Microbial effects on plant phenology and fitness

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SUMMARY

Plant development and the timing of developmental events (phenology) are tightly coupled with plant fitness. A variety of internal and external factors determine the timing and fitness consequences of these life-history transitions. Microbes interact with plants throughout their life-history and impact host phenology. This review summarizes current mechanistic and theoretical knowledge surrounding microbially-driven changes in plant phenology. Overall, there are examples of microbes impacting every phenological transition. While most studies focused on flowering time, microbial effects remain important for host survival and fitness, across all phenological phases. Microbially-mediated changes in nutrient acquisition and phytohormone signaling can release plants from stressful conditions and alter plant stress responses inducing shifts in developmental events. The frequency and direction of phenological effects appear to be partly determined by the lifestyle and the underlying nature of a plant-microbe interaction (i.e. mutualist or pathogenic), in addition to the taxonomic group of the microbe (fungi vs. bacteria). Finally, we highlight biases, gaps in knowledge, and future directions. This biotic source of plasticity for plant adaptation will serve an important role in sustaining plant biodiversity and managing agriculture under the pressures of climate change.

INTRODUCTION

Plant-microbe associations played an important role in the establishment of terrestrial plants (Wang et al., 2010), and remain critical for plant nutrition acquisition, defenses, and overall health (Smith and Read, 2010). Microbes can influence plant traits, ecology, and even the evolution of plant lineages (Osborne et al., 2018; Magnoli and Lau, 2020). Plant phenology—the timing of plant developmental events—is determined by both genotype and environmental factors (Burghardt et al., 2016; Taylor et al., 2017). Compounding evidence suggests that microbes can manipulate environmental cues, impact host gene expression, and affect different traits associated with life history transitions (*i.e.,* phenological traits, (Gundel et al., 2006; Pinedo et al., 2015; Lu et al., 2018). Microbial activities may narrow or widen the duration of plant life history stages, and accelerate or delay life history events, which could have fitness consequences. For example, microbial manipulations in soil affect flowering time, and selection on flowering time (Lau and Lennon, 2011, 2012; Wagner et al., 2014; Chaney and Baucom, 2020). Alterations in flowering time can impact pollinator populations, plant yield, and may lead to premature or prolonged allergy seasons (Derocles et al., 2018; Shrestha et al., 2018; Sapkota et al., 2019). However, flowering is merely a single phenophase; timing of events throughout the entire life cycle matter for plant survival and reproductive success, as changes in one phenological transition have downstream effects on the environments experienced by subsequent developmental stages (Burghardt et al., 2016; Taylor et al., 2017). For these reasons, phenological traits are crucial to the productivity of crop plants and persistence of wild plants, particularly in the face of ongoing climate change.

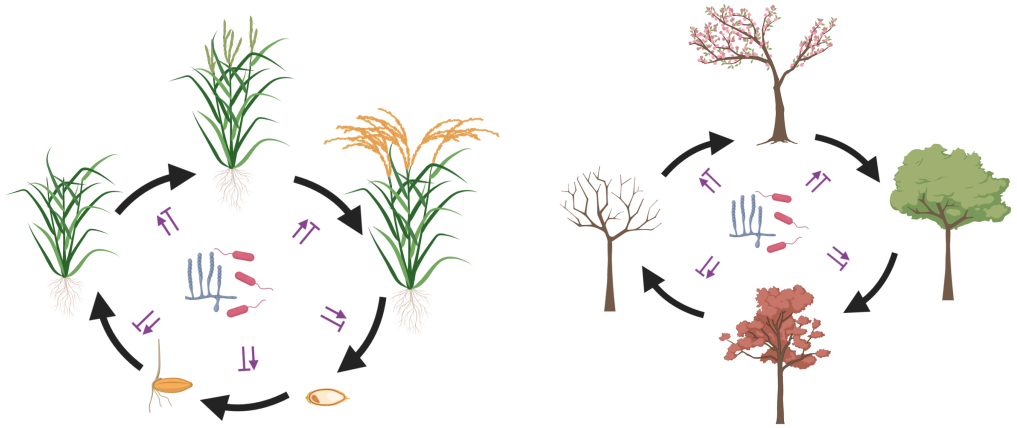

Figure 1. Microbial symbionts and neighbors can alter the timing of life-history transitions in both annual (left) and perennial (right) plants, across all phenological transitions.

Due to the ubiquitous nature of microbes across plant-associated environments and the importance of phenology for plant health, the effects of microbes on plant life history timing deserve attention. Here, we review the impact of microbes on different phenological traits, and synthesize these results based on theoretical predictions from resource allocation and life history theory, mechanisms, and context-dependency. We briefly discuss how plant phenology can also affect microbial communities and life-histories. Finally, we consider the implications of this biotic source of plasticity for agriculture, and plant adaptation to climate change.

PREDICTIONS FROM LIFE HISTORY THEORY

Life history theory predicts that delays in phenological transitions should only be favored if they offset the costs of slower time to reproduction (Roff, 1993). Thus, we would expect the effects of microbes on timing of phenology transitions to depend on the nature of the

interaction (e.g. parasites increasing mortality vs. symbionts providing resources), the life history and reproductive strategy of the plant, and the particular stage in development (Fig. 1).

The first phenological "decision" in the life of a plant is when to germinate. Germination timing determines the conditions that a young seedling will experience, and has downstream effects on the conditions experienced by subsequent plant life stages (Burghardt et al., 2016). Early germination can lengthen growing seasons and let plants secure more resources, ultimately increasing reproductive fitness (Akiyama and Ågren, 2014), and earlier germinants may escape predator- or parasite-induced mortality, increasing survival to reproduction (Beckstead et al., 2007). Yet, earlier germination can decrease fitness, as early germinants may experience harsher conditions, such as frosts or droughts (Thomson et al., 2017). Thus, if microbes ameliorate stressors, plants may germinate earlier in response. If microbes instead are pathogens, plant germination responses might depend on whether the risks to late germinants and dormant seeds are greater than they are for early germinants (as for some fungal pathogens (Enebak et al., 1998; Enebak and Carey, 2004)).

Later in the plant's life, microbes can modify the amounts and kinds of resources available for plants, changing the relative costs and benefits of delays in life history transitions (Charlesworth et al., 1991). Without trade-offs, earlier and longer duration of reproduction is best. However, many factors can favor a delayed onset of flowers. For example, plants might delay reproduction to avoid flower-killing spring frosts (Gezon et al., 2016), if larger size increases total seed output (Fournier-Level et al., 2013), or if there are strong trade-offs between reproduction and survival in perennials (Primack, 1979). There may also be physiological limits:

54 successful flowering and fruit development depends on having enough resources, but
55 reproductive tissue generally has negligible resource acquisition ability. In such cases, microbes
56 that provide nutrients or ameliorate early season stressors can directly shift phenology
57 (Corbesier et al., 2002) and may relax selection against earlier reproduction. High mortality risks
58 late in the growing season can obviate many of these factors (Fournier-Level et al., 2013), and
59 nutrient-providing microbes may lead to earlier and extended flowering when they relieve
60 plants from both resource limitation and mortality risk.

61 **APPROACH**

62 We conducted a literature search in Web of Science (Institute of Scientific Information
63 (Philadelphia, PA), n.d.), requiring either reference to "phenology" or "life history," or words
64 describing phenological events in plants (e.g., "flower*", "fruit*") and words describing
65 microbes (e.g., "microb*", "inoculat*"). This returned 935 records. We scored the first 500
66 (sorted by "relevance" in Web of Science) into two broad categories, discarding those that fit
67 neither category: 1) studies that experimentally tested microbial effects on plant phenology, and
68 2) studies about other links between plants, phenology and microbes, such as how plant or
69 microbial phenology influenced which plants and microbes interact. For both categories, we
70 recorded microbial taxonomy and the location of the microbes (e.g., seed, root, leaf). For records
71 that fell into the first category, we further recorded the phenological trait(s) measured
72 (WordBox 1), and direction of effect (earlier or delayed; expanded or narrowed), as well as the
73 primary mechanism of microbial effects (nutrient-provisioning, phytohormones, other
74 beneficial, pathogen), and other aspects of studies (Appendix S1; see Supplemental Data with

this article). We evaluated whether scored aspects of studies explained the proportion of significant earlier or delayed effects (two separate presence-absence response variables), using linear models with a bernoulli distribution (Appendix S1). Lastly, we noted whether selection on plant phenological traits was measured, and if so, what fitness component(s) was used. Because this type of study was scarce, we inspected the forward and reverse citations of each for additional studies quantifying microbially-driven shifts in selection on phenology.

