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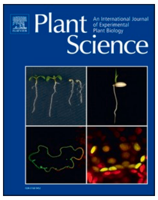

Review article

Review: Plant eco-evolutionary responses to climate change: Emerging directions

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ABSTRACT

Contemporary climate change is exposing plant populations to novel combinations of temperatures, drought stress, [CO_2] and other abiotic and biotic conditions. These changes are rapidly disrupting the evolutionary dynamics of plants. Despite the multifactorial nature of climate change, most studies typically manipulate only one climatic factor. In this opinion piece, we explore how climate change factors interact with each other and with biotic pressures to alter evolutionary processes. We evaluate the ramifications of climate change across life history stages,and examine how mating system variation influences population persistence under rapid environmental change. Furthermore, we discuss how spatial and temporal mismatches between plants and their mutualists and antagonists could affect adaptive responses to climate change. For example, plant-virus interactions vary from highly pathogenic to mildly facilitative, and are partly mediated by temperature, moisture availability and [CO_2]. Will host plants exposed to novel, stressful abiotic conditions be more susceptible to viral pathogens? Finally, we propose novel experimental approaches that could illuminate how plants will cope with unprecedented global change, such as resurrection studies combined with experimental evolution, genomics or epigenetics.

1. Introduction

Atmospheric carbon dioxide concentrations (hereafter: [CO_2]) have risen by 45 % since the Industrial Revolution [1] and temperatures are increasing globally [2]. In addition, climate change is altering precipitation patterns and increasing the frequency of extreme weather events worldwide [3]. Anthropogenic climate change is imposing novel selection on plant populations in increasingly fragmented landscapes [4,5]. Natural populations risk extinction if they do not respond to these shifts in climate by migrating to favorable climates, adapting to novel conditions, or shifting their phenotypes plastically [6,7]. We call for integrative and holistic approaches to generate robust predictions about the fate of natural populations in the face of climate change.

At the organismal level, global change can affect physiology [8], germination success [9], growth [10], flowering success [11], and fruiting phenology [12], as well as leaf senescence [13]. We integrate plant responses to climate change across development and consider how mating systems influence the adaptive potential to climate change. Next we assess how climate change could disrupt biotic interactions between plants and their antagonists (e.g., herbivores and pathogens) and mutualists (e.g., pollinators and beneficial microbes). We further evaluate how climate change could shift the balance between generalist and specialist biotic interactions. Finally, we highlight the complexities of accurately simulating global climate change and discuss emerging experimental approaches aimed at filling gaps in our understanding of the ecological and evolutionary consequences of global change.

2. Organismal and population responses to climate change

Contemporary climate change influences plants at all stages of development. At the organismal level, plants can respond to changing conditions by altering cellular responses and molecular mechanisms, shifting the timing of developmental events, and adjusting morphologically [14]. Here, we explore the developmental consequences of novel environments. Additionally, we consider the role of mating systems in shaping genetic diversity and gene flow within and among populations,

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and ultimately how reproductive strategies will influence the adaptive potential of plant populations.

2.1. Germination

The environmental conditions seedlings experience during germination can have a long-lasting impact across the life cycle [15,16]. Many plant species require specific temperatures and moisture levels to break dormancy, which may be at risk of disruption due to climate change [17]. Additionally, temperature and water availability affect the timing and success of seed germination [18–20]. Increased [CO$_2$] and temperatures might augment seed production [21], yet higher temperatures may reduce seed viability [22]. Furthermore, decreased moisture availability could prevent seeds from breaking dormancy [23]. Studies that evaluate temperature, [CO$_2$] or moisture in isolation risk making inaccurate conclusions about germination responses to climate change.

Despite the considerable effort to understand thermal and moisture requirements for germination [24–27] (Table 1), relatively little is known about how climate change will affect the genetic, molecular, and physiological mechanisms associated with germination [28]. Much of our knowledge of the molecular processes involved with germination comes from crop plants [29], and often ignores a growing body of literature on physiological and morphological seed traits involved in germination [30]. Future studies should examine the fitness consequences of temporal shifts in germination [16,17]. By exploring the effects of climate change on the processes by which seeds germinate, future studies will generate realistic predictions of recruitment from seed under climate change [31,32], and inform conservation strategies [28].

2.2. Plant growth

Temperature, [CO$_2$], and water availability directly affect photosynthesis and growth rates [33,34] (Table 1). For example, elevated [CO$_2$] and mild increases in temperature have enhanced plant growth especially in colder climates [35–38], where growth is generally constrained by low temperatures and short growing seasons. Many models assume that global increase in temperatures and elevated [CO$_2$] will enhance plant growth rates, especially in C$_3$ plants [39]. However, these models often do not accurately predict the responses of communities to climate change [40]. For example, Nitrogen (N) and water limitation can offset the fertilizing effect of [CO$_2$] [41,42]. Additionally, plant growth models often ignore species from the tropics [43] or have oversimplified estimates for some regions [40]. Indeed, climate change has reduced photosynthetic capacity and growth for plants in the tropics [43]. Thus, future models need to incorporate [CO$_2$], temperature, water and nutrient limitations to predict plant growth at regional scales [40,44], especially in highly diverse tropical habitats. Additionally, vapor pressure deficits associated with warming temperatures increases drought stress in plants [45], yet we know little about how this interaction influences plant growth [46]. Multi-factorial manipulations, especially involving drought, vapor pressure deficits and nutrient limitations, will greatly increase our understanding of the long-term effects of climate change on plant growth and improve realism of predictive models.

2.3. Reproductive phenology

Climate change has induced earlier reproduction among spring-flowering angiosperms [47–50]. Climate-change mediated selection generally favors earlier flowering, but at differing rates across elevational gradients [51,52] and geographic regions [53]. Several key questions remain unresolved: What are the fitness and demographic consequences of altered reproductive phenology [54–56]? Does accelerated reproductive phenology lead to greater mismatches with antagonists or mutualists [57]? Will phenology keep pace with climate change

Table 1
Known effects of climate change factors across plant life-history stages.

Life History Stage	Climate Change Effect		
	Elevated Temperature	Disrupted Precipitation	Elevated [CO$_2$]
Dormancy and Germination	High temperatures affect seed metabolism and compromise seedling development [65,66] High temperatures increase probability of germination in alpine plants [24,67] High temperatures delay germination in Mediterranean climates [68,69] Elevated temperatures will exceed optimal germination temperatures in the tropics and decrease germination [70] Warming temperatures may exceed cold stratification requirements for seeds in high elevation and high latitude locales [71]	Altered precipitation affects spring and autumn germination rates differently [72] Seed dormancy may buffer populations from variable precipitation patterns [73] Seeds from drought resistant species will have a germination advantage in more arid climates, which could alter community dynamics [74] Germination of tropical species could be more limited by water availability than temperature [75]	Too few studies to generalize [21,76,77] N availability may influence germination more than CO$_2$ [78]
Growth	Molecular regulation is sensitive to extreme temperatures expected under climate change [79] Plants in historically cool climates at higher latitudes and elevation could experience increased growth [80] Increased temperatures could hinder plant growth in the tropics where plants already experience temperatures near their thermal optima [43,81] Plant growth under higher temperatures depends on water availability [82]	Drought reduces growth in most ecosystems [83] by inducing stomatal closure and decreasing photosynthetic capacity [84] Population responses to altered precipitation patterns depend on environmental heterogeneity and soil moisture [36,85] Flooding due to climate change could hinder growth due to an increase in oxidative stress and decrease in nutrient availability [86,87] Earlier fall precipitation can increase plant growth in arid and semiarid ecosystems [88,89]	Increases plant growth in C$_3$ plants [39], which could alter community composition Increases water use efficiency of leaves [90] Increases photosynthesis [91] Growth may depend on long-term exposure to CO$_2$ and community-level responses to CO$_2$ [42,92]
Reproduction	Warming temperatures accelerate flowering phenology in spring-flowering angiosperms [48,50,93,94,95], and favor earlier flowering in extra-tropical habitats [51,52] Warming temperatures increase flower development in tropical species [96] Warming temperatures disrupt pollen development and fertilization [97], and reduce pollen viability [45,98] Altered fruit sugar concentrations, and reduced resistance to fruit pathogens [99,100]	Reproductive effort declines in response to drought [14,101] Drought reduces flowering and fruit production in tropical species [101,102] Flowering time shifts earlier in response to drought [49,103] Increased precipitation lengthens flowering duration in late-flowering plants [94] Earlier snowmelt advances flowering phenology in alpine plants [104,105]	Increased carbon allocation to flowers could enhance fecundity [106] Elevated [CO$_2$] increases fecundity in crop plants [107,108]

plastically? By addressing these questions through a combination of observational and experimental studies in the field, future research can make robust predictions about population persistence and community dynamics, and target conservation activities toward vulnerable species and ecosystems.

