

12-15-2014

Climate-Induced Changes in the Germination Phenology of *Boechera Stricta*

Samuel Johnson
University of South Carolina - Columbia

Follow this and additional works at: <https://scholarcommons.sc.edu/etd>



Part of the [Earth Sciences Commons](#), and the [Environmental Sciences Commons](#)

Recommended Citation

Johnson, S.(2014). *Climate-Induced Changes in the Germination Phenology of Boechera Stricta*. (Master's thesis). Retrieved from <https://scholarcommons.sc.edu/etd/3020>

This Open Access Thesis is brought to you by Scholar Commons. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of Scholar Commons. For more information, please contact digres@mailbox.sc.edu.

CLIMATE-INDUCED CHANGES IN THE GERMINATION PHENOLOGY OF
BOECHERA STRICTA

by

Samuel Johnson

Bachelor of Science
University of South Carolina, 2012

Submitted in Partial Fulfillment of the Requirements

For the Degree of Master of Earth and Environmental Resources Management in

Earth and Environmental Resources Management

College of Arts and Sciences

University of South Carolina

2014

Accepted by:

Jill Anderson, Director of Thesis

Carol Boggs, Reader

Rudy Mancke, Reader

Lacy Ford, Vice Provost and Dean of Graduate Studies

ACKNOWLEDGEMENTS

I would like to thank my major advisor, Dr. Jill Anderson, for her assistance with defining the parameters of the project, analyzing our findings, and compiling this thesis. I would also like to thank her for giving me the opportunity to work in her lab and develop valuable research skills while also having an enjoyable experience. I would like to thank my fellow labmates for their assistance with this project and data collection, particularly Bashira Chowdhury, Anna Battatia, Cassidy Way, and Caroline Daws. I also would like to thank my committee members, Dr. Carol Boggs and Dr. Rudy Mancke, for their assistance with this thesis.

ABSTRACT

Climate change is having demonstrable, worldwide impacts on ecological systems in ways that have modified aspects of organism behavior. Plant phenologies have responded to warmer temperatures in a variety of ways that may have implications for long-term species survival. How germination phenology changes in response to warmer climate is a largely unexplored question yet the ability of a plant to advance or delay germination in unfavorable conditions is critical for survival. Knowing the relative success and timing of germination under different climate regimes is important in understanding whether species can keep pace with the rate of climate change via migration or adaptation. We examined germination success and phenology under different simulated climate conditions within wild mountain populations of *Boechera stricta*. We found germination success to be heritable within the species. We also found that germination success is lower under snow removal conditions designed to simulate predicted trends in climate. We discovered that *B. stricta* germinants are highly sensitive to environmental conditions and predicted future climate and that the most successful germinants are those inhabiting actual or simulated conditions most similar to those of their home range. Transplanted germinants placed in dissimilar conditions range fare poorly, particularly transplanted high elevation genotypes. Germination occurs earlier under warm-climate conditions with a pronounced effect under both control and warm conditions occurring within low elevation seed families. Implications for these findings

on community dynamics, migratory potential, species survivability and management practices are also discussed. Germination success can limit the migratory potential of a species and the suitable range available for species establishment or relocation and this poorly-understood developmental stage may act as a significant check on a species' or population's ability to survive changing environmental conditions.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	ii
ABSTRACT	iii
LIST OF TABLES	vi
LIST OF FIGURES	vii
CHAPTER 1: INTRODUCTION.....	1
1.1 PURPOSE OF THIS PROJECT	1
1.2 THE ROLE OF THE ENVIRONMENT IN SPECIES SURVIVAL.....	4
1.3 PHENOLOGY, PLASTICITY, AND ADAPTATION	14
1.4 MODELING AND MANAGEMENT	24
1.5 <i>BOECHERA STRICTA</i>	28
1.6 EXPERIMENTAL GOALS AND EXPECTATIONS	33
CHAPTER 2: METHODS.....	36
CHAPTER 3: RESULTS.....	38
CHAPTER 4: DISCUSSION.....	45
REFERENCES	53

LIST OF TABLES

Table 3.1: Heritability of Germination Success.....	38
Table 3.2: Heritability of Germination Phenology	38
Table 3.3: Heritability of Seedling Mortality	39
Table 3.4: Germination Success	40
Table 3.5: Germination Phenology	41

LIST OF FIGURES

Figure 3.1 Interactions between garden and linear/ quadratic effects of source elevation	42
Figure 3.2 Interaction between treatment and linear effects of source elevation.	43
Figure 3.3 Germination phenology at all sites	43
Figure 3.4 Interaction between garden and linear/quadratic effects of source germination	44

CHAPTER 1-INTRODUCTION

1.1 PURPOSE OF THIS PROJECT

Anthropogenic climate change is having demonstrable impacts on biological and physical systems (Root et al 2005, Rosenzweig et al 2008). Climate change can act at different scales and may manifest as small, regional changes or entirely new climates across wide regions (Williams et al 2007). Global and regional climate change has altered ecosystem dynamics in a variety of aquatic and terrestrial settings and across many distinct taxa (Parmesan 2006). Climate change is associated with new diurnal temperature patterns as well as changes in average temperature bounds for a given ecosystem. Average lower and higher temperature bounds are increasing in absolute value with lower bounds exhibiting the greatest rate of change. Average snowfalls and seasonal snow coverage times are also changing in many locations (Mudryk et al 2013). These changes are dramatically altering ecosystem dynamics and will have lasting implications for species survival (Walther et al 2002).

While general trends in global climate are clear, it is difficult to parse out exactly how a given species is responding or will likely respond as localized, non-climate based factors often are responsible for short-term biological changes (Parmesan and Yohe 2003). By identifying and aggregating the ways anthropogenic climate change can influence species, science has been able to identify clear systematic trends. In recent decades climate change has become increasingly viewed as an issue of global importance that demands immediate attention and study. Researchers from many disciplines have

increased efforts to understand the nature and extent of climate and how it is affecting biological systems. As individual effects have become better understood, efforts have also been made to understand how these effects interact with each other and identify potential mitigation strategies. We are beginning to understand how ecosystems may change under warmer conditions. Many of these well-studied characteristics occur at a large scale and are easily observable (eg. melting polar ice) while others manifest in more subtle ways but are no less vital.

Climate responses occur in many forms within and across species and may impact species in different ways based on individual organism sensitivities. Other anthropogenic processes could exacerbate these changes, whether it be through harvesting, depletion of shared resources, or changes in land use. Depending on the nature of the species, these other factors may outweigh the impact of climate or contribute to climate-induced response. Identifying the anthropogenic factors that act on a species and the degree to which they do so is a challenging task in and of itself due to the difficulty in quantifying complex anthropogenic processes. Understanding how these factors manifest across species and ecosystems is much more challenging yet necessary due to the interconnectedness of the natural world. Our understanding of climate impacts in different environments is often assembled piecemeal as many of these investigations focus on single species or aspects of a single species. The irregular focus of climate change research means we may have excellent data on charismatic species or ones that demonstrate clear and easily measurable changes in response to climate. While all of this data is valuable, the complexity of the how climate can alter species means that we may overlook subtle impacts that potentially may be highly influential in the survival of that

species or linked species under a new climate regime. These lurking factors could have major repercussions for ecosystems as a whole and help define limitations to species responsiveness and ecosystem function in a warmer world. Our research is aimed at investigating into one such modest yet potentially critically important factor.

Investigations into the ecology of climate change emphasize the ways in which a given species' suite of survival strategies is modified over time in response to new conditions. These responses can be largely classified as either genetic or ecological level strategies. Ecological-level investigations include examinations of plastic changes within existing populations or changes in range extent resulting from climate-prompted migration or differential die-off rates between populations (Nicotra et al 2010). Genetic responses manifest through gene flow and adaptation. These components are inextricably linked and species respond to changing climate stresses with a mixture of both (Anderson et al 2012). The blending of these components together is a relatively new practice as questions of species-environment interactions are highly complex and require interdisciplinary experience to approach them.

This project examined how environmental changes associated with warmer climate can impact one such ecological level process. We examined plastic responses to warmer temperatures during a key stage of plant life history-germination. Through the use of a well-understood and versatile species (*Boechera stricta*), we simulated how a changing climate may influence germination phenology and impact the distribution and fitness of *B. stricta* and similar species. By addressing this topic, we hope to improve our understanding of how climate change may impact the survival and propagation of this species and the survival of local populations. With an improved understanding of the

climate-induced phenology of germination we can improve our predictions of how responsive this and similar or trophically linked species may respond to anthropogenic climate change and what management and conservation practices are required to ensure species survival and diversity and preserve overall ecosystem function. While this project represents just one small element of a larger approach towards integrated ecological-genetic responses, by focusing on a critical yet little understood stage of plant development we hope to fill in an important gap in the literature.

This experiment examined how germinants of *B. stricta* that originate at different elevations within the same range fare when translocated and placed in simulated warmer-climate conditions. This paper will first examine the literature pertaining to trends in species response due to climate change, the roles of phenotypic plasticity and adaptation in defining these responses, the timing of plant life history events, potential implications for modeling and management, and the unique nature of *B. stricta* that makes it ideal for these purposes. Subsequently we lay out our experimental methodology, findings, and the implications of this research for ecosystem preservation and management.

1.2 THE ROLE OF THE ENVIRONMENT IN SPECIES SURVIVAL

Environmental factors play a critical role in initiating and regulating key stages of life history, especially for plants. Some such factors include the temporal syncing of flowering to increase potential for outcrossing or ensuring that seeds are only released during ideal conditions. (Engelmann and Purugganan 2006, Inouye 2008) Climate-induced changes in phenology have been observed across taxa and manifest in many forms ranging from mammal hibernation and emergence timing (Norquay and Willis

2014), bee emergence and pollination (Bartomeus et al 2011), to the flight season in butterflies (Kharouba et al 2014).

A given organism's or species' ability to survive is driven by many inherent characteristics, some of which may be more malleable or responsive to changing conditions than others. These factors may be large-scale and visible, as with the motility or nonmotility of a species. They may also be difficult to identify and highly species-specific, as is the case for unique genetic architectures or gene interactions. It is becoming clear that while both ecological and genetic approaches are valuable and yield great insights into how ecosystems function, we must also understand how these factors interact as well. Without this, we may miss critical factors when modeling how a species may fare in a changing climate. Improved species-specific knowledge also informs what conservation practices can maximize the chance the species survives with high population numbers and genetic variability (Anderson et al 2012).

There are some clear factors that influence the responsiveness of a species to a new climate. Species that are generalists or have more inherent adaptive capacity in their genetic architecture will be more likely to adjust to climate while species that are highly locally adapted will be at a disadvantage (Thomas et al 2006). This is a relative measure only, and even the most adaptable species may be subject to reduced fitness under new conditions. Specialist species or species that depend on complex systems of interspecies or species-environment interactions may lag behind in speed of response or be unable to respond at all (Thomas et al 2006). This is no surprise, as climate change may affect local environments in complex ways and species that have the most adaptability (whether it be

in diet, behavioral patterns, etc.) have the greatest chance of surviving sudden and major changes.

No two species are alike in the way that they can and may respond to climate change. Some generalist species may be flexible in all other dimensions but have their fate tied to a specific food species or habitat and behave as a specialist if climate negatively impacts that factor. A specialist may be able to better occupy an ecological niche than a generalist species under new climate conditions and be at a competitive advantage in that particular niche. A given specialist species may be fortunate enough to inhabit a local environment that will not be altered significantly by large-scale climate or one that largely disappears. Unique interactions of inherent species characteristics and the environment may lead to species responding in novel ways.

While climate change influences ecosystems in many ways, changes in air temperature are a major driver of environmental change. The rapid rate of change in temperature demands a response from species whose biology is highly dependent on operating within a certain temperature range including ectotherms or the cryophiles. The major early survival strategy under a new climate regime is for a species to shift its active range to one with more ideal conditions similar to those the species is currently adapted or acclimated to (Pearson 2006). This can occur through one of two mechanisms. Motile organisms can physically relocate themselves or alter their seasonal migration phenology to maximize the time within a suitable range. This leads to the rapid establishment of new home ranges for subsequent generations. Nonmotile organisms or motile organisms that reproduce through passive dispersal extend their ranges through a slower process that is dependent on dispersal ability. The ranges of temperature-sensitive species (plant and

animal alike) have shifted more rapidly and more distantly within recent decades than those of their more climate-tolerant peers. This pattern has been clearly documented in a number of sensitive taxa, including the cryophilic bryophytes (Bergamini et al 2009), and is associated with species that must maintain a particular temperature for biological activity.

