



Beneficial microbes ameliorate abiotic and biotic sources of stress on plants

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Abstract

1. Global climate change and shifting land-use are increasing plant stress due to abiotic factors such as drought, heat, salinity and cold, as well as via the intensification of biotic stressors such as herbivores and pathogens. The ability of plants to tolerate such stresses is modulated by the bacteria and fungi that live on or inside of plant tissues and comprise the plant microbiome. However, the impacts of diverse classes of beneficial members of the microbiome and the contrasting stresses that impact plants are most commonly studied independently of each other.
2. Our meta-analysis of 288 experiments across 89 studies moves beyond previous studies in that we simultaneously compare the roles of bacterial versus fungal microbiome members that live within plant tissues and colonize plant surfaces in ameliorating biotic versus abiotic sources of plant stress.
3. The magnitude of microbial stress amelioration can be measured as the greater proportional impact of beneficial microbes on plant performance in more stressful environments. In the plant experiments we examine, the magnitude of microbial stress amelioration is substantial: it is 23% of the effect size of the typical impact of stress and 56% of the effect size of beneficial microbiome members in the absence of stress.
4. The amount of benefit microbiome members confer to plants differs among classes of microbes, depending on whether plants are grown in stressful or non-stressful environments. In the absence of stress, beneficial bacteria tend to confer greater plant benefits than do fungi. However, symbiotic fungi, especially arbuscular mycorrhizal fungi, more strongly ameliorate plant stress than do bacteria. In particular, beneficial microbes ameliorate salinity, foliar herbivory and fungal pathogen stress.
5. These results highlight the fact that the impacts of beneficial and antagonistic components of the microbiome on plant performance depend on biotic and abiotic environmental contexts. Furthermore, beneficial microbes are especially critical for plant health in stressful environments and thus present opportunities to mitigate negative consequences of global change.

KEYWORDS

abiotic stress, biotic stress, context-dependence, global change, meta-analysis, microbiome, plant–microbe interactions, symbiosis

1 | INTRODUCTION

Global climate change, shifting land-use and the intensification of agriculture are increasing plant stress via abiotic factors such as drought, heat, salinity and cold, as well as via the intensification of biotic stressors such as herbivores and pathogens (Isaac-Renton et al., 2018; Lesk, Coffel, D'Amato, Dodds, & Horton, 2017; Neumann, Mues, Moreno, Hasenauer, & Seidl, 2017; Reyer et al., 2013; Seidl et al., 2017; Zhang, Li, & Zhu, 2018). The human population will approach 9.7 billion in 2050 and to achieve the required 1.7-fold increased crop yields (Foley et al., 2011; Tilman, Balzer, Hill, & Befort, 2011; Tilman, Cassman, Matson, Naylor, & Polasky, 2002) on soils of which 69% are moderately to highly degraded (FAO, 2011), we will need to increasingly rely upon marginal lands, which intensify plant stress (Zhang et al., 2018). Components of the plant microbiome, the bacteria and fungi that live on or inside of plant tissues, substantially impact plant performance (Bulgarelli, Schlaeppi, Spaepen, van Themaat, & Schulze-Lefert, 2013; Friesen et al., 2011) and can mitigate the impacts of stress (Kivlin, Emery, & Rudgers, 2010). A frontier in the evolutionary ecology of the microbiome is to identify key beneficial and antagonistic microbes and to understand the magnitude and generality of their main and interactive effects on plant performance across contrasting environments (Busby et al., 2017). We lack an integrated picture of the patterns and magnitudes of these

complex microbial interactions because the impacts of beneficial microbes and stresses on plants are typically studied independently.

Three hypotheses predict the pattern of plant stress amelioration by microbes (Figure 1). The additive model predicts that symbionts confer the same benefits under stressful and non-stressful conditions because the benefits they provide to a plant have similar contributions to plant performance across environments (Larimer, Bever, & Clay, 2018). Here, symbionts serve similar ecological roles and could have similar evolutionary dynamics across environments. Under the positive synergy model, symbionts confer benefits that have a greater contribution to plant performance in more stressful conditions. This could occur if the benefits symbionts provide, such as phosphorous from arbuscular mycorrhizal fungi (AMF) or nitrogen from rhizobium bacteria, are more critical to plant performance under stressful conditions or if microbes modulate plant pathways that only impact performance under stress (Porter & Simms, 2014; Saikkonen, Saari, & Helander, 2010; Thrall, Hochberg, Burdon, & Bever, 2007). Under the negative synergy model, beneficial symbionts play a less important role under stressful conditions. This could occur if stress reduces plants' ability to benefit from symbionts or reduces symbionts' ability to provide resources (Zahran, 1999). Under positive and negative synergy, the impacts of symbionts on plant performance differ across environments and thus symbionts would serve different ecological roles and could have different evolutionary dynamics across environments.

