


## Review

# Plant adaptation to climate change—Where are we?

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**Abstract** Climate change poses critical challenges for population persistence in natural communities, for agriculture and environmental sustainability, and for food security. In this review, we discuss recent progress in climatic adaptation in plants. We evaluate whether climate change exerts novel selection and disrupts local adaptation, whether gene flow can facilitate adaptive responses to climate change, and whether adaptive phenotypic plasticity could sustain populations in the short term. Furthermore, we discuss how climate change influences species interactions. Through a more in-depth understanding of these eco-evolutionary dynamics, we will increase our capacity to predict the adaptive potential of plants under climate change. In addition, we review studies that dissect the genetic basis of plant adaptation to climate change. Finally, we highlight key research gaps, ranging from validating gene function to elucidating molecular mechanisms, expanding research systems from model species to other natural species, testing the fitness consequences of alleles in natural environments, and designing multifactorial studies that more closely reflect the complex and interactive effects of multiple climate change factors. By leveraging interdisciplinary tools (e.g., cutting-edge omics toolkits, novel ecological strategies, newly developed genome editing technology), researchers can more accurately predict the probability that species can persist through this rapid and intense period of environmental change, as well as cultivate crops to withstand climate change, and conserve biodiversity in natural systems.

**Key words:** candidate genes, evolutionary potential, genomics, landscape genomics, selection.

## 1 Introduction

The capacity of plants to adapt to the direct and indirect consequences of climate change will influence extinction risks, agricultural and environmental sustainability, and food security. In the face of persistent and worsening climate change, it has become crucial to investigate how natural populations and communities respond to novel environments. Several clear patterns have emerged. For one, the distributions of many species have shifted to historically cooler regions in poleward and upslope directions (Parmesan et al., 1999; Walther et al., 2002; Parmesan & Yohe, 2003; Parmesan, 2006; Kelly & Goulden, 2008; Poloczanska et al., 2013; Burrows et al., 2014; Fadrique et al., 2018). These shifts have involved local extinctions and population contractions at the warmer range edges as well as range expansions into historically cooler regions at poleward latitudes and upslope elevations (Angert et al., 2011; Chuang & Peterson, 2016; Sheth & Angert, 2018; Anderson & Wadgyamar, 2020). Additionally, many species now emerge and reproduce significantly earlier in the year, which is likely a biological response to shortened winters, earlier onset of the growing season, and prolonged droughts

(Cook et al., 2012; CaraDonna et al., 2014; Hamann et al., 2018; Wadgyamar et al., 2018; Dickman et al., 2019).

Despite these advances, the answers to several key eco-evolutionary questions remain elusive. For one, it is challenging to assess how climate change will disrupt species interactions (Gilman et al., 2010, 2012; Angert et al., 2013; Parida et al., 2015; Pauchard et al., 2015). The ecological consequences of climate change have received extensive investigation, yet fewer studies have tackled the evolutionary consequences of climate change (but see e.g., Franks et al., 2007, 2016; Thompson et al., 2013; Wilczek et al., 2014; O'Hara et al., 2016; Peterson et al., 2018; Anderson & Wadgyamar, 2020). Novel climatic conditions could impose strong selection on natural populations (Bemmels & Anderson, 2019; Exposito-Alonso et al., 2019; Fu et al., 2019). Populations risk declines if they do not have enough genetic variation to adapt to these new pressures and if immigration is insufficient to introduce alleles adapted to warmer conditions in lower latitude or elevation sites (Carlson et al., 2014; Bemmels & Anderson, 2019; Carja & Plotkin, 2019; Kelly, 2019; Razgour et al., 2019). In addition, genetic tradeoffs across traits could constrain adaptive evolution, even under high quantitative genetic variation in functional traits (Etterson & Shaw, 2001). Many species will

fail to migrate fast enough through highly fragmented landscapes to keep pace with climate change (Loarie et al., 2009; Kremer et al., 2012). Furthermore, species that can successfully extend their ranges into previously unoccupied habitats will experience novel selective pressures to which they are not currently adapted (Brown & Vellend, 2014). We still have a limited understanding of how adaptive evolution, phenotypic plasticity, and gene flow will interact to influence population persistence under climate change. By identifying the evolutionary consequences of climate change, we can generate more robust predictions about extinction risks while identifying populations to prioritize for conservation actions.