We uncovered a rich literature on phenological links between plants and microbes (Appendices S2, S3). Strikingly, microbe-induced shifts in phenology were reported in 88% of the studies that tested for them, although this may be an overestimate due to the bias against publishing negative results (Fanelli, 2012). These effects are widespread across diverse microbial and plant taxa and have important implications for the ecology and evolution of these organisms, including in the context of climate change and agricultural sustainability. Our search identified several high-priority topics for future work, motivated by the current lack of available information, their particular importance, or both.

MICROBES CAN INFLUENCE TIMING OF ALL PLANT LIFE HISTORY TRANSITIONS

From seed to seed, plants are exposed to microbes at every point of their life cycles. Microorganisms have been documented to alter every life history transition or phenological trait, from the probability or timing of germination (25/26 and 17/19 studies, respectively, finding an effect of microbes) to flowering time (37/43 studies) to fruit maturation and senescence (6/7 and 1/2 studies, respectively). Bacteria and mycorrhizal fungi (MF) were the microbial groups that most reliably affected plant phenology, with significant effects observed

96 in 24/25 and 16/20 studies, respectively. Bacteria were also more commonly evaluated than non-
97 mycorrhizal fungi and microbial mixtures (18 and 16 studies, respectively). Flowering time was
98 the most studied phenological trait, and frequently sensitive to microbes. All stages other than
99 flowering and germination are relatively understudied (Fig. 2) and could not be included in
100 most of our models. Yet some appear to be more responsive to microbes than flowering and
101 germination time (fruiting time and phyllochron, Appendix S4), and studies on traits with too
102 few tests to evaluate at all (senescence time, maturation time, mid-flowering events) observed
103 effects, suggesting that these life stages deserve greater attention. For example, in the two
104 studies considering senescence, MF had no impact on timing in corn (Colombo et al., 2017), but
105 growth-promoting bacteria advanced senescence in *Arabidopsis thaliana* (Poupin et al., 2013).
106 Microbial effects on phenology of ferns, mosses, and other non-seed plants are critically
107 understudied: these plant groups are missing from our search results (Appendix S5).

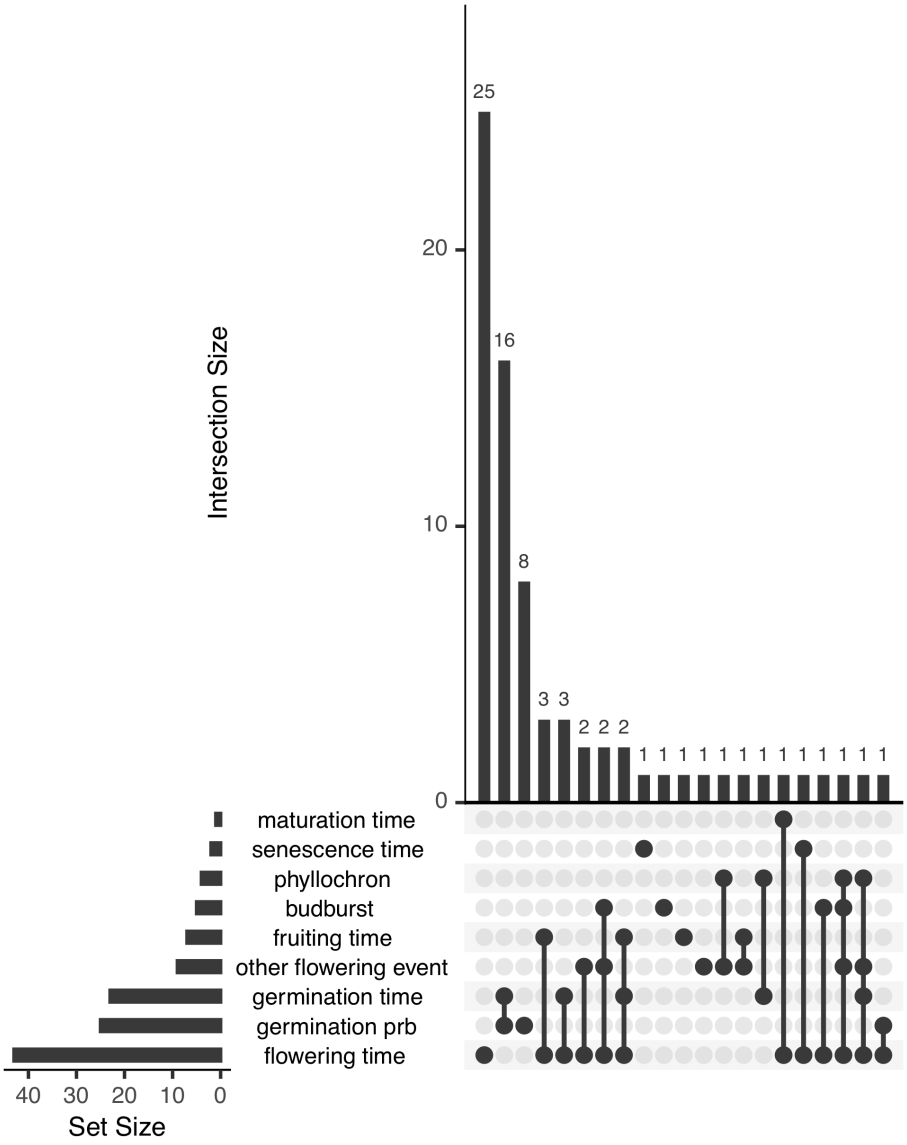

Figure 2. The number of studies out of our 500 scored records that included tests for microbial effects on a particular phenophase (lower left-hand graph), and the same for each combination of phenophases (indicated by connected dots) or studies that only included one phenophase (both, right-hand plot).

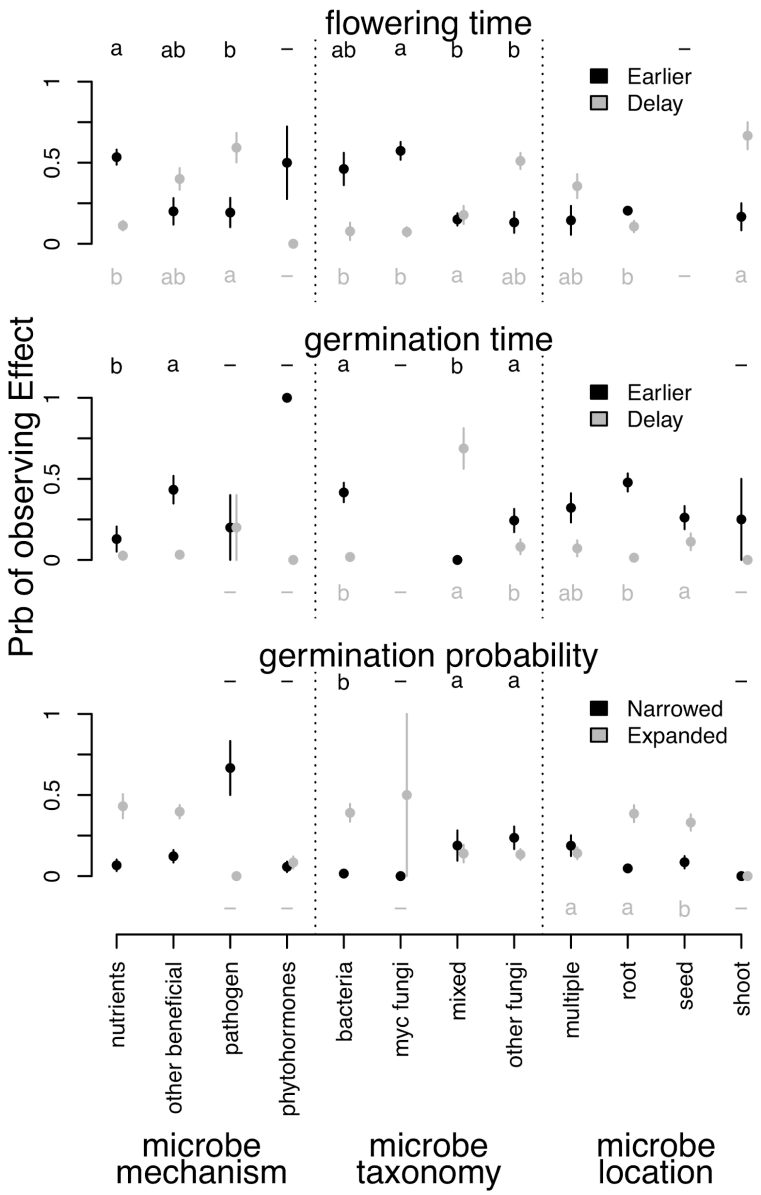

Figure 3: The probability that a test finds flowering time (top) or germination time (middle) to happen significantly earlier (black), or to happen significantly later (grey) when a microbial treatment is applied. On the bottom, the probability that a test that finds a narrowed (black) or expanded (grey) likelihood of germination. Sections separated by vertical lines indicate separate model tests for differences between categories. Letters indicate significant differences in binomial models, where the difference is significant (90%

highest posterior density interval, HPDI, see Appendix S6 for 95% HPDI) at the latent variable level, and the letters are ordered from highest probability to lowest. Points and bars are study-weighted means and +/- standard errors of the mean. Note that because model random effects are fit on the logistic scale, model-fit differences and study-weighted mean probabilities do not perfectly align.

