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# Responses to climate change – insights and limitations from herbaceous plant model species

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## Contents

## Summary

Herbaceous plant species have been the focus of extensive, long-term research into climate change responses, but there has been little effort to synthesize results and predicted outlooks. This primer summarizes research on climate change responses for eight intensively studied herbaceous plant species. We establish generalities across species, examine limitations, and propose a path forward. Climate change has reduced fitness, caused maladaptation, and/or led to population declines in at least part of the range of all six forb species. Plasticity alone is likely not sufficient to allow adjustment to shifting climates. Most model species also have spatially restricted dispersal that may limit genetic and evolutionary rescue. These results are surprising, given that these species are generally widespread, span large elevation ranges, and have substantial genetic and phenotypic variation. The focal species have diverse life histories, reproductive strategies, and habitats, and most are native to North America. Thus, species that are rare, habitat specialists, or endemic to other parts of the world are poorly represented in this review. We encourage researchers to design demographic and field experiments that evaluate plant traits and fitness in contemporary and potential future conditions across the full life cycle, and that consider biotic interactions in climate change responses.

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**Key words:** *Andropogon gerardii* (Big Bluestem), *Arabidopsis thaliana* (thale cress), *Boechera stricta* (Drummond's rockcress), *Clarkia xantiana* (gunsight clarkia), *Ipomopsis aggregate* (Scarlet Gilia), *Mimulus cardinalis* (scarlet monkeyflower), *Mimulus guttatus* (common yellow monkeyflower), *Panicum virgatum* (Switchgrass).

## I. Introduction

A key priority for society is evaluating organismal responses to changing climates – specifically identifying the following: Which species are likely to be threatened by changing climates? Why these species are threatened while others are not? And what the impacts will be on ecological communities and ecosystems (IPCC, 2023)? Empirical studies of plants have played a large role in our current understanding of biological responses to rapid environmental change (Parmesan, 2006; Franks *et al*., 2007; Thompson *et al*., 2013; Wilczek *et al*., 2014; Anderson & Song, 2020). Plants are sessile, which makes them both relatively easy to study through observational and manipulative studies as well as vulnerable to changing climates, as rooted plants cannot behaviorally adjust through movement, as animals can. Indeed, many species exhibit either population declines (Inouye, 2008; Krushelnycky *et al*., 2013; Sheth & Angert, 2018; Campbell, 2019; Reed *et al*., 2021) or spatial lags in adaptation in response to changing climates (Wilczek *et al*., 2014; Kooyers *et al*., 2019; Anderson & Wadgymar, 2020). The effects of climate change on plants have also influenced dynamics at the community and ecosystem scales, including collapsing food webs and altering ecosystem function and services (Avolio *et al*., 2014; Smith *et al*., 2015; Bartley *et al*., 2019; Vahsen *et al*., 2023).

In response to changing climates, plants can acclimate, move, adapt, or risk extinction (Aitken *et al*., 2008). Acclimation through phenotypic plasticity could enable individuals to escape, avoid, or tolerate novel conditions (Nicotra *et al*., 2010). Plants could move to favorable climates through seed or pollen. While only seed dispersal would allow plants to establish in new locations, gene flow through both seed and pollen dispersal could introduce new alleles into existing populations, potentially increasing fitness within a population through reduced inbreeding or demographic increases – a process deemed genetic rescue (Frankham, 2015; Whiteley *et al*., 2015; Bell *et al*., 2019). With or without gene flow, adaptation within populations to novel conditions can result in improved fitness, termed evolutionary rescue (Carlson *et al*., 2014; Bell, 2017). Assessing the type of responses employed by different plant species as well as determining the magnitude of responses is challenging and requires synthesis from different kinds of experiments and fields that may or may not be appropriate for all organisms (Box 1). Researchers can evaluate shifts in species' ranges, phenology, and traits by leveraging herbarium collections and historical surveys as baseline data (e.g. Kelly & Goulden, 2008; Calinger *et al*., 2013; Fadrique *et al*., 2018; DeLeo *et al*., 2020; Büntgen *et al*., 2022). However, documenting the propensity for species to shift their phenotype through phenotypic plasticity or genetic adaptation is more complicated and requires in-depth common garden or manipulative experiments (Gienapp *et al*., 2008; Shaw & Etterson, 2012; Wadgymar *et al*., 2022). Quantifying adaptive potential requires researchers to estimate genetic variation in ecologically important traits (Etterson & Shaw, 2001; Kulbaba *et al*., 2019), often in populations across a species' range (Pennington *et al*., 2021). Furthermore, documenting population dynamics and risk of extirpation requires labor-intensive field studies across life cycles within natural populations (Sheth & Angert, 2018; Campbell, 2019; Reed *et al*., 2021). Needless to say, our understanding of plant responses to changing climates is predominantly shaped by studies of a small proportion of plant species, often in restricted portions of their ranges.

Extensive empirical studies and meta-analyses have been conducted on climate responses in trees (e.g. Langlet, 1971; Aitken *et al*., 2008; Alberto *et al*., 2013; Sork *et al*., 2013; Fei *et al*., 2017), particularly those in northern temperate forests, owing to their economic and ecological importance. These studies suggest that trees are well-adapted to historical climatic conditions (Savolainen *et al*., 2007), are threatened within warmer and drier areas of historical ranges (i.e. the 'trailing-edge' populations (Rebetez & Dobbertin, 2004; Dyderski *et al*., 2018; Browne *et al*., 2019)), have occasionally had recent shifts in range and abundance both latitudinally and longitudinally (Fei *et al*., 2017), but often will require human assistance via assisted gene flow to persist (Aitken & Bemmels, 2016). Meta-analyses of short-lived herbaceous species are far less common (Franks *et al*., 2014; Anderson, 2016). Herbaceous species likely differ in the type and magnitude of responses to changing climates owing to shorter generation time and reduced environmental variability within a lifespan. For instance, herbaceous species with short generation times may adapt rapidly to extreme events (e.g. Franks *et al*., 2007) but are also predicted to be less buffered against climate variability than long-lived species (Morris *et al*., 2008). Additionally, herbaceous plants likely have different trait-based ecological strategies for responding to abiotic and biotic stresses (Kooyers, 2015) and may have different seed bank dynamics (Thompson, 1987).

Here, we explore eight of the model herbaceous plant species that have shaped our current understanding of responses to changing climate (Fig. 1). For each species, we (1) document relevant organismal biology; (2) review the major work on climate change responses; (3) summarize the key results including evidence for population declines, maladaptation, acclimation, genetic rescue, or evolutionary rescue associated with climate change; (4) synthesize the relevance of the results for other plant species, communities, and ecosystems; and (5) highlight the limitations of each model system. Our goal is not to comprehensively summarize the immense literature on all climate responses of herbaceous species. Instead, we aim to provide an introductory primer to eight ecological model species to foster a better understanding of the diversity of and commonalities in climate change responses.

## II. *Arabidopsis thaliana* (Brassicaceae)

### Moi Exposito-Alonso

*Arabidopsis thaliana* (L.) Heynh. ($2n = 10$) is an annual herb whose native range spans Eurasia with sparse relictual populations from Africa to Tibet, and naturalized ranges in every other continent except for Antarctica. Populations occur from sea level to *c.* 4400 m. *A. thaliana* is widespread in North America with small-to-large population sizes depending on region, and rare in South America and Australia (Leventhal *et al*., 2025). The life cycle of *A. thaliana* varies from a winter annual to a spring or summer annual depending on whether germination occurs in fall or spring. Both

**Box 1.** Key experimental designs for detecting climate change responses

Field experiments are critical for understanding a species response to changing climates. However, integrating genetic studies into field and controlled environments has provided greater insight and more feasible logistics for addressing conservation challenges. Here, we summarize several common experimental designs and their utility that reappear for several model herbaceous species (Fig. B1).

Observational demographic studies track key vital rates, such as survival, growth, and reproduction, across the life cycle of a species. These data can be combined together into demographic models and elasticity analyses to determine population growth rates, key life stages, and potential impacts of changing climates. Other observational studies may examine variation in phenotypes within and between populations and associate phenotypic variation with fitness variation. These data are critical for establishing baseline datasets and shifts due to both short- and long-term climatic fluctuations. Field common garden studies include reciprocal transplant experiments, in which populations are transplanted into each other's home environment, as well as provenance studies in which populations from across a range of environmental conditions are transplanted into one or more sites. These studies are designed to detect local adaptation and have been repurposed by the climate community to detect maladaptation in which populations from historically warmer and drier climates have higher fitness than the local population (an 'adaptation lag'). We note that adaptation lags do not necessarily indicate individual populations are threatened – just that populations are not adapting rapidly enough to changing conditions and likely have some decrease in population growth rate. Manipulative experiments are often designed within common garden experiments to manipulate a limited number of agents of selection that are thought to be associated with changing climates (e.g. snowfall removal, ambient heating, water addition, or increased $CO_2$ concentration). Such experiments are positive confirmation of the fitness consequences of individual agents of selection. Resurrection experiments compare phenotypes and fitness between ancestors and descendants within a single population, typically pre- and post-extreme climatic event. Within a common garden, shifts in phenotypes or fitness between generations are associated with evolution, transgenerational plasticity, or reemergence of individuals from a long-term seed bank. Quantitative genetics experiments examine heritability, additive genetic variation, and covariance between phenotypes and fitness within a given population. Phenotypic selection analyses identifying the relationship between phenotypes and fitness are common for both model and nonmodel species. Such experiments provide important predictions for responses to selection to changing climates as well as potential limitations to adaptation. Population genomic experiments examine patterns of genetic variation within and between populations. Neutral marker comparisons among populations allow for assessment of gene flow between populations as well as evidence of population contractions. Gene-environment associations provide evidence of which loci are responsible for climate adaptation and can be used to calculate genetic offsets for assessing the most relevant populations for assisted gene flow. Ancient DNA (Museomics) enables assessment of shifts in both population structure and loci under selection as climates have changed.

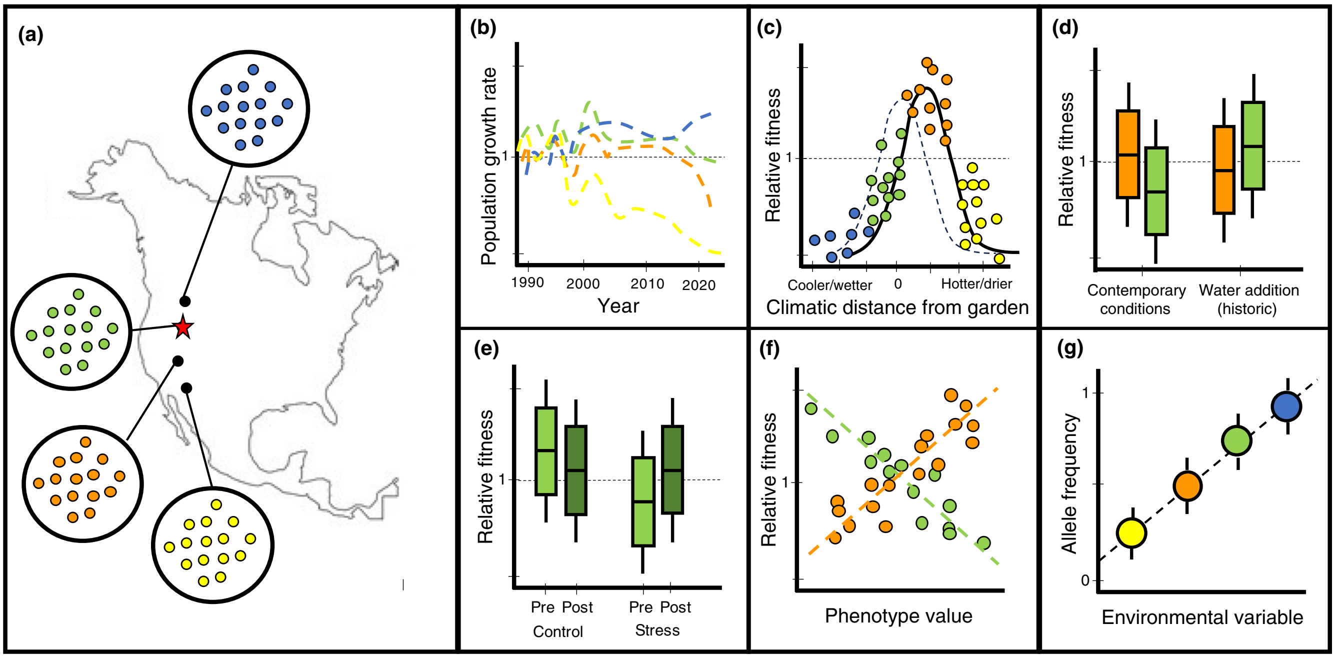

**Fig. B1** Complementary experimental designs for examining climate change responses. (a) Distribution of four populations across the range of a hypothetical species. Focal population represented by the red star. (b) Observational dataset demonstrating declining population growth rates in the warmest/driest population. (c) Provenance study demonstrating an adaptation lag for the focal population. (d) Manipulative experiment demonstrating a key agent of selection for the focal population. The water addition increase water availability to the historic level. (e) Resurrection study demonstrating adaptive evolution following an extreme climatic event. Light green represents the ancestral population while dark green represents the descendent population. (f) Phenotypic selection experiment that depicts differences in directional selection within the green and orange populations. Phenotypic selection experiments represent one kind of quantitative genetic experimental design. (g) Example of a gene–environment association at a single locus from a population genomics experiment. Combining similar effects across the genome can allow genomic prediction of germplasm lines best adapted to future environments.

**Fig. 1** Herbaceous model species for climate change responses: (a) *Arabidopsis thaliana*, (b) *Boechera stricta*, (c) *Clarkia xantiana*, (d) *Mimulus cardinalis*, (e) *Mimulus guttatus*, (f) *Andropogon gerardii*, (g) *Panicum virgatum*, (h) *Ipomopsis aggregata*. Inserts are close-up photographs of flowers. Photographer acknowledgements (top left to bottom right): (a) Anonymous (insert: Jan De Laet); (b) Mary Ellen Harte (insert: Adam Schneider); (c) Geoff Burleigh (insert: Steve Laymon); (d) Seema Sheth; (e) Nicholas Kooyers (insert: Christophe Bornand); (f) Sally & Andy Wasowski (insert: Carolyn Fannon); (g) Bonnie Harper (insert: R.W Smith); (h) Diane Campbell.

life histories result in rapid flowering within the growing season (Donohue, 2002; Montesinos *et al.*, 2009; Picó, 2012). Seed dormancy is variable, and a seed bank exists (Lundemo *et al.*, 2009; Vidigal *et al.*, 2016). Its lack of symbiosis requirements, lack of obligate pollinators or outcrossing, and low competitive ability (Pigliucci, 2002) make it a relatively simple model system with low cultivation requirements. *A. thaliana* is best known as a weed adopted as a genetics laboratory model system in mid-late of the 20th century. We argue that the availability of extensive genetic resources and the expansive climatic range provide a unique opportunity to understand the molecular and genomic basis of environmental adaptation. Its diverse suite of annual life histories, together with a broad geographic range, makes it ideal for studies in ecology, life-history evolution, and population biology (Exposito-Alonso, 2020; Martínez-Berdeja *et al.*, 2020; Leventhal *et al.*, 2025).