The majority of studies of reproductive phenology explore shifts in spring and summer climates and focus on forbs in temperate, boreal, alpine, or subalpine climates [58] (Table 1). Few studies examine the effects of non-growing season temperatures on phenological responses to climate change [12], focus on the tropics [59], or evaluate the duration of reproduction [60–62]. Additionally, warming spring and summer temperatures do not affect fall flowering plant phenology at the same rate as spring flowering plants [58,63]. Future studies that incorporate factors beyond spring and summer climates will shed light on phenological shifts, especially in regions where temperatures are relatively consistent year-round [59,64].

2.4. *Mating system variation*

Plant species vary immensely in their mating systems [110], from completely outcrossing and self-incompatible to entirely self-pollinating [111], with approximately 42 % of seed plants exhibiting mixed mating systems [112]. Mating systems influence gene flow, genetic diversity and population size [110,113], but few studies have empirically evaluated the adaptive potential of mating systems under climate change. Outcrossing populations typically have high within-population genetic variation in contrast to populations of self-pollinating species [110]. Self-compatibility has evolved numerous times from outcrossing systems to enable reproduction when pollinator density is low and when conspecifics are rare [114]. However, inbreeding depression can constrain the evolution of selfing [112,115]. Mixed mating systems offer reproductive assurance when outcrossing fails [114], leading to genetically diverse populations with large effective population size [112].

Outcrossing species may have sufficient genetic variation to adapt to novel selection, but the global loss of pollinators (see *Plant-pollinator interactions* below) has reduced fecundity of outcrossing plant species, potentially favoring the evolution of self-compatibility [111,116,117]. Wind-pollinated plants, in contrast, could maintain high evolutionary potential under climate change, as they do not depend on animal vectors for fertilization [118]. For example, *Festuca rubra* (Poaceae) is a wind-pollinated grass found across the northern hemisphere [118]. Under projected climatic conditions for western Norway, *F. rubra* could adapt readily, as the species has relatively few genetic constraints [118]. We propose that obligately outcrossing mating systems reliant on animal pollinators may decline in future climates. Wind pollinated species may adapt to future conditions, but can still suffer from effects of mate limitation during migration or as a consequences of habitat fragmentation [119,120].

Historical shifts towards self-pollination have been associated with range expansion during periods of warmer temperatures in the Mid-Pleistocene transition. The predominantly self-pollinating *Arabidopsis thaliana* (Brassicaceae) is hypothesized to have evolved from an outcrossing ancestor that transitioned to self-compatibility during a shift towards arid conditions in Africa 1.2-0.8 mya [121]. African accessions of *A. thaliana* display the highest haplotypic diversity at the self-incompatibility locus and all haplotypes can be found in present day Morocco, suggesting that self-compatibility likely evolved in a single geographic area [121]. Populations that increase rates of self-pollinating as a consequence of climate change will initially experience inbreeding depression [122]. However, once deleterious recessive mutations are purged through continued inbreeding, newly self-pollinating species could successfully establish in regions with limited pollinators and mates [112,115]. Self-compatible systems may also be favored as habitat fragmentation reduces population sizes and the number of potential mates [123]. Predominantly self-pollinating systems also face challenges from rapid climate change due to spatially-restricted gene flow and limited within population genetic variation [52,113]. For example, a meta-analysis showed that self-pollinating populations exhibit low levels of additive genetic variation in quantitative traits [124]. Contemporary global change may initially favor self-compatibility, but strictly self-pollinating populations could have low adaptive potential in the long-term.

We hypothesize that mixed-mating strategies could reduce the risk of extinction under climate change [125]; however, inbreeding depression may be exacerbated under novel environments and reduced pollinator availability [125–127] (Table 2). Inbreeding depression has increased significantly under stressful conditions in species with mixed mating systems [126]. Mixed-mating populations may avoid the fitness costs of self-pollination as long as the shift is phenotypically plastic and not a fixed genetic response to selection [125,128]. For example, individuals of the mixed-mating species *Viola praemorsa* spp. *praemorsa* showed a 45 % increase in self-pollination in chasmogamous (open) flowers and a 15 % increase in fruit production in the cleistogamous (closed, self-pollinating) flowers when exposed to increased temperatures and reduced rainfall during one growing season [128]. These plastic responses were not associated with visible effects of inbreeding depression [128]. Self-compatible species with mixed mating systems may have an advantage under novel climates, as self-pollination could provide reproductive assurance in expanding range fronts and fragmented landscapes, and outcrossing populations could harbor the genetic variation necessary to adapt in situ.

Species often reproduce both sexually via flowers and clonally through stolons or tillers [129]. Similarly, some species can reproduce sexually via seeds, but also asexually via apomixis (reproduction

Table 2
An exhaustive list of studies that examine inbreeding depression in plant populations in response to stresses associated with climate change. Studies compared fitness components of inbred individuals with outcrossed individuals in control and treatment settings. Notably, there is only one study that manipulated multiple factors [137].

Species	Climatic stress	Impact of stress on inbreeding depression	Citation
Crepis sancta	Drought	Inbreeding depression increased under stress for number of flower heads and growth rate	[138]
Echium wildpretii	Drought	Inbreeding depression increased under stress for survival	[139]
Lychnis flos-cuculi	Drought	Inbreeding depression increased under stress for survival	[140]
Raphanus sativus	Drought	No increase of inbreeding depression under stress	[141]
Silene vulgaris	Drought	No increase of inbreeding depression under stress	[137]
Solanum carolinense	Herbivory	Inbreeding depression increased under stress for ramet number, biomass and fruit number	[142]
Solanum carolinense	Herbivory	Inbreeding depression increased under stress for ramet number	[143]
Mimulus guttatus	Herbivory	Inbreeding depression increased under stress for aboveground biomass	[144]
Silene vulgaris	Herbivory	No increase of inbreeding depression under stress	[137]
Mimulus guttatus	Herbivory	Inbreeding depression increased under stress for number of flowers and biomass	[145]
Datura stramonium	Herbivory	No increase of inbreeding depression under stress	[146]
Cucurbita pepo	Herbivory	No increase of inbreeding depression under stress	[147]
Cucurbita pepo	Nutrient deficiency	Inbreeding depression increased under stress for number of flowers and fruits per plant	[148]
Schiedea lydgatei	Nutrient deficiency	No increase of inbreeding depression under stress	[149]
Silene vulgaris	Nutrient deficiency	No increase of inbreeding depression under stress	[137]

without fertilization) [130]. Clonal reproduction is a major adaptation of arctic and alpine plants to severe climatic conditions and nutrient shortage in cold environments [129,131]. The extent of clonal reproduction tends to increase with elevation [132,133] and aridity [134] as costs of sexual reproduction increase. Vegetative ramets can forage for resources or optimal conditions in pioneer communities or at range edges, enabling acclimation to novel or stressful conditions under climate change [133–135]. Asexual reproduction and clonal growth could become more prevalent in habitats disturbed by climate change. We encourage future research to examine whether reproductive plasticity and asexual reproduction could ensure population persistence under changing environmental conditions.

