

Local adaption in *Boechera stricta* in the context of climate change

Student: Gabryel Steinmetz

Mentors: Dr. Jill Anderson and Deidre Keating

REU Independent Research

Summer 2018

Abstract

This study examines whether climate change alters patterns of local adaptation in *Boechnera stricta* (Brassicaceae). A common garden experiment was established in sites around the Rocky Mountain Biological Laboratory in Colorado. In the fall of 2017, Dr. Jill Anderson and her lab planted seeds from a broad elevational gradient into four common gardens in four treatments: a control (contemporary climate change condition), snow removal (a climate change simulation), snow addition (historical condition) and snow addition and supplemental water (another historical condition). In the growing season of 2018, we recorded data on three key early life history fitness components germination success, probability of survival of seedlings, and time until mortality for seedlings. As low elevation populations are exposed to hot and dry conditions, we predicted that low elevation maternal families would have greater fitness in treatments simulating ongoing climate change, whereas local adaptation would be more prominent under historical conditions. We found that low-elevation populations had greatest germination success across treatments and gardens. However, families from high elevation populations had enhanced probability of surviving and greater time until mortality. Overall, fitness was low, a likely consequence of the drought experienced during the winter of 2017-2018.

Introduction

The Earth is projected to increase 2-4 °C by the next century (New et al., 2017). Already the earth has increased 1°C from the time of the industrial revolution (New et al., 2017). Climate change disrupts environmental cues that plants depend on for reproduction, such as photoperiod, precipitation, temperature, length of winter, length of the growing season, and soil moisture (Wadgymar et al., 2018). Climate change will not affect certain abiotic factors, such as photoperiod (Anderson, 2015). However, early snowmelt leads to early germination and the developing seedling now finds itself in a novel photoperiod to as result of this decoupling of these historical environmental cues (Wadgymar et al., 2018). Germination onset is occurring earlier as a response to the reduced snowpack and advancing snowmelt, however the timing of frost events has not yet changed (Inouye 2008). No longer is the seedling protected under the insulation of snow (Inouye, 2008). Temperatures are increasing throughout the year, and elevated growing season temperatures increase evapotranspiration in an already water depleted environment due to the lessening snowpack. Predicting whether plants can adapt to this rapidly changing global climate that has multidimensional consequences becomes important in understanding the future impact on plant populations.

Subpopulations of plant species have shown to be optimally adapted to their environment. (Whitlock, 2015). This is called local adaptation, where a population experiences increased fitness in its home site (Hereford, 2009). Charles Darwin's observations on Galapagos finches specializing on different seed sizes through adaptations of beak size and shape were foundational to his development of the theory of evolution (Darwin, 1872). Before speciation of the finches could occur, separate groups first became locally adapted to the seeds they encountered on different islands. Factors that favor local adaptation include low gene flow, selection against genotypes optimally adapted to other habitats, selection against intermediate genotypes, small differences in size and quality of habitats, and constraints on plasticity (Hereford, 2009). Loci with large effects on morphology are disproportionately favorable for

local adaptation (Hereford, 2009). Studies of local adaptation make it possible to identify the selective forces governing specific phenotypic expression and thus provide clues to how plants may respond to climate change.

A superb way to study local adaptation is studying species that are distributed along a broad elevation gradient (Wadgymar, 2017). Elevation gradients are characterized by dramatic changes in climate over short distances due to the rise and fall of elevation and the resulting rapid change of climate (Collins et al., 1993). Plants are exposed to different abiotic factors as elevation increases, such as variance in slope, soil particle size, temperature, precipitation, wind speeds, and intensity of sunlight (Gonzalo-Turpin and Hazard, 2009). In addition, biotic factors change with elevation. Microbial productivity increases with temperature and a more productive microbiome means more nutrients available (Yuste et al., 2007). With elevation, species diversity generally decreases (Wolda, 1987). Another factor plants must confront is herbivory, however insect diversity decreases with elevation (Garibaldi, 2011) which affects how plants allocate resources (Garibaldi, 2011). Severe constraints are imposed on high-elevation populations due to the shortness of the growing season, low temperatures and frequent frost events (Alistair & Penuelas, 2005). As elevation increases snowpack increases, snowmelt date is delayed, and the time between snowmelt and monsoon rains decreases (Anderson and Gezon, 2015). Precipitation in general increases with elevation and so the driest elevations are the lowest and the wettest the highest (Ohsawa et al., 2008). Here, we examine the extent to which climate change disrupts long-standing patterns of local adaptation (Wadgymar et al., 2018).

