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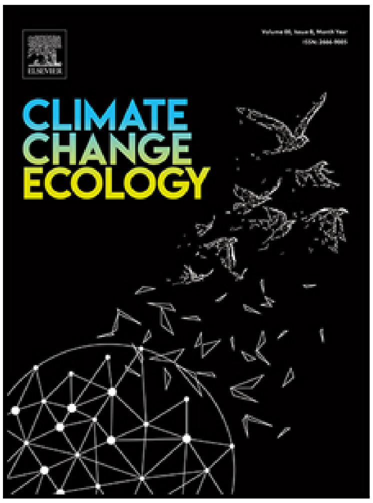

From the ground up: building predictions for how climate change will affect belowground mutualisms, floral traits, and bee behavior

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Highlights

- Climate change affects species and their interactions, reshaping communities.
- Mutualistic soil microbes are likely shifting in phenology and distribution.
- Shifts may affect floral traits, such as flowering phenology and floral rewards.
- Altered floral traits will affect bee behavior and plant-pollinator interactions.
- As a result, soil microbe-plant-pollinator tripartite mutualisms may be disrupted.

From the ground up: building predictions for how climate change will affect belowground mutualisms, floral traits, and bee behavior

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Abstract

Climate change affects species and their interactions, resulting in novel communities and modified ecosystem processes. Through shifts in phenology and distribution, climatic change can disrupt interactions, including those between mutualists. Mutualisms influence the structure and stability of communities and can link species to a common fate. However, research on climate change has focused on pairwise mutualisms, neglecting the higher-order interactions that can arise when species interact with multiple mutualists. We explore the effects of climate change on tripartite interactions involving belowground mutualists, namely soil bacteria and fungi, flowering plants, and pollinators. We outline how climate change is predicted to affect the phenology and distribution of these belowground mutualists, emphasizing the consequent effects on host plant floral traits, plant-pollinator interactions, and bee behavior. We find evidence that warming, advanced snowmelt, and drought are likely to cause phenological and distributional shifts in soil microbes, leading to diminished mutualistic interactions with plants and symbiont switching. Consequently, shifts in flowering phenology, smaller floral displays, and lower quality floral rewards are expected, increasing foraging time and energy demands for bees and altering their floral preferences. Such costs could translate into reduced fitness and novel selection pressures for bees and flowering plants in the short term. We highlight knowledge gaps and ways forward, urging studies on microbe dispersal and phenological cues, experiments that manipulate soil microbe-host plant interactions under simulated climate change conditions, and large-scale field studies across environmental gradients, all with the goal of understanding how climate change will affect soil microbe-plant-pollinator mutualisms.

Keywords: *distribution, higher-order interaction, mycorrhizae, phenology, rhizobia, tripartite*

1. Introduction

Mutualisms are ubiquitous in nature, and most species interact with multiple mutualists simultaneously [1–3]. Mutualistic interactions profoundly influence the structure and stability of ecological communities, in part because they can link species to a common fate, initiating extinction cascades that can follow directly or indirectly from the loss of interdependent species [4–12]. Environmental change can directly affect mutualistic networks by leading to changes in abundances of mutualistic partners. It can also indirectly affect mutualisms by altering traits that structure interactions [13]. For example, temporary removal of dominant bumble bee pollinators from natural communities caused behavioral changes in the remaining pollinator community, resulting in reduced foraging specialization and likely reduced plant reproduction [10]. Mutualistic interactions, and biodiversity in general, are thus critical to the stability and functioning of communities and the provisioning of ecosystem services, such as pollination.

Anthropogenic global climate change is altering the phenology, distribution, trait expression, and, ultimately, evolution of species [14–22]. These climate change-driven effects can in turn alter the incidence and strength of mutualistic interactions [2,23–27]. Because mutualistic partners vary in quality, species are not equivalently effective, with functional roles that depend on the broader community context [10]. As potential partners may respond differently to changing climatic cues and because receptive partners must overlap in both phenology and distribution, the effects of climate change on mutualisms are complex and difficult to predict, even for pairwise mutualistic interactions [25,28–32].

Adding to this complexity is the fact that climate change-induced shifts in phenology, distribution, or trait expression that affect one mutualism can alter the strength and persistence of a second mutualism involving a common focal partner. Higher-order mutualists can interact indirectly with the other partners of a mutualist via a shared partner, and these indirect mutualists can benefit each other [33,34]. Though common, these higher-order interactions, which in this case are mutualistic interactions that are affected by the presence and strength of another mutualism, are greatly understudied relative to pairwise mutualistic interactions [35–37]. To understand the complex ecological implications of climate change on mutualisms, we must move beyond pairwise interactions and incorporate higher-order mutualisms [38–40].

Multiple mutualist effects and emergent higher-order interactions may be particularly important for mutualisms involving soil microbes, flowering plants, and pollinators, as these mutualistic partners span multiple trophic levels that are likely to respond differently to climate change [41]. Whereas mutualisms between plants and pollinators have been relatively well-studied, those between plants and soil microbes have received less attention until recently [e.g., 42–45]. Plant-soil microorganism interactions strongly affect plant survival, phenology, and landscape-scale patterns of floral and faunal diversity [8,46–54; Fig. 1]. Similarly, soil microbial mutualists affect the production of flowers and floral rewards, including nectar and pollen, which in turn affects pollinator foraging behavior [55–59; Fig. 1]. Thus, by studying how the tripartite mutualistic interactions among soil microbes, flowering plants, and pollinators, such as bees, is affected by climate change, we can gain valuable insight into the higher-order interactions that may modify the direct effects of environmental change on species.

Pollinators and soil microbial symbionts, such as rhizobia and mycorrhizal fungi, provide very different benefits to plants, but both guilds of mutualists receive carbon resources (photosynthate) from plants and therefore potentially compete for shared resources or mutually benefit via positive effects on host plants [3,55,56,60]. Though we focus here on mutualistic interactions among rhizobia, arbuscular mycorrhizal fungi (AMF), plants, and pollinators, we note that context-dependent competition between mutualists can also shape these interactions

[61]. Interactions with one mutualist guild (e.g., soil microbes) are likely associated with increased investment in another mutualist guild (e.g., pollinators). Leguminous (Fabaceae) plants in particular can form mutualistic interactions with both rhizobial bacteria and AMF. Many legumes form specialized root structures called nodules that house rhizobial bacteria. Within the nodule, rhizobia fix atmospheric nitrogen (N) to biologically available forms [62]. Increased N benefits the plant in terms of increased growth, photosynthetic capacity, pollen and nectar quality, and flower production [63–69]. Often simultaneously, AMF colonize legume roots. AMF form symbioses with around 80% of all terrestrial plants and develop structures (e.g., hyphae, arbuscules) that increase plant access to resources, namely phosphorus and water [70], especially in dry conditions [71,72], thus increasing plant growth, flower production, and fruit production [55,73]. However, some species of AMF are parasitic and can negatively affect plant growth [2]. Weakening or disruption of soil microbe-plant mutualisms may shift flowering phenology, reduce floral abundances, and decrease plant nutrient content, lowering the quality of nectar and pollen floral rewards, consequently affecting pollinator foraging behavior and fitness [74]. However, few studies bridge the effects of soil microbe-plant mutualistic interactions on plant-pollinator mutualisms [75].

