITY RESEARCH WITH AGRICULTURAL POLICY**

Given the vital role of microbes in agriculture, policy-making domains and stakeholders would benefit from acknowledging the role of microbial biodiversity in farm productivity when developing agricultural policies. In this review, we have summarized the nascent corpus of scientific evidence regarding the role of microbial diversity in the restoration of degraded or disturbed soils; however, understanding the implications of this research for crop yields at the farm scale still requires implementation efforts at the agricultural extension and policy levels. The BEF framework may be a powerful approach to manage the soil microbiome and, ultimately, agroecosystem function. For instance, the use of agrochemicals and other intensive farming practices alter soil microbiome composition and reduce its biodiversity and functionality (for details, see Hussain et al. 2009, Hartmann et al. 2015). Therefore, before introducing new cultivars, agrochemicals, or soil management or agronomic practices, we should assess their effects on microbial functional groups relevant to soil health, fertility, and crop production. To that end, cross-disciplinary research among community ecologists, microbiologists, agronomists, and plant and soil scientists may help us apply ecological theory to increase microbially driven services at the farm scale. More importantly, there is a need for integrated research among soil scientists, growers, extension clientele, ecologists, and policy makers to develop strategies to preserve and utilize microbial resources for soil health and crop production.

## **FUTURE DIRECTIONS**

1. What are the patterns of microbiome biodiversity (taxonomic, functional, phylogenetic, etc.) under different cropping regimes and management practices?
2. Which microbial biodiversity indices best predict microbiome and soil multifunctionality?

3. What are the effects of environmental changes such as nitrogen enrichment, droughts, warming, and other weather extremes on microbiome diversity and services?
4. How does microbial biodiversity confer resilience against such extremes, and how does it help in developing climate-resilient agriculture?
5. How can food producers manage microbiome biodiversity through novel agricultural practices (crop cultivars, amendments, probiotics, etc.) and manipulate soil biophysical conditions to enhance soil fertility? Can scientists develop crop-specific probiotics and synthetic communities that can be applied at the farm scale?
6. Which diagnostic tools could be used to assess the effects of biotic and abiotic disturbances on soil microbiome biodiversity?

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

## ACKNOWLEDGMENTS

We are greatly thankful to the editor and a reviewer for their suggestions and recommendations that improved this manuscript.

## LITERATURE CITED

- Achouak W, Conrod S, Cohen V, Heulin T. 2004. Phenotypic variation of *Pseudomonas brassicacearum* as a plant root-colonization strategy. *Mol. Plant-Microbe Interact.* 17:872–79
- Agaras BC, Scandiani M, Luque A, Fernández L, Farina F, et al. 2015. Quantification of the potential biocontrol and direct plant growth promotion abilities based on multiple biological traits distinguish different groups of *Pseudomonas* spp. isolates. *Biol. Control* 90:173–86
- Awasthi A, Singh M, Soni SK, Singh R, Kalra A. 2014. Biodiversity acts as insurance of productivity of bacterial communities under abiotic perturbations. *ISME J.* 8:2445–52
- Badri DV, Zolla G, Bakker MG, Manter DK, Vivanco JM. 2013. Potential impact of soil microbiomes on the leaf metabolome and on herbivore feeding behavior. *New Phytol.* 198:264–73
- Barea J-M, Pozo MJ, Azcón R, Azcón-Aguilar C. 2005. Microbial co-operation in the rhizosphere. *J. Exp. Bot.* 56:1761–78
- Becker J, Eisenhauer N, Scheu S, Jousset A. 2012. Increasing antagonistic interactions cause bacterial communities to collapse at high diversity. *Ecol. Lett.* 15:468–74
- Bell T, Lilley AK, Hector A, Schmid B, King L, Newman JA. 2009. A linear model method for biodiversity–ecosystem functioning experiments. *Am. Nat.* 174:836–49
- Bell T, Newman JA, Silverman BW, Turner SL, Lilley AK. 2005. The contribution of species richness and composition to bacterial services. *Nature* 436:1157–60
- Bender SF, Wagg C, van der Heijden MGA. 2016. An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. *Trends Ecol. Evol.* 31:440–52
- Berendsen RL, Pieterse CMJ, Bakker PAHM. 2012. The rhizosphere microbiome and plant health. *Trends Plant Sci.* 17:478–86
- Berendsen RL, Vismans G, Yu K, Song Y, de Jonge R, et al. 2018. Disease-induced assemblage of a plant-beneficial bacterial consortium. *ISME J.* 12:1496–507
- Boles BR, Thoendel M, Singh PK. 2004. Self-generated diversity produces “insurance effects” in biofilm communities. *PNAS* 101:16630–35
- Bronick CJ, Lal R. 2005. Soil structure and management: a review. *Geoderma* 124:3–22
- Brophy C, Dooley Á, Kirwan L, Finn JA, McDonnell J, et al. 2017. Biodiversity and ecosystem function: making sense of numerous species interactions in multi-species communities. *Ecology* 98:1771–78