Common garden and provenance experiments have yielded insights into whether adaptation could lag behind climate change in natural plant populations (Wang et al., 2010; Anderson & Wadgyamar, 2020). For example, climate change has already induced local maladaptation in the model organism *Arabidopsis thaliana* (Brassicaceae) (Wilczek et al., 2014) and its congeneric *Boechera stricta* (Anderson & Wadgyamar, 2020). Indeed, under climate change, local maladaptation may become more pronounced, with accessions from historically warmer and more arid environments having a fitness advantage over local accessions (Anderson, 2016; Anderson & Wadgyamar, 2020). One outstanding question is whether populations are able to adapt to ongoing climate change from standing genetic variation (Sheth et al., 2018; Bemmels et al., 2019), introgression via gene flow (Bontrager & Angert, 2019), or novel mutations. Indeed, we must achieve a greater understanding of how these sources of adaptive genetic variation will contribute to climate change responses in a diversity of species that vary in geographic distribution and life history strategies. For example, Qian et al. (2020) estimated the strength of selection acting on standing genetic variations by quantifying changes in allele frequencies of flowering time genes over 28 years in wild barley populations, a timeframe in which flowering time was shortened by 10 days (Nevo et al., 2012). *Arabidopsis thaliana* harbors standing genetic variation in complex traits like adaptation to drought stress; however, the alleles that confer survival under drought are not uniformly distributed across natural populations (Exposito-Alonso et al., 2017). Instead, drought-tolerant alleles currently exist predominantly in arid regions (Exposito-Alonso et al., 2017), raising the question of whether gene flow could spread these alleles rapidly enough to confront projected worsening drought across the native range of the species. Thus, it is critical to investigate how genetic variation is distributed across the landscape, and whether gene flow will be rapid enough to redistribute existing genetic variation, or if conservation practices like assisted gene flow will be necessary to reduce the risk of population decline (Aitken & Whitlock, 2013).

In this review, we seek to evaluate recent progress toward understanding the evolutionary consequences of climate change, while emphasizing how interdisciplinary collaborations could fill critical research gaps. We encourage additional applications of emerging genomic tools, along with interdisciplinary investigations, to enhance our ability to predict the adaptive potential of plants under climate change and to elucidate the genetic basis of complex trait variation (Fig. 1). These integrative approaches could improve

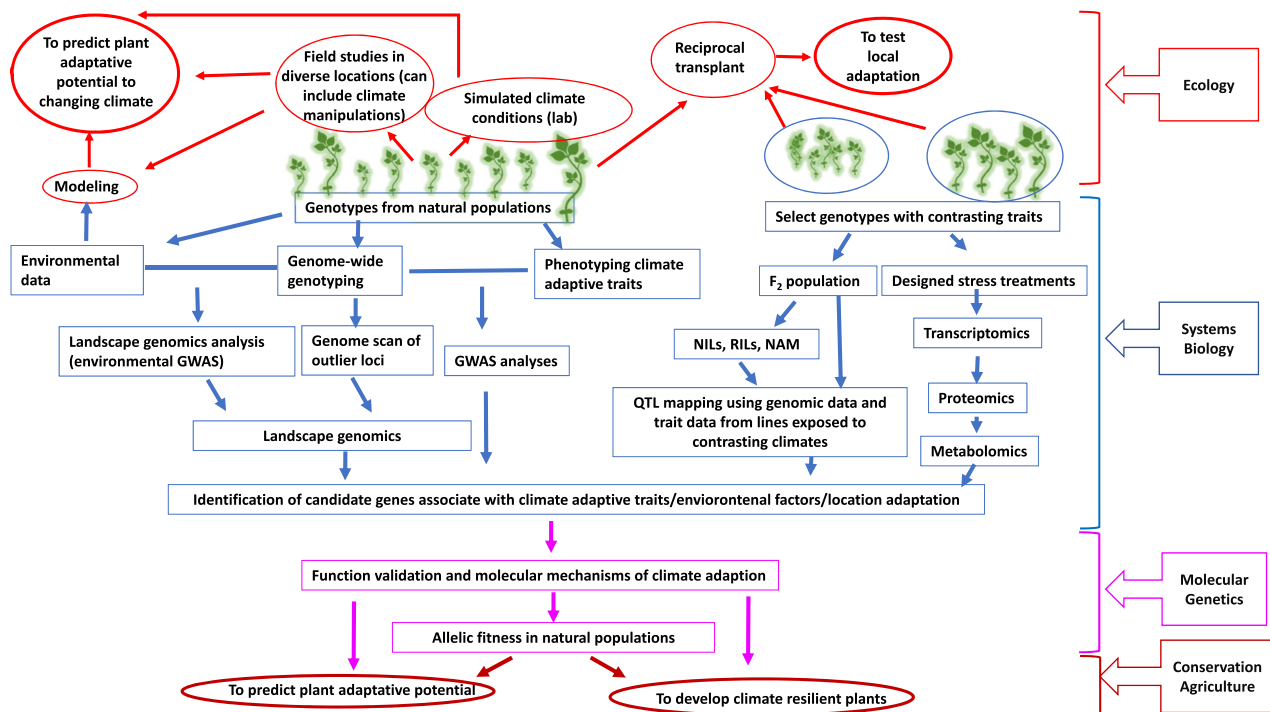
conservation outcomes and facilitate the development of crops that can withstand climate change.