Here, we explore how global climate change can affect higher-order mutualisms by altering the strength and/or outcome of interactions (e.g., those between soil microbes and plants) that in turn affect higher-order partners (e.g., bees). We synthesize what is known about the effects of climate change on the phenology and distribution of soil microbes that interact mutualistically with plants, namely symbiotic N-fixing bacteria and AMF, and how these effects are in turn predicted to alter floral traits and bee behavior and fitness, thereby reshaping plant-pollinator interactions. We conclude by discussing profitable future research areas that will be critical for furthering our understanding of higher-order mutualistic interactions in a rapidly changing world.

2. Known and predicted effects of climate change

The phenologies of flowering plants and pollinating insects are shifting in response to changing climatic cues, including precipitation and temperature [31]. These shifts have been widely documented, and numerous studies have investigated the consequences for plant-pollinator interactions [e.g., 26,76–82]. Similarly, it is well-understood that the distributions of plants and pollinating insects are shifting in response to climate change [83–86]. In contrast, phenological and distributional responses of soil microbes and how these responses will affect interactions with plants have received little attention. In this section, we focus on known and predicted effects of climate change on the phenology and distribution of soil bacteria and fungi. We then consider how phenological and distributional shifts in these belowground mutualists may scale up to influence floral traits and bee foraging behavior.

2.1 *Phenological responses of soil bacteria and fungi*

The phenology of microbes can be defined as periodic life cycle events driven by abiotic or biotic factors [87]. To date, studies on microbe phenology have examined temporal shifts in microbial metabolism, plant root infection, reproductive events, and production of growth structures [87–93]. For example, the warmer temperatures, longer day lengths, and increased soil moisture levels associated with the onset of spring in temperate environments initiate phenological transitions in the metabolic states of soil microbial species [94,95; Fig. 2]. Soil microbial biomass can increase or decrease with snowmelt [96,97], and microbial community composition exhibits seasonality, differing in winter, during snowmelt, and after snowmelt in spring [95,98,99]. Many soil microbes face ecophysiological challenges in drying soils that shape their phenology. In dry conditions, soil microbes are expected to allocate fewer resources to reproduction and more to survival [100–102], thereby shifting the timing of reproduction.

Initial work has indicated that soil bacterial phenology is driven by both stochastic, neutral processes and by niche-driven processes, and that the relative influence of these drivers changes seasonally [103]. Soil carbon availability, itself seasonally variable, may shape soil bacterial phenology [104,105]. For example, low soil carbon availability appears to limit rhizobial growth [106]. Additionally, strigolactones, plant hormones responsible for several plant growth processes, are released under resource limitation and can stimulate rhizobial motility, increasing the chance of infection and potentially also regulating nodule number [107–111]. These seasonally-variable root exudates may provide a link between the phenologies of plants and soil bacteria [112]. At the same time, soil bacteria shape host plant phenology. Numerous agricultural studies have demonstrated that bacteria are able to promote seed germination by excreting phytohormones [113–118], thereby advancing flowering and fruiting [119]. If bacteria are dormant or unable to interact with a host seed, there will be little to no germination stimulation from the bacteria [120,121], delaying downstream plant phenology. Bacteria, in particular, are susceptible to desiccation and cell death in dry conditions [100,122–124]. To avoid losing water to their environment, many cells become dormant [102,125]. For example, drought leads to dormancy in free-living rhizobia, the rapid inhibition of N-fixation in symbiotic bacteroid cells, and denodulation in legumes [126–130]. As a result, the mutualism between legumes and N-fixing bacteria can weaken or break down in the short term due to soil drying. Active cells in dry soils will have difficulty forming interactions with plant roots because decreases in soil moisture negatively affect the signaling abilities of soil bacteria and plants [102,131].

The phenology of belowground fungi, including AMF, is driven both by the phenology of host plants [132,133] and by climatic variables such as temperature and precipitation [93,134–139]. For example, the number of AMF arbuscules peaks during host seed production [88,139], when plants require more phosphorus and nitrogen. Seasonal patterns in percent root colonization by AMF can differ greatly among plant species within a single habitat [140,141], suggesting that phenophase-specific nutritional demands of host plants influence the intensity of plant-AMF interactions. Temperature significantly affects rates of root colonization by AMF, and higher temperatures can have positive, neutral, or negative effects depending on plant species studied [42,140,142,143]. Additionally, in two arid grassland systems, AMF root colonization increased with soil moisture [91,144] and was highest after rain events [89]. In contrast, in two tropical systems, root colonization of AMF occurred predominantly in the dry season [144,145]. The same was found in a long-term experiment in a subalpine ecosystem where increased drought stress led to increased AMF colonization in graminoids [146]. Increased AMF colonization may reflect drought and rainfall-event driven seasonal changes in strigolactone production [147,148], which initiates AMF spore germination and hyphal branching to stimulate AMF-plant interactions [149,150]. However, the variable effects of precipitation on AMF-plant interactions indicate that geographic context may determine the relative strength of abiotic factors and host plant phenology in shaping AMF phenology. Finally, because changing abiotic factors affect the phenologies of fungal guilds differently, temporal reshuffling of fungal symbionts may occur. For example, increasing global temperatures have lengthened the fruiting seasons of fungi that produce aboveground sporocarps [136]. However, among these fungi, the phenologies of saprotrophs and fall-fruiting ectomycorrhizae were strongly linked to temperature, whereas the phenologies of spring-fruiting ectomycorrhizae were linked to primary productivity and precipitation [93,136]. Differing phenological cues among fungal taxa may increase the likelihood of mismatches and symbiont switching with host plants.