- Calderón K, Spor A, Breuil M-C, Bru D, Bizouard F, et al. 2017. Effectiveness of ecological rescue for altered soil microbial communities and functions. *ISME J.* 11:272–83
- Carlson RP, Taffs RL. 2010. Molecular-level tradeoffs and metabolic adaptation to simultaneous stressors. *Curr. Opin. Biotechnol.* 21:670–76
- Chaparro JM, Badri DV, Vivanco JM. 2014. Rhizosphere microbiome assemblage is affected by plant development. *ISME J.* 8:790–803
- Connolly J, Bell T, Bolger T, Brophy C, Carnus T, et al. 2013. An improved model to predict the effects of changing biodiversity levels on ecosystem function. *J. Ecol.* 101:344–55
- Coyte KZ, Schluter J, Foster KR. 2015. The ecology of the microbiome: networks, competition, and stability. *Science* 350:663–66
- Dary M, Chamber-Pérez MA, Palomares AJ, Pajuelo E. 2010. “*In situ*” phytostabilisation of heavy metal polluted soils using *Lupinus luteus* inoculated with metal resistant plant-growth promoting rhizobacteria. *J. Hazard. Mater.* 177:323–30
- Degens BP, Sparling GP. 1995. Repeated wet-dry cycles do not accelerate the mineralization of organic C involved in the macro-aggregation of a sandy loam soil. *Plant Soil* 175:197–203
- Delgado-Baquerizo M, Maestre FT, Reich PB, Jeffries TC, Gaitan JJ, et al. 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nat. Commun.* 7:10541
- Dragoš A, Kiesewalter H, Martin M, Hsu C-Y, Hartmann R, et al. 2018. Division of labor during biofilm matrix production. *Curr. Biol.* 28:1903–13
- Driscoll WW, Pepper JW, Pierson LS, Pierson EA. 2011. Spontaneous Gac mutants of *Pseudomonas* biological control strains: cheaters or mutualists? *Appl. Environ. Microbiol.* 77:7227–35
- Dubuis C, Haas D. 2007. Cross-species GacA-controlled induction of antibiosis in pseudomonads. *Appl. Environ. Microbiol.* 73:650–54
- Dubuis C, Keel C, Haas D. 2007. Dialogues of root-colonizing biocontrol pseudomonads. *Eur. J. Plant Pathol.* 119:311–28
- Eisenhauer N, Schulz W, Scheu S, Jousset A. 2013. Niche dimensionality links biodiversity and invasibility of microbial communities. *Funct. Ecol.* 27:282–88
- Faust K, Raes J. 2012. Microbial interactions: from networks to models. *Nat. Rev. Microbiol.* 10:538
- Fiegna F, Moreno-Letelier A, Bell T, Barraclough TG. 2015. Evolution of species interactions determines microbial community productivity in new environments. *ISME J.* 9:1235–45
- Fierer N. 2017. Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* 15:579
- Freilich S, Kreimer A, Meilijson I, Gophna U, Sharan R, Ruppin E. 2010. The large-scale organization of the bacterial network of ecological co-occurrence interactions. *Nucleic Acids Res.* 38:3857–68
- Freilich S, Zarecki R, Eilam O, Segal ES, Henry CS, et al. 2011. Competitive and cooperative metabolic interactions in bacterial communities. *Nat. Commun.* 2:589
- Fu L, Penton CR, Ruan Y, Shen Z, Xue C, et al. 2017. Inducing the rhizosphere microbiome by biofertilizer application to suppress banana *Fusarium* wilt disease. *Soil Biol. Biochem.* 104:39–48
- Fussmann KE, Schwarzmüller F, Brose U, Jousset A, Rall BC. 2014. Ecological stability in response to warming. *Nat. Clim. Change* 4:206–10
- Gamfeldt L, Snäll T, Bagchi R, Jonsson M, Gustafsson L, et al. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* 4:1340
- Gravel D, Bell T, Barbera C, Bouvier T, Pommier T, et al. 2011. Experimental niche evolution alters the strength of the diversity–productivity relationship. *Nature* 469:89–92
- Griffiths BS, Ritz K, Wheatley R, Kuan HL, Boag B, et al. 2001. An examination of the biodiversity–ecosystem function relationship in arable soil microbial communities. *Soil Biol. Biochem.* 33:1713–22
- Hartmann M, Frey B, Mäder P, Widmer F. 2015. Distinct soil microbial diversity under long-term organic and conventional farming. *ISME J.* 9:1177–94
- Hautier Y, Isbell F, Borer ET, Seabloom EW, Harpole WS, et al. 2018. Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. *Nat. Ecol. Evol.* 2:50–56
- Hector A, Bagchi R. 2007. Biodiversity and ecosystem multifunctionality. *Nature* 448:188–90