Studies have demonstrated local adaptation in many plants species, however climate change is making it difficult to discern these patterns (Kawecki and Ebert, 2004). Detectable patterns of local adaptation are when populations experience an increase in fitness when grown at their home elevation (Anderson, 2015). Local adaptation is common and on average local populations experience a 45% increase in fitness to their local environment versus foreign populations (Hereford, 2009). Trade-offs, when a population has increased in-situ but lower fitness in other environments, were often detected but the magnitude of the loss in fitness in foreign environments due to local adaptation was small (Hereford, 2009). Maladaptation is often reported in other studies and foreign population advantage was also prevalent (Hereford, 2009). Studies may fail to detect local adaptation because climate change is changing the environment these studies are performed in and thus demes (subpopulations or clines) experience decreased fitness in all environments (Wadgymar et al., 2017). The question we pose is whether patterns of local adaptation are more prominent and thus detectable in historical conditions versus climate change conditions.

Boechera stricta (Brassicaceae) provides a great system to explore this question. *Boechera stricta* is a short-lived perennial herb (Wadgymar et al. 2017). It reproduces primarily by self-pollinating and has limited seed dispersal. The lack of outcrossing reduces genetic variation in a population and with low dispersal because seeds are not being distributed from other populations leads to a lack of new genes being introduced to the population (Song et al., 2006; Ohsawa et al., 2007). It has an elevation range between 900 and 3900m (Song et al., 2006; Rushworth et al., 2011). *Boechera stricta* has demonstrated local adaptation in physiology, morphology and phenology traits (Anderson et al., 2015; Wadgymar et al. 2017).

We exposed *B. stricta* seeds to climate change conditions and historical conditions and examined seed germination and establishment. We define establishment as surviving through the growing season. Germination and establishment are important fitness components that represent critical life stages in plants life history (Anderson, 2015). Our hypothesis is climate change

disrupts long-standing patterns of local adaptation, favoring low elevation genotypes that are adapted to hotter and drier conditions and historical conditions will favor high elevation genotypes adapted to cooler and wetter conditions.

Methods

In the fall of 2017, 19,200 seeds from local populations of *B. stricta* along the elevation gradient (2710-3340m) were planted among 4 sites. Before the planting of the seeds, the Anderson lab controlled for maternal effects by growing the seeds from local populations for a generation in a greenhouse to create maternal families. We used one maternal family per population for 54 populations. The seeds were planted in the fall to allow them to synchronize to the environmental conditions and cause dormancy release. The experimental gardens are fenced to protect the plots from cows and gophers. The site elevations are at 2710m (Peanut Mine), 2890 (Gothic), 3133 (Schofield), and 3340 (North Pole). See Table 1 for coordinates of these sites. Within each garden, the seeds were divided evenly into 4 treatment groups, contemporary (control), snow removal (future climate conditions), snow addition (historical condition), and snow addition plus supplemental watering (historical condition). The snow-removal treatment was performed in mid-April by physically removing the snow with a shovel, when snowpack was 1 m deep. For the historical treatments, cylinders were placed around seeds and snow was added during the snow removals; this delayed snowmelt by ~1 week. Historical conditions are based on weather data of Gothic over the past 40 years obtained from the Crested Butte weather station. We used one maternal family per population for 54 populations. We planted 64 seeds per family into each garden, distributed evenly across treatments and thus planted 256 seeds per family total, for an N=19,200 across the four gardens. Seeds were placed in 9x9 cell grids and 2 seeds were planted per cell. In the Summer of 2018, the seeds were censused weekly throughout the growing season to determine the onset of germination. Onset of germination was determined by the presence of a seedling.

We analyzed germination success through a mixed model logistic regression using glmer (R Core Team, 2012) has a function of elevational difference (the difference in elevation between the source population and the garden), treatment, and garden and all two and three-way interactions. Elevational difference values >0 mean that the source population is from a higher elevation than the garden. Values <0 mean that the source population is lower in elevation than the garden. We incorporated random effects for block, and genotype. P-value adjustment was done using Tukey's post-hoc test in order to view comparisons between treatments and gardens.

Establishment is whether a seedling (a germinated seed) survives until the end of the summer. We used the Cox proportional hazards model to jointly model germination success and the timing of mortality among germinated seeds. The Cox proportional hazards model assesses lifetime fitness by modeling the dependence of fitness components on those expressed earlier in life history (Shaw et al. 2008). Here, evaluated lifetime fitness as a function of elevational difference, treatment, their interaction, using random effects for block, garden and maternal family.