2.2 *Distributional responses of soil bacteria and fungi*

Generally, mutualistic interactions ameliorate abiotic stressors, allowing partners to overcome limitations in novel environments [151,152]. For this reason, mutualistic partners are often able to inhabit a broader range of habitats [22–24,34,153]. For example, because rhizobia increase plant N, the mutualism between legumes and rhizobia can help plants expand their ranges to nutrient-poor habitats. Similarly, because AMF associations improve plant water acquisition, host plants may be better equipped to tolerate climate change-induced drought conditions and thus less likely to contract in range [154,155]. In the event that plants shift in distribution, microbes have been shown to improve plant survival in higher-elevation habitats, likely due to improved nutrient and water acquisition [156]. Conversely, the absence of mutualists can negatively affect population persistence and limit species distributions [157–161].

Although the hypothesis that, for microbes, “everything is everywhere, and the environment selects” was universally accepted for many years [162], recent work has shown that host plant range, soil properties, dispersal limitation, and chance are key factors determining the distributions of soil microbial populations [70,163–170; Fig. 3]. Three hypotheses have emerged to describe distributions of AMF: the driver hypothesis, which states that AMF communities drive plant community assembly; the passenger hypothesis, where AMF communities are shaped by changes in plant communities; and the habitat hypothesis, which states that habitat selects for both plant and AMF taxa, causing covariation [171,172]. In any of these scenarios, it will be important to understand how climate change is modifying microbe distributions.

Despite the important role of dispersal in shaping soil microbe distributions, we know very little about the dispersal abilities of soil microorganisms [173,174]. A partnership that lacks co-dispersal is more likely to become spatially mismatched than a symbiosis that is vertically transmitted, as co-dispersal may ensure the spatial co-occurrence of partners [32; Fig. 3]. Non-co-dispersed symbionts, including legumes and rhizobia as well as mycotrophic plants and AMF, may be at higher risk of becoming spatially mismatched as they may track climate differently. Moreover, because AMF reproduce underground [70], they are likely to be dispersal-limited and at a greater risk of spatial mismatch with former interaction partners [45]. Some plant-AMF interactions may, however, be buffered from distributional mismatches by the similar dispersal patterns of host seeds and the spores of their associated AMF taxa, known as “pseudo-vertical transmission” [175,176]. Additionally, in horizontally transmitted mutualisms, cell motility can alter root infection rates [177], such that increased motility could increase competitive ability and thus likelihood of root infection.

Little is known about how and if soil microbial species are shifting spatially in response to climate change [44,178]. Climate change-driven increases in temperature and interannual rainfall variability will likely cause the distributions of some soil-based fungal taxa to move up in elevation, whereas the plants they interact with may shift at a dissimilar rate [179], leading to spatial mismatches between former partners and novel interactions (Fig 3). For example, *Helianthella quinquenervis* formed interactions with dark septate endophytes, beneficial, facultative fungal plant symbionts [180], more so than with AMF when near *Festuca thurberi*, a dark septate endophyte host [181], indicating symbiont switching in *H. quinquenervis*. Similarly, range-shifting plant species were found to have root symbionts more similar to plants in their new range compared to plants in their native range [182,183]. A generalist strategy may be important for establishing in new ranges. Specialist legumes may be less likely to find a compatible rhizobial partner in novel habitats and thus may fail to establish [22,184], although legumes in novel habitats without coevolved rhizobial partners often have relaxed partner choice mechanisms [185]. Although plants may form interactions with different partners, those partners may not confer equivalent benefits to the host plant, affecting flowering and ultimately plant fitness [180,186–188]. Indeed, some AMF species have been shown to be parasitic [189]. Additionally, some soil microbes may decrease in abundance near the soil surface due to climate change-driven increases in temperature, potentially affecting the overlap of plant roots and microbes and the outcomes of interactions [190,191; Fig. 4]. For example, thawing of permafrost led to a shift in fungal communities from beneficial to pathogenic groups [192]; warming could expose plants to different, possibly less beneficial, partners.

2.3 *Effects of soil bacterial and fungal responses on floral traits*

In considering how shifts in the phenology and distribution of soil bacteria and fungi will affect floral traits, we note that obligate mutualisms are expected to have lower risk of mismatch than facultative mutualisms, partly because selection is stronger for partners to maintain obligate interactions [32]. As AMF are obligate symbionts [193], we predict there will be strong pressure to maintain phenological and spatial overlap with host plants, and therefore host plant floral traits that are strongly influenced by AMF mutualisms are less likely to be altered. Conversely, N-fixing bacteria and several other plant-associated soil microbes able to survive as free-living cells can interact with host plants facultatively and are therefore more likely to become mismatched in a changing climate.

Just as floral traits such as nectar quality can be directly related to soil nutrient availability [194], weakening or loss of the interaction between plants and mutualistic soil bacteria due to phenological or distributional mismatches will indirectly affect floral traits by altering host plant nutrient acquisition [119]. Supplemental N increases vegetative growth rates, herbivore defenses, photosynthetic rates, flower production, floral reward quality, pollinator visitation, pollen germination success, and plant reproductive success [63–69,74,195–197]. Increased plant-available N from the interaction between rhizobial bacteria and legumes is expected to have effects similar to supplemental N [58], as nodulating bacteria directly increase the N content of the host plant [198–200]. Indeed, mutualistic rhizobia have been found to affect some of these same traits [119,200–205]. Nectar sugar content [glucose, fructose, and sucrose; 206], volume [65], amino acid diversity [207], and pollen mass [63] vary with plant N and are also altered by the floral microbial community and other plant mutualists [200,208–210]. Disruption of the interaction between N-fixing bacteria and legumes could strongly influence host-plant functional traits, such as flowering phenology and floral reward quantity and quality.

Though drought may decrease interaction strengths between legumes and previously competitively dominant rhizobia as a result of prolonged dormancy, drought-tolerant rhizobia may experience increased nodulation success [211]. Symbiont switching in stressful conditions has been found to negatively affect some host species [212]. For example, seedlings grown without their “home” microbial symbionts experienced decreased growth rates compared to seedlings grown with coevolved root symbionts, with growth benefitting when these plants were later inoculated with coevolved microbes [213]. Similarly, novel soil microbial symbionts may confer lower-quality rewards for the same investment, reducing the net benefit of the mutualism for host plants, and altering floral traits that affect higher-order interactions [214]. Though host plants may impose sanctions on cheating strains of rhizobia in the long-term [215,216], symbiont switching in stressful conditions can cause novel, sometimes negative, effects in the short-term.