## 2 Recent Progress—Cross-Disciplinary Integration

### 2.1 Assessing climatic agents of selection to evaluate whether climate change exerts novel selection and disrupts local adaptation

Field studies hold great promise for identifying the traits and genomic regions associated with climatic adaptation, especially when experimental gardens are arrayed across climatic gradients (Etterson & Shaw, 2001; Fournier-Level et al., 2011; Hancock et al., 2011; Wilczek et al., 2014; Exposito-Alonso et al., 2017, 2019; Sork, 2018; Anderson & Wadgyamar, 2020). However, such experiments cannot readily disentangle the specific agents of selection that have caused adaptive population divergence (Wadgyamar et al., 2017). Only experimental manipulations of key climatic factors can test the causal role of these factors in local adaptation (Wadgyamar et al., 2017; Anderson & Wadgyamar, 2020). For example, in high elevation and high latitude systems, climate change is rapidly reducing winter snowpack and accelerating spring snowmelt (e.g., Fyfe et al., 2017), which can expose plants to spring frost that they would not have experienced historically (Inouye, 2008) and contribute to the decline of native plant species (Campbell, 2019). *Boechera stricta* (Brassicaceae) is a perennial forb native to the Rocky Mountains, where local populations are adapted to historical snowpack levels (Anderson & Wadgyamar, 2020). In common garden experiments, low elevation genotypes adapted to hot and dry conditions outperformed local genotypes under both contemporary snowpack and snow removal, which simulates climate change (Anderson & Wadgyamar, 2020). In contrast, local genotypes had enhanced fitness under snow addition treatments (reflecting historical climates) (Anderson & Wadgyamar, 2020). Additionally, by leveraging data from field manipulations of precipitation in common gardens in Spain and Germany in concert with the rich genomic resources available for *Arabidopsis thaliana*, Exposito-Alonso et al. (2019) evaluated climate-driven selection across the genome of this model organism in its native range. They predicted that intensification of climate change could increase the vulnerability of natural populations to decline by 2050 (Exposito-Alonso et al., 2019). Thus, experimental manipulations of key agents of selection in the field can reveal the extent to which climate change has already disrupted local adaptation.

Field manipulations have demonstrated that climate change can alter ecological processes (Elmendorf et al., 2012; Rudgers et al., 2014; Anderson & Gezon, 2015; Hänel & Tielbörger, 2015; Harte et al., 2015; Smith et al., 2015; Wertin et al., 2015). Recent analyses suggest that experimental warming causes shifts in plant communities that resemble those observed in longitudinal studies (Elmendorf et al., 2015), demonstrating the ecological relevance of experimentally manipulating climatic factors. Nevertheless, field manipulations of abiotic agents of selection have rarely been applied in reciprocal transplant and common garden experiments (Pfeifer-Meister et al., 2013), perhaps because of the large sample sizes needed to estimate quantitative genetic



**Fig. 1.** The integration of methods from multiple disciplines enables us to predict plant climate change adaptive potential and dissect molecular mechanisms of plant climate adaptation. Red: Prediction of plant climate adaptive potential using advanced large-scale field experiments and simulated climate conditions in the lab; Blue: candidate gene identification employing diverse omics strategies; Purple: illustration of research gaps: Gene function validation, molecular mechanisms dissection, and field test of fitness consequences of climate-adapted molecular variation. Dark red: real-world applications in plant conservation and climate-resilient crop development. GWAS, genome-wide association study; NAM: nested association mapping; NIL, near-isogenic line; QTL, quantitative trait locus; RIL, recombinant inbred line.

parameters accurately. Studies of only a few traits can overestimate the potential for adaptation to novel conditions because of genetic constraints (Etterson & Shaw, 2001). Since the adaptive potential of populations is proportional to additive genetic variation in fitness, studies that examine quantitative genetic variation in fitness components in conditions relevant to climate change could generate robust predictions about the adaptive potential of natural populations (Sheth et al., 2018; Bemmels & Anderson, 2019). Owing to the complex nature of global change, we encourage future multifactorial studies that evaluate the interactive effects of climatic change factors (like temperature and atmospheric [CO<sub>2</sub>]) on fitness and adaptive evolution (Matesanz et al., 2009; Eller et al., 2011).

## 2.2 Investigating whether gene flow can facilitate adaptive responses to climate change

Under the rapid environmental change, gene flow could spread beneficial mutations, enhance genetic variation, and introduce preadapted genotypes (Bell & Gonzalez, 2011; Kremer et al., 2012; Aitken & Whitlock, 2013; Bontrager & Angert, 2019). In spatially heterogeneous landscapes, species are often mosaics of populations that have adapted to local biotic and abiotic conditions (e.g., Savolainen et al., 2007; Leimu & Fischer, 2008; Hereford, 2009; Wang et al., 2010; Alberto et al., 2013). If populations have diverged genetically

in response to climatic variation (De Kort et al., 2014), then a genetic variation may already exist within meta-populations that would enable continued adaptation to climate change. Gene flow could promote adaptation to novel suites of environments if alleles adapted to elevated temperatures, drought, reduced snowpack, or other climate change factors become introgressed into locally adapted populations in upslope or poleward locations (Aitken & Whitlock, 2013; Franks et al., 2014).