Results

Germination success was greatest at our low elevation site with the snow addition and water treatment as shown in figure 1. The logistic regression found significant interactions between treatment and linear and quadratic effects of elevational difference. Low-elevation populations had the greatest germination success, however this depended on elevation of site and treatment as shown in figures 2-5. Peanut Mine has a quadratic relationship with elevational difference snow and water treatment ($p < 0.0001$) and shows low-elevation populations experienced a greater germination success than higher elevation. At the Gothic site we found there is a quadratic relationship with elevational difference and snow addition ($p < 0.0001$) and again it was low-elevation populations with greater germination success. Schofield has a linear relationship with elevational difference and snow removal ($p < 0.0001$), while North Pole has a quadratic relationship with elevational difference and snow removal ($p < 0.0001$). These two relationships both had low-elevation populations with greater germination success. Populations planted into sites from the same elevation did not show an increase in fitness (local adaptation).

The Cox proportional hazards model employed analyzed the time until mortality among the successfully germinated seedlings. Figure 6 shows that seedling planted in snow addition and snow addition and water had the greatest the fitness. This greater fitness can be seen by the greater probability of survival and greater number of days until mortality. Across all treatments, high-elevation populations had the greatest fitness. The lowest fitness for seeds was with snow removal.

Discussion

The question we posed was: is local adaptation more prominent and thus detectable in historical conditions versus climate change conditions? We found limited evidence for local adaptation in this study, in contrast with previous work in this system (Anderson et al. 2015). Simulated climate change, represented by our snow removal treatment and contemporary treatment (control), dramatically reduced the fitness of *B. stricta* along our elevation gradient. The increase in germination success with our snow addition and water treatment (figure 2) at our lowest elevation site, Peanut Mine (2710m), reflects greater water limitation at low elevation than higher elevation sites. This year has been a drought year, the snow pack has not been lower since the winter of 1976-1977 (Billy Barr, Rocky Mountain Biological lab, Colorado Weather Station). The increased temperatures likely increased evapotranspiration rates at all sites. Drought stress this past year inflicted on all sites changed the conditions across the entire gradient which is why we believe all populations were maladapted.

The results of our study show that elevation difference had a dramatic effect on germination success. Our hypothesis that lower elevation populations are more adapted to warmer and drier conditions and would demonstrate increased fitness was supported by increased germination success at lower elevations but refuted by increased germination at high elevations as well. While low-elevation populations had the greatest germination success, overall germination success was low as seen in figures 2-5. At the Gothic site, at lower elevation populations experienced increased germination success with the snow addition treatment and Peanut Mine, low-elevation populations experienced an increase in fitness with the snow addition and supplemental watering. This could be due to water being a constraint on germination for lower elevation populations (Gonzalo-Turpin, 2009). The higher elevation sites,

Schofield and North Pole, germination success for low-elevation populations increased with the snow removal, which may be due to extensive snowpack inhibiting germination. The lower elevation populations still benefited from the increase soil moisture and cooler temperatures. The drought this past year may have been too severe for high-elevation populations, causing a low germination rate at all elevations and with all treatments.

High-elevation populations experienced an increase in the probability of survival after germination and recorded more days until mortality, as shown in figure 6. This was unexpected, since high-elevation populations generally depend on higher soil moisture. One explanation is that high elevation populations are no longer experiencing limitations on growth and development that the snowpack provides. The high elevation populations may be better adapted to absorb more water from the snow addition and water treatment, but no longer experience tissue damaging frost because of how warm spring was this past year. Hence, whether frost events will increase or decrease depends on the balance between warmer spring temperatures and earlier snowmelt (Ohsawa et al., 2008). An extension of the first explanation is that high elevation seeds that successfully germinate are capable of living longer. It has been shown that high elevation seeds are larger, and thus they may have more resources (Anderson et al., 2015). Not only is climate getting warmer and drier, extreme weather events are becoming more frequent, such as severe drought or heavy rain events (Jump & Penuelas, 2005). And with climate change bring variability in survival and reproduction and depression in population growth (Morris et al. 2008).

For future studies we could examine native soils along the elevation gradient. *Boechera stricta* populations may be adapted to certain soils with particular water retention properties. A study of water retention in native soils along the elevation gradient could illuminate if precipitation and soil water retention correspond to fitness. Another aspect of soil that a future study could examine is soil nutrient availability. As elevation increases, temperature decreases and so does the metabolism of microbes. Autotrophic root respiration increases and provides more organic carbon for microbes (Wu et al., 2011). Soil nutrient availability depends on the productivity of microbes. However, drought depresses microbe productivity and less rain means less nutrient dispersal throughout the pores of the soil (Papendick & Campbell, 1981; Robertson et al., 1997). As climate change progresses, soils become more depleted. A future study could explore whether low-elevation soils are more productive or if climate change is causing soil productivity to move up in elevation. The performance of *B. stricta* than can be contrasted with soil productivity along the elevation gradient. Herbivory is another component to fitness that can be explored in the context of an elevation gradient. If high elevations experience less herbivory, then they are allocating less resources to defense compounds and giving them increases fitness (for the initial life stages) at all elevations (Anderson et al. 2015). If there is evidence of the existence of allocation costs for *B. stricta*, then this could potentially explain the greater fitness of high elevation populations.