Not all sensitive species or families are capable of responding in the same way or responding as rapidly and may suffer reduced fitness. Climate-sensitive species that can quickly establish themselves within a new range and effectively make use of that range's resources are more successful. Many factors, both environmental and genetic, contribute to this probability of success. Larger body sizes and larger geographic ranges are characteristics of species that exhibit improved dispersal ability, greater competitive advantages, and a tolerance of wide ranges of environmental conditions (Gaston 2003, Roy et al 2002). Dispersal ability is a major factor irrespective of organism size yet the ability of a larger species to disperse is not necessarily an indication that that species will migrate. In some fish species smaller species with rapid life cycles have begun to migrate poleward in response to changing conditions while their larger, long lived counterparts have not (Perry et al 2005). This suggests that initial waves of colonization may be composed of sensitive species whose thermoregulatory need to migrate may outweigh their more limited dispersal ability. This may lead to a short-lived respite as persistent warming prompts generalist migration and specialist species become competitively disadvantaged in the new environment.

Climate change can make areas bordering or connected to a species' native range more hospitable to dispersal where previously that species would have failed to take hold.

This leads to the creation of a 'leading edge' of expansion . Other areas within this given species' home range that are currently hospitable will become less so as temperatures range, which can lead to decreased fitness, population declines, and local extinctions in these 'trailing edge' zones (Angert et al 2011). Differential survival within these zones will lead to a redrawing of species range boundaries, and knowing the direction of movement and size extent of both zones may be useful in projecting future species dynamics.

Range shifts have been well documented in many species across multiple taxa, with consistent patterns emerging as to the extent and direction of edge shifts. Generally, leading edges move poleward in latitude and uphill elevationally. This pattern is directly attributable to climate change as the highest increases in species richness worldwide have been in latitudinal and elevational ranges where local conditions most closely mirror the increase in average global temperatures (Parolo and Rossi 2008). Species may migrate in one or both dimensions based on local topographies and regional climate as well as the species' thermal requirements. Many range-based studies focus on plant, butterfly, and bird species due to their sensitivity to climate, rapidity of response, and ease of tracking (Walther 2002). Invertebrates and large mammals have shown a similar poleward and upward movement pattern. (Hickling et al 2006, Parolo and Rossi 2008, Kelly and Goulden 2008, Lenoir et al 2008)

While the general trend of poleward and upward movement has been widely documented, it is difficult to pin down exactly what the rate of that movement is. Many global averages have been compiled using cross-taxa data but it is unclear what the predictive value of calculating these rates may be. As an example, one study found

changes of an average of 11m elevationally and 16.9km north per decade across many taxa (Chen et al 2011). Another posited an instantaneous velocity of around .42 km/yr poleward as a global mean (Loarie et al 2009). Climate is highly regionalized and species may migrate at rates far above or below the global average or may migrate in unexpected directions. The migration rate of a given species within a specific biome may also be vastly different. These rates also do not take into account factors like habitat fragmentation or geographic barriers though they may be useful in concert with such data. The poleward/upward trend itself is not universal and in some cases species move in a retrograde manner. These inconsistent patterns are particularly prevalent in the center of a species' native range far from either leading or trailing edges. They also occur in areas with a great degree of human activity (La Sorte et al 2007, Popy et al 2010).

Species and taxa respond at vastly different rates to climate change, particularly within the birds and certain plants. Some are highly sensitive and respond within one or a few generations while others do not respond for quite some time or at all, depending on the migratory, plastic, or genetic responses available to them. Potential responses may be constrained by geography or human activity, rendering species unable to respond quickly enough to climate change (Hoffmann and Sgro 2011). Depending on the extent of warming some of these species that are incapable of migrating may eventually go extinct or become highly range-restricted.

Raw air temperature is hardly the only climate-linked factor in a species' survival, as climate change will lead to secondary changes in ecosystem that species must respond to. For some species, temperatures may be less significant or insignificant compared to these secondary factors. Competing or outweighing pressures may negate the ability of a

species to migrate poleward and upward. These species may migrate in an opposite direction or stay in place to remain within the ideal range for other climate-linked limiting factors, including the availability of water as weather patterns change or the availability of prey species (Chen et al 2011, Crimmins et al 2011). Many of these factors are still temperature-linked (if several degrees separated), as with this project's examination of snowfall-derived soil moisture. Each species must respond in a way that is best in line with their particular resource needs, life history timings, interspecific interactions, and interactions with the environment.

Comparative analyses help identify problem areas or vulnerable species and help set management or research priorities. 'Velocities' of climate (ie the rate of migration required to keep pace with the rate of change in air temperature) differ between biomes. There is a strong correlation between topographic slope and velocity, with mountainous environments exhibiting the lowest velocities of climate change while flatter biomes have much higher velocities. This suggests that mountainous areas may provide appropriate shelter for a localized species or offer more time for a species to respond plastically or adaptively to climate (Loarie et al 2009). This seems intuitive, as the physical travel distance required to simulate a given change in air temperature is much smaller elevationally.

Evidence suggests that across biomes, the migratory velocity required to match the rate of climate change may greatly exceed what many contemporary species are capable of (Aitken et al 2008). Areas with high fragmentation may be harder to keep pace within due to artificial barriers while protected areas may offer easier migration (Joppa et al 2008). Species that cannot keep up may need human assistance with migrating or risk

extinction. This may call for a sort of ecological triage, where researchers and managers identify at-risk species or taxa and provide appropriate intervention. Formal climate range modeling may help in identifying at-risk species but comes with its own set of limitations.

Geographic ranges have contracted significantly for polar and mountainous species during recent decades. Many of these species are highly adapted to harsh climates and fare poorly outside of them. While the velocity of climate change is lower in these areas species that inhabit them do not have the same degree of migratory refuge available as there quite simply is less habitable upward or northward space available (Colwell et al 2008, Nogues-Bravo et al 2007). As such, they are at higher risk of going extinct or being confined within isolated refugia within their current native ranges (shaded-out areas, for example). Other highly climate sensitive environments include global coral reef systems, which are vulnerable to minute shifts in temperature, sunlight, and salinity among other factors and have experienced significant global collapse in recent years. Even within more stable biomes, certain taxa are particularly sensitive to climate change, with amphibians as one such example (Parmesan 2006). Models based on amphibians suggest a future defined by upslope movement, population isolation, and localized extinction where land runs out or where thermal/physical barriers prevent migration (Forero-Medina 2011). Similarities in climate response across many taxa and environments suggest that these well-studied sensitives may merely be the first wave of major species migrations, with generalists to follow.

Certain taxa exhibit a large degree of climate lag (delayed response in tracking climate change), as is the case with many North American wind-dispersed trees. When

migration lag occurs in plant species, it tends to be with respect to elevational gradient and not latitude. This may be due to the presence of suitable microclimates (as with shady mountain faces) or local physical characteristics (soil, slope steepness) that hinder or mitigate the need for expansion (Nathan et al 2011, Chen et al 2011).

Microclimates may have a significant impact on the rate and direction of climate-driven range expansion, however they are often overlooked or poorly accounted for in models that are conducted on large scales (in units of kilometers). Local factors can hinder or prevent seed dispersal in plant species, cutting off large areas of potential expansion at geographic chokepoints that may not be adequately represented within a model. Many projections do not account for the variety in local topography across a large area and tend to homogenize regions. It is also difficult to project how a given species or taxa will interact with local ecologies within a potential expansion range (Suggitt et al 2011). This makes it difficult to define just how rigid or porous a species' leading edge border may be, as vegetative cover may prevent wind-dispersed species from establishing themselves or generalist herbivore species within the new range may limit the growth and reproduction of colonists. If crucial lurking factors are underrepresented or omitted entirely then our predictions may be skewed. Without a more complete knowledge, we could miss key leveraging interactions, factors, or stages of life history that determine how successfully a species responds to climate change and its chances of adaptation.

The uncertainty and complexity associated with species-based climate modeling only heightens the need for a better understanding of species life history. This project aims to address two such piece of the larger climate response puzzle, those of germination phenology and success. As plant species have been well-described with

regard to climate migration, (including sensitives and generalists, initial colonists and lagging responders) and function as critical components in the trophic systems and habitat structure of ecosystem, they are useful tools for investigating climate. Plant life history stages have been well investigated at both the ecological and genetic level but it is only in recent decades that life history responses to climate have come to the forefront of research.

Of these life history stages, none may be as important as germination in predicting the success of colonists outside their usual range. Germination is a critical developmental stage for plants and understanding how this process responds to climate stress is essential when modeling the rate, direction, and capability for range expansion for a species. The success of germination, the timing of germination, and the number of germinants that survive to reproductive maturity are all key potentially indicative factors that are not as well understood in an ecological capacity (although the underlying baseline chemical and genetic processes associated with germination are well-known). Poor germination in a leading edge region could serve to restrict species expansion and establishment while successful germination and high adaptability within germinants could give a species a competitive edge in transitional environments. The more flexible and responsive germination (or any other life history stage, for that matter) is to climate, the better chance that species has of surviving.

Changes in phenology represent one flexibility mechanism that could define how well species survive in edge regions. By advancing germination phenology in response to warmer temperatures a species can go a long way towards substituting plastic responses

for migratory demand. This could be important for species in regions with little migratory potential (alpine or high latitudes, for example) or very high inherent plasticity.

1.3 PHENOLOGY, PLASTICITY, AND ADAPTATION

Phenotypic plasticity is an encompassing term that refers to the ability of a single genotype to express different phenotypes depending on ambient environmental conditions, an organism's ability to alter its phenotype based on the environment, or a change in the nature or timing of important life history events in response to environmental cues. While long relegated to mere environmental background noise that had little bearing on the true nature of organism-environment interactions, plasticity has become a substantial area of study for those looking to understand how climate change will alter ecosystems. Plasticity offers a potential 'out' for species that are threatened by changes in climate patterns and cannot adapt or migrate quickly enough to keep pace (Sultan 2000). Plants in particular exhibit a high degree of plasticity in the life history timing and physiology of parent and offspring generations. Studies of plastic responses are complicated and incorporate aspects of both ecological and genetic investigations, including quantitative and molecular approaches (Kelly et al 2012, Sultan 2000).

Plasticity is an especially important consideration for plants and sessile species that are unable to physically relocate. With anthropogenic climate change poised to alter environmental conditions and ecosystems in so many different and interlocking ways, an organism's ability to respond either plastically or adaptively to these pressures might be the difference between persistence or extinction. There have been multiple attempts to generalize plastic responses to climate. One particular hypothesis, the climatic variability hypothesis (CVH), proposes that in general higher latitudes species have more plasticity

due to the greater variation in seasonal temperatures they experience and have experienced over long time periods, a claim that has garnered at least some support (Molina-Montenegro and Naya 2012).

Plasticity may reduce the need and ability for adaptation or may provide new opportunities for selection to adapt but there is at present no single framework that fully accounts for both plasticity and adaptation in evolutionary responses. In some cases, short term plastic responses may reduce population adaptive divergence or result in maladaptiveness in the long term, depending on the particulars of a species niche and which stressors that species is responding to. This can make future fitness and adaptive response harder to predict as entangled stressor variables (temperature, water availability, etc.) change (Ghalambor et al 2007, Fitzpatrick 2012). Phenotypic plasticity offers additional responsive flexibility but presents a headache for researchers and conservation managers that attempt to quantify the nature, direction, and strength of a plastic response.

Plastic responses can act on different components of fitness and may act directionally or antagonistically depending on the type of stress and characteristics of the organism. While the interaction of genetic and environmental variation is a complex issue, plant species provide useful tools for untangling these interactions. Many plant species have been the focus of extensive genetic study in controlled lab settings across many generations. This has provided us with a better understanding of the mechanisms that underlie environmental and ecological response processes. Field experiments provide valuable insight and flexibility for these assessments if performed effectively. The malleability of plants under different climates makes them ideal for plasticity

investigations as they may change physically or in terms of timing under different conditions. (Anderson 2012).

Physical migration is not the only climate response strategy available to species. Species may reduce climate-derived stress by shifting in time as well as in space through the plastic advancement of temperature-triggered processes. By moving these processes up, species can take advantage of warmer spring temperatures and ensure these events happen under ideal conditions. Otherwise, the species would have to migrate northward or upward to find temperature-date pairings similar to those of previous years. Since the 1960s, many species and taxa have been observed advancing spring phenology events. Birds have begun breeding and singing earlier in the season and migratory species leave earlier in the year. Butterflies have emerged earlier and also have advanced their migration timing. Amphibians are spawning and chorusing earlier as well (Walther et al 2002). This advancement pattern is strongly associated with spring but less so with fall, where changes have not been as pronounced (Gatter 1992).

Plants have been observed changing the time of their spring phenology significantly to adjust to warmer climates. Ideally, life history transitions are precisely timed in order to coincide with optimal environmental conditions and mistiming can lead to reduced fitness. Premature germination or emergence risks frost-associated tissue damage (Inouye 2008). Early emergence also can lead to reduced fitness if necessary resources are absent or are not in sufficient quantities to support the emerging population. Timing that misses the presence of pollinators or coincides with high herbivory also reduces fitness (Thomson 2010, Pilon 2000). Late flowering can result in mortality from adverse weather or increased competition from other individuals or species (Franke

2006). These factors would seem to favor selection for intermediate traits and emergence/flowering times that fall within the window of suitable biotic and abiotic conditions. A changing climate shifts this window and impacts species and individuals that fall near the extremes of the spectrum. Under static conditions, earlier emergers would theoretically benefit from climate change and shifting summer conditions. Late emergers would suffer greatly reduced fitness or mortality.