Extensive research has documented range shifts in a diverse array of species in response to rapid climate change (Parmesan, 2006; Angert et al., 2011; Chen et al., 2011). These studies typically focus on the movement of individual animals or seeds into new areas at the cooler edge of the range, and population declines in the warmer edge of the range. However, there have been fewer attempts to investigate how gene flow into established populations within species' current ranges contributes to climate change responses (Bontrager & Angert, 2019). Theoretical and review papers have highlighted the potential advantages and disadvantages of gene flow in changing environments (Kremer et al., 2012; Norberg et al., 2012; Aitken & Whitlock, 2013; Schiffers et al., 2013; Franks et al., 2014), and yeast lab studies have revealed that extensive dispersal across metapopulations enables evolutionary response to stressful environments (Bell & Gonzalez, 2011). Gene flow from populations adapted

to hot and dry climates into populations that historically experienced cooler conditions could facilitate adaptation to changing climates. Alternatively, gene flow could counteract local selection, and constrain adaptation to climate change if gene flow occurs in the opposite direction (e.g., from high to low elevation populations). When will gene flow promote versus restrict adaptive responses to climate change? How much gene flow is needed and from which populations? Will natural levels of gene flow be sufficient, or will conservationists need to adopt practices such as assisted gene flow (Aitken & Whitlock, 2013)? Can we reduce the risk of unforeseen consequences of assisted gene flow? These questions remain vitally underexplored (Etterson et al., 2008; Sexton et al., 2011; Bontrager & Angert, 2019).

### 2.3 Evaluating the contribution of adaptive phenotypic plasticity to the maintenance of population growth rate

Many species display phenotypic plasticity such that individuals can alter their phenotypes in response to the environment they encounter (Murren et al., 2015). Phenotypic plasticity can be adaptive and maximize fitness in heterogeneous landscapes when individuals change their phenotypes across environments in the direction of selection (Dudley & Schmitt, 1996; van Tienderen, 1997; Baythavong, 2011). Numerous species exhibit plasticity in response to environmental stimuli (Valladares et al., 2007; Matesanz et al., 2010). Adaptive plasticity can evolve under fine-grained temporal or spatial environmental variation, if individuals experience temporal variation in conditions during their lifetimes, or if propagules (seeds or pollen) establish in non-parental habitat types (Alpert & Simms, 2002; Sultan & Spencer, 2002; Baythavong, 2011).

Increased climatic variation associated with global change could favor phenotypic plasticity (Crozier et al., 2008; Nicotra et al., 2010), and adaptive plasticity could promote population persistence *in situ* or establishment in new habitats in upslope or poleward locations (Chevin et al., 2013; Frei et al., 2014; Anderson & Gezon, 2015). Indeed, studies have uncovered extensive plasticity to changing climates for some animals and plants (Réale et al., 2003; Bradshaw & Holzapfel, 2006; Teplitsky et al., 2008; Ozgul et al., 2009; Matesanz et al., 2010; Anderson et al., 2012). In most cases, however, we do not know if these plastic shifts can confer a fitness advantage under changing climates, or are maladaptive. One notable exception comes from studies of reproductive phenology in the great tit (*Parus major*; Charmantier et al., 2008; Vedder et al., 2013). Plastic shifts in breeding time in this bird over five decades have been sufficient to track climate-mediated changes in the availability of an important food resource (caterpillars) for *P. major* chicks (Charmantier et al., 2008). Models suggest that adaptive behavioral plasticity in breeding phenology will promote long-term population persistence and that populations would be much more vulnerable to climate change in the absence of plasticity (Vedder et al., 2013).

In the short-term, natural populations could cope with changing conditions via existing plasticity (Teplitsky et al., 2008; Nicotra et al., 2010), but this plasticity could be insufficient when individuals confront future climates outside the range of current environmental variability (Anderson et al., 2012; Kelly et al., 2012). Do populations maintain

enough genetic variation for phenotypic plasticity to adapt to increasingly variable conditions (Chevin et al., 2013)? The evolution of adaptive plasticity requires that individuals can sense and respond to reliable cues of changing environments and overcome the costs of plasticity (Via & Lande, 1985; van Tienderen, 1997; DeWitt et al., 1998; Sultan & Spencer, 2002; Auld et al., 2010). Could reduced reliability of environmental cues under climate change constrain the ongoing evolution of plasticity (Chevin et al., 2013)? Future studies that evaluate plasticity in functional traits under simulated climate change, ideally in the field, will generate answers to these questions.

