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Contemporary Evolution, Range Limits, and Climate Change: An Investigation of Population Adaptation across Species' Ranges

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Contemporary Evolution, Range Limits, and Climate Change: An Investigation of Population Adaptation across Species' Ranges

A dissertation in partial satisfaction of the requirements for the degree of

Doctor of Philosophy

in

Environmental Systems

by

Lillie K Pennington

Committee in charge:

Professor Erin Hestir, Chair
Professor Jason Sexton, Advisor
Professor Emily Moran
Professor Carolin Frank

2023

The Dissertation of Lillie K Pennington is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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2023

To my family, whose love and support I can always feel, wherever I go and whatever I do.

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Okay now let's get to it!

Curriculum Vitae

EDUCATION

Ph.D., Environmental Systems, University of California, Merced. 2017 – present
Focus: Plant adaptation to climate change. Advisor: Dr. Jason Sexton

B.S., Biology, Oklahoma City University. 2015
Magna Cum Laude and Cum Honore. GPA: 3.8/4.0

SELECTED RESEARCH AND PROFESSIONAL EXPERIENCE

Graduate Student Mentor, Summer Undergraduate Research Institute. May – August 2022

- Provide technical assistance, advice, and guidance to a group of 16 undergraduate researchers on their summer research projects, keeping in line with program policies and resulting in 10 students receiving employment offers from their labs in the fall
- Plan programming for students to teach them skills for excelling in undergraduate research and in graduate school, such as searching for graduate programs and funding, presenting research, interacting with principle investigators, and managing lab conflict
- Review student projects and presentations for compliance with program guidelines

Mentor, Competitive Edge Summer Bridge Program, UC Merced.
May – August 2018

- Manage summer programming for a group of 18 incoming PhD students from underrepresented groups

Graduate Student Researcher, UC Merced
June 2017 – August 2023

Advisor: Dr. Jason Sexton

General Lab

- Coordinate and mentor a team of five undergraduate students on research projects, including managing conflict between students as they arise
- Perform statistical analyses on data in R for four publications in preparation
- Attend symposiums on genomic data analysis, La Kretz at UCLA and Summer Institute for Statistical Genetics at UW
- Collaborate with other lab members on two publications in preparation, with one being published
- Present research to academic professional, student, and casual audiences
- Conduct literature searches for publications to be published in scientific journals

Lab Safety Coordinator

- Evaluate lab compliance with Environmental, Health, and Safety (EH&S) department standards
- Perform lab audits with EH&S supervisors to determine consistence with EH&S standards
- Resolve any compliance issues found during lab safety audits
- Coordinate and facilitate lab safety trainings for undergraduate and graduate lab members

Native montane plant adaptation project

- Implement two field common garden experiments with 3 gardens and 900 individual plants per garden to understand climate adaptation in response to drought
- Train and organize undergraduates in field techniques, data collection, and naturalist skills
- Conduct growth chamber drought experiment and collect daily phenology data from over 2000 individual plants from 9 populations to determine plant adaptation to drought

Threatened and endangered vernal pools grass project

- Train undergraduates in lab techniques
- Troubleshoot DNA extraction using a CTAB protocol for rare and endangered vernal pool grasses
- Collaborate with researchers at University of California, Santa Cruz

Intern. Chicago Botanic Garden Conservation Land Management Program, Medford OR.

Supervisor: Stacey Johnson March – September 2016

- Organized rare plant sites to maximize efficiency for site revisits
- Identify plants in field situations to determine community composition

Intern. Chicago Botanic Garden Conservation Land Management Program, Susanville CA.

Supervisor: Valda Lockie June – October 2015.

- Identified and collected seeds from native plant populations for the national seed bank through the Seeds of Success program
- Ensure that seed collections were collected and stored in compliance with Seeds of Success guidelines
- Coordinate monitoring for special conservation project for buffaloberry trees including compliance with NEPA standards
- Identified and monitored special status plant populations
- Coordinate digitization of herbarium samples

Summer Research Intern, UC Merced

Mentor: Dr. Jason Sexton June—August 2014

- Designed an independent research project on the effect of the Rim Fire on White Fir seedling germination in Yosemite National Park
- Analyze data in R to determine differential seedling recruitment according to burn severity

Summer Research Intern, Boston University.

Mentor: Dr. Pamela Templer June – August 2013

- Collected gas samples at Hubbard Brook Experimental Research Forest using static closed chambers and a syringe
- Run samples through a gas chromatograph
- Analyze data in Excel creating baseline gas release graphs for a long-term experiment

Research Assistant. Oklahoma City University, Biology Department.
Mentor: Dr. Laurie Kauffman August 2012 – May 2015

- Collaborate with three member team for ongoing primate research
- Attend lab meetings and lead meetings on data analysis in R and Excel
- Collect data on primate behavior from two orangutans at the Oklahoma City Zoo
- Analyze data to determine baseline behavior to compare future behavior after zoo expansion

PUBLICATIONS

Shay, JE, **Pennington, LK**, Montiel-Molina, JAM, Toews, DJ, Hendrickson, B, Sexton, JP. Rules of plant species ranges: applications for conservation strategies. (2021). Frontiers in Ecology and Evolution, p.664.

Pennington, LK, Slatyer, RA, Ruiz-Ramos, DV Veloz, SD and Sexton, JP. (2021). How is adaptive potential distributed within species ranges?. Evolution, 75(9),.2152-2166.

Dickman, EE, **Pennington, LK**, Franks, SJ, & Sexton, JP (2019). Evidence for adaptive responses

to historic drought across a native plant species range. Evolutionary Applications, 12(8), 1569-1582.

Pennington, LK and JP Sexton. Species Range Limits. Encyclopedia of Biodiversity. Invited article. In review.

Shay, JE, **Pennington, LK**, Toews, DJ, Sexton, JP. "Adaptation and fitness variation is highest near the cold-climate limit of a species range." *In preparation.*

CONFERENCES AND PRESENTATIONS

Pennington L., Sexton J. "A Tale of Two Experiments: How the CA drought affected natural populations of an endemic monkeyflower."

2021: **Invited talk.** Sierra Streams Institute.
2021: **Invited class presentation.** Marymount California University.

Pennington LK, Dickman EE, Sexton JP. "Survival in a Drier World: A Study of Rapid Adaptation in Response to Drought in the Sierra Nevada Endemic Forb, *Erythranthe laciniatus*; *Or: What to Expect When You're Expecting Climate Change*".

2019: Northern California Botanists symposium. Second place winner in poster contest.
2019: **Invited talk**. Botany 2019. Demography of Alpine Plants symposium.

Pennington LK, Sexton JP. "The Effect of the 2013 Rim fir on White Fir seedlings in the Sierra Nevada Range".

2014: Yosemite Environmental Research Training symposium.
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Pennington LK, McCoy E, Kauffman L. "Orangutans: A Study of Activity and Play"

2013: Oklahoma City University Undergraduate Research PowerPoint contest.
2014: American Association of Physical Anthropologists conference, Calgary, Canada. Poster.

2014: Oklahoma City University Undergraduate Research poster contest. First place.

AWARDS AND HONORS

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    Editor-in-Chief. 2017-2019.
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Dissertation Abstract

Climate change is the greatest challenge facing all ecosystems on earth. It is expected to have variable effects on ecosystems, with species potentially facing a myriad of environmental changes across their ranges. Mediterranean climates are biodiversity hotspots marked by climate extremes, which will only be exacerbated by climate change. How climate change will affect plants in these ecosystems is an important question to pursue, as it will have implications for future rates of biodiversity. To understand range-wide effects on plants in response to climate change, we must first understand how species' ranges behave, in particular at range limits, as these are the areas of a species' range where expansion or contraction will occur. I provide a history of range limits research, an overview of how range limits are studied, and a small review of recent range limits work. Then, using the ecological model organism *Erythranthe laciniata*, I examined range-wide implications of the 2012-2016 drought in California, which was exacerbated by climate change.

I implemented a resurrection study, growing pre-drought and drought generation plants in a growth chamber environment, with four treatments testing for range-wide adaptation to drought, and the potential for adaptation to heat; treatments were based on climate predictions for the Sierra Nevada mountains. I found higher fitness for the drought generation in drought conditions, with a strong decline in fitness in the higher heat treatments in both generations. This study shows that adaptation to drought is possible but may not confer higher fitness in higher heat conditions.

Next, in a common garden resurrection study, I tested the fitness of pre-drought and drought generation plants from low, central, and high elevation populations in a reciprocal transplant experiment. The drought generation had higher fitness at the high garden, with the two generations having similar fitness at the central and low gardens. I found evidence of local adaptation in the high populations, while the low elevation populations had the lowest fitness in all gardens. This study shows limited adaptation to contemporary conditions, with the drought generation in the high garden showing the strongest adaptive response.

Finally, to understand how adaptation may vary across species' ranges, I and my collaborators performed a literature review and meta-analysis of range-wide quantitative genetic variation (QGV) studies. It has been theorized that QGV, and therefore adaptability, will be highest at the center of a species geographic and/or niche range, but we found little evidence to support this. This study highlights the need for more research into QGV variation across specie's ranges. Taken together, my dissertation work emphasizes the importance of understanding range-wide patterns of adaptation to climate change.

Chapter 1. Species Range Limits

1.1. Abstract

Species range limits are ubiquitous in the natural world– even “cosmopolitan” species aren’t found everywhere. The study of species range limits has a long history and is resurging in interest due to anthropogenically induced species range shifts. Here we provide a history of the study of species range limits, an overview of range limits research methods, and describe known ecological and evolutionary characteristics of limits while highlighting studies from across the tree of life.

1.2. Introduction

Every species has a geographic area beyond which they are no longer found—that geographic area is that species’ range. Ranges can be bound by geographic features such as rivers, mountains, or oceans, but many are bound by environmental limits like temperature and precipitation, known as the species’ “niche.” The edge of the range is known as the range limit, and populations there often experience unique environmental pressures compared with more central parts of the species range. The unique environments at range limits allow scientists to understand the evolution of tolerance to environmental pressures, the ability of species to adapt or not adapt to varying conditions, and in a more contemporary sense, how changing climates can impact species at the limits of their climate niche.

The range limit is the area beyond which a species can no longer produce viable individuals, whether due to reduced fitness or other factors that limit colonization. Populations at geographic range limits are often called “marginal,” “peripheral,” or “edge” because they exist at the margins of the species range. Note that these terms are sometimes applied to populations existing at the environmental extremes of a species’ distribution or niche, but not necessarily at geographic margins (e.g., very high elevations in the center of a species’ range). In this article, we focus mainly on geographic species range limits. Species ranges can be disjointed, but marginal populations are those at the furthest limit of the range. Ranges can be said to be at equilibrium, indicating that their borders are not shifting (Gaston 2003), but perturbations and evolutionary adaptation can cause ranges to contract or expand, in a process called range shift. Climate change (global warming) is facilitating range shifts– making some parts of the range uninhabitable while opening new areas for colonization (Araujo 2005).

The areas where a range is expanding, or where conditions are becoming favorable even if expansion has not yet occurred, are known as the leading edge of the range. The areas where contraction is more likely, or where conditions are becoming potentially less favorable, are known as the rear edge. For example, in montane species the leading edge is often the higher elevation edge of the species range, and the lower edge of the range is the rear edge (Figure 1). The different edges are hypothesized to have different characteristics—the rear edge may be more impacted by heat-related stress and may show strong local adaptation (Hampe and Petit 2005), whereas the leading edge is impacted by cold stress, is expected to exhibit population growth, and is more likely to be populated by founder events and to be the source of dispersal leading to range expansion (Hampe and Petit 2005).

Ecologically, range limits often match niche limits (Hargreaves et al 2014), meaning that environmental tolerance sets species’ ranges, and niche breadth, or the range of resources a species can use, does tend to correlate well with range size—the greater the niche breadth, the larger the species range (Slatyer et al 2013, Papacostas and Freestone 2016). However, biological interactions and dispersal limitations do play an important role in establishing range constraints (Louthan et al 2015), thus potentially creating mismatches between a species' niche and its realized distribution. Multiple factors can interact to form species ranges (Holt and Keitt 2005), and there is no single unifying factor that explains why every range has a limit (Willi and Van Buskirk 2019).

In this chapter, we highlight major methods in studying range limits, what we have learned so far from range limits studies, and new topics in range limits research. By the end of this chapter, the reader should understand how populations at range limits may differ from more interior populations and how the inclusion of marginal populations can enhance a research program.

1.3. A history of range limits research

Any hunter-gatherer, pastoralist, or farmer through human history likely recognized the important roles that abiotic (e.g., climate) and biotic (e.g., predators) factors play on distributions of plants and animals, and that all species cannot or do not occur everywhere. Thus, humans have long understood the limitation of species, and the finiteness of species distributions. However, the scientific study of species range limits began as early discussions on what limits species distributions in the early 19th Century. Von Humboldt and Bonplan (1807) discussed the great variety of plant species' geographic distributions on Earth and discussed how aspects of climate (e.g., temperature and rainfall) vary across elevational and latitudinal gradients, and how this variation must contribute to plant distribution limits. Merriam (1894) later formalized and extended these concepts and addressed the role of climate in limiting animal distributions. Darwin (1859) and Wallace (1876) also frequently mentioned the importance of range limits to species distributions, and Darwin formulated hypotheses and predictions about how biotic and abiotic factors may affect warm and cold climate limits in different ways (see below).

At the turn of the 20th century, biologists began to frame formal studies examining species and clades in terms of their geographic centers of distribution and abundance (e.g., Adams 1902; Transeau 1905). However, formal study of phenomena at species range limits to test hypotheses about general patterns or mechanisms did not come until later in the 20th century. Griggs (1914) represents one example of a study on range limits, focusing on abundance patterns at the edges of many plant species ranges in the American Midwest and relating these abundance patterns to species interactions (i.e., plant competition) as potential determinants of range limits. Joseph Connell's (1961) study of the intertidal limits of barnacle species is a classic example testing abiotic and biotic mechanisms, but on a local scale of limitation along an environmental gradient.

Throughout the middle part of the 20th Century, range limits science was still in its infancy, but general theories (Table 1) and conceptual models (Table 2) were being developed to address important questions about the ecological and evolutionary causes and consequences of species range limits. A central theory of interest, the Abundant Center Hypothesis (ACH), developed from the idea that species may have their highest abundance, fitness, and population growth rates near their distribution centers, where conditions are assumed to be most favorable; the history of the rise of the ACH is described in Pironon et al. (2017). The ACH reached near-paradigm or rule status and influenced important hypotheses regarding what occurs near species borders, including biogeographic models for speciation such as peripatric speciation (Mayr 1963) and the role that gene flow may play on the formation of range limits (Haldane 1956). Darwin (1859) proposed the idea that colder climate limits should be set more by abiotic stress and warmer limits should be set more by biotic stress. This hypothesis has contributed to ecological theories regarding what an ecological niche is—the environmental and resource parameters a species needs to fulfill its life history (Hutchinson 1957)—and how trade-offs between different factors and opposing adaptations at different ends of niche gradients expressed on the landscape (as range limits) may limit a species' ability to expand geographically (MacArthur 1972). Additionally, how environmental variation changes through time and geographic space may shape range limits in predictable ways, thus ultimately affecting rarity or geographic range size (Janzen 1967). In the latter half of the 20th century and beyond, theoretical studies on the expansion of populations and the formation of species range limits led to the refinement of models to include various factors (reviewed in Sexton et al. 2009) such as how genes or populations spread (Skellam 1951), evolutionary dynamics across spatial and temporal heterogeneity (Levins 1968), the role of gene flow on adaptation at range limits (Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997), and how biological interactions, gene flow, and selection may interact to form limits (Case and Taper 2000).

By the late 20th century, many studies of empirical and theoretical work on species range limits had been conducted or were underway. Studies such as surveys, observations, and experiments of natural populations across species ranges that compared central areas to marginal areas (e.g., Prince and Carter 1985) allowed for tests of the mechanisms behind distributional limits as well as controlled comparisons of parameters such as abundance, fitness, growth rates, and genetic variation in different areas of species ranges. Discussions of the causes of—and phenomena at—species range limits from earlier work allowed for syntheses that provided many testable hypotheses for both empirical and theoretical investigations (e.g., Antonovics 1976, Hoffmann and Blows 1984, Gaston 2003, Bridle and Vines 2007). Moreover, observations on the attributes of species ranges, and of populations in different parts of species ranges, led to an explosion of studies that form the basis of biogeography and macroecology (Rapaport 1982; Brown and Gibson 1983; Brown 1984; Brown et al. 1996).

By the early part of the 21st century, enough data on the essence of species ranges had become available to develop further syntheses, reviews, and meta-analyses to search for generalities about species ranges and range limits (Gaston 2003; Sexton et al. 2009; Pironen at al. 2017; Shay et al. 2021). These works address our current knowledge on many species range limits topics, including the generality of the ACH (Sagarin and Gaines 2002; Sexton et al. 2009; Pironon et al. 2017; Dallas et al. 2017), whether species range limits represent species niche limits (Hargreaves et al. 2014; Paquette and Hargreaves 2021), how genetic variation is distributed within geographical ranges (Eckert et al. 2008; Pennington et al. 2021), patterns of adaptation across species ranges (Angert et al. 2020; Bontrager et al. 2021), and the role of gene flow at species range limits (Kottler et al. 2021). Nevertheless, much is left to learn, and studies continue today, leveraging a combination of state of the art (e.g, genomic, informatic, modeling) and classic methods (e.g., field surveys and experiments).

1.4. How are range limits studied?

Range limits can be studied in a variety of ways, depending on the scientific question and the species of interest. Rangewide studies can be employed to understand how populations perform at range limits as compared to the rest of the range, and to investigate possible local adaptation or unique attributes that exist at the limit. For the most part, factors that can affect range limits include decreased fitness beyond the range, whether that is due to abiotic or biotic factors, and dispersal limitations, both of which can result in range equilibrium or stasis. Studies of how range limits are maintained will address these factors. In plants or other sessile organisms, beyond-range studies are used to determine factors that govern range limits, whether species can exist past the established limit or not, and to determine why. For more mobile organisms, such as many animals, it is harder to study individuals beyond the range (discussed below), but environmental modeling can be used to shed light on the forces at work in setting range limits.

1.4.1. Rangewide studies including marginal populations

Range limits are often studied in a comparative context relative to the full range or more interior or central areas of a species range. Population parameters of interest can vary across species, depending on a researcher’s focus, and often more than one metric is measured to determine population attributes. For instance, rangewide studies are valuable for studying local adaptation to a variety of environments across a species range. Since marginal populations often experience the most extreme climates of a species range, unique phenotypic adaptations may be found there, shedding light on the nature of physiological limits of the species.

Implementing a rangewide study can be a daunting task, even for species with restricted ranges. First, the species’ range must be delineated, either through modeling or aggregating occurrence records. Populations at range limits must be identified, as well as other populations across the range; target traits to be measured across the range will vary by question (e.g., fecundity traits like seed count or litter size). A classic way to compare performance across the range is to perform a reciprocal transplant study. Reciprocal transplant studies in a rangewide context should incorporate populations from across the species range, including the limits. Individuals from each population will be moved to each of the other populations, or to particular populations representing test environments (aka “common gardens”) of interest. Differences in performance among populations at different sites (aka genotype by environment interactions) can reveal local adaptation and measuring a range of traits can reveal unique genetic, population-based attributes.

Transplant studies are common in plants—for instance, Hargreaves et al (2017) tested edge populations in a variety of habitats to understand how different phenotypes from across the range respond to different environmental conditions. This study, which is also a beyond-range study (see below), highlights the importance of local adaptation in survival across a species range and suggests that a species' leading edge may not always be able to expand into environments that are warming under climate change.

Transplant studies are less common in animals since they are mostly mobile. Transplanting mobile species into natural environments is often prohibited, due to concerns for the spread of disease and because it could be difficult to remove the species at the end of the study. In a recent study of the streamside salamander, *Ambystoma barbouri*, Micheletti and Storfer (2020) used a reciprocal transplant study to understand how gene flow impacts range equilibrium for this species, in part by studying local adaptation across the range. To limit interactions with native individuals, they used a mesocosm design with salamanders living in aquariums placed at the site. They called this a "semi-realistic approach," to understand local adaptation in the salamanders without affecting the natural populations. In studying how individuals fared in populations outside of their home range, they found that marginal populations performed better than central populations at range limits, but that in some cases marginal populations performed better overall at central populations. Such experiments illustrate that limits to local adaptation because of general characteristics of marginal populations are not necessarily the limiting factors creating range limits. Nevertheless, range dynamics are complex, and this study shows that multiple factors can impact range limits.

Common garden studies, like transplant studies, can reveal general adaptation patterns. A common garden study does not necessarily require that plants be grown in or near an existing population– individuals from different areas of the species range can all be grown together at the same location. There can be more than one garden—indeed, although reciprocal transplant studies would reveal population-level adaptation to specific locations, including multiple populations and having gardens at different climate zones can reveal adaptive relationships between climates in which populations originate, and the destination climates of the test gardens. For example, finding that fitness declines as climate differences increase between the climates where populations originate and the climates of test gardens indicates a pattern of local adaptation (e.g., Bontrager and Angert 2018).

Common gardens can also be employed indoors. A study of the cutleaf monkeyflower, *Erythranthe laciniata* (formerly *Mimulus laciniatus*), utilized growth chambers to grow individuals from across the range and included marginal populations to understand how a historic drought differentially affected populations (Dickman et al 2019). The study was a rangewide resurrection study, growing plants from seed collected in 2005 (before the drought) and 2014 (the height of the drought). The study found differences in germination and flowering time both across the range and between generations, finding that low elevation and drought-generation plants emerged earlier and that rapid adaptation can occur in a self-fertilizing plant with a restricted range, including at range limits.

1.4.2. Beyond-range studies

Beyond-range studies can be used to determine how range limits are formed and maintained. Whereas reciprocal transplant studies can reveal adaptation and unique population properties found across the range, beyond-range studies establish populations outside of the natural species range to determine how and why that range boundary is maintained–whether through dispersal limitations, ecological limitations like competition or a lack of pollinators, or physiological limitations (Holt and Keitt 2000).

In a long-term, beyond-range study (rare, as most beyond-range studies only take data for one growing season), Cross and Eckert (2021) were able to track population success beyond the range of the beach evening primrose, *Camissoniopsis cheiranthifolia*. They originally planted a beyond-range population in 2005 as part of a rangewide reciprocal transplant study, only to find that their plots were expected to be part of a planned prescribed burn three years later. Nevertheless, they found that not only had their experimental plots not been burned, but that the beyond-range population was thriving fourteen years later. Using the total number of buds, flowers, and fruits at time of sampling as a measure of performance, they found that the beyond-range population did not have reduced performance when compared to the rest of the range. They also found the beyond-range population to have similar density as compared to the rest of the range. Thus, the range limit is not likely to be maintained by low fitness. In fact, northernmost populations had higher fitness at the beyond-range site than at their home climate. This suggests that the range limit is maintained by some other process, such as dispersal limitation, and that global warming may be facilitating a range expansion in northern areas of the species range.

1.4.3. Environmental modeling and range limits

Environmental niche models, also known as species distribution models (SDMs), are a common method used in estimating factors that contribute to species ranges (Elith and Leathwick 2009). In animals, the factors that contribute to range equilibrium are not as straightforward to test– beyond-range transplant studies are uncommon. Various types of modeling can be employed to better understand factors governing range limits in all organisms and are often used in a range-wide context. As animals are mobile, and thus potentially less dispersal-limited, they would be expected to better track changing environments and to seek out habitable areas—although, critical species interactions can still limit animal range expansion. In this vein, the area beyond which an animal may no longer be found may approximate its niche limits. But does it?

In one example of niche modeling to understand range limits, Graham et al (2010) used climate envelope modeling (CEM) to estimate factors that affect range limits of birds in the Andes mountains of Colombia. This study included two levels: determining what affects range occupation of birds for the whole of the Colombian Andes, and what affects range occupation in subsections of the Andes defined by groups of mountain ranges called cordilleras. The team constructed CEMs for 70 bird species whose ranges were restricted to the Andes and mapped the CEM predictions onto the actual ranges of the birds. They found that in most cases, bird ranges were not covering every area deemed habitable by the CEMs across the whole Andes, whereas in the cordilleras, ranges did track the areas predicted with the CEMs. The researchers concluded that for the Andes as a whole, dispersal limitation may be the most important factor for range limits– although competition cannot be discounted since CEMs are unable to include species interactions (i.e., they estimate the realized niche, or the environment in which a species is observed). Nevertheless, for the smaller cordilleras, which are isolated from each other, environmental factors may be sufficient to explain limits. Overall, this study reveals that factors contributing to range limits at a broad scale may be different than the factors at finer scales, lending another layer of complexity to understanding the causes of range limits.

Modeling also reveals that not all range limits are equal. To understand what factors constrain the ranges of three closely related species of freshwater copepods in northeastern North America whose ranges do not overlap, Thum and Stemberger (2006) modeled what abiotic, biotic, or population history factors best explain the species' range limits. As the non-overlapping ranges are suggested to be maintained by isolation and limited dispersal capabilities, the researchers determined how much each factor contributes to the maintenance of the copepod's range limits, specifically why some species are only found in certain lakes. They were able to determine that while environmental factors account for most, but not all, of the species' ranges, one species range was better explained by environmental factors (e.g., water clarity, pH, and depth), whereas the other two were better explained by biogeographic factors such as historical connections between lakes. This study illustrates how range limits can be maintained by different factors even in closely related species, and further shows that environmental factors are not always the main determinant of range limits.

Another type of niche modeling is mechanistic niche modeling. Whereas traditional niche modeling correlates environmental traits with species distributions, mechanistic modeling incorporates specific physiological trait responses to the environment into the model. Theoretically, this should yield both a more intuitive explanation of the causes of range limits as well as stronger predictive power about potential range shifts (Kearney and Porter 2009). In an example of range shift prediction, Thomas et al (2012) used mechanistic niche modeling to model range shifts in ocean phytoplankton. The researchers aggregated temperature-related traits from published studies across a large latitudinal gradient and used mechanistic modeling to infer how phytoplankton populations would respond to warmer future ocean water. They predicted that by 2100, a wide variety of phytoplankton in tropical waters will not be able to persist, which supports the idea that tropical species are more sensitive to warming temperatures– effectively causing rapid shifts in range limits.

It should be noted that while SDMs are commonly used to predict species occurrence, and therefore their ranges, their accuracy has been questioned. In a review of SDMs that were assessed for accuracy, the models were accurate only 50% of the time and may be better suited for hypothesis testing and should be confirmed before use for things like conservation planning (Lee-Yaw et al 2021). At range limits, modeling may be more accurate (Lee-Yaw et al 2016), but species occurrence should be confirmed with occurrence verifications (i.e., ground truthing).

1.5. Range limit ecology

Ecology is the business of understanding the patterns and causes of the abundance and distribution of organisms, their relationships to each other and their environment, and how emergent properties of these phenomena create larger patterns such as ecosystems and biomes. One grand aim of range limits ecology is to define those factors that describe the niche of a given species. Many studies work to detect signals of abundance reductions that signal range limits, such as reduced population growth rates, population density, fitness, or any measure of species or population health that can predict the presence or absence of that species. This is the business of detecting a true range limit, rather than a barrier to dispersal or limiting interactions.

Just as abiotic factors, such as temperature, directly and indirectly influence species abundances and distributions, species are directly and indirectly influenced by the presence or absence of other species. These biological interactions are thus also essential drivers in setting species range limits and are the reason that species range limits are often not found exactly at the edges of the environmental envelope in which a species could live (aka the fundamental niche). Biological interactions set the "realized niche" (Hutchinson 1959), either reducing a species' fundamental niche or its potential range (through negative interactions such as competition or predation) or expanding a species' range (through positive interactions such as provisioning resources or extending tolerances). Thus, interactions between biotic and abiotic factors can determine distribution limits. As mentioned earlier, Darwin hypothesized that abiotic factors should be more limiting at the colder edge of species' distributions (think freeze stress), but that biotic factors should be more limiting at the warmer edges of distributions since there are more species to compete with or escape from in warmer climates (e.g., high species diversity in the tropics). There are strong signals that this pattern generally holds (Paquette and Hargreaves 2021), and it is also true that biotic interactions (positive and negative) are important and in need of study in all areas of species' ranges (Shay et al. 2021).

Biological interactions can have strong implications for range limits, which includes symbiotic relationships with fungi. Fungal interactions may play a large role in setting range limits, and including these interactions in studies will improve our understanding of range limits. In one example, a fungal symbiont was revealed to extend range limits of its grass host, *Bromus laevipes*, by thousands of square kilometers into dryer climates (Afkhami et al. 2014). Mycorrhizal relationships can similarly limit the ranges of plants (Swarts et al 2010), effectively indicating the range limit of the symbiotic fungal species where mutualisms are obligatory—and these relationships can limit the ability for plants to colonize new areas (Delavaux et al 2019). Fungal diseases have been shown to persist throughout their hosts' range and may also play a role in restricting ranges (Bruns et al 2018). However, mutualistic relationships may have a stronger impact on plant species and their ranges as climate change continues to alter environments; these relationships may insulate species from change and mitigate the potential damages that climate change may inflict on species' ranges (Afkhami et al 2014). Indeed, ectomycorrhizal fungi have shown resilience to warming conditions at their range edge (Mucha et al 2018), which may buffer their hosts somewhat against changing conditions—however, across North American pine forests, richness of ectomycorrhizal fungi is expected to decline due to increasing temperatures (Steidinger et al 2020). Leafcutter ants, who are obligate symbionts with the fungi they farm, express behaviors to insulate the fungus they farm from the cold in their more northern colonies (Senula et al 2022). Further variation in symbiotic relationships can be found at range limits of other species of leafcutter ants and show that fungi are able to disperse past the limits of the ants who farm them but are limited by the presence of their hosts (Mueller et al 2011).