A meta-analysis of many European plant species found the vast majority are undergoing an advancement in flowering, leafing, and fruiting with a significant subset (around 30% of the observed species) advancing substantially. These changes are directly attributable to climate change and increased temperatures in the winter months prior to spring phenology. No similar pattern was observed for fall phenology (Menzel et al 2006). When a species advances spring phenological events significantly, it can imperil other species that are linked trophically or reproductively. This can lead to time gaps between spring emergence of a predator species and the presence of its prey, or a gap between pollinator activity and plant flowering. These mismatches in the phenologies of inextricably linked species may have severe ramifications for the ecosystem as a whole. Climate-induced migration by one or more of these linked species can complicate interactions and lead to further breakdowns. Some species have already been observed tracking the range shifts of linked sensitive species. This is particularly common with butterflies and their respective larval food plants (Durant et al 2007, Schweiger et al 2008, Pöyry et al 2009, Gilman et al 2010). While many species are currently exhibiting range expansions as temperatures rise, species in regions where all migratory opportunities are limited or exhausted have moved into the range contraction phase

(Wilson et al 2005). These species are likely to suffer reduced fitness and in some cases, extinction as climate change intensifies.

Plant species are particularly sensitive to climate change and limited migratory capability due to their sessile nature and close association with climate-induced life history timing. As with other taxa, climate alone is not the only factor that restricts the range size of a given plant species but it is a critical one. Plant spatial distributions are controlled not only by a species or population's ability to tolerate local environmental conditions but also by intraspecific variation and competition, species-species interactions, and herbivory (Goslee et al 2005, Becerra 2007, Crutsinger et al 2006, Genung et al 2012). Expansion ranges may introduce new interactions or changes in herbivory rates to colonist populations and limit or prevent establishment beyond what simple range climate range modeling would predict. Knowing the most significant limiting factors for a given species is necessary for accurately detailing the direction and magnitude of migration. To this we add that we must also know the degree to which those characteristics are plastic.

Alpine plant species are particularly vulnerable to climate change due to the narrow temperature and range restrictions characteristic of the region and locally adapted inhabitants. Germination phenology within alpine plants under changing temperatures is a poorly understood process. Historical studies have focused on the survival rates and phenological changes of mature organisms in response to climate change. This is largely due to the new emphasis on the phenology of climate and to the fact that mature organisms are easier to manage in both field and lab settings. While lab germination studies have been conducted on alpine plant species, it is much more difficult to monitor

germination in the field. Seeds that do not germinate and germinants that do not survive cannot become mature plants. Even if the phenological responses to climate and their role in migration are well understood for mature plants, these findings may have lessened value if climate-induced germination failures are a significant limiting factor. Data derived from climate studies on mature plants may be less applicable if those plants never make it past the germination stage. We therefore examined the germination phenology of a malleable alpine plant species in the field setting in an attempt to address this need.

Our project, while novel in many respects, builds upon similar work. Field translocation experiments in alpine settings have proven valuable in understanding life history phenology for other plant species. These experiments are simple in principle yet are effective at simulating intraspecific species dynamics that are shaped by climate. By transferring highly locally adapted genotypes of a species from their native environments to different conditions within the same range, we can simulate climate changes and prompt plastic responses. This approach allows for the monitoring of overall survival of the respective genotypes under different conditions. Careful monitoring also permits the tracking of major life history events in both timing and extent. Samples can also be processed in the lab to examine physiological and genetic responses to translocation, especially across multiple generations.

In alpine environments, lower elevations generally have warmer temperatures while higher elevations are cooler. Reciprocal translocations can therefore be used to simulate future climate (by shifting genotypes downhill a distance proportional to predicted temperature shifts) or explore how species or genotypes fare in vastly different conditions. Other non-temperature factors can also be incorporated. Our work adds to the

literature on how plant species respond to simulated climate and incorporates water availability as an additional factor of study. Our findings resemble to those described in similar experiments. A recent translocation study showed that germinants of *Erysimum capitatum* exhibit greater germination success within home ranges and decreased success when outside the range, suggesting a large degree of local adaptation. Alpine genotypes had a competitive advantage over nonalpine germinants within their native range, an unsurprising result. Alpine germinants only experienced this competitive advantage at higher elevations and suffered high mortality when placed lower in the range (simulated future conditions). Conversely, there was no conclusive survival advantage for low elevation germinants in low elevation conditions, suggesting that warming may have already begun to decrease the fitness of these low elevation inhabitants as the climate becomes unsuitable (Kim et al 2013, Ensuk and Donohue 2011). This is a troubling pattern as populations adapted for alpine environments are at higher risk for climate-induced extinctions (Parry et al 2007).

Germination phenology is important as more than just a measure of survival or mortality under adverse conditions; climate-induced stresses during the germinative phase may have implications for later life history stages. In *Arabidopsis thaliana*, a close relative of *B. stricta*, the timing of germination significantly impacted later life history characteristics. *Arabidopsis* seeds that germinated earlier exhibited significantly larger sizes at the time of reproduction and reproduced earlier. Seeds that germinated later in the year experienced total mortality and did not survive to reproduction. Selective pressures for larger size and faster growth rate were also stronger on later germinants. These latecomers also experienced stabilizing selection on reproduction timing. For

Arabidopsis, changes in the timing of germination may reduce fitness, influence phenology, and alter selective pressures in ways that do not manifest until much later in life (Donohue et al 2005, Barua et al 2012). Natural selection that acts on the early life stages of species like *A thaliana* can influence later traits through pleiotropy across developmental stages and developmental niche construction. (Donohue et al 2002, 2005) Seed dormancy represents a key factor in germination success and can impact later survival. Physiological dormancy is particularly climate sensitive (Willis et al 2014). Dormancy itself can influence life history characteristics independently of germination, suggesting that it is the entire seed stage itself that is critical. In some cases, environmental cues can act on dormant seeds and alter later flowering characteristics without changing germination phenology (de Casas et al 2012).

It is largely unknown whether genotypes within a species germinate based on specific or varying conditions. The degree of variance in physiological mechanisms and what environmental conditions may induce them in natural populations is also poorly understood. *Arabidopsis* has demonstrated germination variation in response to simulated changing conditions but genotypes were not specialized to precise conditions. Instead, genotype sensitivity to phytohormones can influence germination differentially and change the ability of an organism to adapt to new environments. This suggests plants may be able to adjust germination phenology in a somewhat flexible and complex manner based on genotype characteristics (Barua et al 2012).

Species with the proper internal characteristics may be able to undergo rapid genetic adaptation in addition to plastic responses. In many cases, it is difficult to distinguish plastic responses from selective ones. High levels of plastic response may

actually preclude adaptive responses by rendering them unnecessary but have lingering effects for species when the plastic capacity of the organism is exceeded by the adaptive demand imposed by climate. Multiple plastic and nonplastic traits can also act synergistically and create a plastic response (Price et al 2003). Some of these changes may be able to offset the need to migrate in response to climate.

Species are limited in the degree of plastic response. Studies of conifer leaf physiology since the last glacial maximum have shown that physiological changes were more similar within families and differed within co-occurring species assemblages. This suggests that evolutionary history may drive a plant species' future physiological responsiveness to climate change (Becklin et al 2014). Changing environmental conditions create new phenotypic optima and phenotypic distributions that lead to plastic changes. Climate change favors these phenotypic responses initially. Prolonged exposure to changing climate can lead to more permanent genetic responses that mirror the plastic ones. However, the specific conditions, interactions, and genetic or biological mechanisms that determine the degree of plastic responsiveness vs. need for genetic adaptation is often species-specific and difficult to determine (Crozier et al 2008, Moczek et al 2011). Bird species have been documented increasing in size over the past century due to rising temperatures, a substitutive shift equivalent to a migration of 7 degrees of latitude (Gardner et al 2009). Temperate and boreal trees exhibit local adaptation along temperature gradients that result from the small effects of multiple genes, suggesting that climate-induced adaptations will need to occur in those gene linkages to provide sufficient adaptive capacity (Aitken et al 2008)

Leading edge species and populations generally are more likely to adapt while trailing edge species are highly vulnerable to extinction. (Aitken et al 2008) This is likely due to the extra time leading edge species have to adapt before conditions worsen below critical levels or the presence of greater inherent adaptive capacity in those species. Some species can adapt rapidly to drought conditions, even within a single generation, as seen in some brassicas (Franks et al 2007). Adaptive variation is lost when compensating for climate shifts. Translocation experiments have demonstrated that populations in the process of adapting to leading edge ranges suffer reduced fitness when placed back into ancestral ranges (Buckley et al 2014). Leading edge species may suffer from low heritabilities of desirable traits, demographic instability, or cross-environment genetic correlations antagonistic to selection which makes colonization a high-risk proposition (Etterson 2004).

The inherent responsiveness of a species alone is not enough to guarantee survival but can confer major advantages. Adaptable species are still subject to complex and localized suites of stressors, both natural and anthropogenic (Heikkinen et al 2010). Range shifts also are not always due to climate but may also result from human activities. Some of these shifts, especially in some birds, occur in poleward and upward directions but originate from a need to avoid human activities or interactions of biotic and abiotic factors rather than climate itself (La Sorte et al 2007). Climate-associated factors like photoperiods, season lengths, seasonal range or feeding barriers influence species in differing ways. Species may be more influenced by these secondary or tertiary impacts of climate change than temperatures themselves (Davis and Shaw 2001). Plasticity may or

may not offer a way out for species threatened by climate change, but it is a complex process that in some cases may magnify the threat of extinction.

1.4 MODELING AND MANAGEMENT

Attempts to model and predict how climate will impact ecosystems at large are imperfect, generalized, and rely on relative metrics and potentialities. This is not to say that these models do not have great utility for managers and conservationists, as they can help identify at-risk species or identify problem areas. Models are often constructed based on general characteristics of climate or species. These models are functionally useful as experimental evidence suggests that there are indeed characteristics and trends that improve the ability of a species or a population within a species to propagate itself and shift its range to more ideal locales. These factors are not particularly surprising as they suggest that species that can propagate faster and disperse farther are favored. For example, evidence shows that plants with mechanisms that spread seeds farther have been able to shift their ranges farther than plant species with a limited dispersal capacity. Nonthreatened species have shifted their ranges more significantly than threatened ones (which have higher rates of local adaptation and endemism). This is particularly troubling, as it suggests a potential dismal fate for at-risk species and a significant decrease in intraspecific and ecosystem-wide genetic diversity (Angert et al 2011, Pöyry 2009). Species that reproduce earlier in the year, have high fecundity, or reproduce multiple times in a year also have an advantage. (Angert et al 2011) Models incorporate this information to simulate the migratory potential for species that have not yet entered the migratory phase or have migrated at a slower rate.

A species' vulnerability to climate change is described by numerous factors, including its current geographic distribution, whether it exists within anomalous climate regions that are not exhibiting the same warming rate as seen globally, how broad the species' niche is, and whether there are physical barriers to expansion located in or near the natural range (Broenniman et al 2006). Many processes contribute to defining the range of a species as climate change leads to the migration, extinction, and blending of populations and must be accounted for in models. These processes may include Allee effects or gene swamping and may change dramatically as ecosystems are altered. Populations at range edges, while the best poised to expand based on geography are often genetically isolated with high variability in performance between individuals and populations. We do not fully understand how contemporary range boundaries have evolved over time or how genes flow in these areas (Sexton et al 2009) but many attempts have been made to generate models of range limits (Holt et al 2005, Bridle and Vines 2006). Edge populations may be highly distant from those at the heart of the range, both geographically and genetically and have little gene flow between populations. They may also experience different selective pressures as they come into contact with more distinct local ecologies or other species (Eckert et al 2008, Bridle and Vines 2006). Selection for increased dispersal is favored at these edges (Darling et al 2008).

Unfortunately, while these trends are clear models built upon them are limited in their predictive specificity. Climate Envelope Models are the standard tool for species-climate migratory assessments but are based solely on projecting the geographic area that may become temperature-habitable for a species within a given timeframe and do not incorporate local factors, species characteristics, or interspecific interactions effectively.

These models also do not account for a species responding plastically or adaptively to climate stress, (Watling et al 2012, Molina-Montenegro and Naya 2012) even though plastic responses are closely linked to a species' ability to survive extinction in a new climate regime (Hoffmann and Sgro 2011). The rapid rate of climate change puts additional pressure on researchers attempting to fill in data gaps quickly enough for that data to be put to good use in models. Historical provenance tests are an example of one potential data source that adds population and species-specific plasticity data into models within the near-term (Leites et al 2012). This approach is effective where data is readily available but in most cases new work is required to identify what data is needed and establish collection processes. Projects like ours may help fill in these gaps.