Plasticity may be adaptive in portions of the range subject to temporal variation in environmental conditions, and maladaptive or nonexistent where conditions are less variable (Valladares et al., 2014; Duputie et al., 2015). Few studies have evaluated the extent to which plasticity varies intraspecifically across the landscape (but see Baythavong & Stanton, 2010; Baythavong, 2011). Are populations from more climatically variable environments more plastic? Are those populations less vulnerable to climate change? Temporal variation in climate increases from equatorial to poleward latitudes; this observation led to the prediction that thermal tolerances and plasticity should be greater at higher latitudes (Janzen, 1967; Ghalambor et al., 2006). Indeed, this pattern holds for many species, and high latitude species often inhabit locations with temperatures below their physiological tolerances, suggesting that these high latitude species may thrive under warmer climates (Deutsch et al., 2008; Araújo et al., 2013). However, we know very little about the extent to which climatic variability across elevations influences the evolution of plasticity (Vitasse et al., 2013). In mountainous regions with complex terrain, temperatures typically decline with elevation; however, dense cold air settles in valleys and local depressions at night and in the winter, resulting in increased diurnal and seasonal temperature variation at lower elevations relative to exposed mountaintops (Lundquist et al., 2008; Dobrowski, 2011). By testing, if plasticity increases with temporal climatic variation, future studies may be able to identify populations that are most susceptible to climate change. Results could be generalizable across systems if populations in climatically variable sites have the highest plasticity.

### 2.4 Leveraging herbarium and museum collections to evaluate biological responses to climate change

Herbarium and museum collections represent an invaluable resource for characterizing historical distributions, phenologies, and trait values of many plant and animal species (e.g., Losos et al., 2013). By comparing historical collections to contemporary records, Parmesan (1996) documented the first evidence of range shifts in response to climate change in Edith's checkerspot butterfly, with contractions in low latitude and low elevation populations. Other studies have leveraged herbarium records to demonstrate changes in geographic ranges in response to climate change (Feeley, 2012). These historical records can also quantify phenotypic changes through time. For example, DeLeo et al. (2019) used herbarium sheets to monitor shifts in physiology and collection dates of the model species *A. thaliana* across its native range over the course of 200 years. These collections also enable researchers to readily compare how different species have responded to anthropogenic climate

change. By extracting data on flowering time from herbarium sheets for 141 species, Calinger et al. (2013) found that many plant species have advanced the timing of flowering, but that species differ in the magnitude and direction of phenological shifts. Their results corroborated previous findings that species that flower in the spring are highly responsive to changes in temperature (Fitter & Fitter, 2002; Calinger et al., 2013). The digitization of museum and herbarium collections can facilitate research into biological responses to climate change (Meineke et al., 2019), with the caveat that biases in the extent of historical collections across time and space can make it inadvisable to track abundance with these collections (Wepprich, 2019). We encourage future research to capitalize on existing collections to test for phenotypic and genetic changes through time and to evaluate geographic contractions and expansions in response to climate change.

### 2.5 Testing how climate change will influence species interactions

Given the complexity of natural communities, it is challenging to predict how climate change will alter species interactions. Interacting species will differ in their migratory, phenological, and fitness responses to climate change, which could cause mismatches in distribution, abundance, and timing of interactions (Gilman et al., 2010, 2012; Forrest, 2015). By transplanting entire communities across climatic gradients, researchers can examine how climate change will influence species interactions (Alexander et al., 2015). In some cases, the direct abiotic effects of climate change, such as elevated temperature, will strongly affect eco-evolutionary dynamics and population persistence through climate change. In other cases, indirect effects mediated through biotic interactions will be more consequential, leading to increased competition (Alexander et al., 2015), predation and herbivory (Brodie et al., 2012; Rasmann et al., 2014; Romero et al., 2018), as well as disrupted mutualistic interactions (Forrest, 2015). For example, plant populations and their herbivores can be reciprocally locally adapted (Garrido et al., 2012). Climate change has altered fitness and phenotypes for both plants and herbivores (e.g., Stiling & Cornelissen, 2007; Anderson et al., 2012; Robinson et al., 2012). Under global warming in the geological record, herbivores consumed more plant tissue and fossilized leaves show high rates of damage from herbivory (Currano et al., 2008). Herbivores exposed to elevated temperatures and [CO<sub>2</sub>] in contemporary studies also show greater consumption rates of plant tissues (Stiling & Cornelissen, 2007; Robinson et al., 2012), which could depress plant fitness, especially in populations adapted to historically low levels of herbivory (e.g., high elevation *Boechea stricta* populations (Anderson et al., 2015). Evaluating how climate change will alter biotic interactions is crucial for generating robust predictions of population persistence. In addition to predicting species interactions in facing climate change (e.g., Romero et al., 2018; Ohler et al., 2020), scientists can protect against biodiversity loss due to climate change by identifying and preserving species that enhance local diversity, such as keystone species and ecosystem engineers (Bulleri et al., 2018).