In the oldest, relict populations sampled in the Mediterranean, Levant, and Africa, *A. thaliana* inhabits xeric shrublands and rocky outcrops, at elevations from sea level to above 2500 m (Brennan *et al.*, 2014; Fulgione *et al.*, 2022; Leventhal *et al.*, 2025). In relict populations, phenotypes span from extremely fast-flowering plants with low levels of winter germination (Fulgione *et al.*, 2022) to extremely late-flowering plants found at high elevations in Iberia (Méndez-Vigo *et al.*, 2011; Leventhal *et al.*, 2025). Other populations across the range, such as very northern populations of Scandinavia, have strict vernalization and photoperiod control to time overwintering via cold temperature clocks (Dittmar *et al.*, 2014; Duncan *et al.*, 2015), different water use efficiency strategies (Des Marais *et al.*, 2014; Mojica *et al.*, 2016; Exposito-Alonso *et al.*, 2017; Dittberner *et al.*, 2018), and altered root architectures (LaRue *et al.*, 2022). Unlike ruderal populations in Central Europe, relictual populations have been declining in effective population size since the last glacial maxima (1001 Genomes Consortium *et al.*, 2016; Durvasula *et al.*, 2017; Exposito-Alonso *et al.*, 2017).

## 1. Significant work

The vast molecular genetic and genomic resources in *A. thaliana* provide an exceptional context for understanding potential population responses to climate change. For instance, the first genome-wide mutation rate for a plant species ($7 \times 10^{-9}$ mutations per bp per generation; Ossowski *et al.*, 2010) was identified in *A. thaliana*, allowing the parameterization of models to estimate the speed of evolution of natural populations (Exposito-Alonso *et al.*, 2018a). Extensive functional genetic studies allow researchers to understand the potential fitness ramifications of individual mutations. For instance, Ho & Weigel (2014) characterize the ramifications of mutations in 120 of 175 possible codons in FLOWERING LOCUS T (FT) on flowering time. These approaches enable researchers to parse gene × environment interactions, which are necessary for determining how and why (or why not) populations may be phenological tracking changing climates. Surveys of genetic diversity within and across populations across the world allow assessment of which populations have the most adaptive potential (Nordborg *et al.*, 2005; Horton *et al.*, 2012).

While *A. thaliana* has been used as a model for understanding many different types of responses to changing climates, the largest focus has been on characterizing the genomic basis of local adaptation and natural selection to heterogeneous environments. Extensive reciprocal transplant experiments (Ågren & Schemske, 2012; Oakley *et al.*, 2023) and field genome-wide association study (GWAS) experiments (Fournier-Level *et al.*, 2011; Exposito-Alonso *et al.*, 2019) have been conducted, and world-wide panels of *A. thaliana* have been used to identify genotype–environment associations (Hancock *et al.*, 2011; Lasky *et al.*, 2012). Global collaborations (GrENE-net consortium; https://grene-net.org/) are underway to coordinate 45 parallel common gardens across the Northern Hemisphere to examine the tempo, mode, and predictability of natural selection in a changing world (Wu *et al.*, 2025). While these studies may not all directly assess climate change responses, they provide critical information about adaptive and maladaptive responses in future climates.

## 2. Major results

*Arabidopsis thaliana* has a long history of migrating with changing climates (Sharbel *et al.*, 2000; Beck *et al.*, 2008; François *et al.*, 2008). Large population scale genomic sampling was used to reconstruct population histories and suggest populations colonized Eurasia *c.* 100 ka (Durvasula *et al.*, 2017) followed by several admixture events between relictual and nonrelictual expanding populations (1001 Genomes Consortium *et al.*, 2016). Currently, patterns of population structure across the native range strongly suggest range expansion as glaciers receded following the last glacial maximum (LGM) (Beck *et al.*, 2008). Species distribution models (SDMs) suggest that lower latitude populations (often genetically distinct refugial populations) are most threatened by changing climates, but note that *A. thaliana* has clearly colonized novel environments around the globe (Yim *et al.*, 2024). However, accessions associated with humans (i.e. laboratory reference accessions) exhibit patterns of rapid migration across the globe (Exposito-Alonso *et al.*, 2018a). Accessions from low-latitude equatorial or high-elevation environments have lower seed output and slower reproduction rates (Gamba *et al.*, 2024) and have likely been isolated in relictual regions for thousands of years (Brennan *et al.*, 2014; Durvasula *et al.*, 2017). This, along with minimal seed dispersal, suggests that these populations are likely dispersal-limited (1001 Genomes Consortium *et al.*, 2016; Gamba *et al.*, 2024).

Variation in seasonal conditions has driven pervasive natural selection on phenology and local adaptation (Leventhal *et al.*, 2025). Generally, there are strong fitness declines when populations are transplanted into nonlocal environments (Sweden-Italy or Germany-Spain comparisons; Ågren & Schemske, 2012), with an average fitness reduction of 30% (Exposito-Alonso, 2023); climate change could reduce the fitness of local populations relative to those from more equatorial latitudes, which experienced hotter conditions across their evolutionary histories (Wilczek *et al.*, 2014). Natural selection is stronger in water-limiting environments (Mediterranean common gardens; Exposito-Alonso *et al.*, 2019) or very cold environments (Scandinavian common gardens; Ågren & Schemske, 2012), while selection is much weaker when plants are transplanted into more temperate and mesic environments (Exposito-Alonso *et al.*, 2018b, 2019). Selection is sufficiently strong to generate divergent phenotypic clines along different elevation gradients in the native range (Gamba *et al.*, 2024) and parallel latitudinal clines in flowering time following introduction to North America (Samis *et al.*, 2012).

Genomic predictions forecast that regions in Mediterranean-to-temperate climate transitions in Central Europe may have the largest lag in adaptation to climate change (Exposito-Alonso *et al.*, 2019), consistent with maladaptation detected by Wilczek *et al.* (2014) in four European common gardens. This adaptation lag was especially pronounced at the highest latitude site, consistent with greater impacts of warming at more extreme latitudes (Wilczek *et al.*, 2014).

More recently, with over 30 common gardens and experimental evolution, a adaptation lag was detected in accessions originated from warm populations (Wu *et al.*, 2025), highlighting the complex interactions between climate shifts and geography of the species. However, there have been shifts in some phenotypes (including phenology, leaf C:N, and stomatal density) over time that suggest some level of adaptation to changing climates (DeLeo *et al.*, 2020; Lang *et al.*, 2024). The capacity for future adaptation likely depends on the population. There is substantial variation in fitness in experiments with mixtures of global genotypes, with up to $h^2 = 0.5$ for survival in a low precipitation common garden in Spain (Exposito-Alonso *et al.*, 2019). But many local populations will have a fraction of that genetic variation (*c.* 10%) as genetic diversity is generally low within the primarily selfing species (Nordborg *et al.*, 2005; Exposito-Alonso *et al.*, 2022; Hesen *et al.*, 2024). Indeed, common gardens leveraging local populations from Sweden, Toulouse, and Spain (e.g. Toledo *et al.*, 2020) have lower heritabilities in fitness (Leventhal *et al.*, 2025). *De novo* mutation also has been shown to introduce new adaptive variation, as recent studies in isolated populations of Cape Verde colonized 7–10 ka identify multiple independent mutations emerging on several islands (Fulgione *et al.*, 2022).

Phenotypic plasticity plays a clear role in acclimating to changing conditions, although direct tests of selection for plasticity are limited (Stinchcombe *et al.*, 2004; Exposito-Alonso *et al.*, 2018b). Plasticity in water use efficiency is locally favored in drought treatments and is partially heritable and variable across the range (Kenney *et al.*, 2014). Temporal surveys of phenotypic variation in herbarium specimens suggest that populations are able to shift phenology to track yearly variation in climate (DeLeo *et al.*, 2020), although these shifts are likely a product of both fluctuating selection and plasticity. Generalist accessions with greater phenotypic plasticity in flowering time do have higher fitness when transplanted to some warmer environments; but, plasticity (via GxE interactions on flowering) is not always adaptive–low-elevation fast-flowering lines delay flowering at higher elevations and do not have sufficient reproductive output for establishment (Exposito-Alonso *et al.*, 2018b).

Transgenerational plasticity through epigenetics has been demonstrated in *Arabidopsis* (i.e. Kooke *et al.*, 2015; Wibowo *et al.*, 2016), although particular application within natural populations and to changing climate is uncertain.

### 3. Importance for other species

Evolutionary biologists can leverage an extensive genetic and genomic toolkit developed for *Arabidopsis* to identify genes subject to selection in nature. The genetic and genomic advances made in *Arabidopsis* are highly repeatable across Brassicaceae (Koenig & Weigel, 2015; Zhai *et al.*, 2024) and are often able to be extrapolated distantly across the flowering plants. For example, a recent population genomic study capitalized on the *Arabidopsis* genome to find that local adaptation proceeds through similar orthologous loci across 20 species (Whiting *et al.*, 2024). Likewise, similar adaptation lags have been documented in *A. thaliana* as in several other herbaceous species (Wilczek *et al.*, 2014; Kooyers *et al.*, 2019; Anderson & Wadgymar, 2020; Bontrager *et al.*, 2020). Thus, *Arabidopsis* likely represents a generalizable ecological model for herbaceous climate change responses for annual species with mixed mating systems.

### 4. Limitations

*Arabidopsis* is often criticized for the exact traits that make it a spectacular model organism – existence as a cosmopolitan, rapid-cycling, selfing species with a relatively simple genome that often (but not always) occupies degraded habitats. Genome-wide association mapping can be challenging in Arabidopsis as a predominantly selfing reproductive strategy (from *c.* 2% average outcrossing across populations to a 14% in a dense population; Platt *et al.*, 2010; Bomblies *et al.*, 2010) reduces the combinatorics of genomes, and there is significant range-wide population structure to account for within GWAS models (Atwell *et al.*, 2010). Additionally, a lack of competitive ability with other species, limited mycorrhizal associations, and a lack of obvious pollinators may limit extrapolation of conclusions to plant species with more complex ecologies.

## III. *Boechera stricta* (Brassicaceae)

**Jill Anderson**

*Boechera stricta* (Graham) Al-Shehbaz is a short-lived diploid perennial forb ($2n = 14$) that grows in high-elevation meadows and habitats along streams throughout western North America, from Utah through Alaska (Al-Shehbaz & Windham, 2010; Rushworth *et al.*, 2011, 2022). In addition to occurring across a wide range of latitudes, this species spans a broad elevational gradient ranging from 700 to 3900 m above sea level (Al-Shehbaz & Windham, 2010; Rushworth *et al.*, 2011, 2022). Natural populations of the western and eastern subspecies of *B. stricta* (Wang *et al.*, 2019; Lin *et al.*, 2021) have adapted to environmental conditions that vary across the range (Lee & Mitchell-Olds, 2011, 2013; Anderson *et al.*, 2014, 2015; Anderson & Wadgymar, 2020), but much work remains to dissect the relative contributions of various agents of selection to the evolution of local adaptation. Demographic models from natural populations estimate that life expectancy is in the range of 5–7 yr (Anderson & Wadgymar, 2020), but we have seen very large individuals that could be up to 15–20 yr based on the diameter of the plant at the base (J. T. Anderson, pers. obs.). The relatively short-lived nature of the species, in conjunction with its self-pollination mating system (Song *et al.*, 2006), makes it ideal for eco-evolutionary experiments, as many siblings from field-collected accessions and pedigreed lines (such as recombinant inbred lines or near-isogenic lines) can be exposed to multiple environments in the field or laboratory to interrogate fitness and trait expression under realistic ecological conditions (Prasad *et al.*, 2012; Wagner *et al.*, 2014; Keith & Mitchell-Olds, 2019; Carley *et al.*, 2021). Furthermore, climatic projections have been examined extensively for this geographic region (Seager, 2007; Rangwala *et al.*, 2012; Seager *et al.*, 2013; Cook *et al.*, 2018; Talsma *et al.*, 2022; Alizadeh *et al.*, 2023), enabling researchers to simulate climate change in manipulative experiments in glasshouse, growth chamber, and field environments (Anderson & Gezon, 2015; Anderson & Wadgymar, 2020; MacTavish & Anderson, 2022; Denney *et al.*, 2024).

Climate change has already exposed *B. stricta* populations to increased temperatures, reduced snowpack, and accelerated snowmelt, intensifying aridity, and increased risk of fire (Seager, 2007; Rangwala *et al.*, 2012; Seager *et al.*, 2013; Cook *et al.*, 2018; Talsma *et al.*, 2022; Alizadeh *et al.*, 2023). Mean growing season temperatures increased by 0.33–0.52°C per decade from 1979 to 2020 in mountain systems of the western United States and in the Canadian Rockies, with greater rates of warming at higher elevations (Alizadeh *et al.*, 2023). The effects of climate change on *B. stricta* and other high-elevation and high latitude species may be mediated more by shifts in snowpack and snowmelt timing rather than by temperature changes. Snow dynamics drive many elements of *B. stricta's* life history and strongly influence phenology, functional traits, fitness, and local adaptation (Anderson & Gezon, 2015; Wadgymar *et al.*, 2018; Anderson & Wadgymar, 2020; Hamann *et al.*, 2021b). For example, *B. stricta* disperses seeds in the fall, which overwinter and germinate in early spring (Anderson & Wadgymar, 2020), and this species has a vernalization requirement for flowering (Anderson *et al.*, 2011), which occurs within approximately a month after snowmelt (Wadgymar *et al.*, 2018). Thus, snowpack over the winter and the timing of snowmelt in the spring is crucial for eliciting germination and determining the timing of flowering (Wadgymar *et al.*, 2018; Anderson, 2023; Anderson *et al.*, 2025). Increasing temperatures have reduced snow accumulation in the winter by 15–30% since the mid-1900s in the western United States and have hastened the timing of snowmelt in the region (Fyfe *et al.*, 2017; Mote *et al.*, 2018; Campbell, 2019). These changes are projected to increase. For example, by 2080, Colorado may lose 50–60% of its snow cover (Talsma *et al.*, 2022), which could amplify the duration and intensity of spring droughts by increasing the time between snowmelt and monsoonal rains (Seager *et al.*, 2013; Maloney *et al.*, 2014; Pascale *et al.*, 2016; Seth *et al.*, 2019).

## 1. Significant work

*Boechera stricta* has emerged as a model system for evolutionary ecology and ecological genetics (Rushworth *et al.*, 2011, 2022). This species is amenable to large-scale manipulations in field and laboratory settings, and substantial effort has been devoted to identifying environmental drivers of genetic population differentiation (Lee & Mitchell-Olds, 2011, 2012), along with studying the genetic basis of phenotypic variation and fitness (Prasad *et al.*, 2012; Anderson *et al.*, 2013), and examining selection and multivariate trait evolution (Anderson *et al.*, 2012; Keith & Mitchell-Olds, 2019; Carley *et al.*, 2021). Much of the foundational research into the genes underlying key phenotypes in this species can be leveraged to investigate climate change responses. For example, in *B. stricta* and other Brassicaceae, glucosinolates serve a critical role in antiherbivore defense (Prasad *et al.*, 2012; Carley *et al.*, 2021) and drought tolerance (Salehin *et al.*, 2019; Carley *et al.*, 2021), which could influence fitness in future climates if drought stress and herbivory both increase (Hamann *et al.*, 2021a; IPCC, 2023). Recent studies have exposed natural accessions of *B. stricta* to climates that simulate projections through manipulations of snowmelt timing in the field (Wadgymar *et al.*, 2018; Anderson & Wadgymar, 2020; Hamann *et al.*, 2021b), drought stress and nutrient availability in the glasshouse (MacTavish & Anderson, 2020, 2022), and temperature and carbon dioxide concentration in the glasshouse (Denney *et al.*, 2024). Furthermore, ongoing field experiments manipulate snowmelt timing and growing season temperature factorially in four experimental gardens (Anderson, in review). Despite work that mapped quantitative trait loci (QTL) for fitness and identified loci associated with local adaptation to contemporary environments (e.g. Anderson *et al.*, 2013), no studies to date have investigated the fitness consequences of climate change for local alleles at candidate genes implicated in local adaptation.