Community boundaries could signal species range limits and vice versa, as species often influence the distributions of other species. The classic theoretical contrasts of Clements and Gleason on the nature of community assembly (i.e., holistic versus individualistic viewpoints, respectively) (summarized in Nicolson et al. 2002), and the subsequent work of others (e.g., Whitaker et al. 2001) taught us that species distributions do not usually tightly align with each other, with some notable exceptions, including some obligate mutualisms (e.g., senita cactus and senita moth; Fleming and Holland 1998). Thus, we don't expect tight fidelity among the distributions of all species within a community. However, there are often some important associations in the distributions of species, with certain species playing keystone roles that have a dramatic effect on their community. For such species, their range boundaries therefore signal an ecosystem boundary, even if these seem a bit "leaky" depending on the geographic scale sampled. There are many examples: Joshua trees (*Yucca brevifolia*) circumscribing the Mojave Desert (Wilkening et al 2022); mangroves converting and enhancing intertidal communities; elephants transforming entire landscapes and determining the presence or absence of other species (Haynes 2012).

Species are so varied in their niches, dispersal abilities, reproductive capacities, and vulnerabilities to disturbances, there is high variation in species' likelihood of range shifts, collapse, or expansion in the face of modern global change. There is a wide spectrum of range sizes, from tiny-ranged, specialized species, only found in one location (e.g., the Devils Hole Pupfish, *Cyprinodon diabolis*), to wide-ranging generalists (e.g., the Brown Rat, *Rattus norvegicus).* Species range fragmentation from habitat losses can cause rapid retrenchment of species range limits. Also, the shape of a species range, and whether originating from islands or continents, can have important effects on how range limits can shift. Moreover, population attributes, such as size or genetic diversity, are not often predictable based on range position alone. That is, it is possible for wide-ranging species to consist of small populations with low genetic diversity, and conversely, species with small ranges may consist of large populations with high diversity, depending on how widely a species' niche projects onto a resource landscape. Peripheral populations, counter to the abundant center hypothesis, often serve as important areas of refuge for species in decline or collapse (Lomolino and Channell 1995).

Understanding how all these factors may influence distributions can have an impact on species' conservation efforts. For instance, Stevens et al (2019) wanted to understand how different species of snook, a lineage of freshwater fish, could coexist in the same rivers despite having seemingly identical diets. They found that although snooks living in similar areas of the river often do have the same diet, they occupy different spaces of the river—that is, they partition the habitat to coexist. The researchers note that dispersal for some species of snook is limited by environmental factors. As climate change opens up habitat for these fish, they will come into contact with other snook species and will have to further partition habitat if they are to coexist.

1.6. Evolution and range limits

Marginal populations are interesting to consider in the light of evolution– they often experience the harshest conditions for the species, they may be either new colonizers or old glacial relics, and they can be more isolated from the rest of the range, experiencing gene flow from fewer environments. This section is an overview of work that has been done to understand the evolution and the genetics of marginal populations.

1.6.1. Inter- and Intra- population variation and adaptability at range limits

Heritability is the genetic variation in a population that natural selection can act upon, a population's adaptive potential. It is estimated and referred to in various ways (e.g., adaptability, evolvability broad- or narrow-sense heritability), but can generally be thought of as the proportion of phenotypic variation that is influenced by genes rather than environmental variation. As discussed earlier, species' range limits can coincide with geographic barriers, but where no such barrier exists the range limit can represent a limit to niche adaptation– that is, an inability to adapt to conditions beyond the range. It might follow that marginal populations would have low adaptive potential– but is that the case? How genetic variation varies across a species range is an open area of research. To date, no generalized pattern of variation has been found (Pennington et al 2021), meaning that the idea that marginal populations have low adaptability is not supported by empirical studies. Further research into heritability and other measures of adaptability in marginal populations is sorely needed—as these areas are most at risk of range contraction but are also where range expansion will occur due to climate change.

1.6.2. Hardy-Weinberg agents and range limits

Marginal populations have the potential to be affected by the agents or influences of evolution quite differently due to special eco-evolutionary circumstances at range limits and due to often greater isolation. The Hardy-Weinberg Principle (Hardy 1908, Weinberg 2008) characterizes criteria that would result in a population with stable allele frequencies, that is to say, no evolution; deviations from these criteria signal evolutionary change. The five criteria for such a population are that mating must be random and there can be no mutation, genetic drift, gene flow, or natural selection; collectively, these criteria are known as the agents of evolution. Below we discuss work that has been done in marginal populations to understand how populations at range limits are affected by evolutionary processes.

1.6.2.1. Non-random mating

Non-random mating is the result of some choice in the mating process—whether that be for individuals that display certain characteristics, individuals that are nearby, and other factors that result in certain phenotypes being more successful at mating. At range limits, inbreeding, or mating between close relatives, is a relevant factor of non-random mating. Inbreeding can be higher at range margins but this is not necessarily a disadvantage – inbreeding in plants allows for a level of assurance in reproduction and also may conserve local adaptation (Arnaud-Haond et al 2006). In some cases, however, inbreeding depression can reduce fitness (Garcia-Fernandez et al 2012). Therefore, it may be that inbreeding is more advantageous at expanding, leading edges of the range where conserving new adaptations to harsh conditions allows the expansion to continue, but is maladaptive at rear or contracting edges where low genetic variation due to low gene flow prevents adaptation to changing conditions (Garcia-Fernandez et al 2012). In plants, self-fertilization can occur at higher rates at range margins, and indeed may influence the formation of range limits by limiting dispersal (Sun and Cheptou 2012), especially in annual plants. For longer lived species, although there may be local adaptation at range margins, inbreeding does not necessarily increase (Chybicki et al 2014). For obligate outcrossing species, a lack of reproductive opportunities may be a driver of range limits, as a lone colonist would not be able to reproduce (Henry et al 2015). Work has also been done on sexual selection at range limits. For example, sexual selection may play a role in range expansion, or lack thereof, in damselflies (Dudaniec et al 2021). In a field study of sex differences across the species range of the damselfly *Ischnura elegans*, larger males were more likely to survive at the northern edge of the range but smaller males were preferred by females, contributing to the maintenance of this range limit.

1.6.2.2. Mutation

Much theoretical and empirical work has been done to understand the role of mutation at range margins. Species and populations can have different rates at which mutations occur, and deleterious, large-effect mutations do tend to be quickly purged from populations (Glemin 2003). However, mutations with low to moderate negative effects can persist, particularly in small populations experiencing enhanced genetic drift (Henry et al 2015). This is referred to as mutational load and may, along with the decreased genetic variation associated with drift (Peischl et al 2015), reduce the ability of a population to cope with environmental stress (Perrier et al 2022). Populations at range limits may experience higher genetic load or genetic drift if they are small and have decreased genetic variation, which can be further exacerbated by reduced connectivity and gene flow (Higgins and Lynch 2001). In large populations deleterious mutations are purged more readily; in small populations a build-up of mutations can result in population extirpation (Henry et al 2015). Thus, mutational load theoretically can influence the formation of range limits.

Empirical work has been done as well to understand the potential effects of mutational load on the formation of range limits. In *Arabidopsis lyrata*, a perennial plant, range-edge populations were found to have higher mutational load, decreased genetic diversity, and decreased fitness (Willi et al 2018). It was also found that leading- and trailing- edge populations harbor most of the mutational load for the species, which also tends to be self-fertilizing (Perrier, Sanchez-Castro, and Willi 2020). For species that have the ability to self-fertilize and which exhibit decreased genetic variation towards limits, it is possible that deleterious mutations play a role in maintaining those limits. However, as noted above, genetic variation and population size do not always decrease towards limits. In such species, it would be expected that greater rates of mutation would not influence range limits. Empirical work on mutation and range limits has, to the best of our knowledge, been limited to plants. In the work that has been done, increased mutational load at range margins results in lower fitness (Willi 2019). More work is needed to understand the role of mutations in animals, as well as in plants with varying geography and life histories.

1.6.2.3. Genetic drift

Genetic drift is a process by which the frequency of alleles in a population changes due to random chance. Genetic drift increases as population size decreases.

Recently, range limit theoretical research has included genetic drift as a key factor in the formation and maintenance of range limits (Polechová 2018). Empirical work supports this idea. For example, in Canadian hairstreak butterflies, marginal northern populations have a high signature of genetic drift (Keyghobadi et al 2020). For the highly self-fertilizing and widespread plant, *Arabidopsis lyrata*, populations with a greater history of genetic drift had reduced adaptability (Willi et al 2018). In a species of pearl oysters, edge populations exhibited greater genetic drift despite experiencing some gene flow from interior populations, suggesting strong, range-limiting drift effects in smaller edge populations (Lind et al 2007). Further, in a review of genetic variation studies, it was found that many species do exhibit signs of greater genetic drift in marginal populations (Eckert et al 2008). As ranges are shifting due to climate change and marginal populations experience new conditions, drift may play an even more important role in range limits dynamics.

1.6.2.4. Gene flow

Gene flow, or a lack thereof, is sometimes thought to be a key aspect of the formation of range limits– namely, that a lack of gene flow would limit a species' ability to adapt to new conditions and expand its range (Bridle and Vines 2007). Conversely, the genetic swamping hypothesis (Haldane 1956) suggests that gene flow from interior populations is maladaptive and results in failure to adapt to different environments. There is not a lot of support for the swamping hypothesis (Sanford et al 2006, Stanton-Geddes et al 2013, Kottler et al 2021), although see Fedorka et al (2012) and Tamagawa et al (2022) for examples of potential gene swamping at range limits in crickets and river snails, respectively. Conversely, however, there is substantial support for gene flow increasing fitness at range edges (Lopez et al 2009, Sexton et al 2011, Bontrager and Angert 2019). Further, gene flow can counteract the effects of small population size by increasing effective pop size, counteracting drift at range edges (Alleaume-Benharira et al 2006).

Regardless of the benefits of gene flow to marginal populations, gene flow rates are often lower towards range limits. Heterogeneous habitat may reduce gene flow across a species' range (Wang and Bradburd 2014, Sexton et al 2016) and indeed there may be environmental barriers to gene flow that are not obvious but still influence and enforce range limits (Micheletti and Storfer 2016). Across taxa, genetic isolation by environment (IBE) is the most common pattern of genetic isolation, with isolation by distance (IBD) being prominent as well, especially in plants (Sexton et al 2014), and marginal populations do tend to show differentiation from interior populations, indicating reduced gene flow (Hampe and Petit 2005, Eckert et al. 2008, Pironon et al 2017).

1.6.2.4. Natural selection

Natural selection is the broadest agent of evolution: any environmental pressure that influences survivorship and fitness in an organism is a selective force. At range limits, selective pressures may be different than at other points in the range, due to environmental differences and the concordance of the range limit with the niche limit (Gaston 2003). Indeed, selection is expected to be stronger and more directional at range limits, whereas in more interior sections of the range selection may be more stabilizing

(Sexton et al 2009). Temporal variation in an environment may also affect selection at range limits– beyond seasonality, stochastic departures from average conditions can alter demographics at limits through selection (Holt et al 2022). Empirical work suggests that selection is stronger at range limits (Angert et al 2020), and it remains an important area of future research as climates continues to rapidly change.

1.7. What can range expansions and invasive species tell us about range limits?

Species' range limits are not always stable, and range expansions and species invasions can inform our knowledge of range limits. As climates change, we are seeing an increase in range expansions, especially at cool edges of species' ranges where warming results in new habitat for species to colonize—but range expansions have happened in the absence of global climate change as well. Introduced, non-native species that spread aggressively are termed "invasive species." Understanding these two examples of range limits being overcome can help us to understand the complex interactions that can set limits.

Range expansion is a natural process that can increase a species range. In some instances, an event will influence a range expansion. In wasp spiders in Europe, northward expansion of the species range was associated with, and potentially facilitated by, a genetic admixture event (Krehenwinkel and Tautz 2013). Rapid adaptation to new range edge environments facilitates rapid range expansion (Szűcs et al 2017), potentially more important now with climate change. However, following expansion genetic drift may reduce genetic variation at these new range limits (Garroway et al 2011, Swaegers et al 2013). Range expansion can also be affected by abiotic factors. For example, the range expansion of racoons (*Procyon lotor*) in northern North America is facilitated by land use change and the creation of farms but is limited by the inability of raccoons to forage in snow (Walsh and Tucker 2018). So, even seemingly stable ranges can see an expansion at limits following genetic or environmental changes.

Invasive species are marked by the ability to rapidly adapt to new conditions and colonize new areas. The cane toad (*Rhinella marina*) was famously introduced to Australia as a biological pest control for crops before becoming a noxious invasive species that has threatened native biodiversity—and now has evolved thermal tolerance such that it has spread into areas in Australia that are much colder than areas it inhabits in its home range (McCann et al 2014). Other species evolve higher invasibility in their invasive ranges, such as the coastal invasive species *Gladiolus gueinzii*, which has evolved faster germination and increased dispersal ability in eastern Australia (Tabassum and Leishman 2018). However, some species are bound by dispersal limitations in their invasive ranges despite rapidly adapting to new environments (Sanderson et al 2015). Overall, invasive species don't necessarily represent the ability of all species to rapidly adapt to and thrive in new conditions (Moran and Alexander 2014), but are special cases that help us to better understand the factors that limit a range.

1.8. Climate Change and Range Limits

Range limits are not insulated from the hottest topic of our time: climate change. Climate change has the potential to disrupt ranges that were previously more stable and cause rapid demographic changes. As conditions change, populations at range limits may experience a higher magnitude of change than their interior counterparts. One consequence of this rapid change is that ranges can expand or contract.

Range expansions and contractions necessarily start at range limits. Populations at cool-edge limits, when locally adapted, may harbor the necessary genetic variation to colonize new areas as they become more habitable– however, at warm-edge limits populations can be more at risk of extirpation due to anthropogenic activity and increasing temperatures (Rehm et al 2015). In montane habitats, range expansion is only possible up to a point: whereas some species are able to expand their ranges, high elevation species sometimes retract and lose populations at their limits (Moritz et al 2008). Further, favorable conditions beyond the range may not ensure range expansion– expansion may be hindered or facilitated by novel microbial communities if native communities cannot shift at the same rate (Benning and Moeller 2020, Stanton-Geddes and Anderson 2011). Additionally, range shifts may be constrained by asynchrony in the case of biotic interactions (Stewart et al 2022, Alexander et al 2022); e.g., plants not shifting with their pollinators. Novel communities will form as a consequence of range shifts, and these interactions will play an important part in determining the success of range expansion (Descombes et al 2020). Creating models to more accurately predict range shifts that include species interactions is an active area of research (e.g., Romero-Mujalli et al 2019, Walsh et al 2019, Lancaster 2022) and will be important for conservation as climate continues to change.

1.9. Conclusion

The study of range limits continues to be a growing field, partly since the forces behind range equilibrium are complex and require much more study. Often, species ranges are maintained by multiple factors, which can vary not only among species but between range edges within a species. The different methods of studying range limits, from quantifying traits to understanding limit maintenance, all include important avenues of research. Range limits work is gaining new significance due to rapid climate change– populations at limits may be experiencing more stress from changing conditions and can signal how populations will fare in new climates. New work will add to and expand existing knowledge (Table 3). There is work to be done in any study system– from microbes to plants to animals, and we need a more comprehensive understanding of the forces that influence limits across systems and if there are generalizable patterns in these forces.

Range limits, how they are maintained, and how they shift, are important for questions of biodiversity as well. All species have ranges, and the overlap of those ranges creates communities. The maintenance of range limits is important to the stability of communities– and how populations at range limits respond to climate change has further implications for community composition. The study of range limits will continue to provide vital insight into earth’s changing biodiversity.

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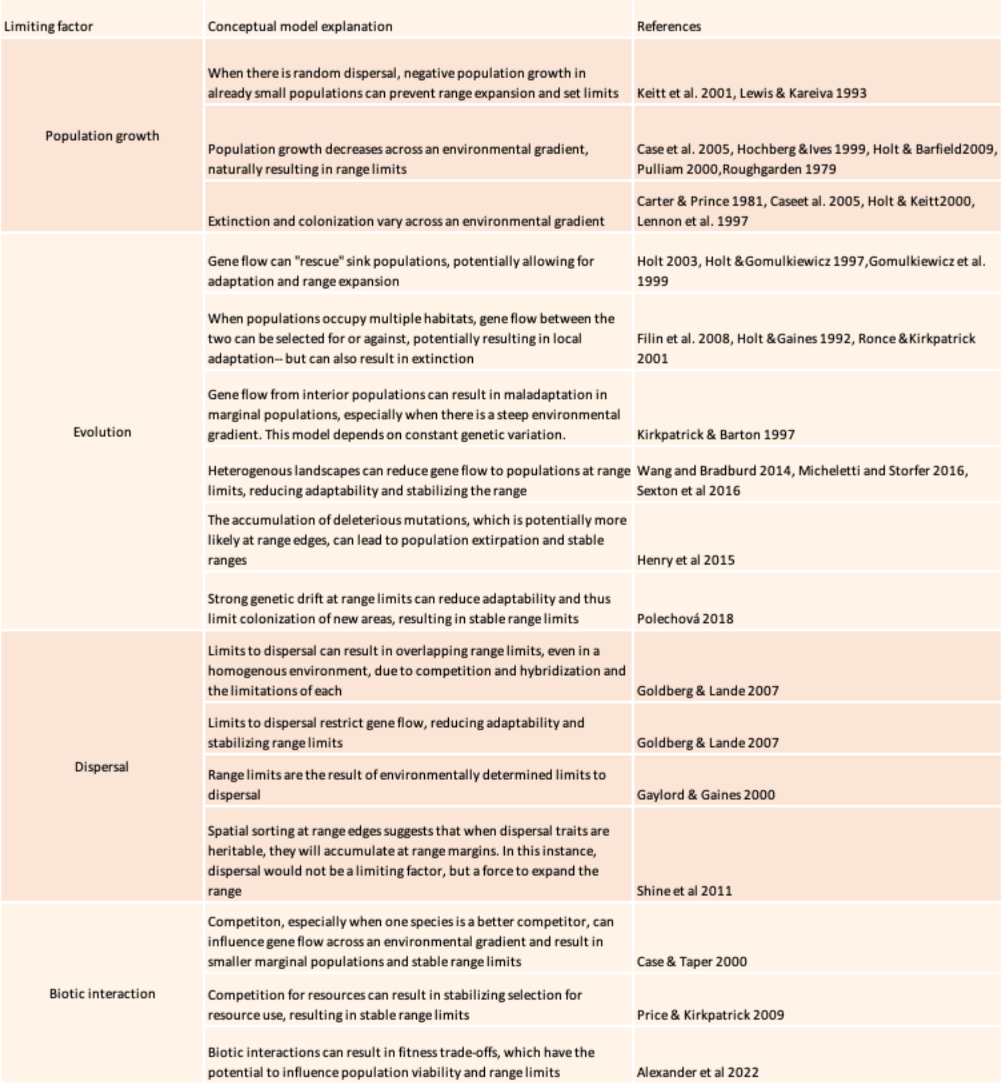
Tables

Table 1. Common hypotheses with range limit implications.

Hypothesis	Reference citation	Hypothesis summary	Sample support paper	Sample opposition paper
Genetic Swamping Hypothesis	Haldane, J.B.S. 1956. The relation between density regulation and natural selection. Proceedings of the Royal Society of London. Series B-Biological Sciences, 145(920), pp.306-308.	Marginal populations are "swamped" with maladaptive gene flow from interior populations, limiting the ability to adapt to new conditions and expand the range.	Fedorka, K.M., Winterhalter, W.E., Shaw, K.L., Brogan, W.R. and Mousseau, T.A. 2012. The role of gene flow asymmetry along an environmental gradient in constraining local adaptation and range expansion. Journal of evolutionary biology, 25(8), pp.1676-1685.	Kottler, E.J., Dickman, E.E., Sexton, J.P., Emery, N.C. and Franks, S.J. 2021. Draining the swamping hypothesis: little evidence that gene flow reduces fitness at range edges. Trends in Ecology & Evolution, 36(6), pp.533-544.
The Center-Periphery Hypothesis	Soule, M., 1973. The epistasis cycle: a theory of marginal populations. Annual review of ecology and systematics, pp.165-187.	Genetic variation and fitness decrease from the center to the margins of a species' geographic range and assumes that that geographic range is correlated with the niche range.	Guo, Q., Taper, M., Schoenberger, M. and Brandle, J. 2005. Spatial-temporal population dynamics across species range: from centre to margin. Oikos, 108(1), pp.47-57.	Pennington, L.K., Slatyer, R.A., Ruiz-Ramos, D.V., Veloz, S.D. and Sexton, J.P. 2021. How is adaptive potential distributed within species ranges?. Evolution, 75(9), pp.2152-2166.
The Abundant-Center Hypothesis (ACH)	Brown, J.H., 1984. On the relationship between abundance and distribution of species. The american naturalist, 124(2), pp.255-279.	Species are more abundant-- more densely distributed-- at the center of their geographic range. The geographic range is correlated with the niche range. Implies geographic range limits are the least suitable areas in a range.	Stanton-Geddes, J., Shaw, R.G. and Tiffin, P. 2013. Insights from population genetics for range limits of a widely distributed native plant. American journal of botany, 100(4), pp.744-753.	Sagarin, R.D. and Gaines, S.D., 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule?. Ecology letters, 5(1), pp.137-147.
Levin's Metapopulation Hypothesis	Holt, R.D. and Keitt, T.H. 2000. Alternative causes for range limits: a metapopulation perspective. Ecology letters, 3(1), pp.41-47.	Employs Levin's Model of metapopulation dynamics to describe three explanations of range limits: 1. insufficient habitat at range limits, 2. higher extinction rates at limits, 3. failure to colonize new patches due to any biotic or abiotic factor that influences survival or dispersal.	Angert, A.L., Bayly, M., Sheth, S.N. and Paul, J.R. 2018. Testing range-limit hypotheses using range-wide habitat suitability and occupancy for the scarlet monkeyflower (Erythranthe cardinalis). The American Naturalist, 191(3), pp.E76-E89.	Channell, R. and Lomolino, M.V. 2000. Dynamic biogeography and conservation of endangered species. *Nature* , *403* (6765), pp.84-86.
The Niche Abundant-Center Hypothesis	Martínez-Meyer, E., Díaz-Porras, D., Peterson, A.T. and Yáñez-Arenas, C. 2013. Ecological niche structure and rangewide abundance patterns of species. Biology letters, 9(1), p.20120637.	Species are most abundant at the center of their niche range, the center of the species' range of habitable environmental conditions. Implies niche range limits are the least suitable areas in a range and that niche limits are range limits.	Osorio-Olvera, L., Yañez-Arenas, C., Martínez-Meyer, E. and Peterson, A.T. 2020. Relationships between population densities and niche-centroid distances in North American birds. Ecology Letters, 23(3), pp.555-564.	Dallas, T., Decker, R.R. and Hastings, A. 2017. Species are not most abundant in the centre of their geographic range or climatic niche. Ecology letters, 20(12), pp.1526-1533.
Species Interactions – Abiotic Stress Hypothesis	Louthan, A.M., Doak, D.F. and Angert, A.L. 2015. Where and when do species interactions set range limits?. Trends in Ecology & Evolution, 30(12), pp.780-792.	Environmental factors are more important in setting range limits in abiotically stressful areas-- in areas that are not abiotically stressful, species interactions are more important in setting range limits.	Ettinger, A.K., Ford, K.R. and HilleRisLambers, J. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. Ecology, 92(6), pp.1323-1331.	Ettinger, A.K. and HilleRisLambers, J. 2013. Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. American Journal of Botany, 100(7), pp.1344-1355.

Table 2. A brief overview of theoretical models on the creation of species range limits. Adapted from Sexton et al 2009.



Limiting factor	Conceptual model explanation	References
Population growth	When there is random dispersal, negative population growth in already small populations can prevent range expansion and set limits	Keitt et al. 2001, Lewis & Kareiva 1993
	Population growth decreases across an environmental gradient, naturally resulting in range limits	Case et al. 2005, Hochberg &Ives 1999, Holt & Barfield2009, Pulliam 2000,Roughgarden 1979
	Extinction and colonization vary across an environmental gradient	Carter & Prince 1981, Caseet al. 2005, Holt & Keitt2000, Lennon et al. 1997
Evolution	Gene flow can "rescue" sink populations, potentially allowing for adaptation and range expansion	Holt 2003, Holt &Gomulkiewicz 1997,Gomulkiewicz et al. 1999
	When populations occupy multiple habitats, gene flow between the two can be selected for or against, potentially resulting in local adaptation-- but can also result in extinction	Filin et al. 2008, Holt &Gaines 1992, Ronce &Kirkpatrick 2001
	Gene flow from interior populations can result in maladaptation in marginal populations, especially when there is a steep environmental gradient. This model depends on constant genetic variation.	Kirkpatrick & Barton 1997
	Heterogenous landscapes can reduce gene flow to populations at range limits, reducing adaptability and stabilizing the range	Wang and Bradburd 2014, Micheletti and Storfer 2016, Sexton et al 2016
	The accumulation of deleterious mutations, which is potentially more likely at range edges, can lead to population extirpation and stable ranges	Henry et al 2015
	Strong genetic drift at range limits can reduce adaptability and thus limit colonization of new areas, resulting in stable range limits	Polechová 2018
Dispersal	Limits to dispersal can result in overlapping range limits, even in a homogenous environment, due to competition and hybridization and the limitations of each	Goldberg & Lande 2007
	Limits to dispersal restrict gene flow, reducing adaptability and stabilizing range limits	Goldberg & Lande 2007
	Range limits are the result of environmentally determined limits to dispersal	Gaylord & Gaines 2000
	Spatial sorting at range edges suggests that when dispersal traits are heritable, they will accumulate at range margins. In this instance, dispersal would not be a limiting factor, but a force to expand the range	Shine et al 2011
Biotic interaction	Competiton, especially when one species is a better competitor, can influence gene flow across an environmental gradient and result in smaller marginal populations and stable range limits	Case & Taper 2000
	Competition for resources can result in stabilizing selection for resource use, resulting in stable range limits	Price & Kirkpatrick 2009
	Biotic interactions can result in fitness trade-offs, which have the potential to influence population viability and range limits	Alexander et al 2022

Table 3. Range limits resources.

Title	Citation	What's in the paper?
Phil. Trans. Roy Soc. B themed issue "'Species' ranges in the face of changing environments'" parts 1&2	'Species' ranges in the face of changing environments'Phil. Trans. R. Soc. 377:20210013.20210013. http://doi.org/10.1098/rstb.2021.0002	Twenty peer reviewed articles highlighting the most up-to-date theory and empirical work on range limits
The nature of limits to natural selection	Antonovics, J., 1976. The nature of limits to natural selection. Annals of the Missouri Botanical Garden, pp.224-247.	A seminal paper on the limits of natural selection and how different factors interact to impose limits on marginal populations.
Limits to evolution at range margins: when and why does adaptation fail?	Bridle, J.R. and Vines, T.H., 2007. Limits to evolution at range margins: when and why does adaptation fail?. Trends in ecology & evolution, 22(3), pp.140-147.	An overview of adaptation at range margins and how studying adaptation at range limits can help us understand evolution more generally.
The Geographic Range: Size, Shape, Boundaries, and Internal Structure	Brown, J.H., Stevens, G.C. and Kaufman, D.M., 1996. The geographic range: size, shape, boundaries, and internal structure. Annual review of ecology and systematics, pp.597-623.	A seminal review of factors that may affect range limits.
Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond	Eckert, C.G., Samis, K.E. and Lougheed, S.C., 2008. Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. Molecular ecology, 17(5), pp.1170-1188.	A meta-analysis of studies that measure genetic variation across ranges. They found high differentiation and low genetic diversity at range margins-- however, most studies report neutral genetic variation which may or may not be correlated with quantitative genetic variation or adaptability.
The structure and dynamics of geographic ranges	Gaston, K.J., 2003. The structure and dynamics of geographic ranges. Oxford University Press on Demand.	A broad prospective on what is known about range limits
Conserving biodiversity under climate change: the rear edge matters	Hampe, A. and Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology letters, 8(5), pp.461-467.	Comprehensive investigation of survival and evolution at range limits, including data from the fossil record. Findings include, as the title would suggest, that the rear edge of a species' range is historically important for the persistance of species.
Are Species' Range Limits Simply Niche Limits Writ Large? A Review of Transplant Experiments beyond the Range	Hargreaves, A.L., Samis, K.E. and Eckert, C.G., 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. The American Naturalist, 183(2), pp.157-173.	A review of transplant experiments, determining what causes range limits through studying what affects fitness beyond the range
Species borders: ecological and evolutionary perspectives.	Hoffmann, A.A. and Blows, M.W., 1994. Species borders: ecological and evolutionary perspectives. Trends in Ecology & Evolution, 9(6), pp.223-227.	Strategies for studying range limits in evolutionary or ecological terms, and a review of current (at the time) research
Adaptation to Marginal Habitats	Kawecki, T.J., 2008. Adaptation to marginal habitats. Annual Review of Ecology, Evolution, and Systematics, pp.321-342.	An overview of adaptation at range limits with ephasis on demographic processes
Where and When do Species Interactions Set Range Limits?	Louthan, A.M., Doak, D.F. and Angert, A.L., 2015. Where and when do species interactions set range limits?. Trends in Ecology & Evolution, 30(12), pp.780-792.	A formal proposal of the "Species Interactions–Abiotic Stress Hypothesis", with supporting and opposing evidence, and future directions
How is adaptive potential distributed within species ranges?	Pennington, L.K., Slatyer, R.A., Ruiz-Ramos, D.V., Veloz, S.D. and Sexton, J.P., 2021. How is adaptive potential distributed within species ranges?. Evolution, 75(9), pp.2152-2166.	Meta-analysis of quantitative genetic variation studies, testing the abundant center hypothesis. Finds little support for ACH.
Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm	Pironon, S., Papuga, G., Villellas, J., Angert, A.L., García, M.B. and Thompson, J.D., 2017. Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. Biological Reviews, 92(4), pp.1877-1909.	An overview of genetic variation and population demographic patterns across species' ranges, testing the Center-Periphery hypothesis (CPH). Finds little support for the CPH.
The 'abundant centre' distribution: to what extent is it a biogeographical rule?	Sagarin, R.D. and Gaines, S.D., 2002. The 'abundant centre'distribution: to what extent is it a biogeographical rule?. Ecology letters, 5(1), pp.137-147.	A review of studies to test the abundant center hypothesis, with inconclusive results.
Evolution and Ecology of Species Range Limits	Sexton, J.P., McIntyre, P.J., Angert, A.L. and Rice, K.J., 2009. Evolution and ecology of species range limits. Annual Review of Ecology, Evolution and Systematics, 40(1), pp.415-436.	Overview of range limits research; thorough review of range limits models
Rules of plant species ranges: Applications for conservation strategies	Shay, J.E., Pennington, L.K., Montiel-Molina, J.A.M., Toews, D.J., Hendrickson, B.T. and Sexton, J.P., 2022. Rules of plant species ranges: Applications for conservation strategies. Predicting and Managing Climate-Driven Range Shifts in Plants.	An overview of purposed biogeographical rules and whether they are reliable. Specific to plants.
A practical guide to the study of distribution limits	Willi, Y. and Van Buskirk, J., 2019. A practical guide to the study of distribution limits. The American Naturalist, 193(6), pp.773-785.	A handy outline of the potential causes of range limits and how to study them, with empirical examples, models, and future directions.

