

The consequences of winter climate change for plant performance

Jill T. Anderson 

Department of Genetics and Odum School of Ecology, University of Georgia, Athens, Georgia 30602, USA

Correspondence: Jill T. Anderson, Department of Genetics and Odum School of Ecology, University of Georgia, Athens, Georgia 30602, USA.

Email: jta24@uga.edu

KEYWORDS

fitness, frost damage, local adaptation, overwinter chilling, phenology

With continually increasing summer temperatures and intense heat waves, it can be easy to neglect the ecological effects of winter climate change. However, shifts in the climate during winter can have profound consequences for eco-evolutionary dynamics in extratropical latitudes and high-elevation locales. Climate change has increased winter temperatures, disrupted snowpack, and reduced ice cover (Rixen et al., 2022). Extreme losses of snowpack are projected for many regions by the end of the century (Talsma et al., 2022). Patterns of climate change are complex and region dependent, but winters are becoming less reliable overall, with elevated temperatures and altered snow dynamics. In ecosystems with cold winters, many plant species require exposure to low, but not necessarily freezing, temperatures for a prolonged period to break dormancy in the spring; this chilling requirement prevents leaf emergence, flowering, or germination from occurring in the middle of winter (Chuine et al., 2016). Warming winters have advanced the onset of spring and could result in insufficient overwinter chilling. In addition, spring and fall frosts that occur after plants become physiologically active can perturb phenology and reduce fitness. Finally, novel winter climates could disrupt biotic interactions among plants, their mutualists, and antagonists. Here, I discuss emerging research frontiers in these domains.

INSUFFICIENT OVERWINTER CHILLING

Species will likely have individualistic responses to declines in the duration of winter. For some, shortening winters and warm snaps during the winter can postpone the fulfillment of chilling needs, delaying phenology, decreasing the rate of leaf production, and increasing vulnerability to spring frosts (Yu et al., 2010; Laube et al., 2014). Models suggest that winter conditions may be insufficient to break dormancy by

the 2050s in the warmest portions of the range of some species, which could lead to local extinctions and crop failures (Chuine et al., 2016). Nevertheless, a recent meta-analysis suggests that warming of $>4^{\circ}\text{C}$ would be necessary to inhibit winter chilling cues for spring-flowering plants in Central Europe (Ettinger et al., 2020).

Laboratory studies (including mine) that have simulated overwinter chilling typically expose plants to a constant 4°C for variable periods. This temperature likely reflects limitations of refrigeration systems rather than mirroring conditions that plants experience during winter. For the past decade, I have been studying fitness and phenotypic responses of *Boechera stricta* (Brassicaceae) to manipulations of snow dynamics in common gardens in montane and subalpine meadows around the Rocky Mountain Biological Laboratory (Colorado, USA). Similar to winter soil temperatures in other snow-dominated systems (Rixen et al., 2022), soil temperatures in these common gardens remain within a very stable range (0°C – 1.2°C ; see Figure 1) during winters that can last 5–7 months. Winter temperatures deviate from this range only when snow is absent, which has occurred at our low-elevation site (2553 m a.s.l.). In the growth chamber, flowering success of *B. stricta* is significantly dampened at 4 weeks of exposure to 4°C compared with 6 weeks (Anderson et al., 2010), although this result may have limited bearing on climate change responses, given that future winters may not be as short as 4 weeks in this system. Rather, reduced snowpack and frosts may play a stronger role in determining future fitness and phenology. Thus, 4°C may be sufficient for meeting chilling requirements, but lab experiments at this temperature likely poorly reflect natural conditions.

Considerable uncertainty remains about the extent to which climate change could disrupt overwinter chilling. What is the actual range of temperatures needed for chilling? How do short bursts of warmer temperatures or periods without snow influence the accumulation of chilling