We advocate for comparative studies evaluating the role of mating systems and reproductive modes in climate change responses. Future work can address whether pollinator loss and mate limitation favor self-compatibility [117] or plastic shifts between sexual and vegetative reproduction [134], and whether inbreeding depression will rise in species with mixed mating systems due to heightened self-pollination and environmental stress [115,127]. Few studies have addressed the degree to which populations maintain sufficient genetic variation to shift from outcrossing to mixed mating systems under rapid contemporary climate change. By identifying closely related species or populations with different rates of self-pollination located in disparate environments, researchers can identify ecological factors that impose selection on mating systems and reproductive plasticity, quantify variable selection on traits related to self-pollination or outcrossing (e.g., flower size and anther-stigma distance in space and time), and identify loci under selection. Studies which use quantitative genetic approaches to measure phenotypic responses of multiple species or populations to climate change manipulations in a common garden environment can evaluate the consequences of mating systems for persistence through climate change [52,124,136].

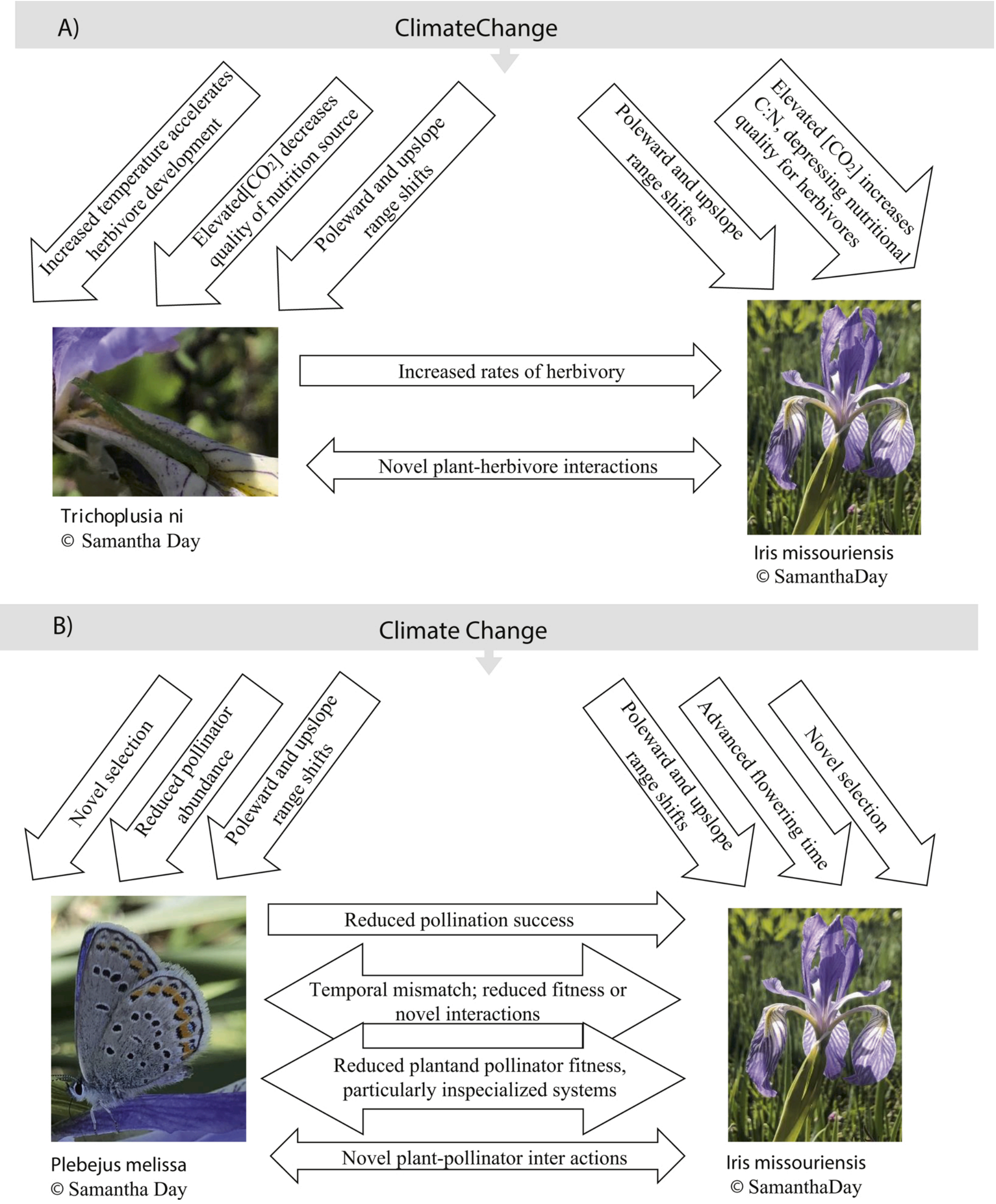

Fig. 1. An overview of the impacts of anthropogenic climate change on both plant-herbivore (A) and plant-pollinator (B) interactions. This outline acknowledges the variety of ways in which the abiotic factors associated with climate change disrupt these sensitive interactions.

3. Biotic interactions

Climate change directly influences natural communities through increased atmospheric [CO_2] and global temperatures along with altered precipitation patterns [reviewed in 150,151]. These direct effects can diminish overall fitness, reduce migratory and adaptive potential [152,153], and disrupt local adaptation [154–156]. Additionally, climate change indirectly affects plant populations through altered biotic interactions (e.g., Fig. 1). Plant populations adapted to historical conditions at local microsites have evolved in response to interactions with biotic associates, be they antagonists or mutualists. Shared evolutionary histories strongly influence the performance of interacting species [157]. It is unclear whether natural plant populations will adapt to novel environments created by the indirect effects of climate change [158,159]. We recognize that pairwise comparisons between plants and discrete taxonomic groups (e.g., bacteria) are incomplete, but they can be useful nonetheless. Here, we consider differences between generalized and specialized interactions between plants and their antagonists and mutualists. As the climate continues to change, the balance between generalists and specialists at the regional [160], community [161] and even species levels [162] could change for plants and their biotic associates. What are the ecological and evolutionary consequences of disrupted biotic interactions for plants?

3.1. Plant-insect interactions

3.1.1. Plant-herbivore interactions

Since 1960, species of pathogens and herbivores have been migrating toward the poles at an average rate of 2.7 km per year [163]. During the same timeframe, global temperatures have increased by 0.12 °C per decade [1], which translates into a latitudinal median velocity of long-term temperature change of 2.73 km per year, reflecting the rate of migration of the natural enemies of plants [164]. Insect herbivores appear to be migrating faster than their plant counterparts [165], which is leading to novel plant-herbivore interactions in the expanding range of the herbivores [166,167]. Some plants may already exhibit defenses that can protect against novel herbivores assemblages [168]. In other instances, native plants may be poorly adapted to new herbivores. For example, the mountain pine beetle (*Dendroctonus ponderosae*) has expanded into historically cooler forests in high latitude and high elevation locations in North America, resulting in massive pine forest mortality across 71,000 km^2 in the western United States [169]. We do not have precise maps of the distributions of most herbivores [170]. Future studies that compare available historical distribution data with contemporary distribution patterns could generate early predictions of the degree of novel plant-herbivore interactions along the migration routes of herbivores.