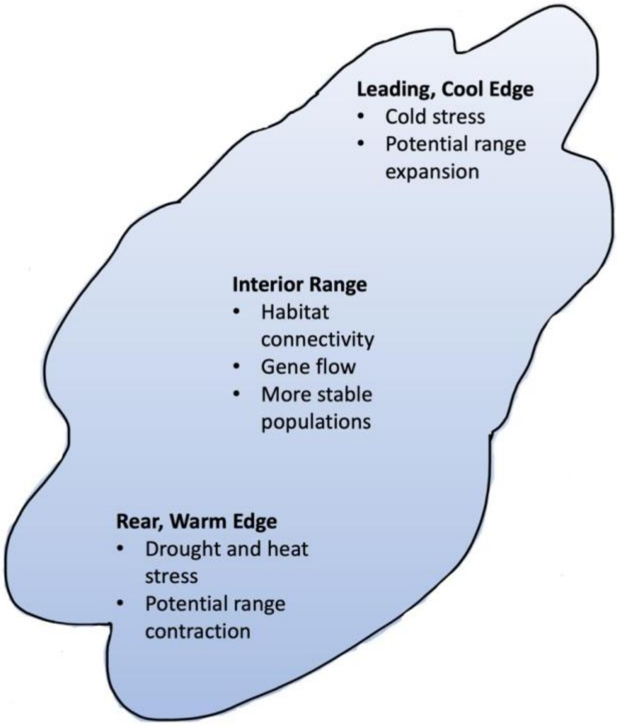


Figure 1. A cartoon depiction of a species range.

Chapter 2. Recent climate stress has resulted in rapid drought adaptation, but not heat adaptation, across a native plant species' range

2.1. Abstract

Climate change has the potential to disrupt climate suitability for endemic montane plants as temperatures increase and more precipitation falls as rain rather than snow, increasing summer aridity. Using a resurrection approach, I designed an experiment to understand how the 2012-2016 drought in California, the worst drought in the last 2000 years, affected natural populations of an endemic plant in the Sierra Nevada, *Erythranthe laciniata*. I grew seeds collected in 2005 and 2014 (prior to and at the height of the drought), in common growth chamber conditions. I manipulated temperature and water availability, resulting in four factorial treatments of current or elevated temperature and moist or drought conditions, meant to simulate current climate and potential climates in the future. I collected phenology data daily and fitness and morphological data at the end of the study. Drought generation plants emerged earlier than pre-drought generations, with flowering time depending on treatment. However, using phenotypic selection analysis I found that this change was not a determinant of fitness in drought treatments. Furthermore, while drought generation plants performed better in the average treatments, the pre-drought generation had marginally higher fitness in the hot treatments, though the overall poor response in drought conditions suggest there is little adaptive variation to cope with heat stress in either generation. Finally, I found that genetic variation was severely reduced in the drought treatments, reduced in the drought generation, and reduced in all populations across experimental treatments (drought, heat) compared to control conditions. In this novel range-wide examination of adaptation to drought and heat, I found that while these endemic plants may have rapidly adapted to drought conditions, they may still be vulnerable to increased heat and drought stress. Further, earlier phenology, which is commonly thought to be a drought escape strategy, may not always confer higher fitness in extreme conditions.

2.2. Introduction

Worldwide, species are responding to climate change with range shifts and contractions, and habitat unsuitability, as a result of changing climate, has resulted in some population or species extinctions (Parmesan 2006). Species' ability to respond quickly to climate perturbations is an active area of research (Hoffman and Sgro 2011, Catullo et al 2019), with evidence of species responding to long-term climate change (see Kannan and James 2009, Poloczanska et al 2013, Nunez et al 2019, Román-Palacios and Wiens 2020, Hill et al 2021, among others). Population dynamics play a role in the evolutionary trajectory of a species (Kinnison and Hairston 2007) and while the ability of a population to respond to change relies heavily on genetic variation within that population (Kokko et al 2017), it is unknown if the genetic shifts in response to changing conditions will be able to mitigate the negative effects for many species (Parmesan 2006). Despite the importance of long-term climate change research, few studies have examined the effects of specific climate events (for example, extreme drought, flooding, and fires) on evolution of climate responses. As climate continues to change, more climate events like drought and extreme wet years are predicted, but it is unclear how these events affect populations and if those effects will persist or lead to evolutionary change.

To deal with climate change, plant species must adapt, migrate, or risk extinction or local extirpation (Aitken et al 2008). Plants are moving— climate change has been measurable since the early 1980s (Barnett et al 2008) and range shifts in response to changing conditions have been globally documented for some time (Parmesan and Yohe 2003), although the pace of shifts do not always match the pace of climate change (Lustenhouwer et al. 2017). To tolerate climate change, plants have also changed the timing of their phenology to avoid unfavorable conditions (Walther et al 2002). Paradigms on the speed of niche evolution during rapid environmental shifts have shifted from niches being immutable, to the possibility of rapid niche contraction or expansion (Bennet 1997). Further, plants were able to respond to rapidly changing conditions during the Quarternary age (Davis et al 2005), suggesting that adaptation and range shifts can occur at the same rate as climate change (although see McLachlan et al. 2005 who found that tree range shifts lagged behind climate change post-ice-age). In contemporary times, there is evidence of rapid adaptation in both invasive species (Franks et al 2007) and native species (Dickman et al 2019) to drought, as detected by resurrection studies (Franks et al 2018). The resurrection approach involves growing past and present seed collections in common conditions to observe genetic changes at the population level. This approach can can allow detection of not only evolutionary changes across time but also across space, if multiple populations are included.

Species range limits theory suggests that adaptive responses at the cold (leading) and warm (rear) climate edges of species ranges may vary due to potential differences in abundance, gene flow, or historical effects (e.g., glaciation) (Hampe and Petit 2005). In a warming climate, populations at the warm edge of the range, that is the lowest in elevation or latitude, are most often the areas where habitat becomes unsuitable, i.e., when the environment no longer matches the species niche (Lee-Yaw et al., 2016). Because of this, they are termed the “rear” or “trailing” range margins. Higher or cooler populations may be able to migrate and shift the range into areas that had once been too cold, and hence are termed “forward” or “leading” range margins. Range margins are dynamic areas and understanding how persistent drought and warming temperatures affect genetic variation at range margins will be important in predicting both range shifts and adaptive capacity.

Plant adaptation to stressful environments, such as unfavorable soil types (Brady, Kruckeberg, and Bradshaw Jr. 2005), has been studied extensively. Plant adaptation to climate change is a growing field of research and will become increasingly more important. Adaptation (or adaptive evolution) is change of a population in the mean phenotype that confers greater fitness (Davis and Shaw 2001) and depends on the amount of quantitative genetic variation available in a population for natural selection to act on (Conner and Hartl 2004; Hoffmann, Sgrò, and Kristensen 2017). Fisher’s Fundamental Theorem of Natural Selection (Fisher 1930) suggests that any increase in plant fitness is a direct result of the evolvability available in a population. As such, measures of genetic variation in fitness in populations can be used as a proxy for adaptive potential.

Montane habitats provide an ideal “natural laboratory” to test plant species response to climate, as the elevation change provides a variety of climates on a small spatial scale (Tito et al 2020). The Sierra Nevada of California are a biological diversity hotspot and home to a high number of endemic herbaceous plants, which make up the bulk of this biodiversity (Myers et al 2000). Climate in this region is changing rapidly, but it is unknown how herbaceous plants are responding to these changes. As climate change is likely not reversible on a century-scale timeline (Solomon et al 2008), it is imperative to understand the adaptive potential of native plant populations and how it may affect the future of species distributions in a warmer, drier California (Reich et al 2018, Goss et al 2020). An historic drought impacted the Sierra from 2012-2016—this drought was extreme in its lack of precipitation, high temperatures, and duration and is thought to have been exacerbated by climate change (Griffen and Anchukaitis 2014, AghaKouchak et al 2016). It thus provides a natural opportunity to understand rapid adaptation to extreme conditions.

Rapid adaptation to climate change has previously been observed using the resurrection method in the eco-evolutionary model genus *Erythranthe* (monkeyflowers, formerly *Mimulus*) (Wu et al 2008) in California and the Sierra. In *E. cardinalis* (scarlet monkeyflower), populations did not evolve advanced phenology to avoid drought conditions (Vtipil and Sheth 2020), but were found to rapidly evolve drought tolerance traits, with southern populations losing plasticity in these traits due to strong selective pressures (Anstett et al 2021). In *E. guttata* (common yellow monkeyflower), populations were found to vary widely in trait responses to drought, with drought generation plants having higher fitness in drought conditions than pre-drought generation plants in one population (Kooyers et al 2021). Finally, the evolution of early emergence and flowering was detected in nine populations from across the range of the highly self-fertilizing endemic monkeyflower, *Erythranthe laciniata* (cutleaf monkeyflower) (Dickman et al 2019) (Fig. 1). These studies affirm the prevalence of rapid adaptation, while highlighting differences in how that adaptation plays out between populations and related species.

Here, I utilize a resurrection design to study how the 2012-2016 drought in the western US impacted populations of *E. laciniata*. This work seeks to build on the research by Dickman et al. (2019) to test whether observed changes in emergence and flowering time are adaptive. Specifically, I address the following questions:

1. *Are the evolutionary changes observed in the drought generation adaptive?*
2. *Are evolutionary changes observed in the drought generation adaptive in future, warmer climates? And if so, which populations are better adapted to predicted, warmer climates?*
3. *Has evolution in response to contemporary drought come at a cost to genetic variation or adaptive potential?*

2.3. Methods

2.3.1. Study species

Erythranthe laciniata is endemic to the Sierra Nevada, where it has specialized on mossy patches in snowmelt seeps on exposed outcrops (Fig. 1). It is a highly self-fertilizing annual plant, which allows for easier estimation of heritability (i.e., no pollinations or understanding of parentage is required) and lifetime fitness. Prior work in this system showed that although the plant primarily self-fertilizes, there is some gene flow between populations (Sexton et al 2011, Ferris et al 2017, Sexton et al 2016) and evidence of rapid phenology adaptation to drought (Dickman et al 2019). Its range is wholly restricted to the western slopes of the Sierra, allowing for rangewide sampling. Sampling across the range allows assessments of genetic variation at leading and rear edges of the range, where population expansion or contraction occurs (Sexton et al 2016). Higher elevation populations have been shown to be locally adapted to their climatic conditions (DeMarche et al 2013, Dickman et al 2019, Chapter 3, Shay et al. *in prep*). Low elevation edge populations already experience hotter, drier conditions than populations at other elevations and have shown higher survival rates compared to high elevation populations in a low-elevation common garden experiment (Shay et al *in prep*).

2.3.2. Growth chamber experiment

Nine populations from across the species range (Fig. 2) were collected from 2005-2008 (pre-drought generations) and during 2014 (drought generation) (Table 1). Prior work with these populations (Dickman et al 2019) revealed variation in the magnitude of phenology advancement by population and population elevation. Families from all populations were grown in common conditions for two generations before being used in this experiment to further reduce maternal effects.

I sowed seeds into Sta-green potting (Lowes 2020) mix in 72-well plastic planting trays. The cutleaf monkeyflower often germinates over winter depending on elevation, and to simulate these germination conditions, plant trays were watered and placed in germination cabinets in the dark at 4°C for two weeks. I used two Conviron PGR Flex growth chambers (Conviron Ltd., Winnipeg, Canada) to simulate average and predicted future average temperatures across the species range (Table 2). The average temperature treatment was a 23 °C day temperature and 10 °F night temperature, with a 16 hour day. In the Sierra Nevada, temperatures are expected to be 7 °F warmer on average by the end of the century (Reich et al 2018, reported in degrees F). I set the future temperature as a 30 °C day temperature with a 17 °C night temperature, simulating an much warmer—but but not improbably so—growing season. Within each temperature treatment, I included two watering treatments: a non-drought and a drought treatment. As the Sierra Nevada have a Mediterranean climate, plants experience a seasonal drought every growing season once the summer dry period begins, but the window of water availability can differ greatly among years. To emulate more benign, average conditions, I provided water to the non-drought treatment for 35 days, the point at which 75% of plants had flowered in prior breeding experiments. For the drought treatment, I withheld water after 16 days—the average day of the first flower in prior breeding experiments. Due to space limitations, the experiment was run one half at a time, split into two cohorts or experimental trials that included all treatments and families from each population. Midway through each experimental trial, plants were switched between growth chambers to reduce conflation of chamber and treatment effects.

Planting for the experiment began in Summer 2020. For each population, I planted three representatives from ten families for each generation and each treatment, for a total of 2,160 plants: 4 treatments x 10 families x 3 reps x 9 pops x 2 generations. I used a randomized block design in which seeds were randomly sown into trays, with all populations represented in each tray four times. Plant phenology was recorded daily, with day one being the first day in the growth chamber. I recorded days to germination and days to first flower. Plants were thinned after true leaves formed on whichever plant was most central in the cell. After senescence, I measured the total fruit production for each plant.

2.3.3. Analysis

All analyses were completed in R (R Core Team, 2021). For lifetime fitness tests, I used total fruit production as a proxy for fitness (Sexton et al. 2011, DeMarche et al. 2013, Sexton and Dickman 2016, Dickman et al. 2019), with zeros included for plants that did not germinate or did not produce fruits. The main explanatory, fixed effect variables were generation (drought or pre-drought), treatment (Average Non-drought, Hot Non-drought, Average Drought, and Hot Drought), and the elevation of the population, which was treated as a continuous variable. I included population and tray as random effects. I used the lrtest function in the lmtest package (Zeileis and Hothorn 2002) to produce p-values from regression models.

2.3.3.1. Are the evolutionary changes observed in the drought generation adaptive?

First, I used logistic regression to understand patterns of survival across the experiment and to test whether drought generation plants had higher rates of survival to reproduction than pre-drought generation plants in drought conditions. I scored plants with 0 if they did not produce fruit and 1 if they did produce fruit. I used the lme4 package (Bates et al 2015) to run a generalized linear model using the glmer function with a binomial family specification and a logit link. I regressed survival on treatment, generation, and their interaction, elevation, population, and/or tray.

Next, I analyzed fitness trends across treatments and fitness plasticity between treatments. I grouped the populations into low, intermediate, and high elevation bins in order to detect broad genotype by environment (GxE) interactions. I then used a generalized linear model to regress fitness on treatment, generation, and their interaction, with a poisson distribution specified and with tray and population as random effects.

Due to finding a significant the interaction of treatment and generation, I then split the dataset by just the drought treatments and used a generalized linear model with a poisson distribution, regressing fruit count on the interaction between generation and population elevation, with population and tray as random effects.

Finally, I tested whether phenology differences affect fitness in drought conditions. I first used a cox proportional hazards mixed effects model to test whether the drought generation emerges and flowers earlier than the pre-drought generation, as it did in our prior study (Dickman et al. 2019). I then used phenotypic selection analysis to test whether the drought generation has shallower selection gradients, due to prior selection during the drought. I estimated relative fitness by dividing the total flower count estimates by the total number of plants to obtain an average flower count, and then divided flower count by the average flower count. I then transformed each morphological and phenological variable (days to emergence, days to first flower, height at first flower, flower width, final height, and biomass) to a standard measure using the scale function in base R. I correlated the traits using the cor function in the stats package of base R to evaluate them for their use in phenotypic selection analysis. I then used a multiple regression linear model using the lm function of base R to simultaneously regress relative fitness on the scaled traits.

2.3.3.2. Are evolutionary changes observed in the drought generation adaptive in future, warmer climates? And if so, which populations are better adapted to predicted, warmer climates?

Increased temperature (predicted in climate change models) can have detrimental effects on plants, even in average water conditions. In order to understand the impact of heat on fitness, I analyzed the Hot, Non-drought treatment separately to understand heat responses between generations. I used the glmer function in the lme4 package (Bates et al 2015) to model fruit count in a generalized linear model on generation and elevation, and their interaction, with population and tray as random effects.

To determine if there is an elevational response to heat, I grouped populations by their elevations into categorical groups of low, medium, and high, with three populations in each group, to compare fitness variances between the Average Non-drought and Hot Non-drought treatments. First, to test the effects of elevation group, generation, and treatment on fitness I used a generalized linear model with a poisson distribution specified, and with population nested in elevation group, and tray and population included as random effects. I then used the pairs function in the emmeans package (Lenth 2022), which uses a Tukey test on least square mean values computed from the model, to compare fruit count means between the two treatments and generations. I used these pairwise tests in order to test whether increased temperatures impact fitness in each generation and to what extent. For example, I compared the drought generation in the high elevation group in the Average Non-drought treatment to the drought generation in the high elevation group in the Hot Non-drought treatment.

2.3.3.3. Has evolution in response to contemporary drought come at a cost to genetic variation or adaptive potential?

In my experimental design, I included family level replication to understand how genetic variation varies between treatments. These data were not normally distributed, so I used a non-parametric test of variances, the Kruskal-Wallis test in base R, to determine if there is variation amongst the families in fruit count in both drought and pre-drought generations.

2.4. Results

2.4.1 Are the evolutionary changes observed in the drought generation adaptive?

2.4.1.1. Survival

The environmental differences among treatments caused dramatic differences in survival, and these survival responses varied by elevation. The Average Non-drought treatment had the highest survival, followed by the Hot Non-drought and Average Drought treatments, with the Hot Drought treatment having the lowest survival (Fig. 3). In all treatments, low elevation populations had the highest survival. Treatment, generation, elevation, and their interactions all showed significant effects on survival (Table 3). The drought generation had marginally higher survival overall, with the highest variation between the two generations occurring in the central and high elevation populations.

2.4.1.2. Fitness

Increasing heat and reducing water had a strong impact on fitness. There was evidence for fitness plasticity between treatments, but not between generations (Table 4,

Fig. 4). Although all elevation groups had severely reduced fitness in the Hot Drought treatment, the low group had higher fitness than the intermediate and high groups in the Average Drought and Hot Non-drought treatment, signifying a GxE interaction. This fitness response also indicates plasticity in fitness, as fitness varied for all populations across all treatments.

The drought generation had higher fitness in average temperature, while population elevation affected fitness in the hot temperature treatment. I analyzed fitness separately for each drought treatment. In the Average Drought treatment, the drought generation had higher fitness ($p = 0.035$), with no significant effect from elevation or the interaction between generation and elevation (Figure 5, Table 5). In the Hot Drought treatment, the pre-drought generation had marginally higher fitness ($p = 0.05$, Figure 6), and fitness of all plants was extremely low, with significant effects from elevation ($p = 0.03855$) and the interaction between elevation and generation ($p = 0.01871$) (Figure 6, Table 6).

2.4.1.3. Phenotypic Selection Analysis

The cox proportional hazards confirmed earlier emergence in the drought generation ($p = <0.001$, Fig. 7) and found that emergence was influenced by elevation ($p = <0.0001$), but not treatment ($p = 0.133$). Days to first flower differed by generation ($p = 0.021$), treatment ($p = 0.003$), and elevation ($p = <0.0001$) (Fig. 7). In the Average and Hot Non-drought treatments, the drought generation flowered later than the pre-drought generation as population elevation increases; in the Average Drought treatments, trends were similar between the two generations, whereas in the Hot Drought treatment lower elevations flower later in the pre-drought, low elevation populations, but earlier in the pre-drought, high elevation populations (this is a slight relationship due to overall low survival in this treatment.

There were significant correlations between days to first flower and final height ($p = 0.02$), biomass and flower width ($p = 0.04$), and final height and height at first flower ($p = 0.01$), while days to emergence was significantly negatively correlated with all other traits in the analysis (Fig. 8). In the Average Non-drought treatment, selection favored later flowering in both generations; in the Hot Drought treatment, selection very strongly favored later flowering in the Drought generation. I found evidence for directional selection favoring later flowering, indicating that in Average Non-drought and Hot Drought treatments that later flowering confers higher fitness. Selection gradients were not shallower in the Drought treatment (Figure 9), and in fact the steepest gradient was in the Drought generation in the Hot Drought treatment.

2.4.2. Are evolutionary changes observed in the drought generation adaptive in future, warmer climates? Are some populations better adapted to predicted, warmer climates?

I found evidence that drought-generation plants are better adapted to hotter temperatures, but this depended on elevation and water availability. In the Hot, Non-drought treatment, the drought generation had higher fitness overall ($p = <0.0001$). This was primarily driven by the drought generation's higher fitness in the high elevation groups, as source elevation and the interaction between elevation and generation were significant ($p = <0.0001$, $p = <0.0001$, respectively) (Fig. 9). However, the pre-drought generation had higher fitness in the Hot, Non-drought treatment in the low and central elevation groups. In the Hot, Drought treatment pre-drought generation plants had significantly higher fitness, but fitness differences were extremely slight (0.025 fruits). Moreover, even in the Hot, Non-drought treatment, pre-drought generation populations had higher fitness in low and intermediate elevation groupings (Fig. 10). Post-hoc Tukey tests revealed that all groupings were significantly different, with the exception of the low-elevation pre-drought generations (Fig. 10, Table 8). In the significant pairings, plants produced fewer fruits in the Hot, Non-drought treatment, suggesting that all populations were negatively affected by increased temperatures.

2.4.3. Has evolution in response to contemporary drought come at a cost to genetic variation or adaptive potential?

The Kruskal-Wallis tests showed that for both generations and across treatments, there was significant family-level genetic variation in fruit count; however, family trait variation dropped precipitously in more stressful treatments in each generation, where fitness was universally low (Fig. 11, Table 9).

2.5. Discussion

In a rapidly warming world, extreme climate events like more intense droughts or hotter heat waves are becoming more common. How plants will deal with these perturbations will determine the fate of ecosystems. Further, studying plant response in self-fertilizing plants is an area of research need (Wright et al 2013). Here, I show that a highly self-fertilizing, native plant can rapidly adapt to drought, although potentially at the expense of heat tolerance. There was evidence of plasticity across all treatments, which may have a strong impact on plant response to climate perturbations (Fenollosa and Munné-Bosch 2019). Selection analysis showed some support for directional selection in flowering timing in the Hot Drought treatment. Variation was not greatly reduced between generations but was reduced in hot and dry treatments (Fig. 11). Nevertheless, the findings here show reduced fitness in response to both heat and drought treatments, which were based on predictions of future climatic conditions.

In all treatments and in both the pre-drought and drought generation, the low elevation populations had the highest fitness (Fig. 4), with elevation being a significant effect in the models. They also had the highest variation in fitness (Fig. 11). These populations are at the "rear edge" of *E. laciniata*'s range—they are among the lowest elevation populations for the species. As such, they experience higher water and heat stress when compared with the rest of the range. Rear edge populations often harbor unique variation, sometimes as relic populations (Hampe and Petit 2005). For example, Gugger et al (2010), found important adaptive diversity at the southernmost extent of the range of the Douglas Fir (*Pseudotsuga menziesii*), potentially as a result of southward range expansion during the Pleistocene. However, higher variation at warm edges is not a rule. In cold-adapted species in particular, the warm edge may be depauperate in variation (Stewart et al 2010), and the interactions of past refugia can be complex (Stewart et al 2010). For example, in the range restricted, cold-adapted shrub *Bupleurum euphorbioides*, rear edge populations have reduced variation, potentially owing to a past range expansion into favorable areas that are now unfavorable (Meng et al 2019). Lower elevation plants may have an advantage beyond their climate tolerances, having stronger defenses against herbivory (Pellissier et al 2014) and stronger plasticity in phenological traits (Schmid et al 2017). There is a general trend for lower elevation plants to grow larger than high elevation counterparts (Clausen et al 1948, Halbritter et al 2018), potentially allowing lower elevation plants to be heartier and more resilient in hotter, drier conditions.

There was a decrease in fitness between the average non-drought treatment, which is meant to simulate optimal conditions, and all other treatments. Increased heat caused a reduction in fitness regardless of water availability, with hot drought conditions resulting in the lowest fitness across the experiment. Other plants also exhibited reduced fitness as a result of increased heat. Canola (*Brassica napus*) seed production was reduced after a single 12-hr exposure to intense heat (Lohani et al 2021). Experimental heat waves impacted milkweed (*Asclepias syriaca*) and the local insect community differently depending on when the heat wave occurred, further suggesting that punctuated heat events can have long term effects on plant fecundity (Cope et al 2023). In Europe, a continent-wide drought in 2003, linked to extreme heat and reduced summer rainfall, reduced primary productivity in plants (Ciais et al 2005). Finally, climate change may result in longer growing seasons for commercial vegetables but reduced overall crop yield due to rapid development and reduced seed set (Bisbis et al 2018). These negative fitness responses to heat reported both in crops and native plants may portend warm edge range contractions in the future.

The results of the phenotypic selection analysis suggest that among the treatments, phenological changes in the drought generation are not drought or heat adaptive, with the exception of the hot drought treatment where later flowering in the drought generation improved fitness. I expected to find shallower selection gradients in the drought generation as a result of past selection during the 2012-2016 drought—however, clines were almost identical between the generations with the exception of drought generation time to flowering in the Hot Drought treatment, which was steep and showed strong directional selection for later flowering. Globally, plant phenology is advancing, presumably to track favorable conditions (Parmesan 2007, Menzel et al 2020). This work shows that not all phenology changes are adaptive to new conditions. Huckleberries (*Vaccinium membranaceum*) in North America are on track to have maladaptive phenology: climate change will result in flowering and fruiting up to twenty days earlier than contemporary averages, resulting in potential exposure to winter frost conditions and decoupling with their pollinators (Prevey et al 2020). Here in *E. laciniata*, more research is needed to understand how changes in phenology manifest in the field if there are other ecological interactions that result in higher fitness due to changes in phenology that I was not able to capture in this controlled growth chamber study.

I found evidence of adaptive evolution in response to severe drought, but not heat. In the Average Drought, the drought generation had higher fitness. This is a similar treatment to conditions experienced in the 2012-2016 drought—an early end to water availability, although the 2012-2016 drought is referred to as a hot drought, it did not get as hot as the Hot Drought treatment. In the Hot Drought treatment, the pre-drought generation had a significant but very small increase in fitness, but all generations experienced extremely reduced fitness (Fig. 4). Conversely, for all populations, generations, and elevation groups, fitness was drastically higher in the Average Non-drought treatment. The reduction in fitness associated with each derivation from the

Average Non-drought signals potential range-wide reductions in fitness in the predicted warmer, drier conditions of the future. While growth chamber studies are not entirely realistic environments, this study shows negative responses to controlled conditions similar to predicted future conditions.

Although family level genetic variation is maintained across generations, the data show that variation falls between treatments, with the Average Non-drought treatment having the highest variation between populations and the Hot Drought treatment having the least. Variation between populations was maintained in the Average and Hot Non-drought treatments, with fitness being reduced across populations in the Hot Non-drought treatment. As variation in fecundity is considered a measure of a population's immediate ability to adapt (Fisher 1930, Shaw and Etterson 2012), this reduction in the magnitude of fitness suggests that increased temperatures decrease not only fitness of the individual but the adaptability of populations across a species' range.