- Hibbing ME, Fuqua C, Parsek MR, Peterson SB. 2010. Bacterial competition: surviving and thriving in the microbial jungle. *Nat. Rev. Microbiol.* 8:15–25
- Hillebrand H, Matthiessen B. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecol. Lett.* 12:1405–19
- Hol WHG, de Boer W, de Hollander M, Kuramae EE, Meisner A, van der Putten WH. 2015a. Context dependency and saturating effects of loss of rare soil microbes on plant productivity. *Front. Plant Sci.* 6:485
- Hol WHG, de Boer W, Termorshuizen AJ, Meyer KM, Schneider JHM, et al. 2010. Reduction of rare soil microbes modifies plant–herbivore interactions. *Ecol. Lett.* 13:292–301
- Hol WHG, Garbeva P, Hordijk C, Hundscheid MPJ, Gunnewiek PJA, et al. 2015b. Non-random species loss in bacterial communities reduces antifungal volatile production. *Ecology* 96:2042–48
- Hu J, Wei Z, Friman V-P, Gu S, Wang X, et al. 2016. Probiotic diversity enhances rhizosphere microbiome function and plant disease suppression. *mBio* 7:e01790–16
- Hu J, Wei Z, Weidner S, Friman V-P, Xu Y-C, et al. 2017. Probiotic *Pseudomonas* communities enhance plant growth and nutrient assimilation via diversity-mediated ecosystem functioning. *Soil Biol. Biochem.* 113:122–29
- Hunt HW, Wall DH. 2002. Modelling the effects of loss of soil biodiversity on ecosystem function. *Glob. Change Biol.* 8:33–50
- Hussain S, Siddique T, Saleem M, Arshad M, Khalid A. 2009. Impact of pesticides on soil microbial diversity, enzymes, and biochemical reactions. *Adv. Agron.* 102:159–200
- Irikiin Y, Nishiyama M, Otsuka S, Senoo K. 2006. Rhizobacterial community-level, sole carbon source utilization pattern affects the delay in the bacterial wilt of tomato grown in rhizobacterial community model system. *Appl. Soil Ecol.* 34:27–32
- Ji P, Wilson M. 2002. Assessment of the importance of similarity in carbon source utilization profiles between the biological control agent and the pathogen in biological control of bacterial speck of tomato. *Appl. Environ. Microbiol.* 68:4383–89
- Jiang L, Pu Z, Nemergut DR. 2008. On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. *Oikos* 117:488–93
- Jiang X, Zerfaß C, Feng S, Eichmann R, Asally M, et al. 2018. Impact of spatial organization on a novel auxotrophic interaction among soil microbes. *ISME J.* 12:1443–56
- Jousset A, Becker J, Chatterjee S, Karlovsky P, Scheu S, Eisenhauer N. 2014. Biodiversity and species identity shape the antifungal activity of bacterial communities. *Ecology* 95:1184–90
- Jousset A, Bienhold C, Chatzinotas A, Gallien L, Gobet A, et al. 2017. Where less may be more: how the rare biosphere pulls ecosystems strings. *ISME J.* 11:853–62
- Jousset A, Eisenhauer N, Materne E, Scheu S. 2013. Evolutionary history predicts the stability of cooperation in microbial communities. *Nat. Commun.* 4:2573
- Jousset A, Eisenhauer N, Merker M, Mouquet N, Scheu S. 2016. High functional diversity stimulates diversification in experimental microbial communities. *Sci. Adv.* 2:e1600124
- Jousset A, Schmid B, Scheu S, Eisenhauer N. 2011a. Genotypic richness and dissimilarity opposingly affect ecosystem functioning. *Ecol. Lett.* 14:537–45
- Jousset A, Schulz W, Scheu S, Eisenhauer N. 2011b. Intraspecific genotypic richness and relatedness predict the invasibility of microbial communities. *ISME J.* 5:1108–14
- Kiers ET, Denison RF. 2008. Sanctions, cooperation, and the stability of plant–rhizosphere mutualisms. *Annu. Rev. Ecol. Syst.* 39:215–36
- Kim W, Levy SB. 2008. Increased fitness of *Pseudomonas fluorescens* Pf0–1 leucine auxotrophs in soil. *Appl. Environ. Microbiol.* 74:3644–51
- Kinkel LL, Schlatter DC, Xiao K, Baines AD. 2014. Sympatric inhibition and niche differentiation suggest alternative coevolutionary trajectories among *Streptomyces*. *ISME J.* 8:249–56
- Koechler S, Farasin J, Cleiss-Arnold J, Arsène-Ploetze F. 2015. Toxic metal resistance in biofilms: diversity of microbial responses and their evolution. *Res. Microbiol.* 166:764–73
- Krause S, Le Roux X, Niklaus PA, Van Bodegom PM, Lennon JT, et al. 2014a. Trait-based approaches for understanding microbial biodiversity and ecosystem functioning. *Front. Microbiol.* 5:251