## 2. Major results

Reduced winter snowpack and early snowmelt (Fyfe *et al.*, 2017) accelerated flowering in *B. stricta* (Bemmels & Anderson, 2019), and climate change has advanced *B. stricta*'s reproductive phenology by 3.7 d per decade in natural populations around the Rocky Mountain Biological Laboratory (Gothic, CO) since the mid-1970s (Wadgymar *et al.*, 2018), likely through a combination of plasticity and adaptation (Anderson *et al.*, 2012). This rate is nearly identical to phenological shifts in other plant species at that site (CaraDonna *et al.*, 2014; Wadgymar *et al.*, 2018), and very similar to changes in spring phenology in a diversity of plant and animal species in temperate ecosystems world-wide (Amano *et al.*, 2010; Diamond *et al.*, 2011; Pöyry *et al.*, 2011; Jakoby *et al.*, 2019; Bates *et al.*, 2023). Thus, *B. stricta* may serve as a reliable model of climate change responses for other species. Furthermore, manipulations of snowmelt timing in the field suggest that *B. stricta* is adapted to historical climates and that climate change has already disrupted local adaptation (Anderson & Wadgymar, 2020). Specifically, low-elevation accessions, which evolved under relatively hot and dry conditions, have a fitness advantage over local accessions in contemporary environments (Anderson *et al.*, 2025). Importantly, snow additions, which simulate historical climates, can restore local adaptation (Anderson & Wadgymar, 2020). Furthermore, this experiment revealed strong costs of reproduction under arid and hot projected climates, suggesting that climate change could favor the evolution of shorter lifespans (Hamann *et al.*, 2021b).

To date, research suggests that local populations in the Colorado Rocky Mountains may not maintain sufficient genetic variation to respond to rapid changes in the climate (Bemmels & Anderson, 2019; Anderson *et al.*, 2025), but it is possible that populations at the leading edge in high-elevation and high-latitude locations could expand if climate change dampens the harsh winters and cold temperatures there (Anderson *et al.*, 2025). Gene flow is spatially restricted across populations of this selfing species (Song *et al.*, 2006; Wang *et al.*, 2019; Anderson *et al.*, 2025), and we hypothesize that upslope or poleward migrations will not be rapid enough for variants from trailing edge and central populations to remain within their locally adapted climate niche (Anderson *et al.*, 2025). Nevertheless, field (Anderson & Wadgymar, 2020), growth chamber (Denney *et al.*, 2024), and glasshouse (MacTavish & Anderson, 2020) experiments have found that low-elevation accessions display greater fitness than high-elevation accessions when exposed to conditions that reflect climate change projections, including early snowmelt (Anderson & Wadgymar, 2020), high temperatures, elevated atmospheric carbon dioxide levels (Denney *et al.*, 2024), and drought stress (MacTavish & Anderson, 2020). Additionally, low-elevation accessions show greater resistance against insect herbivory than their higher elevation counterparts when transplanted into common gardens at various elevations (Anderson *et al.*, 2015). This heightened resistance could reduce the vulnerability of low-elevation accessions to any increases in herbivory that may occur with climate change (Robinson *et al.*, 2012; Hamann *et al.*, 2021a). These results highlight that relevant genetic variation in climatic responses exists across the range of the species even if it is not found within any given population and that assisted gene flow (Aitken & Whitlock, 2013) could stabilize local populations as climate change proceeds (Anderson *et al.*, 2025).

### 3. Importance for other species and limitations

As a primarily selfing species, *B. stricta* may lack the within-population genetic variation necessary to adapt to ongoing environmental change (Bemmels & Anderson, 2019), and this species has limited interactions with pollinators. Selfing species are often assumed to have restricted genetic variation within populations. Additional research could estimate quantitative genetic variation in adaptive potential across the range, which would be especially illuminating if experiments exposed transplants to simulated climate change. Furthermore, *B. stricta* has gravity and wind-dispersed seeds, which likely restrict its ability to migrate in response to climate change (Anderson *et al.*, 2025). These elements of the natural history of *B. stricta* make it less suitable for studies focused on phenological mismatches with pollinators and seed dispersers or novel interactions that could arise from divergent range shifts. However, hybridization in the genus *Boechera* (Al-Shehbaz & Windham, 2010), including between *B. stricta* and other members of the genus (Rushworth *et al.*, 2018, 2020), indicates that animal-mediated pollination occurs. In some portions of the geographic range, this hybridization could potentially lead to introgression of alleles associated with tolerance of heightened temperature and drought stress, which could facilitate population persistence in areas where multiple *Boechera* species exist in sympatry.

Furthermore, researchers can address plant–animal interactions through investigations of herbivory at the ecological, genetic, and evolutionary levels (Prasad *et al.*, 2012; Carley *et al.*, 2021; Jameel *et al.*, 2025). Detailed experiments have elucidated the genetic basis of glucosinolates and have examined the effects of glucosinolates on both herbivory and drought responses (Prasad *et al.*, 2012; Carley *et al.*, 2021). Drought is projected to increase across the range of *B. stricta* (Seager, 2007; Cook & Seager, 2013; Cook *et al.*, 2018; Talsma *et al.*, 2022; IPCC, 2023), and it is possible that rates of herbivory could also shift with climate change (Hamann *et al.*, 2021a). Thus, multifactorial experiments are required to evaluate how climate and biotic environments interact to impose novel selection and shape global change responses in *B. stricta* and other species. To date, few studies have manipulated the herbivore community (Carley *et al.*, 2025; Jameel *et al.*, 2025) to examine the strength of selection imposed by herbivory – or specific herbivore species – on functional traits, defenses, and plant phenology. Furthermore, we know very little about how mammalian herbivores influence eco-evolutionary dynamics in this system. Exciting questions also remain about how microbiota interact with roots and aboveground biomass to influence trait expression and fitness in *B. stricta* (Wagner *et al.*, 2014, 2016). Finally, we have limited understanding of how climatic drivers influence root phenotypes, interactions of roots with soil microbes or leaves with leaf microbiota, the soil seed bank and seed dormancy, and plant ecophysiology.

## IV. *Clarkia xantiana* (Onagraceae)

**David Moeller**

*Clarkia xantiana* is a diploid ($2n = 18$), self-compatible, winter annual plant endemic to southern California, occurring primarily in the southern Sierra Nevada (Lewis & Lewis, 1955; Eckhart & Geber, 1999). The species is currently divided into two subspecies that are differentiated by phenology, floral traits, and geography (Moore & Lewis, 1965; Eckhart & Geber, 1999). Substantial evidence indicates that the two taxa are phylogenetically distinct and reproductively isolated (Pettengill & Moeller, 2012b; Briscoe Runquist *et al.*, 2014); therefore, they are more appropriately considered sister species (Sianta *et al.*, 2024). Both taxa occupy small geographic ranges that are parapatric, with a narrow zone of overlap. *C. xantiana* ssp. *xantiana* is primarily outcrossing and bee-pollinated (Moeller, 2006; Pettengill & Moeller, 2012a) and occupies the western foothills of the Sierra Nevada where precipitation is higher and less variable than in the eastern foothills where the primarily selfing *C. xantiana* ssp. *parviflora* occurs. Most research with relevance to climate change has occurred on subspecies *xantiana* (hereafter *C. x. xantiana*).

Populations of *C. x. xantiana* are typically large and discrete, with hundreds to hundreds of thousands of individuals (Eckhart *et al.*, 2011). Plants primarily occur on slopes in open areas and co-occur with other herbaceous forbs and grasses, especially non-native annual grasses. Seeds germinate in winter (November–March) and flower in late spring in response to the onset of summer drought (May–June; Eckhart & Geber, 1999). Population dynamics are driven primarily by precipitation (Eckhart *et al.*, 2011), which is highly variable in the Sierra Nevada (historically varying 50–200% of average; Dettinger *et al.*, 2011). The southwestern United States has experienced the most severe 'megadrought' since 800 CE (2000–present: Cook *et al.*, 2015; Williams *et al.*, 2022) and anthropogenic climate change has caused *c.* 42% of the soil moisture anomaly (Williams *et al.*, 2020). In this region, climate change is expected to result in reduced mean but higher variance in precipitation (Dettinger *et al.*, 2018).

### 1. Significant work

The genus *Clarkia* has been an important model system for studies of plant adaptation and speciation since the 1950s (Lewis & Lewis, 1955). *Clarkia x. xantiana* is among the most intensively studied plants in the context of geographic range dynamics. Long-term research (20+ yr of continuous study) integrates data on abiotic variation, species interactions, population dynamics, and local adaptation. This work includes long-term demographic studies, reciprocal transplant experiments, population genetic studies, and resurrection studies.

### 2. Major results

SDMs were developed to examine range dynamics in response to Holocene climate change and to first evaluate alternative explanations for the causes of current geographic range limits. At the LGM (21 000 BP), predicted suitable habitat occurred only at the very southern end of the current distribution and at the lower extreme of elevations where contemporary populations occur (Pettengill & Moeller, 2012b). Since the LGM, populations have migrated north and to higher elevations, which is reflected in patterns of population genomic structure (Pettengill & Moeller, 2012b; Sianta *et al.*, 2024). Populations are now infrequent in the southern

**Box 2.** Organismal responses to a historic California drought (2012–2015)

Extreme events provide exceptional opportunities to examine the resilience and capacity for adaptation within natural populations. Studies on three model species (*Clarkia xantiana, Mimulus cardinalis*, and *Mimulus guttatus*) all take advantage of a notable extreme drought affecting western North America from 2012 to 2015. This 4-yr drought was most severe in central and southern California, with vegetation indexes dropping more severely in Southern than in Northern California (Dong *et al*., 2019). Just the 2012–2014 drought period was assessed as a 10 000-yr event, with the full 2012–2015 period having an almost incalculable return period (Robeson, 2015). In Southern California, the drought persisted through an additional growing season (the 2016 water year). This event occurs in the background of a longer 'megadrought' encompassing the first two decades of the 2000s. This drought is the combination of anthropogenic warming intensifying an already moderate drought period (Williams *et al*., 2020).

The three species studied across the drought overlap in range and were subjected to reasonably similar common garden experiments. Conclusions on the adaptive potential of the three focal species studied during the 2012–2015 drought are remarkably consistant. Annual species generally had reduced population sizes, with some populations not establishing during drought years. Dormancy is a critical strategy for surviving extreme events but may hinder adaptive evolution. Some southern populations of perennial *M. cardinalis* went extinct. All species exhibited evolution in a minority of populations, but not as widely as expected. Both *C. xantiana* and *M. guttatus* evolved faster flowering in a minority of populations, and *M. guttatus* also evolved slower flowering in a limited number of populations. However, *M. cardinalis* evolved greater drought avoidance range-wide, with slower time to flowering and increased carbon assimilation under dry conditions. It is clear that spatial variation in evolutionary responses in all species is not easily predicted. These studies highlight the importance of collecting long-term data for providing the opportunity to study extreme events that may mimic future climatic conditions.

portion of the range but common in the northern portion of the range. The northern range limit coincides with the Greenhorn Mountains, and SDMs suggest that potentially suitable habitat is found to the north (i.e. dispersal limitation; Eckhart *et al*., 2011). Those SDMs also suggest that the eastern range margin is limited by adaptation (not dispersal) and that precipitation is a key limiting factor (Eckhart *et al*., 2011). Long-term work on *C. x. xantiana* has focused on this broad eastern range limit, which falls along a continuous abiotic gradient, consistent with the context of most theoretical models on range limits (e.g. Kirkpatrick & Barton, 1997; Polechová & Barton, 2015).

Guided by distribution models, subsequent work sought to distinguish the causal agents of maladaptation to novel conditions beyond the range. Understanding the ecological and evolutionary causes of range limits is central to predicting range shifts with climate change. Reciprocal transplant studies have shown that lifetime fitness is at or below replacement just inside and beyond the eastern range limit (Geber & Eckhart, 2005). While quantitative genetic variation for fitness is elevated at the range limit and beyond, no genotypes have fitness above replacement even when crosses were used to generate novel recombinants among populations (D. A. Moeller *et al*., unpublished data). Patterns of population variation indicated that abiotic stress and physiology contribute to the location of the range limit (Eckhart *et al*., 2010). However, a series of experiments have shown that a major source of mortality at the range margin was fatal herbivory by small mammals (Geber & Eckhart, 2005; Benning & Moeller, 2021); populations could persist beyond the range margin if such biotic interactions were removed (Benning *et al*., 2019; Benning & Moeller, 2021). Similarly, fecundity is limited by pollinator availability at the range limit and beyond (Geber & Eckhart, 2005; Moeller *et al*., 2012; Benning & Moeller, 2021). Notably, both biotic interactions exhibit steep nonlinear gradients that coincide with the range limit (Moeller, 2006; Moeller *et al*., 2012; Benning *et al*., 2019; Benning & Moeller, 2021), whereas abiotic factors exhibit shallow and linear gradients. Such steep gradients have been suggested by theoretical studies to promote range limit formation (Polechová & Barton, 2015). Despite a focus in the literature on how abiotic factors govern distributions, our results emphasize that the biotic environment is similarly important even in the presence of a strong and obvious abiotic gradient.

Population persistence in the face of climate change may occur if populations adapt *in situ* and/or if plasticity is adaptive such that plastic responses result in higher fitness. Persistence may also occur when populations remain dormant through periods of unsuitable conditions. While range shifts have been observed in many systems in response to contemporary climate change, *C. x. xantiana*'s range limits have remained stable over 25 yr of monitoring (and in relation to records as far back as the 1950s). At the eastern range limit where drought is most prevalent, we have observed substantial climate and population fluctuations but no local population extinctions (Eckhart *et al*., 2011; Siegmund *et al*., 2023; Vergara *et al*., 2024). Long-term demographic studies spanning 20 yr have demonstrated that the seed bank is key to population persistence through periods of low precipitation (Eckhart *et al*., 2011; Siegmund *et al*., 2023; Vergara *et al*., 2024).

We have also tested for rapid evolution in response to a multiyear episode of severe drought from 2012 to 2015 (Box 2) (Benning *et al*., 2023). Although all populations experienced similar levels of drought stress and expressed similar levels of quantitative genetic variation in ecologically relevant traits, only one of three populations exhibited rapid evolution in phenology (time to first flower). Flowering occurred earlier in genotypes from 2015 than from 2011 and even earlier for genotypes from 2017 (2 yr after drought ended). Evolutionary simulation models (developed in SLiM) incorporated field data and tested alternative hypotheses on the causes of a lack of rapid evolution using approximate Bayesian computation. There was strong evidence that gene flow from the seed bank (gene flow through time) prevented the evolution of early phenology in two populations (Benning *et al*., 2023). These results suggest that the same mechanism that may facilitate persistence through unsuitable periods (dormancy) may also prevent adaptive evolution to climate change.