2.6. Conclusion

Rapid adaptation in response to drought was detected in populations of the self-fertilizing, endemic forb *Eryhtranthe laciniata*. These findings support prior findings from resurrection studies in this genus, which also show adaptation to drought (Anstett et al 2021, Kooyers et al 2021). This study is a novel examination of adaptation across the entire range of a native species, utilizing a resurrection approach. Furthermore, it is an important examination of the ability of a self-fertilizing plant to adapt to rapid environmental change. The transition to self-fertilization from outcrossing is common in plants, and around 15% of flowering plants are self-fertilizing (Barrett 2002). Self-fertilization can be advantageous when mates or pollinators are scarce but also has the potential to limit adaptability due to a lack of recombination of genes. Climate change has the potential to disrupt plant/pollinator relationships, which would favor self-fertilization (Eckert et al 2010).

Lower elevation plants outperform higher and central elevation plants in every treatment, despite experiencing more stressors in their home range, suggesting their high conservation value for adaptive gene flow and seed sourcing. The drought generation outperformed the pre-drought generation, except in the hot treatments, suggesting a potential trade-off in drought versus heat stress adaptation. As the climate in the Sierra Nevada continues to change, these plants will experience new stressors. This study suggests that this plant will be able to persist, but populations may shrink or go extinct as phenotypes that can handle both drought and heat may be lost after concurrent droughts and heat spells. Further work includes investigating what phenotypes exist in the seed bank, how earlier phenology effects plants in the field, and how populations fare in contemporary conditions.

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Tables

Table 1. Population information with collection dates for the pre-drought and drought generation.

Population Code	Population Name	Elevation (meters)	Pre-drought Collection Year	Drought Collection Year
R	R Property	947	2006	2014
HWY	HWY 168	1000	2006	2014
HH	Poopenaut Valley	1020	2006	2014
MC	McLeod Flat	1280	2006	2014
HS	Hetch Hetchy Sign	1400	2005	2014
JM	Jackass Meadow	2200	2008	2014
ML	May Lake	2774	2006	2014
ME	Mammoth Edge	3049	2006	2014
HE	Hilgard Edge	3095	2006	2014

Table 2. Growth chamber conditions for the average and hot temperature treatments. Nested within each treatment is a non-drought and a drought treatment, resulting in four treatments: Average Non-drought, Average Drought, Hot Non-drought, and Hot Drought.

Growth chamber	Average	Hot
Daytime temperature	25°C	32°C
Nighttime temperature	10°C	15°C
Light day	16 hour	16 hour
Light intensity	500mmol	500mmol

Table 3. Likelihood Ratio results from binomial regression. Degrees of freedom, log likelihood, chi-square value, and p-value reported.

Fixed Effect	DF	LogLik	Chi^2	p value
Interaction	8	-1024.4	40.56	**<0.0001**
Treatment	5	-1070.8	97.388	**<0.0001**
Generation	7	-1043	41.806	**<0.0001**
Elevation	7	-1046.7	49.071	**<0.0001**

Table 4. Likelihood Ratio results from the full generalized linear regression model. Degrees of freedom, log likelihood, chi-square value, and p-value reported.

Fixed Effect	DF	LogLik	Chi^2	p value
Interaction	8	-5644.2	59.639	**<0.0001**
Treatment	5	-5656	83.198	**<0.0001**
Generation	7	-5648.1	67.517	**<0.0001**
Elevation	7	-5647.5	66.33	**<0.0001**

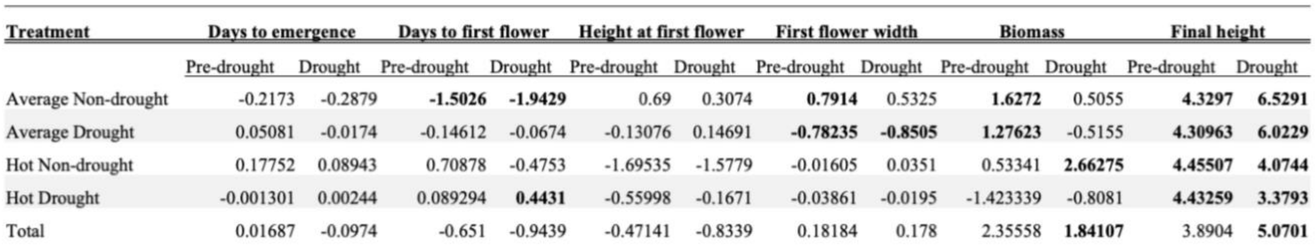
Table 5. Likelihood Ratio test results for the Average Drought treatment model. Degrees of freedom, log likelihood, chi-square value, and p-value reported.

Fixed Effect	DF	LogLik	Chi^2	p value
Interaction	5	-568.02	0.6432	0.4225
Generation	4	-571.05	6.7014	**0.035**
Elevation	4	-5710.1	4.8056	0.09

Table 6. Likelihood Ratio test results for the Hot Drought treatment model. Degrees of freedom, log likelihood, chi-square value, and p-value reported.

Fixed Effect	**DF**	**LogLik**	**Chi^2**	**p value**
Interaction	5	-281.8	5.528	**0.019**
Generation	4	-282.03	5.9947	**0.05**
Elevation	4	-282.29	6.5118	**0.039**

Table 7. Coefficients from multiple regressions on flower number; phenotypic selection analysis. Significant effects (0.05>) are bolded.



Treatment	**Days to emergence**		**Days to first flower**		**Height at first flower**		**First flower width**		**Biomass**		**Final height**	
	Pre-drought	Drought	Pre-drought	Drought	Pre-drought	Drought	Pre-drought	Drought	Pre-drought	Drought	Pre-drought	Drought
Average Non-drought	-0.2173	-0.2879	**-1.5026**	**-1.9429**	0.69	0.3074	**0.7914**	0.5325	**1.6272**	0.5055	**4.3297**	**6.5291**
Average Drought	0.05081	-0.0174	-0.14612	-0.0674	-0.13076	0.14691	**-0.78235**	**-0.8505**	**1.27623**	-0.5155	**4.30963**	**6.0229**
Hot Non-drought	0.17752	0.08943	0.70878	-0.4753	-1.69535	-1.5779	-0.01605	0.0351	0.53341	**2.66275**	**4.45507**	**4.0744**
Hot Drought	-0.001301	0.00244	0.089294	**0.4431**	-0.55998	-0.1671	-0.03861	-0.0195	-1.423339	-0.8081	**4.43259**	**3.3793**
Total	0.01687	-0.0974	-0.651	-0.9439	-0.47141	-0.8339	0.18184	0.178	2.35558	**1.84107**	3.8904	**5.0701**

Table 8. Tukey test results from the GLM of fruit count on generation, elevation and their interaction between treatments. Contrasts are between the Average, Non-drought and the Hot, Non-drought treatment for each elevation group; for example “Drought High” is a contrast between the fitness response in high elevation populations of the drought generation in Average, Non-drought treatment and the drought generation in the Hot, Non-drought treatment. This comparison of fitness within a generation between each Non-drought treatment allows for a better understanding of the role of heat on fitness. Ratio of geometric means standard error, and p-value reported.

Contrast	Ratio	SE	P value
Drought High	2.33	0.491	**0.003**
Pre-drought High	2.985	0.6981	**<0.001**
Drought Central	3.165	0.6977	**<0.001**
Pre-drought Central	4.835	1.5825	**0.001**
Drought Low	2.38	0.4612	**<0.001**
Pre-drought Low	1.701	0.3462	0.1037

Table 9. Results of the Kruskal-Wallis tests, comparing family variance for each generation. Results confirm that for all generations, family level genetic variation remains. Chi-square value, degrees of freedom, and p-value reported.

Generation	Treatment	Chi^2	DF	P value
Pre-drought	Average Non-drought	203.62	86	**<0.001**
Drought	Average Non-drought	184.84	89	**<0.001**
Pre-drought	Hot Non-drought	187.62	86	**<0.001**
Drought	Hot Non-drought	181.86	89	**<0.001**
Pre-drought	Average Drought	132.91	86	**<0.001**
Drought	Average Drought	131.66	89	**0.0022**
Pre-drought	Hot Drought	166.53	86	**<0.001**
Drought	Hot Drought	161.84	89	**<0.001**

Figures

Figure 1. *Erythranthe laciniata*, the cutleaf monkeyflower, and habitat (left) and confirmed range (right).

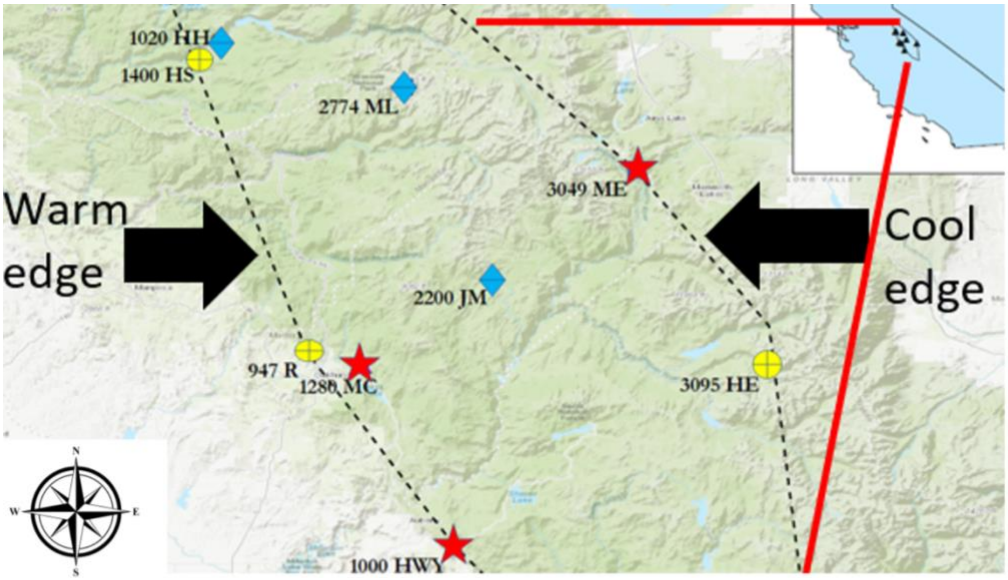


Figure 2. Population locations with elevation in meters. The dotted line is the geographic range for the *E. laciniata*. Populations are distinguished by size, with blue diamonds representing small populations, yellow circles are medium sized, and red stars are large.

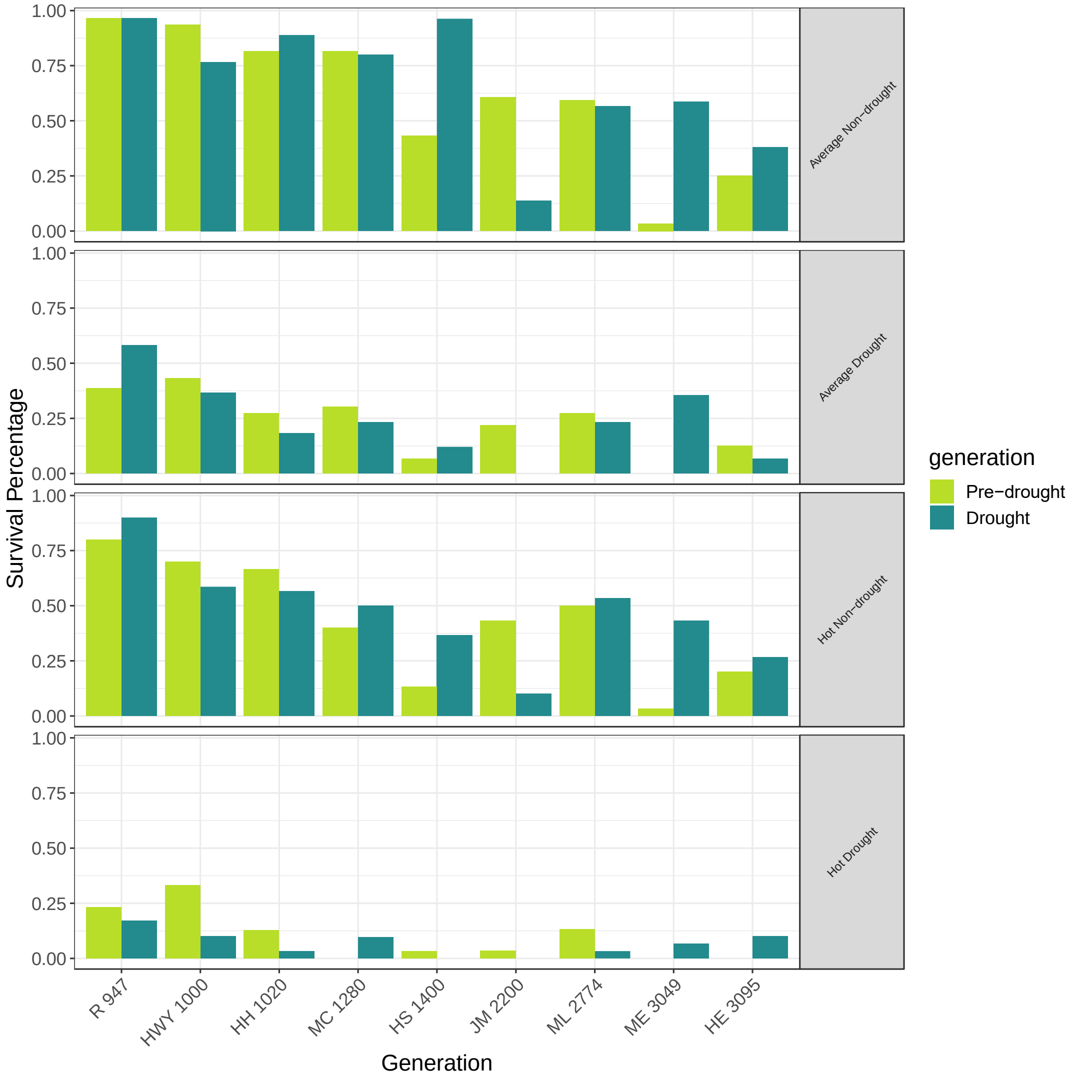


Figure 3. Percentage of plants that survived to fruiting by generation and population elevation.

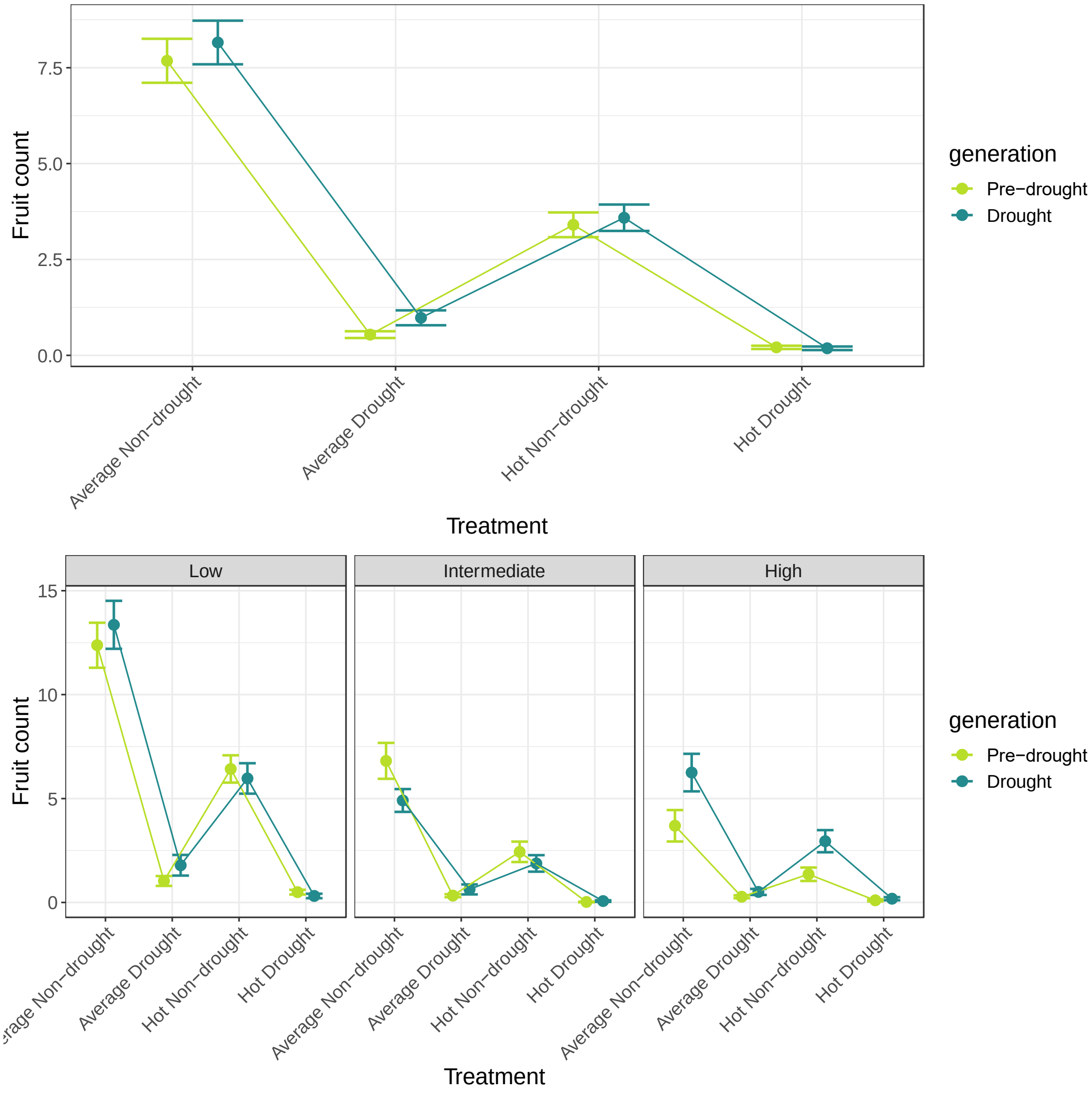


Figure 4. Reaction norms between treatments by generation (top) and elevation group (bottom). Treatment is on the X-axis with mean fruit count on the Y-axis.

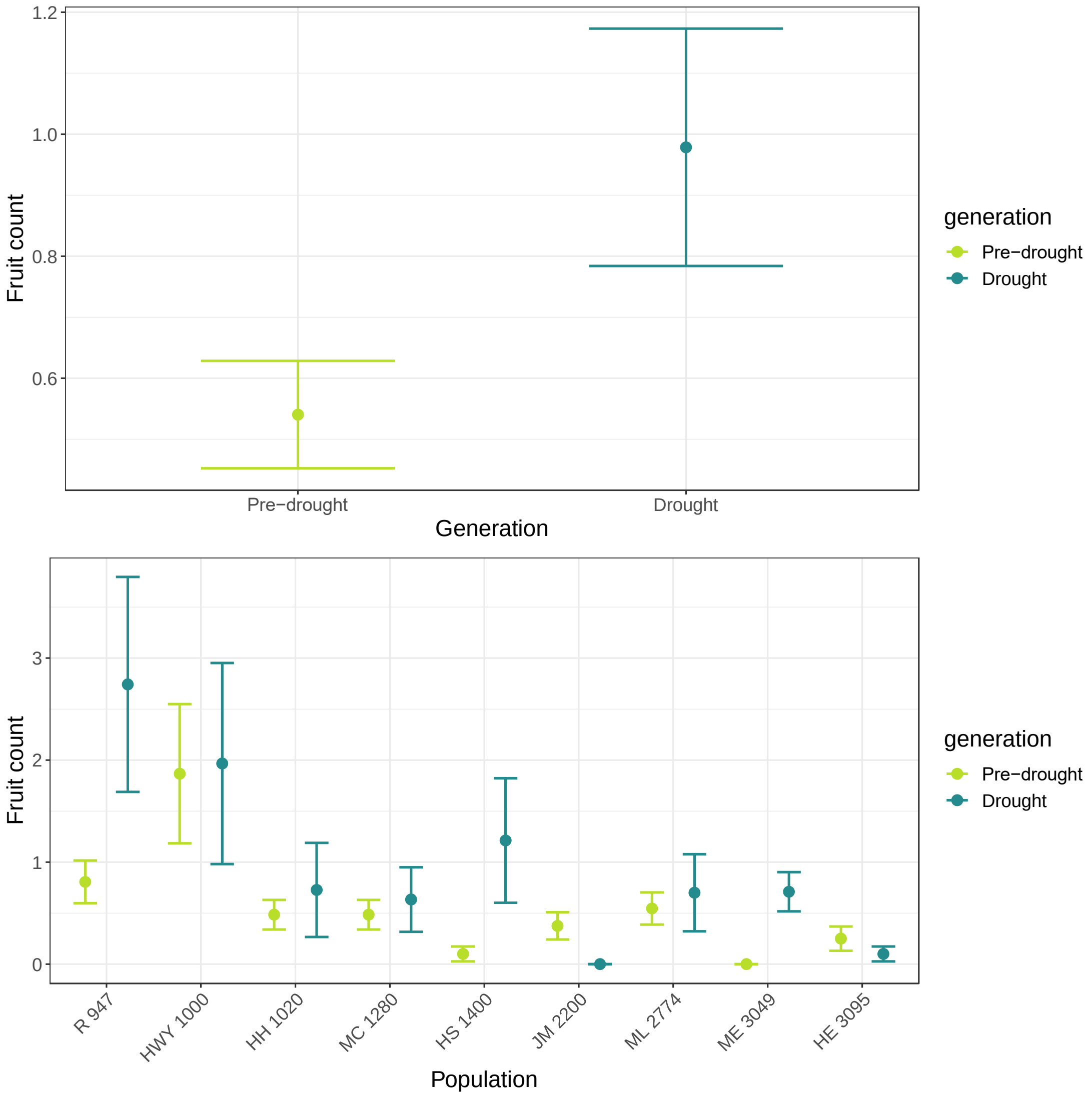


Figure 5. Fitness means by generation (top) and population (bottom) in the Average Drought treatment. Bars represent standard error.

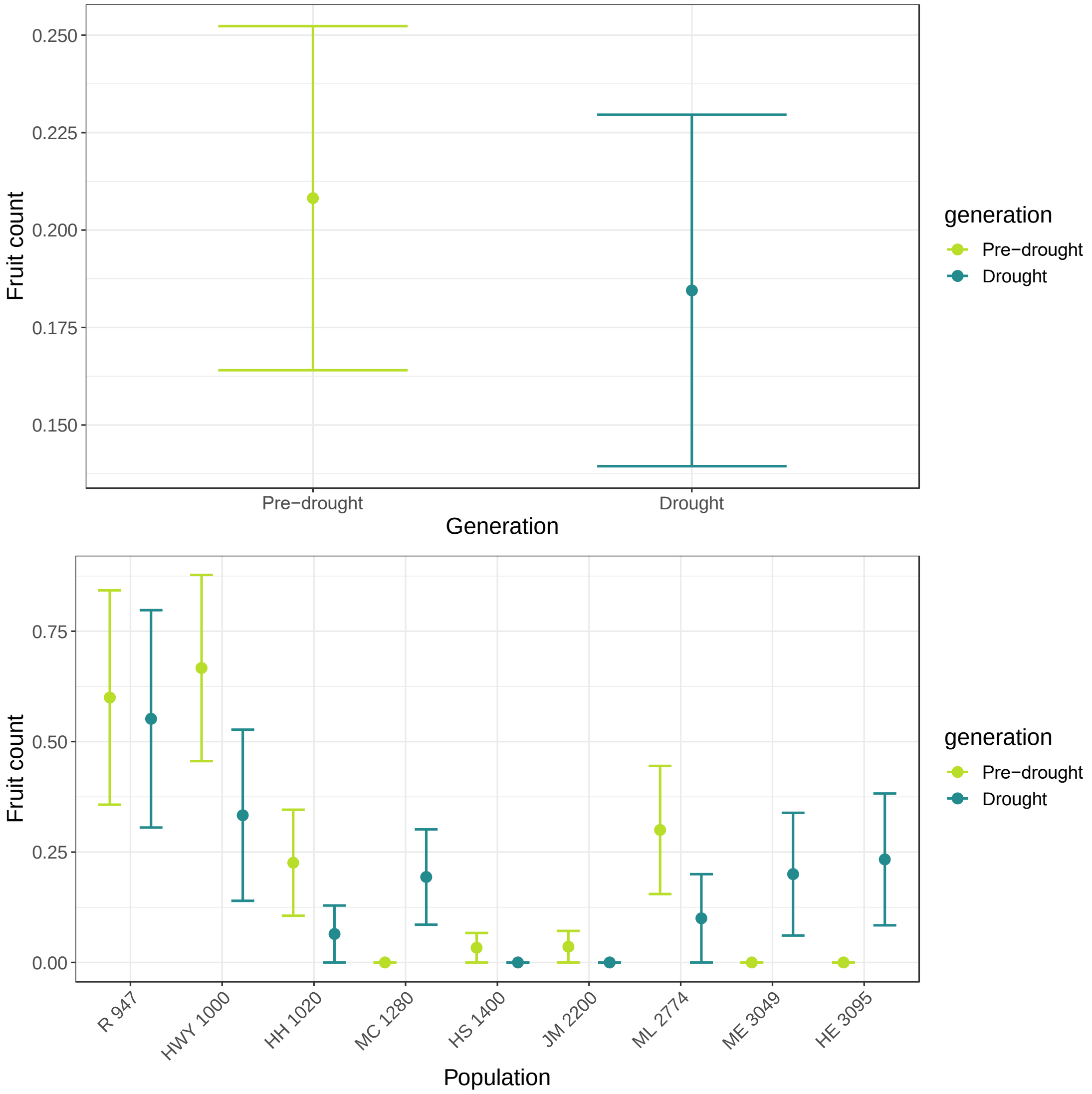


Figure 6. Fitness means by generation (top) and population (bottom) in the Hot Drought treatment. Bars represent standard error.

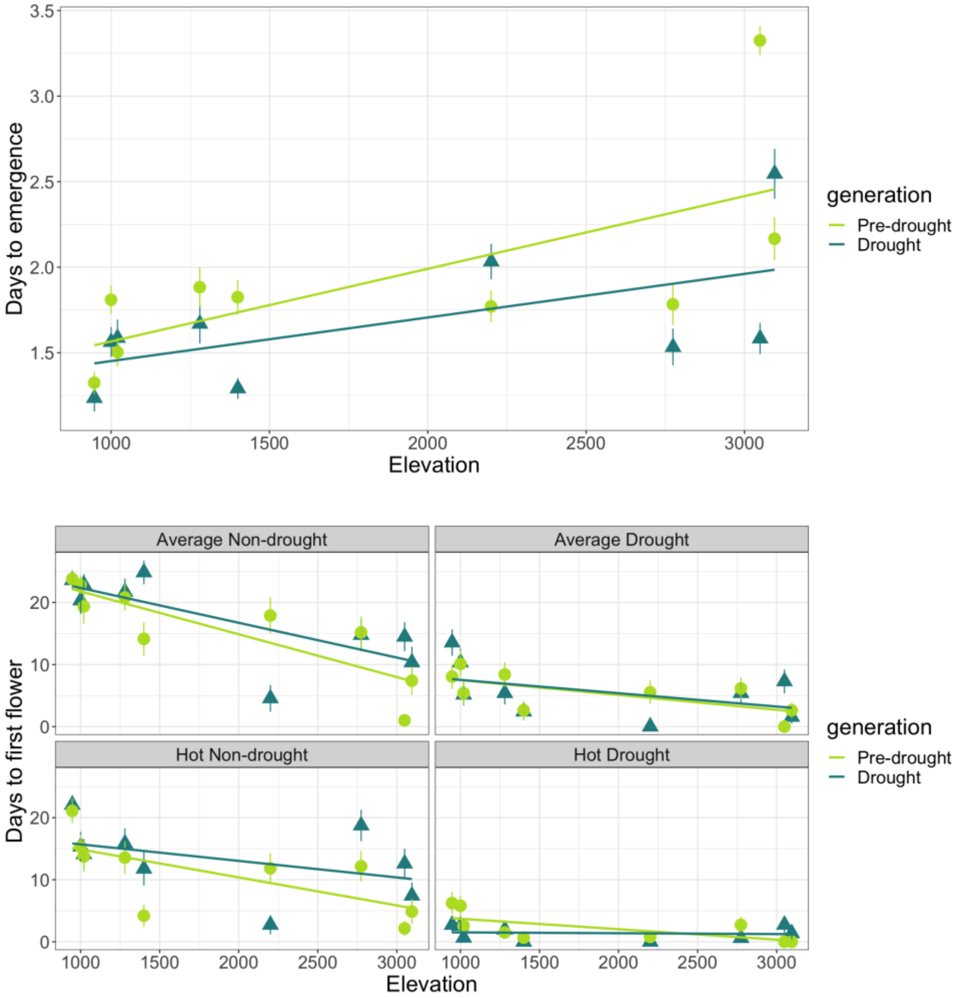


Figure 7. (Top) Days to emergence for each generation for all treatments. (Bottom) Days to first flower for each generation, by treatment. Regression trend lines on population means across elevation are plotted for reference only.