Most work linking belowground symbionts to floral traits has been focused on AMF. While it has long been understood that AMF play an important role in plant productivity and nutrient cycling [217–219], more-recent work has established that plant-AMF interactions also affect the production of flowers and floral resources [58,220]. AMF colonization of plants can increase flower number in some plant species and flower size in others [55], potentially a result of increased water availability [221]. While this effect may in some cases be linked to the positive effect of AMF on plant biomass, some plants colonized by AMF preferentially allocate resources to reproductive rather than vegetative structures [222]. Interactions with AMF on the parasitic end of the continuum may decrease floral display size [2,186,223–225]. By using extraradical hyphae to hydrolyze organic phosphates and transporting the resultant inorganic phosphorus to plants [226], AMF increase pollen production, pollen grain size, nectar volume, and nectar sugar content [55,227,228]. AMF also decrease concentrations of the alkaloid nicotine in pollen [229]. Although the effects of AMF on floral micronutrients have received little study, AMF-colonized plants have higher levels of foliar potassium [230], indicating that micronutrients in floral resources may indeed be affected by AMF.

Switching of AMF symbionts in response to climate change-driven phenological or spatial shifts may affect host plants in various ways, as the effects of plant-AMF symbioses on floral traits appear to depend on both the species and strain of AMF [222,228,230]. For example, among plants inoculated with either *Glomus hoi* or *G. claroideum*, plants inoculated with *G. claroideum* were more likely to produce flowers than those inoculated with *G. hoi* [228]. As distributions shift, plant species that are more positively affected by interactions with novel AMF can increase in abundance, leading to shifts in floral evenness [56]. Habitat type and soil fertility may also be important predictors of how floral traits will be affected by altered plant-AMF interactions. For example, fungicide application increased nectar sugar content in an alpine krummholz habitat but had no effect on floral rewards in a tundra habitat. As plants and AMF shift in distribution, they are likely to experience novel soil fertility regimes that similarly alter their dynamics [231].

Although we focus here on nodulating rhizobial bacteria and AMF, other soil microbes are known to influence floral traits. For example, soil *Streptomyces* bacteria, when in the rhizosphere, have been found to protect both flowers and honey bees from pathogens [232]. Natural soil microbes, including fungal, bacterial, and archaeal operational taxonomic units (OTUs), affect the mean flowering time of *Boechera stricta* [53]. Endophytic *Pseudomonas* bacteria enhanced the drought tolerance of host plants in serpentine soils [233], which could increase flower production and longevity under stressful conditions. Low-abundance strains of *Pseudomonas* increased root biomass and leaf chlorophyll content in host plants [181], which could affect floral traits. Dark septate endophytic fungi increased flower and fruit density in tomato plants [234], and exhibited increased host plant colonization rates after 20 years of experimental soil warming [146]. Ericoid mycorrhizae, which associate only with plants in the order Ericales, increased the number of *Vaccinium* inflorescences and flowers per plant, though this response was dependent on host plant genotype [235]. Additionally, plants grown in soils with experimentally simplified bacterial communities produced fewer flowers than those grown with more complex soil communities [48].

2.4 *Consequences for bee behavior and plant-pollinator interactions*

Altered resources for leaf, flower, fruit, and seed growth will mediate species interactions, including those with pollinators [43,58,65,236–240]. The quality and quantity of floral resources have dramatic effects on bee energetics, fitness, and population sizes [66,241–

245]. Pollen and nectar provide carbohydrates, lipids, protein, and micronutrients that bees [246–248] and other pollinating insects [249] rely upon to maintain existing populations and establish new broods [250]. Dietary protein content is crucial for reproduction, growth, and survival of bees and other insects [64,242,244,251–254]. Diets deficient in protein (e.g., a lack of essential amino acids) can negatively affect larval bee development and shorten adult lifespan [64,255,256]. Both nectar and pollen quality have been shown to alter feeding preferences of pollinators [207,252,257,258]. Most bees and many other insect pollinators prefer floral rewards with higher protein content [207,252,259–263]. In nectar, the concentrations of sugars influence the thoracic temperatures of social bees [264,265] and thus foraging energetics and behavior [266,267].

Though many studies have assessed the effects of altered soil N on plant fitness and floral functional traits, none to our knowledge have directly tested the effects of N-fixing bacteria on plant-pollinator interactions. Under severe abiotic stress, bacteria will become dormant, affecting interaction outcomes with legumes and influencing higher-order interactions with pollinators [268]. A reduction in or loss of germination stimulation by soil bacteria will delay host plant germination phenology and alter downstream phenophases, such as flowering onset [119], which will alter phenological overlap and interaction strengths between host plants and pollinators [269]. A shift in flowering phenology without a corresponding shift in pollinator phenology could decrease the fitness of both mutualists [79,82,269,270]. In the long-term absence of pollinators, traits that facilitate selfing may be selected for [271].

N-fixing bacteria may also allow plants to produce higher quality rewards, increasing pollinator visitation. A reduction in the strength of the interaction between legumes and rhizobia will affect plant N and negatively affect bee feeding preference via decreased flower number and nectar and pollen quality, which may affect bee fitness [272–274]. A change in reward quality and quantity would be especially important for oligolectic bees which feed on just one genus or species of plant. For example, *Osmia iridis* are Fabaceae-specialists which forage exclusively on *Lathyrus lanszwertii* var. *leucanthus* and *Vicia americana* flowers in parts of their range [275,276]. Reduced floral reward quality, caused by a mismatch between these legumes and N-fixing bacteria, could alter the foraging behavior of *O. iridis* and lead to fitness costs for both adults and larvae [274–276]. If flowers offer lower-quality rewards, more time and energy will be required to provision brood cells [277] increasing time and energy allocated to foraging and decreasing reproductive output of oligolectic bees.

The increased size and number of flowers produced by AMF-colonized plants [55,222], as well as effects on inflorescence structure [278], are likely to influence the behavior of bees and other pollinating insects. Indeed, plants colonized by AMF tend to receive higher rates of visitation [55] and are visited by different assemblages of pollinators [56]. In particular, floral visitation patterns of Hymenoptera were strongly affected by plant AMF colonization [55]. The mechanism for increased visitation differed among plant species: one species produced larger flowers, one produced more flowers, and one produced more nectar [55]. Additionally, suppression of AMF induced a shift in the insect visitor community from larger-bodied bees to smaller-bodied bees and flies, which was attributed to altered patch-level display [56]. Long-term loss of AMF may lead to selection for nutrient absorption traits, such as cluster roots or carnivory [212,279,280] and exert selection on pollinator foraging behavior in response to altered floral reward availability [281].