References

- Anderson, J. T. (2015). Plant fitness in a rapidly changing world. *New Phytologist*, 210(1), 81-87. doi:10.1111/nph.13693
- Anderson, J. T., Perera, N., Chowdhury, B., & Mitchell-Olds, T. (2015). Microgeographic Patterns of Genetic Divergence and Adaptation across Environmental Gradients in *Boechera stricta* (Brassicaceae). *The American Naturalist*, 186(S1). doi:10.1086/682404
- Billy Barr, Rocky Mountain Biological lab, Colorado Weather Station. (n.d.). Retrieved from <https://wrcc.dri.edu/weather/rbil.html>
- Chevin, L., Lande, R., & Mace, G. M. (2010). Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. *PLoS Biology*, 8(4). doi:10.1371/journal.pbio.1000357
- Darwin, C. (1860). On the origin of species by means of natural selection: Or the preservation of the favoured races in the struggle for life. *Werner Company*, 1. doi:10.1037/14088-000
- Garibaldi, L. A., Kitzberger, T., & Chaneton, E. J. (2011). Environmental and genetic control of insect abundance and herbivory along a forest elevational gradient. *Oecologia*, 167(1), 117-129. doi:10.1007/s00442-011-1978-0
- Gonzalo-Turpin, H., & Hazard, L. (2009). Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of Ecology*, 97(4), 742-751. doi:10.1111/j.1365-2745.2009.01509.x
- Hereford, J. (2009). A Quantitative Survey of Local Adaptation and Fitness Trade-Offs. *The American Naturalist*, 173(5), 579-588. doi:10.1086/597611
- Jump, A. S., & Penuelas, J. (2005). Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letters*, 8(9), 1010-1020. doi:10.1111/j.1461-0248.2005.00796.x
- Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, 7(12), 1225-1241. doi:10.1111/j.1461-0248.2004.00684.x
- Manzaneda, A. J., Prasad, K. V., & Mitchell-Olds, T. (2010). Variation and fitness costs for tolerance to different types of herbivore damage in *Boechera stricta* genotypes with contrasting glucosinolate structures. *New Phytologist*, 188(2), 464-477. doi:10.1111/j.1469-8137.2010.03385.x
- New, M., Liverman, D., Schroder, H., & Anderson, K. (2010). Four degrees and beyond: The potential for a global temperature increase of four degrees and its implications. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 369(1934), 6-19. doi:10.1098/rsta.2010.0303

- Ohsawa, T., & Ide, Y. (2008). Global patterns of genetic variation in plant species along vertical and horizontal gradients on mountains. *Global Ecology and Biogeography*, 17(2), 152-163. doi:10.1111/j.1466-8238.2007.00357.x
- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Robertson, G. P., Klingensmith, K. M., Klug, M. J., Paul, E. A., & Crum, J. R. (1997). Soil Resources, Microbial Activity, and Primary Production Across an Agricultural Ecosystem. *Ecological Applications*, 7(1), 158. doi:10.2307/2269414
- Song, B., Clauss, M. J., Pepper, A., & Mitchell-Olds, T. (2006). Geographic patterns of microsatellite variation in *Boechera stricta*, a close relative of *Arabidopsis*. *Molecular Ecology*, 15(2), 357-369. doi:10.1111/j.1365-294x.2005.02817.x
- Wadgyamar, S. M., Daws, S. C., & Anderson, J. T. (2017). Integrating viability and fecundity selection to illuminate the adaptive nature of genetic clines. *Evolution Letters*, 1(1), 26-39. doi:10.1002/evl3.3
- Wadgyamar, S. M., Ogilvie, J. E., Inouye, D. W., Weis, A. E., & Anderson, J. T. (2018). Phenological responses to multiple environmental drivers under climate change: Insights from a long-term observational study and a manipulative field experiment. *New Phytologist*, 218(2), 517-529. doi:10.1111/nph.15029
- Whitlock, M. C. (2015). Modern Approaches to Local Adaptation. *The American Naturalist*, 186(S1). doi:10.1086/682933
- Wolda, H. (1987). Altitude, habitat and tropical insect diversity. *Biological Journal of the Linnean Society*, 30(4), 313-323. doi:10.1111/j.1095-8312.1987.tb00305.x
- Wu, Z., Koch, G. W., Dijkstra, P., Bowker, M. A., & Hungate, B. A. (2011). Responses of Ecosystem Carbon Cycling to Climate Change Treatments Along an Elevation Gradient. *Ecosystems*, 14(7), 1066-1080. doi:10.1007/s10021-011-9464-4
- Yuste, J. C., Baldocchi, D. D., Gershenson, A., Goldstein, A., Misson, L., & Wong, S. (2007). Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. *Global Change Biology*, 13(9), 2018-2035. doi:10.1111/j.1365-2486.2007.01415.x