MECHANISMS OF MICROBE-INDUCED PHENOLOGICAL SHIFTS

Plant development is orchestrated by intricate source-sink pathways: the bidirectional movement of photosynthates via the phloem provides nutrients and energy to different plant tissue destinations as phenological stages progress. Vegetative growth periods direct resources to new leaves and root storages, whereas costly flowers and fruits are the major sinks during reproductive growth (Zamski, 2017). This source-sink resource partitioning is regulated by hormonal, sugar, and environmental cues (e.g. temperature, moisture, bioavailable nitrogen). Signaling pathways involved in growth and development can be interrupted by plant-microbe interactions (Huot et al., 2014), and microbes can supply or degrade plant hormones and nutrients (Egamberdieva et al., 2017; Kuypers et al., 2018), potentially modifying phenological signals. In turn, plant hormones can modulate the plant-associated microbiome (Huot et al., 2014; Carvalhais et al., 2015; Lebeis et al., 2015). Therefore, it is not surprising that numerous bacteria and fungi that shift host phenology have also been linked to alterations in nutrient acquisition and hormonal cues related to growth and defense.

Microbial alleviation of nutrient limitation—especially bioavailable N, which is required in large amounts for flower and fruit production (Corbesier et al., 2002)—can allow phenological transitions. We hypothesized that microbes supplying nutrients would be likely to defray costs of early flowering and earlier germination, and would be more likely to lead to earlier events than pathogens or other microbes. A number of results support this hypothesis. Microbes known to supply nutrients were marginally more likely to accelerate flowering and least likely to delay it, though other beneficial microbes (where mechanism of benefit is unknown, or not nutrients or phytohormones) were marginally more likely to increase the speed of germination (Fig. 3, Appendix S6). Likewise, MF were likely to accelerate flowering time, whereas inoculations with mixed taxonomic groups or whole communities were more likely to delay this transition (Fig. 3). Notably, both the bacteria, and non-mycorrhizal fungi taxonomic categories include both nutritional mutualists and pathogens (Appendix S7). Bacteria on average accelerate germination time (Fig. 3), though this could not be compared to the effects of MF on germination due to a scarcity of studies.

Often, microbial effects on phenology were specifically linked to nutrients, including for stages that were infrequently studied (fruiting, 7 studies, and vegetative stages, 9 studies). Rhizobia and a beneficial *Pseudomonas* strain accelerate flowering in lentils and other legumes by increasing uptake of N and P (Thakur et al., 1999; Singh et al., 2008). MF inoculation of orchid seeds in low-nutrient media restored germination and early development growth to levels seen on high-nutrient media (Guimarães et al., 2013). The acceleration of budburst and flowering by MF can also be due to enhanced nutrient uptake (Sohn et al., 2003; Vaingankar and

Rodrigues, 2012; Yguel et al., 2014), or increased carbon resources in storage organs (Scagel, 2003; Scagel and Schreiner, 2006), but MF do not always accelerate budburst (Berdeni et al., 2018). Nutrient effects of microbes on phenology may even pass through seeds and extend across generations (Shumway and Koide, 1994). Cumulative nutrient-acquisition effects may be more likely in perennials and especially evergreen perennials, which maintain active tissue year-round. While fewer studies focused on these types of plants (28 and 4, respectively), their phenological responses to microbes may differ (Appendix S8). Indeed, because timing shifts could generally accumulate across life stages, it is unclear whether similar effects (e.g., mixed microbial taxa treatments delay both germination and flowering) are independent effects, as only 8 studies considered both early-life and late-life phenological stages (Fig. 2).

Notably, microbes known to affect phytohormone signaling had similar effects on flowering time as microbes known to affect nutrients (Fig. 3). Hormones and nutrients often interact in the signalling cascades leading to major phenology events. Studies that clearly link microbially-driven nutrient acquisition to both hormonal pathways and phenology are rare, but suggest that microbial manipulation of hormones and nutrients may generally co-mediate flower induction. For instance, (Lu et al., 2018) found that root exudates of certain plant varieties can select distinct microbiota that increase N availability through nitrification. The increased N availability, in turn, delays flowering via tryptophan-dependent production of IAA, a phytohormone that stimulates vegetative growth and suppresses flowering. In another example, MF accelerated flowering in wildtype tomato but not in mutants deficient in the

perception of ethylene and light, which also failed to acquire P from the MF (Chialva et al., 2016).

In addition to nutrition, hormone signaling in plants relates information about biotic and abiotic stressors. Stress related hormones (e.g., salicylic acid, SA, and jasmonic acid, JA) can suppress growth hormones (e.g., auxin and gibberellin), and resource allocation to physical defenses can stunt or delay plant development. Recent evidence shows that SA and JA also affect microbial community assembly (Huot et al., 2014; Carvalhais et al., 2015; Lebeis et al., 2015). During stress, altered hormone levels trigger immune defenses, affect microbial community assembly, and could have downstream consequences on flowering time. For example, the fungus *Pochonia chlamydosporia* accelerates flowering in *Arabidopsis thaliana*, but its successful recruitment to the microbiome depends on JA (Zavala-Gonzalez et al., 2017). Similarly, the plant growth promoting *Burkholderia phytofirmans* PsJN induces early bolting in multiple hosts, an effect linked to JA signaling (Pinedo et al., 2015), auxin homeostasis, and gibberellin biosynthesis (Poupin et al., 2013; Pinedo et al., 2015). Indeed, recruitment of microbes capable of manipulating flowering time may be an important stress response strategy.

On the other hand, microbes can alter plant phenology through mechanisms not primarily related to hormones and nutrition. For example, rhizobia effects on soybean germination, flowering, and fruiting time were similar to a chemical treatment attracting water to seeds and seedlings (Gayathri et al., 2008). Seed-borne bacterial pathogens inoculated during flowering can delay transcription of seed developmental genes without impacting the timing of fruiting (Terrasson et al., 2015), and plant-associated microbes capable of heavy metal

detoxification improve germination probability and seedling survival (Sánchez-López et al., 2018). Clearly, microbes regulate host phenology through a variety of mechanisms, and much more work is needed to understand why and how distinct microbes affect plant phenology. Characterizing underlying mechanisms is even more challenging considering that pathway regulation and impacts can be transient and context-dependent.

CONTEXT DEPENDENCY: INTERACTIONS WITH THE ABIOTIC AND BIOTIC ENVIRONMENT

Context dependency is rampant in all categories of species interactions (Chamberlain et al., 2014). Plant-microbe interactions are no exception and depend on adjacent biotic interactions and abiotic properties of the local environment (Morris et al., 2007; Shantz et al., 2016). It has long been hypothesized that biotic interactions are more likely to be mutually beneficial when the *abiotic* environment is more stressful to one or both partners (Bertness and Callaway, 1994), and more recently, that this might result in evolution of increased mutualism in stressful sites (O'Brien et al., 2018).