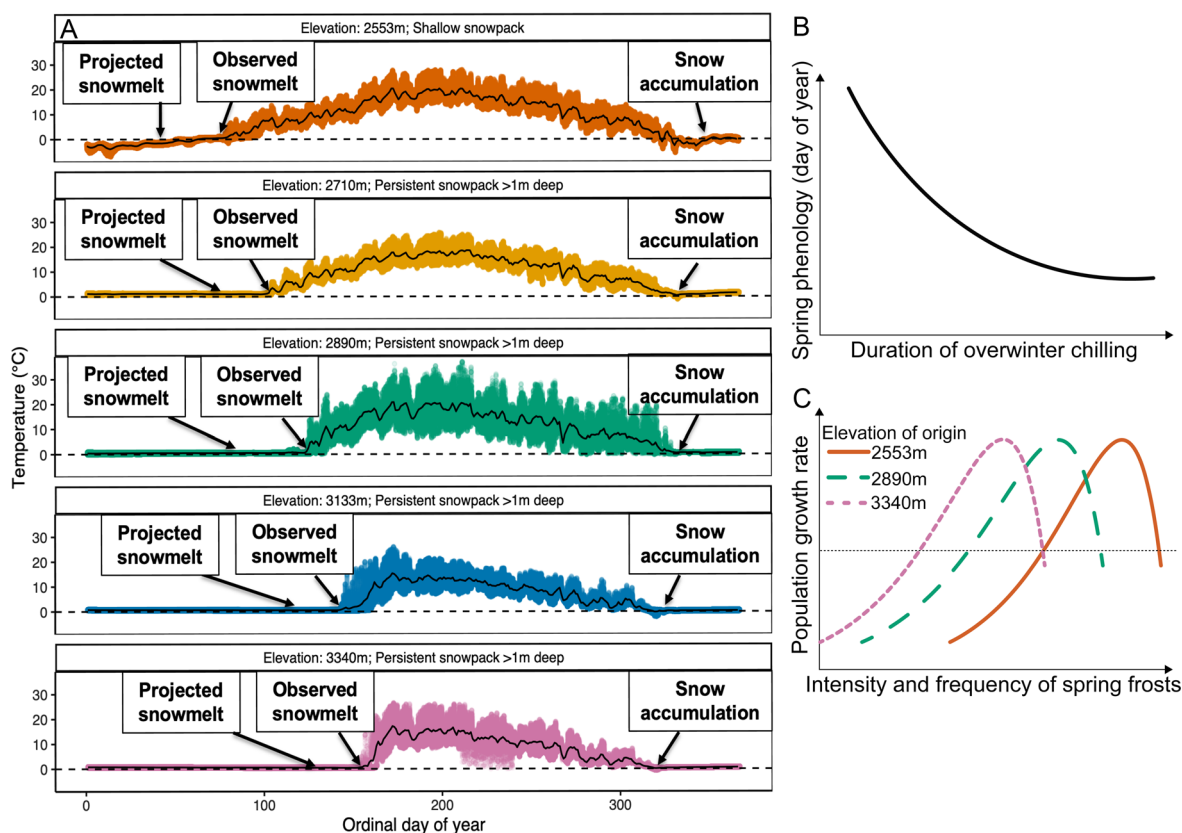


FIGURE 1 (A) Winter soil temperatures remain stable in the Colorado Rocky Mountains, USA, at common gardens with persistent snowpacks. The snowbank at the lowest-elevation site is minimal, and snow-free days can occur during winter, leading to freezing soil temperatures. Shown are soil temperatures for one representative year (2016) at 10 cm depth, logged every 15 minutes with ECH20 sensors in 5–10 blocks/garden. The black lines show daily mean temperatures across blocks, with dashed horizontal lines at 0°C. I have indicated the observed snowmelt date in each site along with end-of-century projections under Representative Concentration Pathway 8.5 (Lute et al., 2022). (B) Models project continued reductions in snowpack under climate change (Lute et al., 2022), which could reduce the duration of winter chilling and delay spring phenological events, such as germination, leaf-out, and flowering. Although many species have advanced the timing of spring events in response to climate change, accelerated phenology is not a universal response to early springs (Yu et al., 2010). A failure to track climate change in time can arise through lack of exposure to sufficient winter chilling. (C) Variation in winter climates could favor the evolution of specialization to local climates. For example, I hypothesize that low elevation populations and species (red) have evolved greater freezing tolerance than mid- (green) or high (pink) elevation populations/species, owing to strong selection from freezing spring temperatures. I have depicted asymmetrical fitness curves based on typical findings from the thermal performance literature, and used plant population growth rates as a metric of fitness integrated across life history. Horizontal dotted line indicates growth rates at which populations are stable; values above line represent expanding populations, and values below line indicate contracting populations. Reduced snowpack under climate change could expose higher-elevation populations to novel frost events, and depress population growth rates. Shifts in other winter conditions also risk increasing the susceptibility of locally adapted genotypes to decline. Studies characterizing plant performance curves in response to variable winter conditions could generate predictions about population persistence and inform conservation practices.

requirements? How do other factors—such as frosts and spring water availability—interact with winter conditions to influence budbreak, flowering, and germination (Laube et al., 2014)? Future mechanistic lab or field studies that more closely mimic actual winters, and periods of warming during the winter, will yield crucial information about the extent to which winter conditions will remain suitable for breaking dormancy.

FROST DAMAGE

Delayed snowfall in late autumn could subject plants to freezing temperatures before full dormancy. Furthermore, increased winter temperatures can melt snow prematurely

in spring, exposing plants to frosts they would not have experienced historically when insulated under snow (Rixen et al., 2022). Even in areas without persistent snowbanks, spring frosts after plants become physiologically active can injure developing vegetative and floral tissues (Chamberlain et al., 2019). These false springs have severe economic consequences. For instance, farmers in Georgia lost \$1.2 billion in peach, blueberry, and other fruit crops due to a frost in March 2017 after a warm winter in which plants had already begun flowering (Smith, 2020).