Climate can impact an ecosystem directly by thermally stressing sensitive organisms or indirectly by changing ecosystem dynamics (Thomas 2006, 2010), complicating management practices as those impacts manifest differentially. Most species track spatial ecological niches as they change with climate (Davis and Shaw 2001), while others may lag behind (Svennig et al 2008). External non-climate anthropogenic factors like increased habitat fragmentation can hinder or prevent species from expanding into a suitable range or isolate populations that otherwise would become widespread, increasing the risk of extinction (Jump and Penuelas 2005). Changes in land cover use can also create barriers to migration (Damschen et al 2006). Models also may vary based on which climate projection scenarios are used (IPCC 2000). Alternatives to CEMs are often appropriated from other sources rather than specifically designed, as with invasion models (Angert et al 2011). While there is much skepticism towards just how reliable climate-based range models are at predicting future ranges, it may still be

possible to at least *a priori* predict how sensitive a species will be to climate change with the proper data and emphasis on redesigning how these models are structured (Broenniman et al 2006).

In order to build more rigorous models that are useful for creating species-specific range projections and the makeup and dynamics of future ecosystems we need to incorporate our current knowledge of the specific life history traits, interactions, and plastic/adaptive capacity of species (Ibanez et al 2006, Angert et al 2011, Parolo and Rossi 2008, le Roux 2008). While some work has been done in this area, only weak associations have been observed between specific life history traits and higher dispersal success at leading range edges (Angert et al 2011). Historical data may be of use here, with one such example being the dispersal rates of large trees during the late Pleistocene (Clark 1998, Davis and Shaw 2001) Risk can be modeled as a factor of inherent characteristics that make a species poorly suited for new conditions or a vulnerability to unique geographic or historical conditions and events. Understanding previous extinction events that were linked to creeping environmental changes or significant rapid events (extreme weather, natural disasters, human activities) can help us predict future ones (Purvis et al 2005, Kolar and Lodge 2001) and improve management practices. High-risk species may need to be manually relocated to match the pace of climate change (Aitken et al 2008). Protecting at-risk areas can influence a species' ability to survive climate change (Hannah 2008).

Modeling strategies should incorporate as much site-specific detail as possible, especially that which is already readily available through GIS services. Desirable local detail includes local topographies, the amount and distribution of vegetative cover,

species compositions, etc. (Holzinger et al 2008). Data is easily collected and analyzed in areas with high spatial heterogeneity (Walther et al 2002). Unique microhabitats or potential interactions between previously noninteracting species can impact ecosystem dynamics in unforeseen ways and complicate models (Suggitt et al 2011). Even so, equilibrium species responses to climate change are difficult to determine when temperatures are changing far more rapidly than previous warming events (Clark 1998).

Since collecting life history and interaction data for a wide array of species is expensive and time consuming, surrogate species may be an efficient, if imperfect way to model general patterns of climate response. While this approach is not foolproof and by design overlooks nuanced responses and sensitive species, it may represent a valid middle ground approach that maximizes our predictive ability.

1.5 *BOECHERA STRICTA*

Boechea stricta (also known as Drummond's rockcress) is an exemplary model for functional genomics and ecological investigations. *Boechea* is a member of the family Brassicaceae, a genus that contains dozens of well-understood species. Most of these are sexually diploid with high levels of inbreeding and homozygosity resulting from mixed mating systems. *Boechea stricta* is a strongly selfing species. A minority of highly heterozygous asexual species also exist within the Brassicaceae. Representatives of *B. stricta* and related species are found in a wide range of environments and environmental conditions (Song et al 2006). Individuals have rapid development cycles and are perennial. The genus has been shown to be genetically pliable in both lab and field settings and is widespread enough yet also untouched enough to be an ideal model organisms for examining a plethora of life history traits (Rushworth et al 2011).

Native *Boechera* populations are relatively undisturbed and are widespread across a wide variety of North American environments (Rollins 1993). Within the Rocky Mountain range there is a great deal of partitioning along a north-south axis and multiple isolated refugia available. Glaciation has had a profound effect in shaping the genetic architecture and distribution of *B. stricta* within this range (Song et al 2006). Within these environments, *Boechera* exhibits a high degree of adaptation to local range characteristics like temperature and rainfall (Anderson et al 2010). Its close relation to *Arabidopsis thaliana* and high degree of genetic linkage means there are a suite of genomic tools available for use in ecological studies. *Boechera stricta* has also been sequenced in recent years. While there is a high proportion of hybridization between *Boechera* species and subspecies, this allows for genetic and mapping and the ability to track speciation (Rushworth et al 2011). *Boechera* community dynamics can be influenced by biotic and abiotic factors. *Boechera* spatial distributions within its native range are driven by preference for specific microhabitats and a limited dispersal ability in addition to intraspecific interactions and insect herbivory (Naithani et al 2014). *Boechera stricta* has smaller populations than its *Arabidopsis* cousins with lower diversity, possibly due to local extinctions and founder effects (Nordborg et al 2005).

Studies of evolutionary ecology are most effective when the examined species have existed in relatively undisturbed environments over long periods of time, allowing for natural selection alone to act on these species. *Boechera* populations have existed in some areas for around 3,000 years in an undisturbed state (Brunelle et al 2005). While they may not be at perfect genetic or ecological equilibrium, certain Rocky Mountain *Boechera* populations are virtually untouched and have not been contaminated by foreign

genotypes or fragmented by human activities. This range is ideal for field experiments on ecological and genetic response to stress (Rushworth et al 2011). Glaciation cycles and the rugged Rocky Mountain topography are responsible for a complex arrangement of *Boechea* species and populations within the range, with the highest species biodiversity west of the Rockies (Kiefer et al 2009). Eastern and western North American populations of *B. stricta* exhibit significant genetic differences (Song et al 2006). Within the eastern group, there is also a significant degree of genetic differentiation along a north-south axis (Lee and Mitchell-Olds 2011).

Each year, multiple *Boechea* generations can be grown under controlled settings. Major life history events like bolting and flowering occur quickly in the lab with the proper vernalization procedures. Individuals produce many seeds that are relatively easy to collect and crossbreeding is simple. Individuals are also hardy and can be relocated easily, allowing lab-grown experimental plants to be introduced into natural populations. This allows for easier and more robust analyses of many life history characteristics and their impact on fitness (Anderson et al 2010). The interactions of *Boechea* members with other local species are also relatively well studied, either directly or by proxy through our understanding of *Arabodopsis* dynamics. These include pathogens (Roy 2001) and herbivores (Carmona et al 2011). The genetics of herbivory resistance involves tradeoffs between it and other components of fitness (Anderson and Mitchell-Olds 2010, Manzaneda et al 2010). *Boechea* also holds potential for quantitative trait locus (QTL) mapping and gene-wide association studies across multiple wild populations, a relative unexplored practice (Anderson et al 2011). The species is also suited for small to

medium scale shotgun sequencing for cheap and rapid examinations of specific evolutionary or functional genetic frameworks. (Windsor et al 2006)

Many components of *Boechea* fitness and life history are well understood. Characteristics like age at first flowering and the timing phenology of flowering have been examined at the genetic level in both *Arabidopsis* and *Boechea*. The selective pressures on these characteristics have also been studied in the field, with flowering phenology favoring genotypes that reproduce during optimal conditions. (Metcalf and Mitchell-Olds 2009, Anderson et al 2010) Lab experiments have proven less indicative suggesting that we do not fully understand how to model the signaling of flowering in a lab setting and emphasizing the need for undisturbed field sites in order to continue our work. Advancing climate change within this undisturbed range has allowed for the tracking of selection under new pressures, as with flowering. Warming climates have favored genotypes that flower earlier in the year and relocation experiments have shown that local alleles are favored in their home environments (Anderson et al 2010). Flowering is advanced temporally to adapt to drought conditions. Reproductive phenology is impacted by genetic and environmental factors and directional selection towards earlier flowering is occurring. This trend is consistent with local and global warming patterns over the past forty years. Advancement in flowering is also strongly associated with earlier snowmelt. The rate of flowering advancement also is likely to accelerate in coming decades concurrently with warming accelerations, requiring at least some degree of adaptation in order to survive in the current range. (Anderson et al 2012) At the same time, flowering in *B. stricta* is not controlled by water alone. Microbial communities may have a role to play as well. Natural soil biomes and chemistries can

influence flowering phenology independently or in concert. Changes to soil composition or the microbial balance in soils can prompt plastic responses as well as selection on the time of first flowering. Different microbial communities may be influencing selective pressures between habitats or microhabitats and may act in concert with water concentrations to drive flowering (Wagner et al 2014). This reiterates that climate alone is not the only factor driving phenological changes in organisms like *B. stricta* and that the balance of phenological vs. selective response is malleable.

This organism is well suited for range limitation studies and has been thus utilized to test an important theory on how ranges limits are maintained. The Defense Constraint (DC) hypothesis suggests that the evolution of tolerance to stressful conditions across range boundaries in many plant species is constrained allocations to chemical defensive mechanisms. Biotic/abiotic stress tolerance pathways are theorized to crosstalk and act antagonistically (Siemens et al 2012).

The presence or absence of water plays a critical role in both the germination and overall success of *Boechera* species. *Boechera stricta* is generally found in moister regions and is sensitive to drought. A reciprocal transplant experiment observed high local adaptation for water conditions within a close cousin species (Knight et al 2006). Herbivory is possibly the most defining factor that acts in concert with climate to determine the range of *Boechera stricta* as the species is commonly found in regions with few generalist herbivores. Plasticity across generations should allow *Boechera* to temporarily expand its range in response to climate change; however herbivorizers may create a barrier to migration. Multigeneration lab experiments on *B. stricta* have found that genetic changes can surmount these barriers but that plastic change may act

antagonistically. This may limit the ability of *B. stricta* to migrate to more significant degree than a climate range model alone would suggest (Alsdurf et al 2013). One aspect of *Boechera stricta* life history that was previously unexplored is that of germination timing, particularly with respect to different climatic conditions. Our project addressed this need and strengthened the species' role as a valuable indicator of climate response and useful experimental organism.

1.6 EXPERIMENTAL GOALS AND EXPECTATIONS

Reciprocal transplantation experiments are useful tools for studying phenotypic plasticity and degrees of local adaptation (Reznick 1996, Kawecki and Ebert 2004, Kim et al 2013, Ettreson 2004). In this study, we conducted one such assessment using natural populations of *Boechera stricta* in order to simulate how projected warming air temperatures would affect germination success and seedling mortality. By isolating and relocating a large number of highly locally adapted alpine genotypes to new elevations within the range we hoped to understand how increases in temperature and associated decreases in available water during the critical germination period manifest phenologically.

Similar germination experiments and experiments using closely related organisms have demonstrated that organisms that are well adapted to local conditions unsurprisingly fare well when in those conditions and less so when removed from them. We expected a similar finding with one major caveat. As climate warms, mid and high elevation alpine reaches experience increases in air temperature and decrease in seasonal snowpack that more closely resembles that of neighboring lower elevations. This could lead to alterations in the dynamics of a given population as currently well-adapted low elevation

inhabitants become more favored in higher elevation settings. Current mid and high elevation inhabitants may experience reduced fitness or upward migration as the range for suitable habitation shrinks or disappears entirely. We anticipate that this may result in decreases in fitness and variation for the population as a whole and a degree of plastic response in the short term as these at-risk populations shift the timing of germination.

By adding to the available literature on how germination phenology responds to climate we hope to improve our understanding of how this sensitive stage of development impacts life history and overall mortality for plant species as the planet warms. If germination is a critically climate-sensitive process, contemporary range modeling and species management practices may greatly underestimate the degree to which species can adapt plastically for long enough to establish themselves and survive in new ranges or adapt to existing ones. Conversely, if germination is highly plastic and able to compensate for rapid warming and earlier snowmelt, then it may not be as significant a constraint on species range and species fitness.

Warming temperatures are associated with earlier snowmelt and shallower snowpack in alpine regions. We anticipate that in control settings, seed families that originate from elevations similar to those of the respective gardens will show increased germination success and reduced and delayed mortality compared to those from above or below the range. We may also find that in some cases germinants from slightly lower in altitude than each experimental garden may be favored due to recent warming trends already beginning to change local conditions to ones more similar as downhill. In addition, we anticipate that high-altitude seedlings will fare more poorly than lower altitude seedlings across the range due to the increased unsuitability of these highly

locally adapted genotypes in warmer conditions, with high unsuitability at the lowest altitudes. High elevation genotypes are accustomed to deeper snowpacks and later snowmelts as well as cooler temperatures, conditions which are rapidly disappearing within our study range. Of our experimental gardens, all but one were sited at elevations within the range represented by our seedlings. Our lowest elevation garden is lower than that of any of our seed families, therefore we anticipate lower germination success for all genotypes in this environment across the board (as none would be particularly adapted in either contemporary or future conditions), with lower elevation genotypes faring much better than high elevation counterparts.