Garden	Elevation (m)	Latitude	Longitude
Peanut Mine	2710	38.885075	-106.99724
Gothic	2890	38.9514333	-106.99108
Schofield	3133	39.0391	-107.06363
North Pole	3341	39.0315806	-107.07846

Table 1. Spatial data of sites.

Effect	Chisq	Df	P-value(>Chisq)
(Intercept)	30.7109	1	3.00E-08
Elevational_diff	0.0469	1	0.8286087
Treatment	20.6987	3	0.0001216****
garden	37.2593	3	4.06E-08****
I(Elevational_diff^2)	0.0492	1	0.8245475
Elevational_diff:Treatment	7.9089	3	0.0479316*
Elevational_diff:garden	1.3407	3	0.7194839
Treatment:garden	91.5483	9	7.96E-16****
Treatment:I(Elevational_diff^2)	0.7039	3	0.8722786
garden:I(Elevational_diff^2)	3.4069	3	0.3330442
Elevational_diff:Treatment:garden	98.922	9	< 2.2e-16****
Treatment:garden:I(Elevational_diff^2)	81.6752	9	7.51E-14****

Table 2. Three-way interaction between of treatment, garden and quadratic effect of elevation difference.

Analysis via logistic regression assessing the probability of germination using a binomial distribution. Significance codes: 0 '****' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Treatment	Site	Germination Success	SE
Snow Removal	Gothic	1.31E-09	4.86E-09
	North Pole	3.04E-03	2.00E-03
	Peanut Mine	3.83E-02	1.94E-02
	Schofield	4.94E-02	2.20E-02
Control (Contemporary)	Gothic	1.19E-03	8.82E-04
	North Pole	2.72E-03	1.82E-03
	Peanut Mine	3.72E-02	1.90E-02
	Schofield	1.80E-02	8.59E-03
Snow Addition	Gothic	7.69E-03	4.02E-03
	North Pole	1.16E-03	9.35E-04
	Peanut Mine	5.13E-02	2.52E-02
	Schofield	2.22E-02	1.04E-02
Snow Addition and Water	Gothic	2.30E-03	1.46E-03
	North Pole	5.24E-11	1.40E-10
	Peanut Mine	2.00E-01	8.05E-02
	Schofield	1.97E-02	9.51E-03

Table 3. Garden by treatment interaction.

	loglik	Chisq	Df	Pr(> Chi)
Elevational_diff	-5600.4	156.9319	1	< 0.001
Treatment	-5542.4	115.9532	3	< 0.001
l(Elevational_diff^2)	-5539.5	5.7905	1	0.01611
Elevational_diff:Treatment	-5520.1	38.799	3	< 0.001
Treatment:l(Elevational_diff^2)	-5515.9	8.3781	3	0.03881

Table 4. The linear and quadratic relationships between treatment and elevational difference. Analysis via the Cox proportional hazards model.