Climate change-driven switching of AMF symbionts may affect floral display and pollinator behavior and, because some pollinating insects prioritize nectar rewards whereas others prioritize floral abundance [282,283], shifts in plant-AMF interactions may lead to floral patches that are more or less attractive to different groups of pollinators. For example, AMF inoculation increased flower number and number of pollen grains, but bumble bees did not respond to these effects while dipterans and other hymenopterans visited AMF-inoculated plants more frequently [228]. Similarly, among plants inoculated with either individual species and strains of AMF species or an assemblage of AMF species, bumble bees visited plants inoculated with one AMF strain frequently, but honey bees probed fewer flowers of plants inoculated with a different AMF strain. Patterns of increased visitation by bumble bees and decreased visitation by honey bees were not related to the number or size of flowers; instead, the preferences may have been driven by unmeasured traits such as nectar quantity or floral volatile organic compounds that varied among plants inoculated with different fungal assemblages, species, and strains [230]. Similarly, AMF colonization increased insect visitation rates across three plant species, but the mechanisms (flower abundance, flower size, and nectar standing crop) driving this pattern were species-specific [55]. Differences in attractiveness may be particularly pronounced if some plants are colonized by AMF species on the parasitic end of the mutualism-parasitism continuum [186,189,224–227], leading to decreased floral displays and resource production.

Further, mycorrhizal plants may also be able to provide pollinating insects with higher quality floral rewards by increasing availability of micronutrients and phosphorus. These micronutrients play an important role in linking mycorrhizal fungi and pollinators. For example, by affecting nutrients in pollen and nectar, AMF can in turn reduce parasitism of bumble bees [229]. Likewise, by increasing plant potassium, which may be an important micronutrient for bee overwintering [284], AMF symbioses can indirectly shape pollinator fitness.

3. Ways forward

In section 2, we highlighted the predicted effects of climate change on the phenology and distribution of N-fixing bacteria and AMF, with an emphasis on how these shifts may affect plant traits important to higher-order mutualists, such as bee pollinators. Many of our predictions stem from work on pairwise interactions, agricultural studies, and nutrient supplementation or limitation studies. In this section, we outline lab-, greenhouse-, and field-based studies that could advance our understanding of higher-order interactions and multiple mutualist effects. We also identify key gaps in our understanding of the bottom-up effects of soil microbe-plant interactions on pollinator behavior and fitness.

3.1 *Phenological responses of soil bacteria and fungi*

As described in section 2.1, little is known about the phenology of soil microbes. Most work has examined soil microbial phenology in the context of plant phenology and does not address how climate change-driven shifts in temperature and precipitation may affect soil microbial phenology itself. To move forward, we first need to build on our understanding of how temperature and soil moisture influence microbial life history stages and transitions among them. This work could be performed in a field setting by sequencing the active microbial soil community throughout seasons [88,285]. Active communities could be examined by direct microscopy, using RNA-based FISH (fluorescence *in-situ* hybridization) [286,287] with complementary staining, and microbial growth approaches [285]. These methods may help to identify species that are active at each time point and avoid underestimating the abundance of microbes due to RNA decay in soil [285]. Quantifying structures, such as AMF hyphae, spores, and arbuscules [139], or comparing gas fluxes to identify functional groups that are active in soils [288] may also offer insight into how microbial communities change seasonally. To understand how plant phenology affects microbial phenology, similar studies could be performed with sampling during specific plant phenophases. Quantum dots, nanoparticles that fluoresce under fluorescent light, could be used to track periods of nutrient and water transport and inactivity in microbes [289]. It may also be important to identify how and when microbes form “seed banks”, or reserves of propagules that are resilient and last in soil for long periods of time [125]. This work could be performed by collecting and identifying spores of AMF [290] or by sequencing soil for inactive rhizobial species, though relic DNA should be controlled for in analyses [291].

To more directly assess the effects of temperature and soil moisture on microbial phenology, plants and microbes could be grown together under different abiotic conditions representing different climate change scenarios, and plant and microbial phenophases could be compared. It is understood that changes in plant phenology alter the phenology of AMF and rhizobia; the host plant life cycle shapes AMF phenophases [139] and can alter the timing of nodule formation and bacterial release to the environment [292,293]. However, disentangling the effects of microbial phenology on plant phenology from the effects of plant phenology on microbial phenology presents a significant hurdle. Examining how the phenologies of plants and microbes respond to abiotic treatments may provide a step forward. For example, greenhouse studies could compare the effects of an “extended summer” treatment on duration of flowering versus AMF arbuscule formation. If the treatment causes plants to flower longer but does not extend periods of arbuscule formation, this would suggest that AMF and plants respond differently to climatic cues.

To assess the effects of potential phenological mismatches between plants and soil microbes, experimental studies could simulate novel partner interactions, weakened interaction strength, and mutualism breakdown. These studies could be performed in a greenhouse setting, by growing plants of the same genotype with partners they would be expected to interact with given a phenological shift, with current mutualistic partners in dormant stages, and without any mutualists present. Antibiotics could be applied to soil [231] to decrease bacterial or fungal growth at certain plant phenophases to simulate the potential effects of partner mismatch and loss. Then, functional traits of these plants and microbes could be measured under different climate change scenarios.

3.2 *Distributional responses of soil bacteria and fungi*

To form a predictive framework for how climate change will affect the distributions of soil microbes, it will be crucial to better understand how microbial distributions are affected by the current climate. This could be achieved by sampling soils across large environmental gradients, identifying and quantifying the abundances of microbes such as rhizobia and AMF in these samples, and combining microbe abundance with climatic data to produce species distribution models [294]. Joint species distribution models and co-occurrence networks could also be used to assess how the distributions of microbes and plants are affected by one another and by the environment [295,296]. Recent work using species distribution modeling to compare plant and bacterial ranges revealed that the presence of one group of bacteria explained absence of one plant species [297] and that soil microbe distribution can determine competitive outcomes in plants [298]. To improve our understanding of how distributional shifts may affect tripartite interactions among microbes, plants, and pollinators, future species distribution models could focus on microbial taxa that are known to affect flowering [such as *Rhizophagus irregularis*; 230]. However, our knowledge of soil microbe dispersal, a component critical to accurate species distribution modelling [299], is currently limited.