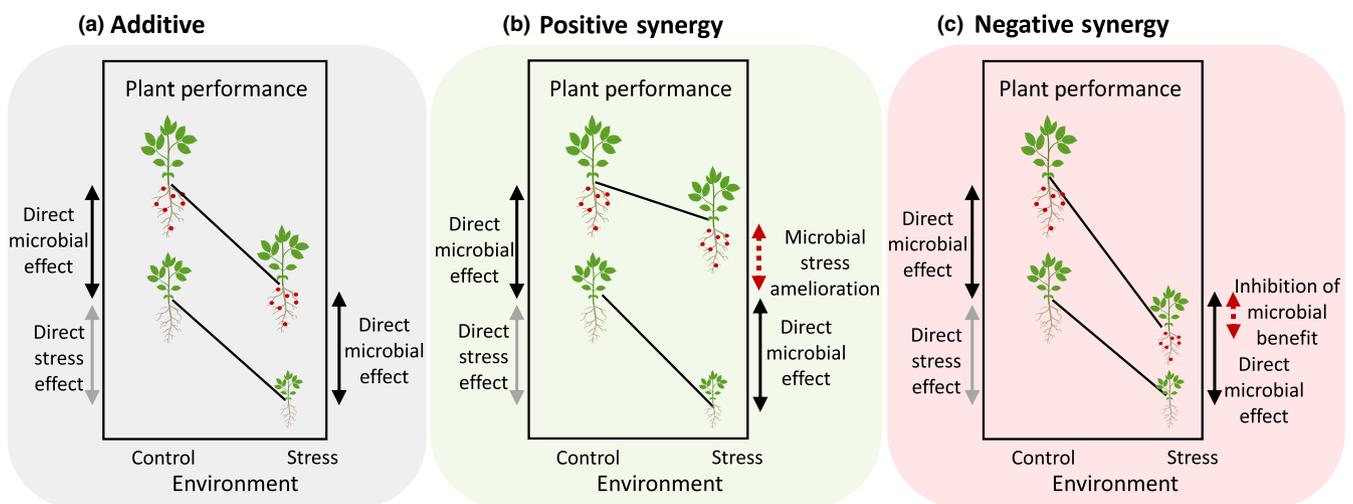


FIGURE 1 Possible models of the impact of beneficial symbiotic microbes on plant stress. Experimental manipulation of microbial inoculation factorially with stress treatment is required to estimate the degree to which microbes ameliorate the detrimental effect of stress on plant growth and yield. (a) *Additive Model*: Symbionts confer the same benefits under stressful and non-stressful conditions. (b) *Positive Synergy Model*: Symbionts confer benefits that ameliorate plant stress because they have a greater contribution to plant performance in more stressful conditions. (c) *Negative Synergy Model*: Beneficial symbionts play a less important role under stressful conditions; stress may inhibit the benefits of microbes for plants

Biotic and abiotic stress impose fundamentally different challenges for plants that could result in contrasting patterns of amelioration by beneficial microbes. Under biotic stress, plants interact simultaneously with antagonistic and beneficial biota in a complex balancing act. Plants under biotic stress could experience a larger benefit from symbionts (positive synergy) if the resources provided by microbes are more critical for plants burdened with the costs of enemy defence, or if the symbionts confer enemy defence and thus improve plant health only with enemies present (Mayerhofer, Kernaghan, & Harper, 2007; Omacini, Semmartin, Pérez, & Gundel, 2012; Saikkonen, Lehtonen, Helander, & Koricheva, 2006; Saikkonen et al., 2010). Positive synergy could also result from priming, which occurs when microbes induce a physiological state of super-activation of defences against environmental challenges (Jung, Martinez-Medina, Lopez-Raez, & Pozo, 2012; Martinez-Medina et al., 2016). On the other hand, pathogen defence can trade-off with symbiont benefits, resulting in negative synergy whereby plants under greater biotic stress benefit less from mutualistic microbes. This trade-off could result when plants regulate antagonists and beneficials via shared molecular pathways (Cao, Halane, Gassmann, & Stacey, 2017; Chen et al., 2017). For example inactivation of the plant gene *RAM2* leads to resistance to oomycete pathogens but this trades off with the ability to form mycorrhizal symbioses (Gobbato et al., 2013; Wang et al., 2012), and pathogenic nematode resistance trades off with the ability of legumes to nodulate with nitrogen fixing rhizobium bacteria (Wood, Pilkington, Vaidya, Biel, & Stinchcombe, 2018). Furthermore, resources conferred by symbionts can alter plant nutritional quality and defence allocation to leave plants more vulnerable to enemies (Godschalx, Schädler, Trisel, Balkan, & Ballhorn, 2015; Simonsen & Stinchcombe, 2014).

Under abiotic stress, plants must cope with physiological challenges while supporting mutualistic symbionts. Under abiotic stress plants could benefit more from symbionts (positive synergy), if resources provided by microbes are more critical for plants coping with harsh conditions, which can require a large proportion of a plant's resources (Kaschuk, Kuyper, Leffelaar, Hungria, & Giller, 2009). On the other hand, abiotic stress could reduce the benefits plants receive from symbionts (negative synergy). Plants cope with abiotic stress via complex multicomponent signalling pathways to restore cellular homeostasis and promote survival (Choudhury, Rivero, Blumwald, & Mittler, 2017; Golladack, Li, Mohan, & Probst, 2014), leaving fewer plant resources to allocate to beneficial symbionts (Hoeksema et al., 2019; Porter & Simms, 2014; Thrall et al., 2007). Abiotic stress that limits carbon acquisition could also reduce plant resources available to exchange with microbial symbionts (Lau et al., 2012; Taylor & Menge, 2018), though AMF and rhizobia can stimulate plant photosynthetic rates and compensate for their carbon costs (Kaschuk et al., 2009). Furthermore, associating with beneficial microbes can leave the host more vulnerable to stress because microbes that spur early growth can leave plants vulnerable to long-term drought stress (Ulrich et al., 2019) and abiotic stress can reduce the ability

of symbionts to provide benefits to plants (Manzoni, Schimel, & Porporato, 2012; van der Heyde, Ohsowski, Abbott, & Hart, 2017).