Even outside of the context of range expansions, climate change can expose plants to greater levels of herbivory locally through several mechanisms [171]. For one, in temperate regions, warming springs and delayed winters lengthen the herbivore growing season [172]. In areas such as the western United States, climate change has reduced winter snowpack [173,174], leading to increased early season vertebrate herbivory on woody species [175]. In contrast, warming winters in arctic zones have hardened snowpack, preventing herbivore vertebrates from foraging during the winter [176]. Increased atmospheric [CO_2] and temperature can alter the physiology and metabolism of herbivores and plants [177]. For example, elevated [CO_2] increases the ratio of carbon to nitrogen in plant tissue, thereby decreasing the nutritional quality for herbivores. In response, herbivores may increase consumption rates or shift to host plants that can meet their nutritional requirements [178,179]. Yet, increasing atmospheric [CO_2] may induce greater production of plant defenses [178]. Few studies have investigated the direct impacts of prolonged drought stress on herbivores [180], however, drought stress reduces plant fitness in many systems [181]. Additionally, climate change could accelerate the developmental rates of insect herbivores and increase the number of life cycles a species completes in a growing season [177]. For example, the mountain pine beetle (*D. ponderoae*) has shifted from a semivoltine lifecycle that takes two years to complete to a univoltine lifecycle of one year, resulting in larger outbreaks that significantly damage whitebark pine trees (*Pinus albicaulis*) in Yellowstone National Park [182]. However, rapid development can be costly; juvenile herbivores may not reach the appropriate developmental stage before the onset of winter [183].

Few studies investigate the synergistic effects of temperature, [CO_2], and new precipitation patterns on herbivory [179,180]. We call for multifactorial field experiments to test how climate change factors interact to influence plant-herbivore interactions. In addition, multidisciplinary approaches could shed light on the ecological and evolutionary consequences of mismatched migration rates between herbivores and plants. For example, herbivores expanding into novel ranges could behave as invasive species and may escape from their own natural enemies [184], which could increase population growth rates and result in greater herbivory to plant tissues. Experiments conducted outside of the contemporary range of herbivores could evaluate novel plant-herbivore interactions, but these studies must be designed carefully to prevent the establishment of non-native herbivores. Studies of plant-herbivore interactions under climate change focus almost exclusively on arthropod herbivores [but see 175]. Future studies of mammalian herbivores, especially large ungulates and their movement across landscapes will test how climate change is altering the diversity of herbivorous interactions in nature [185].

3.1.2. Plant-pollinator interactions

Insect pollinators have declined globally [186], as has the abundance of insect-pollinated plant species [187]. Pesticide use, and the direct and indirect consequences of climate change are all causal factors involved in the decline of insect pollinators [116]. Pollinator loss may lead to pollinator limitation and reduced fecundity in some plants; additionally, pollinators could face starvation if sufficient floral resources are not available [188]. For example, reduced flowering success under drought stress depressed bumble bee abundance [189]. However, reductions in bumble bee population sizes are not uniform across species [190–192]. What are the fitness costs of climate change for plants and pollinators, and are these costs greater in highly specialized pollination systems? Future studies of fitness costs can quantify the extent to which climate change could destabilize natural communities [193].

An estimated 94 % of plants in tropical zones require animal pollination [194], yet the tropics are experiencing the fastest loss of pollinators [191]. In the tropics, insects are more sensitive to temperature changes, and population growth rates could decrease by up to 20 % [195]. Additionally, tropical zones have the largest proportion of specialized plant-pollinator interactions [196], and pollinator specialists may not be able to adapt to climate change to the same extent as generalists [57]. We call for funding to support future studies in tropical biodiversity hotspots addressing the consequences of climate change for plant-pollinator interactions, plant phenology, and biodiversity conservation.

Increasingly novel climates may lead to mismatched range shifts for plants and pollinators, which could be particularly problematic for specialized plant pollinator systems [57]. The tree bumble bee, *Bombus hypnorum*, expanded its range northward, from mainland Europe to the southern United Kingdom in 2001 and is now found as far north as Scotland where it acts as a pollinator for many native plants [197]. Interestingly, many species of butterfly pollinators have stalled their range shifts in response to climate change in both Canada and Europe, indicating that these species may not be able to keep pace with warming climates via range shifts [198–200]. A known barrier to butterfly range migration is habitat fragmentation, as it can severely limit dispersal abilities [200,201]. As plants move into novel environments, increased interspecific competition for pollinators could reduce fitness [202].

Climate change could generate strong temporal mismatches between flowering time and pollinator emergence [203,204]. Warming springs have accelerated flowering times and the arrival of pollinators [50], but not always at the same rates. For example, in the Colorado Rocky Mountains, climatet change has decoupled spring arrival dates of broad-tailed hummingbirds (*Selasphorus platycercus*) and first flowering of various plant species [205]. These temporal mismatches could depress population growth rates of flowering plants that require pollinator services for reproduction and of pollinators that are sustained by floral resources [188]. Some studies, however, have demonstrated a lack of temporal mismatches between flowering time and pollinator emergence when early flowering plants are pollinated by early season pollinators [206]. Future research should explore how the degree of pollinator specialization influences plant-pollinator temporal mismatches and investigate the proximate environmental factors that elicit pollinator emergence vs. flowering. For example, climate change could exacerbate mismatches if a specialized pollinator is highly responsive to temperature cues and its host plant is responsive to photoperiod. Moreover, climate change could increase competition for floral resources, which may differentially influence generalist and specialist pollinators. Generalist pollinators will likely fare better than specialized pollinators due to greater flexibility in their diet [188]. We call for future studies testing whether the loss of specialized pollinators will reduce fecundity in their plant counterparts, or whether generalist species will maintain pollination services for these plants [188].

Climatic conditions shape selection on both plant and pollinator traits [172,207], and climate change can impose novel selection on these interacting species. For example, in the Colorado Rocky Mountains, two species of long-tongued bee specialists, *Bombus balteatus* and *Bombus sylvicola*, have historically pollinated flowers with deep corolla tubes; however, climate change has reduced the abundance of flowers with deep corolla tubes, leading to a decline in tongue length in bee pollinators [208]. Climate change has induced smaller body size in several bumble bee species over the past century, which is likely a plastic response to stressful conditions [192]. Morphological mismatches can occur between flower and pollinator due to changes in pollinator size, thereby resulting in ineffective pollinator services [209].

Given the importance of climatic factors in the evolution of plant and pollinator traits, we hypothesize that climate change will exert novel selection on these traits, which could further disrupt the quantity and quality of pollination. Indeed, climate change imposes strong selection on floral traits, such as nectar quality and flower size [207]. Drought-stressed plants produce fewer flowers, which often have reduced volumes of nectar [210]. In addition, the concentration of amino acids and carbohydrates in floral nectars is sensitive to temperature, [CO_2], and N availability [211]. Some pollinators, such as the honeybee (*Apis mellifera*), have strong preferences for nectar composition and experience increased mortality under low concentrations of sucrose [212]. Other floral traits, such as floral size, are also subject to climate-mediated selection [213]. In Israel, flower size of several species of *Oncocyclus* irises decreases with increased aridity, suggestive of drought-mediated selection [214]. Additionally, drought stress selects for reduced floral size in female alpine forbs, *Polemonium viscosum*, even though large flowers attract more pollinators [213]. As pollinators generally prefer larger flowers, flower size could be subject to conflicting selection, with abiotic factors favoring smaller flowers and biotic factors favoring larger flowers. Increasing aridity under climate change could shift the balance toward selection for smaller flowers, reducing the quantity of floral resources available to pollinators.