As little is known about how soil microbial species disperse, it is difficult to predict how microbial ranges will expand and contract in a changing climate. Foundational studies on the dispersal mechanisms and limitations of important fungal and bacterial clades would be an important start. For example, regular soil coring along elevational gradients will reveal if isotopically labeled microbes are dispersing to higher elevations or moving down in the soil profile to track cooler, wetter conditions [44,300,301]. Similarly, greenhouse and growth chamber experiments that manipulate soil moisture and temperature, among other factors, would help us understand if soil microbial communities will undergo reshuffling in the soil profile under different climatic conditions. If soil microbes that were previously at a soil position where they could interact with host plant roots subsequently move down in the soil profile to access cooler temperatures, soil microbe-plant interactions, and thus plant traits, will be affected (Fig. 4). Additionally, some species of AMF are dispersed by animals, including small insects [302]. Next-generation sequencing could be used to identify the particles carried by belowground insects, and based on their life histories, inferences could be made about how far AMF spores are able to travel. Finally, by sampling across environmental gradients and performing a distance-based redundancy analysis, it may be possible to infer the importance of dispersal versus environmental processes in shaping AMF distribution [303].

Field experiments could be used to assess how plant traits important to pollinators may be affected by interactions with novel soil microbial communities. For example, sterile seeds from a single source population could be planted at various elevations, including beyond the current elevational range of an upward range-expanding plant. The floral traits of these plants could be quantified, then plant roots could be stained and sequenced to assess which microbial symbionts are present and to what extent they associate with plants across elevational gradients. This could give insight into how floral resources may be affected as seeds disperse into novel ranges with potentially novel soil symbionts. Similar work has been performed successfully in alpine systems with a focus on vegetative growth [156].

3.3 ***Effects of soil bacterial and fungal responses on plant-pollinator interactions***

We know of no studies that have examined how the effects of climate change on soil microbe-plant interactions will affect plant-pollinator interactions. Profitable areas of research in this field include the use of experimental studies that manipulate the incidence and strength of interactions among N-fixing bacteria, AMF mutualists, and host plants under simulated climate change conditions. Treatments involving elevated temperatures and more frequent, intense periods of drying could be applied to determine the effects of stressful environmental conditions not only on bacterial and fungal performance (e.g., hyphal growth, nodulation capacity, spore formation) but also on floral traits important to bees, and plant-pollinator interactions. Floral functional traits, such as flowering phenology, floral abundance, nectar and pollen protein content and amino acid diversity, volatile organic compound production, and nectar sugar content, could be quantified and pollinator foraging behavior measured. Field studies in sites that differ in mycorrhizal and rhizobial community composition can relate floral functional traits to sequenced root symbionts and pollinator foraging behavior. Additionally, in systems where snowmelt timing can be experimentally manipulated, the abundances and OTUs of N-fixing bacteria and AMF could be compared between advanced snowmelt and control plots and linked to floral functional traits and bee behavior.

To better understand what factors influence pollinator visitation to flowers of soil microbe-symbiotic plants, choice trials, wherein pollinators of different taxonomic and functional groups are given the choice to forage on plants inoculated with or without rhizobial bacteria and/or AMF could provide insight into pollinator preferences. Multi-generational studies measuring pollinator fitness could then be used to understand how N-fixing bacteria and AMF indirectly affect pollinator behavior, survival, and reproduction. To date, most work has ignored the effects of mutualistic soil microbes on insect pollinator fecundity [but see 229].

To elucidate the pathways through which rhizobia and mycorrhizae affect flowering and pollination, it may be useful to examine the gene functions of these microbes. Transposon insertion sequencing allows high-throughput gene functional analysis of microbes [304,305] and has been used to identify the functions of genes driving basic physiological processes in *Rhizobium leguminosarum* under different growth media [306]. By identifying genes in microbial taxa that affect mutualistic interactions and those that affect responses to changing climatic conditions, we may be able to determine which microbes are most likely to positively affect flowering and how they will respond to climate change. Additionally, the use of quantum dots may help inform which microbial genes are responsible for nutrient transport from soils to pollen and nectar [289]. A genome-wide association study or coexpression network approach could be implemented to identify loci that connect plant-microbial association with plant flowering [60,307,308].

It is also important to note that AMF and rhizobia interact to affect plant traits. Co-inoculation of rhizobia and mycorrhizae positively affects plant biomass and fitness [309,310], and harboring both N-fixing bacteria and AMF has been shown to synergistically increase legume fitness in particular [39,60,307,311]. How co-inoculation affects floral traits is an important area to explore. For example, co-inoculation with rhizobia and AMF increased legume photosynthetic rates by 51% [67], which could alter nectar quality and quantity [312]. Work on multiple belowground mutualists has found that N-fixing rhizobia increased colonization and sporulation of AMF on plant roots [313–315], whereas other lab studies have found that rhizobia inhibit or have no effect on AMF colonization [39]. AMF inoculation also affects bacterial communities. AMF increased the number and biomass of nodules, traits correlated with the presence and strength of rhizobia-legume mutualism [316,317], likely due to increased host phosphorus [313–315]. AMF-inoculated treatments had greater total bacterial biomass and a lower ratio of soil fungal biomass to bacterial biomass [318]. All in all, promotion of co-inoculation by both symbionts will increase plant fitness and may positively affect floral traits that shape plant-pollinator interactions.

4. Conclusions

Based on current understanding, we have generated predictions about how climate change will affect the phenologies and distributions of mutualistic soil bacteria and fungi, projecting how those shifts will affect the floral traits of host plants, and ultimately bee foraging behavior and plant-pollinator interactions. In part because the effects of climate change on soil microbes are inconspicuous relative to phenological and distributional responses of plants and pollinators, fewer data exist on how these mutualists will shift temporally and spatially in response to changing climatic conditions. Despite the paucity of data, we predict that elevated mean temperatures and prolonged drought will cause rhizobia and AMF to exhibit shifts in the timing of metabolic activity, dormancy, root colonization, and reproductive events, though the direction and magnitude of shifts will likely be shaped by environmental context. Phenological shifts are expected to alter the timing of interactions with host plants and the costs and benefits of these mutualisms. We further predict that these climatic changes will cause belowground mutualists to shift in distribution, both laterally and vertically, reshuffling soil microbial communities and leading to symbiont switching by host plants [180–183]. Consequently, we predict that changes in interaction timing or symbiont identity will alter host plant flowering phenology and generally reduce floral display sizes and the quality of nectar and pollen floral rewards [58,220]. These shifts in flowering time, driven by altered interactions with microbial mutualists rather than by altered abiotic cues, are predicted to reduce phenological overlap with some pollinators, particularly oligolectic solitary bees that have specialized diets and relatively short foraging seasons. Similarly, reduced floral resource availability will decrease pollinator foraging efficiency, potentially reducing reproductive output, and alter visitation patterns for bees with labile preferences. Finally, because pollinators differ in their effectiveness [e.g., 269,319], these changes in bee foraging behavior will likely affect pollination success and plant reproductive output.