Although plasticity may contribute to population persistence through environmental fluctuations, we find mixed evidence for it in this system. For flowering time, transplant experiments beyond the eastern range limit of *C. x. xantiana* have shown that flowering time is later; however, selection favors earlier flowering time (Eckhart *et al*., 2004). This counter-gradient plasticity is maladaptive and has important consequences for lifetime fitness (Eckhart *et al*., 2004; Anderson *et al*., 2015). By contrast, there is evidence that flowering phenology has adaptively differentiated even over fine spatial scales (highest estimated Qst; Gould *et al*., 2014). Flowering time is also a key trait that differentiates *C. x. xantiana* from its sister subspecies (Eckhart & Geber, 1999) and contributes to reproductive isolation (Briscoe Runquist *et al*., 2014). Therefore, while flowering time is an important trait mediating local adaptation, plasticity in flowering time in response to novel environments may impede rather than facilitate population persistence.

The last 20+ yr of megadrought in the southwestern United States has provided a potential preview of future climate change – multiyear severe drought episodes punctuated by intermittent wet years. Our continuous study of *C. x. xantiana* over this period has revealed significant declines in abundance in some areas but no population extinctions or range shifts. While we have observed some rapid evolution in response to drought, seed banks have simultaneously hindered adaptation and prevented local extinctions. Unlike most systems where studies of climate change examine upslope elevational movement and northward migration, research on *C. x. xantiana* offers insights into climate change effects on biotas in which precipitation is a more important driver of population and community dynamics than temperature.

### 3. Importance for other species

Beyond the effects on single species, climate change may also modulate the process of divergence between lineages. The expression of traits that confer premating reproductive isolation may be affected by adaptation and/or plasticity to changing environments (e.g. flowering phenology during the megadrought). If changes in trait expression (in one or both taxa) weaken premating isolation, hybridization may occur more often. In *C. xantiana*, the magnitude of historical admixture between sister taxa is highest in sites where interannual variation in precipitation during the spring growing season is most pronounced (Sianta *et al*., 2024). Given that climate change is predicted to cause greater interannual variance in precipitation in the southern Sierra Nevada (Dettinger *et al*., 2018), one might predict higher rates of hybridization over time. However, the extent of introgression will depend upon the fitness consequences of admixed ancestry under climate change and requires further study.

*C. x. xantiana* is also an important model for plant biotic interactions in a changing climate. The east–west environmental gradient over which the range limit occurs is complex, with both abiotic and biotic factors influencing population dynamics and adaptation. For example, precipitation drives the population dynamics of *C. xantiana*, which affects populations of its specialized bee pollinators in subsequent years (Moeller *et al*., 2012). The lagged effects of plant population dynamics on bee pollinators can cause mismatches between years of high plant and pollinator abundance and limit reproduction. Interestingly, the same climate-driven lags have been observed in interactions between *C. xantiana* and generalist insect herbivores, in which the intensity of herbivory can be predicted by precipitation in prior years (unpublished data). Future studies of climate change will need to consider the direct effects of abiotic variation on plant populations along with the complex indirect effects on its pollinators and herbivores.

### 4. Limitations

Studies of *C. xantiana* have spanned a long time period and involved substantial environmental fluctuations, but attempts have not yet been made to simulate climate change with experimental manipulations. While the seed bank is important for population persistence through short-term fluctuations (Eckhart *et al*., 2011; Siegmund *et al*., 2023), it remains unclear whether seed dormancy can facilitate population persistence through the more extreme interannual variance in precipitation that has been predicted with climate change (Dettinger *et al*., 2018). We have also found that fluctuations in precipitation are associated with greater admixture between sister taxa of *C. xantiana* (Sianta *et al*., 2024). Our observations suggest that droughts are associated with greater flowering overlap between sister taxa, especially at higher elevations, thereby allowing greater heterospecific pollen transfer. However, experiments have not been conducted that link drought to weakened premating isolation and greater hybridization in this region. While experimental manipulations are important, only long-term experiments would likely provide strong insights given high variability in precipitation before human-induced climate change (Dettinger *et al*., 2011).

## V. *Mimulus cardinalis* (syn. Erythranthe cardinalis; Phrymaceae)

**Amy Angert and Seema Sheth**

*Mimulus cardinalis* is a short-lived self-compatible perennial herb ($2n = 16$) with red, tubular flowers pollinated primarily by hummingbirds. Reproduction occurs sexually via copious, tiny seeds and asexually via rhizomes. The species grows in moist, disturbed riparian habitats such as mossy crevices in water-splashed boulders and sandy cobble bars along stream banks. It ranges from central Oregon, USA, to northern Baja California, Mexico, and from sea level to < 2400 m asl (Fraga, 2018). This latitudinal and elevational breadth encompasses substantial variation in macroclimate, with > 12°C difference in mean annual temperature and 3000-mm difference in mean annual precipitation observed among populations (Sheth & Angert, 2018b). Northern populations occupy cooler and more reliably wet conditions, while southern populations inhabit warmer and unpredictably dry conditions (Muir & Angert, 2017). For all populations, growing season precipitation is negligible; soil moisture is recharged by winter precipitation and spring snowmelt and gets progressively drier across the growing season.

Across the species range, warming has already increased mean annual temperatures by 1–2°C (California EPA, 2018). While changes in total annual precipitation are more difficult to project, there is high confidence that drought severity will increase due to increasing evaporative demand and changing intensity and seasonal distribution of rainfall events (California EPA, 2018). During the historic 2012–2015 CA drought (Box 2), many populations of *M. cardinalis* declined, and some southern populations were extirpated (Sheth & Angert, 2018). For riparian species such as *M. cardinalis*, climatic changes are compounded by changes in the hydrological regime. For example, warming-driven shifts in precipitation falling as rain instead of snow change the timing and size of the spring freshet, with important consequences for flood disturbance regimes and soil moisture availability in the subsequent growing season (California EPA, 2018).

## 1. Significant work

*Mimulus cardinalis* has been the subject of a wide variety of observational and experimental studies for many decades (Decker, 1959; Hiesey *et al.*, 1971; Schemske & Bradshaw, 1999). Observational work across range-wide climatic gradients includes demographic observations of vital rates and population dynamics in 21 wild populations (ongoing since 2010); stratified, random sampling of population presences and absences for unbiased estimates of habitat suitability and occupancy; and estimates of population genetic diversity and differentiation. Experimental work has tested the effects of climatic drivers on performance by assaying physiological responses to thermal and drought stress and conducting reciprocal transplants and common gardens. Experiments have also quantified evolutionary potential using artificial selection and quantitative genetic breeding designs and tracked real-time evolution during extreme climate events via resurrection studies. Collectively, these studies have fostered the collection and creation of numerous resources for further study, such as 750 whole-genome sequences, curated records of occurrence, ecological niche models independently validated by field surveys, and tissue and seed samples (including pedigreed crosses allowing for estimation of additive genetic variances and covariances) spanning > 20 yr and most of the climatic and geographic range of species.

## 2. Major results

Several lines of evidence suggest that the geographic range is not at equilibrium with recent–past climate. Projected population growth rates increase with elevation (Angert, 2006) and latitude (Sheth & Angert, 2018), consistent with leading-trailing dynamics (Hewitt, 1996; Davis & Shaw, 2001). Natural dispersal appears to be insufficient to track changing climates. The species is underfilling climatically suitable habitat in the north compared to the central and southern portions of the range (Angert *et al.*, 2018), while experimental translocations indicate that experimental populations beyond the northern range edge grow as well or better than experimental populations transplanted within the northern range (Bayly & Angert, 2019). During the 2012–2015 drought, demographic surveys documented high mortality and low seedling recruitment, leading to significant declines in 19 of 32 populations spanning the latitudinal gradient (Sheth & Angert, 2018), especially in populations experiencing the most anomalous winter precipitation conditions (Anstett *et al.*, 2024). The intensity of decline was greatest in the south, where researchers observed two local extinctions; to date, one of these populations remains extirpated. Although life-history shifts were consistent with demographic compensation (i.e. more negative correlations between vital rates than expected by chance), higher reproduction in southern populations was insufficient to offset their low survival and growth during the unprecedented drought (Sheth & Angert, 2018). Consistent with an adaptation lag, experiments of northern-edge, central, and southern-edge populations transplanted into northern, central, and southern common gardens reveal that southern populations had the highest fitness and northern populations had the lowest fitness in all gardens (Sheth *et al.*, 2025). Collectively, these findings strongly support the hypothesis that the northern range edge is dispersal-limited, not climate-limited, while the southern range edge is under increasing climate stress. If southern range contraction proceeds faster than northern range expansion because of limited dispersal, the range will shrink.

Field and laboratory common gardens reveal how population divergence in physiological, phenological, and life-history traits mediates responses to climatic variation and sets the baseline for the direction and pace of future evolutionary responses. For example, populations diverge along a fast–slow life-history axis (Reich *et al.*, 2003) from the less predictable environments of the south to the more reliably wet north, with southern populations demonstrating more rapid germination, higher photosynthesis, greater growth, and a more annualized life history than northern populations (Sheth & Angert, 2016; Muir & Angert, 2017). Populations also differ in breadth and optima of thermal performance curves along latitudinal gradients (Angert *et al.*, 2011). Interestingly, different analyses on these independent datasets both suggest that gene flow among populations has constrained adaptation to historical climates (Paul *et al.*, 2011; Muir & Angert, 2017). Despite ample variation among populations in trait means, there is less consistent evidence for population divergence in trait plasticity in response to climatic variation. Muir & Angert (2017) did not detect strong plasticity for performance traits in response to temperature or watering treatments. By contrast, Branch (2023) showed that southern populations exhibited greater within-generation plasticity but lesser transgenerational plasticity for leaf traits in response to soil moisture relative to northern ones.

Glasshouse studies suggest that some populations of *M. cardinalis* harbor substantial levels of genetic variation in ecologically important traits. A study of two northern-edge, two central, and two southern-edge populations of *M. cardinalis* found that the trailing-edge populations have ample genetic variation to respond to climate-driven selection on flowering time and that the evolution of delayed flowering for drought avoidance could lead to an overall shift to slower life-history traits (Sheth & Angert, 2016). Muir *et al.* (2022) quantified genetic variance in another phenological trait, germination timing, for five latitudinally arrayed populations of *M. cardinalis* in a glasshouse setting, and found that populations harbored substantial genetic variance for germination timing, with similar levels of variation among and within populations. Nonetheless, genetic variance in winter survival in a northern and southern common garden was negligible, implying that genetic variation in germination time did not contribute to variation in winter survival (Muir *et al.*, 2022). Since glasshouse studies can overestimate quantitative genetic variation (Charmantier & Garant, 2005), we ultimately need to measure quantitative genetic variation in traits and fitness, along with selection on a suite of drought resistance traits (Kooyers *et al.*, 2015) in climatically distinct field gardens to fully evaluate the evolutionary potential of populations across the species' range, and this is the focus of ongoing work (Sheth *et al.*, 2025). Preliminary reports of additive genetic variances of drought resistance traits, along with fitness, in latitudinally arrayed common gardens highlight the challenges of detecting population-level variation in field settings (Sheth *et al.*, 2025).

Resurrection studies to date suggest that the likelihood of *in situ* evolution of trait means and plasticities depends on the populations, timescales, and traits examined. They also demonstrate how populations entering an extreme event (Box 2) with different baseline phenotypes diverge along different trajectories. In six populations (two each from the south, central, and northern portions of the range), Wooliver *et al.* (2020) observed limited evolution of thermal performance curves; Vtipil & Sheth (2020) found no evolution of flowering phenology despite high standing genetic variation in southern-edge populations (Sheth & Angert, 2016). By contrast, Anstett *et al.* (2021) sampled 11 populations from across the range and detected evolution of later phenology range-wide and lower specific leaf area, especially in the south and center of the range, consistent with a shift from traits promoting drought escape (live fast, die young) to traits promoting drought avoidance (conserve water and grow slow). Branch *et al.* (2024a,b) focused on leaf anatomy and biochemical function across six populations (a subset of those studied by Anstett *et al.*, 2021) and found that populations from all regions evolved to maintain photosynthetic carbon assimilation under dry conditions, but via different anatomical changes within leaves. In the south, drought adaptations appear to have become more canalized. The anatomical changes that maintain photosynthesis during drought incur a cost to photosynthesis under wet conditions for southern populations, but not northern populations, and southern populations have lost plasticity in specific leaf area (Anstett *et al.*, 2021). Preston *et al.* (2022) also observed loss of plasticity, in this case in high-temperature gene expression in northern populations.

Differences in the extent of trait evolution do not appear to be a simple outcome of differences in the strength of selection; although the north is wetter than the south in absolute terms, the drought anomaly (relative to historical baselines) was similar in the north and the south. Rather, differences in evolutionary response might be better explained by historical differences in environmental predictability and the evolution of transgenerational plasticity. Branch (2023) found that northern populations in historically predictable climates had both less trait evolution and more (grand) parental inherited stress memory, while southern populations evolved more rapidly and showed less transgenerational plasticity. Although the detection and magnitude of evolutionary responses vary among studies, populations, and traits, this work represents unique evidence for rapid evolution in a perennial plant species and highlights the potential for adaptive evolution to rescue some declining populations from extreme climatic events. Genomic analyses reveal that the frequency of drought-adapted alleles has increased in some populations and that variability at climate-associated loci predicted population recovery postdrought (Anstett *et al.*, 2024). This provides one of few empirical examples of evolutionary rescue – whereby evolution by natural selection allows a population that was on an extinction trajectory after an environmental change to rebound and persist–in the wild.

### 3. Importance for other species

While most resurrection studies examining plant responses to climate change have focused on annual species (e.g. Franks *et al.*, 2007; Hamann *et al.*, 2018; Dickman *et al.*, 2019; Kooyers *et al.*, 2021), little is known about whether perennial species will be able to adapt fast enough to keep up with climate change. Although we often assume that perennial species evolve more slowly, *M. cardinalis* includes populations that have high evolutionary potential, can rapidly respond to selection in the glasshouse, and have rapidly evolved in response to recent drought. This work documents that evolutionary rescue can occur in herbaceous perennial plants, which are long-lived than most focal organisms in evolutionary rescue studies.

### 4. Limitations

Disturbance and postdisturbance successional dynamics can have overriding effects on population dynamics that make climatic signals hard to discern. For example, riparian habitat is subject to stochastic flood-driven disturbances that can cause high mortality of established adult *M. cardinalis* and pulses of juvenile recruitment, followed by successional development of willow and alder stands that gradually displace *M. cardinalis*. Fire disturbance has a similar effect: Fires stimulate high recruitment both directly (by clearing canopy and increasing light along riparian corridors) and indirectly (because deadfall alters streamflows). The perennial life history of *M. cardinalis* poses challenges for adequately capturing long-term fitness and population trajectories in short-term common garden experiments. As with many plant species, seed bank dynamics are not well-studied, and whether seed banks hinder evolutionary responses or allow ecological buffering and bet-hedging in variable environments remains an open question. While there have been numerous studies of climatic drivers of performance in this system, species interactions (e.g. with hummingbird pollinators, herbivores, and fungal leaf endophytes) and their interplay with climate stress need further study.