- Krause S, van Bodegom PM, Cornwell WK, Bodelier PLE. 2014b. Weak phylogenetic signal in physiological traits of methane-oxidizing bacteria. *J. Evol. Biol.* 27:1240–47
- Lawrence D, Fiegna F, Behrends V, Bundy JG, Phillimore AB, et al. 2012. Species interactions alter evolutionary responses to a novel environment. *PLOS Biol.* 10:e1001330
- Li M, Wei Z, Wang J, Jousset A, et al. 2019. Facilitation promotes invasions in plant-associated microbial communities. *Ecol. Lett.* 22:149–58
- Ling N, Zhu C, Xue C, Chen H, Duan Y, et al. 2016. Insight into how organic amendments can shape the soil microbiome in long-term field experiments as revealed by network analysis. *Soil Biol. Biochem.* 99:137–49
- Locey KJ, Fisk MC, Lennon JT. 2017. Microscale insight into microbial seed banks. *Front. Microbiol.* 7:2040
- Lori M, Symnaczik S, Mäder P, Deyn GD, Gättinger A. 2017. Organic farming enhances soil microbial abundance and activity—a meta-analysis and meta-regression. *PLOS ONE* 12:e0180442
- Lugtenberg B, Kamilova F. 2009. Plant-growth-promoting rhizobacteria. *Annu. Rev. Microbiol.* 63:541–56
- Lupatini M, Korthals GW, de Hollander M, Janssens TKS, Kuramae EE. 2017. Soil microbiome is more heterogeneous in organic than in conventional farming system. *Front. Microbiol.* 7:2064
- Meng L, Sun T, Li M, Saleem M, Zhang Q, Wang C. 2019. Soil-applied biochar increases microbial diversity and wheat plant performance under herbicide fomesafen stress. *Ecotox. Environ. Saf.* 171:75–83
- McDaniel MD, Tiemann LK, Grandy AS. 2014. Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. *Ecol. Appl.* 24:560–70
- Mehrabi Z, McMillan VE, Clark IM, Canning G, Hammond-Kosack KE, et al. 2016. *Pseudomonas* spp. diversity is negatively associated with suppression of the wheat take-all pathogen. *Sci. Rep.* 6:29905
- Mendes R, Kruijt M, de Bruijn I, Dekkers E, van der Voort M, et al. 2011. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science* 332:1097–100
- Messiha NAS, van Bruggen AHC, Franz E, Janse JD, Schoeman-Weerdesteijn ME, et al. 2009. Effects of soil type, management type and soil amendments on the survival of the potato brown rot bacterium *Ralstonia solanacearum*. *Appl. Soil Ecol.* 43:206–15
- Netzker T, Fischer J, Weber J, Mattern DJ, König CC, et al. 2015. Microbial communication leading to the activation of silent fungal secondary metabolite gene clusters. *Front. Microbiol.* 6:299
- Pang G, Cai F, Li R, Zhao Z, Li R, et al. 2017. *Trichoderma*-enriched organic fertilizer can mitigate microbiome degeneration of monocropped soil to maintain better plant growth. *Plant Soil* 416:181–92
- Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH. 2013a. Going back to the roots: the microbial ecology of the rhizosphere. *Nat. Rev. Microbiol.* 11:789–99
- Philippot L, Spor A, Hénault C, Bru D, Bizouard F, et al. 2013b. Loss in microbial diversity affects nitrogen cycling in soil. *ISME J.* 7:1609–19
- Pineda A, Kaplan I, Bezemer TM. 2017. Steering soil microbiomes to suppress aboveground insect pests. *Trends Plant Sci.* 22:770–78
- Prabhukarthikeyan R, Saravanakumar D, Raguchander T. 2014. Combination of endophytic *Bacillus* and *Beauveria* for the management of *Fusarium* wilt and fruit borer in tomato. *Pest Manag. Sci.* 70:1742–50
- Raaijmakers JM, Mazzola M. 2016. Soil immune responses. *Science* 352:1392–93
- Rabbi SMF, Daniel H, Lockwood PV, Macdonald C, Pereg L, et al. 2016. Physical soil architectural traits are functionally linked to carbon decomposition and bacterial diversity. *Sci. Rep.* 6:33012
- Ravanbakhsh M, Sasidharan R, Voesenek LACJ, Kowalchuk GA, Jousset A. 2017. ACC deaminase-producing rhizosphere bacteria modulate plant responses to flooding. *J. Ecol.* 105:979–86
- Reich PB, Tilman D, Isbell F, Mueller K, Hobbie SE, et al. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* 336:589–92
- Ren D, Madsen JS, Sørensen SJ, Burmølle M. 2015. High prevalence of biofilm synergy among bacterial soil isolates in cocultures indicates bacterial interspecific cooperation. *ISME J.* 9:81–89
- Rillig MC, Aguilar-Trigueros CA, Bergmann J, Verbruggen E, Veresoglou SD, Lehmann A. 2015. Plant root and mycorrhizal fungal traits for understanding soil aggregation. *New Phytol.* 205:1385–88
- Rolli E, Marasco R, Viganì G, Ettoumi B, Mapelli F, et al. 2015. Improved plant resistance to drought is promoted by the root-associated microbiome as a water stress-dependent trait. *Environ. Microbiol.* 17:316–31
- Saleem M, Arshad M, Hussain S, Bhatti AS. 2007. Perspective of plant growth promoting rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. *J. Ind. Microbiol. Biotechnol.* 34:635–48