CHAPTER 2-METHODS

Jill Anderson and Bashira Chowdhury planted seeds in four gardens at different elevations within the Rocky Mountain Biological Laboratory (RMBL) in October of 2013, and inspected gardens for germination from mid-April to late July 2014. Our experimental gardens were located at elevations of 2540m (designated 'Estess'), 2710 ('Peanut Mine'), 2890m ('Gothic Valley'), and 3430m ('North Pole'). Seeds were collected from populations that ranged in elevation from 2693-3690m. Field collected seeds were grown in a lab setting for one generation in an effort to reduce maternal effects. Planting plots were established by a 13x13 grid of plastic diffusion-screen blocks that contained a total of 169 individual 1cm² planting sites. Each site contained randomized germinants from all across the elevational gradient arranged within treatment blocks. Germination blocks at each site were exposed to either contemporary or simulated future snow dynamics.

Projected future conditions were simulated via the physical removal of snow in the garden area. The snow removal treatment served to simulate both warmer air temperatures and decreased water availability associated with most alpine climate change projections. Upon the winter snowfall reaching 1m in depth, in snow removal plots all snow in excess of 10cm depth was removed. This process was maintained until the end of the snow season and the onset of snowmelt, at which point plots were monitored for germination. Three of our four experimental sites were able to be maintained in this manner. The lowest elevation garden (Estess) did not attain 1m in snowfall depth at any

point of the experiment, reaching only .4m in depth at maximum. Snow removal proceeded in Estess as it did in the other sites, though control plots had decreased snowpack and water availability compared to our other control plots.

Prior to the snowy season, two seeds from the same seed family were planted in their corresponding individual 1cm² plot, with control cells left empty. Seedlings were monitored throughout the year, especially during the spring snowmelt. As soon snowmelt began in late May of 2014 and plots became exposed, Anderson and Chowdhury monitored all blocks for visible germinants. Plots were checked every other day and any visible germinants were recorded. The Julian day for the first day of observed germination in a given plot was recorded along with the success or failure of the plot's paired seedling. Additional germinants and associated germination date were added to our records through a regular monitoring process that continued throughout the spring and summer months. Germinant mortality was also recorded and tracked by Julian day of death.

Anderson analyzed the timing of germination as well as germination success. Data was analyzed using SAS (ver 9.3) and examined for trends in heritabilities, success of germination at the individual and population levels, phenology (timing) of germination at both levels, success by garden and treatment, and the timing and degree of mortality. Interactions between linear and quadratic effects associated with garden and treatment were also analyzed.

CHAPTER 3-RESULTS

We examined heritabilities for germination success, germination phenology, and mortality timing within each of our four producing gardens. We first present the broad sense heritabilities (\pm SE) of germination success in our organisms. Heritabilities were estimated from variance components in REML (Proc Mixed) using individual seedling data. Results are as follows and all p-values are based on likelihood ratio tests (χ^2 , df=1). Bolded p-values correspond to significant heritabilities after a Bonferroni correction for 3 trait x 4 gardens ($\alpha=.05/12=.0042$)

Table 3.1: Heritability of Germination Success

Germination success	H ²	χ^2	p-value
Estess (2540m)	0		1
Peanut Mine (2710m)	0.106 \pm 0.025	9.0	<0.0001
Gothic (2884m)	0.105 \pm 0.024	39.0	<0.0001
North Pole (3430m)	0.124 \pm 0.029	36.9	<0.0001

Table 3.2: Heritability of Germination Phenology

Germination phenology	H ²	χ^2	p-value
Estess (2540m)	0.132 \pm 0.197	0.4	0.53
Peanut Mine (2710m)	0.122 \pm 0.036	38.0	<0.0001
Gothic (2884m)	0.062 \pm 0.033	5.6	0.018
North Pole (3430m)	0.045 \pm 0.030	3.9	0.048

Table 3.3: Heritability of Seedling Mortality

Seedling mortality	H^2	χ^2	p-value
Estess (2540m)	0		1
Peanut Mine (2710m)	0.043 ± 0.027	3.3	0.069
Gothic (2884m)	0.131 ± 0.055	8.2	0.0042
North Pole (3430m)	0.057 ± 0.051	1.5	0.22

We examined how germination success varied based on garden, source elevation of genotype, and all 2 and 3-way fixed effect interactions using a generalized linear mixed model with binomial distribution. (Proc Glimmix, SAS ver 9.3). This logistic regression incorporated random effects for genotype nested within source population and block crossed with treatment nested within garden. Those random effects account for non-independence of siblings from the same maternal family and plants in the same block. Family level analyses that include population within treatment within crossed garden as a substitute for block averaging effects returned similar results as the population level analysis.

Table 3.4:Germination Success

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F-value	p-value
Treatment	1	18	6.52	0.02
Source elevation	1	3641	1.58	0.21
Treatment × Source elevation	1	3641	5.95	0.0148
Garden	3	18	4.76	0.0129
Garden × Treatment	3	18	1.84	0.18
Garden × Source elevation	3	3641	4.66	0.0030
Garden × Source elevation × Treatment	3	3641	1.82	0.14
Elevation ²	1	3641	2.85	0.0915
Elevation ² × Garden	3	3641	3.69	0.0114
Elevation ² × Treatment	1	3641	0.25	0.62
Elevation ² × Garden × Treatment	3	3641	1.81	0.14
Block nested within treatment crossed garden			$\chi^2=292.99$	<0.0001
Genotype (population)			$\chi^2=110.96$	<0.0001

Table 3.5: Germination Phenology

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F-value	p-value
Treatment	1	1124	0.7	0.40
Source elevation	1	1124	0.33	0.56
Treatment \times Source elevation	1	1124	0.84	0.36
Garden	3	18	1.36	0.29
Garden \times Treatment	3	1124	3.94	0.0082
Garden \times Source elevation	3	1124	1.96	0.12
Garden \times Source elevation \times Treatment	3	1124	3.98	0.0078
Elevation ²	1	1124	1.02	0.31
Elevation ² \times Garden	3	1124	3.86	0.0092
Elevation ² \times Treatment	1	1124	0.00	0.96
Elevation ² \times Garden \times Treatment	3	1124	4.05	0.0071
Block nested within treatment crossed with garden			$\chi^2=157.4$	<0.0001
Genotype (population)			$\chi^2=25.4$	<0.0001

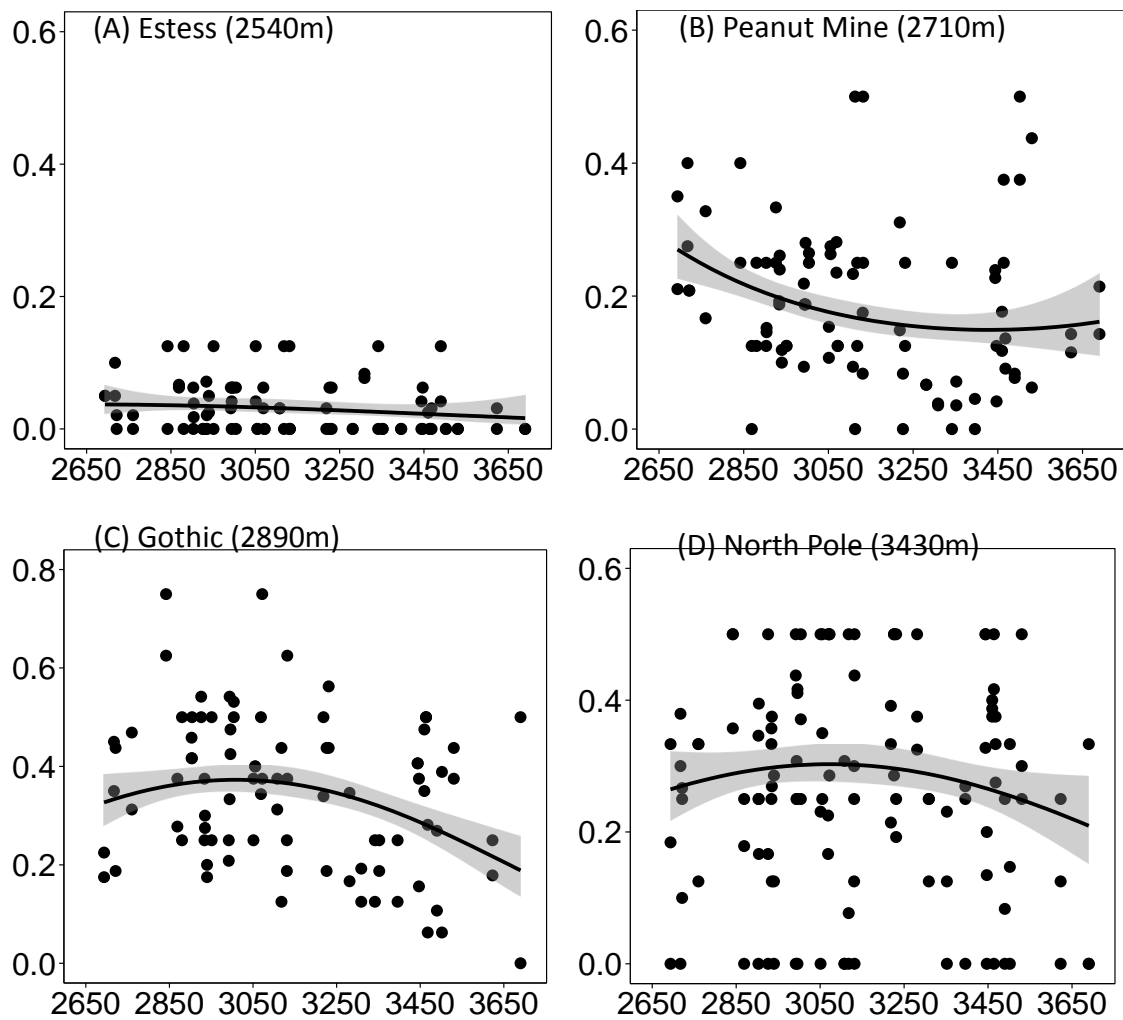


Figure 3.1 Interactions between gardens and linear and quadratic effects of source elevation within all four gardens. Axes are elevations of seed origin (in m) vs. germination success as a proportion of seedlings within a family. Regression line and confidence intervals are represented in black and gray respectively.

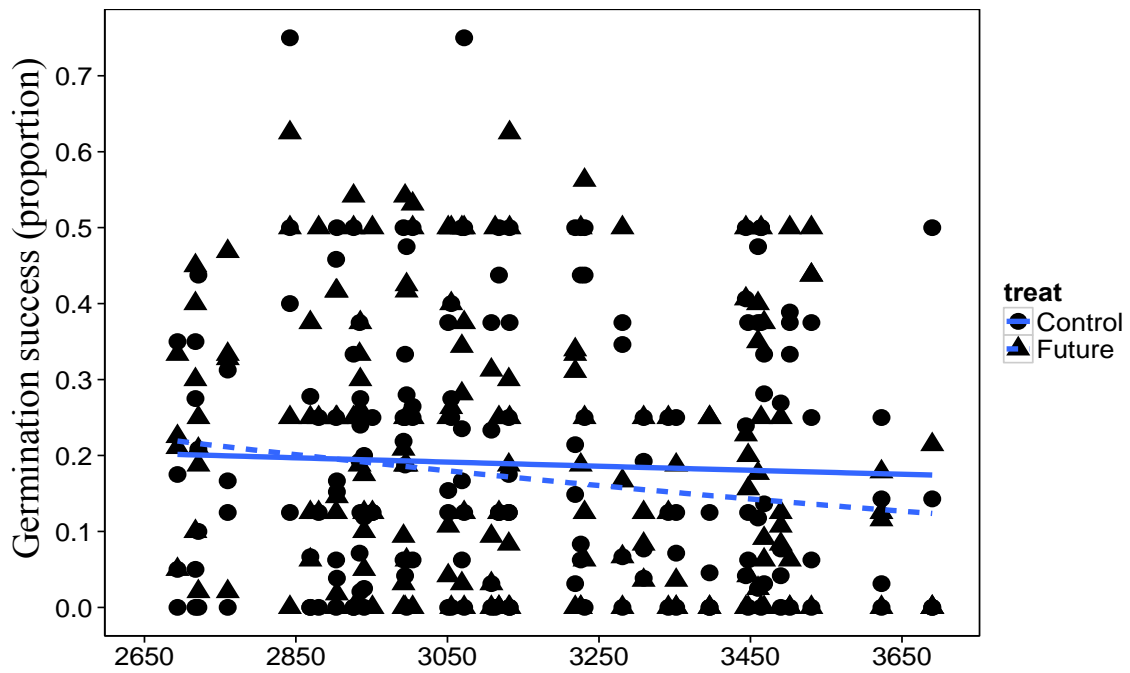


Figure 3.2 Interaction between treatment and linear effects of source elevation.