Accumulating evidence from plant-microbe systems suggests that microbial effects on phenological traits may be a key mechanism supporting these hypotheses, particularly for germination. Soil and endophytic microbes may enhance germination in nutrient-deficient soils, as observed in the Florida rosemary scrub ecosystem (David et al., 2020) and under salt stress (Piernik et al., 2017). Beneficial microbes, including pre-treatment of seeds with the best local strains (Balshor et al., 2017) could be useful to improve seed germination, a major bottleneck in large-scale ecosystem restoration plantings (Larson et al., 2015) especially for restoration or

224 phytoremediation projects in stressful environments. Conversely, these effects could contribute
225 to invasion success across distinct habitats: the same soil microbiota that improved germination
226 of St. John's wort in limestone barrens had the opposite effect in more hospitable old-field
227 environments (Petipas et al., 2020).

228 Microbial effects on flowering time were also linked to improving stress tolerance. In
229 *Arabidopsis thaliana*, a mixed microbial community accelerated flowering only under drought
230 conditions ((Fitzpatrick et al., 2019). Likewise, a *Burkholderia* strain accelerated bolting in *A.*
231 *thaliana* only under salt stress (Pinedo et al., 2015), a live soil slurry restored normal flowering
232 time in *Elsholtzia splendens* under copper stress (Jin et al., 2015), and mycorrhizal alleviation of
233 nutrient and water stress was tied to earlier flowering and higher fitness in *Erodium*
234 *oxyrrhynchum* (Sun et al., 2008). Notably, either faster or slower flowering can be an adaptive
235 response to stress (Charlesworth et al., 1991; Fournier-Level et al., 2013; Gezon et al., 2016) and
236 various studies document microbially-induced reproductive delays that increase host fitness
237 under stressful conditions. For instance, *Phyllobacterium brassicacearum* increases the duration of
238 vegetative growth in *A. thaliana*, but also increases biomass and water use efficiency under
239 drought (Bresson et al., 2013). Importantly, not every study that tested stress-dependent effects
240 and benefits observed them: effects of AMF on *Medicago truncatula* flowering and biomass were
241 consistent across nutrient treatments (Liu et al., 2017), and in *Zantedeschia* sp., nutrient
242 availability impacted microbial effects on flowering time, but not fitness (Scagel and Schreiner,
243 2006).

While microbes indeed generally ameliorate plant stressors (Porter et al., 2020), microbes can exist on a mutualist-parasite spectrum (David et al., 2018); e.g., AMF effects shift from mutualism to parasitism under certain, rare, conditions (Johnson et al., 1997; Frederickson, 2017). Stress exacerbation could also act through phenology: for example, microbial communities more often *reduced* germination of several plant species in the presence of a stressful allelopathic chemical (David et al., 2018). While there are few similar examples, our results might be biased towards studies testing species with known plant-promoting-growth effects. We also note that fitness effects may trade off across life stages: for instance, an endophyte that increases growth also reduces germination probabilities (Kazenel et al., 2015).

Mechanistically, microbes may have stress-dependent effects by constitutively priming plant stress responses, as was seen in response to salt (Pinedo et al., 2015). Alternatively, microbes may alter the ability of plants to sense the abiotic environment. Endophytic fungi delay germination in *Lolium multiflorum* by altering the ability of seeds to sense and respond to chilling and light requirements (Gundel et al., 2006). Such microbial signal-blocking could explain effects of fungi on germination timing that were only observed under certain cold treatments in *Elymus canadensis* (Connolly and Orrock, 2015).

Not all context-dependency in species interactions is due to abiotic conditions; biotic context can also have dramatic impacts on outcomes (Cardinale et al., 2003; Morris et al., 2007). Indeed, complex communities were more likely to delay flowering and germination (Appendix S8). For example, a whole soil community generally reduced germination rate and success across 19 species, but a single strain from the community mostly increased germination (Balshor

et al., 2017). Sub-additive effects were common, such as among phyllosphere fungi that delayed flowering in *Arabidopsis thaliana (Zahn and Amend, 2019)* and for acceleration of flowering in lentils by *Rhizobium* and *Pseudomonas* (Singh et al., 2008) In contrast, multiple microbial agents had increasing effects on germination, when co-inoculated (Fatemeh et al., 2014). However, effects can be more complex: MF influence on a range of phenological traits in *Brodiaea laxa* and *Zephyranthes* sp. sometimes weakened, strengthened or even shifted in direction when the native soil community was present (Scagel, 2003, 2004). Even the abundance of a single microbe can change the direction of the effect on flowering (Garrido et al., 2010). Such complex interactions suggest that microbe-microbe interactions can alter microbe-plant interactions, emphasize the importance of studying natural communities, and are a key reason why single-inoculant experiments must be interpreted with caution (Vorholt et al., 2017).

Some microbe-induced shifts in flowering time, or the corresponding fitness consequences, accrue via other types of biotic context, such as herbivory and competition. In *Datura stramonium*, the effects of MF reversed from accelating to delaying flowering when 50% of leaf area was removed to mimic herbivory (Garrido et al., 2010). Inoculation with *Bradyrhizobium* did not directly alter soybean phenology, but strengthened the effects of neighboring plants on the timing of flowering and fruiting (Viana et al., 2009). The fitness consequences of germination timing—which often responds to soil biota—depend on the density and growth rate of neighboring plants (Weinig, 2000). For outcrossing zoophilous plants, flowering overlap with pollinator activity is critical for reproduction (Rafferty and Ives, 2011). Reciprocally, changes to flowering time could have indirect impacts on plant fitness by

altering pollinator survival (Davis et al., 2019). Although very few studies considered microbial effects on host phenology as well as plant interactions with other macro-organisms, these forms of context-dependence are likely to be ecologically and evolutionarily important.

PATHOGENS, COMMENSALS, AND MUTUALISTS AS DRIVERS OF PLANT PHENOLOGY EVOLUTION

Like insect herbivores, phytopathogenic microbes have played a critical role in shaping plant evolution (Upson et al., 2018). The most virulent pathogens can devastate entire plant populations, creating extremely strong selection pressure favoring genetic variants that confer resistance. On the other end of the spectrum, some mutualistic microbes (e.g., rhizobia and mycorrhizal fungi) confer such strong growth benefits that plants have evolved intricate molecular and physiological machinery to communicate with them (Streng et al., 2011). These important groups of microbes are not particularly noted for their effects on plant phenology; yet many examples of such effects exist (Thakur et al., 1999; Liu et al., 2017; Berdeni et al., 2018; Davis et al., 2019). Thus, selection for optimal phenology may also have shaped plant interactions with pathogens, rhizobia, MF, and other phenology-shifting microorganisms.

The few studies that have explicitly linked phenological impacts of microbes to evolutionary processes have found that selection on phenology can change across microbial contexts. Several studies report that manipulation of the soil microbiota changed directional selection on flowering time from positive to neutral or even negative (Lau and Lennon, 2011, 2012; Wagner et al., 2014). In both *Ipomoea purpurea* and *Arabidopsis thaliana*, selection for earlier flowering was stronger in the presence of a complex soil microbiome, relative to sterile

conditions (Fitzpatrick et al., 2019; Chaney and Baucom, 2020). And in maize, viral infection reversed the sign of the genetic correlation between flowering time and breeder-selected performance traits (Horn et al., 2013). So far, the mechanism linking microbes to the relationship between fecundity and flowering time has not been determined.

Microbes can also act as agents of selection on germination; in particular, multiple studies report a negative impact of fungal pathogens on the probability of germination. This suggests that pressure to avoid pathogens has likely shaped selection on germination timing. More generally, fungi other than mycorrhizae more often reduce the likelihood of germination than increase it (Fig. 3). In Canadian wild rye (*Elysmus canadensis*), for example, fungicide treatment increased both the speed and probability of germination (Connolly and Orrock, 2015). Alternatively, some microbes (particularly bacteria) induce faster germination, which can help plants escape pathogens that specialize on new germinants, as observed in loblolly pine (Enebak et al., 1998; Enebak and Carey, 2004). In such cases, responsiveness to germination-accelerating microbes should be evolutionarily favored, perhaps when pathogens are slower to get established in a season.