Previous meta-analyses reveal that both biotic and abiotic factors modulate the impacts of beneficial symbionts on plants. Plant functional group, phylogenetic history and the biological complexity of microbial inocula are important drivers of plant benefit from fungal symbionts (Hoeksema et al., 2018, 2019). Both bacterial and fungal endophytes mitigate drought, nitrogen deficiency and salinity stresses (Rho et al., 2018). Fungal symbionts can ameliorate drought stress (Jayne & Quigley, 2014; Kivlin et al., 2013; Mayerhofer et al., 2013; Worchel, Giauque, & Kivlin, 2013), and impact stomatal conductance more under drought (Augé, Toler, & Saxton, 2015). Diverse mutualistic beneficial microbes can ameliorate biotic stress (Morris et al., 2007) and symbiotic fungi are particularly important (Larimer et al., 2018)—they alter the impact of herbivores (Borowicz, 2013; Koricheva, Gange, & Jones, 2009) and reduce fungal pathogen stress but exacerbate nematode stress (Borowicz, 2001). Furthermore, the interactive impacts of multiple classes of plant enemies can depend on environmental conditions (Hauser, Christensen, Heimes, & Kiær, 2013).

Our meta-analysis is novel in that we compare the roles of bacteria versus fungi living within plant tissues and colonizing plant surfaces in ameliorating biotic versus abiotic plant stresses. We use the log response ratio (Hedges, Gurevitch, & Curtis, 1999) as a measure of effect size, to quantitatively integrate results from 89 studies comprising 288 experiments to ask, (a) Which of the three hypotheses for the interaction between beneficial microbial symbionts and plant stress are supported? Next, we compare different classes of players in the microbiome on different forms of stress by asking, (b) Do bacteria and fungi differ in their impacts on the outcomes of abiotic or biotic plant stress? We consider the effects of modifying variables, including (i) subclasses of microbes and stressors, (ii) co-evolutionary history (as captured by plant domestication) and (iii) biotic complexity (as captured by the potential impact of experimental protocols on the background microbial communities). Finally, to compare the effect size of microbial stress amelioration in this study, we ask, (c) What are the magnitudes of the direct effects of beneficial microbes and stress on plant performance?

2 | MATERIALS AND METHODS

2.1 | Data compilation

We compiled data from manuscripts in which bacteria or fungi with known plant growth-promoting properties are inoculated onto plants factorially with biotic or abiotic stress, resulting in a dataset containing 288 experiments across 89 studies (Table 1; Supporting Information S2; Friesen et al., 2019). We obtained 66 relevant studies included in related meta-analyses (Larimer et al., 2018; Morris et al., 2007; Worchel et al., 2013). To sample additional studies, we used search strings in ISI Web of Science: plant abiotic endo* [775], plant abiotic rhiz* [405], plant abiotic fung* [979], plant abiotic bact* [749], plant pathogen* rhizosphere [1595], plant pathogen*

Microbe	Epiphytic bacteria	Endophytic fungi	Endophytic bacteria	EMF	Combined AMF, EMF	AMF
Stress						
Salinity	16	1	8	0	1	2
Oomycete pathogen	1	0	4	0	0	4
Herbivory-nematode	0	4	0	0	0	24
Herbivory-foliar	0	0	0	0	0	6
Heavy metal	4	1	0	0	0	0
Fungal pathogen	53	0	46	6	0	18
Drought	1	23	0	0	0	57
Cold	8	0	0	0	0	0

Abbreviations: AMF, arbuscular mycorrhizal fungi; EMF, ectomycorrhizal fungi.

endophyt* [1060], PGP* plant stress [292]. The order of these studies was randomized and we skimmed title and abstract for 1,194 of these to add 29 additional studies.

We accepted studies that measured plant performance as: above-ground dry biomass, above-ground fresh weight, total biomass, total fresh weight, root biomass, root fresh weight, survival, seed number, fruit number and leaf number. The microbe being manipulated was bacterial or fungal and we designated microbes inhabiting the interior of a plant's tissue endophytes and designated mycorrhizal fungi separate from other endophytic fungi. We recorded whether plants were monocots, dicots or multicotyledonous, type of photosynthesis (C3 or C4), growth conditions (greenhouse, growth chamber or field), daylength, and whether plants were wild or domesticated. We recorded the biotic complexity of the background soil microbial community as (a) whole field soil in the field, (b) whole field soil or potting soil with soil microbial wash in pots, (c) sterilized field soil or potting soil passively colonized by microbes during the experiment and (d) sterile. We required that studies contain means, a measure of variance and sample size for each treatment combination of the full factorial of microbe by stress.

2.2 | Data analysis

We used the METAFOR version 2.0-0 package in R version 3.5.0 (R Core Team, 2017) which allowed "study" to be treated as a random effect. For plant growth response to microbial inoculation in the absence of stress, we calculated the log response ratio (L_m), standard deviation (SD_m) and degrees of freedom (DF_m).

$$L_m = \log \frac{\bar{m}}{\bar{c}},$$

$$SD_{L_m} = \frac{SD_m^2}{N_m \bar{m}^2} + \frac{SD_c^2}{N_c \bar{c}^2},$$

$$DF_m = N_m + N_c,$$

where \bar{m} is the mean value of performance for plants inoculated with beneficial microbes in the absence of stress, \bar{c} the mean value of

TABLE 1 Number of experiments that investigate the six classes of beneficial microbes for each of the abiotic and biotic stresses examined in the meta-analysis. In total there are 288 experiments across 89 studies

performance for uninoculated control plants in the absence of stress and N is the number of replicates in a treatment combination.