- Saleem M, Fetzer I, Dormann CF, Harms H, Chatzinotas A. 2012. Predator richness increases the effect of prey diversity on prey yield. *Nat. Commun.* 3:1305
- Saleem M, Fetzer I, Harms H, Chatzinotas A. 2013. Diversity of protists and bacteria determines predation performance and stability. *ISME J.* 7:1912–21
- Saleem M, Fetzer I, Harms H, Chatzinotas A. 2016a. Trophic complexity in aqueous systems: bacterial species richness and protistan predation regulate dissolved organic carbon and dissolved total nitrogen removal. *Proc. R. Soc. B* 283:20152724
- Saleem M, Law AD, Moe LA. 2016b. *Nicotiana* roots recruit rare rhizosphere taxa as major root-inhabiting microbes. *Microb. Ecol.* 71:469–72
- Saleem M, Law AD, Sahib MR, Pervaiz ZH, Zhang Q. 2018. Impact of root system architecture on rhizosphere and root microbiome. *Rhizosphere* 6:47–51
- Saleem M, Meckes N, Pervaiz ZH, Traw MB. 2017. Microbial interactions in the phyllosphere increase plant performance under herbivore biotic stress. *Front. Microbiol.* 8:41
- Saleem M, Moe LA. 2014. Multitrophic microbial interactions for eco- and agro-biotechnological processes: theory and practice. *Trends Biotechnol.* 32:529–37
- Saleem M, Pervaiz ZH, Traw MB. 2015. Theories, mechanisms and patterns of microbiome species coexistence in an era of climate change. In *Microbiome Community Ecology: Fundamentals and Applications*, ed. M Saleem, pp. 13–53. Berlin: Springer
- Scherer-Lorenzen M. 2005. Biodiversity and ecosystem functioning: basic principles. In *Biodiversity: Structure and Function*, ed. W Barthlott, E Linsenmair, S Porembski, pp. 68–88. Oxford, UK: EOLSS
- Schindler DE, Armstrong JB, Reed TE. 2015. The portfolio concept in ecology and evolution. *Front. Ecol. Environ.* 13:257–63
- Schlatter D, Kinkel L, Thomashow L, Weller D, Paulitz T. 2017. Disease suppressive soils: new insights from the soil microbiome. *Phytopathology* 107:1284–97
- Seth EC, Taga ME. 2014. Nutrient cross-feeding in the microbial world. *Front. Microbiol.* 5:350
- Shoemaker WR, Locey KJ, Lennon JT. 2017. A macroecological theory of microbial biodiversity. *Nat. Ecol. Evol.* 1:0107
- Singh BK, Quince C, Macdonald CA, Khachane A, Thomas N, et al. 2014. Loss of microbial diversity in soils is coincident with reductions in some specialized functions. *Environ. Microbiol.* 16:2408–20
- Singh M, Awasthi A, Soni SK, Singh R, Verma RK, Kalra A. 2015. Complementarity among plant growth promoting traits in rhizospheric bacterial communities promotes plant growth. *Sci. Rep.* 5:15500
- Slade EM, Kirwan L, Bell T, Philipson CD, Lewis OT, Roslin T. 2017. The importance of species identity and interactions for multifunctionality depends on how ecosystem functions are valued. *Ecology* 98:2626–39
- Steinbauer MJ, Field R, Fernández-Palacios JM, Irl SDH, Otto R, et al. 2016. Biogeographic ranges do not support niche theory in radiating Canary Island plant clades. *Glob. Ecol. Biogeogr.* 25:792–804
- Tang J, Zhou S. 2011. The importance of niche differentiation for coexistence on large scales. *J. Theor. Biol.* 273:32–36
- Thijs S, Weyens N, Sillen W, Gkorezis P, Carleer R, Vangronsveld J. 2014. Potential for plant growth promotion by a consortium of stress-tolerant 2,4-dinitrotoluene-degrading bacteria: isolation and characterization of a military soil. *Microb. Biotechnol.* 7:294–306
- Tiemann LK, Grandy AS, Atkinson EE, Marin-Spiotta E, McDaniel MD. 2015. Crop rotational diversity enhances belowground communities and functions in an agroecosystem. *Ecol. Lett.* 18:761–71
- Tsoi R, Wu F, Zhang C, Bewick S, Karig D, You L. 2018. Metabolic division of labor in microbial systems. *PNAS* 115:2526–31
- Tyc O, van den Berg M, Gerards S, van Veen JA, Raaijmakers JM, et al. 2014. Impact of interspecific interactions on antimicrobial activity among soil bacteria. *Front. Microbiol.* 5:567
- Tyc O, Zwers H, de Boer W, Garbeva P. 2015. Volatiles in inter-specific bacterial interactions. *Front. Microbiol.* 6:1412
- van der Plas F, Manning P, Allan E, Scherer-Lorenzen M, Verheyen K, et al. 2016. Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. *Nat. Commun.* 7:11109
- van Elsas JD, Chiurazzi M, Mallon CA, Elhottová D, Křišťůfek V, Salles JF. 2012. Microbial diversity determines the invasion of soil by a bacterial pathogen. *PNAS* 109:1159–64

- Wagg C, Bender SF, Widmer F, van der Heijden MGA. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *PNAS* 111:5266–70
- Wagner MR, Lundberg DS, Coleman-Derr D, Tringe SG, Dangl JL, Mitchell-Olds T. 2014. Natural soil microbes alter flowering phenology and the intensity of selection on flowering time in a wild *Arabidopsis* relative. *Ecol. Lett.* 17:717–26
- Wei F, Hu X, Xu X. 2016. Dispersal of *Bacillus subtilis* and its effect on strawberry phyllosphere microbiota under open field and protection conditions. *Sci. Rep.* 6:22611
- Wei Z, Yang T, Friman V-P, Xu Y, Shen Q, Jousset A. 2015. Trophic network architecture of root-associated bacterial communities determines pathogen invasion and plant health. *Nat. Commun.* 6:8413
- Weidner S, Koller R, Latz E, Kowalchuk G, Bonkowski M, et al. 2015. Bacterial diversity amplifies nutrient-based plant-soil feedbacks. *Funct. Ecol.* 29:1341–49
- Weisser WW, Roscher C, Meyer ST, Ebeling A, Luo G, et al. 2017. Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: patterns, mechanisms, and open questions. *Basic Appl. Ecol.* 23:1–73
- Williams LJ, Paquette A, Cavender-Bares J, Messier C, Reich PB. 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nat. Ecol. Evol.* 1:0063
- Wittebolle L, Marzorati M, Clement L, Balloi A, Daffonchio D, et al. 2009. Initial community evenness favours functionality under selective stress. *Nature* 458:623–26
- Wood SA, Bradford MA, Gilbert JA, McGuire KL, Palm CA, et al. 2015. Agricultural intensification and the functional capacity of soil microbes on smallholder African farms. *J. Appl. Ecol.* 52:744–52
- Xiong W, Guo S, Jousset A, Zhao Q, Wu H, et al. 2017. Bio-fertilizer application induces soil suppressiveness against *Fusarium* wilt disease by reshaping the soil microbiome. *Soil Biol. Biochem.* 114:238–47
- Yachi S, Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *PNAS* 96:1463–68
- Yang T, Han G, Yang Q, Friman V-P, Gu S, et al. 2018. Resource stoichiometry shapes community invasion resistance via productivity-mediated species identity effects. *Proc. R. Soc. B* 285:20182035
- Yang T, Wei Z, Friman V-P, Xu Y, Shen Q, et al. 2017. Resource availability modulates biodiversity–invasion relationships by altering competitive interactions. *Environ. Microbiol.* 19:2984–91
- Yang W, Xu X, Li Y, Wang Y, Li M, et al. 2016. Rutin-mediated priming of plant resistance to three bacterial pathogens initiating the early SA signal pathway. *PLOS ONE* 11:e0146910
- Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD. 2010. Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *PNAS* 107:1443–46
- Zhang Q, Saleem M, Wang C. 2017. Probiotic strain *Stenotrophomonas acidaminiphila* BJI1 degrades and reduces chlorothalonil toxicity to soil enzymes, microbial communities and plant roots. *AMB Express* 7:227
- Zolla G, Badri DV, Bakker MG, Manter DK, Vivanco JM. 2013. Soil microbiomes vary in their ability to confer drought tolerance to *Arabidopsis*. *Appl. Soil Ecol.* 68:1–9