To improve our ability to predict how climate change will affect the tripartite mutualism among soil microbes, flowering plants, and pollinators, we recommend three major research avenues. First, foundational studies are needed to determine the drivers of rhizobia and AMF phenology and to document the dispersal abilities of these microbes. These studies will enable us to better anticipate how climate change will affect microbial phenology and distribution. Second, we urge greater use of experiments that manipulate soil microbe-host plant interactions to isolate the effects of reduced interaction strengths, novel partners, and complete mismatches on plant functional traits, particularly floral traits that structure interactions with pollinators. Third, we advocate for large-scale field studies, both observational and experimental, on communities of soil microbes and flowering plants across environmental gradients. Observational studies would serve to characterize the relationships between soil microbial community composition and abiotic factors, particularly factors such as temperature and precipitation that are affected by climate change. Experimental studies, such as reciprocal transplants of seeds and/or microbes, would yield data on the outcomes of novel interactions and environmental contexts that accompany distributional shifts. By incorporating data on floral traits and pollinator visitation, such studies could also shed light on the consequences of novel soil microbe-plant interactions for plant-pollinator mutualisms.

Beyond the fundamental importance of these multipartite mutualisms for community stability and ecosystem services, such as pollination and nutrient cycling, our understanding of the ecology of rhizobia and AMF has implications for native plant conservation and restoration. For example, there are advantages to inoculating restoration sites with soils from the home range of the focal plant species. Coevolved microbial symbionts increase plant germination success, growth, and fitness [320–324], whereas commercially available microbial inoculum containing AMF and/or rhizobia that are not coevolved with the focal plants have been found to negatively affect plant establishment and growth in restoration sites [325]. In addition, conserving and restoring soil microbe-plant mutualisms in natural communities will benefit native bee populations, many of which are declining [326,327], by improving the quantity and quality of floral resources.

The study of multiple mutualists offers key insights into how climate change will reshape communities, yet these multipartite interactions have received little attention relative to bipartite interactions. In neglecting the potential higher-order interactions that can arise from multipartite mutualisms, we risk mischaracterizing how species and the ecosystem services they provide will be affected by climate change. For example, studies on plant-pollinator phenological synchrony that focus on abiotic drivers, without considering the influence of belowground mutualists on flowering time, may misjudge the risk of mismatch. We therefore advocate for greater study of the effects of changing climatic conditions on tripartite mutualisms involving soil microbes, flowering plants, and pollinators. With the advent of more-sophisticated sequencing technologies to characterize soil microbial communities, there is much opportunity to push forward our understanding of how these mutualisms will fare in a changing climate.

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure Legends

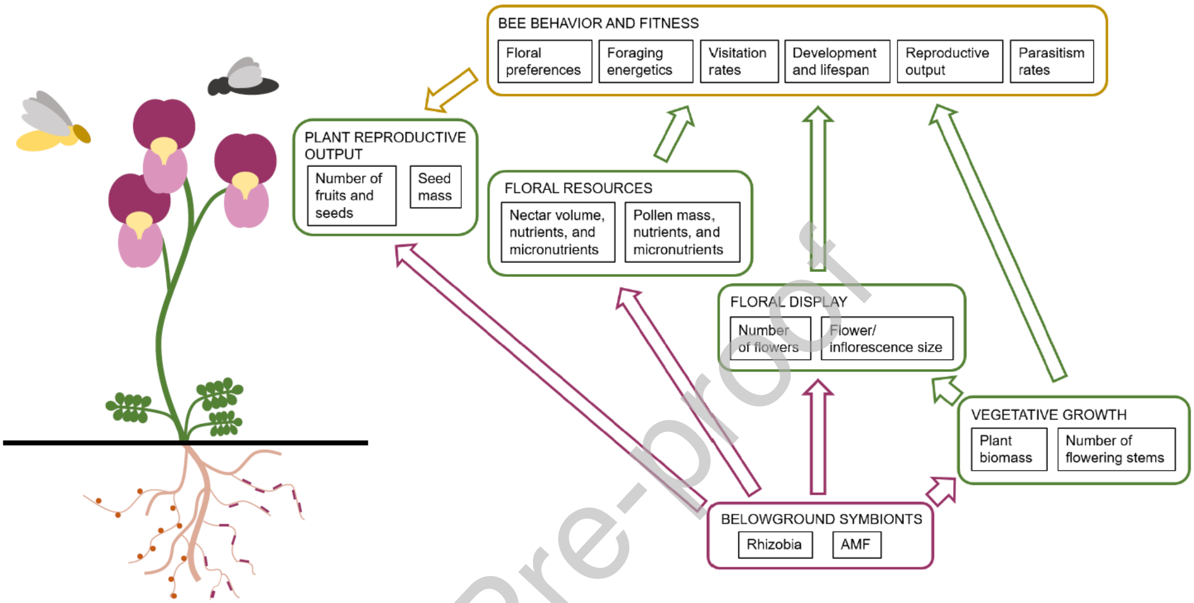

Figure 1. Links among belowground microbial symbionts rhizobia and arbuscular mycorrhizal fungi (AMF), host plant traits and fitness, and bee behavior and fitness. Mutualistic interactions with microbes affect plant vegetative growth, floral display, floral resources, and plant reproductive output. The affected plant traits in turn affect bee behavior and fitness. Bee behavior affects plant reproductive output.