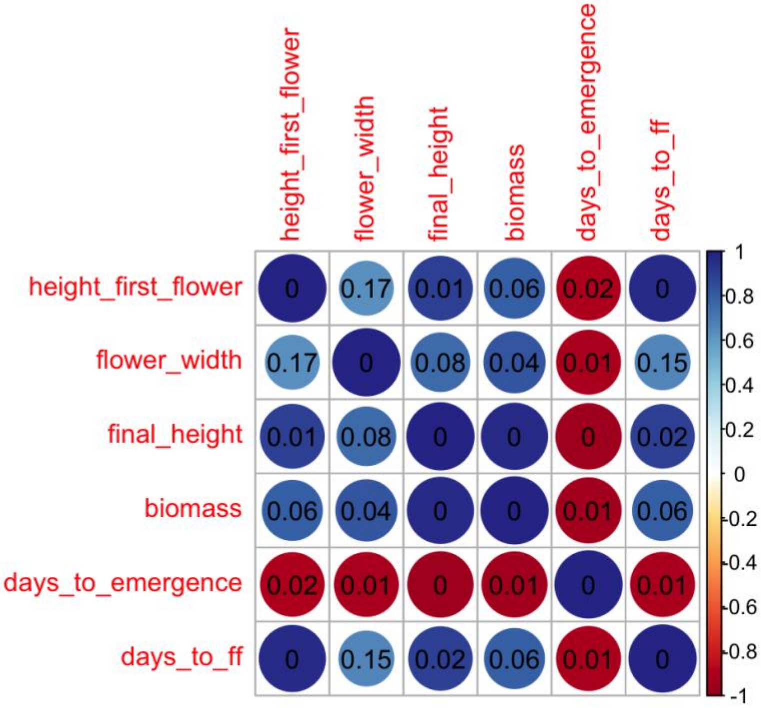


Figure 8. Correlation plot reporting p-values for traits included in the phenotypic selection analysis. Red coloring denotes a negative correlation, with blue denoting a positive correlation.

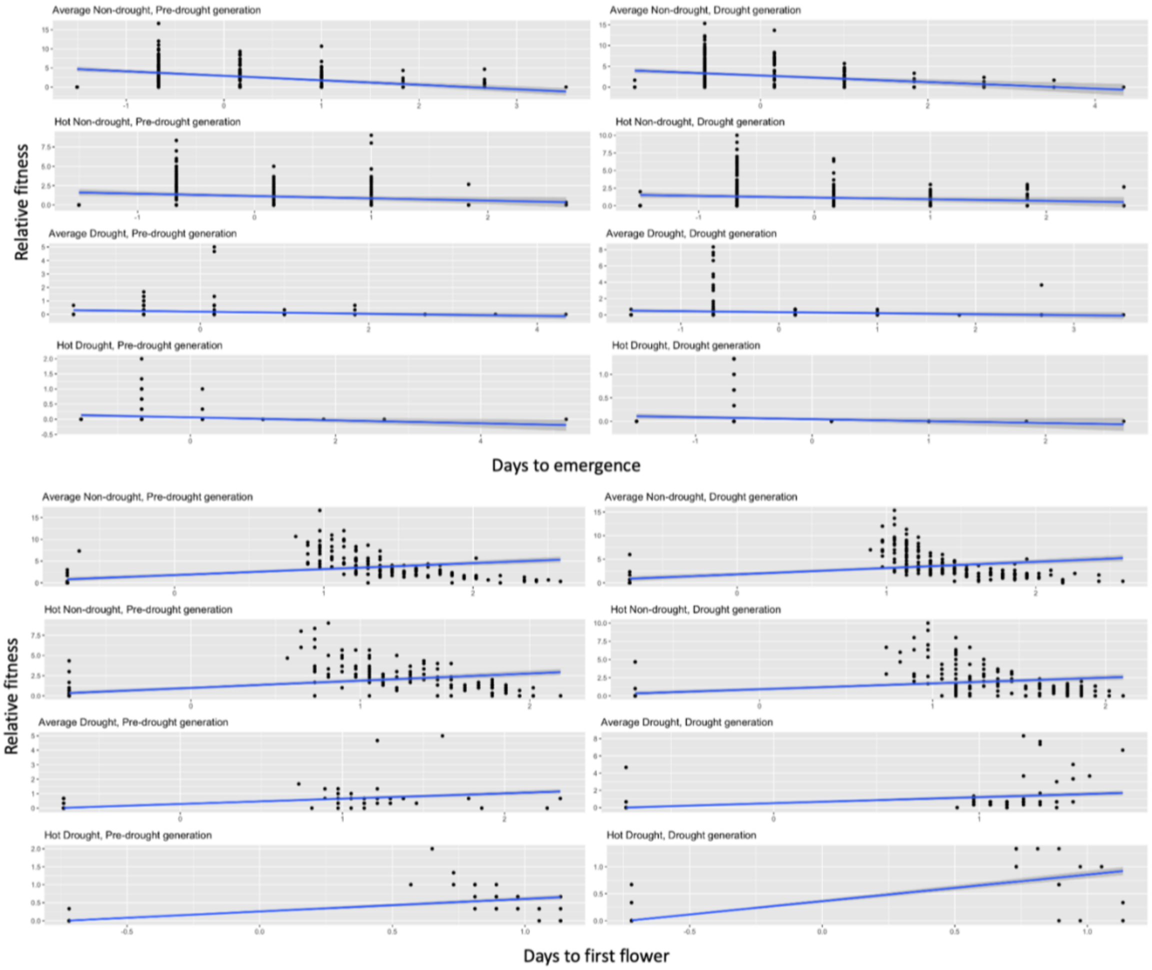


Figure 9. Selection gradients for phenology traits from multiple regression analysis, days to emergence and days to first flower. Stars indicate a significant effect. Days to emergence (top 8 graphs) and days to first flower (bottom 8 graphs) are graphed on the X-axis. Relative fitness is graphed on the Y-axis.

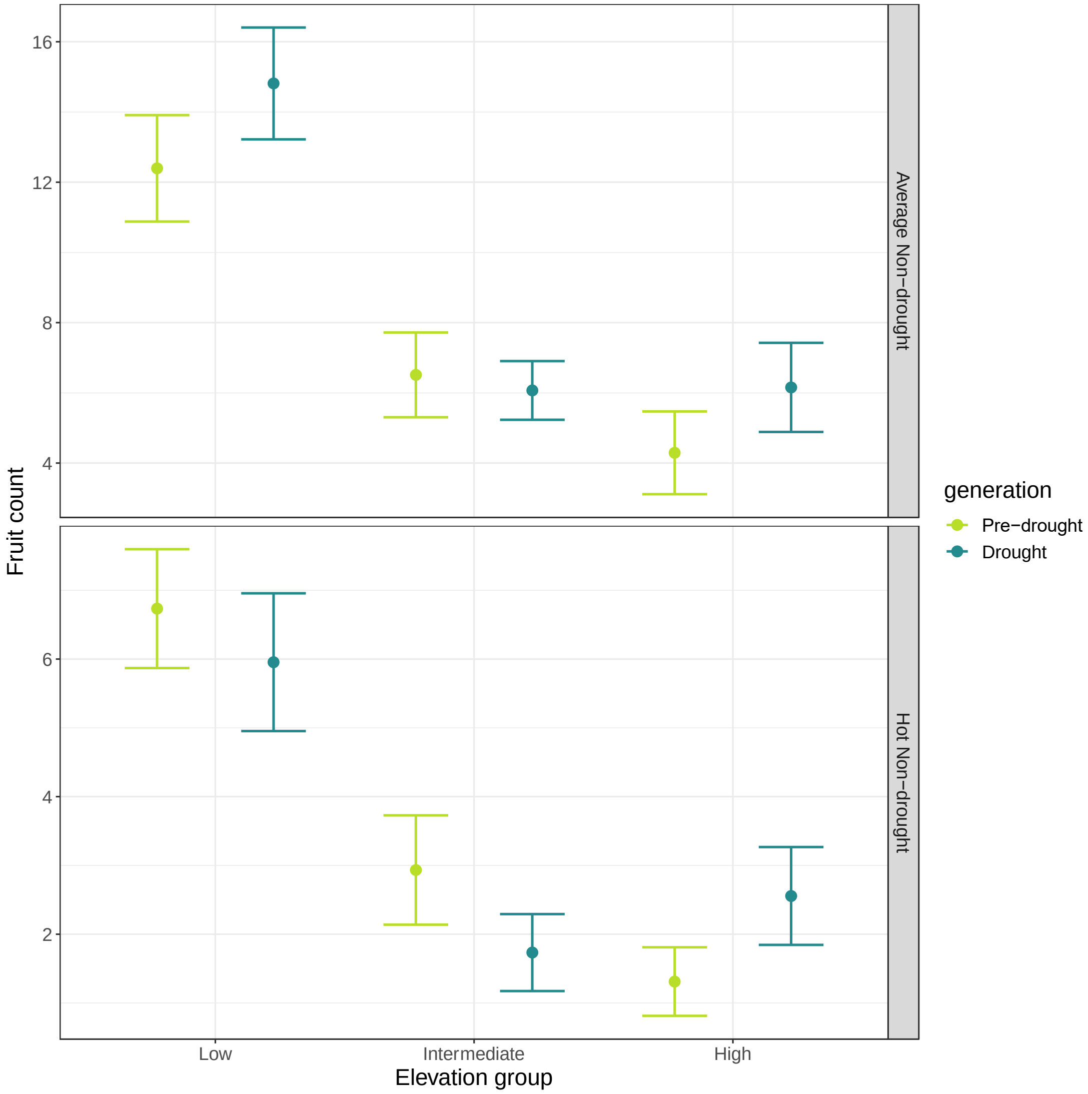


Figure 10. Fitness means by elevation group, separated by the drought treatments. Bars represent standard error. Note the Y-axis scale change between the two treatments.

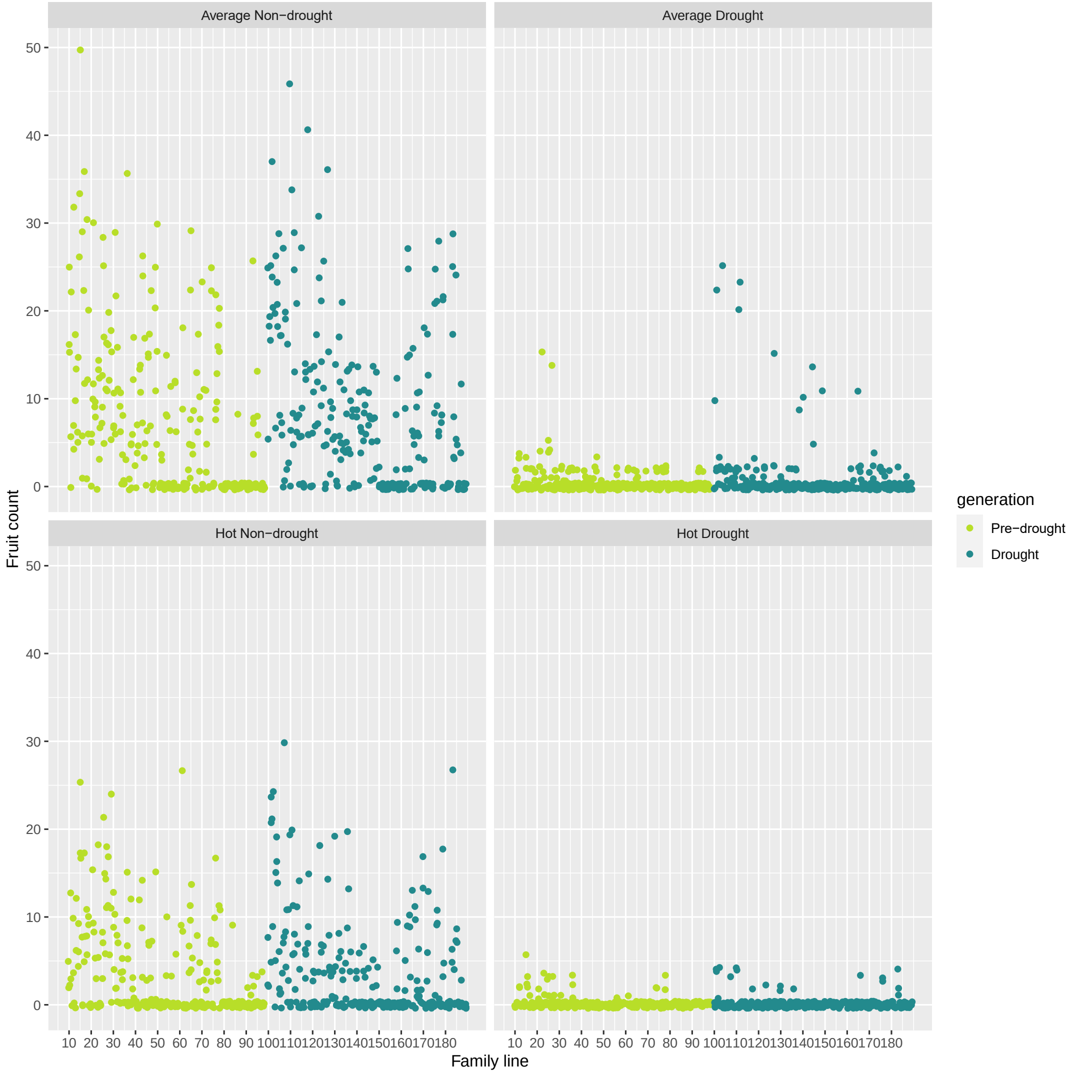


Figure 11. Raw fruit count data by family line. Family lines are numbered based on population, with the lowest number (10) being the lowest population (R – 947m) in the pre-drought generation, and the highest number (180) being the highest population in the drought treatment (HE – 3095m).

Chapter 3. Resurrected in the field: benefits of adaptation to historic drought seen mainly at the leading edge of a plant species range

3.1. Abstract

In California, contemporary climate conditions are consistently shifting from prior averages, resulting in warmer, drier summers and winters marked by severe water events and oftentimes reduced snowpack. Utilizing the ecological model organism *Erythranthe laciniata*, I designed a resurrection experiment to understand how seeds from before the 2012-2016 drought and seeds collected during the drought vary in their fitness in contemporary conditions. I implemented a common garden experiment with populations from across the species range, growing families at low-, central-, and high-elevation established populations. 2,430 plants were grown in the experiment. I recorded fruit production for each plant to estimate lifetime fitness. This experiment took place in 2021, a year marked by low precipitation and high temperatures. In these conditions, the drought generation had much higher fitness than the pre-drought generation in the high garden, while the two generations had similar fitness in the central and low gardens. I found evidence of local adaptation in high elevation populations, which had the highest fitness at the high garden. Finally, I found that overall fruit production was much lower at the lower garden than at the high garden, even for the low-elevation populations, suggesting the potential for range contraction.

3.2. Introduction

Climate change is a global issue affecting all ecosystems, making the species living in those systems vulnerable (Leemans and Eikhout 2004, Li et al 2018, Nolan et al 2018; Kannan and James 2009). In the face of climate change, understanding the ability of species to rapidly adapt to change is a major conservation concern (Anderson and Song 2020). Climate change may also exacerbate other anthropogenic factors such as habitat fragmentation (Jaureguiberry et al 2022). Plants are sessile and therefore are particularly vulnerable to rapid changes in their environment; species will either have to adapt to change, shift their ranges, or face range contraction or extinction (Aitken et al 2008; Alexander et al 2017). Climate often varies across the species range; as such, the effects of climate change will also vary (Anstett et al 2021). Thus, understanding population-level adaptability is a pressing research issue.

The Sierra Nevada of California are a biological diversity hotspot and home to a high number of endemic herbaceous plants (Myers et al., 2000), making them an ideal system to study climate change effects on plants. By the end of the century, the Sierra are expected to be 7°F warmer during the growing season with decreased snowpack (Reich et al. 2018), leading to a potentially contracted growing season due to warmer temperatures and decreased water availability imposing earlier seasonal drought. Already, the Sierra have experienced reduced snowpack and increased temperatures (Huang et al 2018).

Range limits theory suggests that adaptive responses at the cold (leading) and warm (rear) climate edges of species ranges may vary due to potential differences in abundance, gene flow, or historical effects (see Chapter 1). Plants at the leading edge of a range may be able to colonize beyond-range areas that were previously uninhabitable, while rear edge populations may face extirpation unless adaptation to warmer, drier conditions rapidly evolves. In montane environments, plants are physically limited to how far their ranges can shift upward by the height of the mountain. Further, plants may have difficulty tracking climate change due to limited dispersal (Alexander et al 2017). As conditions warm, there may be niche mismatch, especially for alpine species as conditions are changing rapidly in high elevation environments, potentially resulting in range shifts and local extirpation (Parmesan and Yohe 2006). Low-elevation populations have been shown to experience extirpation at the same rate as high-elevation colonization of newly habitable areas (Rumpf et al 2018), and in some species, upslope migration is outpacing new colonization (Mamantov et al 2018). Adaptation to warmer conditions could hold the rear edges of ranges stable where it occurs, but climate change may also eventually outpace a species' ability to adapt (Jump and Peñuelas 2005). Plants in the Sierra are already responding to climate change through range shifts and adaptation. For example, in the cutleaf monkeyflower, *Erythranthe laciniata* (formerly *Mimulus laciniatus*), adaptive changes in phenology have been observed (Dickman et al 2019, Ch. 2). Resurrection studies can detect rapid adaptation to new climates (Franks 2007, Shaw and Etterson 2012, Franks 2018, Dickman et al 2019), and rapid adaptation has been recorded in a wide variety of plants, especially invasive plants, to drought conditions and conditions not found in the home range of the plant (Franks et al 2007, Boheeman et al 2018).

Drought is a major selective force on plant populations (Chaves et al 2003), and influences the evolution of plant morphology, phenology, and physiology. Drought events can drastically increase mortality (Senf et al 2020, Marchin et al 2020, Breshears et al 2021), which can have a long-term effect on community composition and result in range contractions (Kelly and Goulden 2008). In order to adapt to drought, plants need genetic variation for selection to act on (Connor and Hartl 2004, Hoffman et al 2017). However, existing variation within populations may be constrained to traits that are adaptive to non-climatic features of the local environment, constraining local adaptation to novel climate conditions (Anderson and Wadgymar 2020). Although it is known that plants are responding to climate change, it is unclear if these changes are adaptive (increased fitness in the changed conditions) or to what degree plants can adapt.

The 2012-2016 drought in the western United States provided a natural experiment of contemporary evolution to climate change; specifically studying the impact of climate change in the Sierra Nevada provides opportunities to study climate impact across a broad climatic gradient (Tito et al 2020). The drought was extreme in both high temperatures and lack of precipitation, which both contribute to aridity (Griffen and Anchukaitis 2014, AghaKouchak et al 2016). In the mountains, the lack of snowpack was exceptional (Belmecheri et al 2016, Mote et al 2016). More than 129 million trees died during the drought (USDA 2017). However, how this drought impacted herbaceous plants in the Sierra—the majority of the plant biodiversity—is still largely unknown.

This work studies local adaptation, rapid adaptation to drought, and how rapid adaptation may affect drought in the endemic, highly self-fertilizing, Sierra Nevada forb, *E. laciniata*. Prior resurrection research on *E. laciniata* showed earlier emergence and flowering in drought generation plants, sustained after two generations, with variation in phenology across the range (Dickman et al. 2019, Chapter 2). This sustained change in phenology suggests that drought-adapted genotypes were selected for during drought.

Further, drought generations, especially those from higher elevations, experienced a reduction in trait variation after drought. This is notable because the cutleaf monkeyflower has shown evidence of local adaptation (Dickman et al 2019, Sexton et al 2011, Shay et al., *in prep*), and it is possible that drought selection has reduced locally adapted genetic variation in these populations.

Although there have been other resurrection studies performed in this genus (Vtipil and Sheth 2020. Wooliver et al 2020, Anstett et al 202, Kooyers et al 2021), this is the first common garden, resurrection field study for *E. laciniata* and, to my knowledge, it is the first range-wide field resurrection study of a native plant. I performed a climate change resurrection study in field conditions, at multiple locations across a wide climate gradient, and in range limits context. This experiment took place in a warm, dry year, providing an opportunity to test for advantages in the drought generation. I grew seeds collected before the 2012-2016 drought and seeds collected at the height of the drought in 2014 in a common garden, rangewide transplant design to address the following questions:

1. *How has evolution during historic droughts affected performance in contemporary conditions?*
2. *Has the recent severe drought affected climate adaptation and local adaptation across the species range?*
3. *Are rear edge populations more drought-adapted than populations from central and leading edge areas of the range?*

3.3. Methods

3.3.1. Study System

In this experiment I used an ecological model organism, *Erythranthe laciniata* (formerly *Mimulus laciniatus*). This plant is likely to be heavily affected by climate change for two reasons. First, it depends on spring snowmelt for water during its growing season, and precipitation as snowpack is decreasing. Second, as a self-fertilizing plant with a restricted range, it may not have sufficient genetic variation available to respond to changing conditions (Loarie et al. 2008). Here, I use a resurrection paradigm (Franks et al., 2017) in combination with a common garden study to determine the effect of drought across the species' range of this endemic plant.

3.3.2. Experimental Design

Seeds from the ancestral "pre-drought" generation were collected from 2005-2008 and seeds from the drought generation were collected in 2014 (Table 1) [see Dickman et al. 2019]. Collections from nine populations across the species' range (Fig. 1) were grown for two generations before sowing to reduce maternal effects. Populations from the species' range edge are included in this study, to examine range edge effects on adaptation. Earlier emergence and flowering of the drought generation was confirmed in a growth chamber experiment (Chapter 2).

Seeds were randomly sown into small tray blocks set into the field, as in Sexton et al. (2011), with five seeds sown per cell. Each block consisted of 3 rows and 6 columns into which a representative from each of the nine populations and each generation (9 populations x 2 generations) was sown. Sta-Green outdoor potting soil was used (Lowes, Sta-Green Potting Mix Plus Fertilizer) with a layer of sand added as a protective mulch. For both generations, each population was represented by fifteen family lines with three replicates each, for a total of 810 plants in each garden and 2,430 plants total across the three gardens. Each garden had 45 trays (blocks) placed in Fall 2020 to overwinter before the growing season.

Three gardens were established within existing *E. laciniata* populations that represent different climate bands across the range, with gardens at 1000 m, 1555 m, and 2500 m above sea level (Fig. 2). One of the garden sites, the low-elevation HWY site (Table 1), is the source of one of the nine study populations. Wildfires in 2020 prevented the use of previously planned middle and upper elevation garden sites that also represented wild populations in the study, so alternate locations that also host natural popualtions of *E. laciniata* were established. Data were collected in Spring 2021—the 2021 water year was considered to be drier and warmer than average (CDWR 2021) (Fig. 3). I visited each garden at least four times to collect germination and phenology data, thin trays of excess sprouts, and to maintain the experiment over the course of the growing season.

3.3.3. Data Analysis

All analyses were performed in R 4.3.1. I used fruit count as a proxy for lifetime fitness. In the analyses, population elevation was treated as a continuous variable, while garden, generation, and population group (i.e. low, central, and high) were coded as categorical. Population group and population elevation were not used in the same model together. The trays that the plants were grown in are treated as a random effect, nested in garden. Significant effects were determined using the LR test function in the lmtest package in R. Significance was set at 0.05.

3.3.3.1. How has evolution during climate change affected performance in contemporary conditions?

I assessed differences in fitness between the two generations using a generalized linear model with a poisson distribution. I modeled fruit production on population elevation, garden, generation, and their interactions, with tray nested in garden as a random effect.

I also modeled differences in survival between the two generations. I created a binary survival variable where individuals that survived to fruiting received a 1 and all others 0. I then used a generalized linear model with a binomial distribution family, regressing survival on population elevation, garden, generation, and their interactions, again with tray nested in garden as random effect.

3.3.3.2. Has the severe drought affected climate adaptation and local adaptation across the species range?

One definition of local adaptation is populations having higher fitness at their home environments than when they are grown away from their home environment; this is known as the home versus away definition (Blanquart et al 2013). I used two approaches to testing local adaptation in this study. The first is a direct test using home versus away:

I compared the fitness of both generations of the HWY population at the HWY garden to the HWY population at the central (TBD) and high (TL) elevation gardens using a post-hoc test on both the fitness and survival regressions from above.

The second test is an indirect approach. Due to fire conditions in 2021, I wasn't able to have my central and high gardens at populations that are represented in the study. So, in order to test for local adaptation, I grouped the nine populations in the study into three groups—low, central, and high—based on population elevation. Then, I reran the fitness models using these elevational groupings in place of population elevation. Finally, I used a post-hoc Tukey test on this linear model to compare the fitness of each elevational group at each garden.

3.4. Results

3.4.1. How has evolution during climate change affected performance in contemporary conditions?

Fitness is strongly affected by population elevation, generation, garden, and their three-way and two-way interactions (Table 2). The drought generation had higher fitness in the high elevation garden, but lower fitness in the low elevation garden, with the two generations having similar fitness in the central garden (Fig 4, top). Almost all populations had higher fitness at the high garden. The drought generation of a population also tended to have higher fitness than the pre-drought generation. Fitness in the pre-drought generation decreased as garden elevation increased (Fig. 4, bottom).

The drought generation had higher survival in all gardens, with the most pronounced difference in the high garden (Fig. 5, top). Survival was impacted by population elevation, garden, generation, and the interaction between population elevation and generation (Table 3). Lower elevation populations in the low elevation had slightly higher fitness in the pre-drought generation, whereas high elevation populations had higher fitness in the drought generation. Overall, the drought generation had more consistent survival whereas the pre-drought generation had lower survival in the high elevation populations and more variability across the range (Fig. 5, bottom).

3.4.2. Has the severe drought affected climate adaptation and local adaptation across the species range?

For the HWY population, fitness was greatest at the high garden for both generations, with the drought generation having a greater magnitude increase at the high garden compared to the central and low gardens (Fig. 6). Pre-drought generation HWY plants had highest mean fruit counts at the central garden—however, this difference was not detected as significant in the post-hoc test. Regardless, this test would suggest the HWY population is no longerlocally adapted or is mismatched to its home environment (the low-elevation garden), as it performs better away.

The pre-drought and drought generations followed the same patterns in each elevation group—that is, the low group had the highest fitness in the central garden and the central and high groups had the highest fitness in the high garden (Fig. 7). Fitness varied significantly by generation, garden, elevation group, and their interaction (Table 4). There was very little difference between the generations in the low elevation group; the pre-drought generation had higher fitness in each garden in the central group, and the drought generation has higher fitness in the high elevation group. Fitness at all gardens was significantly different (Table 5). The only group that showed a signal of local adaptation was the high group, and in fact the drought generation in the high group had much higher fitness at the high garden than the pre-drought generation, suggesting that high-elevation populations are adapting to recent drought stress.

3.5. Discussion

In this study I detected rapid adaptation to drought in field conditions. These results suggest that wild populations are evolving rapidly to the new conditions climate change is imposing—however, declining fitness at lower elevations signals that this evolutionary change may not be enough to mitigate the effects of climate change at the warmer, drier parts of the range, potentially resulting in range contraction.

3.5.1. Fitness

The experiment took place during a warmer and drier than average year—which is expected to be more common as climates warm (Mallakpour et al 2018). In these conditions, it is expected that if rapid adaptation to drought occurred during the “big drought,” that the drought generation would have higher fitness (Franks et al 2007). The drought generation had higher fitness, but only in mid- and high-elevation gardens. Fitness was much higher in the drought generation in the high garden, while at the central garden the two generations had similar fitness, and at the low garden the pre-drought generation had slightly higher fitness.

Survival was higher for the drought generation across gardens and was highest for both generations in the high garden. However, overall survival of germinated seedlings was low—fewer then 50% of all individuals planted survived to produce fruit. In a warm, dry year this is not surprising. However, if populations exhibit such reductions in survival year after year, extirpation is possible, potentially resulting in range contraction. Range shifts as a result of climate change have been documented in the Santa Rosa Mountains of southern California. A comparison of surveys between 1977 and 2007 revealed an upward trend in the elevation centers of tree species distributions, a result of population reductions at lower elevations (Kelly and Goulden 2008). In many montane environments, climate change is thus far resulting in increased biodiversity as plants are able to track change and shift their ranges (Dornelas et al 2014), and sometimes resulting in the formation of novel communities (Williams and Jackson 2007). However, *E. laciniata* lives in a harsh environment, which few other species can tolerate. For this species and other herbaceous plants like it, understanding fitness responses to climate change will be critical for their conservation.

Climate responses of self-fertilizing plants is an area of research need (Wright et al 2013). The transition to self-fertilization from outcrossing is common in plants, and around 15% of flowering plants are self-fertilizing (Barrett 2002). Self-fertilization is advantageous where mates or pollinators are scarce, but also has the potential to limit adaptability due to a lack of diverse recombinants. Additionally, climate change has the potential to disrupt plant-pollinator relationships, resulting in even higher selfing rates for plants (Eckert et al. 2010). This study addresses a gap in our understanding of self-fertilizing plants and their ability to respond to climate events—historic drought, in this case.

Across the range, each population showed its own pattern of fitness variation, and it was not always the drought generation that has higher fitness. In some populations, the pre-drought generation had higher survival and fitness than the drought generation—this, along with the significant effect of population elevation in both models, suggests that populations had varying evolutionary responses to drought (Fig. 4 and 5). Population response to climate change is variable and can lead to contrasting evolutionary fates across a species' range (Tredennick et al 2016). Responses in *E. laciniata* populations loosely follow those modeled in the endangered alpine plant, *Argyroxiphium sandwicense*—the results of which show decreased population stability and size at lower elevations but more robust populations at higher elevations (Fortini et al 2022). Variable population responses can muddle species response predictions and can require specific modeling based on local climate estimates (Tredennick et al 2016).