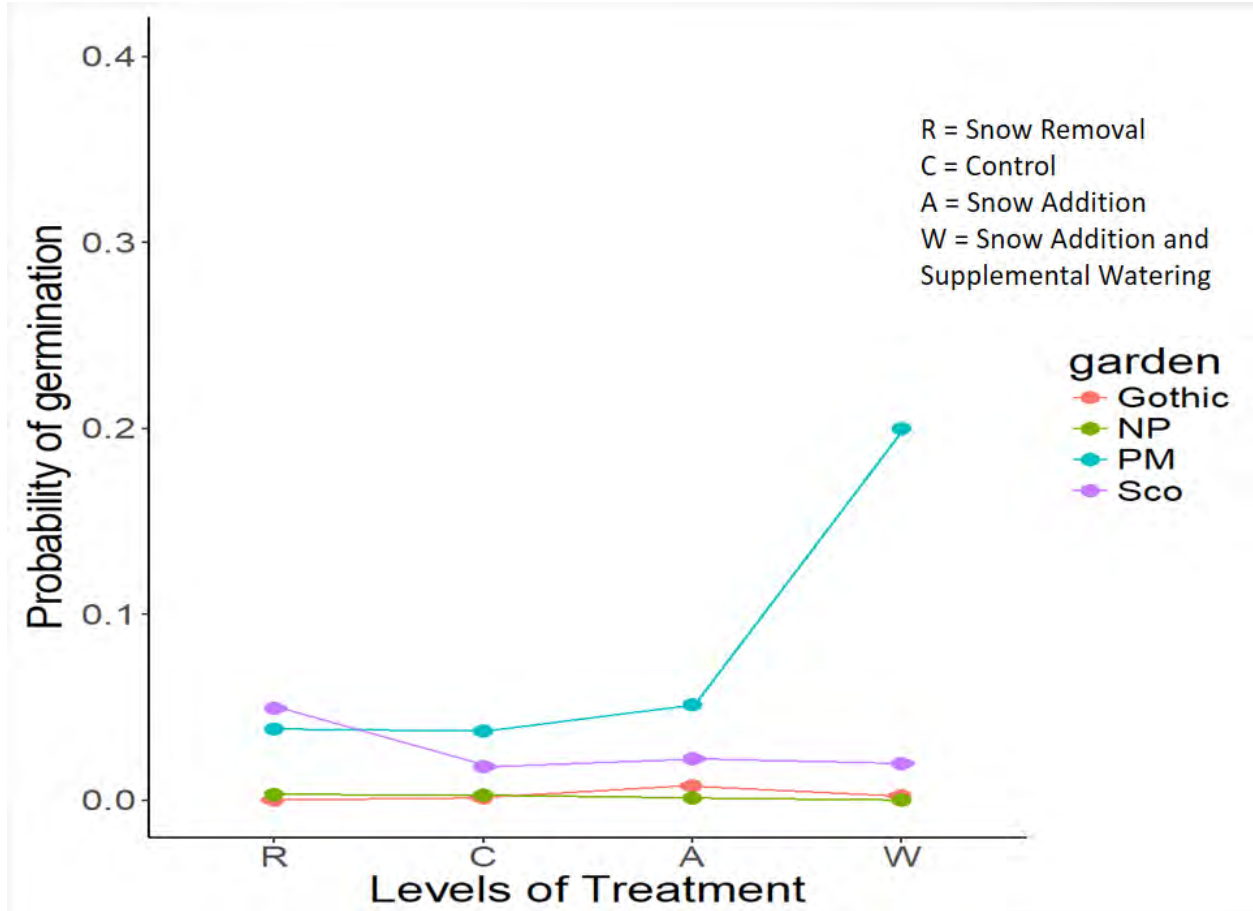


Figure 1. Probability of germination by garden and treatment interaction.