In addition to their direct evolutionary impacts as agents of selection, microbes can alter plant fitness by simply shifting a phenological trait that is under selection for any reason. In plant populations where germination timing is under strong selection to ensure proper plant size during cold winter temperatures (Donohue et al., 2005), microbes that delay or speed germination could either reinforce or disrupt this coordination, depending on the direction of their effect. Similarly, in challenging environments selection often favors earlier-flowering

phenotypes that can reproduce before late-season drought becomes too severe. In one such montane habitat, soil microbiota shifted flowering time of a perennial mustard by up to 3 days, corresponding to a 12% change in fecundity under the local selective regime (Wagner et al., 2014). In crop breeding programs, slow or unreliable germination can preclude an otherwise high-performing genotype from selection for the next generation. Observations of microbe-induced germination delays are common in crop species including soybean and corn (Naveed et al., 2014; Andrade et al., 2019). Notably, many "nonpathogenic" microbes with no direct negative effects on the plant could nevertheless decrease host fitness if they shift phenological traits in an unfavorable direction. However, the extent to which microbe-induced shifts in phenology align with selective pressures on phenology is currently unclear, due to the rarity of studies that quantified selection on phenological traits in any microbial context.

Beyond causing selection on and phenotypic plasticity of phenological traits, microbes can drive plant evolution in more subtle ways. In teosinte, for instance, rhizosphere communities altered patterns of genetic variance and covariance among flowering time and other traits (O'Brien et al., 2019), which determine these traits' potential to respond to both direct and indirect selection. The activity of floral microbes affects pollinator behavior, with implications for patterns of gene flow within and among plant populations (Rebolleda-Gómez et al., 2019; Russell and Ashman, 2019); seed and fruit microbes may have similar effects on dispersal and migration. Overall, genetic variation within plant species for phenological responses to microbes appears to be plentiful (Krauss et al., 2007; Chialva et al., 2016; Fitzpatrick

et al., 2019; O'Brien et al., 2019), reinforcing the need for more research into the evolutionary causes and implications of these interactions.

Plant phenology has the potential to influence microbial fitness, and microbial effects on phenology may evolve in microbial genomes, or as joint traits (Metcalf et al., 2019; Rebolleda-Gómez et al., 2019; O'Brien et al., 2021). From the perspective of microbes, it can be advantageous to manipulate the development of the host plant to increase resources. For example, in annual plants, soil priming (exudation of organic C from roots) intensifies throughout the vegetative growth period and starts to decline after flowering (Cheng et al., 2003). Indeed, pathogens have evolved to manipulate life history transitions in order to increase their probability of transmission (Jennersten, 1988). For such joint traits, we have often expected genes in closer temporal or physical proximity to the trait to have greater impacts (Dawkins, 1982). This logic would suggest that microbes located in shoots and reproductive structures would be more likely to influence flowering time. However, compared to microbes in roots, microbes in shoots were less likely, and multi-location microbes equally likely, to affect flowering time. Similarly, microbes in seeds were more likely than root microbes to affect germination timing, but less likely to affect germination probability (Fig. 3). However, we relied only on author information for the location when the microbe was not well-known (MF, rhizobia), and the ecology of many plant-associated microbes is poorly characterized. Further, few studies considered flower-inhabiting microbes, which manipulate the attraction of pollinators (Rering et al., 2018; Tsuji and Fukami, 2018; Cellini et al., 2019; Russell and Ashman, 2019). Floral microbes can be mutualistic or pathogenic, and some species can migrate to the

vascular bundles, becoming systemic and even passing on to seeds (Piqué et al., 2015; Kim et al., 2019; Chesneau et al., 2020). Thus, they have high potential for downstream consequences on plant traits, such as the timing of floral senescence and fruiting.

THE OTHER SIDE OF THE COIN: PLANTS INFLUENCE PHENOLOGY OF MICROBES

When considering all studies relevant to microbes, plants, and phenology, half addressed how microbes influence plant phenology (74 of 148), and the rest address the reverse in some way: how plant phenology influences which microbes colonize tissues and microbial fitness, or how microbe phenology changes interactions (82 of 148). Biases in all these relevant records were similar to biases observed for effects of microbes on phenology alone: most studies consider soil or root microbes (118 of 148), especially mycorrhizae (50 studies), and comparatively few consider microbes residing in multiple plant organs (only 21; Appendices S9, S10).

While the activities of microbes can affect plant phenology and selection on plant phenology, the reciprocal is also true: plants influence microbial phenology. Indeed, it is well-known that roots influence germination of arbuscular MF spores (Gianinazzi-Pearson et al., 1989), and the absence or presence of high-quality nutrients often promotes or breaks dormancy, respectively, in many microbes (Bever et al., 2012; Dijkstra et al., 2013). This likely has evolutionary consequences for microbes. For example, changes in source-sink sugar transport across plant phenophases or tissues could select between microbes that initiate

388 growth more rapidly versus those that tolerate long periods of low nutrients (Moreno-Gámez
389 et al., 2020).

390 Microbial community composition also changes across plant development. For example,
391 microbial succession patterns in developing rice can accurately predict plant age (Edwards et
392 al., 2018). Plant age was associated with rhizosphere microbiome composition in sorghum
393 (Schlemper et al., 2017; Xu et al., 2018) and *Boechera stricta* (Wagner et al., 2016), while
394 communities also shifted across age of apple flowers (Shade et al., 2013). One limitation of these
395 studies is that composition of microbial communities is determined by DNA and it does not
396 distinguish between active and dormant species ((Lennon and Jones, 2011; Carini et al., 2016).

397 However, while the presence and time of residency of *Arabis alpina* were important
398 factors in structuring soil communities, the transition to flowering did not affect the microbial
399 community composition of the roots (Dombrowski et al., 2017). This observation calls into
400 question whether tissue age or background fluxes in microbial propagules, rather than plant
401 phenology per se, drives shifting patterns of microbial colonization through time. We
402 recommend that more studies leverage flowering mutants, which have revealed short-term
403 influences of the circadian clock on microbiomes (Hubbard et al., 2018), or evergreen plants,
404 because both separate tissue age from reproductive stage effects.

405 **IMPLICATIONS FOR AGRICULTURE AND CLIMATE CHANGE**

406 As the climate crisis directly alters microbial communities (Castro et al., 2010), these
407 effects will likely feed forward to alter plant phenology. Therefore, microbial responses to

408 climate have the potential to either exacerbate or mitigate damaging phenological mismatches
409 observed between plants and the other organisms with which they interact, such as insect
410 herbivores and pollinators (Burgess et al., 2018). Microbe-driven shifts on budburst and
411 senescence (Poupin et al., 2013; Yguel et al., 2014) could also impact the duration of plants'
412 atmospheric C sequestration, and therefore the progression of climate change. While our
413 understanding of microbe-induced phenology shifts currently remains rudimentary, the fact
414 that plant phenology so often responds to microbes suggests that microbial manipulation could
415 become an important tool for tackling the climate crisis.

416 Along the same lines, naturally-occurring microbes have potential to influence the
417 evolutionary trajectories of wild native plants through their impact on phenology. Phenological
418 traits have evolved in part due to pressure to escape stressors such as drought, pathogens, and
419 temperature extremes, which are expected to continue increasing over the coming decades (Pau
420 et al., 2011; Dantec et al., 2015). Ongoing range shifts (e.g., to higher elevations) in response to
421 climate disruption will expose wild plant species to novel microbial communities, potentially
422 with different effects on their phenology relative to the communities in their original range. The
423 implications for the survival and future evolution of these species are unclear, because it
424 remains unknown whether soil microbes' effects on phenology are generally aligned with the
425 direction of selection on phenology in a given habitat, and how often microbes alter the
426 associations between phenology and fitness, as discussed above.

427 In addition to the effects of climate change, induction of phenological shifts by microbes
428 has many potential applications for sustainable agriculture. Microbial inoculants to increase

crop yield are already used on some commercial farms, and have high potential to displace a larger proportion of chemical inputs in future years (Parnell et al., 2016). Food crop phenological models predict plant performance in a particular growing region, planting season, or under future climate conditions (Soltani et al., 2020). Phenophase timing models are also a powerful tool to optimally time pesticide sprays, irrigation, fertilizer treatment, and harvest,increasing both quality and yield, particularly in fruit trees and other specialty crops (e.g. citrus, (Mechlia and Carroll, 1989)). However, these models fail to incorporate microbial activities that influence plant growth and reproduction across a variety of food crops and microbial types, as discussed above (Thakur et al., 1999; Fan et al., 2008; Gayathri et al., 2008; Singh et al., 2008; Naveed et al., 2014; Chialva et al., 2016; Masangwa et al., 2017; Andrade et al., 2019; Shaik and Thomas, 2019).