3.2. Plant-microbial interactions

Interactions between plants and microbes (fungi, bacteria or viruses) can influence plant fitness, physiological performance and adaptive potential, particularly when microbiomes are vertically transmitted between plant generations [215]. The majority of land plants enter into positive associations with a diversity of fungal species [216,217], above- and below-ground bacterial communities [218,219] and viruses [220,221]. Together, plants and microorganisms form a co-evolved biological unit of organization (the holobiont) that experiences ecological and evolutionary processes jointly [222]. Holobionts, in which hosts and microbes are adapted to each other, represent specialized systems [223] that may be influenced by abiotic conditions. Thus, to predict outcomes of plant-microbe interactions under changing environments, it is helpful to include microbes as part of a holistic organismal response to environmental conditions, both in co-adapted holobionts and in novel interactions. We suggest expanding the classical definition of ‘resident genotypes’ in locally-adapted demes [224] to include host-associated microbes, which could result in more realistic predictions of plant responses to global change. Indeed, a recent review, suggested that microbes contribute ‘extra’ genes upon which selection acts [225]. We recognize microbial community dynamics are important in determining host outcomes [215]. However, we focus here on adaptive plant-microbe interactions observed in plant-microbial studies. We encourage future research into the effects of climate change on plants and their microbial associates, and the emergent adaptive potentials therein [226].

3.2.1. Effects of changing resource availability on plant-microbial interactions

Novel climates coul exert differential selective pressures on hosts and microbes, changing the adaptive stability of plant-microbial systems. While plants acquire many microbial symbionts from their environment, vertical transmission of microbes and the inheritance of microbe-related alleles between host generations suggest that climate change will influence both incidental plant-microbe associations as well as those co-evolved over time [227]. The stability and flexibility of adaptive host-microbe systems to abiotic stress depends on genetic and behavioral responses across generations [228], differential reproductive rates and strategies between hosts and microbes, and microbial community interactions [reviewed in 217]. For example, in *Boechera stricta* (Brassicaceae), changing environmental conditions alter leaf microbial communities with impacts on plant fitness across complex abiotic clines [229]. We suggest that it is important to consider the historical and future role of microbial associations with plant hosts in predicting adaptation to climate change, which will require more fully-reciprocal field studies.

Climate change, especially warming temperatures and novel soil moisture can disrupt abiotic soil conditions, and directly influence microbial communities [230,231]. For example, drought stress alters soil microbial abundance [232] and shifts microbial community functionality from opportunistic and sensitive taxa toward drought-tolerant taxa, altering soil carbon and mineral processing [233]. Moreover, shifts in soil microbial community structure can accelerate litter decomposition, increase heterotrophic microbial respiration, and release carbon (C) and nutrients into the atmosphere and bioavailable sediment pools [234]. While climate change effects on soil C cycles and plant-soil C interactions are relatively well understood [235], we still know little about the impacts of nutrient cycling on soil microbial communities. For example, changes in soil microbiota could disrupt species coexistence [236]. Additionally, variation in the physical, chemical and biological soil environment will alter plant-soil feedback, potentially influencing ecosystem productivity and biodiversity [237]. Future research should consider how climate change-induced shifts in soil microbiota scale up to communities and ecosystems.

Climate change increases microbial enzymatic activity and elevates bioavailable soil N, which increases aboveground plant tissue N pools and foliar $\delta^{15}N$ in experimental warming plots [238]. However, increased N availability may only be temporary, as soil nitrogen was depleted after 2 years of a long-term meadow warming study [239]. In addition to summer warming, climate change also increases the frequency of freeze/thaw cycles in natural communities [240], which can increase short-term bioavailable N availability, C mineralization, CO_2

release, and N_2O emissions [241–243]. In contrast with higher latitude systems, tropical ecosystems are generally warm and humid yearlong, and bioavailable N and P are already among the most limiting resources for plants [244,245]. Rising [CO_2] and temperatures further reduce litter quality (increasing C:N and C:P) in these systems [246] and excess eutrophication decreases microbial diversity [247]. Future research should investigate indirect effects of disrupted biogeochemical cycles on plant-microbe associations by asking how climate change affects microbial soil activity, nutrient regulation, and associated plant communities. In particular, studies should urgently concentrate on tropical biodiversity hotspots, which are severely understudied.

3.2.2. *Abiotic stressors on plant-microbial interactions*

Thermal tolerance varies between species and genotypes of microbial symbionts in natural plant host systems [248]. Temperature stress influences numerous plant physiological processes, which mediate the interaction with intra- and extra-cellular microbes. For example, heat stress can increase fluidity of plant membranes, thus facilitating systemic infections of microbial pathogens [249,250]. Additionally, heat stress can create reactive oxygen species that dampen plant immune and defense responses [251], or trigger stomatal closure or cuticle production that limit carbon and nitrogen resources for leaf-associated microbes [252]. Heat may also impact plant microbial associations by disrupting competition between non-pathogenic and pathogenic microbes [253] or inducing host responses that favor certain microbes or microbial genotypes over others [254]. For example, the tropical panic grass *Dichantheliu lanuginosum* (Poaceae) is more heat tolerant when associated with a virus-infected fungal symbiont as compared to the fungal symbiont alone [255]. Understanding the different biological scales at which host-microbial interactions will be impacted by rising temperatures should be explored in community and population frameworks.

Climate change is reducing snowpack in high elevation and latitude systems [174]. Under novel snow-free conditions, plants are exposed to frosts that they would not have experienced historically [93]. Extreme cold temperatures in these locations could lead to the formation of intracellular ice crystals, which reduce survival for plants and microbes alike. Cold-adapted organisms exhibit an array of responses to sub-0 °C temperatures that plant genotypes adapted to snow cover may not maintain [256,257], while beneficial interactions, such as rhizobia nodulation, may decrease under freezing temperatures [258]. Thus, in some systems, elevated global temperatures could have the paradoxical effect of increasing exposure to cold conditions in late winter, early spring, and late fall despite global warming trends.

Changing precipitation patterns coupled with warming temperatures will increase drought stress in many regions [1]. Plant adaptations to drought range from physiological adjustments to structural changes such as induction of waxy cuticles and modified root morphology [reviewed in 259]. Thick leaf cuticles attenuate desiccation, but may negatively impact host immune responsiveness to pathogens [260]. Root hair density is positively correlated with both water uptake and rhizosphere abundance of bacterial symbionts in particular [259]. Stomatal pore density and conductance may cool plants and reduce water loss [261] while also mediating microbial access to the plant apoplast and triggering innate immunity against bacterial pathogens [262]. Thus, plant functional traits (e.g., higher stomata density) may improve host adaptation to drought while also regulating interactions with microbes.

Changing water availability will impact microbial symbionts differently. For example, drought impacts root-associated bacterial symbionts more negatively than fungal associations [259]. Furthermore, bacterial and fungal functional types may be divergently adapted to abiotic and host factors. For example, drought tends to enrich relative abundance of Gram positive bacteria, such as mutualistic Actinobacteria [263], which may lead to an adaptive shift towards more fungus- and Actinobacteria-plant associations under increasing aridity. However, severe drought can increase fungal pathogen infections as well [264], suggesting that the type of interactions may shift based on the severity of stress and plant condition [265]. Finally, drought may impact viruses directly and in the context of the microbial community. Not all plant viruses are necessarily antagonistic [266]. In one example, infection by each of four RNA viruses improved host survival under drought [267]. In another study, both fungal and viral associations conferred drought resistance to tobacco plants by mediating plant metabolism and the expression of drought resistance genes [268]. Further research into plant virus diversity and virus-plant associations is necessary to better understand how climate change may alter these interactions. Investigating conditional amensalism and drought-triggered mutualism may be a fruitful area for future research, though the outcome of combined drought and pathogen stress is likely pathosystem dependent [264,269].