Figure 2. Gothic

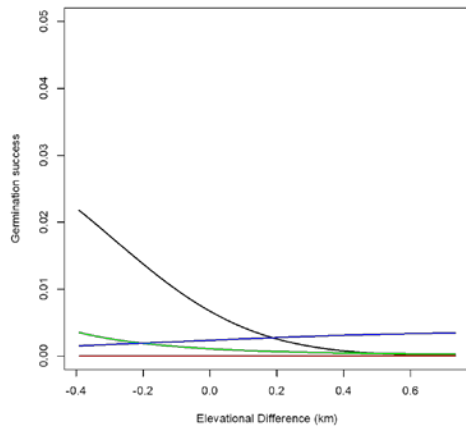


Figure 3. Peanut Mine

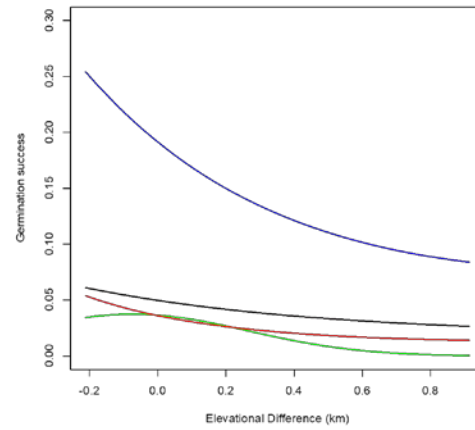


Figure 4. Schofield

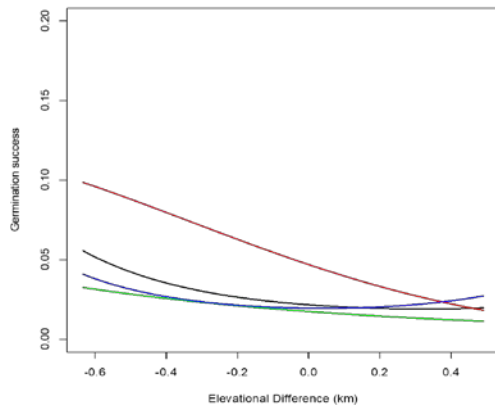


Figure 5. North Pole

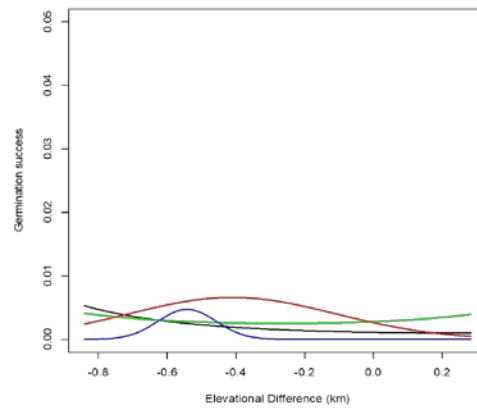


Figure 2-5. The graphs model relative fitness (fitness/average fitness) using germination success as a function of elevational difference in the four treatments. The color scheme: black is addition; green is control; red is removal; blue is watered.

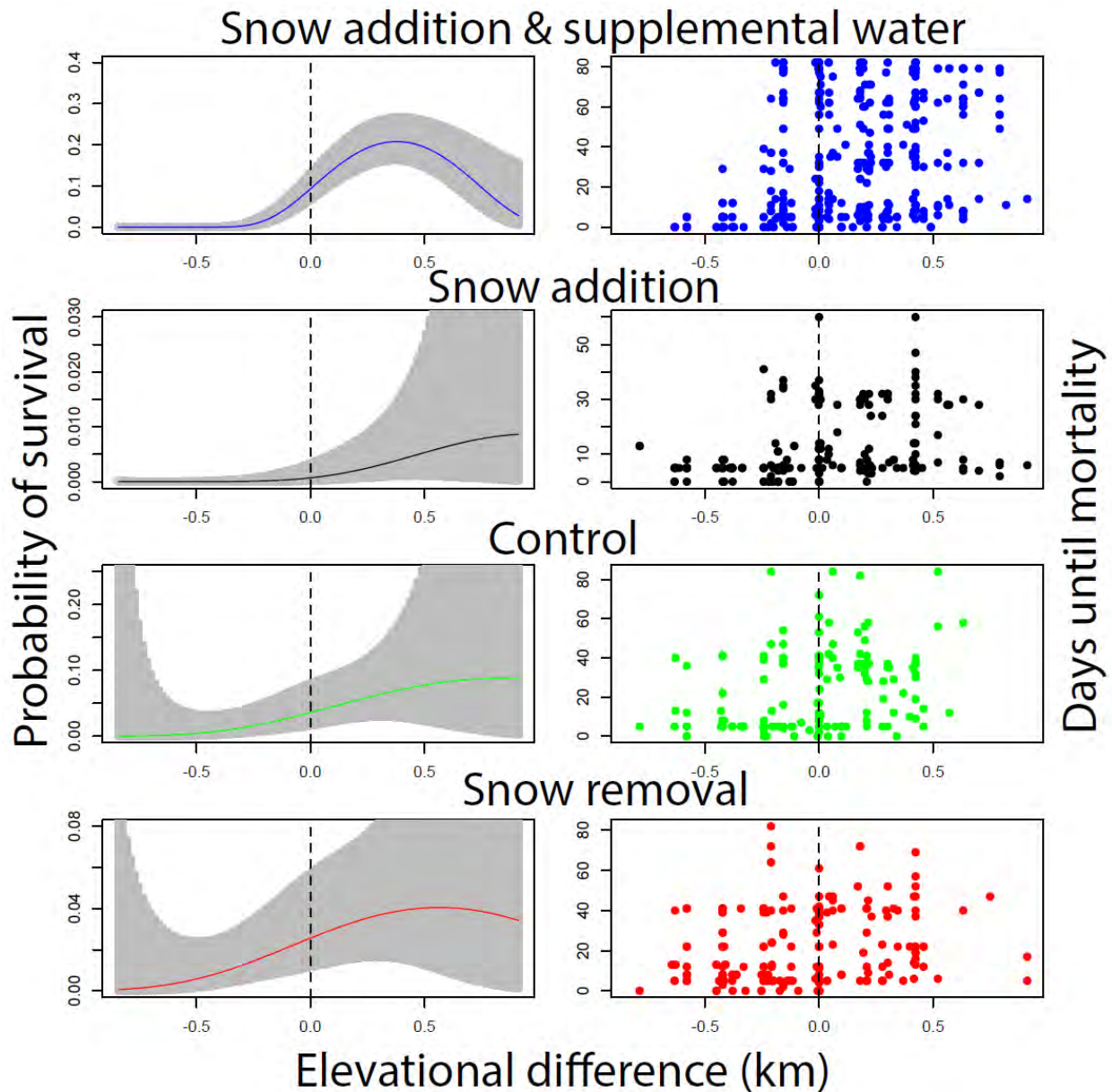


Figure 6. Joint modeling of germination success and time until mortality via Cox proportional hazards model. The panels on the left of the figure indicate the probability of survival as a function of source elevation. The panels on the right indicate the number of days until mortality.