Additionally, biological control agents can have non-target phenological consequences, such as fungal entomopathogens for controlling insect pests that also impact germination timing and decrease germination probability (Heinz et al., 2018). On the other hand, phenology regulation can be an advantageous mode of action. Babalola et al. (2007) discovered three rhizobacteria strains which cause a parasitic weed to germinate early, before a host is available to colonize. Even disease agents could be useful: a weakened viral pathogen can increase yield in zucchini by delaying flowering (Spence et al., 1996). Testing biocontrols for negative phenological impacts and exploitation of microbial control of plant phenology could be novel crop management strategies. Organic farming and precision agriculture could greatly benefit from improved understanding of microbial-host phenology interactions.

NEXT STEPS FOR RESEARCH ON MICROBE-DEPENDENT PLANT PHENOLOGY

We have three main recommendations for future research in this area. First, more work is needed on less-studied phenological transitions (vegetative, fruiting, and senescence) and microbe locations (reproductive structures, phyllosphere, and other shoot tissues). Knowledge of what happens at intermediate phenophases is particularly essential for applying whole life-cycle models (Burghardt et al., 2016). Second, there is a need for more studies that measure microbe-mediated selection on phenology, which appears potentially important based on evidence from the few existing studies. All that is required is to 1) include at least two plant genotypes in multiple microbial conditions (they do not even have to be the same genotypes in each microbe treatment), 2) measure both a phenological trait and a fitness trait (e.g., biomass, survival, fecundity, yield), and 3) test whether the microbial treatment alters the regression of fitness onto the trait. We note that many of the studies reviewed here already collected all the necessary data to do this, and were only missing the analysis step. For example, (Kalkal et al., 2018) measured time to flowering and yield in 20 chickpea genotypes, as affected by two rhizobia strains or one MF strain. They concluded that there was sufficient genetic variation to select for the phenological response to microbes, but did not test for associations between flowering time and fitness or yield. All that is needed to address this gap is awareness; this extra analysis could provide valuable insights for minimal extra effort. Third, finer-resolution methods for fractionating microbiomes are needed to learn more about mechanisms. It is much easier to identify the mechanistic basis of the effect in one or a few microbes, than to tease out microbes with similar effects from complex communities. In particular, synthetic community

approaches (Vorholt et al., 2017) and community enrichments (Sanchez et al., 2021) are likely to be useful for studying microbial effects on plant phenology in a tractable yet ecologically realistic system. Progress in each of these three priority areas will be crucial for gaining a clearer picture of this important phenomenon.

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AUTHOR CONTRIBUTIONS

AMO performed statistical analyses. All authors reviewed and synthesized literature and contributed to manuscript writing and editing.

DATA AVAILABILITY STATEMENT

Search results and associated extracted data are available in Appendices S2 & S3, and with code online. Code will be available at https://github.com/amob/MicrobesAndPhenology upon publication or by request.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

Appendix S1: Detailed methods of the literature search and analysis.

Appendix S2: Database of reported microbial effects on phenology.

Appendix S3: Database of studies found in search and other links scored.

Appendix S4: Summary of microbial effects on plant phenology across different plant phenological events.

Appendix S5: Taxonomic breakdown of studies and unique tests within them for effects of microbes on plants.

Appendix S6: Results reported in Fig. 3 of main text, but with 95% HPDI for determining different groups.

Appendix S7: Overlap of tests across microbial effect mechanism, taxonomy, and location.

Appendix S8: Summary of microbial effects on plant phenology for studies featuring different inoculum types, host lifeforms (perennial *vs.* annual), and host mating strategies (predominantly selfing *vs.* outcrossing).

Appendix S9: Summary of the numbers of studies considering microbes residing in each plant organ.

Appendix S10: Summary of the numbers of studies considering microbes belonging to various taxonomic groups or categories.

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WordBox 1	
Term	**Definition**
flowering time	date of first flower
fruiting time	time to fruit maturity or seed abscission
maturation time	age at first flowering (perennials)
senescence	either the onset of seasonal dormancy (perennials), or death (annuals)
phyllochron	transition through distinct vegetative developmental stages (e.g. from juvenile to adult type leaves)
budburst	emergence of shoot tissue from a dormant vegetative state (i.e. a twig or rhizome).
germination time	days post planting until, or date of, germination within a single season
germination probability/proportion	proportion of seeds germinating within a defined timeframe - e.g., a single season or duration of an experiment
phenophase	any distinct phase of the life-cycle

889 **SUPPORTING INFORMATION**

890 **Microbial effects on plant phenology and fitness**

891 Anna M O'Brien, Nichole A. Ginnan, María Rebolleda-Gómez, Maggie R. Wagner

892 **Appendix S1: Detailed methods of literature search and analysis.**

893 *Detailed search methods*: We conducted a literature review in order to quantify the amount
894 of research on this topic. We first curated a list of search terms based on plant phenology and
895 microbial interactions. We then conducted several rounds of exploratory searches to expand
896 search words to those not on the initial list and to eliminate words that produced a high amount
897 of non-relevant results. We required either reference to "phenology" or "life history," or words
898 describing phenological events in plants ("flower*", "fruit*") to be within two words from a
899 timing word to filter to records referencing the phenology of the event (i.e. "date of flowering"),
900 not simply the character (i.e. "the phylogeny of flowering plants"). We further required that
901 search words describing microbes appear within a number of words within a reasonable
902 sentence. We defined this as an average (english) sentence in peer-reviewed literature (Moore,
903 2011), or 30 words. We conducted this search in Web of Science (Institute of Scientific
904 Information, Philadelphia, PA, n.d.) using a topic search with the syntax: plant AND *((phenology*
905 *OR "life history") OR ((flower* OR bolting OR bolt OR anthesis OR fruit* OR ripen* OR senesc* OR*
906 *dehisc* OR budburst OR germinat* OR dormancy OR dormant OR maturation OR pollination OR*
907 *reproduct* OR emergence)* ***NEAR/2*** *(time OR timing OR day OR date)))* **NEAR/30** (microbiome
908 OR bacteria OR plant-soil-feedback OR microb* OR mycorrhiz* OR arbuscular OR

ectomycorriz* OR AMF OR EMF OR Rhizobia* OR Frankia OR nodul* OR rhizosphere OR rhizoplane OR phyllosphere OR phylloplane OR phytobiome OR endophyte OR anthosphere OR fungi* OR antibiotic OR inoculat* OR microflora OR PGPR OR "plant growth promoting bacteria"). Italics separate the major parentheticals, and bold highlights the word spacing requirements. We further restricted to results of document type "Article." We evaluated the results of this search with respect to year of publication. The search was conducted on the 11th of September, 2020.

We next downloaded the records, sorted by relevance in Web of Science (Institute of Scientific Information, Philadelphia, PA, n.d.), and then extracted information from individual records. We sorted records into two broad categories. First, we marked records that documented the influence or association of plant phenology with changes in microbes, or documented microbe phenology itself. Second, we marked records that manipulated microbes and measured changes (or lack thereof) in plant phenology. For both sets of records, we recorded the taxonomic group of microbe or microbes at a coarse level (fungi, bacteria, virus), but noting a few specific categories of special interest (mycorrhizal fungi and bacteria), and "mixed" if the community is expected to include various taxonomic groups of microbes. We noted if the study plant was annual or perennial, and whether it was known to primarily self or outcross. We also recorded the location of the microbes on plants, defined broadly for the plant, with the possible values of shoot, root (including soil), reproductive or seed tissues, or combinations, and restricted to author manipulation, mention, or measurement (i.e. we did not use independent information of microbe location), except for very well-known groups, such as

mycorrhizal fungi and rhizobia. If the abstract did not suggest work linking plants, microbes and phenology, we discarded the record. We did not score all records (935), but instead worked from the most relevant record towards the least relevant record (as ranked by Web of Science), and stopped extracting information after 500 records.

We used UpsetR (Conway et al) to plot intersections of categories in concise figures from these 500 records, and evaluated the records accumulated over time, both in R (R Core Team, 2017).

When scoring tests for records that quantified microbial effects on plant phenology, we prioritized author language, model results, tables with confidence intervals, and then figures to determine whether differences between treatments with and without the focal microbe or inocula were significant. We included differences between microbial treatments if these were discussed and reported, and if the effect of one treatment could be polarized relative to more than one other microbial treatment.