## VI. *Mimulus guttatus* (syn. Erythranthre guttata; Phrymaceae)

**Nicholas Kooyers**

The common yellow monkeyflower (*Mimulus guttatus*; syn. *Erythranthe guttata*; $2n = 28$) is widespread through Western North America, occurring in wet areas including coastal bluffs, riversides, thin-soiled meadows, rock walls, and roadside ditches from sea level to *c.* 3000-m elevation (Wu *et al.*, 2008). *M. guttatus* is highly genetically and phenotypically variable, with life-history strategies ranging from stoloniferous perennial populations living on ocean-adjacent bluffs and riversides to inland annual populations rapidly completing life cycles in habitats with ephemeral water supplies. This species is primarily outcrossing, with pollination by bee species, and it has an obligate long-day photoperiod requirement with variable vernalization requirements for flowering (Friedman & Willis, 2013). Populations are both locally and regionally common; thus, *M. guttatus* is not typically considered vulnerable to changing climates and is even considered an invasive species in some regions (Vallejo-Marín *et al.*, 2021). Moreover, *M. guttatus* contains some of the highest levels of genetic diversity found within any plant population (Friedman *et al.*, 2015; Puzey *et al.*, 2017), suggesting extensive capacity for adaptation to changing conditions. However, recent studies indicate that populations of *M. guttatus* in part of its range (the central Oregon Cascades) are threatened by shifting and shortening growing seasons as well as extreme events (Kooyers *et al.*, 2019, 2025; McDonald *et al.*, 2023). This area has the shortest growing season across the range of *M. guttatus*.

## 1. Significant work

*Mimulus guttatus* has not traditionally been considered a model species for climate change, but it is an important model for speciation (Vickery, 1964, 1978; Fishman & Willis, 2001; Brandvain *et al.*, 2014; Ferris *et al.*, 2014; Oneal *et al.*, 2016), hybridization (Sweigart *et al.*, 2006; Coughlan *et al.*, 2020; Ivey *et al.*, 2023), evolutionary genomics of adaptation (Hendrick *et al.*, 2016; Monnahan & Kelly, 2017; Nelson *et al.*, 2018; Selby & Willis, 2018), evolution of chemical defense (Holeski, 2007; Holeski *et al.*, 2013; Colicchio, 2017; Kooyers *et al.*, 2017), plant evo-devo (Yuan, 2019; Ding *et al.*, 2020), and life-history evolution (Hall & Willis, 2006; Lowry & Willis, 2010; Twyford *et al.*, 2015; Peterson *et al.*, 2016; Troth *et al.*, 2018). This work has provided context and resources (e.g. annotated genomes, seed stocks, and functional genetics protocols) for understanding climate change responses. Nearly all work on climate change responses has been conducted in inland annual populations. Provenance experiments including populations throughout the range that were designed to examine local adaptation in the central Oregon Cascades provided the first evidence for an adaptation lag in *M. guttatus* (Kooyers *et al.*, 2019). Additional common garden experiments and phenotypic selection analyses conducted in high-elevation Oregon populations have documented patterns of fluctuating selection (Mojica *et al.*, 2012; Troth *et al.*, 2018; Kelly, 2022) and the genomic consequences of inbreeding (Brown & Kelly, 2020). These studies have often been paired with evolutionary genomics to examine the genetic basis of rapid adaptation (Nelson *et al.*, 2018; Monnahan *et al.*, 2021). Demographic and observational experiments tracking populations across many years are rare; however, there are now six continuous years of data in 12 central Oregon high-elevation populations tracking survival, phenology, and fecundity (Kooyers *et al.*, 2025).

Additionally, researchers in the *Mimulus* community are prolific seed collectors, leading to collections of the same populations before and after extreme events – such as the historical CA drought (Box 2). These collections have been used in resurrection experiments to identify phenotypic and genetic responses across populations to extreme events (Kooyers *et al.*, 2021). Finally, extensive work on the evolution of flowering time variation via controlled growth chamber experiments, QTL mapping, and field experiments has provided insights into potential phenological responses across monkeyflower populations (Friedman & Willis, 2013; Kooyers *et al.*, 2015).

## 2. Major results

Provenance studies have identified adaptation lags in both low- and high-elevation annual populations in Oregon where populations from California that better match contemporary growing season conditions have higher fitness (Kooyers *et al.*, 2019). While this adaptation is identifiable across multiple different years (2014 and 2019; Scharnagl *et al.*, 2023; McDonald *et al.*, 2023), the exact California populations that are favored change between years in high-elevation sites, depending on temporal variation in the timing of snow melt and duration of the growing season (McDonald *et al.*, 2023). At the low-elevation site, plants that develop faster, flower earlier in the growing season, and have a chemical defense arsenal more similar to California populations have a fitness advantages (Kooyers *et al.*, 2019; Scharnagl *et al.*, 2023). At the high-elevation site, early-season survival of heat and low water availability (McDonald *et al.*, 2023) as well as flowering later and at a larger size underlie fitness differences (Kooyers *et al.*, 2019). Such adaptation lags suggest that monkeyflowers are able to neither move (i.e. disperse via pollen or seeds) nor adapt quickly enough to respond to changing climate conditions, at least in this region.

The adaptation lag results fit into the context of over two decades of work within a few highly diverse populations in the central Oregon Cascades. These studies identify a key trade-off between rapid flowering and flower size, in which extensive variation is maintained due to temporally heterogeneous selection associated with growing season variation (Mojica *et al.*, 2012; Monnahan & Kelly, 2017; Troth *et al.*, 2018). More broadly, nearly 15 yr of temporal studies at the Iron Mountain field site suggest that large portions of the genome exhibit signs of balancing selection, with similar shifts in allele frequency at *c.* 1800 single nucleotide polymorphism (SNPs) across the genome (Kelly, 2022). The large levels of segregating variation within this population (and at a large Quarry population; Monnahan & Kelly, 2017) suggest that these populations already contain the variation to adapt to small shifts in the growing season by altering phenology and that they could contribute to genetic rescue in nearby populations. At a range-wide scale, substantial heritable phenotypic variation exists in nearly all morphological, physiological, and phenological traits examined (Friedman *et al.*, 2015; Kooyers *et al.*, 2015, 2017). Gene flow through pollen flow is likely to be substantial at fine spatial scales (< 5 km) as little population structure has been observed between nearby populations, even with whole-genome sequencing of many individuals (Twyford *et al.*, 2020; Colicchio *et al.*, 2021).

Notably, other nearby populations are much smaller in physical size, number of individuals, and levels of genetic variation and may have greater difficulty with evolutionary rescue.

Observational studies in 12 nearby smaller natural populations over the last 6 yr have demonstrated that growing season fluctuations and extreme heat events do indeed threaten smaller *M. guttatus* populations (McDonald *et al*., 2023; Kooyers *et al*., 2025). A short 9-d heatwave in 2019 occurring early in the growing season caused complete mortality in one of the 12 populations and caused an average of 50.3% mortality across plots. A heat dome event in 2021 occurring midway through the growing season caused early mortality in all plots but did not reduce fecundity despite occurring during the flowering and fruiting period. Instead, seed mass was 30% less than earlier years, and seeds germinated later and less readily. Germination rates remained low in the following year but recovered 2 yr following the drought. These results indicate that the timing of extreme events within growing seasons is important for determining outcomes. Notably, mortality from these heatwaves is mediated by faster dry down of the thin-soiled meadows (McDonald *et al*., 2023). Water addition treatments increased survival and fecundity of local *M. guttatus* populations (S. Holt; Unpublished Data). These results suggest that water availability – mediated by temperature and snow melt and impacting growing season duration – is the key selection factor for climate adaptation in these populations. While there are risks of complete mortality in a given year, both seed banks and intrapopulation variation in water availability may provide important buffers (Friedman *et al*., 2019; McDonald *et al*., 2023). The population with complete mortality after the 2019 heatwave had a small number of new germinants in 2021 and has maintained a minimal population size.

Climate-change-mediated extreme events may also have range-wide impacts in *M. guttatus*. Resurrection experiments similar to those conducted in *C. xantiana* and *M. cardinalis* surrounding the 2012–2016 CA drought (Box 2) examine the rapid evolution in *M. guttatus*. Annual *M. guttatus* populations are often thought of as drought-escaping plants that grow and reproduce quickly before terminal drought, but some populations also are competent at physiologically avoiding drought to extend the growing season (Wu *et al*., 2008; Kooyers *et al*., 2015). Early resurrection studies suggest that only < 20% of surveyed populations evolved earlier flowering or greater drought avoidance during the drought. Patterns of evolution were not geographically structured, but evolutionary responses varied in magnitude based on the amount of phenotypic variation in the population before the drought (Kooyers *et al*., 2021). This study has two major limitations. First, this study only examined two phenotypes, and evolution of drought resistance can occur through many different mechanisms. Second, several populations were not observed during the drought; this suggests that seed dormancy may be an important yet unexplored way to cope with poor conditions. Combined, these results suggest that evolutionary rescue may occur in a subset of cases, largely in more phenotypically diverse populations. However, further investigation is needed to evaluate whether rapid evolution facilitated population recovery or benefits these populations during future drought events (i.e. creates silver-linings).

Other key considerations for the future performance of range-wide populations exist. First, annual *M. guttatus* populations have an obligate long-day photoperiod requirement (Friedman & Willis, 2013; Kooyers *et al*., 2015). Tracking growing seasons that are consistently moving earlier in the year may be a challenge for this species. However, substantial variation in critical photoperiod thresholds exists within populations that should facilitate evolutionary rescue (Friedman & Willis, 2013). Second, the reproductive dynamics of *M. guttatus* will also depend on the availability of pollinators. While *M. guttatus* is capable of selfing, strong inbreeding depression has been observed in natural populations (Brown & Kelly, 2020). Loss or limited activity of bee species from hotter and drier areas of the range could be problematic, causing an initial loss of fitness and driving life-history evolution (Bodbyl Roels & Kelly, 2011).

## 3. Importance for other species

Owing to the high levels of genetic diversity, the large abundance of individuals within a population, and an extensive distribution, *M. guttatus* provides a model system for species that *should* be able to respond to changing climates. Despite its wide distribution, *M. guttatus* also occupies a very specific ecological niche – sites that have copious water, high levels of sunlight, little soil, and little competition from other species. The plant communities in these sites are largely different from surrounding meadows and forests and tend to be specialized (Arceo-Gómez & Ashman, 2014). The previously discussed results likely are most directly applicable to specialist species within seeps and rockwall communities, some of which are threatened, as well as other annual species that experience terminal droughts in Mediterranean ecosystems. *M. guttatus* also hosts a diverse community of microbes, mycorrhizal fungi, and both generalist and specialist herbivores (Bowsher *et al*., 2020; Rotter, 2020; McIntosh *et al*., 2024). However, few herbivores are likely exclusively dependent on this monkeyflower, and impacts on microbes and fungi are unknown.

## 4. Limitations

*Mimulus guttatus* might provide a limited model for understanding climate responses of threatened species because populations harbor high levels of genetic diversity, and it is extremely common compared with other plant species. We know little about mortality and selection directly following germination because nearly all field studies transplant seedlings. This is important because individual plants produce many seeds compared with the number of censused individuals within a population. Likewise, while the existence of a seed bank is likely (McDonald *et al*., 2023), the abundance and long-term viability of seeds in the ground is unknown. These factors make it challenging to produce demographic models that realistically project the impacts of climate change and extreme events on populations (DeMarche *et al*., 2016).

*Mimulus guttatus* is part of a larger species complex that includes multiple different ecotypes (inland annuals, coastal perennials, high-elevation perennial populations, and perennial river populations) and closely related species (*M. nasutus*, *M. tilingii*, *M. glacescens*, etc.) (Ivey *et al.*, 2023). Despite some reproductive isolation between these ecotypes and species, there is hybridization that could impact the long-term evolution of these populations (Brandvain *et al.*, 2014; Ivey *et al.*, 2023). Because these different ecotypes are often relatively proximate geographically, there are likely genetic variants of large effects introduced at a high frequency that could potentially be adaptive in a rapidly changing environment (Coughlan & Willis, 2019). However, this is a feature that is not common for other plant species and may increase the relative climate resilience of *M. guttatus.*

## VII. *Andropogon gerardii* (Poaceae)

**Meghan Avolio**

Big Bluestem (*Andropogon gerardii*, Poaceae) is a dominant $C_4$ grass species that characterizes tallgrass prairies across North America, from the eastern Atlantic coast to the western Rocky Mountains, and from southern Canada down to northern Mexico (Keeler, 2004). *A. gerardii* is a long-lived species (Keeler *et al.*, 1987), composed of two common coexisting cytotypes ($2n = 6x = 60$ and $2n = 9x = 90$), with intermediate cytotypes, $7x$ and $8x$, being present but rare (Keeler, 1992; McAllister *et al.*, 2015). Geographically, $9x$ cytotypes are more common in drier habitats, with $6x$ being more widespread overall and more common in the northern part of the species range (McAllister *et al.*, 2015). The species reproduces mainly asexually (Benson & Hartnett, 2006), recruiting buds on rhizomes at the start of the growing season (Ott & Hartnett, 2011). Estimates of the size of clones vary from meters (Keeler *et al.*, 2002) to tens of meters in diameter (Avolio *et al.*, 2013) or larger (Chang & Smith, 2013), and clones are intermixed with one another (Avolio *et al.*, 2011). Although a clone is long-lived, individual tillers are rapidly lost and gained due to annual senescence and recruitment of new tillers from the bud bank (Hartnett & Bazzaz, 1985; Ott & Hartnett, 2012). Flowering and sexual reproduction commonly occur, but most plants do not produce viable seeds (Keeler, 2004) *A. gerardii* is self-incompatible, and fertilization occurs across all combinations of $6x$ and $9x$ cytotypes (Norrmann *et al.*, 1997). Crosses between $6x$ cytotypes result in the most viable seeds (Keeler, 2004); however, viable seed is possible from other crosses (Norrmann & Keeler, 2003).

Large-scale population genetic studies of *A. gerardii* spanning its range in the United States indicate there are high levels of genetic variation (Gray *et al.*, 2014), including southeastern US populations where the species is not as common or dominant (Tompkins *et al.*, 2012). The most recent study of population structure using SNP data found four differentiated clusters: one in the eastern United States and three in the Midwest. Midwest clusters include a northern, a southeastern, and a southwestern cluster that co-occur in Kansas (McAllister & Miller, 2016).

### 1. Significant work

Despite the challenges of working with a long-lived perennial species with mixed ploidy, *A. gerardii* has a substantial body of work examining potential responses to climate change. Importantly, there is a reference genome available from the Joint Genome Institute for this allopolyploid. Most of this work consists of observational and manipulative field experiments examining growth and physiology.

### 2. Major results

Historic observations suggest that *A. gerardii* is sensitive but resilient to changing climate conditions, particularly water availability. During the intense drought of the 1920s (the dust bowl), *A. gerardii* only persisted in small areas with wetter soils (Weaver, 1954). After the drought, *A. gerardii* was able to recover through asexual spread of rhizomes that persisted through the drought (Weaver, 1954).