Elevated [CO_2] alters plant-microbial interactions. In some studies, elevated [CO_2] increased the abundance of mutualistic mycorrhizal fungi and host root colonization, augmenting plant biomass productivity [270,271]. Similarly, elevated [CO_2] stimulated rhizobia growth and nitrogen fixation across multiple grass hosts grown under Free-Air Carbon Dioxide Enrichment (FACE) experiments [272], and elevated [CO_2] could enhance the mutualistic interaction between plant hosts and mycorrhizal associates [273]. Increased [CO_2] may also alter plant-virus interactions [reviewed in 274]. For example, infection with pathogenic Barley Yellow Dwarf Virus (BYDV) attenuated aphid herbivory in wheat plants under elevated [CO_2], but viral incidence of BYDV increased across wheat genotypes, although the mechanisms leading to increased viral incidence remain unclear [274]. These studies suggest that some aspects of plant-virus interactions may benefit plant hosts indirectly through multitrophic interactions, but that viral presence may become more common and widespread under elevated [CO_2]. Future research should examine whether [CO2]-mediated microbial or viral boosts may buffer plants against other stressors associated with climate change and investigate insect-plant-pathogen interactions. Furthermore, studies regarding leaf-associated microbial responses to elevated [CO2] are fewer than those focused on soil communities; this gap should be addressed.

3.2.3. *Range shifts and plant-microbial interactions*

Plant-microbe associations will also experience novel conditions as range limits shift [50,275]. Climate change will alter the distributions of plants, microbes and microbial vectors, which will enable microbes to colonize new hosts [237,276]. Simultaneously, plants could experience novel microbe communities in their expanding ranges. For example, non-native plants undergoing range expansions may benefit from escaping co-evolved pathogens (the enemy release hypothesis) [277], but be colonized by novel microbes to which plant immune responses are not adapted. Similarly, microbial dispersal may occur as insect vectors track environmental shifts [278] or through assisted migration (i.e. translocation).

Adaptive plant-microbe interactions depend on the degree of evolved cooperation [217], which requires sufficient time for co-adaptation [279]; yet over the short term, plants may show maladaptive responses to invading microbes. For example, high latitude plants may be at high risk of emergent diseases as pathogens move poleward in a warming world [163], especially in circumstances of vectored microbes which may experience rapid range expansions. For example, viruses requiring vector transmission account for approximately half of emergent plant diseases [280]. For pathogenic viruses like Cucumber Mosaic Virus (CMV), generalist aphid vectors may increase the geographic and host range by infecting new plant populations and species [281] . [282,283]. While emergent epidemics are possible, environmental conditions and shifting microbial distributions may also facilitate greater plant survival in new regions because of the complex nature of plant-microbial interactions across entire communities rather than simple paired species interactions. If mutualistic interactions persist or expand under changing conditions, it is possible that plant fitness could be stable or improve under novel environments (Fig. 2). Thus, 'microbial rescue', like

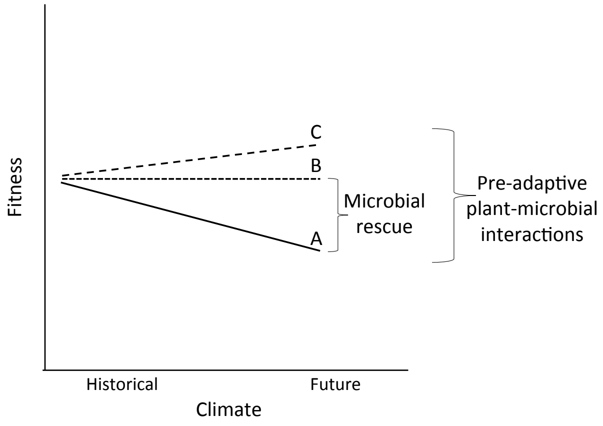

Fig. 2. Theoretical adaptive outcomes for plant-microbe systems under future climate changed scenarios. In this figure, line A predicts plant fitness without adaptive microbes. If plants inoculated with a particular microbial symbiont perform the same in the future as they have historically (B), the microbe has 'rescued' the host from climate-induced extinction or extirpation. If plants perform better when inoculated with a microbial associate than they have historically, the host-microbe system may have been climate-limited historically (C). Experiments and field work across appropriate environmental gradients may simulate future climate scenarios and provide data to test these graphical hypotheses.

ecological and evolutionary rescue, may provide an option for plants experiencing rapid climate change [284]. More research into wild plant-microbe biogeography is needed before the microbial rescue hypothesis can be tested effectively, though it is a compelling framework that considers the adaptive nature of all plant-microbial outcomes [284].

Microbial associations mediate functional host traits in a variety of ways [285], and may contribute to adaptive host responses in some circumstances [229] (Table 3). The complexity of interacting stressors and the biological scale of their interactions is not well understood. Field studies examining standing microbial diversity across environments and between host populations will provide insight into the consequences of plant-microbe interactions under divergent environments. Furthermore, the sustainability of agricultural production may depend on the stability of plant-microbial associations, which enhance plant growth, nutrient-use efficiency, abiotic stress tolerance, and disease resistance [286]. Given the threats to the stability of biotic interactions under climate change, agricultural research examining beneficial plant-microbial associations is urgently needed to investigate the potential impacts of plant-microbe range shifts on future food production. We echo previous calls for field experiments addressing the adaptive potential of host-microbe symbioses in a systematic way for both cultivated and wild systems.

4. Common challenges, methodological advancements, and future directions

The persistence of species through anthropogenic climate change depends on their ability to track favorable conditions by shifting distribution ranges [50,289,290], acclimate via phenotypic plasticity [6,291,292], and evolve adaptations to novel stresses [293]. Most often, combinations of these strategies will be necessary for population persistence, and a central goal in evolutionary ecology has been to disentangle the relative role of these processes in shaping species responses to climate change [294]. Mirroring the multitude and complexity of species responses, a combination of approaches and tools are often needed to examine the relative contributions of distributional shifts, phenotypic plasticity and adaptation to biological responses to rapid global change. Evolutionary ecologists now use combinations of field studies, including provenance trials, reciprocal transplant experiments, and resurrection studies to test key hypotheses about population persistence under climate change. These field approaches offer unique predictive power when conducted in concert with manipulations of climate variables, biotic interactions, or when combined with population dynamics, quantitative genetics and ecological genomics. In this section, we discuss common challenges in the study of ecological and evolutionary responses to climate change, and examine emerging experimental approaches aimed at filling gaps in our understanding of species adaptive potential to global change.

4.1. *On the complexity of simulating global climate change*

One particular challenge in generating robust predictions is the need to adequately simulate future or past conditions for a given region. Since climate change is simultaneously altering multiple agents of selection, including CO_2, temperature, growing season length, and precipitation patterns [1,151], studies must use an integrative approach with multifactorial manipulations. Global change factors interact in complex ways, and can have additive, synergistic or antagonistic effects. For example, increased CO_2 may positively affect plant growth, yet these effects are largely offset when associated with warming and drought [295]. Multifactorial experimental manipulations can more realistically simulate future climatic conditions, identify agents of selection, and disentangle the interactive effects of selective drivers [296,297]. However, few studies have manipulated multiple global change factors simultaneously [298], and such endeavors are often complicated by rapidly growing experimental sizes. In certain regions, one driving selective factor can be identified and used to simulate changes in associated environmental variables. For example, in high-elevation and latitude systems, flowering phenology is mainly driven by timing of snowmelt [297]. In those regions, snow removal manipulations can be used to reduce winter snowpack and simulate advanced snowmelt, which also realistically simulates the associated decreased water availability and prolonged growing seasons [299]. Moreover, multiyear experimental manipulations in natural settings increase ecological realism and capture the complexity of interannual variation in abiotic and biotic conditions [297,300,301].