3.5.2. Local adaptation

Recent climate change may be eroding patterns of local adaptation in the warmer areas of species ranges as the climates there become more stressful over time. Although the low populations have worse fitness at the low garden—including the HWY population growing at its home population—in both generations, lower elevations have higher fitness at the central garden. For instance, Shay et al. (*in prep*) showed low elevation populations having higher in high elevation garden, and Chapter 2 showed low elevation populations having the highest fitness in average, mild growth chamber environments—cooler and wetter than what those populations currently experience in the wild. However, high elevation populations show strong local adaptation, both in Shay et al. and in the current study. This finding partially supports expectations outlined in a meta-analysis (Bontrager et al 2021), which reported that adaptation may be constrained at range edges due to reduced habitat quality. The low garden is hotter and drier than the other gardens in the study and is similar to other low elevation populations. However, Bontrager et al. (2021) found that local adaptation was reduced at high elevation populations, either due to the age of the population or reduced genetic variation; here I find that high elevation populations show the strongest signal local adaptation.

In *Silene cilata*, drought stress induced high mortality across the species range (Giménez-Benavides 2007), similar to the survival results of this study. However, in *S. cilata* it was found that gardens in the center of the species range had the highest survival, which is opposite to the findings here of highest survival at the high garden. It could be that in *E. laciniata*, climate change is negatively impacting the low elevations while making higher elevations more favorable. This study provides evidence of local adaptation persisting at high elevations despite extreme climatic disruption.

3.6. Conclusion

To my knowledge, this is the first resurrection study to take place in the field with a native plant in a range-wide, climate change context. Field studies can be unpredictable—there are always variables that will be uncontrollable. Nevertheless, field studies provide important insight into what is happening on the ground at populations, and in this case, provide a real-world test of local adaptation and fitness variation. This study shows that rapid adaptation to extreme drought confers fitness in contemporary, high elevation conditions. Further, all populations had higher fitness at the high elevation garden, suggesting that higher elevations are becoming more suitable and less harsh as the climate warms. This is consistent with our growth chamber experiment, which found that “hot drought” conditions severely reduced fecundity (Chapter 2). Reduced fruit production at lower elevations may hint at future range contraction. However, overall, the results show that this restricted range, self-fertilizing, endemic plant has the adaptive potential to persist under climate change.

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Tables

Table 1. Population information with collection dates for the pre-drought and drought generation.

Population Code	Population Name	Elevation (meters)	Pre-drought Collection Year	Drought Collection Year
R	R Property	947	2006	2014
HWY	HWY 168	1000	2006	2014
HH	Poopenaut Valley	1020	2006	2014
MC	McLeod Flat	1280	2006	2014
HS	Hetch Hetchy Sign	1400	2005	2014
JM	Jackass Meadow	2200	2008	2014
ML	May Lake	2774	2006	2014
ME	Mammoth Edge	3049	2006	2014
HE	Hilgard Edge	3095	2006	2014

Table 2. Results of from the generalized linear model of fitness modeled on population elevation, generation, garden, and their interactions.

Fixed Effect	DF	Log Likelihood	Chi^2	P value
Interaction	12	-1627.2	131.82	< 0.001
Generation	11	-1628.5	134.45	< 0.001
Garden	10	-1670.3	218.05	< 0.001
Population elevation	4	-1656.9	191.13	< 0.001
Pop. Elevation*Garden	28	-1595.4	63.551	< 0.001
Pop. Elevation* Generation	20	-1600.8	52.755	0.04
Generation*Garden	14	-1624.1	6.2366	< 0.001

Table 3. Results of the logistic model of survival regressed on population elevation, generation, garden, and their interactions.

Fixed Effect	DF	Log Likelihood	Chi^2	p value
Interaction	12	-758.61	59.872	0.036
Generation	11	-759.93	62.51	0.027
Garden	10	-778.68	100.01	< 0.001
Population elevation	4	-776.3	95.253	< 0.001
Pop. Elevation*Garden	28	-745.5	26.212	0.051
Pop. Elevation* Generation	20	-748.53	20.165	0.01
Generation*Garden	14	-757.58	2.057	0.3573

Table 4. Results from the generalized linear model of fitness regressed on elevational group, generation, garden, and their interactions.

Fixed Effect	DF	Log Likelihood	Chi^2	P value
Interaction	6	-1647.4	64.633	< 0.001
Generation	5	-1648.8	67.288	< 0.001
Garden	4	-1690.5	150.86	< 0.001
Elevation Group	4	-1656.9	83.511	< 0.001
Elevation Group*Garden	10	-1625.8	43.3	< 0.001
Elevation Group* Generation	8	-1638.6	17.634	< 0.001
Generation*Garden	8	-1644.3	6.3124	0.043

Table 5. Results from the post-hoc Tukey Tests on the GLM of fitness regressed on elevational group, generation, garden, and their interactions.

Elevation Group	Contrast	p value	
Low Group			
	Low Drought / High Drought	< 0.0001	
	Low Drought / Central Drought		0.0321
	Low Pre-Drought / Central Pre-Drought		0.0321
	HWY Pre-Drought / High Pre-Drought	< 0.0001	
Central Group			
	Low Drought / Central Drought		0.0321
	Central Drought / High Drought	< 0.0001	
	Central Pre-Drought / High Pre-Drought	< 0.0001	
	Low Pre-Drought / Central Pre-Drought		0.0321
High Group			
	Low Drought / High Drought	< 0.0001	
	Central Drought / High Drought	< 0.0001	
	Low Pre-Drought / High Pre-Drought	< 0.0001	
	Central Pre-Drought / High Pre-Drought	< 0.0001	

Figures

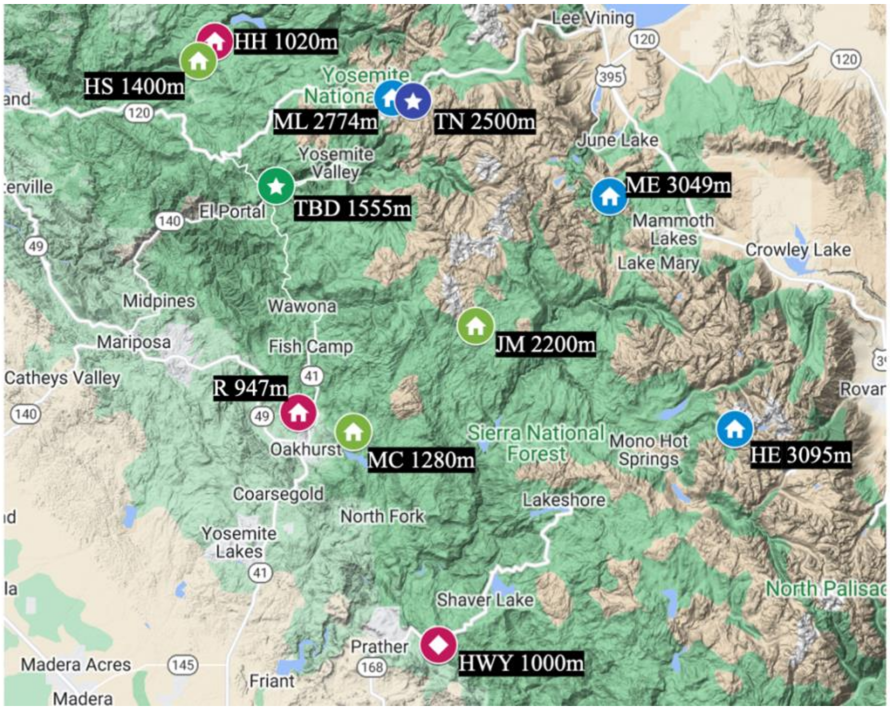
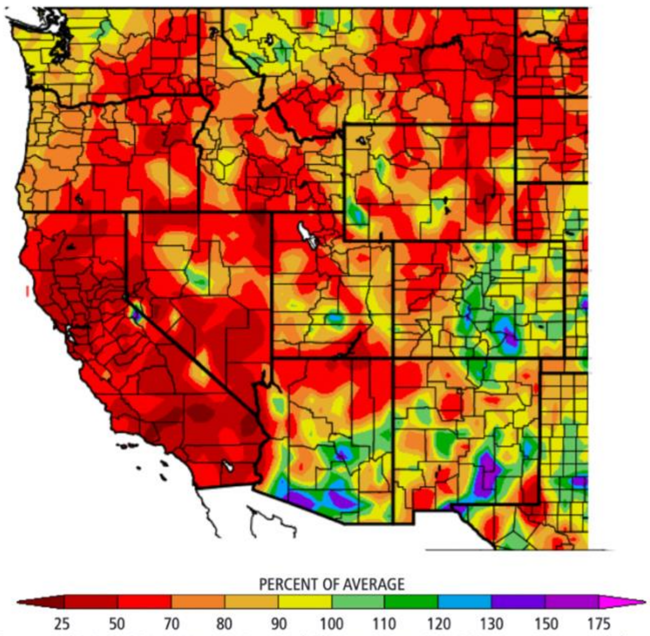


Figure 1. Map of the source populations and garden locations. Collection sites are marked with a house symbol and with elevation groups marked by color: Low = red, Central = green, High = blue. The low garden is marked with a diamond as it is a garden as well as a source population. The other two gardens are marked with a star.

Figure 2. Trays at the HWY garden (left), TBD garden (center), and TL garden (right), with an inset picture of a monkeyflower growing in a tray between the HWY and TBD pictures.

Water Year 2021 was California's second driest year based on statewide precipitation. (Water Year 1924 was California's driest year for that metric.)



Generated 9/16/2021 at Western Regional Climate Center (WRCC) using provisional data.

Figure credit: Western Regional Climate Center

Figure 3. Statewide precipitation shown as percent of average precipitation. Figure taken from California Department of Water Resources, originally from Western Regional Climate Center.

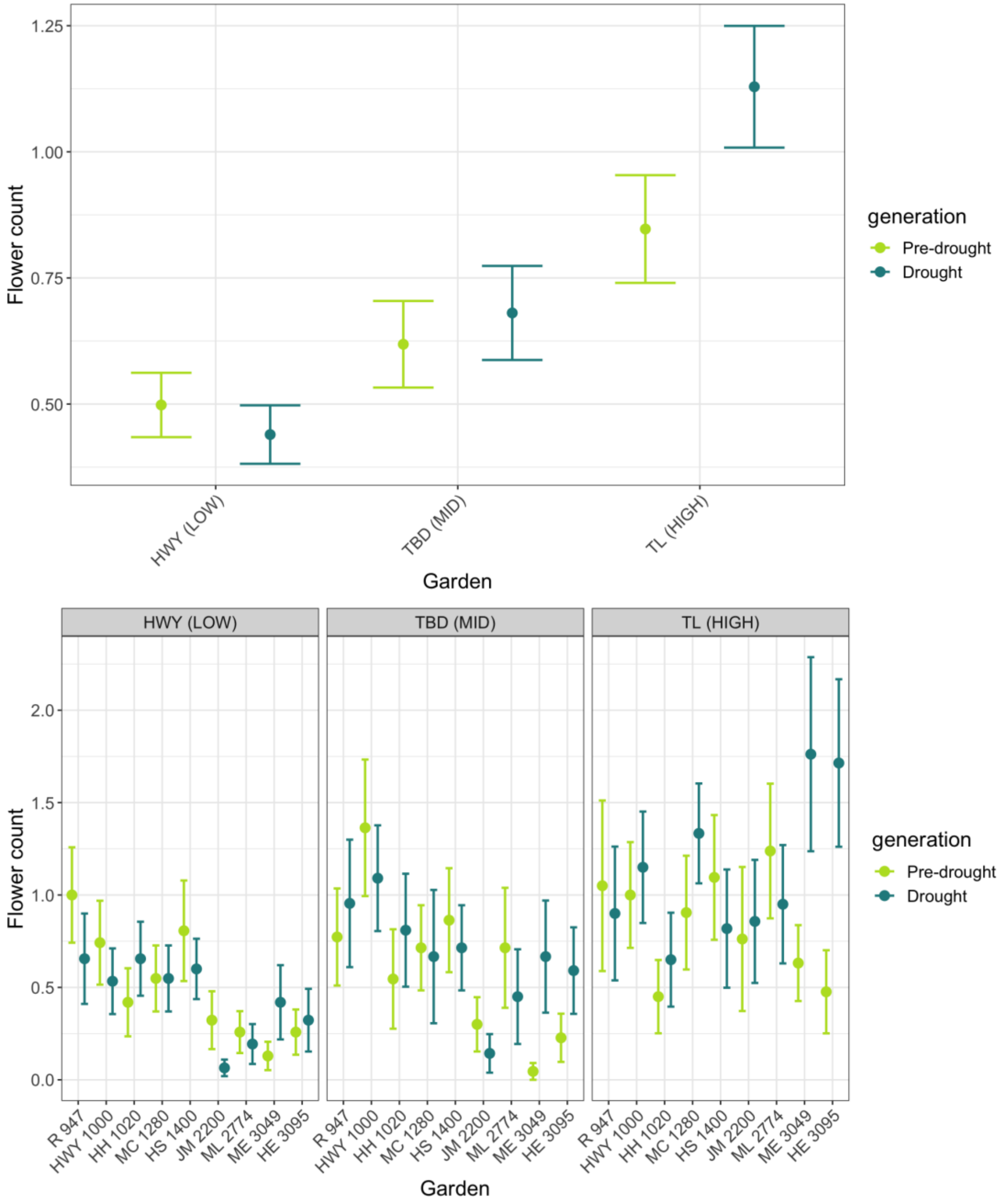


Figure 4. (Top) Mean flower counts at each garden with pre-drought generation in green and drought generation in blue. Bars represent the standard error. (Bottom) Mean flower counts at each population, by garden.

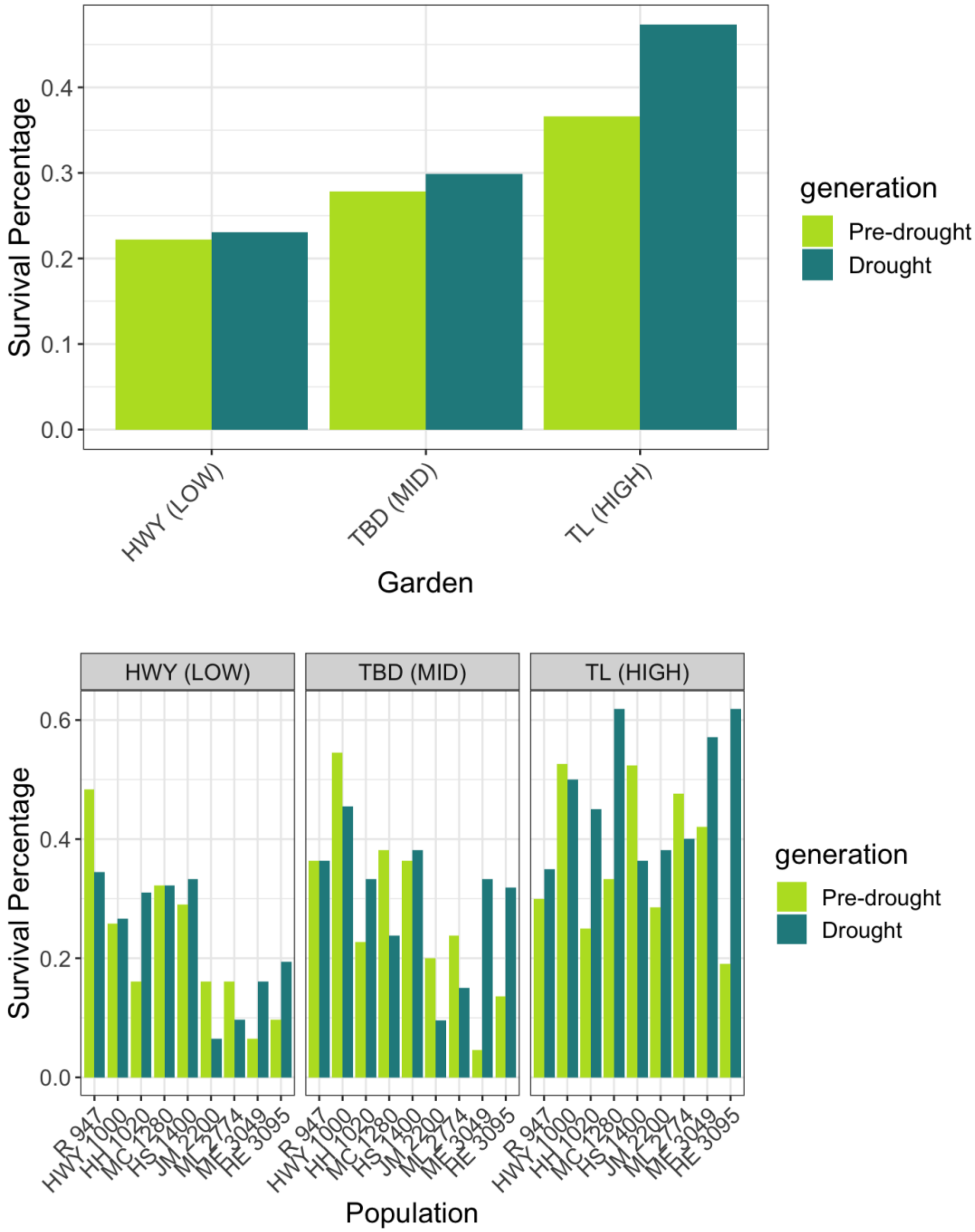


Figure 5. (Top) Survival represented as percentage of seeds sowed that survived to fruiting, at each garden. Pre-drought generation is in green and drought generation is in blue. (Bottom) Survival at each garden, by population.

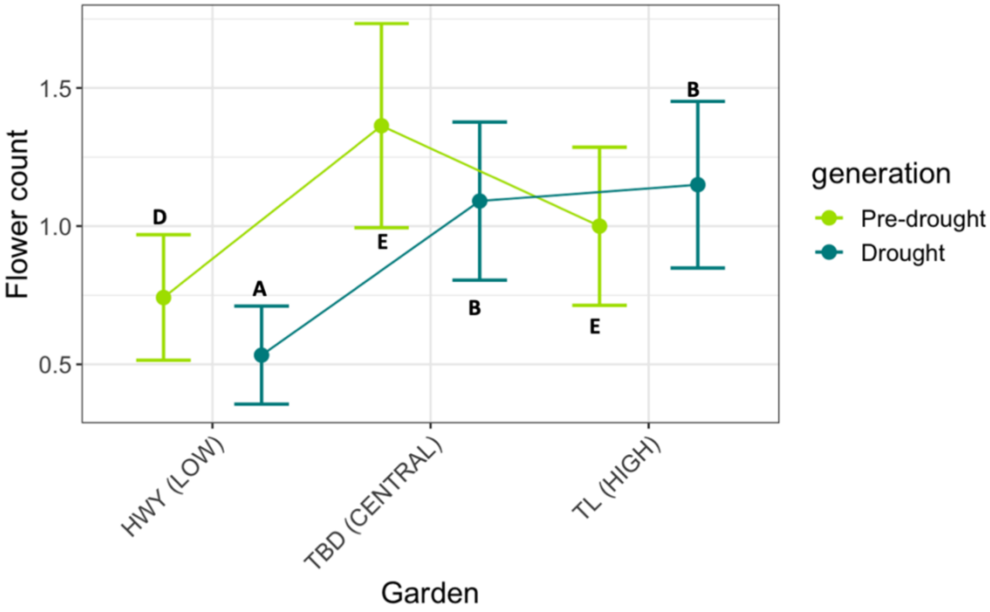


Figure 6. Reaction norms for just the HWY population at its home garden vs away gardens, for each generation. Letters represent similarity results from the post-hoc Tukey test. The pre-drought and drought generations are significantly different from each other at the low garden, and significantly different to the two generations at the central and high garden (p = < 0.001).

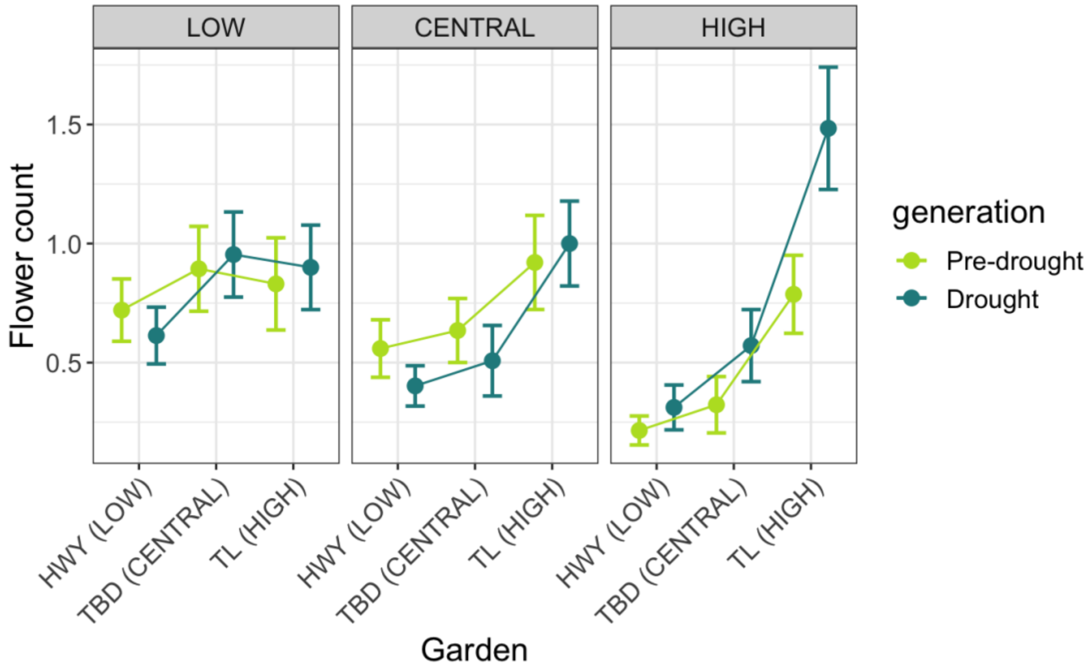


Figure 7. Grouped reaction norms by elevation group for each generation at each garden. Bars represent 1 standard error.

Chapter 4. How is adaptive potential distributed within species ranges?

4.1. Abstract

Quantitative genetic variation (QGV) represents a major component of adaptive potential and, if reduced toward range-edge populations, could prevent a species' expansion or adaptive response to rapid ecological change. It has been hypothesized that QGV will be lower at the range edge due to small populations—often the result of poor habitat quality—and potentially decreased gene flow. However, whether central populations are higher in QGV is unknown. We used a meta-analytic approach to test for a general QGV-range position relationship, including geographic and climatic distance from range centers. We identified 35 studies meeting our criteria, yielding nearly 1000 estimates of QGV (including broad-sense heritability, narrow-sense heritability, and evolvability) from 34 species. The relationship between QGV and distance from the geographic range or climatic niche center depended on the focal trait and how QGV was estimated. We found some evidence that QGV declines from geographic centers but that it increases towards niche edges; niche and geographic distances were uncorrelated. Nevertheless, few studies have compared QGV in both central and marginal regions or environments within the same species. We call for more research in this area and discuss potential research avenues related to adaptive potential in the context of global change.

4.2. Introduction

Climate change is affecting the evolutionary trajectory of natural populations (Parmesan and Yohe 2003), and the ability of populations to respond to change relies on their adaptive potential (Lynch and Walsh, 1998; Conner and Hartl 2004). Adaptive potential depends mainly on the amount of quantitative genetic variation (QGV) in a population, as it is largely this variation upon which selection can act (Lande and Shannon 1996). The geographic distribution of genetic variation could either facilitate adaptation and range expansion or constrain adaptive evolution (Lande and Shannon 1996; Kawecki 2008). Low QGV could thus limit genetic adaptation and niche evolution at species range margins (Holt and Gomulkiewicz 1997; Pujol and Pannell 2008), preventing range expansion (Hoffman and Blows 1994; Eckert et al 2008; Sexton et al 2011). Despite this implication, QGV remains relatively unexplored across geographic and niche space contexts and is a missing piece in our understanding of species ranges. The limits to a species' geographic range are difficult to explain where no discrete environmental or geographic barriers exist (Sexton et al 2009). Range limits, where species transition from being present to being absent, can represent frontiers of evolutionary change (Brown et al 2014) or the manifestation of limits to adaptation (Hoffman and Blows 1994; Bridle and Vines 2007; Hargreaves et al 2014; Lee-Yaw et al 2016). These margins are therefore important for understanding the underlying causes of species distributions and their potential responses to environmental change. Conversely, central regions of species ranges may be areas of stability or equilibrium—where populations are well within the geographic territory where their climatic niche is manifested (Brown 1984; Hampe and Petit 2005; Lira-Noriega and Manthey 2014). In this vein, identifying general patterns across species ranges would be useful for understanding the processes, mechanisms, and constraints that dictate the ecology and evolution of species' distributions.

QGV across species ranges could vary due to a variety of interacting factors (discussed in Eckert et al 2008; Pironon et al 2016). The major processes of evolution affect QGV at the population level. Variable selection regimes across the range of a species might drive differences in QGV patterns (Antonovics 1976). For example, classical genetic theory suggests that directional selection, which may be greater towards range limits, should deplete QGV as alleles conferring higher fitness rapidly become fixed, resulting in a narrower range of trait values (Kimura 1958; Bulmer 1971). QGV can also be depleted by strong stabilizing selection (Bulmer 1971; Houle 1992; Lande and Shannon 1996), which may be more prevalent in central areas of species ranges (Sexton et al 2009). Further, genetic drift may also deplete QGV in small populations. Small population size may reduce adaptive potential by genetic mechanisms in addition to drift, such as inbreeding depression (Hoffman et al 2017), and so population size may be critically linked to QGV across species ranges. Finally, gene flow may be limited in more marginal populations if they receive gene flow from fewer sources, whereas central populations may benefit from gene flow from many sources (Garcia-Ramos and Kirkpatrick 1997). Thus, QGV may be reduced in such situations.

In addition to being influenced by the above effects, genetic variation might not be expressed because of inherent limits– that is, certain phenotypes might simply be unable to emerge by the available standing genetic variation, or the expression of genetic variation may be dampened by poor environmental quality resulting in developmental constraints (Charmantier and Garant 2005). Furthermore, not all traits should be considered equal: different trait types might show different patterns in QGV across species ranges where the strength and type of selection may vary. For instance, fitness-related traits, such as fecundity, generally exhibit lower heritability than other trait categories (e.g., morphological traits) (Mousseau and Roff 1987). Fisher's Fundamental Theorem of Natural Selection (1930) predicts that this is a result of fitness-related traits being under greater selection pressure. Thus, variance in fitness traits should predict a population's immediate capacity for adaptation (Shaw and Etterson 2012), but fitness may have lower heritability than other trait types. These theories and observations lead to the question: are there predictable patterns of QGV across species ranges?

Based on theory and empirical findings to date, we describe three conceptual models (hypotheses) for how QGV may be distributed across a species range, acknowledging that other scenarios are possible: a null model, a center effect model, and an edge effect model (Fig. 1). First, the null model describes a scenario where population size is randomly or unpredictably distributed across the species range, gene flow is generally equal and non-directional, and populations are equally likely to be adapted (e.g., Tigerstedt 1973; sensu Gotelli and Graves 1996). Thus, any population in the species range has the potential to be high or low in QGV and range or niche position does not predict QGV. Second, a center effect model describes a decrease in population size away from the center of the geographic range (Brown 1984) or climatic niche (Lira-Noriega and Manthey 2014), in accordance with the abundant center hypothesis (ACH). The ACH has often been invoked to explain how species' range limits may evolve, including adaptive constraints, via a lack of genetic variation in marginal populations, or a surplus of maladaptive genetic variation through swamping gene flow (Eckert et al 2008; Kawecki 2008; Sexton et al 2016; although see Polechová and Barton 2015). The ACH has been disputed as a general phenomenon for lack of evidence, although this pattern is found in some species (Sagarin and Gaines 2002; Sexton et al 2009; Pironon et al 2016; Dallas et al 2017); but, consistent with some ACH predictions, neutral genetic variation shows a negative relationship with distance from the niche center (Lira-Noriega and Manthey 2014) and declines in the geographic peripheries of many species ranges (Eckert et al 2008). Nevertheless, such patterns could also arise from increased isolation near range limits as potential sources of gene flow are reduced (Eckert et al 2008). Moreover, quantitative trait differentiation is not strongly correlated with measures of neutral genetic variation (McKay and Latta 2002; Mittell et al 2015) and thus, whether adaptive genetic variation decreases for ecologically relevant traits away from central regions is still unknown (Hoffman and Kellermann 2006; Kawecki 2008; Gould et al 2014).

Third, an edge effect model combines aspects of the null and center effect models. It describes a scenario where populations have random or unpredictable patterns of QGV across the species range, similar to the neutral model, but then QGV falls precipitously in the most marginal populations due to increased directional selection at the edge (described above), increased isolation, increased drift related to reduced habitat suitability (Hoffman and Blows 1994; Polechová 2018), or a combination of the above (Fig.1). Several analyses have accommodated such platykurtotic distributions (i.e. a steep drop-off in fitness and abundance at the edge; see Sagarin and Gaines 2002; Samis and Eckert 2007). It is important to note that the above conceptual models assume range equilibrium, or stasis, between the range and the niche. Nevertheless, range disequilibrium processes have been occurring due to contemporary climate change (reviewed in Sexton et al 2009). This is creating "leading" cool edges, where species ranges are expanding due to the release of cold-climate niche constraints, and warm "rear" (or sometimes "trailing") edges, where the warmest regions of species ranges are heating up and causing local extinctions (range contractions) or pushing such warm-edge populations to new limits of adaptive response (Hampe and Petit 2005; de Lafontaine et al 2018; Angert et al 2020). Thus, not all edges are necessarily equal. How and whether QGV patterns differ in cool and warm edges of species' ranges under rapid climate shifts, and how this may affect modern adaptive species responses, is an open and important question. For example, QGV could be inflated in warm edges that represent glacial refugia and lower in cool edges that represent post-glacial colonization (see Hampe and Petit 2005), but we can also envision scenarios where cool edges become enriched due to new migration or gene flow as a result of climate warming. Nevertheless, we were unable to address such questions (and we do not include such scenarios in Fig. 1) due to a lack of studies that permit testing disequilibrium hypotheses (see Discussion).