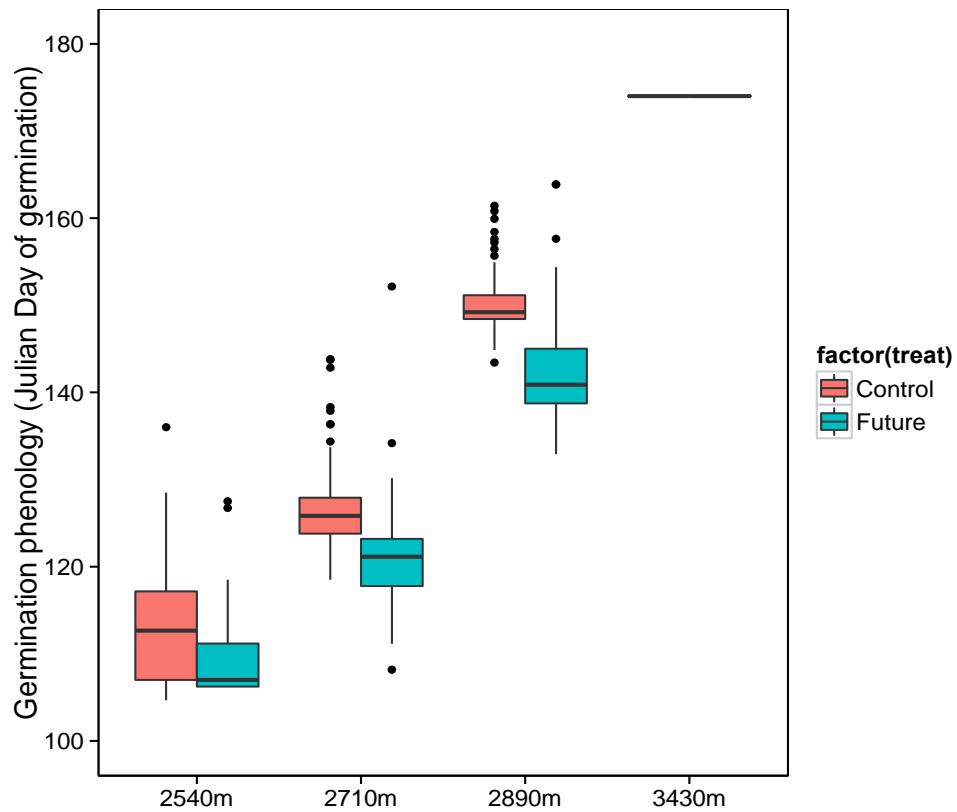


Figure 3.3 Germination phenology at all sites.

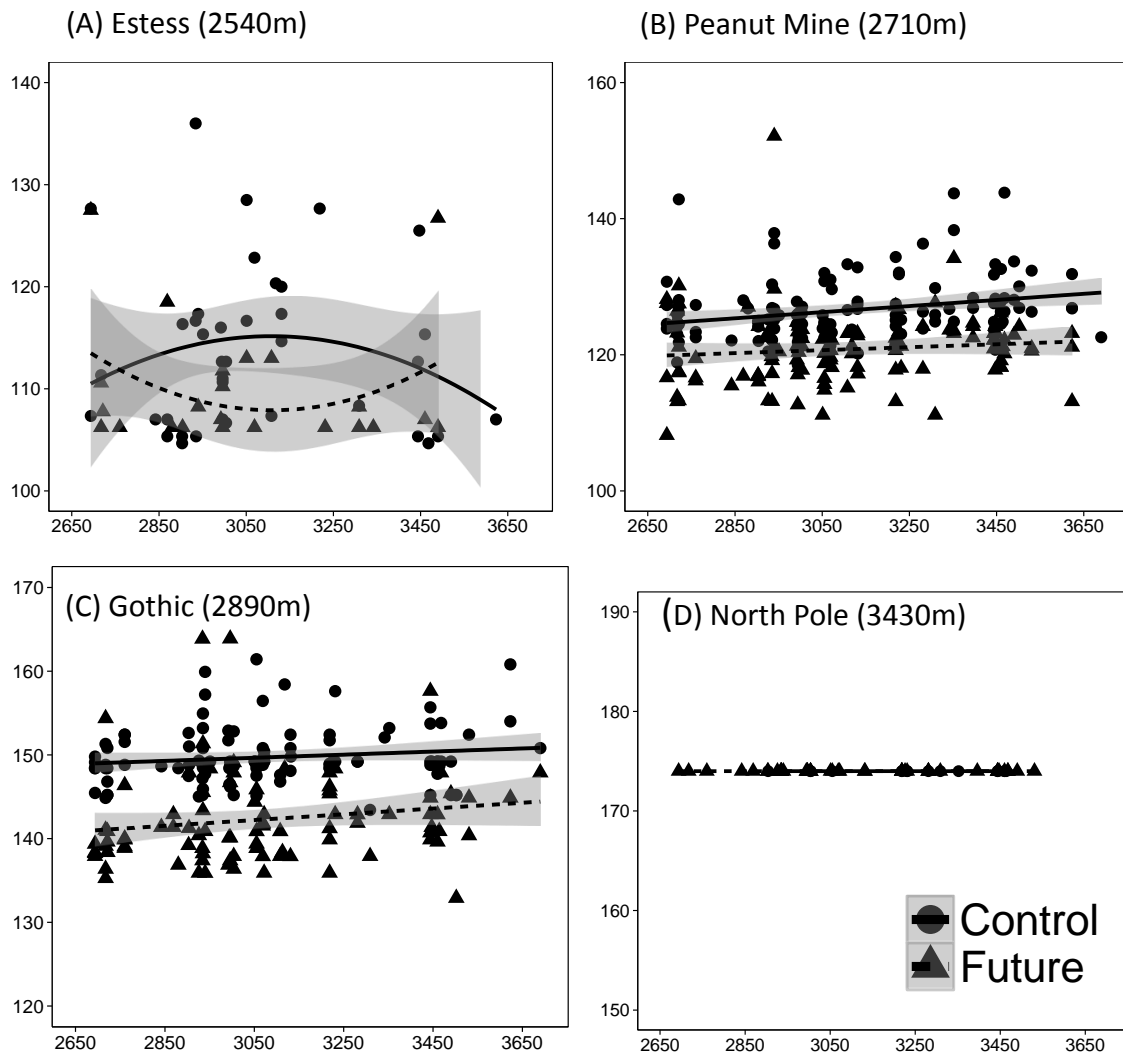


Figure 3.4 Interaction between garden and linear and quadratic effects of source germination. Axes are elevation of origin (in m) vs. Julian Day of first emergence

CHAPTER 4-DISCUSSION

Our estimated heritability tables demonstrate that our *B. stricta* population displays a clear heritability for germination success ($p < .001$ for 3 gardens with similar H^2 values) and likely heritability for germination phenology as well as mortality timing. Germination success appears to have the strongest evidence supporting heritability as similar significant heritabilities were found in all three sites that produced useful heritability results. (Table 1) Phenology and mortality exhibited less conclusive heritabilities but individual experimental gardens did provide significant results. (Tables 2-3) These heritabilities were low in strength (not unsurprising for factors that are so susceptible to changes environmental conditions) but likely high enough to provide for future directional selection in a garden setting. This provides the regional *B. stricta* population with the genetic flexibility to at least partially adapt to climate change in concert with plastic responses. These findings were consistent across or present within three of our four major experimental gardens with the remaining garden's failure to demonstrate significant heritabilities likely attributable to experimental design. Findings from our lowest elevation garden (Estess) contradict the observed pattern but is easily explainable and likely due to characteristics associated with our seeds. Our seeds were highly locally adapted (a must for a study of this sort) and the lower bound for the elevational range of our seeds families was higher than the elevation that the Estess garden sits at. Selecting this site aids us in understanding trailing edge dynamics and how these particular *B. stricta* germinants fare in regions both outside their usual range and

thermal tolerance. This is useful in understanding trends in phenology but less so in describing characteristics of the seeds themselves.

Table 4 details our findings on the factors influencing germination success in these plants. We found a significant effect for treatment and confirmed that germination success is lower under snow removal conditions. This is sobering, as it suggests the potential for across-the-board germination failures and significant changes to population dynamics as the region warms and snowpacks become shallower and more short-lived. We also discovered a significant effect for the interaction between source elevation and treatment. (Fig 2) In all observed gardens, germination success declines with an increase in source elevation without regard to treatment but the slope of the decline is steeper under snow removal conditions. Germinants fare poorly when relocated into conditions dissimilar to those of their area of origin, suggesting a high sensitivity to changes in climate that could jeopardize their ability to undergo the critical germinative process. This also has implication for conservation and management practices associated with this species and those with similar response patterns. Poor germination results in fewer mature plants and subsequent seedlings, which may impair the dispersal ability and the dispersal range of that species. Active seedling or relocation to ideal climate conditions may be required to keep pace with the velocity of climate change. In addition, the poorer germination response associated with snowpack may indicate that there is little recourse for high elevation populations that rely on deep cover and cooler temperatures to germinate.

There was no substantial difference in germination success across treatments for low elevation genotypes while their high elevation counterparts exhibited a significantly

higher probability of germination under control conditions. This suggests that earlier snowmelt associated with increased temperatures could present difficulties for high elevation genotypes used to longer winters and consistently deep snowpacks. These genotypes appear to be very sensitive to the depth of snow and associated water available during melting and will be placed in a perilous situation as climate changes. Suitable habitat will disappear within the current range and their migratory capacity will be irrelevant due to the nonexistence of suitable conditions uphill. These populations would need to undergo rapid and extensive adaptation or risk dramatically reduced fitness and being placed at a competitive disadvantage in relation to lower elevation migrants. Relocation is not an option for these populations as no suitable local environment will exist.

Germination success was also significantly lower within Estess . This is concerning, as climate change will replicate the hot and dry conditions of the Estess site at higher elevations within coming years, suggesting that current populations may be at a high risk of mortality due to failed germination. These populations will need to respond via migration, rapid genetic adaptation, or a mixture of both processes or risk local extinction. Climate-induced stresses may exceed the plastic capacity of these populations.

We found a significant interaction between the garden and both the linear and quadratic effects of seed source elevation. This conclusively demonstrates there is a great degree of local adaptation to elevation within the regional pool of genotypes. For the 2710m and 2890m gardens (Fig.1), higher source seed elevation leads to declines in germination success. Lower elevation seed origins correspond with higher probabilities of germination success, which is consistent with what we would predict for populations

exhibiting local adaptation. It is not surprising that seeds that originate from elevations similar to those of our experimental gardens would be most suited to those conditions and others would be less so. Our highest elevation garden (3430m) continues this trend and features a peak in germination success within middle elevations at around 3200m, with drop-offs in success for genotypes that originate at higher and lower elevations. This gap between garden elevation and peak in germination success somewhat inconsistent with what one would predict and may indicate that climate change is already having a demonstrable effect at these elevations. Maladaptiveness may have been introduced into native populations at the North Pole site as they become less favored and slightly lower elevation natives become more so. Lower elevation seeds (from 3200m) with a high degree of adaptation to their home environments are able to find purchase higher up in the range, suggesting that warming temperatures have already made these new territories suitable for colonization. These lower elevation populations may be poised to outcompete native ones at high elevations.

Family level data were also analyzed alongside the population level and yielded similar results for treatment, treatment by elevation, garden, and garden by elevation as well as quadratic effects of elevation. These findings corroborate those of the population level and demonstrate that successful garden genotypes come from local seed families and conditions closest to the current norm.

We would expect a similar pattern to that indicated at the North Pole site to propagate downrange and through our gardens as climate warms. This would correspond with a localized leading edge of population migration. As detailed earlier, we can already begin to see the early stages of a localized trailing edge at the Estess site (though here we

use ‘edges’ as relative trackers of movement and not as formal measures of the range of *B. stricta* populations). In review, this experiment has demonstrated that germination success is definitively influenced by climate and that warming has already begun to change *B. stricta* population distributions and dynamics in the Rocky Mountains. These populations’ ability to respond to climate adequately enough for survival at current fitness levels depends on the degree to which they can both adapt via natural selection (a capacity that is at least present to some degree) and to shift phenology.

Our analysis of germination phenology provides interesting insights into how responsive these populations are. (Table 5) No significant treatment effect was present in this data, nor were there clear source elevation effects yet we did discover a significant interactive effect between garden and treatment. Restricting the snowfall present in our experimental gardens accelerated the timing of germination at all sites, excluding North Pole. North Pole is harder to access compared to our other experimental sites and significantly fewer germination timing data points were obtained from that garden compared to others and the inconclusive results from this site are likely attributable to this fact. Otherwise, our gardens showed clear evidence that simulating climate change via reducing the snowpack prompted germinants to emerge earlier than they ‘should’ have, which is consistent with general observed phenological trends associated with climate change.