Biological responses to changes in *mean* temperature and precipitation have already been well documented [38,302]; however, much less work has focused on plant responses to changes in climatic *variability*. Climate change does not proceed at a constant rate; models project increases in frequency and severity of drought events and heat waves in many areas of the world [1,303], and variability between and within years has become the rule rather than the exception [49]. We need to separate the impact of changes in climate mean values from those produced by changes in the magnitude and/or frequency of extreme events by transitioning from *trend-based* to *event-based* ecological research [304]. Primary studies that compared the effects of events vs. trends found that climatic variability affected population dynamics and community functioning even more than climatic means [305,306]. For example, one experiment in a tallgrass prairie in Kansas, found that manipulations of the variability in rainfall reduced productivity significantly more than a simple overall 30 % reduction in rainfall quantity [307,308]. Similarly, pronounced changes in phenology, productivity and community composition occurred when grasslands and heath communities were exposed to extreme droughts or heavy rainfall [309–311]. Yet, drought resistance improved when communities experienced recurrent milder drought simulations, and stress memory or soil biotic legacies may enable plants to acclimate to increasing climatic variability [310].

Beyond the severity of extreme events, the timing of events is particularly important [304]. A recent study found that timing, but not frequency, of temperature stress affected the phenology and performance of *Arabidopsisthaliana*(Brassicaceae) [312]. Periods of accelerated growth and reproduction are generally most susceptible to extreme

Table 3
Key studies and hypotheses regarding adaptive plant-microbe interactions under changing abiotic conditions.

Climate-change mediated stress	Adaptive plant-microbe symbioses	Citations	Example mechanisms	Future directions
Increasing summer drought	Drought tolerance conferred by fungal, bacterial and viral microbes	[267,268, reviewed in 287]	Water acquisition by below-ground symbionts; microbe-mediated delayed desiccation	What is the fitness impact of microbe-mediated drought tolerance? Are drought-tolerant mutualisms more commonly found in arid environments?
Winter droughts	Adaptive protection against freezing-tolerant and cold-tolerant pathogens	[reviewed in 258]	Cold-induced synthesis of pathogenesis-related (PR) proteins	Are there microbial associates that confer direct or indirect benefits to cold-stressed host plants?
Elevated [CO_2]	Below-ground microbial symbionts benefit from elevated CO_2 and augment plant nutrient acquisition	[270, reviewed in 272,273]	Increased carbon and nitrogen exchange between hosts and symbionts	How does elevated [CO_2] influence interactions with leaf-associated microbial species and communities?
	Virus infection attenuates plant response to elevated [CO_2]	[274]	Viral infection increases relative plant performance through elevated leaf nitrogen and biomass	Do host fitness outcomes improve for virus coinfections with fungal and bacterial mutualists that augment plant nutrients and quality?
Heat stress	Fungal endophytes confer heat tolerance in some habitats	[288]	Symbiotic fungi attenuate osmolyte production and associated damage when exposed to heat	Do heat-tolerant symbiotic interactions improve host fitness? If so, how important is fungi fidelity over generational time, and what is the consequence of symbiont loss for offspring?
	Fungal endophytes infected by certain viruses can improve host plant thermal tolerance	[255]	Heat-induced osmolyte concentrations do not rise in the presence of the virus; mechanism unknown	What is the mechanism through which heat affects microbe-microbe interactions? Do induced stress mechanisms for the host impact microbial interactions?
Range shifts of interacting organisms	Microbial rescue through host-microbe cooperation during host range shifts	[284]	Associations with microbes attenuate novel stressors in the hosts' expanded range	Can microbial mutualists improve host survivorship during range shifts or relocation?

weather events [93]. Experimental manipulations that simulate variability in the timing, frequency, duration, and severity of extreme events that reflect projections for regional climates will produce more robust predictions about community responses to climate change (Fig. 3). Additionally, populations may differ in their tolerance to climate fluctuations based on past selection in their home sites [313,314]. Investigating intraspecific variation in responses to climatic variability will inform predictions of the evolutionary potential for adaptation to projected increases in spatial and temporal variability [312].

4.2. Detecting contemporary evolution

We still do not know whether local populations will keep pace with ongoing climate via adaptation [155,315,316]. To study contemporary evolution, resurrection approaches can be used in species with dormant propagules (e.g., seeds), where an ancestral base generation is preserved and revived for comparison with descendants under common conditions after several generations of exposure to climate change [317]. Using this approach, researchers can directly quantify evolutionary response to environmental change [318,319]. For example, studies resurrecting stored seeds, have shown rapid evolution of earlier flowering or seedling emergence following drought [49,320–322] and warming [323], directional and/or stabilizing selection on flowering time in response to changes in precipitation patterns [49,324], rapid evolution of phenotypic plasticity in an invasive species [325], and evolution of herbicide resistance [326].

The resurrection approach cannot in itself determine whether evolutionary change is caused by mutation, gene flow, genetic drift or selection, nor can this approach reveal the agent of selection [317]. To evaluate the adaptive nature of evolutionary changes in functional traits, the resurrection approach can be combined with reciprocal transplants across ancestral and descendant environmental conditions; if descendants perform better than ancestors under contemporary conditions, then the evolutionary changes are adaptive [320]. Furthermore, biases can arise in the resurrection approach when the sampled genetic pool is not representative of standing genetic variation within the species, for example when sampling is done too early or late, or on an insufficient number of genotypes [317]. Similarly, selection that occurs during storage of dormant propagules could bias estimates of trait means and lead to over- or under-estimates of the extent of evolutionary change [327]. Although early resurrection studies often depended on fortuitously collected seeds, there are now seed collections made specifically to facilitate evolutionary research via future resurrection studies [318]. Coordinated large-scale efforts such as Project Baseline in the US [328], and Back to the Future in Europe [329], ensure the productive continuance of resurrection studies, and offer an unprecedented capacity to monitor and understand contemporary evolution in response to rapid climate change. Few tropical species have been included in these efforts, however, biasing future research to the Global North. We call for funding for seed banking of tropical species, as these habitats harbor the vast diversity of plants globally.

Here, we suggest several frameworks that have rarely been explored via resurrection approaches. Combining the resurrection approach with population genomics has started to shed light on the genetic basis of evolutionary change to altered climatic conditions [317,330] and offers an advantage over more traditional landscape or spatial population genomics studies that indirectly infer signatures of selection. Genome-wide DNA or RNA sequencing can be compared between ancestors and descendants to detect changes in allele frequencies or gene expression, and ultimately uncover the genetic basis and mechanisms underlying phenotypic selection in response to climate change [159,317]. With this method, uncovered evolutionary shifts in allele frequencies were uncovered between ancestral and descendant lines [331], and significant differential gene expression was related to drought stress responses based on available functional gene annotations in *Brassica rapa*(Brassicaceae) [332]. To our knowledge, this complementary approach has never been used in other resurrection systems outside of the context of experimental evolution [330,333], nor to examine the role of epigenetic responses to climate change [334,335]. In another novel framework, the resurrection approach was recently used to examine the evolution of thermal performance curves across a plant species' range [336]. Such studies can test whether rapid adaptation and evolutionary rescue are more likely at the leading edge of a species distribution range [290,337,338]. Additionally, so far, most resurrection studies have concentrated on evolutionary responses to abiotic components of climate change [317]. However, climate change has also altered biotic interactions (as described in the previous section), imposing selection that has, for example, led to evolutionary changes in