Similarly, for plant growth response to stress in the absence of microbes, we calculated the log response ratio (L_s), standard deviation (SD_s) and degrees of freedom (DF_s).

$$L_s = \log \frac{\bar{s}}{\bar{c}},$$

$$SD_{L_s} = \frac{SD_s^2}{N_s \bar{s}^2} + \frac{SD_c^2}{N_c \bar{c}^2},$$

$$DF_s = N_s + N_c,$$

where \bar{s} is the mean value of performance for uninoculated plants subject to stress.

Finally, we calculated the effect of microbial stress amelioration by considering the difference between stress impacts on uninoculated plants versus stress impacts on inoculated plants. Microbial amelioration was calculated as the log response ratio (L_a), standard deviation (SD_a) and degrees of freedom (DF_a).

$$L_a = \log \frac{\bar{i}}{\bar{m}} - \log \frac{\bar{s}}{\bar{c}},$$

$$SD_a = \frac{SD_m^2}{N_m \bar{m}^2} + \frac{SD_s^2}{N_s \bar{s}^2} + \frac{SD_c^2}{N_c \bar{c}^2} + \frac{SD_i^2}{N_i \bar{i}^2},$$

$$DF_a = N_m + N_s + N_c + N_i,$$

where \bar{i} is the mean value of performance for inoculated plants in the presence of stress. Our metric of microbial stress amelioration takes into account beneficial direct effects of microbes on plant performance by calculating what is effectively an interaction between microbial inoculation and stress treatment, namely the degree of non-additivity between microbes and stress similar to the interaction term in Morris et al. (2007). Positive values of amelioration indicate microbes ameliorate growth decreases due to stress in addition to the stress-independent beneficial effects they may have on plants. This stress amelioration metric allows us to test our hypothesis that

microbes ameliorate stress under models of positive synergy (positive values), additivity (zero) or negative synergy (negative values).

The significance of fixed-effect model terms and their interactions was assessed using the metafor function `rma.mv` including study as a random effect and allowing the model to fit an intercept term. Treatment combination pooled mean effects and confidence intervals were calculated using `rma.mv` without an intercept term and a fail-safe number was calculated for single factor tests (Rosenthal, 1979). Post-hoc Tukey tests of different treatment pooled effect sizes were conducted with the `multcomp` 1.4-8 function `glht` (see Supporting Information S1).

3 | RESULTS

3.1 | Beneficial microbes ameliorate plant stress

Overall, beneficial microbes ameliorate stress (pooled mean effect = 0.1158, $SE = 0.0384$, $p = .0026$, fail-safe number [fsn] = 42,627; Figure S1c), supporting positive synergy in the overall interaction between microbial symbionts and stress. The overall effect size of stress amelioration was 23% of the effect size of stress and 56% of the effect size of microbes in the absence of stress.

3.2 | Bacterial and fungal amelioration of abiotic and biotic stress

Fungi more strongly ameliorate stress than do bacteria ($p < .0001$) and bacterial and fungal stress amelioration is different for abiotic versus biotic stress ($p = .0007$; Table 2). Bacteria do not ameliorate stress overall (pooled mean effect = 0.0156, $SE = 0.0414$, $p = .7065$), whereas fungi do ameliorate stress (pooled mean effect = 0.1737, $SE = 0.0408$, $p < .0001$; Figure 2). Within both abiotic and biotic stress, fungi have a stronger stress amelioration effect than bacteria (Tukey test $p < .001$ for both comparisons; Figure 2). The difference between fungal and bacterial stress amelioration is greater under abiotic stress (Figure 3), and there is no difference within either bacteria or fungi for amelioration of abiotic versus biotic stress.

We further categorized type of microbe and stress to assess variation in microbial stress amelioration. AMF are the most

effective at ameliorating stress (pooled mean effect = 0.2216, $SE = 0.0450$, $p < .0001$, Figure 4a) and endophytic bacteria are marginally greater than zero (pooled mean effect = 0.0858, $SE = 0.0454$, $p = .0589$; Figure 4a). Microbes are effective at ameliorating fungal pathogens (pooled mean effect = 0.1949, $SE = 0.0616$, $p = .0016$), salinity (pooled mean effect = 0.2027, $SE = 0.0737$, $p = .0059$) and foliar herbivory (pooled mean effect = 0.5412, $SE = 0.2311$, $p = .0192$). Microbes make oomycete pathogen stress worse (pooled mean effect = -0.1917 , $SE = 0.0729$,

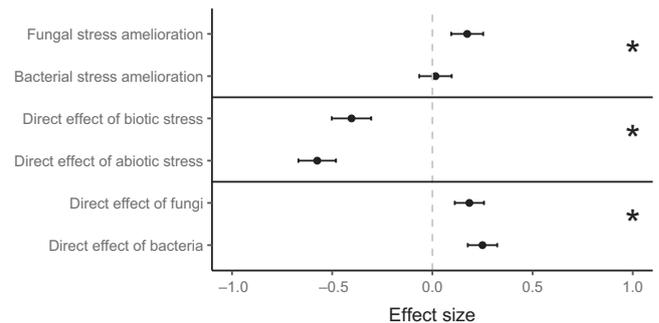


FIGURE 2 Influence of the type of microbe and type of stress on both the direct effects of microbes and stress and the strength of microbial stress amelioration. Effect sizes are standardized as the log of the response ratio and can thus be compared to one another. *Each of the pairs of points represent significant model terms