Linear model details: To fit models to our bernoulli response variables (ones and zeros for significant, and non-significant results to tests), we used package MCMCglmm (Hadfield, 2010) in R, fixing the residual variance at 1 (with 10,00,000 iterations, thinning by 50, and burn-in 1,000). We included random effects for study, but pooled all studies with 12 or fewer tests in one study. We set a strong prior on random effects to be 0 (nu = 8) -- when there is insufficient information to fit a good random effect for a study, this assumes that the difference between the data in that study and the mean must be due to variation at the fixed effects alone. We first fit models with phenophase trait as the fixed effects to ask whether the likelihood of observing a

951 significant early, or significant delay effect differs across traits. We also estimated differences in
952 the probability of significant effects across treatments or categories within traits (as we do not
953 necessarily expect traits to respond in the same way to, i.e. inoculation with mycorrhizal fungi),
954 by subsetting data to each and fitting each categorical variable as an explanatory variable one
955 by one (there was insufficient data to fit models with multiple categorical variables). Before
956 fitting each model, we removed datapoints associated with fixed effects where the total number
957 of datapoints for estimating that fixed effect was 12 or fewer. For modelling differences
958 between phenophases in probability of responses, this meant that we did not include
959 maturation time, senescence time, and mid-flowering events (peak flowering, senescence of
960 flowers). For other models, insufficient data is indicated in the figure with a "-". To determine
961 significant differences between categories on the model fitting scale, we re-fit each model,
962 changing the value associated with the intercept until all values of the treatment/category were
963 compared. This determined our significant differences groups.

964 Web of Science. Institute for Scientific Information,; Thomson Reuters,; Clarivate Analytics
965 (Firm). Philadelphia, PA, Institute for Scientific Information [Philadelphia,
966 Pennsylvania]. Thomson Reuters [Philadelphia, Pennsylvania], Clarivate Analytics.
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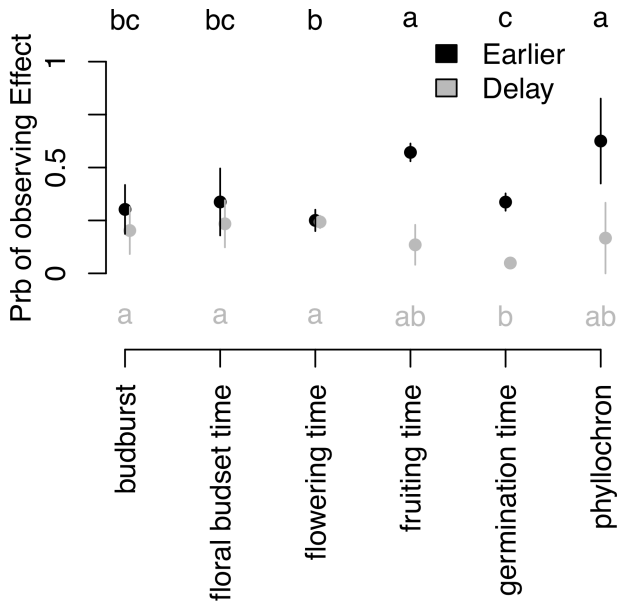
Appendix S2: Database of search and relevant records.

See attached tab-delimited file ('search_results.tsv').

Appendix S3: Database of reported microbial effects on phenology.

See attached tab-delimited file ('split_records.tsv').



Appendix S4: Significant differences among different phenophase traits across all other categories at 90% HPDI. The proportion of tests that found the phenological event to happen significantly earlier (black), or to happen significantly later (grey) when a microbial treatment is

applied. Letters indicate significant differences in binomial models, where the difference is significant at the latent variable level, and the letters are ordered from highest probability to lowest. Points and bars are study-weighted means and +/- standard errors of the mean note that because models including random effects are fit on the logistic scale, model-fit differences and study-weighted mean probabilities do not perfectly align.

Appendix S5: Table of studies and unique tests within those studies for microbial influence on plant phenology, by plant family. Note taxonomic bias towards agriculturally important plant families, especially angiosperms. Indeed no studies considered non-seed plants.

Plant Family	Number of Tests	Number of Studies
Amaranthaceae	28	2
Amaryllidaceae	60	1
Anacardiaceae	8	1
Araceae	48	1
Asparagaceae	38	2
Asteraceae	48	7
Boraginaceae	6	1
Brassicaceae	279	15
Caryophyllaceae	8	1
Chenopodioideae	4	1
Cistaceae	4	1
Cleomaceae	4	1
Convolvulaceae	1	1
Cucurbitaceae	3	1
Cyperaceae	1	1
Ericaceae	1	1
Fabaceae	113	15
Fagaceae	1	1
Geraniaceae	6	2
Hypericaceae	8	1
Iridaceae	8	1
Lamiaceae	6	1
Lythraceae	3	1
Malvaceae	6	1
Orchidaceae	8	2

Orobanchaceae	3	1
Papaveraceae	4	1
Pinaceae	54	2
Plantaginaceae	4	2
Poaceae	219	14
Polygonaceae	4	1
Rosaceae	74	3
Solanaceae	45	5

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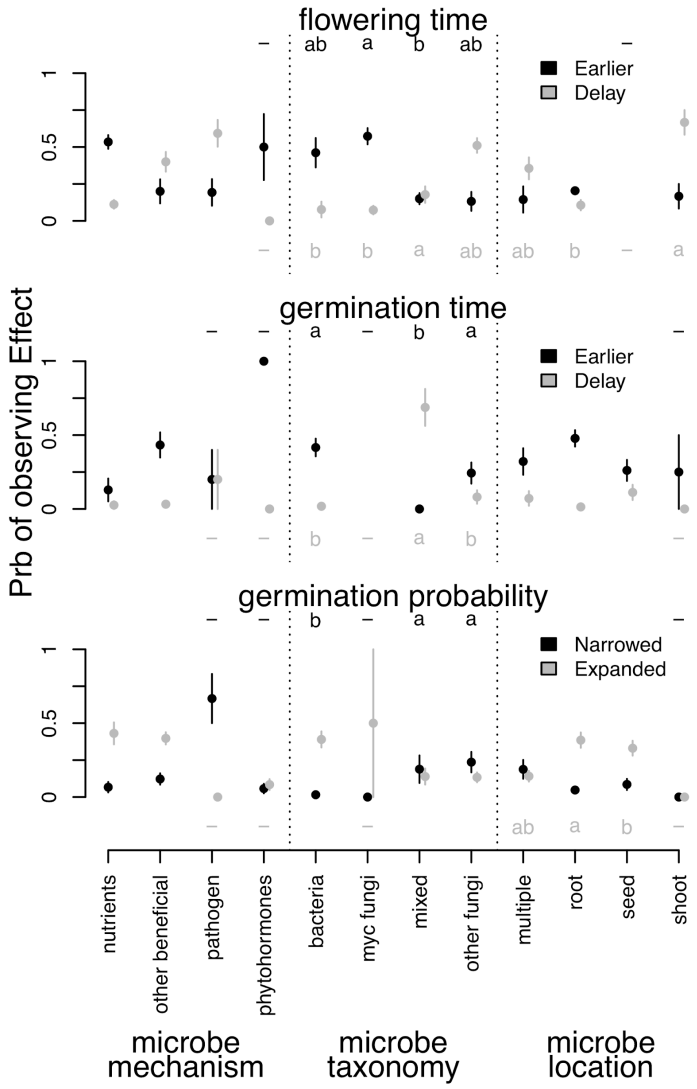


Appendix S6: Significant differences among categories related to hypotheses at 95% HPDI. The proportion of tests that found flowering time (top) germination time (middle) to happen significantly earlier (black), or to happen significantly later (grey) when a microbial treatment is applied. On the bottom, the proportion of tests that found a narrowed (black) or expanded (grey) likelihood of germination. Sections separated by vertical lines indicate separate model tests for differences between categories. Letters indicate significant differences in