Our two mid-elevation gardens demonstrated significantly earlier germination under snow removal conditions across the board but the exact timing of that germination increased with source elevation. (Fig 3) In other words, low elevation genotypes germinated significantly earlier than their high elevation counterparts even as

germination timing phenology advanced overall. This is somewhat unexpected, as previous research on flowering phenology in *B. stricta* has suggested that lower elevation genotypes flower later in the season than high elevation ones (Anderson and Gezon). Snowfall provides the water necessary for germination and early plant growth and in low elevation alpine conditions soils dry out more quickly than in moister higher elevation conditions. This may suggest that selection has acted on low elevation genotypes of *B. stricta* that favors rapid germination that coincides with a shorter moist period, while high elevation genotypes do not need to respond as quickly to water-poor conditions. Our highest garden exhibits no similar interactive link, likely due to limited sample size for germinants.

Snow removal also appears to have generated an interesting quadratic effect within our lowest elevation garden. Under contemporary conditions, a negative quadratic relationship exists that shows rapid germination in high and low elevation genotypes with delayed germination in mid-ranges. Conversely, under snow removal conditions mid-range germinants are the first to emerge, with other ranges delayed. It is difficult to assess what factor(s) may be responsible for this pattern at present but it does appear that snow removal can drastically and rapidly alter the germination practices of an environment. The unpredictability of this finding and its unclear implications further emphasize the complexity of natural systems and the difficulty in untangling the balance of factors responsible for an ecological response.

Our analysis of seedling mortality for successful germinants in the dimensions of total mortality and lifespan did not yield conclusive results. These probabilities do not appear to be linked to the gardens themselves, either treatment, or the population of

origin. We will continue to monitor seedlings to see if any patterns emerge over the lifespan of these plants.

Our experimental methodology was sound due to the numerous and diverse seed families we used, the multiple gardens located at different and useful elevations, and the large seed sample sizes planted within the garden. Our statistical models yielded interpretable results and patterns that could be easily distinguished in future iterations of this experiment. Logistical difficulties associated with monitoring certain gardens can be compensated for now that local dynamics are better understood. This work can be extended in the near term by monitoring current germinants and improving our mortality dataset and replicating this experiment or an extended version of it over the coming years. This experiment could be replicated in a more carefully controlled lab setting with precise manipulation of water availability and temperature as well as other climate-associated variables like light availability or carbon dioxide levels. Extending the elevational range associated with our seed families is an additional short-term strategy that could help us pin down at what low elevations overall fitness is being reduced at (similar to the Estess site). As *B. stricta* is a widespread organism, comparative studies in these other environments could also contribute to understanding its adaptive and plastic capacity.

In the long term, continuous monitoring at these sites could conclusively establish if the peaks in germination success are shifting to favor genotypes at slightly lower elevations than our respective garden sites and establish a rate at which this pattern is propagating downhill. In addition, we can calculate average and site-level rates of advancement in germination timing. When compared with local velocities of climate

change, we can determine if locally adapted *B. stricta* seed families are migrating at a rate sufficient enough to compensate with climate change. In concert with other concurrent work investigating plastic responses in this species, we can continue to pick apart the mix of factors that influence the rate and direction of local migration as well as the relative strength of those factors.

Previous analyses of herbivory resistance, stomatal density and response to drought, genetic architecture, and reproductive phenology can complement this project and strengthen overall predictions on the survivability of *B. stricta* under a new climate regime. As this organism is widespread and malleable, it also may be useful as a surrogate model for other organisms responding to climate change. By understanding germination phenology in more detail we can improve our understanding of how this developmental stage may act to restrict adaptation to climate and improve range modeling for sensitive species. This will in turn aid in managing and preserving these species by identifying at risk species or subsets and establishing clear limits on how far they can migrate/be relocated before adverse effects ensue.

REFERENCES

- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S “Adaptation, migration or extirpation: climate change outcomes for tree populations.” *Evolutionary Applications* (2008) 1: 95–111
- Alsdurf JD, Ripley TJ, Matzner SL, Siemens DH. “Drought-induced trans-generational tradeoff between stress tolerance and defence: consequences for range limits?” *AoB PLANTS* (2013) 5: plt038
- Anderson, J.T., A.M. Panetta, T. Mitchell-Olds. “Evolutionary and ecological responses to anthropogenic climate change.” *Plant Physiology*. (2012) 160:1728-1740
- Anderson, Jill T., David W. Inouye, Amy M. McKinney, Robert I. Colautti, and Tom Mitchell-Olds “Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change” *Proc Biol Sci*. (2012) 279(1743): 3843–3852.
- Anderson, JT., John H. Willis, and Thomas Mitchell-Olds “Evolutionary genetics of plant adaptation” *Proc Biol Sci*. (2012) 279(1743): 3843–3852.
- Anderson J, Lee C-R, Mitchell-Olds T. “Life history QTLs and natural selection on flowering time in *Boechera stricta*, a perennial relative of *Arabidopsis*.” *Evolution*. (2010) 65:771–787.
- Anderson J, Mitchell-Olds T. “Ecological genetics and genomics of plant defenses: Evidence and approaches.” *Functional Ecology*. (2010) 25:312–324
- Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ “Do species’ traits predict recent shifts at expanding range edges?” *Ecol Lett* (2011) 14: 677–689
- Barua, D., Butler, C., Tisdale, T. E., & Donohue, K. “Natural variation in germination responses of *Arabidopsis* to seasonal cues and their associated physiological mechanisms.” *Annals Of Botany*, (2012) 109(1), 209-226.
- Bartomeus, Ignasi, John S. Ascher, David Wagner, Bryan N. Danforth, Sheila Colla, Sarah Kornbluth, and Rachael Winfree “Climate-associated

phenological advances in bee pollinators and bee-pollinated plants.”
PNAS. (2011) 108:51

Becerra, J. X. “The impact of herbivore-plant coevolution on plant community structure.” *Proc. Natl. Acad. Sci. U.S.A* (2007)104, 7483–7488.

Becklin K, Medeiros J, Sale K, Ward J. “Evolutionary history underlies plant physiological responses to global change since the last glacial maximum.” *Ecology Letters* (2014) 17(6):691-699.

Bergamini, A., S. Ungricht, H. Hofmann “An elevational shift of cryophilous bryophytes in the last century—an effect of climate warming?” *Divers. Distrib.* (2009).15, 871

Bridle JR, Vines TH. “Limits to evolution at range margins: When and why does adaptation fail?” *Trends Ecol. Evol.* (2006) 22:140–47

Broenniman, O., Thuiller, W., Hughes, G., Midgley, G.F., Alkemade, J.M.R. & Guisan, A. “Do geographic distribution, niche property and life form explain plants’ vulnerability to global change?” *Glob. Change Biol.* (2006). 12, 1079–1093.

Brunelle A, Whitlock C, Bartlein P, Kipfmüller K. “Holocene fire and vegetation along environmental gradients in the Northern Rocky Mountains.” *Quaternary Science Reviews*. (2005) 24:2281–2300.

Buckley J, Bridle J. “Loss of adaptive variation during evolutionary responses to climate change.” *Ecology Letters*. (2014) 17(10):1316-1325.

Carmona D, Lajeunesse MJ, Johnson MTJ. “Plant traits that predict resistance to herbivores.” *Functional Ecology*. (2011) 25:358–367.

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas C. “Rapid range shifts of species associated with high levels of climate warming.” *Science* (2011) 333: 1024–1026

Clark, J.S. “Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord.” *Am. Nat.*, (1998). 152, 204–224

Colwell, Robert K., Gunnar Brehm, Catherine L. Cardelús, Alex C. Gilman, and John T. Longino. “Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics” *Science* (2008) 322 (5899), 258-261.

- Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. "Changes in climatic water balance drive downhill shifts in plant species' optimum elevations." *Science* (2011) 331, 324–327.
- Crozier LG, Hendry AP, Lawson PW, Quinn TP, Mantua NJ, Battin J, Shaw RG, Huey RB "Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon." *Evolutionary Applications* (2008) 1: 252–270
- Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C. C., and Sanders, N. J. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* (2006) 313, 966.
- Damschen, Ellen I., Nick M. Haddad, John L. Orrock, Joshua J. Tewksbury, and Douglas J. Levey. "Corridors Increase Plant Species Richness at Large Scales." *Science* (2006) 313 (5791), 1284-1286
- Darling E, Samis KE, Eckert CG. "Increased seed dispersal potential towards geographic range limits in a Pacific coast dune plant." *New Phytol.* (2008) 178:424–35
- Davis MB, Shaw RG "Range shifts and adaptive responses to quaternary climate change." *Science* (2001) 292: 673–679
- de Casas, R. R., Kovach, K., Dittmar, E., Barua, D., Barco, B. and Donohue, K. (2012), Seed after-ripening and dormancy determine adult life history independently of germination timing. *New Phytologist*, 194: 868–879.
- Donohue, Kathleen. "Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*." *Ecology* 83, no. 4 (April 2002): 1006.
- Donohue, Kathleen, et al. "The evolutionary ecology of seed germination of *Arabidopsis thaliana*: variable natural selection on germination timing." *Evolution* 59, no. 4 (April 2005): 758-770
- Donohue, Kathleen, et al. "Environmental and genetic influences on the germination of *Arabidopsis thaliana* in the field." *Evolution* 59, no. 4 (2005): 740-757
- Durant, J.M., Hjermmann, D.O., Ottersen, G. & Stenseth, N.C. "Climate and the match or mismatch between predator requirements and resource availability." *Climate Res.* (2007) 33, 271–283.

- Eckert CG, Samis KE, Loughheed SC. "Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond." *Mol. Ecol.* (2008) 17:1170–88
- Engelmann K, Purugganan MD. "The molecular evolutionary ecology of plant development: Flowering time in *Arabidopsis thaliana*." *Advances in Botanical Research.* (2006) 44:507–526.
- Etterson, J.R. "Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change- Clinal patterns of selection along an environmental gradient in the Great Plains." *Evolution* (2004) 58, 1446–1458
- Eunsuk, K., & Donohue, K. "Demographic, developmental and life-history variation across altitude in *Erysimum capitatum*." *Journal Of Ecology* (2011) 99(5), 1237-1249.
- Fitzpatrick, Benjamin M. "Underappreciated Consequences of Phenotypic Plasticity for Ecological Speciation," *International Journal of Ecology* (2012) Article ID 256017, 12 pages,
- Forero-Medina, G., L. Joppa, S. L. Pimm "Constraints to species' elevational range shifts as climate changes." *Conserv. Biol.* (2011) 25, 163
- Franke D., Ellis A., Dharjwa M., Freshwater M., Fujikawa M., Padron A., Weis A. "A steep cline in flowering time for *Brassica rapa* in Southern California: Population-level variation in the field and the greenhouse." *Int. J. Plant Sci.* (2006) 167, 83–92
- Franks SJ, Sim S, Weis AE "Rapid evolution of flowering time by an annual plant in response to a climate fluctuation." *Proc Natl Acad Sci USA* (2007) 104: 1278–1282
- Gardner, J.L., Heinsohn, R. & Joseph, L. "Shifting latitudinal clines in avian body size correlate with global warming in Australian passerines." *Proc. R. Soc. Lond. B Biol.*, (2009). 276, 3845–3852.
- Gaston, K.J. "The Structure and Dynamics of Geographic Ranges." (2003). Oxford University Press, Oxford.
- Gatter, W. "Timing and patterns of visible autumn migration: Can effects of global warming be detected?" *J. Ornithol.* (1992)133(4), 427-436
- Genung, M. A., Bailey, J. K., and Schweitzer, J. A. "Welcome to the neighbourhood: interspecific genotype by genotype interactions in *Solidago* influence above- and belowground biomass and associated communities." *Ecol Lett.* (2012) 15(1):65-73

- Ghalambor, C. K., McKay, J. K., Carroll, S. P. and Reznick, D. N. "Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments." *Functional Ecology*. (2007), 21: 394–407.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. "A framework for community interactions under climate change." *Trends Ecol. Evol.*, (2010) 25, 325–331.
- Goslee, S. C., Niering, W. A., Urban, D. L., and Christensen, N. L. "Influence of environment, history and vegetative interactions on stand dynamics in a Connecticut forest." *J. Torrey Bot. Soc.* (2005)132, 471–482.
- Hannah, L. "Protected Areas and Climate Change." *Annals of the New York Academy of Sciences* (2008) 1134: 201–212.
- Heikkinen, R.K., Luoto, M., Leikola, N., Pöyry, J., Settele, J., Kudrna, O. *et al.* "Assessing the vulnerability of European butterflies to climate change using multiple criteria." *Biodivers. Conserv.*, (2010). 19, 695–723.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. "The distributions of a wide range of taxonomic groups are expanding polewards." *Glob. Change Biol.*, (2006). 12, 450–455.
- Hoffmann AA, Sgrò CM. "Climate change and evolutionary adaptation." *Nature* (2011) 470: 479–485
- Holt RD, Keitt TH, Lewis MA, Maurer BA, Taper ML. "Theoretical models of species' borders: single species approaches." *Oikos* (2005) 108:18–27
- Holzinger, B., K. Hulber, M. Camenisch, G. Grabherr, "Changes in plant species richness over the last century in the eastern Swiss Alps: Elevational gradient, bedrock effects and migration rates." *Plant Ecol.* (2008)195, 179
- Ibanez, I., Clark, J.S., Dietze, M.C., Feeley, K., Hersh, M., LaDeau, S. *et al.* "Predicting biodiversity change: outside the climate envelope, beyond the species-area curve." *Ecology* (2006) 87, 1896–1906.
- Inouye DW "Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers." *Ecology*. (2008 Feb); 89(2):353-62.
- IPCC special report on emission scenarios (2000).
- Joppa, Lucas N., Scott R. Loarie, and Stuart L. Pimm "On the protection of 'protected areas'" *PNAS* (2008) 105 (18) 6673-6678