# Contents

|  |     |
|--|-----|
| <i>AREES</i> at 50: A Semicentennial Celebration<br><i>Douglas J. Futuyma</i> .....  | 1   |
| Cultural Evolution in Animals<br><i>Andrew Whiten</i> .....  | 27  |
| Somatic Mutation and Evolution in Plants<br><i>Daniel J. Schoen and Stewart T. Schultz</i> .....   | 49  |
| Beyond Reproductive Isolation: Demographic Controls<br>on the Speciation Process<br><i>Michael G. Harvey, Sonal Singhal, and Daniel L. Rabosky</i> .....   | 75  |
| An Integrative Framework for Understanding the Mechanisms<br>and Multigenerational Consequences of Transgenerational Plasticity<br><i>Alison M. Bell and Jennifer K. Hellmann</i> .....  | 97  |
| Origins and Assembly of Malesian Rainforests<br><i>Robert M. Kooyman, Robert J. Morley, Darren M. Crayn,<br/>Elizabeth M. Joyce, Maurizio Rossetto, J.W. Ferry Slik,<br/>Joeri S. Strijk, Tao Su, Jia-Yee S. Yap, and Peter Wilf</i> ..... | 119 |
| More Than the Sum of Its Parts: Microbiome Biodiversity as a Driver<br>of Plant Growth and Soil Health<br><i>Muhammad Saleem, Jie Hu, and Alexandre Jousset</i> .....  | 145 |
| Consequences of Multispecies Introductions on Island Ecosystems<br><i>James C. Russell and Christopher N. Kaiser-Bunbury</i> .....   | 169 |
| Importance of Pollinator-Mediated Interspecific Pollen Transfer for<br>Angiosperm Evolution<br><i>Juan Isaac Moreira-Hernández and Nathán Muchbala</i> .....   | 191 |
| Haploid Selection in “Diploid” Organisms<br><i>Simone Immler</i> .....   | 219 |
| Mycorrhizal Fungi as Mediators of Soil Organic Matter Dynamics<br><i>Serita D. Frey</i> .....  | 237 |

|  |     |
|--|-----|
| What Have Long-Term Field Studies Taught Us About Population Dynamics?<br><i>Beth A. Reinke, David A.W. Miller, and Fredric J. Janzen</i> .....  | 261 |
| History and Geography of Neotropical Tree Diversity<br><i>Christopher W. Dick and R. Toby Pennington</i> .....   | 279 |
| Climate Change in the Tropics: Ecological and Evolutionary Responses at Low Latitudes<br><i>Kimberly S. Sheldon</i> .....  | 303 |
| Experimental Studies of Evolution and Eco-Evo Dynamics in Guppies ( <i>Poecilia reticulata</i> )<br><i>David N. Reznick and Joseph Travis</i> .....  | 335 |
| The Invasion Hierarchy: Ecological and Evolutionary Consequences of Invasions in the Fossil Record<br><i>Alycia L. Stigall</i> .....   | 355 |
| Interactive Effects of Global Change on Forest Pest and Pathogen Dynamics<br><i>Allison B. Simler-Williamson, David M. Rizzo, and Richard C. Cobb</i> .....                                    | 381 |
| Phylogenetic Comparative Methods and the Evolution of Multivariate Phenotypes<br><i>Dean C. Adams and Michael L. Collyer</i> .....   | 405 |
| Spatial Population Genetics: It's About Time<br><i>Gideon S. Bradburd and Peter L. Ralph</i> .....   | 427 |
| Evolutionary and Ecological Consequences of Gut Microbial Communities<br><i>Nancy A. Moran, Howard Ochman, and Tobin J. Hammer</i> .....   | 451 |
| A Bird's-Eye View of Pollination: Biotic Interactions as Drivers of Adaptation and Community Change<br><i>Anton Pauw</i> .....   | 477 |
| Life Ascending: Mechanism and Process in Physiological Adaptation to High-Altitude Hypoxia<br><i>Jay F. Storz and Graham R. Scott</i> .....  | 503 |
| Evolution in the Anthropocene: Informing Governance and Policy<br><i>Peter Søgaard Jørgensen, Carl Folke, and Scott P. Carroll</i> .....   | 527 |
| Revisiting the Fate of Dead Leaves That Fall into Streams<br><i>Jane C. Marks</i> .....  | 547 |
| The Paradox Behind the Pattern of Rapid Adaptive Radiation: How Can the Speciation Process Sustain Itself Through an Early Burst?<br><i>Christopher H. Martin and Emilie J. Richards</i> ..... | 569 |