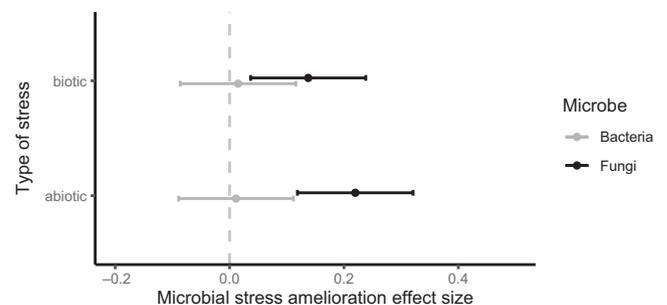


FIGURE 3 Interaction between type of microbe and type of stress on the strength of microbial stress amelioration. Fungi show greater amelioration of plant stress than do bacteria, and this difference is larger for abiotic stress. Effect sizes are standardized as the log of the response ratio and can thus be compared to one another

TABLE 2 Overall impact of microbe type (fungi vs. bacteria) and type of stress (biotic vs. abiotic) on plant stress amelioration. The significance of fixed-effect model terms and their interactions including study as a random effect and allowing the model to fit an intercept term

Factor	Estimate	SE	Z-value	p-value	CI lower	CI upper
Intercept	0.0112	0.0512	0.2193	.8264	-0.0891	0.1116
Microbe type	0.2085	0.0194	10.7368	<.0001	0.1704	0.2466
Stress type	0.0035	0.0597	0.0589	.953	-0.1135	0.1205
Microbe × Stress	-0.0858	0.0253	-3.3926	.0007	-0.1353	-0.0362

Bold indicates significant p -values.

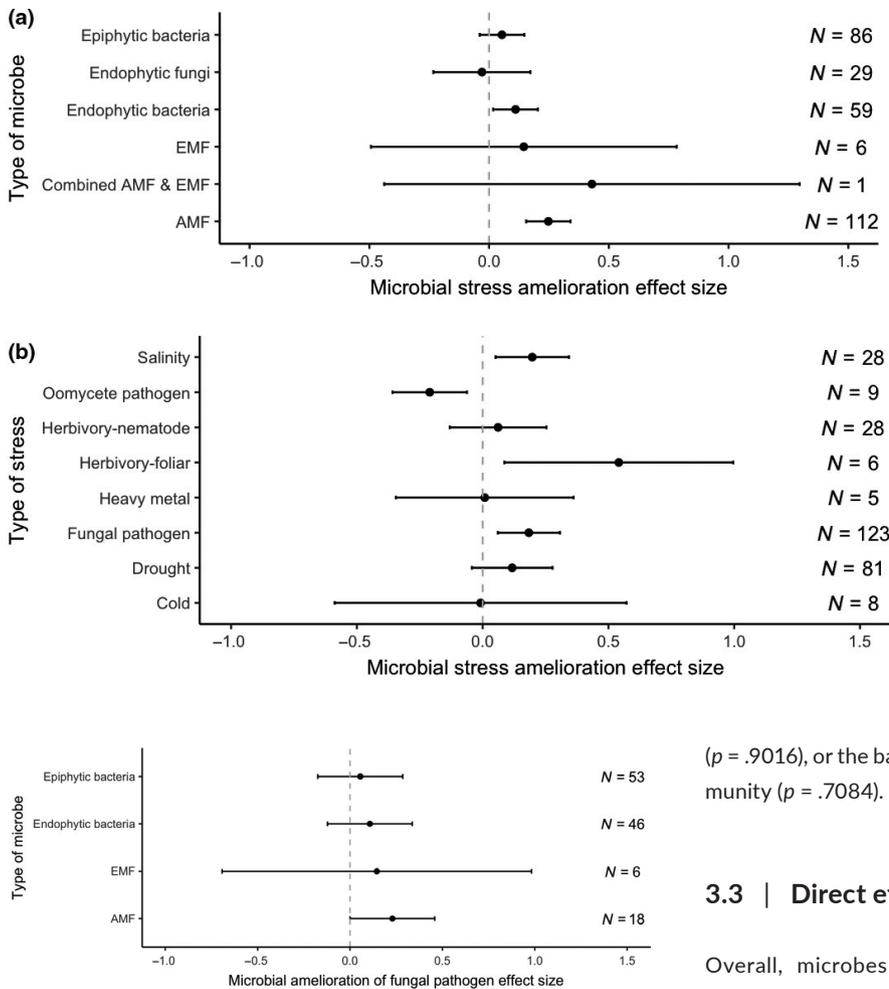


FIGURE 5 Fungal pathogens are ameliorated more by arbuscular mycorrhizal fungi than by bacteria. Effect sizes are standardized as the log of the response ratio and can thus be compared to one another

$p = .0086$; Figure 4b); this is the sole case of negative synergy that we observe.

Due to low sample sizes for some subsets of the data (Table 1), we further analysed only two well sampled subsets of our dataset. For drought, we dropped the one epiphytic bacterial study and found that AMF and endophytic fungi provide indistinguishable drought stress amelioration ($p = .7420$). The type of microbe affects fungal pathogen stress ($p < .0001$). Only AMF ameliorate fungal pathogen stress (pooled mean effect = 0.2293, $SE = 0.1169$, $p = .0498$; Figure 5) and the effect of AMF is higher than both endophytic bacteria and epiphytic bacteria (Tukey test, $p < 1e-07$).