### 2.6 Predicting the adaptive potential of plants under climate change

To prioritize populations and species for conservation, it is critical that we generate reliable predictions about the adaptive potential of species to climate change. The availability of large data from genome-wide genotyping and whole-genome sequencing, as well as germplasm collection, has enabled researchers to begin making such predictions. Recently, Exposito-Alonso et al. (2019) planted over 500 ecotypes of *A. thaliana*, collected across the range of the species, into common gardens in Spain and Germany to investigate how unique combinations of alleles influence climatic adaptation. Some alleles showed clear fitness trade-offs across environments, with positive selection in one environment being counteracted by negative selection in another environment (Exposito-Alonso et al., 2019). Fournier-Level et al. (2016) studied the seasonal adaptation of *A. thaliana* under four climate scenarios with advanced generation intercross lines developed from multiple parents. The results indicated that, in *Arabidopsis*, and likely other species, the maintenance of sufficient standing genetic variation is essential for adaptation to rapid climate change (Fournier-Level et al., 2016), which corroborates previous results (Fournier-Level et al., 2011). Recently, spatial modeling of biodiversity has been applied to map the geographic distribution of genomic variation in response to current and future environmental adaptation (e.g., Gugger et al., 2013; Fitzpatrick & Keller, 2015). For example, Jia et al. (2020) employed gradient forest modeling, integrating geographic, environmental, and genomic data, to investigate the climate adaptive potential of *Platycladus orientalis* (Cupressaceae), an ecologically and medicinally important conifer species. The results suggested that factors associated with temperature best explained the distribution of genomic diversity. The model also predicted that the northern and southern margins of the species distribution are at high risk in facing climate change (Jia et al., 2020). Future studies that investigate the adaptive potential to climate change in diverse species will enable researchers to detect more generalized patterns. By quantifying the fitness of specific alleles, and combinations of alleles across loci, researchers will be able to test the extent to which populations could adapt. A multidisciplinary approach integrating ecology, genetics, and genomics, and computational approaches will elucidate species' response to climate change (e.g., Exposito-Alonso, 2020; Segar et al., 2020; Waldvogel et al., 2020). We summarize a schematic of how to investigate thoroughly the adaptive potential of plants by integrating these diverse fields in Fig. 1 (red color).

### 2.7 Dissecting the genetic basis of plant climate change adaptation

The surge of omics technologies, databases and newly developed genome editing tools have facilitated the dissection of the genetic basis of complex traits associated with climatic adaptation in natural populations for better mitigating the negative consequences of climate change and developing climate-adaptive crops (e.g., Sork, 2018; Ogura et al., 2019; Zaidem et al., 2019). These approaches include quantitative trait locus (QTL) mapping, genome-wide association studies (GWAS), landscape genomics,

transcriptomics, and metabolomics, among others. By approaching the same question using multiple complementary methods, researchers can gain a more complete understanding of the genes underlying adaptation to climate. For example, GWAS use hundreds of ecotypes from natural populations to examine associations between genome-wide molecular markers (e.g., single nucleotide polymorphisms, SNPs) and ecologically important phenotypes. These ecotypes from natural populations have experienced many recombination events, often resulting in low levels of linkage disequilibrium (LD; high resolution); however, GWAS results can be confounded by a population structure (e.g., Frichot et al., 2013; Zhang et al., 2016; Kofsky et al., 2020; Pais et al., 2020). In contrast, cross-based QTL mapping studies use mapping populations developed from crosses among individuals with contrasting traits (often from different populations, or even from different species). Quantitative trait locus mapping studies are not confounded by population structure; however, QTL approaches are not applicable for most natural systems, especially for woody plants, which comprise ~45% of plant species globally (FitzJohn et al., 2014). Additionally, QTL studies suffer from low resolution due to fewer recombination events (e.g., Mitchell-Olds, 2010; Zaidem et al., 2019). Both QTL mapping and GWAS can be done using populations exposed to climate change factors, such as elevated temperature or drought stress, either in the field or in the lab. These experiments will reveal which regions of the genome—and ultimately candidate genes—are involved in climate change responses.