- Jump, A.S. & Penuelas, J. "Running to stand still: adaptation and the response of plants to rapid climate change." *Ecology Letters* (2005) 8, 1010–1020
- Kawecki, T.J. & Ebert, D. "Conceptual issues in local adaptation." *Ecology Letters* (2004) 7, 1225–1241
- A. E. Kelly, M. L. Goulden, "Rapid shifts in plant distribution with recent climate change." *Proc. Natl. Acad. Sci. U.S.A.* (2008).105, 11823
- Kelly, Scott A., Tami M. Panhuis, Andrew M. Stoeckl. "Phenotypic Plasticity: Molecular Mechanisms and Adaptive Significance" *Compr Physiol.* (2012) (2):1417-39.
- Kharouba, Heather M., Sebastien R. Paquette, Jeremy T. Kerr and Mark Vellend "Predicting the sensitivity of butterfly phenology to temperature over the past century" *Global Change Biology*. (2014) 20(2): 504-514
- Kiefer C, Dobes C, Sharbel TF, Koch MA. "Phylogeographic structure of the chloroplast DNA gene pool in North American *Boechera* - A genus and continental-wide perspective." *Molecular Phylogenetics and Evolution*. (2009) 52:303–311
- Kim E, Donohue K, Jacquemyn H. "Local adaptation and plasticity of *Erysimum capitatum* to altitude: its implications for responses to climate change." *Journal Of Ecology*. (2013) 101(3):796-805.
- Knight CA, Vogel H, Kroymann J, Shumate A, Witsenboer H, Mitchell-Olds "Expression profiling and local adaptation of *Boechera holboellii* populations for water use efficiency across a naturally occurring water stress gradient." *T Mol Ecol*. (2006) 15(5):1229-37.
- Kolar, C.S. & Lodge, D.M. "Progress in invasion biology: predicting invaders." *Trends Ecol. Evol.*, (2001) 16, 199–204.
- le Roux, P. C., M. A. McGeoch, "Rapid range expansion and community reorganization in response to warming." *Glob. Change Biol.* (2008) 14, 2950
- La Sorte, F.A. & Thompson, F.R. "Poleward shifts in winter ranges of North American birds." *Ecology* (2007) 88, 1803–1812.
- Lee C-R, Mitchell-Olds T. "Quantifying effects of environmental and geographical factors on patterns of genetic differentiation." *Molecular Ecology*. (2011) in press.

- Leites, L. P., Rehfeldt, G. E., Robinson, A. P., Crookston, N. L. and Jaquish, B. "Possibilities and limitations of using historical provenance tests to infer forest species growth responses to climate change." *Natural Resource Modeling* (2012) 25: 409–433.
- Lenoir, J., J. C. Gégout, P. A. Marquet, P. de Ruffray, H. Brisse, "A significant upward shift in plant species optimum elevation during the 20th century." *Science* (2008).320, 1768
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. "The velocity of climate change." *Nature*, (2009). 462, 1052–1055
- Manzaneda AJ, Prasad K, Mitchell-Olds T. "Variation and fitness costs for tolerance to different types of herbivore damage in *Boechera stricta* genotypes with contrasting glucosinolate structures." *New Phytologist*. (2010) 188:464–477.
- Menzel, A. et al. "European phenological response to climate change matches the warming pattern." (2006) *Glob. Change Biol.* 12, 1969
- Metcalf C, Mitchell-Olds T. "Life history in a model system: opening the black box with *Arabidopsis thaliana*." *Ecology Letters*. (2009) 12:593–600.
- Moczek AP, Sultan SE, Foster S, Ledón-Rettig C, Dworkin I, Nijhout HF, Abouheif E, Pfennig DW "The role of developmental plasticity in evolutionary innovation." *Proc Biol Sci* (2011) 278: 2705–2713
- Molina-Montenegro MA, Naya DE "Latitudinal Patterns in Phenotypic Plasticity and Fitness-Related Traits: Assessing the Climatic Variability Hypothesis (CVH) with an Invasive Plant Species." *PLoS ONE* (2012) 7(10): e47620
- Mudryk, LR, PJ Kushner, C Derksen. "Interpreting observed northern hemisphere snow trends with large ensembles of climate simulations" *Climate Dynamics*. (2013) 43 (1-2): 345-359
- Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F. M. and Katul, G. G. "Spread of North American wind-dispersed trees in future environments." *Ecology Letters* (2011), 14: 211–219.
- Naithani, Kusum J., Brent E. Ewers, Jonathan D. Adelman, and David H. Siemens. "Abiotic and biotic controls on local spatial distribution and performance of *Boechera stricta*." *Frontiers In Plant Science* (2014) 5, 1-11.

- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, et al. "Plant phenotypic plasticity in a changing climate." *Trends Plant Sci* (2010) 15: 684–692
- Nogués-Bravo, D., M.B. Araújo, M.P. Errea, J.P. Martínez-Rica. "Exposure of global mountain systems to climate warming during the 21st Century" *Global Environmental Change*. (2007) 17(3-4):420-428
- Nordborg M, Hu TT, Ishino Y, et al. "The pattern of polymorphism in *Arabidopsis thaliana*." *Plos Biology*. (2005) 3:e196
- Norquay, K. J. O. & C. K. R. Willis "Hibernation phenology of *Myotis lucifugus*" *Zoology*. (2014) 294(2) 85-92
- Parmesan, C. "Ecological and evolutionary responses to recent climate change." *Annu. Rev. Ecol. Evol. Syst.* (2006) 37, 367–669.
- Parmesan C., Yohe G. 2003. "A globally coherent fingerprint of climate change impacts across natural systems." *Nature* 421, 37–42
- Parolo, G., G. Rossi. "Upward migration of vascular plants following a climate warming trend in the Alps." *Basic Appl. Ecol.* (2008) 9, 100
- Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. & Hanson, C.E. "Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change." (2007). Cambridge University Press, New York
- Pearson, RG. "Climate change and the migration capacity of species." *Trends in Ecology and Evolution*. (2006) 21(3):111-113
- Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. "Climate change and distribution shifts in marine fishes." *Science*. (2005). 308, 1912–1915.
- Pilson D. "Herbivory and natural selection on flowering phenology in wild sunflower, *Helianthus annuus*." *Oecologia* (2000) 122, 72–82
- Popy, S., L. Bordignon, R. Prodon, "A weak upward elevational shift in the distributions of breeding birds in the Italian Alps." *J. Biogeogr.* (2010). 37, 57
- Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. Species traits explain recent range shifts of Finnish butterflies. *Glob. Change Biol.* (2009) 15, 732–743.

- Price, Trevor D., Anna Qvarnström, and Darren E. Irwin “The role of phenotypic plasticity in driving genetic evolution” *Proc. R. Soc. Lond. B* (2003) 270 1523 1433-1440
- Purvis, A., Cardillo, M., Grenyer, R. & Collen, B. “Correlates of extinction risk: phylogeny, biology, threat and scale.” In: *Phylogeny and Conservation* (eds Purvis, A., Gittleman, J.L. & Brooks, T.) (2005). Cambridge University Press, Cambridge, pp. 295–316
- Reznick, D. & Travis, J. “The empirical study of adaptation in natural populations.” *Adaptation* (eds M.R. Rose & G.V. Lauder). (1996) Academic Press, California, USA.
- Rollins RC. “The Cruciferae of Continental North America.” Stanford, CA: Stanford University Press; 1993
- Root, Terry L., Dena P MacMynowski, Michael D. Mastrandrea, and Stephen H. Schneider “Human-modified temperatures induce species changes: Joint attribution.” *PNAS* (2005) 102 (21) 7465-7469
- Rosenzweig, Cynthia, David Karoly, Marta Vicarelli, Peter Neofotis, Qigang Wu, Gino Casassa, Annette Menzel, Terry L. Root, Nicole Estrella, Bernard Seguin, Piotr Tryjanowski, Chunzhen Liu, Samuel Rawlins¹ & Anton Imeson. “Attributing physical and biological impacts to anthropogenic climate change.” *Nature* 453, (2008) 353-357
- Roy BA. “Patterns of association between crucifers and their flower-mimic pathogens: Host jumps are more common than coevolution or cospeciation.” *Evolution*. (2001) 55:41–53
- Roy, K., Jablonski, D. & Valentine, J.W. “Body size and invasion success in marine bivalves.” *Ecol. Lett.*, (2002) 5, 163–167.
- Rushworth, C. A., Song, B.-H., Lee, C.-R., and Mitchell-Olds, T. “Boechera, a model system for ecological genomics.” *Mol. Ecol.* (2011)20, 4843–4857.
- Schweiger, O., Settele, J., Kudrna, O., Klotz, S. & Kuhn, I. “Climate change can cause spatial mismatch of trophically interacting species.” *Ecology* (2008). 89, 3472–3479
- Sexton, Jason P, Patrick J. McIntyre, Amy L. Angert, Kevin J. Rice, “Evolution and Ecology of Species Range Limits” *Annual Review of Ecology, Evolution, and Systematics* (2009) Vol. 40: 415 -436
- Siemens, D. H., Duvall-Jisha, J., Jacobs, J., Manthey, J., Haugen, R., & Matzner, S. “Water deficiency induces evolutionary tradeoff between stress

tolerance and chemical defense allocation that may help explain range limits in plants.” *Oikos*, (2012) 121(5), 790-800.

- Song B-H, Clauss M, Pepper A, Mitchell-Olds T. “Geographic patterns of microsatellite variation in *Boechera stricta*, a close relative of *Arabidopsis*.” *Molec Ecol.* (2006) 15:357–369.
- Suggitt, A. J., Gillingham, P. K., Hill, J. K., Huntley, B., Kunin, W. E., Roy, D. B. and Thomas, C. D., “Habitat microclimates drive fine-scale variation in extreme temperatures”. *Oikos* (2011) 120, 1
- Sultan, SE. “Phenotypic plasticity for plant development, function and life history.” *Trends Plant Sci.* 2000 Dec 5(12):537-42.
- Svenning JC, Normand S, Skov F. “Postglacial dispersal limitation of widespread forest plant species in nemoral Europe.” *Ecography* (2008) 31:316–26
- Thomas, C. D., A. M. A. Franco, J. K. Hill “Range retractions and extinction in the face of climate warming” *Trends Ecol. Evol.* (2006). 21, 415
- Thomas, C. D. “Climate, climate change and range boundaries.” *Divers. Distrib.* (2010) 16, 488.
- Thomson JD “Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte.” *Philos Trans R Soc Lond B Biol Sci.* (2010) 365(1555):3187-99.
- Wagner, M. R., Lundberg, D. S., Coleman-Derr, D., Tringe, S. G., Dangl, J. L., & Mitchell-Olds, T. “Natural soil microbes alter flowering phenology and the intensity of selection on flowering time in a wild *Arabidopsis* relative.” *Ecology Letters* (2014) 17(6), 717-726.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. et al “Ecological responses to recent climate change.” *Nature* 416 (2002),389–395
- Watling, J.I., S.S. Románach, D.N. Bucklin, C. Speroterra, L.A. Brandt, L.G. Pearlstine, F.J Mazzotti. “Do bioclimate variables improve performance of climate envelope models?” *Ecological Modelling* (2012) 246: 79-85.
- Williams, John W., Stephen T. Jackson, and John E. Kutzbach “Projected distributions of novel and disappearing climates by 2100 AD.” *PNAS* (2007) 104 (14) 5738-5742
- Willis CG, Baskin CC, Baskin JM, Auld JR, Venable DL, Cavender-Bares J, Donohue K, Rubio de Casas R; NESCent Germination Working Group.

“The evolution of seed dormancy: environmental cues, evolutionary hubs, and diversification of the seed plants.” *New Phytol.* 2014 Jul;203(1):300-9.

Wilson, R. J. et al., “Changes to the elevational limits and extent of species ranges associated with climate change.” *Ecol. Lett.* (2005) 8, 1138.

Windsor, A. J., Schranz, M. E., Formanová, N., Gebauer-Jung, S., Bishop, J. G., Schnabelrauch, D., Mitchell-Olds, T. “Partial Shotgun Sequencing of the *Boechera stricta* Genome Reveals Extensive Microsynteny and Promoter Conservation with *Arabidopsis*.” *Plant Physiology*, (2006) 140(4), 1169-11