Plants rely on multiple cues to break winter dormancy, including temperature and photoperiod; species that are more responsive to temperature likely face greater threats of damage from false springs. Global shifts in the prevalence of late spring frosts (Liu et al., 2018) could heighten damage to

plants with limited evolutionary exposure to these conditions (Zohner et al., 2020). For example, mid- and high-elevation *B. stricta* genotypes, which have limited exposure to freezing temperatures (Figure 1), may be increasingly vulnerable to frosts as snowmelt advances. Future experiments should evaluate the extent and distribution of genetic variance in frost tolerance in a diversity of species with divergent life forms in different ecosystems. For example, variation in freezing tolerance underlies local adaptation to disparate latitudes in the model organism *Arabidopsis thaliana* (Oakley et al., 2014). Nevertheless, we know very little about the extent to which natural populations have adapted to spatially variable winter conditions. Experiments that quantify the extent of local adaptation to winter conditions could illuminate whether conservation programs such as assisted gene flow (Aitken and Whitlock, 2013) could introduce adaptive alleles into populations facing novel winter climates.

ALTERED BIOTIC INTERACTIONS

In addition to spring events, atypical midwinter heat waves could break dormancy and elicit flowering and leaf production at inopportune times in species cued by temperature and with limited overwinter chilling needs. For example, in the past 5 years in the upland forests of Georgia (USA), I have observed plants like *Vaccinium elliotii* (Ericaceae) flowering as early as late January, after which temperatures have declined and snow has fallen. Historically, this buzz-pollinated native plant flowered from mid-March to mid-April, after the last frost date (Anderson et al., 2021). In addition to damaging sensitive floral tissues, these warm winter spells could have negative ramifications for plant-pollinator interactions. Questions remain about the extent to which climate change induces temporal mismatches between plants and their pollinators and the fitness effects of these asynchronies (Iler et al., 2021). Nevertheless, it seems clear that pollinators will not visit flowers that mature at aberrant midwinter times, increasing the risk of fertilization failure for obligately outcrossing species and potentially disrupting seed dispersal mutualisms. Biologists may miss these abnormal winter events because they fall outside our regular field seasons, such that we only witness any reductions in fitness months later.

In addition to its effects on plant-pollinator interactions, winter climate change can influence plant eco-evolution indirectly through other altered biotic interactions. For example, warming can ameliorate conditions for pathogens and herbivores, allowing these antagonists to expand their ranges into regions that were previously inhospitable. The most notable case involves the mountain pine beetle (*Dendroctonus ponderosae*); warming winters, in part, explain its recent range expansion into northern and high-elevation locales, where the species has killed trees across millions of hectares (Sambaraju et al., 2019). Warming winters can also augment herbivory by large mammals

(Martin and Maron, 2012) and facilitate the spread of invasive plants (Osland et al., 2023), both of which could have serious community-level consequences. Climate change in the winter may also influence plant-microbe interactions, but researchers are just beginning to understand the roles of soil microbes on plant fitness and functional traits (Rudgers et al., 2020).

CONCLUSIONS

Winter climate change has disrupted the timing of critical life-history transitions in many areas worldwide. Community science programs that monitor phenology during the winter could detect flowering and leaf-out at unusual times, and researchers could then examine the fitness consequences. Future studies could consider the effects of winter climate change on germination phenology and recruitment dynamics, given that early life history stages are often overlooked (Wang et al., 2018). Furthermore, I encourage additional work that disentangles the contributions of winter vs. summer climate change to plant population growth rates (Iler et al., 2019) to test the relative importance of winter climate change in population persistence. Experimental studies exposing plants to manipulated false springs, winter warming, reduced snowpack, and accelerated snowmelt in field settings with interacting species will illuminate the fitness consequences of winter climate change, and the degree of local adaptation to winter. In sum, these studies will enable more reliable predictions about the vulnerability of local populations to climate change.

ACKNOWLEDGMENTS

I thank T. Pendergast, M. Rochford, S. Day, I. Jameel, D. Denney, and K. McCrum for comments on the manuscript. I am grateful to Pamela Diggle and the two anonymous reviewers for their suggestions and critiques. The National Science Foundation funded the research that generated these insights (DEB-1553408 and IOS-2220927).