Landscape genomics has emerged as a powerful approach for testing the relationship between genomic variation and environmental heterogeneity among natural populations (e.g., Rellstab et al., 2015; Li et al., 2017; Pais et al., 2017, 2018, 2020; Dalongeville et al., 2018). Two strategies have been widely used to identify candidate genes involved in environmental adaptation in landscape genomic studies. One involves scanning the genome of two or many populations in different habitats to detect outlier loci showing excess of population differentiation ( $F_{ST}$ ; genome scan method; e.g., Storz, 2005; Foll & Gaggiotti, 2008; Excoffier et al., 2009; Wittkopp & Kalay, 2011; Pais et al., 2017, 2018, 2020; Gould et al., 2018), and the other is genome-wide association study between molecular markers and environmental variables, which are treated as phenotypes (GWAS method; e.g., Rellstab et al., 2015; Li et al., 2017; Frachon et al., 2018; Razgour et al., 2019). These two methods require different sampling strategies. The former requires population samples growing in distinct environments, while the latter requires hundreds or thousands of genotypes across the range of a species with only one individual per location (Yoder et al., 2014; Anderson et al., 2016; Pais et al., 2020). Both methods benefit from the rapid progress of genome-wide genotyping technologies and statistical techniques. The latter (GWAS method) is also facilitated by the accessibility of large-scale climatic data. For example, Yoder et al., (2014) applied the GWAS-method and identified candidate loci responsible for the adaptation of *Medicago truncatula* to different climatic gradients with an association panel of over 202 accessions and almost two million genome-wide

SNPs. The integration of both methods can be applied to dissect the genetic basis of climate adaptation, especially for the tree species in which QTL mapping and reciprocal transplantation are not applicable due to long life cycles. For example, Pais et al. (2020) employed both genome scan method and GWAS method and identified 72 genetic variants showing signal of local adaptation to biotic or abiotic pressures in an endangered flowering dogwood tree (*Cornus florida* L.) in the Cornaceae family.

Systems biology integrating various “omics” technologies has facilitated the discovery of candidate genes conferring complex trait variation (e.g., Civelek & Lusk, 2014; Cloney, 2016; Palit et al., 2020). Transcriptomics, proteomics, and metabolomics are well suited to handle complex traits by quantitatively and dynamically determining the activities of transcripts, proteins, and metabolites over a time course. Data generated from these approaches may directly support the prediction of candidate genes that underlie significant QTLs, or link proteins, metabolites, and pathways with traits of interest. In Fig. 1 (blue), we illustrate how to integrate genomics, landscape genomics, and systems biology in identifying candidate genes involved in plant climate adaptation. Once appropriate genes or pathways are discovered and validated, modern biotechnology, genome editing, and pathway engineering can be applied to develop plants that can withstand climate change (Fig. 1, purple and dark red color).

Over the past decade, numerous studies have reviewed methods employed in dissecting the genetic basis of climatic adaptation, as well as identified candidate genes involved in environmental adaptation (e.g., Franks & Hoffmann, 2012; Sork, 2018; Kelly, 2019; Zaidem et al., 2019; Ding et al., 2020; Waldvogel et al., 2020). In a comprehensive literature review, Franks & Hoffmann (2012) suggested that candidate genes, genetic regulatory networks, and epigenetic effects are involved in climate change adaptation. Recently, Sork (2018) reviewed studies on the genetic architecture of plant environmental adaptation in natural populations, with a focus on model plants, including *A. thaliana* and tree species. Ogura et al. (2019) took a genomic approach (GWAS) to identify an *Arabidopsis* gene (*EXO70A3*) that influences drought tolerance and, then, used genome editing to elucidate the molecular mechanisms regulating soil root architecture and depth of the root system by controlling the auxin pathway. This discovery could ultimately enable scientists to develop crops that produce deeper roots. This study highlights the complementary nature of these genomic tools/approaches.

### 3 Research Gaps

#### 3.1 Expanding research focus from model species to a diverse array of ecologically and agronomically important species

The majority of studies dissecting the genetic and genomic basis of climate adaptation focus on the model plants, *Arabidopsis thaliana*, because of its rich genomic and germplasm resources, short life history, well-developed transformation system, and a large research community. Few studies have investigated the molecular mechanisms of climate adaptation of diverse natural species. Climate change can strongly influence some natural populations and may

increase the risk of extinction for many native species (Anderson, 2016). Thus, we suggest that future research should apply cross-disciplinary integration to study climate adaptation in a more diverse array of species. One of the priorities should target crop wild relatives (CWR), closely related to domesticated crop species, as climate change can dramatically reduce crop yield production and further lead to the food security crisis. Increasing effort is urgently needed to develop climate-adaptive crops (Lobell & Gourdj, 2012; Nelson et al., 2014; Zhao et al., 2017). Crop wild relatives harbor rich genetic variation and can provide new genetic variation for agriculture sustainability (Henry, 2014; Brozynska et al., 2016; Fu et al., 2019; Zhang et al., 2017, 2019). For example, Henry (2019) highlighted several recently identified wild rice species with most divergent genotypes in northern Australia containing novel alleles for various important traits, which could enhance the capacity of cultivated rice to tolerate climate change. During the past decade, dozens of review/perspectives have been published to highlight the potential and importance of crop wild relatives in meeting global challenges (e.g., Brozynska et al., 2016; Zhang et al., 2017, 2019; Mammadov et al., 2018; Fernie & Yan, 2019; Henry, 2019). Nevertheless, few climate-adaptive casual genes identified in CWR have been applied to the development of crops that can withstand climate change.