Common garden experiments in Texas during the 1950–1960s leveraged sampling across the United States and Mexico to find signatures of local adaptation via superior survival of geographically proximate populations (McMillan, 1969a). Differences were driven by phenological variation in which local southern populations started the growing season earlier, flowered later, and had greater dormancy than more northern populations (McMillan, 1964, 1965a, 1967). More recently, a large reciprocal transplant experiment suggests that contemporary populations are locally adapted to their home sites across the Great Plains (Johnson *et al.*, 2015). Plants from three locations, including central Kansas, eastern Kansas, and southern Illinois, were planted in four common gardens (the three collection locations plus a fourth location in western Kansas), spanning a precipitation gradient from drier conditions in the west to wetter conditions in the east (Johnson *et al.*, 2015). Plants from the drier and wetter end of the spectrum did considerably better when grown in their home environment than nonlocal populations (Johnson *et al.*, 2015; Galliart *et al.*, 2019, 2020). Local adaptation was not necessarily based on growth patterns – populations from the mesic area grew equally well across all sites (Galliart *et al.*, 2019), and flowered relatively more and set more seed at wetter sites (Galliart *et al.*, 2020). Plants collected from more xeric locations appeared to have adaptive traits, such as thicker leaves, that may underlie the advantage in the drier sites (Olsen *et al.*, 2013; Kramer *et al.*, 2018). Indeed, synthesis of published trait data from *A. gerardii* found substantial variation in plant functional traits (e.g. specific leaf area) across natural populations likely due to plasticity as there are few trait–environment associations (Bachle *et al.*, 2018). However, more work documenting heritable trait variation across climate gradients is necessary in the system. This work highlights the degree to which there is substantial phenotypic variation within *A. gerardii*, a high degree of phenotypic plasticity, yet broad local adaptation.

Species and phenotypic distribution models project that climate change is likely to cause range shifts and potential maladaptation (Smith *et al.*, 2017). Climate suitability for species abundance is most dependent on maximum temperature in the hottest month, but phenotypic variance throughout the range was most closely associated with precipitation metrics. Models suggest that *A. gerardii* will decline in abundance across most of its present range, with the suitable climatic range moving considerably northward. Notably, phenotype variation will shift dramatically, with shorter plants, which currently prevail in the most xeric populations, spreading to a greater proportion of the range (Smith *et al*., 2017). Since there are already established populations in areas with future climate suitability (i.e. Canada; Gorrie, 2002), persistence of this species is likely. However, dispersal is likely limited, given the overwhelming reliance on clonal reproduction and low fertility of seeds (Keeler, 2004).

Several field studies have investigated how different agents of selection associated with changing climates influence fitness and population abundance. The majority of recent field studies on *A. gerardii* took place in or around Manhattan, KS, near the center of the species range. One study found that *A. gerardii* only responded to increased $CO_2$ when water was limiting (Knapp *et al*., 1993). Additionally, long-term elevated soil moisture reduced *A. gerardii* abundance in lowlands (Collins *et al*., 2012), but not in more xeric upland environments. Field experiments on drought timing found that drought in the middle of the growing season strongly depresses the number of flowering stalks and may reduce sexual reproduction (Dietrich & Smith, 2016). Finally, extreme drought over the whole growing system greatly reduced *A. gerardii*; but then, there was strong recovery following drought (Hoover *et al*., 2014a). There is also evidence from an extreme drought and heatwave experiment that *A. gerardii* is more sensitive to water stress than heat stress in terms of leaf-level physiology (Hoover *et al*., 2014b). Together, these studies may suggest that increased precipitation variability, as likely in future climates, may alter population dynamics and shift the range of *A. gerardii*.

The existence of considerable phenotypic plasticity (Avolio & Smith, 2013b; Galliart *et al*., 2020; Hoffman & Smith, 2021) and substantial intraspecific variation across the range (Bachle *et al*., 2018) suggest that populations may be able to evolve *in situ* to changing conditions. Studies of variation in natural populations and manipulative field experiments suggest that there is substantial genetic variation in leaf-level physiological traits as well as differences in biomass accumulation and allocation that could act as fodder for natural selection in changing climates (Avolio & Smith, 2013a,b). Avolio *et al*. (2013) also examined the effect of a decade of experimentally more variable rainfall patterns on the genetic diversity and genotypic composition of *A. gerardii* in intact tallgrass prairies. In this experiment, precipitation was manipulated to have fewer, larger rainfall events, but the same total amount of precipitation as in the ambient treatment. They found that the altered rainfall treatments reduced the number of genotypes but that surviving individuals were less related to one another, increasing overall genetic diversity (Avolio *et al*., 2013). Follow-up field studies found that the remaining genotypes had different phenotypes, with one genotype growing faster and being taller and another having higher specific leaf area (Avolio & Smith, 2013a). Downstream glasshouse studies found that successful genotypes were either more drought-tolerant or had greater plasticity in leaf-level physiology (Avolio *et al*., 2018). These experiments suggest that evolution may indeed facilitate population persistence in future climates.

Given dispersal limitations and evidence of *in situ* evolution, assisted gene flow has been an important topic for *A. gerardii*. Some researchers have suggested that assisted gene flow might have unintended negative consequences as plants from drier areas have much lower belowground biomass and productivity, which could alter local ecosystem function (Mendola *et al*., 2015). However, others hypothesize that using drier adapted plants now in restoration efforts may be prudent, given how climate is likely to change (Smith *et al*., 2017).

### 3. Importance for other species

*Andropogon gerardii* is the dominant species in tallgrass prairies and can account for up to 80% of biomass production (Smith & Knapp, 2003). When removed, no other species can replace it, and ecosystem productivity does not recover (Smith & Knapp, 2003; Chaves & Smith, 2021). Given the dominance of *A. gerardii*, when present, it reduces community richness (Collins *et al*., 2002). Genetic diversity within the species across the landscape has conflicting impacts on productivity and no relationship with species richness (Avolio & Smith, 2013c; Chang & Smith, 2014). Thus, range shifts of genotypic variation may have localized effects on productivity. In addition, *A. gerardii* is a good model for studying evolutionary processes as a contrast to *Panicum virgatum* (Section VIII). Both of these species are widespread $C_4$ grasses, and the differences or similarities found between them will give important insights into the generalities or contingencies of long-lived clonal tallgrass species.

### 4. Limitations

There are three key organismal characteristics that stand as challenges for understanding climate change responses in *A. gerardii*: mixed ploidy cytology, predominant asexual reproduction, and long generation times. As a polyploid with mixed ploidy levels across the range, basic population genetic studies are challenging (Meirmans *et al*., 2018) as is determining the potential for genetic or evolutionary rescue with unknown reproductive barriers among populations. Both a predominantly asexual reproduction strategy and long lifespan make it challenging to accurately assess lifetime fitness, maladaptation, and the agents and targets of selection. However, given the ecological importance of this species within prairie ecosystems, it is essential that we continue parsing potential climate responses.

## VIII. *Panicum virgatum* (Poaceae)

**Joseph Napier & Thomas Juenger**

Switchgrass, *P. virgatum*, is a large, perennial $C_4$ grass that is widespread throughout much of the grassland, woodland, and riparian areas in eastern and central North America from Mexico to Canada (McMillan, 1964; Zhang *et al*., 2011a,b; Triplett *et al*., 2012; Lovell *et al*., 2021). As a wind-pollinated, obligate outcrosser, and allopolyploid species (Talbert *et al*., 1983; Martínez-Reyna & Vogel, 2002; Triplett *et al*., 2012; Lowry *et al*., 2014), it exhibits extensive phenotypic variability and adaptation across its range, especially related to latitude and precipitation gradients (Casler *et al.*, 2004, 2007; Meyer *et al.*, 2014). Specifically, phenological traits such as flowering time and winter dormancy strongly vary along these clines (Casler, 2012; Aspinwall *et al.*, 2013). McMillan (McMillan, 1956, 1959, 1964, 1965a, 1967, 1969a,b) provided pioneering experimental evidence linking genetic variation with these large-scale environmental gradients.

Beyond the strong link between phenotypic variability and broad environmental gradients, there are two major diversity partitions within the switchgrass complex: ecotypes and ploidy level. Switchgrass populations have been traditionally classified as one of two major ecotypes, lowland and upland (Porter, 1966; Cortese *et al.*, 2010; Morris *et al.*, 2011; Zhang *et al.*, 2011a,b; Lu *et al.*, 2013; Lowry *et al.*, 2014). In comparison with upland plants, lowlands have bluish waxy leaves, fewer tillers per plant, thicker leaves and tillers, and are generally taller with a strong bunchgrass habit (Cortese *et al.*, 2010; Zhang *et al.*, 2011a,b). Upland ecotypes have greener leaves, thinner tillers, more tillers per plant, are less resistant to rust infection, and have a more rhizotomous and spreading growth form (Cornelius & Johnston, 1941; Porter, 1966; Cortese *et al.*, 2010). Lowland plants have a more southern range, being typically found in riparian areas, whereas uplands have a more northern range and are found in grasslands with seasonally lower soil moisture when the ecotypes co-occur (Porter, 1966; Brunken & Estes, 1975). More recently, a third phenotypically intermediate coastal ecotype has been described as originating from a second southern ancestry group with a broad distribution across the Atlantic seaboard (Lovell *et al.*, 2021; Napier *et al.*, 2022).

Switchgrass ecotypes are reproductively compatible and hybridize along several contact zones. Ploidy level has typically been considered a secondary division within switchgrass, with the dominant cytotypes considered to be tetraploids ($2n = 4x = 36$) and octoploids ($2n = 8x = 72$) (Brunken & Estes, 1975; Hopkins *et al.*, 1996; Narasimhamoorthy *et al.*, 2008; Costich *et al.*, 2010; Triplett *et al.*, 2012). The upland ecotype contains both $4x$ and $8x$ individuals, while the lowland ecotype was traditionally assumed to be dominated by $4x$ individuals (Costich *et al.*, 2010; Triplett *et al.*, 2012). The switchgrass $4x$ allopoloid genome is large (haploid genome size of 1.129 Mb), is highly heterozygous, with large repeat expansions and likely considerable content and copy number variability (Lovell *et al.*, 2021). Much less is known about the $8x$ genome, although octoploid individuals are likely the product of both auto- and allopolyploidization within and among switchgrass ancestry groups (Napier *et al.*, 2022). Switchgrass populations have likely experienced range shifts and population expansion and contraction along the latitudinal gradient in response to recent glacial–interglacial cycles (McMillan, 1959; Zhang *et al.*, 2011b; Lovell *et al.*, 2021). Historic switchgrass populations were likely enormous, given the wide extent of habitat and its ecological dominance across much of North America. However, populations in the Great Plains and Midwestern prairies have recently been disrupted by conversion to row crop agriculture. Many of the relictual prairie populations in the Midwest are small (often < 1 acre) and isolated, resulting in dramatic bottlenecks and potential loss of local diversity.

## 1. Significant work

Switchgrass has been the target of extensive common garden experiments, field trials, and natural collections for over seven decades (e.g. Nielson, 1947; McMillan, 1959, 1965a; Quinn, 1969; Hopkins *et al.*, 1995a,b; Casler *et al.*, 2004, 2007; Lowry *et al.*, 2019; Lovell *et al.*, 2021; Napier *et al.*, 2022). Much of this work has been motivated by agronomic interest in switchgrass as a forage crop and more recently as a candidate biofuel feedstock. Observational work across the range of switchgrass has provided information on the habitat differentiation between ecotypes, variation structured along environmental gradients, presence/absence data for niche modeling, occurrence of ploidy variation, genetic population structure, and introgression patterns. Complementary experimental work has documented plant performance in common gardens, ecotypic performance, and genotype by environment interactions using genetic mapping and natural populations. A number of field experiments have studied plant physiological and growth responses to potential climate drivers including elevated $CO_2$ and altered patterns of precipitation (Aspinwall *et al.*, 2016; Heckman *et al.*, 2024). From the applied perspective, a small number of breeding programs have generated cultivars through recurrent phenotypic selection. Genomic prediction has been explored for increasing the speed of switchgrass improvement in modern breeding programs (Tilhou *et al.*, 2024). Ongoing studies integrating field observations, experimental results, climate data, and sequenced genomes provide opportunities to test long-standing ecological and evolutionary theories and provide insight into the basis of local adaptation. These studies also provide considerable insight into current and future responses to changing climates.

## 2. Major results

Decades of field research indicate that growing season length is one of the primary drivers of adaptation within the species and, potentially more broadly, in $C_4$ perennial grasses. Independent studies have concluded that adaptation in the northern range of switchgrass is driven by short growing seasons and tolerance to colder winter temperatures (Nielson, 1947; Hope & McElroy, 1990; Moser & Vogel, 1995; Casler *et al.*, 2004, 2007; Berdahl *et al.*, 2005; Casler & Smart, 2013). By contrast, longer growing seasons and higher summer temperatures are the major adaptive drivers in the southern portion of the switchgrass range (McMillan, 1965b, 1969a; Casler *et al.*, 2004, 2007). Recent work argues that these patterns provide a link between leaf economic strategies and physiological acclimation (Wright *et al.*, 2004; Heckman *et al.*, 2024). Specifically, southern switchgrass genotypes from the warmer part of the species range exhibit conservative economic strategies including later flowering times and producing thicker, long-lived leaves with lower nitrogen concentration than switchgrass genotypes from cooler climates with shorter, less stochastic growing seasons (Aspinwall *et al.*, 2013; Lovell *et al.*, 2021). In part, these results imply that switchgrass climate adaptation is linked with variation in flowering time and resource allocation strategies (Heckman *et al.*, 2024).

Understanding how plant species respond to climate shifts is central to predicting future ecological and evolutionary dynamics of species. Correspondingly, many retrospective studies have focused on how plant populations responded during major periods of climate upheaval, particularly glacial maximums, and subsequent postglacial periods (De Lafontaine *et al.*, 2018). A paradigm-shifting study in this field argued that rather than focusing on the discrete processes of migration and adaptation, it is the interplay of these forces that is central to plant responses to climate change (Davis & Shaw, 2001). Switchgrass provided one of the first opportunities to directly observe this interplay when an expansive genomics study uncovered a suite of introgressions from a Midwestern genetic subpopulation into an Atlantic genetic subpopulation that coincided with northern range expansion after the LGM (Lovell *et al.*, 2021). The Atlantic genotypes with higher levels of Midwest introgressions exhibited a more upland suite of traits and were also overrepresented along the northern margin of the predominantly subtropical and temperate distribution of the Atlantic subpopulation. Multivariate analyses demonstrated a strong relationship between climate and these introgressions. Lovell *et al.* (2021) hypothesize that these introgressions facilitated the postglacial colonization by switchgrass of colder habitats in the northeastern coastal region of the United States and broadly support the role of adaptive introgressions in facilitating range expansions.

Genetic architectures of local adaptation likely play an important role in rapid adaptation to changing climates, and studies of the genetics of adaptation in switchgrass provide key insights. Theoretical models have consistently predicted that local adaptation will likely involve strong fitness trade-offs at the level of single loci (Levene, 1953; Felsenstein, 1976; Hedrick, 1986; Kawecki & Ebert, 2004). Genes increasing fitness in one environment may, through antagonistic pleiotropy, result in decreases in fitness in other environments. Alternatively, local adaptation may arise through mutations that improve fitness locally but that are neutral and generally have no fitness impact in other environments (Anderson *et al.*, 2013). The ratio of antagonistic pleiotropic to conditionally neutral architectures may be a key determinant of species responses to climate change. Two analyses of switchgrass common garden studies (Lowry *et al.*, 2019; Lovell *et al.*, 2021) provide a unique opportunity to test how often and to what extent loci confer benefits and costs across geographic space. Results from these studies suggest trade-offs were largely rare, weak, or nonexistent, although there was substantial evidence for standing genetic variation in performance across much of the species range. This is surprising, as most theories would predict beneficial (or conditionally neutral) alleles should spread by gene flow across habitats and ultimately fix in natural populations (Anderson *et al.*, 2013; Mee & Yeaman, 2019). Interestingly, both studies identified alleles strongly impacting general vigor across broad geographical ranges, which suggests that there is ample genetic variation for adaptation to climatic variation and there is tremendous agronomic opportunity to breed generalist high-yielding cultivars by recombining and selecting on this standing variation.