ORCID

Jill T. Anderson  <http://orcid.org/0000-0002-3253-8142>

REFERENCES

- Aitken, S. N., and M. C. Whitlock. 2013. Assisted Gene Flow to Facilitate Local Adaptation to Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 44: 367–388.
- Anderson, J., C.-R. Lee, and T. Mitchell-Olds. 2010. Life history QTLs and natural selection on flowering time in *Boechera stricta*, a perennial relative of *Arabidopsis*. *Evolution* 65: 771–787.
- Anderson, J. T., M. I. Jameel, and M. A. Geber. 2021. Selection favors adaptive plasticity in a long-term reciprocal transplant experiment. *Evolution* 75: 1711–1726.
- Chamberlain, C. J., B. I. Cook, I. García De Cortázar-Atauri, and E. M. Wolkovich. 2019. Rethinking false spring risk. *Global Change Biology* 25: 2209–2220.
- Chuine, I., M. Bonhomme, J.-M. Legave, I. García De Cortázar-Atauri, G. Charrier, A. Lacoite, and T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The

- unrevealed hurdle of endodormancy break. *Global Change Biology* 22: 3444–3460.
- Ettinger, A. K., C. J. Chamberlain, I. Morales-Castilla, D. M. Buonaiuto, D. F. B. Flynn, T. Savas, J. A. Samaha, and E. M. Wolkovich. 2020. Winter temperatures predominate in spring phenological responses to warming. *Nature Climate Change* 10: 1137–1142.
- Iler, A. M., P. J. CaraDonna, J. R. K. Forrest, and E. Post. 2021. Demographic Consequences of Phenological Shifts in Response to Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 52: 221–245.
- Iler, A. M., A. Compagnoni, D. W. Inouye, J. L. Williams, P. J. CaraDonna, A. Anderson, and T. E. X. Miller. 2019. Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *Journal of Ecology* 107: 1931–1943.
- Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20: 170–182.
- Liu, Q., S. Piao, I. A. Janssens, Y. Fu, S. Peng, X. Lian, P. Ciais, et al. 2018. Extension of the growing season increases vegetation exposure to frost. *Nature Communications* 9: 426.
- Lute, A. C., J. Abatzoglou, and T. Link. 2022. SnowClim v1.0: high-resolution snow model and data for the western United States. *Geoscientific Model Development* 15: 5045–5071.
- Martin, T. E., and J. L. Maron. 2012. Climate impacts on bird and plant communities from altered animal–plant interactions. *Nature Climate Change* 2: 195–200.
- Oakley, C. G., J. Ågren, R. A. Atchison, and D. W. Schemske. 2014. QTL mapping of freezing tolerance: links to fitness and adaptive trade-offs. *Molecular Ecology* 23: 4304–4315.
- Osland, M. J., B. Chivoiu, L. C. Feher, L. L. Dale, D. Lieurance, W. M. Daniel, and J. E. Spencer. 2023. Plant migration due to winter climate change: range expansion of tropical invasive plants in response to warming winters. *Biological Invasions* 25: 2813–2830.
- Rixen, C., T. T. Høye, P. Macek, R. Aerts, J. Alatalo, J. Andeson, P. Arnold, et al. 2022. Winters are changing: snow effects on Arctic and alpine tundra ecosystems. *Arctic Science* 8: 572–608.
- Rudgers, J. A., M. E. Afkhami, L. Bell-Dereske, Y. A. Chung, K. M. Crawford, S. N. Kivlin, M. A. Mann, and M. A. Nuñez. 2020. Climate Disruption of Plant-Microbe Interactions. *Annual Review of Ecology, Evolution, and Systematics* 51: 561–586.
- Sambaraju, K. R., A. L. Carroll, and B. H. Aukema. 2019. Multiyear weather anomalies associated with range shifts by the mountain pine beetle preceding large epidemics. *Forest Ecology and Management* 438: 86–95.
- Smith, A. B. 2020. U.S. Billion-dollar Weather and Climate Disasters, 1980 - present (NCEI Accession 0209268). Website: <https://www.ncei.noaa.gov/archive/accession/0209268>, accessed 25 August 2023.
- Talsma, C. J., K. E. Bennett, and V. V. Vesselinov. 2022. Characterizing Drought Behavior in the Colorado River Basin Using Unsupervised Machine Learning. *Earth and Space Science* 9: e2021EA002086.
- Wang, G., C. C. Baskin, J. M. Baskin, X. Yang, G. Liu, X. Ye, X. Zhang, and Z. Huang. 2018. Effects of climate warming and prolonged snow cover on phenology of the early life history stages of four alpine herbs on the southeastern Tibetan Plateau. *American Journal of Botany* 105: 967–976.
- Yu, H., E. Luedeling, and J. Xu. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences* 107: 22151–22156.
- Zohner, C. M., L. Mo, S. S. Renner, J.-C. Svenning, Y. Vitasse, B. M. Benito, A. Ordonez, et al. 2020. Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. *Proceedings of the National Academy of Sciences* 117: 12192–12200.

How to cite this article: Anderson, J. T. 2023. The consequences of winter climate change for plant performance. *American Journal of Botany* e16252. <https://doi.org/10.1002/ajb2.16252>