### 3.2 Expanding research focus from the identification of candidate genes to function validation and elucidation of molecular mechanisms

Despite an impressive body of literature identifying candidate genes associated with various traits related to climate conditions, such as drought and thermal stress, few studies have evaluated the function of candidate genes that may influence climatic adaptation. We know very little about the molecular mechanisms involved in climate adaptation. For example, Anderson et al. (2016) used GWAS to identify candidate genes for abiotic stress tolerance in *Glycine soja*, the wild progenitor of cultivated soybeans. This study identified two significant SNPs associated with mean temperature, which were close to an Arabidopsis ortholog, *MYB88*, which encodes a putative transcription factor involved in stomata development in Arabidopsis. Genotypes with nonreference alleles were more prevalent in *G. soja* than in cultivated soybeans. Another candidate gene, *PECT1*, involved in respiration capacity in leaves, was significantly associated with both monthly precipitation and precipitation in the wettest quarter (Anderson et al., 2016). Efficient transformation strategies and emerging genome editing technology are expected to facilitate gene function validation in more diverse species.

### 3.3 Expanding research focus from identification of casual genes to testing fitness in natural environments

Even when studies detect causal genes associated with an important adaptive phenotype, we typically lack information on the fitness effect of the alleles in natural environments. Prasad et al. (2012) identified a gene (*CYP79F*) that controls variation in glucosinolate compounds and insect herbivory in a wild relative of Arabidopsis by QTL mapping and positional cloning. They then used functional validation and allele-specific fitness testing by planting the near-isogenic lines in the

environment where the parents were originally collected. One allele at the *CYP79F* locus showed higher fitness in its native environment, but allelic variation did not affect fitness in the other environment (Prasad et al., 2012). This kind of study is challenging but can shed light on the molecular mechanisms and evolutionary dynamics of plant environmental adaptation.

### 3.4 Expanding research focus from single environmental stress factor to multiple factors

Most studies evaluate the genetic basis of adaptation to a single stress factor at a time. However, plants face multiple stressors under climate change, from elevated CO<sub>2</sub> concentrations to increased temperatures and disrupted precipitation. A response to a combination stresses cannot be extrapolated from each individual stress alone; rather, plants may show non-additive responses to interacting stresses, including unique expression profiles (e.g., Suzuki et al., 2014; Gray et al., 2016; Pandey et al., 2017). For example, abiotic stress, such as drought, can weaken plant defense mechanisms against pathogens (e.g., Prasad & Sonnewald, 2013). Recent work suggests that the response to the combined stress of soybean cyst nematode (SCN) and drought is different from each stress alone (Song Lab, unpublished data). Identifying the genetic basis of multiple traits relevant to fitness under global change will significantly advance predictions on global change effects (Reusch & Wood, 2007). Thus far, omics strategies, such as, transcriptomics, metabolomics, and proteomics, have shed light on plant responses to stress. Future interdisciplinary collaborations hold great promise for predicting plant adaptation to climate change and uncovering pathways and networks that underlie these responses. Particularly, we suggest future research should focus on conditions that mimic the field environment, to develop plants and crops with enhanced tolerance to climate change conditions.

## 4 Conclusions

Evaluating complex biological responses to climate change requires an interdisciplinary approach that leverages ecological, evolutionary, and genomic tools to test the extent to which climate change disrupts eco-evolutionary processes and to predict whether species can withstand deteriorating conditions. At an evolutionary scale, natural populations respond to climate change through shifts in geographic distributions, adaptation to novel conditions, or a plastic response to changing environments. If climate change severely depresses individual fitness and population growth rates ( $\lambda$ ), species risk extinction locally, regionally, or globally (Anderson, 2016). Within natural communities, interacting species vary in dispersal capacity, as well as the environmental cues that trigger key life-history events, such as reproduction and annual migrations. These species will differ in their spatial and temporal responses to climate change. Thus, at the ecological level, climate change will re-shape communities. Interdisciplinary research will more effectively address critical questions about the biodiversity consequences of climate change, from genetic diversity within and among populations of one species to species diversity within and across communities.

The expanding omics and statistical toolbox could enable us to generate more robust predictions about plant adaptive potential under climate change. Promising progress has been made, however, we still have many research gaps to fill. For example, we still have an incomplete understanding of the relative role of regulation of gene expression versus gene changes in plants' responses to climate change, as well as the relative contributions of standing genetic variation versus novel mutations to climate adaptation. Furthermore, we have a very limited understanding of whether common genes and pathways underlie climatic adaptation across plant species and families. A more complete understanding of plant responses to climate change will only emerge through integrative studies and international collaboration that include field fitness tests across diverse environments and countries (Losos et al., 2013; Taylor et al., 2019).

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## Competing Interests

The authors declare that they have no conflict of interest.

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