Switchgrass also provides a key opportunity for understanding how mixed-cytotype species respond to changing climates. Napier *et al.* (2022) contrasted the molecular and quantitative genetic diversity of 4*x* and 8*x* switchgrass across 10 common gardens to evaluate the scale of climate adaptation, ecological niche breadth, and growth performance. A main result from the study was the detection of differential environmental sensitivity between switchgrass cytotypes, suggesting a generalist–specialist trade-off and niche evolution between 4*x* and 8*x* cytotypes linked to climate adaptation. Specifically, in common gardens with climates most similar to the climate of the original collection locations, 4*x* genotypes demonstrated higher relative fitness than the 8*x* genotypes; however, fitness declined more slowly in the 8*x*, with the 8*x* eventually having higher relative fitness than the 4*x* in climates more different from the climate of origin. These results suggest that ploidy increases may expand the diversity of suitable habitats and niche breadth, providing a path to range shifts under changing climate.

Switchgrass is extremely robust and tolerant of most environmental extremes, in part because of the buffering provided by its robust belowground growth pattern and extensive bud banks. Field trials and agronomic crop modeling suggest that under most climate change scenarios, switchgrass should persist and even increase in terms of biomass productivity, as it generally benefits from the warming winters, long growing seasons, and the increased precipitation predicted across much of its range (Behrman *et al.*, 2013). The most vulnerable populations are likely associated with the desert southwest and western margins of the species distribution, where extreme and persistent drought may threaten new establishment and the persistence of existing populations. Moreover, remnant populations in the Midwest are likely threatened by climate-change-driven shifts in community composition and woody encroachment in small prairie preserves (Symstad & Leis, 2017).

## 3. Importance for other species

Results from a long history of switchgrass studies combined with modern genomic approaches provide insight into the interplay between gene flow, demography, and adaptation in responses to past climate change. An especially interesting discovery is the role of adaptive introgressions from one genetic subpopulation into another enabling range expansion during rapid climate shifts (Lovell *et al.*, 2021). Second, the discovery of links between ploidy, niche breadth, and the spatial scale of climate adaptation (Napier *et al.*, 2022) may hold true for other species with complex ploidy series, including other grass species in North America that are widely distributed. This suggests changes in ploidy might play a key role in abiotic stress responses and that ‘ploidy hops’ might be a generalized response to persist through periods of pronounced climatic fluctuations.

## 4. Limitations

While there have been many insights gleaned from studies of switchgrass, it is important to acknowledge that many of the field studies have been conducted in agronomic settings rather than in more realistic and complex natural habitats. For example, many of the riparian habitats where lowland switchgrass occurs experience seasonal flooding, while northern upland prairie habitats were once grazed or periodically burned by wildfires. Incorporating these disturbances into ongoing experiments is challenging and rare. Moreover, most studies are based on transplants that exclude the establishment stage and lack the strong competition expected in grassland habitats. Measures of performance (i.e. fitness) are also often estimated by biomass production as a proxy, which, while highly correlated with sexual and asexual reproduction in switchgrass (Palik *et al.*, 2016; Lowry *et al.*, 2019), might provide only a partial view of adaptation and fitness. New studies incorporating demographic tracking of individuals from dispersal to establishment, in more natural habitats, and allowing more realistic competitive environments would be especially valuable. The switchgrass research community continues to develop genomic resources and tools to study diversity. To date, the community has relied on the gulf lowland genome (AP13 genotype) as the primary reference for studies of gene content and population genetic diversity. New high-quality genome assemblies of the upland and coastal ecotypes, along with more sampling within each of the described ecotypes, will likely improve our understanding of ecotype divergence and climate adaptation across the species range.

## IX. *Ipomopsis aggregata* (Polemoniaceae)

**Diane Campbell**

Scarlet gilia (*Ipomopsis aggregata*) is a monocarpic perennial forb ($2n = 14$) that occurs throughout mountainous western North America from southern British Columbia to north-central Mexico (Grant & Wilken, 1986). Eight subspecies are currently recognized (Porter *et al.*, 2010) and are usually mainly hummingbird or hawkmoth pollinated, with occasional flower visits by other insects to the self-incompatible plants (Price *et al.*, 2005). Most ecological or evolutionary work has focused on *I. aggregata* subsp. *aggregata* in western Colorado (Campbell, 2004) or on *I. aggregata* subsp. *candida* and *I. aggregata* subsp. *collina* in the Front Range (Juenger & Bergelson, 1998; Campitelli *et al.*, 2018). Plants of *I. aggregata* subsp. *aggregata* spend 2 to 10 yr or more as a vegetative rosette of leaves before putting up a flowering stalk, reproducing and dying in a single season (Campbell, 1997). Mammalian herbivory, either before or after flowering, can release apical dominance and cause the production of multiple flowering stalks (Brody *et al.*, 2007). Seeds are frequently consumed by a fly (Anthomyiidae) that is a predispersal seed predator, laying an egg on the inside of the sepals, and typically consuming all seeds in the fruit (Brody, 1997). Seeds rarely move > 1 m (Campbell *et al.*, 2017), and there is virtually no seed bank, with 96% of seedlings that germinate doing so in the first year (Campbell *et al.*, 2008). In many localities, plants of *I. aggregata* hybridize naturally with *Ipomopsis tenuituba* (Aldridge, 2005). Long-term demographic studies show that certain local populations at relatively high elevation (2500–3000 m) are threatened by earlier snowmelt in the spring that leads to a longer period of drought before the onset of summer monsoon rains (Campbell, 2019). But establishment of vegetative rosettes can be enhanced by disturbance and open ground (Juenger & Bergelson, 2000), and the species as a whole occupies a wide variety of habitats, including sagebrush, forests, and subalpine meadows (Grant & Wilken, 1986), likely allowing widespread persistence of the species.

### 1. Significant work

*Ipomopsis aggregata* has long served as a model species for understanding the evolution of floral traits (Grant, 1949; Campbell, 1989; Mitchell, 1993; Campitelli *et al.*, 2018; Campbell *et al.*, 2022a,c). It has also served to model demographic effects of pollination (e.g. Juenger & Bergelson, 2000; Price *et al.*, 2008) and hybridization and speciation (e.g. Wu & Campbell, 2007; Campbell *et al.*, 2008, 2024). Work on climate change has focused on consequences for trait variation, natural selection, and population persistence. Two approaches have been employed: (1) long-term (> 30 yr) studies of natural populations and common gardens, and (2) experimental manipulations of snowmelt timing, summer precipitation, and temperature. Twenty-five years of data from experiments involving planting seeds in the field and tracking survival and reproduction were incorporated into integral projection models (Campbell, 2019). Those studies were supplemented by estimates of seedling establishment from naturally sown seeds (Waser *et al.*, 2010), such that the integral projection models included all steps of the lifecycle from seed germination to seed production. Those initial demographic models described the impacts of earlier snowmelt with climate change in the absence of changes in trait expression, and more recent models now examine whether phenotypic plasticity or evolutionary responses to selection can rescue otherwise threatened populations (Campbell *et al.*, 2025). These rely on estimates of plasticity, primarily from experimental manipulation of snowmelt timing and summer precipitation over 3 yr (Navarro *et al.*, 2022; Powers *et al.*, 2022). Estimates of natural selection and how it depends on snowmelt timing were obtained from > 20 yr of phenotypic selection estimates in natural populations (Campbell & Powers, 2015; Campbell *et al.*, 2024). Genetic variances and heritabilities of traits, also necessary to examine evolutionary rescue, were measured in the field using hand-pollinations to generate paternal half-sib families of seeds and planting them in common gardens and performing reciprocal transplants (Campbell *et al.*, 2022c).

### 2. Major results

In years of early snowmelt, populations of *Ipomopsis* have lower seedling establishment and survival to the next year, and flowering individuals produce fewer seeds (Campbell, 2019). Based on the demographic models, one hybrid population (*I. tenuituba* × *I. aggregata*) is already below replacement, and one *I. aggregata* population could be within a few decades given the trend toward earlier snowmelt (Powers *et al.*, 2022) and early-season drought (Campbell, 2019). Moreover, based also on 13 yr of pollen supplementation experiments, the impact of early snowmelt has stronger effects on demography in a given year than does pollen limitation due to few pollinators or interactions with seed predators (Campbell *et al.*, 2022b). Early snowmelt or reduced precipitation leads, in the same year, to shorter and narrower corollas, shorter styles, narrower sepals, and reduced production of more concentrated nectar (Powers *et al.*, 2022), altered floral volatile emissions (Powers *et al.*, 2025), and reduced stomatal conductance and specific leaf area (Navarro *et al.*, 2022; Campbell *et al.*, 2022c). Elevated temperatures of 2–3°C during flowering alter floral volatile emissions and increase nectar production but have little or no effect on flower color or seed production in that same season (Wu *et al.*, 2023). Long-term estimates of natural selection in wild populations indicate adaptive plasticity for low specific leaf area (Campbell *et al.*, 2025). For floral traits, selection sometimes counters plasticity, favoring for example wider flowers (Campbell *et al.*, 1996, 1997, 2022a) even though early snowmelt directly causes narrower flowers. In other cases, selection changes in intensity with snowmelt date in the spring. For example, corolla length and aliphatic emissions from flowers both experience weaker selection with earlier snowmelt (Campbell & Powers, 2015; Powers *et al.*, 2025). Several other floral traits are also under selection because of effects on pollination, seed predation, or both. These include not only flower morphology but also the floral volatiles α-pinene and indole (Campbell *et al.*, 2022a). Many of these traits exhibit genetic variation under natural field conditions (Campbell *et al.*, 2022c), as does fitness based on survival, reproduction, and age at reproduction (Campbell, 1997).

Putting this information together shows the possibility of evolutionary rescue in the hybrid population, but not for the *I. aggregata* population and only if plasticity along with evolution *in situ* is included in the model (Campbell *et al.*, 2025). This prediction is based on a shift toward lower specific leaf area (thicker leaves) with earlier snowmelt. Low specific leaf area is adaptive under extreme drought conditions seen with early snowmelt, as it reduces water loss through the stomates (Navarro *et al.*, 2022). Without accounting for adaptive plasticity in the trait, the evolutionary response to selection appears too slow to counter changes in snowmelt. But including the adaptive plasticity response of thicker leaves along with evolution would allow certain local populations to survive early snowmelt under climate change. By contrast, seed dispersal upslope is unlikely by itself to keep up with changing climates. The hybrid and *I. aggregata* populations are 700 m apart and differ in snowmelt date by 11 d on average, meaning that 64 yr of seed dispersal of <1 m would be required to move to an environment where snow melts just 1 d later, and yet in that time period the snow is expected to melt *c.* 13 d earlier on average (Campbell *et al.*, 2025). Additionally, while pollen moves over longer distances (Campbell & Waser, 1989), allowing introduction of adaptive alleles into lower elevation populations, pollen flow alone could not rescue a population at the upper elevation edge, nor allow the range to move farther upslope. Phenological responses are small in *Ipomopsis*, as it is relatively late to bloom, and later blooming species in this habitat show less advancement of first and peak flowering time (CaraDonna *et al.*, 2014) than do early bloomers, but earlier flowering could increase the rate of pre-dispersal seed predation (Freeman *et al.*, 2003).

### 3. Importance for other species

Reduced snowpack and early snowmelt are likely major risk factors for plant species in mountainous areas around the world. *I. aggregata* is an excellent model for understanding how herbaceous species are affected, as it is a common species that shares subalpine meadows with a wide variety of other species. In addition, as a monocarpic perennial, *I. aggregata* is well-positioned to allow estimation of lifetime fitness on a moderate timescale. Its generation time of *c.* 5 yr slows its ability to respond adaptively to climatic shifts in comparison with annuals, but models indicate that its trait changes can still be rapid enough to counter reduced snowpack under climate change (Campbell *et al.*, 2025). The results from demographic models likely presage similar effects for other species, and indeed, there is evidence that negative effects on survival due to drought imposed by early snowmelt also affect the co-occurring insect-pollinated sunflower *Helianthella quinquenervis* (Iler *et al.*, 2019). Interestingly, both species are impacted more by negative effects on survival than by changes in flowering phenology. Whereas few other plant study systems provide sufficient information to parameterize an evolutionary rescue model, combining published ranges of heritabilities and those of selection intensities suggests that other short-lived species besides *I. aggregata* could also experience evolutionary rescue from early snowmelt due to evolution of leaf traits (Campbell *et al.*, 2025). Impacts could cascade to other trophic levels, as climate effects on floral rewards and volatiles in *Ipomopsis* affect resources available for pollinators (Powers *et al.*, 2022) and behavioral responses of seed predators (Powers *et al.*, 2025).

### 4. Limitations

*Ipomopsis aggregata* in areas of most study has a mean generation time of 5 yr (Campbell, 1997), generating results that apply more widely than just to annual plants, but making it difficult to perform experiments following evolutionary change. One study did show changes in corolla length over 25 yr similar to those predicted from estimates of selection and heritability (Campbell *et al.*, 2018). Because of the long history of quantifying phenotypic selection and genetic variances/covariances, *I. aggregata* is more useful as a model species for quantitative genetic approaches to understanding evolutionary rescue than for those identifying specific genes involved in climate adaptation. Only a relatively small amount of genomic work has been carried out (Campitelli *et al.*, 2018), showing a large QTL for flowering time and another for flower color localized to a gene in the anthocyanin biosynthesis pathway. Seeds are difficult to store as they do not retain long-term viability, but leaf tissue samples have been collected and stored from most plants used in long-term studies. These resources exist for future genetic mapping and for following genomic changes in natural populations as far back as the 1980s.

## X. Synthesis

These case studies of herbaceous species responses to climate change demonstrate the variety of approaches that characterize the early days of understanding biological responses to changing climates. The majority of these focal species are model systems (predominantly from North America) developed to address foundational questions in evolutionary ecology, evolutionary genetics, or molecular genetics, and have been co-opted for climate change research. However, together these species provide valuable insights into the degree of commonality in climate change responses. A basic conclusion is that climate change affects all of these species and that they are evolving in response to novel conditions. We note that not all species have had comparable amounts of work – for instance, several species (*B. stricta*, *I. aggregata*, and *C. xantiana*) have had dozens of studies targeting climate change over the past two decades. However, work on the dominant prairie grasses (*P. virgatum* and *A. gerardii*) has focused on patterns, mechanisms, and genetics of local adaptation. Below, we attempt to generalize the results from the previously discussed case studies and then synthesize these results within three contexts: the characteristics of our focal species, notable knowledge gaps, and a path forward.

## 1. Generalities in climate change responses across focal species

Despite differences in the experimental methodologies and organismal biologies of our focal systems, we note clear commonalities in climate responses between species. We synthesize these in the same format as previously discussed, first examining patterns of decline and maladaptation, and then assessing the ability for plasticity, genetic rescue, or evolutionary rescue to allow persistence or expansion.