Finally, we considered whether other moderators impacted microbial stress amelioration. Dicotyledonous hosts have more microbial stress amelioration than monocots (Tukey test, $p = .0191$; dicot pooled mean effect = 0.2067, $SE = 0.0513$, $p < .0001$, $N = 88$; monocot pooled mean effect = 0.0082, $SE = 0.0551$, $p = .8824$, $N = 194$). There is no effect of daylength ($p = .1529$), type of photosynthesis ($p > .7038$), whether the study occurs in a growth chamber, greenhouse, or field ($p > .6517$), whether the plant is wild or domesticated

FIGURE 4 Mean amelioration by different types of microbes and stressors. (a) Microbial stress amelioration effect size for different classes of beneficial microbes. (b) Microbial stress amelioration effect size for different types of abiotic and biotic stresses. Effect sizes are standardized as the log of the response ratio and can thus be compared to one another. Numbers on the right indicate the number of experiments in the meta-analytic dataset that examined particular microbes or stresses

($p = .9016$), or the background biotic complexity of the microbial community ($p = .7084$).

3.3 | Direct effects of microbes and stress on plants

Overall, microbes are beneficial for plants (pooled mean effect = 0.2051, $SE = 0.0376$, $p < .0001$, $fsn = 882,838$; Figure S1a). Both bacteria and fungi are beneficial (bacteria pooled mean effect = 0.2500, $SE = 0.0376$, $p < .0001$; fungi pooled mean effect = 0.1846, $SE = 0.0373$, $p < .0001$; Figure 2), even if rhizobia are excluded. Bacteria provide greater benefit to plants than fungi in the absence of stress (microbe type mean effect = -0.0654 , $SE = 0.0077$, $p < .0001$; Figure 2), even if rhizobia are excluded. Studies investigating abiotic and biotic stress do not differ in the effect of microbial inoculation ($p = .1821$). Overall, stress is detrimental to plant performance (pooled mean effect = -0.5008 , $SE = 0.0442$, $p < .0001$, $fsn = 1,735,591$; Figure S1b). Both abiotic and biotic stress are detrimental (abiotic pooled mean effect = -0.5748 , $SE = 0.0479$, $p < .0001$; biotic pooled mean effect = -0.4036 , $SE = 0.0503$, $p < .0001$; Figure 2) but abiotic stress is more detrimental than biotic stress ($p < .0001$). The effect of stress treatment does not differ among experiments investigating bacteria or fungi ($p = .8125$).

4 | DISCUSSION

We find beneficial microbes contribute to plant health more strongly in stressful environments, ameliorating the negative impacts of stress on plant health, consistent with the positive synergy model (Figure 1). The magnitude of microbial stress

amelioration is substantial—27% of the effect size of the typical impact of stress and 66% of the effect size of beneficial microbes in the absence of stress. Classes of microbes differ in the amount of benefit conferred to plants. In the absence of stress, beneficial bacteria, including plant growth promoting strains from *Bacillus*, *Pseudomonas*, *Achromobacter*, *Rhizobium* and other genera, tend to confer greater plant benefits than do fungi, even when nitrogen-fixing rhizobium bacteria, well known bacterial mutualists, are excluded from the analysis. However, fungi tend to confer greater stress amelioration than do bacteria, particularly under abiotic stress. The high prevalence of AMF studies (112 of 148 fungal experiments) likely drives this trend. As wild and agricultural plants will experience increasing stress due to global change (Reyer et al., 2013; Seidl et al., 2017; Wheeler & Braun, 2013), our results suggest that the ecological importance of beneficial components of plant microbiomes will increase.

4.1 | Microbial stress amelioration depends on type of microbe and stress

Overall, we find positive synergy, whereby benefits from microbes are especially valuable to plants under stress. Therefore, the impact of biological antagonists on plant performance depends on the presence or absence of beneficial symbionts in the microbiome, and vice versa. This finding is congruent with that of a meta-analysis examining a broader swath of plant mutualists (pollinators, defensive insects and microbial symbionts) and their impact on plant enemy effects (Morris et al., 2007). Our finding could be viewed as either the presence of beneficial microbes reducing the impact of pathogens, or as the presence of pathogens enhancing the beneficial effects of mutualists. Microbial amelioration of biotic stress could result from the increased importance of resources provided by beneficial microbes under the burden of enemy defence costs (Mayerhofer et al., 2013; Omacini et al., 2012; Saikkonen et al., 2006, 2010) or by symbionts priming plant defence (Jung et al., 2012; Martinez-Medina et al., 2016). Unlike abiotic stress, biotic stress is driven by antagonistic organisms that can co-evolve with host plants and beneficial members of the microbiome. The fact that ecological interactions amongst components of the plant microbiome differ across environments suggests that co-evolutionary dynamics in plant-microbiome interactions could show similar variation across environments (O'Brien, Sawers, Ross-Ibarra, & Strauss, 2018; Thompson, 2013).