## Related Articles

From the *Annual Review of Animal Biosciences*, Volume 7 (2019)

Functional Annotation of Animal Genomes (FAANG): Current Achievements and Roadmap

*Elisabetta Giuffra, Christopher K. Tuggle, and The FAANG Consortium*

Mammalian Sex Chromosome Structure, Gene Content, and Function in Male Fertility

*Wan-Sheng Liu*

Multiple Facets of Marine Invertebrate Conservation Genomics

*Jose V. Lopez, Bisboy Kamel, Mónica Medina, Timothy Collins, and Iliana B. Baums*

The Role of Reproductive Technologies in Amphibian Conservation Breeding Programs

*Aimee J. Silla and Phillip G. Byrne*

Tigers of the World: Genomics and Conservation

*Shu-Jin Luo, Yue-Chen Liu, and Xiao Xu*

From the *Annual Review of Earth and Planetary Sciences*, Volume 47 (2019)

Seawater Chemistry Through Phanerozoic Time

*Alexandra V. Turchyn and Donald J. DePaolo*

Flood Basalts and Mass Extinctions

*Matthew E. Clapham and Paul R. Renne*

Soil Functions: Connecting Earth's Critical Zone

*Steven A. Banwart, Nikolaos P. Nikolaidis, Yong-Guan Zbu, Caroline L. Peacock, and Donald L. Sparks*

Marsh Processes and Their Response to Climate Change and Sea-Level Rise

*Duncan M. FitzGerald and Zoe Hughes*

The Mesozoic Biogeographic History of Gondwanan Terrestrial Vertebrates: Insights from Madagascar's Fossil Record

*David W. Krause, Joseph J.W. Sertich, Patrick M. O'Connor, Kristina Curry Rogers, and Raymond R. Rogers*

Droughts, Wildfires, and Forest Carbon Cycling: A Pantropical Synthesis  
*Paulo M. Brando, Lucas Paolucci, Caroline C. Ummenhofer, Elsa M. Ordway,  
Henrik Hartmann, Megan E. Cattau, Ludmila Rattis, Vincent Medjibe,  
Michael T. Coe, and Jennifer Balch*

From the *Annual Review of Environment and Resources*, Volume 44 (2019)

The State and Future of Antarctic Environments in a Global Context  
*Steven L. Chown and Cassandra M. Brooks*

Island Biodiversity in the Anthropocene  
*James C. Russell and Christoph Kueffer*

Mammal Conservation: Old Problems, New Perspectives, Transdisciplinarity,  
and the Coming of Age of Conservation Geopolitics  
*David W. Macdonald*

The State of the World's Mangrove Forests: Past, Present, and Future  
*Daniel A. Friess, Kerrylee Rogers, Catherine E. Lovelock, Ken W. Krauss,  
Stuart E. Hamilton, Shing Yip Lee, Richard Lucas, Jurgenne Primavera,  
Anusha Rajkaran, and Subua Shi*

Status, Institutions, and Prospects for Global Capture Fisheries  
*Christopher Costello and Daniel Ovando*

Illegal Wildlife Trade: Scale, Processes, and Governance  
*Michael 't Sas-Rolfes, Daniel W.S. Challender, Amy Hinsley, Diogo Veríssimo,  
and E. J. Milner-Gulland*

Ecotourism for Conservation?  
*Amanda L. Stronza, Carter A. Hunt, and Lee A. Fitzgerald*

Co-Producing Sustainability: Reordering the Governance of Science, Policy,  
and Practice  
*Carina Wylborn, Amber Datta, Jasper Montana, Melanie Ryan, Peat Leith,  
Brian Chaffin, Clark Miller, and Lorrae van Kerkhoff*

Social Synergies, Tradeoffs, and Equity in Marine Conservation Impacts  
*David A. Gill, Samantha H. Cheng, Louise Glew, Ernest Aigner, Nathan J. Bennett,  
and Michael B. Mascia*

From the *Annual Review of Entomology*, Volume 64 (2019)

The Ecology of Collective Behavior in Ants  
*Deborah M. Gordon*

Invasion Success and Management Strategies for Social *Vespula* Wasps  
*Philip J. Lester and Jacqueline R. Beggs*

Invasive Cereal Aphids of North America: Ecology and Pest Management  
*Michael J. Brewer, Frank B. Peairs, and Norman C. Elliott*

Movement and Demography of At-Risk Butterflies: Building Blocks for Conservation

*Cheryl B. Schultz, Nick M. Haddad, Erica H. Henry, and Elizabeth E. Crone*

Epigenetics in Insects: Genome Regulation and the Generation of Phenotypic Diversity

*Karl M. Glastad, Brendan G. Hunt, and Michael A.D. Goodisman*

Molecular Evolution of the Major Arthropod Chemoreceptor Gene Families

*Hugh M. Robertson*

Systematics, Phylogeny, and Evolution of Braconid Wasps: 30 Years of Progress

*Xue-xin Chen and Cornelis van Achterberg*

Water Beetles as Models in Ecology and Evolution

*David T. Bilton, Ignacio Ribera, and Andrew Edward Z. Short*

Phylogeography of Ticks (Acari: Ixodida)

*Lorenza Beati and Hans Klompen*

From the *Annual Review of Genetics*, Volume 53 (2019)

Crossover Interference: Shedding Light on the Evolution of Recombination

*Sarah P. Otto and Bret A. Payseur*

Evolutionary Ecology of *Wolbachia* Releases for Disease Control

*Perran A. Ross, Michael Turelli, and Ary A. Hoffmann*

Living with Two Genomes: Grafting and Its Implications for Plant Genome-to-Genome Interactions, Phenotypic Variation, and Evolution