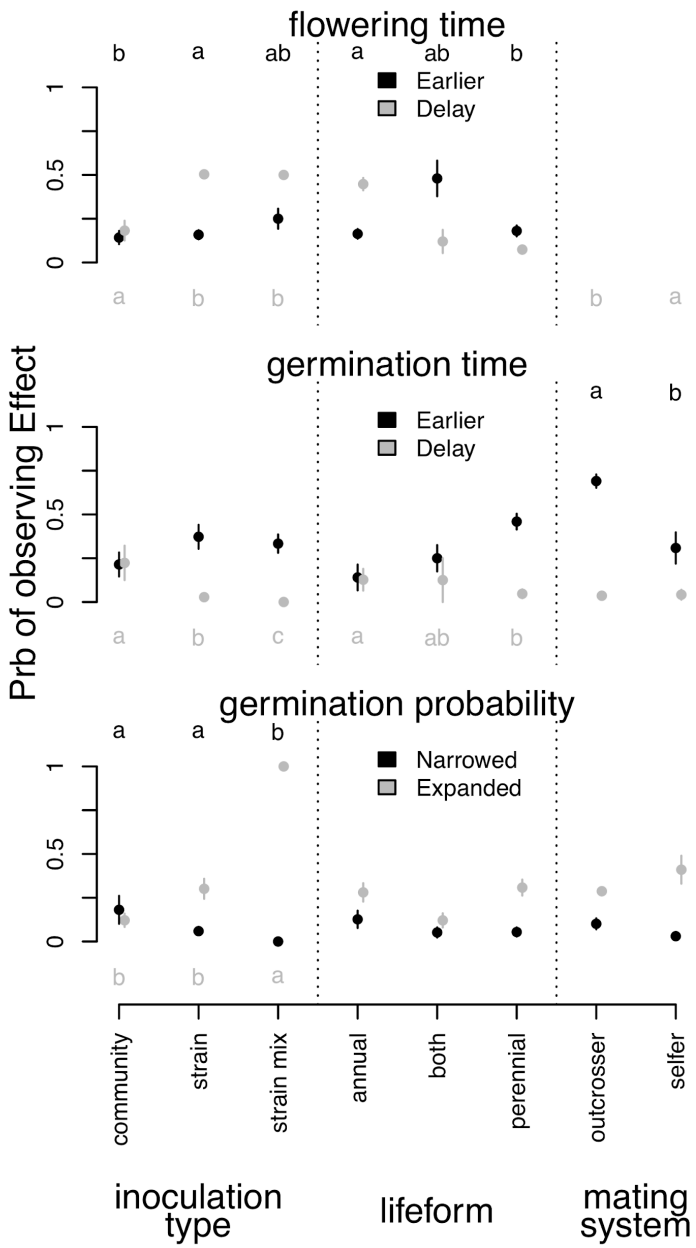
binomial models, where the difference is significant at the latent variable level, and the letters are ordered from highest probability to lowest. Points and bars are study-weighted means and +/- standard errors of the mean note that because models including random effects are fit on the logistic scale, model-fit differences and study-weighted mean probabilities do not perfectly align.

Appendix S7: Contingency tables showing overlap between the number of tests in each of the categories of microbe location, taxa and effect on plants that we hypothesized would influence the prevalence and direction of effects.

		Microbe location			
		multiple	**root**	**seed**	**shoot**
Microbial effect	**nutrients**	1	352	8	8
	other beneficial	129	30	82	29
	pathogen	41	6	8	9
	phytohormones	2	10	0	0
	unknown	0	298	88	0

		Microbe location			
		multiple	**root**	**seed**	**shoot**
Microbial taxonomic group	**bacteria**	44	187	121	8
	MF	0	180	0	0
	mixed	0	299	35	0
	otherfungi	129	30	30	29
	virus	0	0	0	9

		Microbial effect				
		nutrients	**other beneficial**	**pathogen**	**phytohormones**	**unknown**
Microbial taxonomic group	**bacteria**	138	128	3	8	83
	MF	180	0	0	0	0
	mixed	49	12	0	0	273
	otherfungi	2	130	52	4	30
	virus	0	0	9	0	0



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1018 **Appendix S8:** The proportion of tests that found flowering time (top) germination time

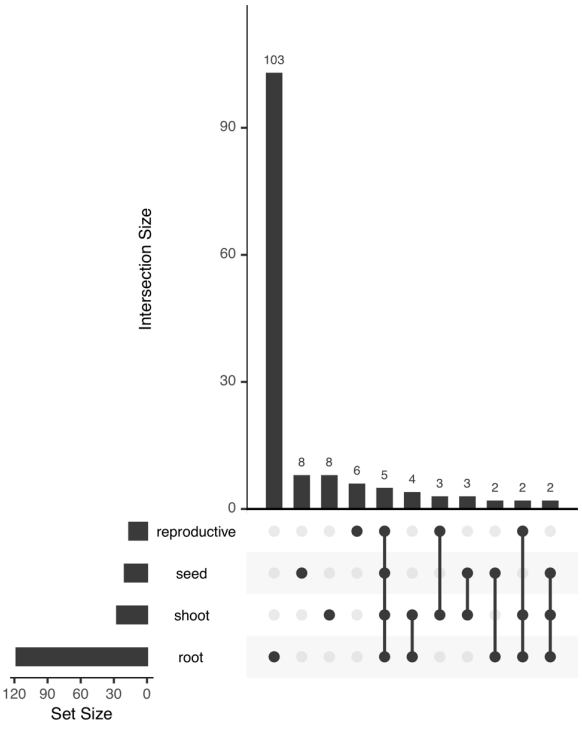
1019 (middle) to happen significantly earlier (black), or to happen significantly later (grey) with

1020 different experimental methods, lifeforms, or mating strategies. On the bottom, the proportion

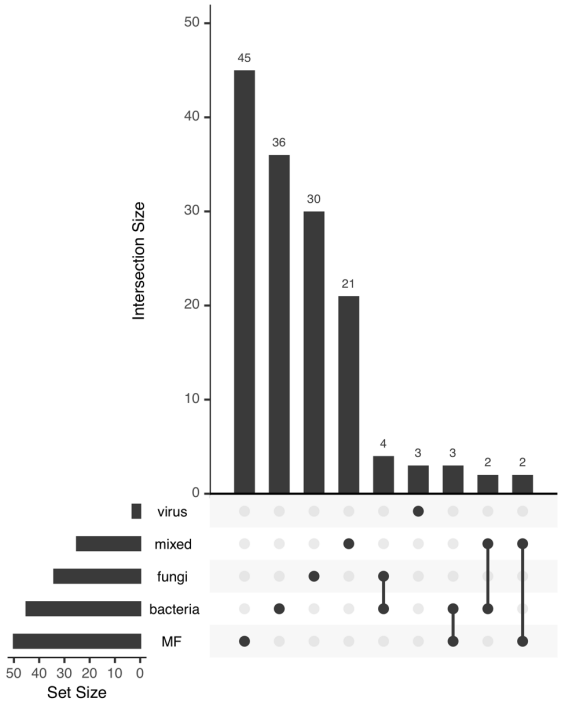
1021 of tests that found a narrowed (black) or expanded (grey) likelihood of germination. Sections

1022 separated by vertical lines indicate separate model tests for differences between categories.

Letters indicate significant differences in binomial models (at 90% HPDI), where the difference is significant at the latent variable level, and the letters are ordered from highest probability to lowest. Points and bars are study-weighted means and +/- standard errors of the mean; note that because models including random effects are fit on the logistic scale, model-fit differences and study-weighted mean probabilities do not always perfectly align.



Appendix S9: Out of all the scored records, the numbers of studies considering microbes residing in each plant tissue.



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1033 **Appendix S10**: Out of all the scored records, the numbers of studies considering microbes in

1034 different coarse taxonomy categories.

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FIGURE LEGENDS

Figure 1. Microbial symbionts and neighbors can alter the timing of life-history transitions in both annual (left) and perennial (right) plants, across all phenological transitions.

Figure 2. The number of studies out of our 500 scored records that included tests for microbial effects on a particular phenophase (lower left-hand graph), and the same for each combination of phenophases (indicated by connected dots) or studies that only included one phenophase (both, right-hand plot).

Figure 3: The probability that a test finds flowering time (top) or germination time (middle) to happen significantly earlier (black), or to happen significantly later (grey) when a microbial treatment is applied. On the bottom, the probability that a test that finds a narrowed (black) or expanded (grey) likelihood of germination. Sections separated by vertical lines indicate separate model tests for differences between categories. Letters indicate significant differences in binomial models, where the difference is significant (90% highest posterior density interval, HPDI, see Appendix S6 for 95% HPDI) at the latent variable level, and the letters are ordered from highest probability to lowest. Points and bars are study-weighted means and +/- standard errors of the mean. Note that because model random effects are fit on the logistic scale, model-fit differences and study-weighted mean probabilities do not perfectly align.