We find that fungal stress amelioration exceeds that of bacterial symbionts. Our meta-analysis indicates fungi ameliorate both abiotic and biotic plant stress, whereas symbiotic bacteria as a general group do not ameliorate either type of stress—although they do provide substantial direct growth benefits. This supports previous findings that the ecological impact of beneficial soil bacteria can be modest relative to mutualists like AMF (Morris et al.,

2007). However, functional groups within the symbiotic bacteria differed in their role in stress amelioration. Endophytic bacteria ($N = 59$) significantly ameliorate stress, albeit to a lesser degree than do fungi, whereas epiphytic bacteria ($N = 86$) do not. The significant interaction between microbe type and type of stress indicates that while fungi ameliorate biotic stress more than do bacteria, fungi provide even greater stress amelioration under conditions of abiotic stress. Two-thirds of the experiments we examine focus on AMF, and we find AMF result in greater stress amelioration than other classes of microbes, so AMF likely drive this trend.

As the living connection between plants, soil, water and other microbiota (Thompson, 2013), mycorrhizae are well-positioned to exert major impacts on plant fitness. Our meta-analysis supports AMF as particularly effective at ameliorating plant stress. Previous meta-analyses demonstrate that mycorrhizae ameliorate the impacts of drought stress and pathogen stress on plants (Jayne & Quigley, 2014; Larimer et al., 2010). However, our results are novel in that we quantify the magnitude of stress amelioration symbiotic fungi provide and find they provide a similarly important role in ameliorating both abiotic and biotic stresses for plants.

Our findings suggest promising avenues for evolutionary microbiome research. Future work could identify strains most useful for plant stress amelioration in agriculture or conservation (Meena et al., 2017). Microbes differ in both abiotic stress tolerance (Porter & Rice, 2013; van der Heyde et al., 2017) and benefit offered to a plant (Friesen et al., 2011; Heath & Stinchcombe, 2014; Porter, Faber-Hammond, Montoya, Friesen, & Sackos, 2018), but less is known about standing variation for plant stress amelioration. Furthermore, microbiome evolutionary dynamics under biotic versus abiotic stress could differ. Antagonists can co-evolve with the plant and other members of the microbiome and may impose more dynamic and fluctuating selection on plant-microbiome interactions, whereas abiotic stresses may provide a more stationary fitness peak.

4.2 | Microbial stress amelioration: Mechanistic bases and ecological predictions

Microbial amelioration of plant stress differs among types of biotic stressors. Beneficial microbes ameliorate fungal pathogens and foliar herbivory. AMF drive fungal pathogen stress amelioration, corroborating previous findings (Larimer et al., 2010). The proportional benefit plants receive from beneficial microbes is greater under herbivore stress, consistent with experimental evidence that symbionts that defend against herbivores can provide less benefit in their absence (Mayerhofer et al., 2013; Omacini et al., 2012; Thamer, Schadler, Bonte, & Ballhorn, 2011). For example fungal endophyte alkaloids can increase herbivore resistance in plants, but do not increase other axes of plant performance (Saikkonen et al., 2006, 2010). AMF in particular hold promise for mitigation of biotic stresses like fungal pathogens in agriculture and wildland management.

In contrast, we did not detect microbial amelioration of nematode antagonists, and more strikingly, beneficial microbes show negative synergy with oomycete pathogens. Nematode antagonists can initiate plant infection via molecular pathways similar to those used by beneficial microbes and can render plants less able to form symbiotic structures (Wood et al., 2018), which could constrain plant benefit from microbes. Negative synergy could result if symbiotic structures or suppression of the plant immune system during symbiosis renders plants more susceptible to oomycetes or if oomycetes interfere with plants' ability to benefit from symbionts. This would be congruent with findings that oomycete resistance trades off with the functionality of mycorrhizal symbiosis (Gobbato et al., 2013; Wang et al., 2012). Within the microbiome, the role of beneficial microbes depends critically on the identities of antagonists.

Beneficial microbes ameliorate abiotic plant stress, except for heavy metal and cold stress. Soil salinity is a growing problem due to rising sea levels and irrigation practices that affects over 20% of irrigated agriculture (Qadir et al., 2014). The overall microbial amelioration of salinity stress we observe is congruent with findings for endophytes (Rho et al., 2018), AMF (Selvakumar, Shagol, Kim, Han, & Sa, 2018), and rhizobia (Egamberdieva, Jabborova, & Berg, 2016). Beneficial fungi can reduce the impacts of salinity stress by mitigating the overaccumulation of Na⁺ ions in roots (Selvakumar et al., 2018), increasing soluble sugar concentrations in roots which enhances resistance to salt-induced osmotic stress (Feng et al., 2002), and reducing the accumulation of toxic reactive oxygen species (Azad & Kaminskyj, 2016). Bacteria associated with AMF can enhance amelioration of salinity stress (Selvakumar et al., 2018) and many studies that attribute salinity stress amelioration to AMF do not control for these bacteria, which could inflate the importance of AMF to plant salinity tolerance. While heavy metal and cold stress were not ameliorated in our meta-analysis, this inference should be tempered by the few relevant studies we examined.