Understanding patterns in QGV may provide clues to general mechanisms of the formation of species range limits and species resilience under global change. We gathered published estimates of QGV to test whether adaptive potential decreases from the center to the margins of species' geographic range or niche. We took several analytic approaches to test for a general QGV-range position relationship, including geographic and climatic niche distance from range center (hereafter "distance") and type of QGV estimate among a variety of trait categories. We did not find consistent evidence for greater adaptive potential near species range centers for geographic nor niche distances. Few studies have sampled QGV approaching range limits in comparative range contexts (e.g., warm vs cool edges or edge vs center), likely due to sample sizes required for quantitative genetic analyses and the large number of traits that could be important for adaptive potential. Insightful studies are emerging (e.g., Paccard et al 2016; Sheth and Angert 2016), but there are clear and important research gaps to be filled by future studies.

4.3. Material and Methods

4.3.1. Literature search and QGV estimation

We used two approaches to compile our dataset of studies measuring QGV in multiple populations of a species. First, we searched the literature using the ISI Web of Science database, with the search terms [narrow sense heritability OR broad sense heritability OR additive genetic variation] and [population] in October 2014. This literature search was updated in October 2019, and although new studies with estimates of QGV were found, they were not included as they did not include samples across the species' range and were unlikely to change the results of the analyses. Second, we retrieved all publications citing two relevant reviews (Hoffmann and Kellermann 2006; Eckert et al 2008). This search procedure yielded a total of 1567 unique references that were checked for suitability according to three criteria: (1) QGV was measured in two or more populations; (2) the set of populations had a total geographic range of at least 10 km; (3) the species had at least 10 georeferenced occurrence points in the Global Biodiversity Information Facility. Although 10 records were the minimum for study inclusion, most studies had many more records: median n = 1,084, max n = 75,526 (Appendix 2). Occurrences were truncated to one per grid cell in analyses to reduce sampling bias.

QGV estimates from the literature were aggregated accordingly as the coefficient of additive genetic variation (CVA), narrow-sense heritability (h2), or broad-sense heritability (H2). For criterion 1, we included studies that reported or provided data with which heritability and/or CVA could be calculated. The different metrics are a result of standardization: when comparing evolutionary potential among traits, species or populations, additive genetic variation should be standardized as its value is dependent upon the trait values themselves. Heritability, measured as the proportion of total phenotypic variance that is attributable to broad-sense genetic variance or additive genetic variance, is a common standardized metric (Falconer and Mackay 1996). However, several authors have argued against the use of heritability as a metric of evolutionary potential, as it is affected by other sources of variance such as environmental variation and is expected to be negatively correlated with the strength of selection (Houle 1992; Hansen et al 2011). As an alternative, Houle (1992) proposed standardizing additive genetic variation by the trait mean (CVA), commonly referred to as "evolvability" (Houle 1992; Garcia-Gonzalez et al 2012). Variance-scaled and mean-scaled measures of additive genetic variation are uncorrelated (Hansen et al 2011) and can produce very different conclusions (Kruuk et al 2000). Although the latter is more appropriate for comparative analyses, heritability is the more common metric (Hansen et al 2011; Garcia-Gonzalel et al 2012). Therefore, wherever possible, we extracted both heritability and CVA from published studies and ran analyses with both metrics. Where possible, we calculated CVA ourselves from population-specific estimates of additive genetic variation (VA) and trait means (Garcia-Gonzalel et al 2012). We classified all measured traits as either morphological, growth, developmental, fecundity, or physiological to test for differences in QGV patterns among these categories. Studies that did not provide population-specific estimates were excluded.

For criterion 2, we chose 10 km as a threshold range across the population set because at this scale, populations are clearly discrete and will differ appreciably in their distance from the range center and in their niche characteristics. For criterion 3, georeferenced occurrence data were required to calculate distance metrics. A total of 35 studies met these criteria, yielding 345 estimates of evolvability (CVA), 365 estimates of narrow-sense heritability (h2) and 181 estimates of broad-sense heritability (H2) from 34 species and 147 populations (2 – 15 populations per species, mean 3.8).

The species in our dataset included arthropods (12 species from 8 orders), vertebrates (4 species from 4 orders) and plants (16 species from 13 families), as well as one mollusc and one bacterium. The traits measured were mainly morphological (44%), but also included growth traits (16%), development traits (19%), measures of fecundity (15%) and physiological traits (6%) (see data available at: https://doi.org/10.6084/m9.figshare.13871867.v1).

The theoretical range of narrow-sense heritability, which describes the proportion of phenotypic variance between individuals in a population attributable to additive variance, is between zero and one, with a value greater than 0.5 generally considered moderate heritability (Falconer and Mackay 1996). Most studies in our analysis examined traits with moderate QGV. Twenty percent of the h2 estimates in our study were > 0.5 with a mean of 0.242, ranging from 0 to 1. Some studies reported negative heritability values and values greater than 1. This is relatively common when heritability is very low or very high and can be due to small sample sizes and noise in the error terms (Gill and Jensen 1968)—these numbers were scaled up to zero or down to one in order to meet the beta regression requirements (see below).

4.3.2. Range and niche quantification

The geographic range of each species was estimated by constructing minimum convex polygons (MCPs) around geo-referenced occurrence points from GBIF, which were truncated to one occurrence per grid cell, using adehabitat HR 0.4.14 (Calenge 2006) in R 3.6.3 (R Core Team 2020), with polygons cropped to match continental landmasses. The geographic centroid of each polygon was then calculated in ArcGIS 10.4 (ESRI 2015). We calculated the geographic distance (km) between species populations and the species geographic centroid using SP 1.2-3 (Pebesma and Bivand 2005) in R. Additionally, we estimated the geographic distance from each population where QGV was measured to the edge—the distance to the nearest edge of the MCP. MCPs have some limitations in that they can overestimate range sizes and distort the placement of a population in a species' geographic range. However, these challenges are considered to be less important for inter-species comparisons (Nilsen et al 2008).

We characterised climatic niches using bioclimatic layers from the WorldClim v1.4 data set (Hijmans et al 2005). We selected six layers that were not highly correlated with one another (|r| = 0.12-0.7) and represented climate extremes and variability: temperature seasonality (BIO4), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO9), precipitation of wettest month (BIO13), precipitation of driest month (BIO14), and precipitation seasonality (BIO15). All subsequent analyses were also run using the full set of WorldClim variables, but the results did not change qualitatively (data not shown). We used the Mahalanobis function in R to calculate both the niche centroid (vector of means from the multivariate environmental space) and the squared Mahalanobis distance from each point to this centroid. The niche centroid of each species was calculated using the mean value of each climate variable sampled from all occurrence locations for the species. We used the Mahalanobis distance (D2) to calculate the distance in niche space from each population to the niche centroid and to the niche edge, which is estimated as the maximum D2 distance for all distribution points of the species. Both geographic and niche distances were centered using the scale function in base R (R Core Team 2020) for use in regression analysis.

4.3.3. Statistical analyses

Statistical analyses were conducted separately for the two measures of distance (geographic and niche) and three metrics for QGV (h2, H2 or CVA). To test the distance-QGV relationship, we used three statistical methods. First, we used beta regression mixed models, using the betareg package in R (Simas and Rocha 2006) to test for QGV response variation with distance, including trait type, their interactions, and species effects. To improve comparison among species, which varied greatly in sampled geographic and niche distances, we transformed the geographic and niche distance measures described above to proportional distance (i.e., proportion of the total distance from the centroid to the edge). We did this by dividing a given population's distance to its species centroid by the total of that distance plus the distance of that population to its geographic or niche edge. Proportional distance measures were included in models as linear effects as well as second-degree polynomial (i.e., quadratic) effects to test for curvilinear responses of QGV. Trait type was a fixed effect and species was a random effect. Interactions between trait type and distance (linear and curvilinear) were initially included. If found to be non-significant, interactions and curvilinear distance effects were removed from the final models. When trait type-distance interactions were significant, we ran separate models for each trait type. Beta regressions (Ferrari and Cribari-Neto 2004) are commonly used to model variables that are scaled between 0 and 1, such as QGV and the transformed distance metrics. If the center or edge models are supported (Fig. 1), the expected outcome of these statistical models is for negative linear estimates between distance and QGV, or potentially negative quadratic estimates if QGV reductions occur abruptly near range limits. Non-significant estimates would support the null hypothesis (Fig. 1). The significance of fixed effects was evaluated using likelihood ratio tests, implemented with the lrtest function in the lmtest package in R. Tukey post-hoc tests were used to test for significant differences between trait types when an effect of trait type was detected. In order to describe how niche and geographic distances are related to each other across the study, we ran a Spearman correlation test—correlation between the two distance measures, or lack thereof, could explain parallels or incongruities in QGV patterns between geographic and niche space. All statistics were performed in R 3.6.3 (R Core Team 2020).

Second, we used a meta-analysis to incorporate the effect sizes of multiple studies in testing for QGV-distance relationships. We converted the r2 values obtained from linear regressions of QGV on distance, as calculated during our sign tests (see below), to the standardized effect size, Fisher's z. The meta-analysis was limited to studies that measured QGV in four or more populations, as this is the minimum number required to calculate the variance of z. Fisher's z can have positive or negative effect values. In our case, a negative z symbolizes a negative relationship between distance from geographic or niche centroids and QGV. When a species had multiple effect sizes for a given trait category, we calculated the mean of the estimated effects for that trait category. This produced effect size estimates for a total of 84 trait/QGV/distance type combinations from 11 species. We then performed a random-effects meta-analysis with a restricted maximum likelihood estimator, using species-level effects and a null hypothesis of zero mean effect, with METAFOR V1.9-9 (Viechtbauer 2010) in R.

Third, in order to test for broad signals of QGV decline or increase from centroids to range limits, we tested the null hypothesis that the slopes between QGV and distance are not different than zero using sign tests. For the sign tests, we first estimated the slope of the relationship between QGV and distance using linear regression. As we were interested solely in the slope of the relationship, we did not attempt to normalize the data prior to analysis. So that each species contributed equally to the analysis, we calculated average slopes for each species and did this in two different ways. First, we averaged QGV across traits for each population within a species, prior to running the linear regression ("slope of averages" approach). Second, we estimated the slope of the relationship between QGV and distance for each trait separately, then calculated the average slope ("average of slopes" approach). For both approaches, we then tested whether the average slope differed significantly from zero using a Wilcoxon sign-rank test in R.

4.4. Results

4.4.1. Distance correlation

Climatic niche and geographic distances were not significantly correlated ($r = -0.041$, $p = 0.33$) (Fig. 4).

4.4.2. Beta regression mixed models

In the mixed beta regression models, we found a range of QGV responses, some contradictory, across geographic and niche distances and QGV trait types (Fig. 3). When testing for linear relationships in geographic distance, we found a significant relationship for CVA only, with a negative estimate and consistent with the center-effect model—H2 and h2 non-significant results were more consistent with the null model. Polynomial distance relationships were significant for all QGV metrics in geographic distance, with CVA and h2 having a positive slope. This indicates that intermediate areas, those between the range center and limits, are reduced in QGV (Fig. 3). H2 had a negative polynomial relationship, indicating that intermediate areas are higher in QGV. Linear relationships were more consistent for niche distance—all QGV metrics had a positive linear relationship with distance from the niche centroid, indicating that QGV increased further away from the centroid. The polynomial relationship was significantly negative for h2 and significantly positive for H2 (Fig. 3). Significant interactions between linear distances and QGV trait types were found for geographic distance and CVA, and for niche distance and h2 (Table 1), indicating differing slopes in QGV change with distance among trait types. In beta regression models for individual traits, within CVA, fecundity traits significantly decreased away from the geographic centroid (physiology was also weakly negatively significant) (Table S1). For individual traits in h2, no traits were found to differ significantly with distance from the niche centroid (Table S2). Trait type was significant in all mixed models. Traits varied in terms of which had the least and greatest estimates of QGV among distance measures (geographic or niche) and QGV estimates (h2, H2 or CVA) (Table S1), but physiology traits usually had the highest estimates of QGV, whereas fecundity (fitness) measures often had the lowest QGV estimates (Table S3, Table S4, Fig. S1).

4.4.3. Meta-analysis

The meta-analysis for the relationship between QGV and distance from centroid revealed an overall mean effect size (z) of -0.1950, meaning that QGV decreases slightly, but non-significantly, away from central regions of species ranges or climate niches (Fig. 2).

The 95% confidence intervals on z estimates all overlapped zero, meaning there was no conclusive directionality in the pattern of QGV across species ranges.

4.4.4. Sign tests

Similar to the meta-analysis results, no significant signals of QGV decline or increase with geographic or niche distance were found in sign tests (Table S5).

4.5. Discussion

Using mixed model approaches, meta-analysis, and sign tests on the slope of the relationship between QGV and distance, we found mixed evidence for change in QGV towards species’ range or niche margins (Table 1, Figs. 2-3). These findings lend partial support to all the models of QGV variation we described (Fig. 1), depending on the statistical test or QGV measure, but we believe that this signals a need for further study. Results differed by statistical approach and QGV metric, with the only statistically significant results being found in the mixed model beta regressions. Surprisingly, QGV increased significantly away from niche centers in these models, whereas QGV was reduced away from geographic centers (for narrow-sense heritability and evolvability; Fig. 3). Nevertheless, there is a large gap in estimations of QGV from outer or marginal niche environments of species ranges; this is especially true for broad-sense heritability in this dataset (Fig. 3). Finally, sampling of central and peripheral populations within the same species range in studies examining QGV is extremely rare and remains a major research gap.

If QGV does not vary consistently across species ranges, this could signal that marginal and central populations are equally likely to be locally adapted (Fig. 1). There is a mixture of evidence to date regarding local adaptation at species range limits; in fact, local adaptation may even generally be greater toward some niche limits (Angert et al 2020), but this is an active area of research and a mixture of evidence exists (see Hargreaves et al 2014). Adaptation at the range margin depends on the slope of the environmental gradient and the efficacy of selection – itself a product of QGV, genetic architecture (the number of loci influencing a trait and the nature of interactions among loci) and the strength of selection (Etterson and Shaw 2001; Polochevá and Barton 2015). The efficacy of selection relative to genetic drift can be estimated and compared among populations, and recent studies have found evidence for adaptive evolution occurring across species ranges (e.g., Gould et al 2014; Volis et al 2016a), but more studies are needed. Local adaptation at range margins could partly account for why declines in population size, performance, or variability are not often observed towards species range limits (Sagarin and Gaines 2002; Sexton et al 2009; Pironon et al 2016; Dallas et al 2017). Accordingly, where there is no decrease in QGV, reductions in local adaptation should not be expected, unless QGV is being elevated by maladaptive gene flow (Eckert et al 2008; Polechová and Barton 2015). Nevertheless, geographically marginal populations are often observed to be more differentiated and genetically isolated (Eckert et al 2008), making "swamping gene flow" scenarios unlikely to be a cause of variation in QGV near range limits or of range limits themselves (Kottler et al. In press.). Finally, moderate or high QGV for certain traits may be maintained, even in edge populations, if there is not strong directional selection on those traits.

Several studies not included in our dataset have examined adaptive potential near niche or range limits using a variety of methods. Taken together, these studies also suggest a mixed pattern in adaptive potential across species ranges. Pujol and Pannell (2008) demonstrated that cool range-edge populations of the herb, annual mercury (*Mercurialis annua*), have a weaker response to artificial selection than populations in the species' putative Pleistocene refugia in southern Europe. Sheth and Angert (2016) similarly found a relatively weak response to artificial selection in cool edge populations of the cardinal monkeyflower, *Mimulus cardinalis*, in western North America when compared to warm-edge populations; nevertheless, central populations had a similarly low selection response. In the American badger, *Taxidea taxus*, Rico et al. (2016) found that major histocompatibility complex diversity is high in small populations near northern range limits relative to large, central populations. Further, Martínez-Padilla et al. (2017) uncovered highest evolvability in climates of intermediate suitability across 12 European bird species. The authors reasoned that evolvability may be low in bird populations occupying harsh environments, but also in high-quality environments competition may be strongest.

Four studies published after our initial literature search found mixed or contrasting patterns in QGV towards limits. Volis et al. (2016b) found that central populations had higher quantitative trait variation than those from northern or southern edge populations in wild emmer, *Triticum dicoccoides*, in Israel. Moreover, central-population plants had higher performance than edge-populations plants when grown in extreme conditions beyond the species range. In contrast, a study of northern populations of European wild cherry, *Prunus avium*, found central regions to be depauperate when compared with populations at the northern extent of the species' range (Lobo et al 2018), though this study did not include QGV estimates from the southern extent of the range. Moreover, a study measuring QGV across the range of the emerald damselfly, *Lestes sponsa*, in Europe found again that central regions are depauperate in genetic variance for life history traits—in this case, southern populations have the highest variation, followed by northern populations (Sniegula et al 2016). Finally, using a more holistic approach in which traits were regarded in a multivariate fashion (i.e., evaluation of traits within a variance-covariance G-matrix), Paccard et al (2016) found that genetic independence among traits in the North American lyre-leaved rockcress, *Arabidopsis lyrata*, is greater towards range limits. This greater independence among traits could allow for potentially greater responses to selection in peripheral populations, despite a decline in QGV detected in this study and despite reduced neutral genetic diversity detected towards range margins in a prior study (Griffin and Willi 2014).

Taken together, the above studies point to a clear knowledge gap: Do some peripheral or marginal regions of species ranges (e.g., cool or warm edges) have greater adaptive potential than others? Also, what would it mean to find no general pattern in adaptive potential across geographic or niche space for the properties of peripheral populations or range limits? There are several implications. First, peripheral populations can have significant adaptive potential, and in these cases, it should not be a population-level lack of QGV that sets range limits. Second, some types of range peripheries may differ in QGV. A prevalent hypothesis, which we were unable to test with the current dataset, is that warm-edge populations harbour the greatest amount of genetic variation due to their role as refugia during ice ages (Hampe and Petit 2005; Prionon et al 2016), a scenario not in conflict with the results of case studies described above. In this vein, the age and history of a population may play an important role in the amount of QGV found there, regardless of population size (Marko and Hart 2011). Reductions in QGV, if occurring, might only be detected in the most marginal populations (not often sampled) or in ranges undergoing contemporary shifts. Further studies that replicate range margin and central populations, and measure populations from both the cool and warm margins, will help resolve these issues. Due to the paucity of studies assessing QGV at or near niche limits, and to the fact that few studies have simultaneously compared QGV at geographic and central regions within species ranges, we were unable to assess whether center-edge patterns may differ between cool and warm-edge regions, but this is an important future research direction. Moreover, since niche and geographic positions are often uncorrelated (as found in this study) or even negatively correlated (Dallas et al 2017) (Fig. 4), many novel environments occur in the interior of species ranges and should be investigated for adaptive trait variation.

Third, in assessing QGV in wild populations, heritability may be inflated in more favourable conditions, and depressed in unfavourable conditions (Wood and Brodie 2016)—more so for morphological traits than fitness-related traits (i.e. fecundity) (Charmantier and Garant 2005). We found lower QGV in fecundity traits in general, consistent with expectations that these traits are under greater natural selection (Fisher 1930; Mousseau and Roff 1987). Additionally, QGV-distance relationships occasionally varied by trait type, indicated by significant distance-trait type interactions. QGV, specifically evolvability, decreased significantly from geographic centers for fecundity traits only (Table S1), which may indicate increased selection and reduced adaptive potential towards geographic range limits. Will this hold as a general relationship as more studies are conducted and what traits should be estimated? Estimating and comparing QGV for fitness, while challenging, is a good start for determining whether adaptive constraints exist at a particular population or geographic limit (see Shaw and Etterson 2012). Understanding which traits are actually related to range limits is a challenging enterprise, but it is possible that QGV for range-limiting traits are lowest right at the edge (Magiafoglou and Hoffmann 2003). Low expressed QGV in the field may actually be a property of peripheral populations if conditions near range limits are harsh or stressful, thereby supressing the expression of heritable phenotypic variance through selection for phenotypes that can tolerate those conditions. Many studies estimate QGV under more benign, controlled conditions, such as in greenhouses or incubators, but studies that estimate and compare QGV in range limit contexts in the field or in conditions mimicking range-limiting conditions are greatly needed (Eckert et al 2008). We acknowledge that it can be challenging to obtain QGV estimates as they often require breeding designs or observations of multiple generations. Practically speaking, QGV requires greater sample sizes, but more easily allows simultaneous quantification of genetic variation for multiple traits and the G matrix. In contrast, in artificial selection studies, it is challenging to select on more than 1-2 traits at a time and one cannot derive a G matrix. Genomic quantitative genetics provide new avenues for estimating adaptive potential in the wild (Gienapp et al 2017) . As genomic techniques are developed and utilized (e.g., Robinson et al 2013; Bérénos et al 2014), hopefully studies will frame questions in a range wide context and include marginal populations.

Finally, whether populations across species ranges are equally likely to serve as important sources of genetic variation for conservation, adaptation to novel conditions, and under climate change stress is an open question. Indeed, central regions are not necessarily the most important conservation strongholds; for instance, species ranges are equally likely to contract to their peripheries as to their central regions during range contraction and extinction (Channell and Lomolino 2000b, a). Knowing whether adaptive potential generally does not decline at or towards range margins should promote the development of more effective conservation theory and basic theory to better understand the formation of species range limits and the processes that facilitate, or limit, climatic niche expansion. In cases where peripheral populations are adapted to their local conditions, genetic novelty may be high in peripheral populations, and so peripheral populations may serve as important sources of genetic variation (Lesica and Allendorf 1995; Macdonald et al 2017). It is risky to assign value to any part of a species range as a general rule. More research is needed, but we suggest a case-by-case evaluation of populations before assigning conservation priorities across a species range, including assessment of genetic variation, private or rare alleles, and phenotypic variation. We advocate that managers and researchers err on the side of caution and conservation.

SUPPORTING INFORMATION

SI 1. Tukey post-hoc tests and sign test results

SI 2. Summary of QGV study inclusion, with sample sizes.

4.6. References

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Tables

Table 1. Mixed beta regression model results. “Interactions” refer to linear distance x trait type interactions. Interaction and quadratic effects were included in models when significant. Interaction terms were unable to run on all models, and when able to run did not have one estimate. Psuedo-R-squared values for the full model are reported. Significant values (α < 0.05) marked with an asterisk.

Organism type	**CV_a** n = 316	**h^2** n = 313	**H^2** n = 179
Invertebrate an other n = 15	**Arthropod:** *Bemisia tabaci* (Ma 2014) *Callosobruchus maculatus* (Messina 1993) *Coelopa frigida* (Day 1996) *Drosophila melanogaster* (Mitchell 2010, Service 2000) *Ischnura elegans* (Shama 2011)* **Mollusc:** *Cornu aspersum* (Nespolo 2014) **Bacterium:** *Pseudomonas fluorescens* (Pompini 2013)	**Arthropod:** *Achroia grisella* (Zhou 2008)* *Asellus aquaticus* (Eroukhmanoff 2009) *Bemisia tabaci* (Ma 2014) *Callosobruchus maculatus* (Messina 1993) *Coelopa frigida* (Day 1996) *Drosophila melanogaster* (Mitchell 2010, Service 2000) *Epiphyas postvittana* (Gu 1992) *Orchesella cincta* (Posthuma 1993) *Pirata piraticus* (Hendrickx 2008) *Plutella xylostella* (Jallow 2006) **Mollusc:** *Cornu aspersum* (Nespolo 2014)	**Arthropod:** *Daphnia magna* (Messiaen 2013) *Ischnura elegans* (Shama 2011)*
Plant n = 15	*Amsinckia spectabilis* (Bartkowska 2009) *Austrocedrus chilensis* (Aparicio 2010) *Avena sterilis* (Volis 2007)* *Betula pendula* (Billington 1991) *Betula pubescens* (Billington 1991) *Chamaecrista fasciculata* (Etterson 2004)*, *Datura stramonium* (Fornoni 2003) *Hordeum spontaneum* (Volis 2007)* *Lythrum salicaria* (O’Neil 1993) *Senecio integrifolius* (Widen 1993)	*Amsinckia spectabilis* (Bartkowska 2009) *Austrocedrus chilensis* (Aparicio 2010) *Betula pendula* (Billington 1991) *Betula pubescens* (Billington 1991) *Chamaecrista fasciculata* (Etterson 2004)* *Datura stramonium* (Fornoni 2003) *Senecio integrifolius* (Widen 1993) *Zamia fairchildiana* (Lopez-Gallego 2014)	*Avena sterilis* (Volis 2007)* *Clarkia xantiana ssp xantiana* (Gould 2014)* *Hordeum spontaneum* (Volis 2007)* *Populus fremontii* (Grady 2013)* *Salix exigua* (Grady 2013)* *Triticum turgidum ssp. dicoccoides* (Volis 2014)*

Vertebrate n = 8	*Oryzias latipes* (Kiso 2012) *Parus caeruleus* (Charmentier 2004) *Rana arvalis* (Knopp 2007) *Rana temporaria* (Laurila 2002, Sommer 2003, Uller 2002)	*Oryzias latipes* (Kiso 2012) *Parus caeruleus* (Charmentier 2004) *Rana arvalis* (Knopp 2007 Merila 2004) *Rana temporaria* (Laurila 2002, Sommer 2003)	*Gasterosteus aculeatus* (Snyder 1991) *Rana temporaria* (Uller 2002)

Table 2. Mixed beta regression model results. “Interactions” refer to linear distance x trait type interactions. Interaction and quadratic effects were included in models when significant. Interaction terms were unable to run on all models, and when able to run did not have one estimate. Psuedo-R-squared values for the full model are reported. Significant values ($\alpha < 0.05$) marked with an asterisk.

	Source	**Estimate**	**Chi^2**	**Pseudo-R^2**	***p***
Geographic					
CV_a	Distance	-0.13613	17.005	0.08912	0.004491 **
	Trait type	0.05255	42.564		1.061e-06 ***
	Interaction		15.148		0.004404 **
	Distance^2	5.10207	5.9569		0.01466 *
h^2	Distance	-0.49539	1.1632	0.04189	0.2808
	Trait type	0.0438325	11.761		0.01922 *
	Distance^2	3.31043	4.1164		0.04247 *
H^2	Distance	0.04113	0.0038	0.2127	0.9507
	Trait type	-11.53475	24.985		0.001564 **
	Distance^2	-7.1316	5.5583		0.01839 *
Niche					
CV_a	Distance	0.23915	5.0015	0.00065	0.02533 *
	Trait type	0.34924	25.326		4.326e-05***
	Interaction		7.6036		0.1072
	Distance^2	-0.47161	0.0313		0.8596
h^2	Distance	1.68041	61.509	0.1576	5.924e-12 ***
	Trait type	-0.03458	36.904		1.199e-05 ***
	Interaction		31.618		2.29e-06***
	Distance^2	-2.62784	15.832		6.922e-05 ***
H^2	Distance	37.5510	39.381	0.299	3.487e-10 ***
	Trait type	-1.5469	49.057		5.682e-10 ***
	Distance^2	191.5917	34.612		4.025e-09 ***

Figures

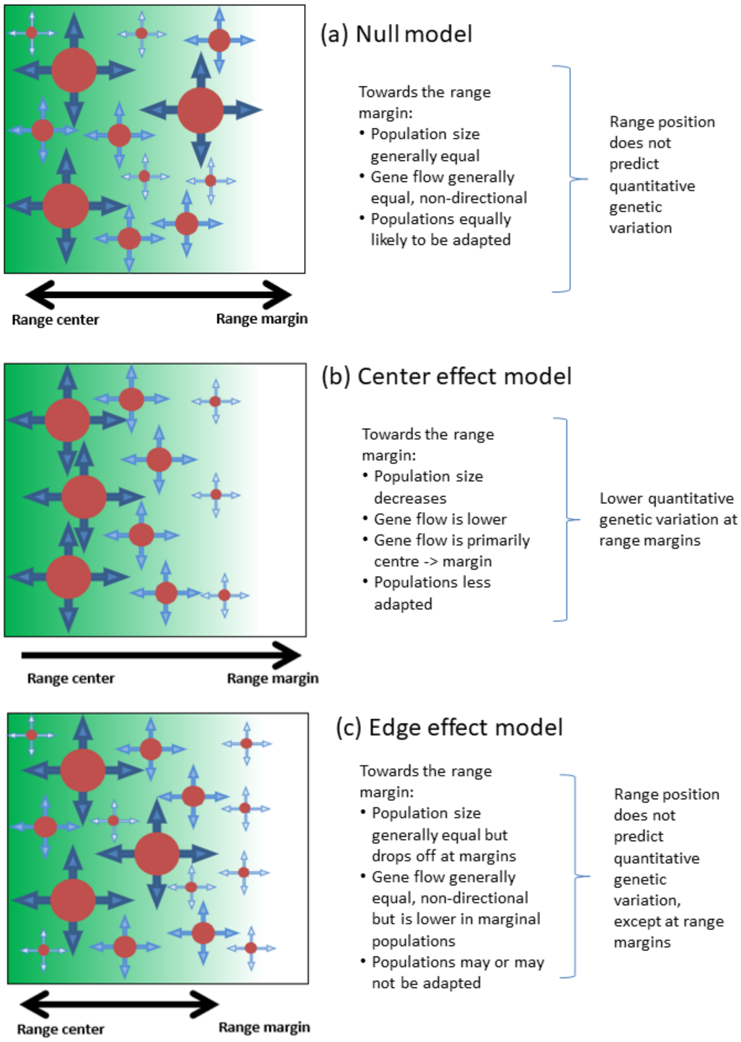


Figure 1. QGV models across species ranges at equilibrium. (a) The null model predicts that population size and QGV do not consistently decrease towards the range margin. (b) The center effect model is based on the abundant center hypothesis (ACH), which predicts smaller populations (red circles, with blue arrows representing gene flow emigration potential scaling with population size) towards the range margin, which in turn generates the prediction of reducing genetic variation or maladaptation towards range margins. (c) The edge effect model has aspects of the null and center effect models, having reduced population size and QGV at marginal populations due to strong selection and demographic instability near species niche limits. Black arrows represent the predominant direction of gene flow.