*Brandon S. Gaut, Allison J. Miller, and Danelle K. Seymour*

Standard Deviations: The Biological Bases of Transmission Ratio Distortion

*Lila Fishman and Mariab McIntosh*

The Microbiome and Aging

*Bianca Bana and Filipe Cabreiro*

Zebrafish Pigment Pattern Formation: Insights into the Development and Evolution of Adult Form

*Larissa B. Patterson and David M. Parichy*

From the *Annual Review of Genomics and Human Genetics*, Volume 20 (2019)

The Genetics of Human Skin and Hair Pigmentation

*William J. Pavan and Richard A. Sturm*

Measuring Clonal Evolution in Cancer with Genomics

*Marc J. Williams, Andrea Sottoriva, and Trevor A. Graham*

The Causes and Consequences of Genetic Interactions (Epistasis)

*Júlia Domingo, Pablo Baeza-Centurion, and Ben Lebner*

Thinking About the Evolution of Complex Traits in the Era of Genome-Wide Association Studies

*Guy Sella and Nicholas H. Barton*

From the *Annual Review of Marine Science*, Volume 11 (2019)

Planktonic Marine Archaea

*Alyson E. Santoro, R. Alexander Richter, and Christopher L. Dupont*

Arctic and Antarctic Sea Ice Change: Contrasts, Commonalities, and Causes

*Ted Maksym*

Biologically Generated Mixing in the Ocean

*Eric Kunze*

Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience?

*John F. Bruno, Isabelle M. Côté, and Lauren T. Toth*

Marine Metazoan Modern Mass Extinction: Improving Predictions by Integrating Fossil, Modern, and Physiological Data

*Piero Calosi, Hollie M. Putnam, Richard J. Twitchett, and Fanny Vermandele*

From the *Annual Review of Microbiology*, Volume 73 (2019)

Ecology and Evolution of Plant Microbiomes

*Viviane Cordovez, Francisco Dini-Andreote, Víctor J. Carrión, and Jos M. Raaijmakers*

Algal Sex Determination and the Evolution of Anisogamy

*James Umen and Susana Coelbo*

The Ultimate Guide to Bacterial Swarming: An Experimental Model to Study the Evolution of Cooperative Behavior

*Jinyuan Yan, Hilary Monaco, and Joao B. Xavier*

Biogeography of the Oral Microbiome: The Site-Specialist Hypothesis

*Jessica L. Mark Welch, Floyd E. Dewhirst, and Gary G. Borisy*

Diversity, Genomics, and Distribution of Phytoplankton-Cyanobacterium Single-Cell Symbiotic Associations

*Rachel A. Foster and Jonathan P. Zehr*

Paleomicrobiology: Diagnosis and Evolution of Ancient Pathogens

*Kirsten I. Bos, Denise Kühnert, Alexander Herbig, Luis Roger Esquivel-Gomez, Aida Andrades Valtueña, Rodrigo Barquera, Karen Giffin, Aditya Kumar Lankapalli, Elizabeth A. Nelson, Susanna Sabin, Maria A. Spyrou, and Johannes Krause*

From the *Annual Review of Plant Biology*, Volume 70 (2019)

Molecular Interactions Between Plants and Insect Herbivores

*Matthias Erb and Philippe Reymond*

A Molecular View of Plant Local Adaptation: Incorporating Stress-Response Networks

*Acer VanWallendael, Ali Soltani, Nathan C. Emery, Murilo M. Peixoto, Jason Olsen, and David B. Lowry*

Comparative and Functional Algal Genomics

*Crysten E. Blaby-Haas and Sabeeha S. Merchant*

CRISPR/Cas Genome Editing and Precision Plant Breeding in Agriculture

*Kunling Chen, Yanpeng Wang, Rui Zhang, Huawei Zhang, and Caixia Gao*

Risk Assessment and Regulation of Plants Modified by Modern Biotechniques: Current Status and Future Challenges

*Joachim Schiemann, Antje Dietz-Pfeilstetter, Frank Hartung, Christian Kohl, Jörg Romeis, and Thorben Sprink*

From the *Annual Review of Phytopathology*, Volume 57 (2019)

Revisiting the Concept of Host Range of Plant Pathogens

*Cindy E. Morris and Benoît Moury*

Durability of Quantitative Resistance in Crops: Greater Than We Know?

*Christina Cowger and James K.M. Brown*

Molecular Dialog Between Parasitic Plants and Their Hosts

*Christopher R. Clarke, Michael P. Timko, John I. Yoder, Michael J. Axtell, and James H. Westwood*

Ecology and Evolution of the Sudden Oak Death Pathogen *Phytophthora ramorum*

*Niklaus J. Grünwald, Jared M. LeBoldus, and Richard C. Hamelin*

Understanding Adaptation, Coevolution, Host Specialization, and Mating System in Castrating Anther-Smut Fungi by Combining Population and Comparative Genomics

*Fanny E. Hartmann, Ricardo C. Rodríguez de la Vega, Fantin Carpentier, Pierre Gladieux, Amandine Cornille, Michael E. Hood, and Tatiana Giraud*

Surviving in a Hostile World: Plant Strategies to Resist Pests and Diseases

*Samuel W. Wilkinson, Melissa H. Magerøy, Ana López Sánchez, Lisa M. Smith, Leonardo Furci, T.E. Anne Cotton, Paal Krokene, and Jurriaan Ton*