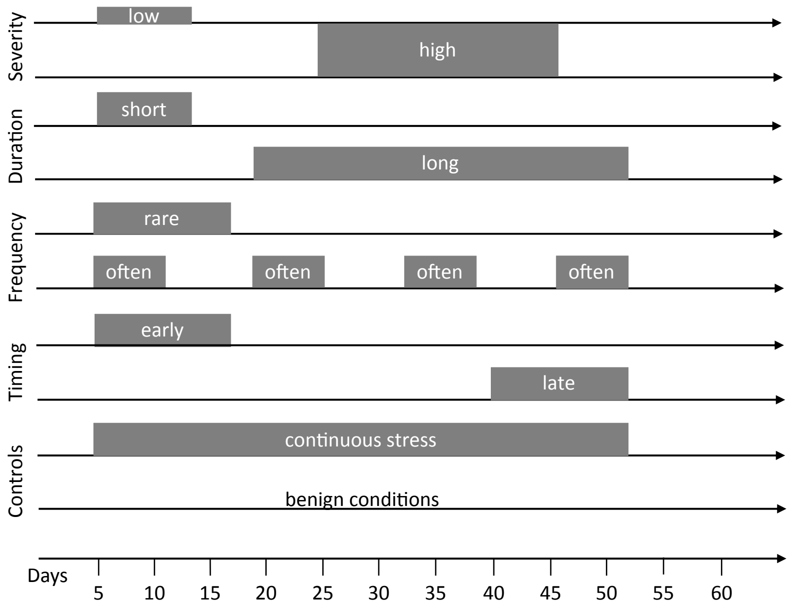

Fig. 3. Event-based ecological experiments can examine the tolerance of populations to climatic variability by manipulating the timing, frequency, duration, and severity of stress experienced by plant populations. The grey blocks represent periods of stress during the growing season (illustration inspired by Fig. 1A from [312]). We can consider experimental rainfall manipulations aimed at investigating the effects of drought stress, though this framework can be adapted to other conditions. Along with control manipulations that maintain continuous rainfall or drought stress, investigators can manipulate the timing of drought stress (i.e. early or late in the growing season) and the frequency of drought stress (i.e. rare or common). To disentangle the effects of timing and frequency of drought stress, manipulations should keep the amount of rainfall constant across factors. Alternatively, or in parallel, the duration of drought stress can be manipulated by withholding water for different periods of time (i.e. short or long), and severity of drought stress can be simulated by varying the amount of provided rainfall (i.e. low or high). The combination of factor manipulations and experimental levels should reflect regional projections for the climatic variability in the examined abiotic factor.

plant resistance to herbivory [339,340] and pollinator availability [117]. The resurrection approach offers a promising avenue to study rapid evolution to changes in biotic interactions between plants and herbivores or pollinators, and to examine co-evolutionary dynamics between species.

4.3. Emerging directions

One major gap in our understanding of evolutionary responses to climate change is in linking adaptive traits to their underlying molecular basis to facilitate a broader understanding of how adaptations can arise in the face of climate change [341], how local adaptation may facilitate climatic adaptation or be disrupted by climate change [154,155,342], or how novel selection shapes genes and gene expression underpinning organismal phenotypes [343].

One particular challenge lies in identifying the genetic basis of intraspecific variation in climatic tolerances, and translating those insights into spatial predictions of current and future range-wide climate adaptation [344,345]. Quantitative trait locus (QTL) mapping provides a powerful forward genetic approach to linking phenotype to genotypes, and has been applied to short lived plants where recombinant inbred lines (RILs) or near-isogenic lines (NILs) can be generated [341]. For example, two large-effect loci explained pathogen resistance between locally adapted switchgrass ecotypes [346]. Alternatively, under conditions when the relatedness of individuals in natural populations is unknown and pedigree lines cannot be generated (for long-lived species for example), genome-wide association studies (GWAS) identify genomic regions that exhibit polymorphisms associated with phenotypic variation [347–350]. By combining GWAS approaches with environmental niche models, studies predicted genetic changes of *A.thaliana* populations under future climate change [351]. Furthermore, using trained and field-validated genome-wide environment selection (GWES) models, follow-up studies predicted that many *A. thaliana* populations across the native range will experience more negative selection in the future, with local genotypes having lower fitness due to a diminished degree of local adaptation in the face of climate change, putting populations at evolutionary risk [352]. Similarly, other studies used multivariate community-level models (Generalized Dissimilarity Modelling: GDM, and Gradient Forests: GF) to analyze and map intraspecific adaptive genetic diversity under current or future environmental conditions in balsam poplar (*Populus balsamifera*) [345]. Based on candidate genes (i.e. GIGANTEA-5), rapid turnover in allele frequencies was identified in the north-western portion of balsam poplar’s range in response to small changes in temperatures, and models predicted these populations to have the strongest variation in genetic composition in the future. Such studies, integrating spatial modelling with large-scale environmental, phenotypic and genomic population data, will be key to predicting the fate of natural populations and the genetic change needed to track climate change [345,353,354].

Furthermore, gene expression patterns shape trait variation in natural populations [355], and affect abiotic stress tolerance and local adaptation to climate [356]. However, discerning the functional implications of variation in gene expression remains challenging, and very little is known about intrinsic and extrinsic factors that drive adaptive evolution via gene expression regulation [343,357]. Increasing research focus on transcriptomic profiles will further our understanding of the genetic basis of complex traits and interactions between the environment and genetics in trait expression [358,359]. For example, one recent study examined how winter storms drive rapid phenotypic, regulatory, and genomic shifts in green anole lizards, where gene expression of southern populations shifted towards patterns of northern populations with increased cold tolerance [360]. Such studies shed light on how climatic events can rapidly induce selection at the phenotypic, regulatory and genetic levels. Using phenotypic selection analysis on gene expression patterns across the entire genome, a novel study estimated the strength and type of ongoing selection that acts on gene expression and opened up the possibility of dissecting the factors that drive adaptive evolution via gene expression regulation [343]. However, linking gene expression to fitness remains challenging, thus we have a poor understanding of the adaptive nature of variation in gene expression and the magnitude of selection that occurs at the regulatory level [343,357, 361,362].

5. Conclusions

In response to unprecedented rates of climate change, plants and their mutualists and natural enemies have already shifted their geographic distributions and adjusted to novel conditions plastically and genetically. However, it is not always clear whether these changes will enable long-term persistence through increasingly novel climates. We have posed a series of research questions and hypotheses aimed at filling critical gaps in our current knowledge about the eco-evolutionary consequences of climate change. We argue that to generate more robust predictions about plant responses to global change, researchers need to integrate across the entire life cycle, from germination to reproduction, in studies that simultaneously manipulate multiple climate change factors. Single factor experiments do not reflect the complexity of contemporary climate change and could result in inaccurate inferences about the stability of populations under future climates. In addition, future studies will illuminate the extent to which specialized biotic interactions may be vulnerable to climate change. These studies could also lead to generalizable predictions about when spatial and temporal mismatches between plants and their mutualists or antagonists could jeopardize plant population growth. Resurrection approaches can evaluate the extent to which local populations have already adapted to climate-change mediated shifts in biotic interactions and abiotic conditions. Once such studies have been conducted in a diversity of systems, researchers will be able to test which characteristics enable rapid adaptation and which traits constrain adaptive responses to novel conditions. Such generalizations could inform conservation priorities. Emerging genomic and transcriptomic tools that dissect the genetic basis of climate change responses could test whether metapopulations can adapt to ongoing environmental change through standing genetic variation and provide key information for improving the efficacy of conservation strategies like assisted migration. We call for additional funding to support holistic manipulative experiments aimed at resolving the ecological and evolutionary consequences of climate change, especially in tropical ecosystems.

Declaration of Competing Interest

The authors report no declarations of interest.

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