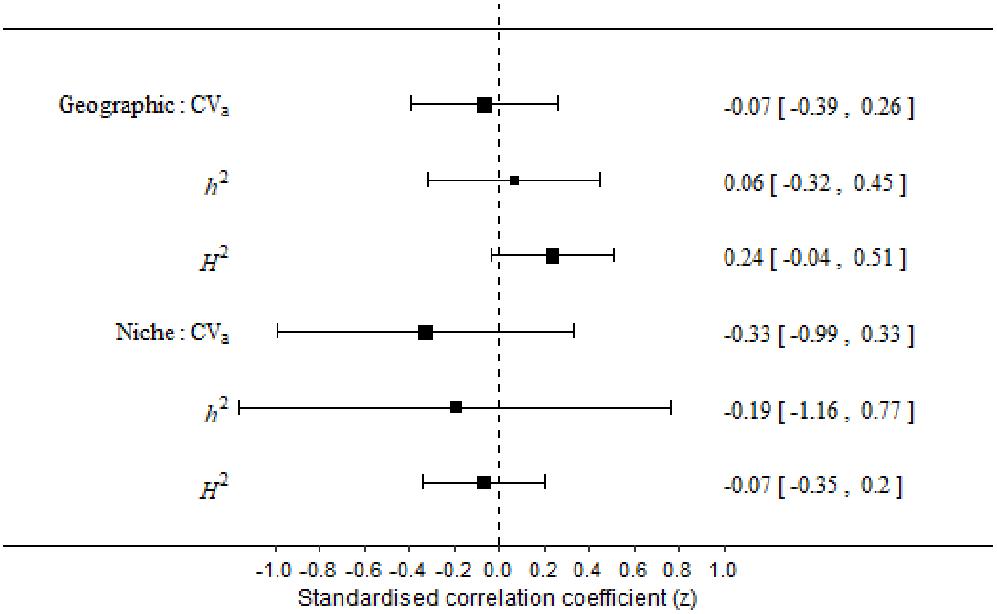


Figure 2. Summary of results from random effects meta-analysis, testing the relationship between QGV and distance. QGV was measured as either the coefficient of additive genetic variation (CV_A), narrow-sense heritability (h^2) or broad-sense heritability (H^2). Mean effect sizes ± 95% confidence intervals are shown, with the size of the point scaled to the number of species-level effects included (sample sizes: geographic margin, CV_A: 16, h^2: 10, H^2: 14; niche margin, CV_A: 16, h^2: 10, H^2: 14). The dashed line indicates an effect size of zero and negative values indicate a decline in QGV towards the range/niche margin. Values for the mean effect size for each QGV metric are provided, along with lower and upper 95% confidence intervals, on the right-hand side of the figure.

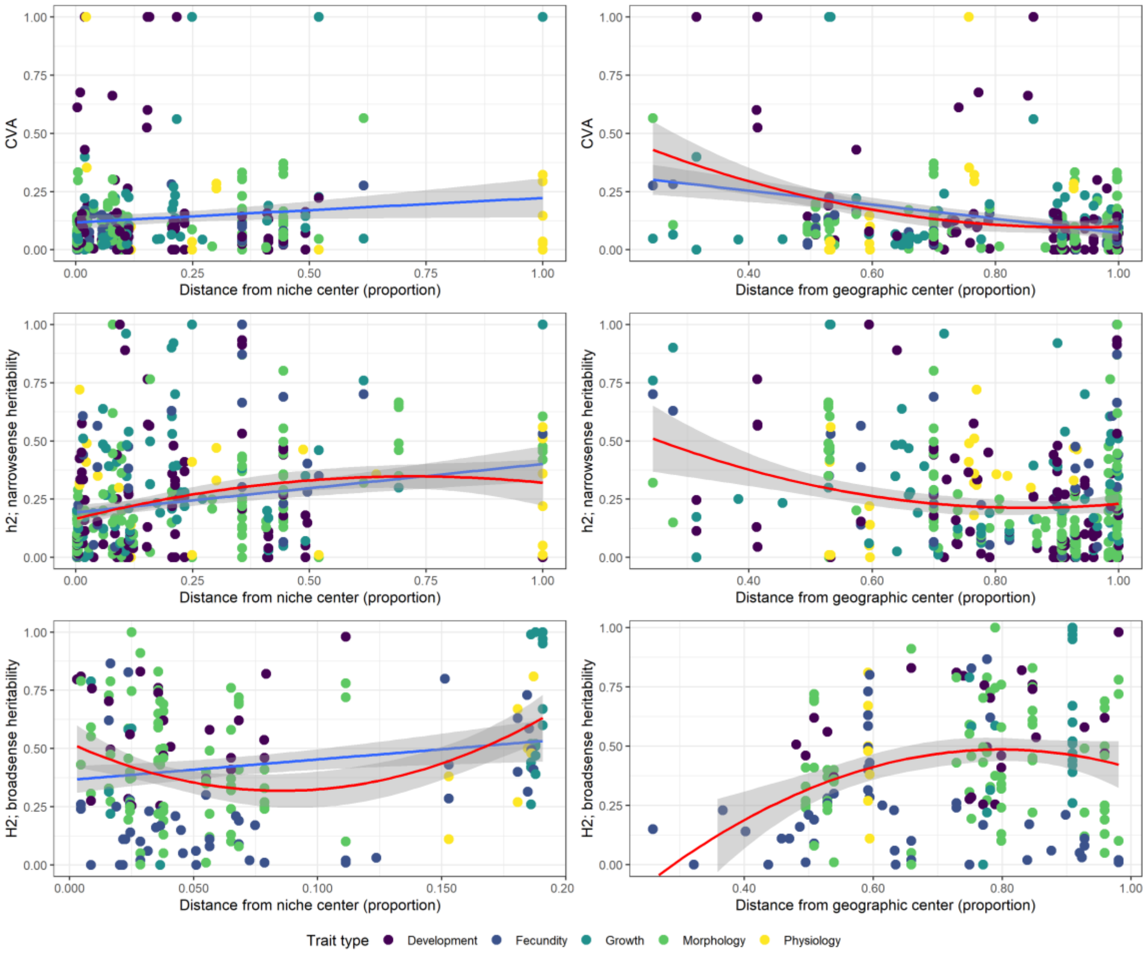


Figure 3. Scatterplots of QGV estimates against proportional distance to geographic and climate niche centers of species ranges. Blue lines are linear regression lines and red lines are quadratic regression lines—only included when the relationship was found to be significant. Estimates from different trait types are sometimes from the same study species. Note that the x-axis is greatly truncated, due to limited data, in the panel showing broad-sense heritability (H2) across niche distance (lower left).

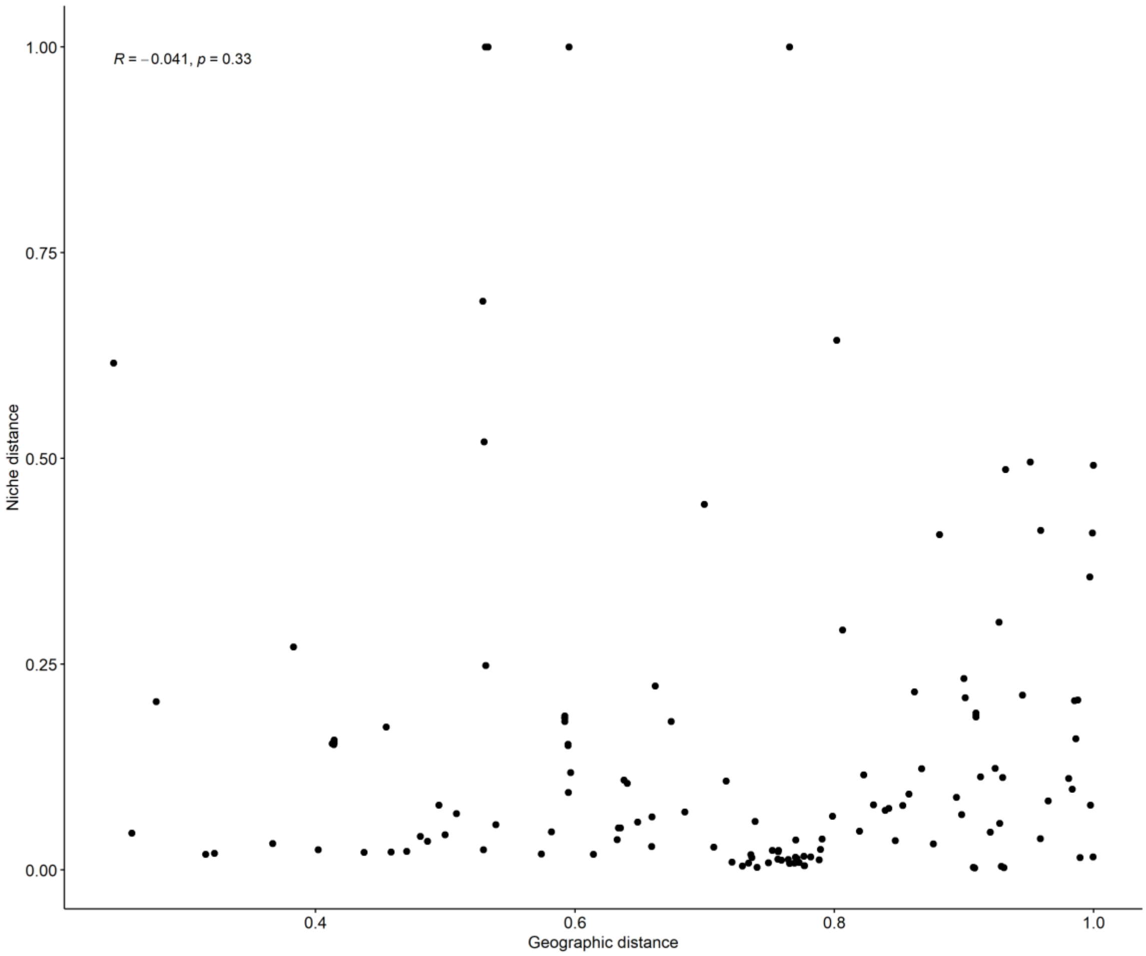


Figure 4. Spearman's correlation between calculated distance from geographic and niche centers.

Appendix A. Chapter 4 Supporting Information
SI 1. Tukey post-hoc tests and sign test results

Table S1. Beta regression results of CVA on specific trait type in geographic distance. Growth trait types did not have sufficient observations to run alone.

Trait Type	Chi sq.	Estimate	P value
Development	0.0124	0.05861	0.9112
Physiology	3.3633	-0.96643	0.06666
Morphology	2.7239	-0.56538	0.09885
Fecundity	9.5098	-2.7110	0.002044 **

Table S2. Beta regression results of h^2 on specific trait type in niche distance. Fecundity and morphology trait types did not have sufficient observations to run alone.

Trait type	Chi sq.	Estimate	P value
Development	0.2309	-0.3461	0.6308
Physiology	0.0483	-0.10634	0.826
Growth	3.1531	0.64719	0.07578 .

Table S3. Niche distance Tukey test results for trait type from beta regression mixed models.

contrast: CVA niche distance	**estimate**	**SE**	**z.ratio**	**p.value**
Development - Fecundity	0.010129	0.012708	0.797018	0.93156
Development - Growth	-0.03391	0.012332	-2.74951	0.04709
Development - Morphology	-0.00206	0.008712	-0.23674	0.999307
Development - Physiology	-0.16233	0.011721	-13.8502	<.0001
Fecundity - Growth	-0.04404	0.015548	-2.83225	0.037285
Fecundity - Morphology	-0.01219	0.01259	-0.96834	0.869446
Fecundity - Physiology	-0.17246	0.01509	-11.4292	<.0001
Growth - Morphology	0.031845	0.01247	2.553638	0.0792
Growth - Physiology	-0.12843	0.014315	-8.97127	3.40E-14
Morphology - Physiology	-0.16027	0.011873	-13.4987	<.0001

contrast: h^2 niche distance	**estimate**	**SE**	**z.ratio**	**p.value**
Development - Fecundity	0.019855	0.037117	0.534926	0.983745
Development - Growth	0.003711	0.030143	0.12312	0.999948
Development - Morphology	0.043548	0.027653	1.574769	0.513657
Development - Physiology	-0.09179	0.030214	-3.03791	0.020156
Fecundity - Growth	-0.01614	0.033934	-0.47575	0.989548
Fecundity - Morphology	0.023693	0.03149	0.752395	0.943944
Fecundity - Physiology	-0.11164	0.033991	-3.28444	0.009045
Growth - Morphology	0.039836	0.022856	1.742959	0.407488
Growth - Physiology	-0.0955	0.026211	-3.64333	0.002497
Morphology - Physiology	-0.13533	0.022923	-5.90392	3.54E-08

contrast: H^2 niche distance	**estimate**	**SE**	**z.ratio**	**p.value**
Development - Fecundity	0.470587	0.021078	22.32602	<.0001
Development - Growth	0.363717	0.066461	5.472656	4.42E-07
Development - Morphology	0.20962	0.025833	8.11435	6.69E-14
Development - Physiology	0.404414	0.071679	5.641993	1.68E-07
Fecundity - Growth	-0.10687	0.065659	-1.62766	0.479546
Fecundity - Morphology	-0.26097	0.033788	-7.72367	1.43E-13

Fecundity - Physiology	-0.06617	0.070443	-0.93938	0.88156
Growth - Morphology	-0.1541	0.073256	-2.10355	0.218423
Growth - Physiology	0.040697	0.078742	0.516836	0.985711
Morphology - Physiology	0.194794	0.078265	2.488917	0.093084

Table S4. Geographic distance Tukey test results for trait type from beta regression mixed models.

contrast: CVA geographic distance	**estimate**	**SE**	**z.ratio**	**p.value**
Development - Fecundity	0.025489	0.013534	1.88327	0.32631
Development - Growth	0.023144	0.008241	2.80839	0.039915
Development - Morphology	0.012102	0.009232	1.31087	0.684452
Development - Physiology	-0.13738	0.03844	-3.57398	0.003237
Fecundity - Growth	-0.00234	0.012704	-0.18458	0.999741
Fecundity - Morphology	-0.01339	0.012805	-1.04537	0.83417
Fecundity - Physiology	-0.16287	0.039678	-4.10487	0.000389
Growth - Morphology	-0.01104	0.007946	-1.38952	0.634426
Growth - Physiology	-0.16053	0.038087	-4.21468	0.000242
Morphology - Physiology	-0.14948	0.038406	-3.89218	0.000943

contrast: h^2 geographic distance	**estimate**	**SE**	**z.ratio**	**p.value**
Development - Fecundity	-0.01448	0.04129	-0.35066	0.996765
Development - Growth	-0.00347	0.032705	-0.10616	0.999971
Development - Morphology	0.047336	0.028292	1.67314	0.450672
Development - Physiology	-0.07275	0.029951	-2.42901	0.107598
Fecundity - Growth	0.011007	0.040472	0.271966	0.998802
Fecundity - Morphology	0.061815	0.036869	1.6766	0.448498
Fecundity - Physiology	-0.05827	0.038732	-1.50447	0.559524
Growth - Morphology	0.050808	0.027421	1.852906	0.343145
Growth - Physiology	-0.06928	0.029416	-2.35512	0.127859
Morphology - Physiology	-0.12009	0.023701	-5.06673	4.02E-06

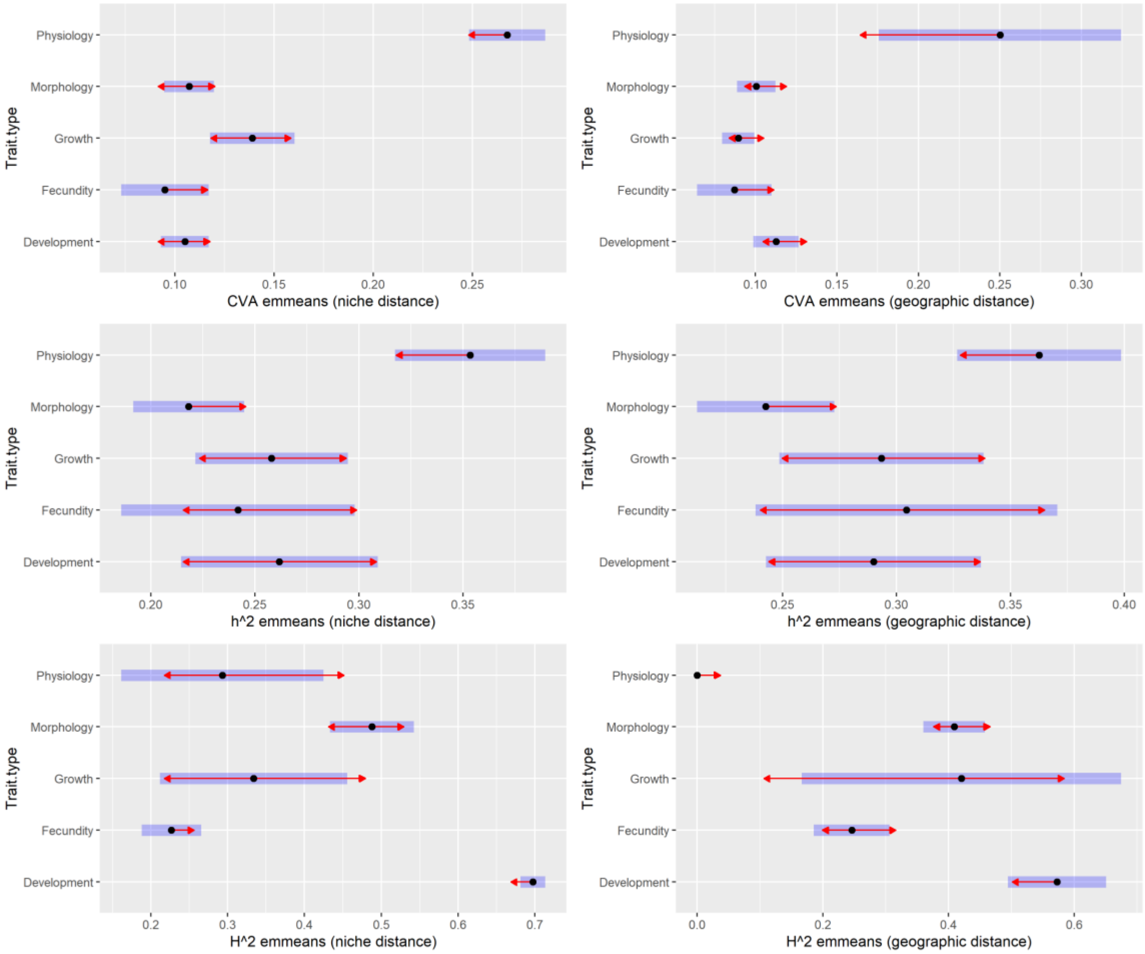
contrast: H^2 geographic distance	**estimate**	**SE**	**z.ratio**	**p.value**
Development - Fecundity	0.326354	0.050229	6.497337	8.17E-10
Development - Growth	0.151817	0.135093	1.123802	0.794017

Development - Morphology	0.163441	0.04699	3.47824	0.004594
Development - Physiology	0.572339	0.039854	14.36085	<.0001
Fecundity - Growth	-0.17454	0.132694	-1.31533	0.68166
Fecundity - Morphology	-0.16291	0.03928	-4.14743	0.000324
Fecundity - Physiology	0.245985	0.030719	8.007619	7.84E-14
Growth - Morphology	0.011624	0.131873	0.088145	0.999986
Growth - Physiology	0.420521	0.129658	3.243299	0.010389
Morphology - Physiology	0.408897	0.024925	16.40543	<.0001

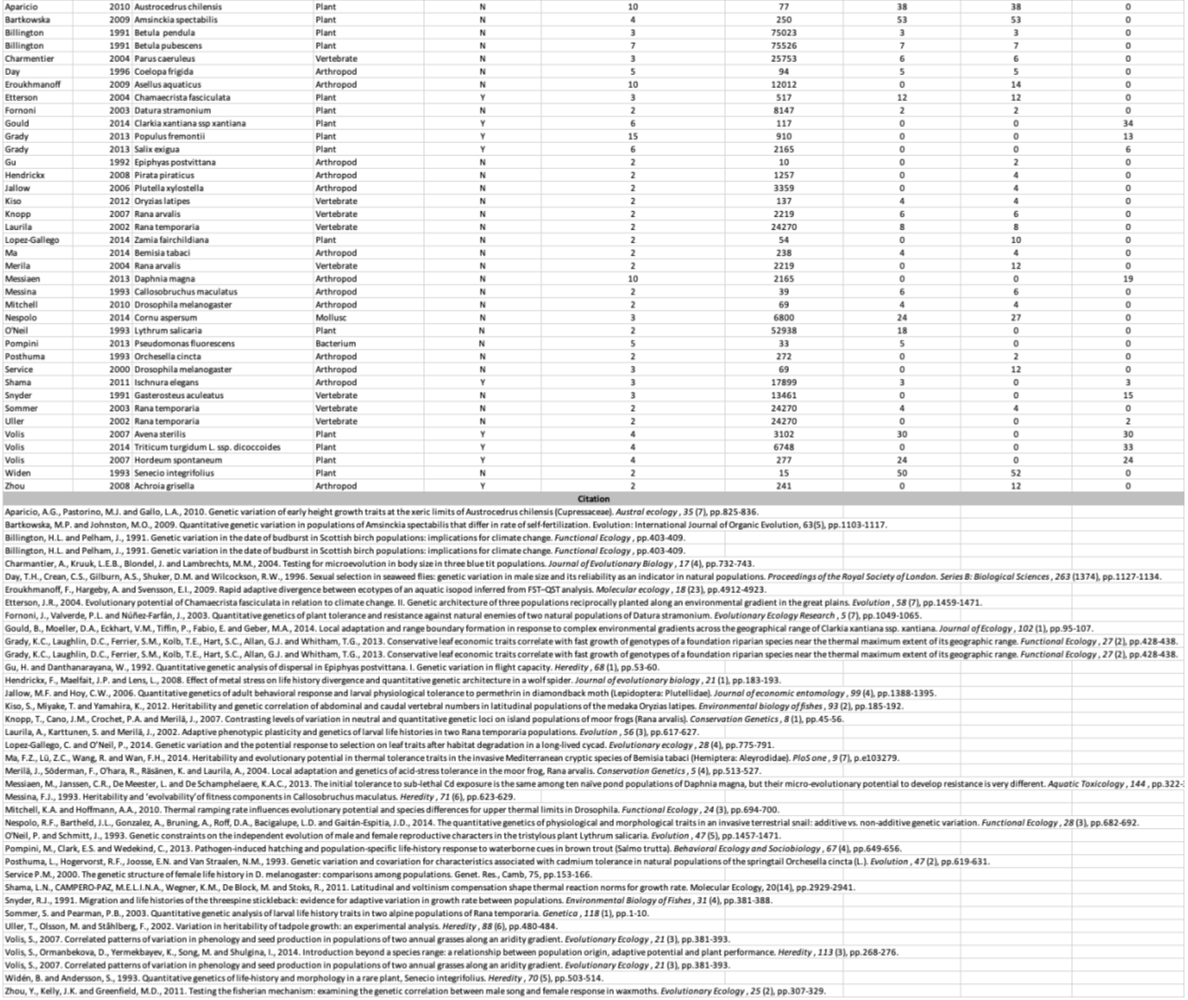
Table S5. Summary of results from sign tests of QGV across species ranges. Sign tests were conducted using one value per species, calculated as either the mean slope of linear regressions of population-specific trait values and distance (mean of slopes) or as the linear regression of the mean of population-specific trait values and distance (slope of mean).

Sign tests			
Mean of slopes		Slope of mean	
p	*n*	*p*	*n*
0.3604	28	0.1539	29
0.7191	23	0.3317	26
0.2101	18	0.1671	18
0.8804	28	0.6358	29
0.07092	23	0.09837	26
0.8288	18	0.6476	18

Figure S1. Graphical representation of Tukey test estimates and contrasts. The blue bars are confidence intervals for the estimated marginal means (EMMS, emmeans, also called least square means), and the red arrows are for the comparisons among them. If an arrow from one mean overlaps an arrow from another group, the difference is not “significant,” with alpha set at 0.05.



SI 2. Summary of QGV study inclusion, with sample sizes.



First author	Year	Species	Classification	Range Limit Context Y/N	Number of populations sampled for QGV	Species Occurrence Points	Number of CVA estimates	Number of h2 estimates	Number of H2 estimates
Aparicio	2010	Austrocedrus chilensis	Plant	N	10	77	38	38	0
Bartkowska	2009	Amsinckia spectabilis	Plant	N	4	250	53	53	0
Billington	1991	Betula pendula	Plant	N	3	75023	3	3	0
Billington	1991	Betula pubescens	Plant	N	7	75526	7	7	0
Charmentier	2004	Parus caeruleus	Vertebrate	N	3	25753	6	6	0
Day	1996	Coelopa frigida	Arthropod	N	5	94	5	5	0
Eroukhmanoff	2009	Asellus aquaticus	Arthropod	N	10	12012	0	14	0
Etterson	2004	Chamaecrista fasciculata	Plant	Y	3	517	12	12	0
Fornoni	2003	Datura stramonium	Plant	N	2	8147	2	2	0
Gould	2014	Clarkia xantiana ssp xantiana	Plant	Y	6	117	0	0	34
Grady	2013	Populus fremontii	Plant	Y	15	910	0	0	13
Grady	2013	Salix exigua	Plant	Y	6	2165	0	0	6
Gu	1992	Epiphyas postvittana	Arthropod	N	2	10	0	2	0
Hendrickx	2008	Pirata piraticus	Arthropod	N	2	1257	0	4	0
Jallow	2006	Plutella xylostella	Arthropod	N	2	3359	0	4	0
Kiso	2012	Oryzias latipes	Vertebrate	N	2	137	4	4	0
Knopp	2007	Rana arvalis	Vertebrate	N	2	2219	6	6	0
Laurila	2002	Rana temporaria	Vertebrate	N	2	24270	8	8	0
Lopez-Gallego	2014	Zamia fairchildiana	Plant	N	2	54	0	10	0
Ma	2014	Bemisia tabaci	Arthropod	N	2	238	4	4	0
Merila	2004	Rana arvalis	Vertebrate	N	2	2219	0	12	0
Messiaen	2013	Daphnia magna	Arthropod	N	10	2165	0	0	19
Messina	1993	Callosobruchus maculatus	Arthropod	N	2	39	6	6	0
Mitchell	2010	Drosophila melanogaster	Arthropod	N	2	69	4	4	0
Nespolo	2014	Cornu aspersum	Mollusc	N	3	6800	24	27	0
O'Neil	1993	Lythrum salicaria	Plant	N	2	52938	18	0	0
Pompini	2013	Pseudomonas fluorescens	Bacterium	N	5	33	5	0	0
Posthuma	1993	Orchesella cincta	Arthropod	N	2	272	0	2	0
Service	2000	Drosophila melanogaster	Arthropod	N	3	69	0	12	0
Shama	2011	Ischnura elegans	Arthropod	Y	3	17899	3	0	3
Snyder	1991	Gasterosteus aculeatus	Vertebrate	N	3	13461	0	0	15
Sommer	2003	Rana temporaria	Vertebrate	N	2	24270	4	4	0
Uller	2002	Rana temporaria	Vertebrate	N	2	24270	0	0	2
Volis	2007	Avena sterilis	Plant	Y	4	3102	30	0	30
Volis	2014	Triticum turgidum L. ssp. dicoccoides	Plant	Y	4	6748	0	0	33
Volis	2007	Hordeum spontaneum	Plant	Y	4	277	24	0	24
Widen	1993	Senecio integrifolius	Plant	N	2	15	50	52	0
Zhou	2008	Achroia grisella	Arthropod	Y	2	241	0	12	0

Citation
Aparicio, A.G., Pastorino, M.J. and Gallo, L.A., 2010. Genetic variation of early height growth traits at the xeric limits of Austrocedrus chilensis (Cupressaceae). *Austral ecology* , *35* (7), pp.825-836.
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