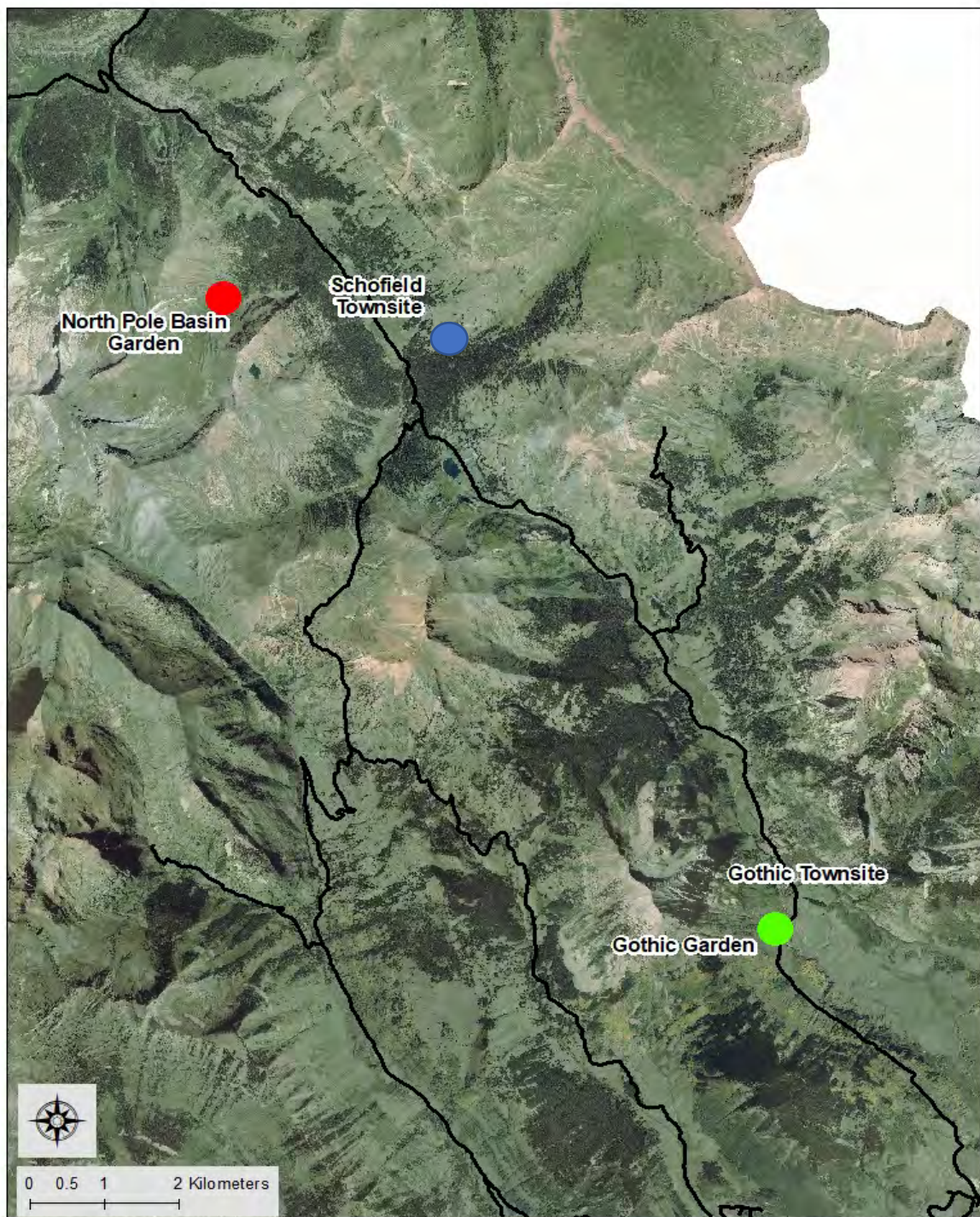


Figure 7. Map of North Pole Basin, Schofield, and Gothic common garden sites.