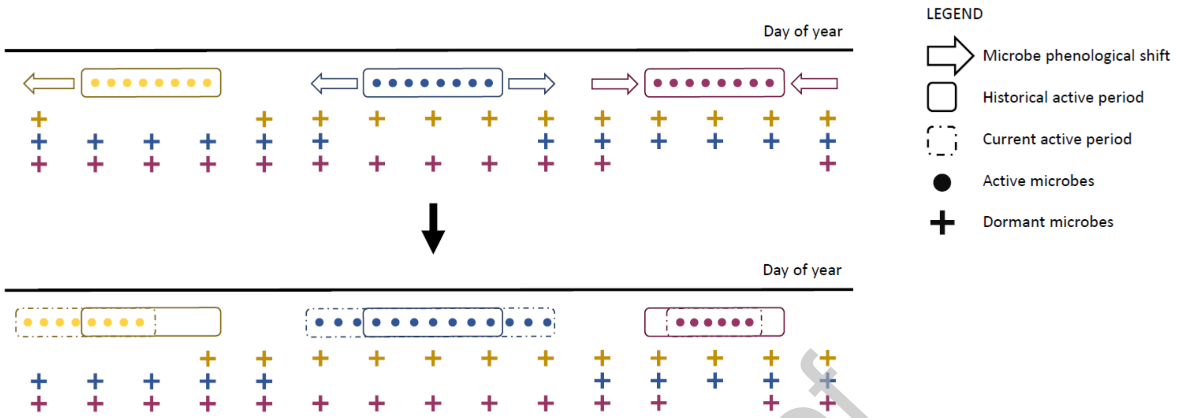

Figure 2. Potential outcomes of microbe phenological shifts. Climate change may induce shifts in the seasonal timing of microbial activity and dormancy. Active periods may be shifted earlier (yellow microbes), lengthened (blue microbes), or shortened (purple microbes). Dormant periods may be lengthened (purple microbes) or shortened (blue microbes).

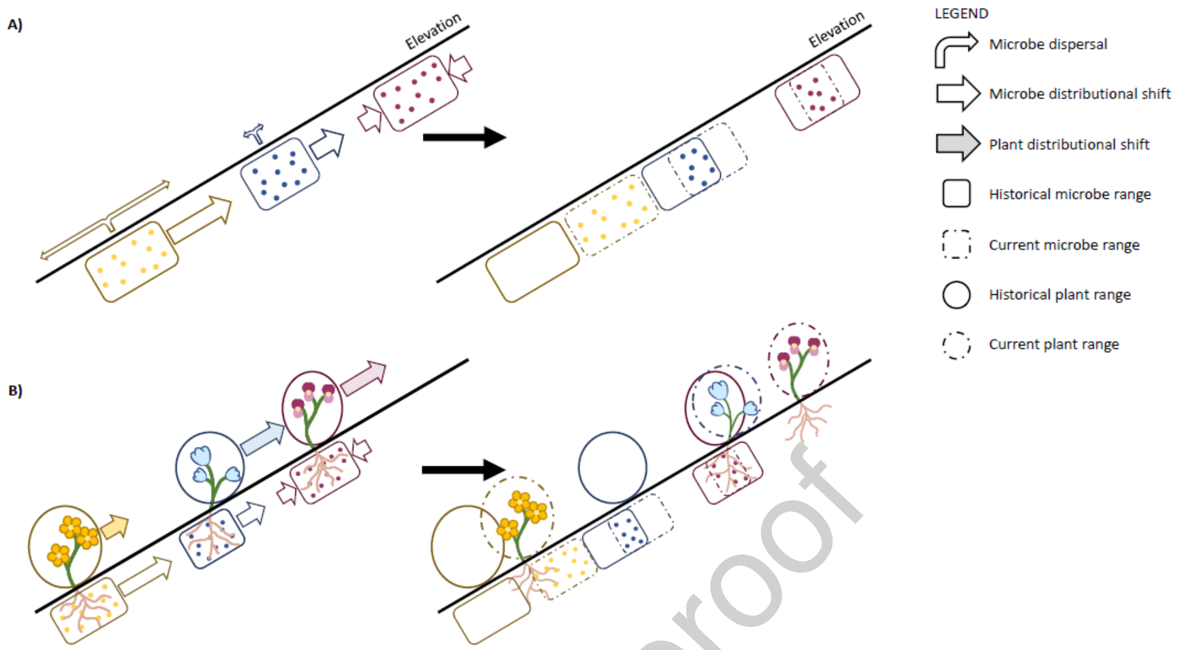

Figure 3. Potential outcomes of microbe and plant distributional shifts. **(A)** Climate change and microbe dispersal may interactively shape microbe distributional shifts, such that some microbial taxa shift upward in elevation to a greater (yellow microbes) or lesser extent (blue microbes) and others constrict in distribution (purple microbes). **(B)** Some plants may shift upward in elevation to a lesser extent than their historical microbial partners, resulting in reduced interaction strength (yellow plant). Some plant taxa may shift upward in elevation to a greater extent than their historical microbial partners, resulting in novel interactions (blue plant) or interaction loss (purple plant). However, vertically transmitted mutualists are less likely to experience partner mismatches than horizontally transmitted mutualists.

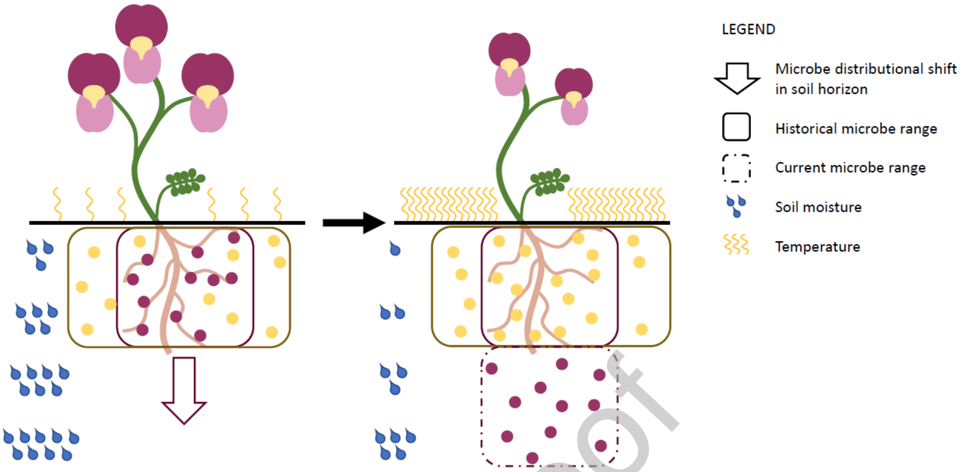

Figure 4. Potential outcomes of microbe distributional shifts in soil horizons. Higher temperatures and drier conditions near the soil surface (indicated by yellow lines and blue drops, respectively), driven by climate change, may cause soil microbes to shift downward, thereby disrupting interactions with host plants. This could potentially affect floral display or floral resource production.