**Decline** A number of species exhibit signs of population decline in at least part of their geographic range. Population growth rates below one, indicative of contracting populations, have been observed in *I. aggregata*, *B. stricta*, *C. xantiana*, and *M. cardinalis*, and extirpation of natural populations has been observed in *M. guttatus* and *M. cardinalis*. Declining populations are often on the edges of the range, typically the trailing edge that occurs in the hottest and driest part of the range. But high-elevation subalpine populations of *I. aggregata*, *B. stricta*, and *M. guttatus* are also at risk due to earlier snowmelt and shifting growing seasons (Campbell, 2019; Kooyers *et al.*, 2019; Anderson *et al.*, 2025). Earlier snowmelts shift phenology, change water availability patterns during the growing season, can expose seedlings to greater freezing risk (Anderson, 2023). Population dynamics for several species have been observed during extreme events (i.e. droughts or heatwaves), which can exacerbate declines. For all model species, precipitation and altered growing seasons are key agents of selection. The only species without evidence of any population declines due to climate change is a dominant perennial grass in which such demographic data have not been collected (*P. virgatum*). Range-wide demographic experiments need to be a priority.

**Maladaptation** Patterns of maladaptation have been documented in *A. thaliana*, *B. stricta*, *M. cardinalis*, and *M. guttatus*. In each instance, populations from historically hotter and drier environments have higher fitness than native populations; often, the contemporary conditions in the common garden are more similar to the historical conditions of the foreign population than the local population. These patterns occur not only in populations with low growth rates but also within large populations that do not appear to be threatened by climate change. Such patterns of adaptation lag will inevitably vary between individual years in association with environmental conditions but appear in a high proportion of years in species in which multiple years have been surveyed (*B. stricta* and *M. guttatus*).

**Plasticity** While plasticity is consistently observed among all focal species, plasticity alone does not seem sufficient to allow adjustment to the multitude of factors changing during climate change. Plasticity may contribute to species persistence, giving currently threatened populations more time to adapt, as in *I. aggregata* (Campbell *et al.*, 2025). Phenology seems to be particularly plastic, enabling some subalpine species to keep up with shifting growing seasons (Anderson & Gezon, 2015). However, there are also multiple instances of plasticity being maladaptive by producing counter-gradient effects on key ecological traits such as flowering time and dormancy. In *A. thaliana*, typically fast-flowering low-elevation accessions may flower too late for reproductive success in higher elevation populations (Exposito-Alonso *et al.*, 2018b). Similarly, plasticity is in the opposite direction as selection in *C. xantiana* (Eckhart *et al.*, 2004). In *M. cardinalis*, plasticity was lost (canalized) during an extreme drought, a key result that may not have been anticipated (Branch *et al.*, 2024b). The nuance associated with each of these results suggests that there must be greater emphasis on understanding the mechanisms underlying acclimation and examining the fitness consequences of plasticity in response to climate change.

**Genetic and evolutionary rescue** Importantly, there are populations for each of the focal species that are not threatened or maladapted and exhibit reasonably high population growth rates. These populations may also contain valuable standing genetic variation for ecologically important traits that could facilitate genetic or evolutionary rescue. Theory predicts that genetic variation in traits and fitness should represent a population's potential to adapt to changing climates (Fisher, 1930; Lande, 1979; Lande & Arnold, 1983; Falconer & Mackay, 1996; Shaw, 2019). Notably, evolutionary rescue has been observed in a subset of *M. cardinalis* populations following an extreme drought (Anstett *et al.*, 2024), and *all* of the systems have exhibited rapid responses to selection in at least some populations. Unfortunately, many of these species, including *M. cardinalis*, *I. aggregata*, *C. xantiana*, *A. gerardi*, *B. stricta*, and *A. thaliana*, are likely dispersal-limited to the extent that potentially adaptive alleles are unlikely to get to the declining populations unless the declining population is only a short geographic distance away. These results indicate that more drastic management strategies, including assisted gene flow or even assisted migration, may be necessary for many species (Aitken & Whitlock, 2013). However, we note that the species mentioned previously are widespread and have extensive ecologically relevant variation – other species may not have the same advantage.

## 2. Notable characteristics of focal species and studies

Understanding the ways our focal species are similar and different provides insight into the interpretation and generality of the previously discussed synthesis. We selected the focal species for this

**Table 1** Organismal attributes of herbaceous model species.

| Model species | Life history | Mating system | Main pollinator | Genome size | Chromosome count | PPD req. | Vern. req. | Seed bank |
|---|---|---|---|---|---|---|---|---|
| *A. thaliana* | A | S | Fly | 135 Mb | 2*n* = 10 | F. LD | Variable | Yes |
| *B. stricta* | P | S | Bee | 190 Mb | 2*n* = 14 | *Unkn.* | Yes | Yes |
| *C. xantiana* | A | FO | Bee | 1.1 Gb | 2*n* = 18 | F. LD | No | Yes |
| *M. cardinalis* | P | M | H.bird | 450 Mb | 2*n* = 16 | *Unkn.* | No | *Unkn.* |
| *M. guttatus* | B | FO | Bee | 430 Mb | 2*n* = 14 | O. LD | Variable | Yes |
| *A. gerardi* | P | OO | Wind | 7 Gb | 2*n* = 6*x* = 60<br>2*n* = 9*x* = 90 | SD | No | Yes |
| *P. virgatum* | P | OO | Wind | 1.12 Gb | 2*n* = 4*x* = 36<br>2*n* = 8*x* = 72 | SD | No | Yes |
| *I. aggregata* | P | OO | H.bird | *Unkn.* | 2*n* = 14 | *Unkn.* | Yes | Limited |

Genome is estimated haploid genome content in mega- or gigabases. Life histories are coded as A (annual), P (perennial), or B (both). Mating systems are coded as S (selfing), FO (facultative outcrosser), OO (obligate outcrosser), or M (mixed mating system). H. bird refers to a hummingbird pollinated species. PPD req. is the photoperiod requirement; O.LD (obligate long day), F.LD (facultative long day) or SD (short day). Vern req. is the presence of a vernalization requirement to flowering. Binomial nomination of model species: *Arabidopsis thaliana, Boechera stricta*, *Clarkia xantiana*, *Mimulus cardinalis*, *Mimulus guttatus*, *Andropogon gerardi*, *Panicum virgatum*, *Ipomopsis aggregata*.

review both for the extensive history of research with them and because the coauthors are collaborators from previously established research networks based in North America (i.e. Cocciardi *et al.*, 2024). Several other species could have been included: *Mimulus laciniatus*, *Chamaecrista fasciculata*, *Echinacea angustifolia*, *Brassica rapa, Arabidopsis lyrata, Rhinanthus minor, Protea sp.*, *Arabis alpina*, or *Trifolium repens*. However, these species have similar biologies, and we do not believe that including these species would have altered the overarching conclusions. Below, we assess similarities and differences in the characteristics of our organisms and provide suggestions for future work that can address pertinent knowledge gaps.

Our focal species demonstrate several commonalities that also characterize the literature on organismal responses to changing climates (Table 1). Notably, all species besides *A. thaliana* are native to North America, and all species inhabit seasonal environments in the temperate zone. This bias is likely caused not only by the gap in research funding between global north and south but also because of how we prioritized a specific type of climate response research. This review focused on organismal and evolutionary responses within individual species, which often necessitate approaches (e.g. deep sampling from natural populations and common garden or manipulative experiments) that impose financial and logistical constraints. A broader world-wide focus has used observational data to evaluate changes in abundance or phenology within plant populations or communities. There are substantial overlaps in the conclusions from our focal species and these other studies, for example clear shifts and often lags in phenology (Cleland *et al.*, 2007; CaraDonna *et al.*, 2014; Piao *et al.*, 2019). Connecting our population-level data with these community ecology studies could guide conservation and management decisions and provide information on holistic responses that drive changes in ecosystems. For instance, if the demography of our focal species (or other model species) parallels changes in abundance and richness of other community members, there could be simplified decision-making on which populations to target for conservation action.

The species chosen for this review are generally both widespread and locally abundant. Exceptions include *C. xantiana*, which is locally abundant but has a relatively limited distribution in south-central California, and *A. thaliana*, which is often locally rare but geographically widespread. As with most widespread species, these species may have substantial range-wide levels of genetic and phenotypic diversity relative to species with more limited ranges (Enquist *et al.*, 2019; Boyd *et al.*, 2022). Our focal species, except for *A. gerardii* and *P. virgatum*, also span impressive elevational gradients, likely reflecting either a priority to study species within climate-change-threatened subalpine and alpine environments or because these systems were logistically feasible models for studying local adaptation. However, we may miss important species declines or unique climate responses across non-mountainous ecosystems. Since environmental conditions are more uniform across flatter ecosystems, declines of a species could impact large areas and could have important ecosystem level consequences, e.g., prairie carbon sinks. Our species, aside from *A. gerardii*, *P. virgatum*, and arguably *M. guttatus*, are also not considered dominant species in their ecosystems. By focusing on these models rather than on the systems most important to ecosystem function, we may miss the species declines that influence ecosystem services.

Our species encompass a wide variety of organismal characteristics (Table 1). We have variation in life-history strategies including obligately annual species (*A. thaliana*, *C. xantiana*), species with both annual and perennial forms (*M. guttatus*), short-lived perennials (*B. stricta*, *M. cardinalis*, *I. aggregata*), and long-lived perennial species (*A. gerardii* & *P. virgatum*). There is variation in reproductive strategy (degree of selfing vs outcrossing), dormancy and seed bank duration, and flowering cues (i.e. photoperiod and vernalization responses). These are likely critical phenotypes for predicting climate change responses, and the responses we observe in the model species previously can serve as predictions for nonmodel species with similar characteristics. However, interestingly, these species characteristics are not strongly linked with similarities or differences in climate change responses in our focal species – with the caveat that we only examine eight species. Future comparisons need to focus on accumulating studies across many species with similar experimental designs.

### 3. Notable knowledge gaps

Knowledge gaps are largely caused by the limitations associated with the model systems or by the limitations or lack of methods available to examine climate change responses. We highlight four gaps, including the following: the lack of experiments identifying clear agents and targets of selection associated with climate change, limited information on species responses to extreme events, the role of seed bank dynamics within climate change responses, and determining the eco-evolutionary roles of biotic interactions in climate change responses.

While some model systems (i.e. *B. stricta* and *I. aggregata*) have excellent long-term manipulative experiments that demonstrate clear selective pressures and phenotypes likely to be selected in future climates, most other systems have not isolated the key agents and targets of selection in future climates (Wadgymar *et al.*, 2022). The previously discussed synthesis suggests that changes in water availability and growing season length are key for the focal species surveyed here, but this may not extend to species in different ecosystems. Additionally, there may be key interactions between agents of selection that we miss without manipulative experiments. For instance, snow-removal treatments in *B. stricta* reveal that nighttime freezing temperatures can be a key selective factor when snowmelt occurs earlier in the year (Jameel *et al.* in preparation). Costly and labor-intensive transplant experiments could be supplemented by using herbarium specimens collected across time within a particular location or across climate gradients to understand changing population dynamics (i.e. employing a space-for-time substitution; Kharouba & Williams, 2024, Perret *et al.*, 2024).

Extreme events are becoming increasingly frequent and severe (Diffenbaugh *et al.*, 2017; Kornhuber *et al.*, 2024). Multiple systems (*M. cardinalis*, *M. guttatus*, and *C. xantiana*) have taken advantage of extreme climate events to document responses to selection (Box 2), but we have a limited understanding of how populations will respond to extreme events of different magnitudes and durations across species ranges (Grant *et al.*, 2017). Studies in *M. guttatus*, *M. cardinalis*, and *C. xantiana* all suggest that spatial variation in evolutionary responses is not easily predicted (Box 2). Moreover, successive extreme events could have iterative effects on populations, with potential responses either dampened or enhanced by prior events. Manipulative experiments and experimental evolution studies could provide insight into future species responses. Long-term demographic studies have been used effectively within multiple different model systems (*M. cardinalis* and *I. aggregata*) and may be the only studies that can catch lagged impacts of climates on plant populations – impacts that have received increasing attention (Evers *et al.*, 2021). Additionally, long-term demographic datasets that capture extreme climatic events and subsequent population recovery are essential for fully testing predictions from evolutionary rescue theory (Anstett *et al.*, 2024). We note that these experiments can be more challenging in long-lived perennial species but are equally important as there may be critical differences in how annual and perennial species respond to changing climates.

A key black-box for many plant species is the existence of seed banks. Multiple model species have documented seed dormancy and seed banks (i.e. *M. guttatus*, *M. cardinalis*, *C. xantiana*, and *B. stricta*), but even these studies have limited resolution of variation over space and time. The role of seed banks as a buffer to population extirpation during extreme events will likely be important – especially for annual species that would need to depend on yearly fecundity with limited seed banks (Cohen, 1966). However, seed banks may also act to limit evolutionary rescue within populations or create lagged responses to selection events (Templeton & Levin, 1979). Continuous population-level monitoring and time series of allele frequencies within populations can provide any idea of the limitations and extent of the seed bank (*C. xantiana* studies). Likewise, these same studies may be informative for transitions between life stages that are difficult to observe, such as early-life survival and establishment.

Species interactions can make a substantial difference in the outcomes for a population or for ecosystem services (Hamann *et al.*, 2021a). Indeed, we find that biotic interactions play clear roles in patterns of adaptation, hybridization, and species range limits for several of the previously discussed model systems. However, it is less clear how the herbivore and pollinator communities will shift with changing climates and the relative extent that abiotic vs biotic selection pressures will play in shaping species responses (but see Campbell *et al.*, 2022b, for an example using *Ipomopsis*). Including realistic biotic interactions in field studies is challenging, both because additional manipulative treatments exponentially increase the sample sizes of experiments and because precisely manipulating the diversity and abundance of community members is nearly impossible. In reality, many common garden experiments (whether provenance studies or reciprocal transplants) often remove competition and/or alter biotic interactions in order to simplify large and logistically challenging experiments (Hargreaves *et al.*, 2020). While including more realistic ecological interactions would likely improve our assessment of how species respond to changing climates, changes in the abundance or evolution in individual plant species also impact communities and ecosystem dynamics – a link that is important to managers (Vahsen *et al.*, 2023). One way forward is leveraging ecological studies, including those conducted at LTERs, NEON sites, or field stations, to better understand changing species interactions and the ecological impacts of focal species declines (Cocciardi *et al.*, 2024). Notably, all of our model species are found on at least one NEON site.

## XI. Conclusions and a path forward

In this manuscript, we have summarized the conclusions from multiple decades of research on climate responses in eight prominent herbaceous species. Despite substantial differences in organismal biology, our focal species have remarkably similar climate change responses, including population declines or maladaptation likely related to climate change in all species. Future researchers in these focal systems must seek to identify mechanisms – highlighting key climatic factors underlying declines or maladaptation and working toward more predictive models.

Efforts within these species are not enough – there are clear biases in the species chosen that may hide risks to narrowly distributed and/or rare species. A clearer focus on dominant herbaceous species within ecosystems will also provide more insight into how responses of individual species resonate across communities and ecosystems, as well as a comparison to the extensive literature from the tree community. Efforts to combine resources and synchronize experiments across focal species research communities will be valuable as we evaluate to what degree climate change responses are predictable.

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## Competing interests

None declared.

## Author contributions

NJK conceived the project and coordinated the synthesis. NJK, JTA, ALA, MLA, DRC, ME-A, TEJ, DAM, JDN and SMS wrote first drafts of their own sections and contributed to the revision of the manuscript.

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## Data availability

There is no original data associated with this manuscript.

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