We find AMF and fungal endophytes ameliorate abiotic drought stress, though as a group, beneficial microbes do not show a unified pattern. The importance of AMF and fungal endophytes to plant drought tolerance is broadly supported (Jayne & Quigley, 2014; Kivlin et al., 2013; Mayerhofer et al., 2013; Rho et al., 2018). Beneficial fungi can alleviate drought stress by altering plant hormonal profiles and physiology (Ruiz-Lozano et al., 2016), for example, by reducing damaging reactive oxygen species in plant tissues (Azad & Kaminskyj, 2016). Drought can trigger plants to increase strigolactone production to increase associations with beneficial fungi as a means to cope with drought (Ruiz-Lozano et al., 2016). Our findings indicate AMF and endophytic fungi do not differ in their amelioration of drought stress. As drought stress increases due to global climate changes (Trenberth et al., 2014) and agricultural intensification (Wheeler & Braun, 2013), our findings predict that the importance of symbiotic fungi to plant health could increase correspondingly (Gehring, Sthultz, Flores-Rentería, Whipple, & Whitham, 2017). While increased fertilization under agricultural intensification could reduce the magnitude of AMF benefits to plants (Hoeksema

et al., 2010) it is not clear if this would alter the magnitude of microbial stress amelioration.

4.3 | Microbial stress amelioration is generalizable across evolutionary and ecological contexts

We find dicotyledonous plants benefit more from microbial stress amelioration than do monocotyledonous plants, supporting previous findings that plant functional and phylogenetic classification can predict the benefit a plant obtains from microbes (Augé et al., 2015; Hoeksema et al., 2010, 2018). We could not investigate finer-scale taxonomic resolution, but note that cool versus warm-season grasses have been previously found to respond differently to soil microbes (Bennett, Daniell, & White, 2013). We find that plants with different photosynthesis systems (C3 $N = 248$, C4 $N = 44$) do not differ in benefit from stress amelioration in our meta-analysis.

Unlike the meta-analysis of Hoeksema et al. (2010), which focused on AMF, we did not find that biotic complexity of the rhizosphere microbiome impacted the benefits provided to the host. This is surprising because a more diverse microbiome could contain antagonists that could enhance the apparent effect of the focal symbiotic microbe. More complex experimental designs, such as co-inoculating with focal symbionts and diverse communities in a factorial design, are needed to better understand these interactions. One such study found that rhizobia reduce the effects of antagonists in live soil inocula (Jack, Wozniak, Porter, & Friesen, 2019). Our findings appear to be robust across a variety of experimental conditions and co-evolutionary contexts. For those studies that report conditions, day length and experimental environment (growth chamber vs. greenhouse vs. field) do not drive differences in microbial plant stress amelioration. Plant growth promotion by beneficial microbes tends to be higher with co-evolved sympatric symbionts and when partners interact in their native soil (Johnson, Wilson, Bowker, Wilson, & Miller, 2010; Rúa et al., 2016). Domesticated and wild plants have different co-evolutionary dynamics with members of their microbiomes yet we did not detect differences in our findings among domesticated ($N = 264$) versus wild plants ($N = 29$). The unbalance in this comparison highlights a need for additional work in wild systems, particularly in forests.

4.4 | Conclusions and future priorities

In the face of increasing global change, there is growing momentum to incorporate microbial symbiosis into efforts to mitigate increasing plant stress in agriculture and wild systems (Kivlin et al., 2013; Rho et al., 2018; Vimal, Singh, Arora, & Singh, 2017). The studies we examine manipulate the presence or absence of individual types of plant symbionts. However, plants associate simultaneously with diverse communities of microbes that can have complex interactive

effects on host performance (Afkhami, Rudgers, & Stachowicz, 2014; Lekberg et al., 2018). This indicates a need to investigate microbial plant stress amelioration by manipulating the presence and absence of many microbial taxa in factorial combinations. Furthermore, plants shape microbial communities of soil microbes in ways that feed back to impact subsequent plant growth and survival (Bever, Platt, & Morton, 2012; Lekberg et al., 2018; van der Putten, 2017). It will be important to examine mutualistic microbial stress amelioration in the context of these more complex microbial communities that include diverse antagonists, commensals and free-living organisms, over both ecological and evolutionary timescales.

The large effect sizes we observe indicate that there are dramatic potential gains from optimizing the microbiome in the face of increasing plant stress. A greater impact of fungi on amelioration of plant stress suggests that soil and root-dwelling fungi, particularly AMF, present an important opportunity to reduce the negative impacts of stress on plant health. Such a goal could be attained via management practices that promote a robust AMF community, or cause less disruption to AMF communities resident in the soil (Verbruggen, Heijden, & Rillig, 2012; Verbruggen & Van der Heijden, 2012); though previous meta-analysis finds AMF can frequently be non-beneficial to crops (Ryan & Graham, 2018) others identify substantial benefits (Rillig et al., 2019; Zhang, Lehmann, Zheng, You, & Rillig, 2019). AMF inocula in wild and agricultural environments can have substantial impacts on resident AMF communities and plant health, though evidence for their efficacy in the field remains scant (Hart, Antunes, Chaudhary, & Abbott, 2018; Verbruggen et al., 2012). Understanding how multiple members of the microbiome interact with one another to ameliorate plant stress is a critical research priority and knowledge of the underlying mechanisms will enable informed management.

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AUTHORS' CONTRIBUTIONS

M.L.F., R.B., C.A.F., A.G., K.G., B.M.M., P.S. and E.S. conceived and designed the study; R.B., K.I., C.A.F., A.G., K.G., B.M.M., P.S., E.S. and M.L.F. collected the data; M.L.F. and S.S.P. analysed the data; S.S.P. and M.L.F. led the writing of the manuscript with contributions from all authors.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.4mw6m906t> (Friesen et al., 2019). Photo credits: Rachel Bomberger, WSU (upper left), PublicDomainPictures/18042 images (CC0 1.0) (upper right), Maren L. Friesen, WSU (lower left), Ashley Finnestad, T.E. Cheeke lab, WSU (lower right).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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