

MICROCLIMATE AND PHENOLOGY AT THE H.J. ANDREWS EXPERIMENTAL
FOREST

by
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THESIS ABSTRACT

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Master of Science

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Title: Microclimate and Phenology at the H.J. Andrews Experimental Forest

Spring plant phenology is often used as an indicator of a community response to climate change. Remote data and low-resolution climate models are typically used to predict phenology across a landscape; however, this tends to miss the nuances of microclimate, especially in a mountainous area with heterogeneous topography. I investigated how inter-annual variability in regional climate affects the distribution of microclimates (i.e., areas $<100\text{m}^2$) and spring plant phenology across a 6400-hectare watershed within the Western Cascades in Oregon. Additionally, I created species-specific models of bud break at the microclimate scale, that could then be applied across a wider landscape. I found that years with warm winters, few storms and low snowpack have a homogenizing effect on microclimate and spring phenology events, and that bud break models developed at a local scale can be effectively applied across a broader landscape.

This thesis includes previously unpublished coauthored material.

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CHAPTER I

INTRODUCTION

Phenology – the study of recurring seasonal life cycle events – is a simple metric that can be used to elucidate patterns among communities and across ecosystems. Plant phenology is easily observable and can be measured by citizens and scientists alike. Regional climates across the globe have been steadily increasing in temperature (IPCC 2014), and as temperatures continue to warm, the timing of annual leaf emergence and flowering has advanced as much as 2 to 3 days per decade (Parmesan and Yohe 2003, Menzel et al. 2006). These advancements can have sweeping impacts beyond a single trophic level, and can reduce the fitness of plants, animals and insects within a community (Walther et al. 2002, Parmesan and Yohe 2003, Both et al. 2009, Thackeray et al. 2016). Local climates (areas <100m²) driven by variable topographies, canopy cover and temperature inversions have been shown to buffer temperature advances and in turn have the potential to minimize advanced phenological events (Daly et al. 2010, Dobrowski 2011, Pepin et al. 2011, Frey et al. 2016b, Novick et al. 2016, Lenoir et al. 2017). I investigated the effects of regional climate patterns on the distribution of microclimates in a 6400-hectare watershed in the Western Cascades, and in turn, how those microclimates affect the spring plant phenology of 18 native species of herbs, shrubs and trees. Because each species has evolved a unique physiological response to climate (Kreyling 2010), I was interested in creating species-specific models to predict bud break using local temperature metrics. Most predicted effects of regional warming are derived using low resolution spatial models and then downscaled to higher spatial resolutions. This method misses the nuances of local microclimates and can over or under predict the effects of regional change on a community. By creating local scale models at high spatial resolution that can then be applied to a wider region, I hoped to remove this source of error, and create models that can accurately predict bud break across a landscape.

Chapters II and IV of this thesis are both co-authored material and will be published with Bitty Roy and Mark Schulze listed as co-authors. Chapters I, III and V are all sole authored by Sarah Ward.

CHAPTER II

A LONG TERM PERSPECTIVE OF MICROCLIMATE AND SPRING PLANT PHENOLOGY IN THE WESTERN CASCADES

Acknowledgements

This chapter includes materials currently under review and co-authored by Sarah Ward, Mark Schulze, Bitty Roy.

Introduction

Over the past several decades, scientists and land managers have become increasingly concerned about the effects of current warming trends and the potential threat warming poses to biodiversity and ecosystem services (Grimm et al. 2016). Phenology – the timing of seasonal events of an organism’s life cycle – is a common measure of the response of a species to climate change, and phenological shifts can have significant impacts on the dynamics of an ecosystem (Walther et al. 2002, Parmesan 2006, Both et al. 2009). For example, because not every species responds equally to changes in climate, trophic levels with historically synced phenologies, such as plants and pollinators, may become decoupled due a shift in one or both species’ phenologies (trophic asynchrony), and result in localized population declines and biodiversity loss (Harrington et al. 1999, Walther et al. 2002, Visser et al. 2004, Visser and Both 2005, Parmesan 2006, Inouye 2008, Both et al. 2009, Forrest and Thomson 2011, Thackeray et al. 2016). Parmesan and Yohe (2003) reviewed data time series data on the phenology of 677 species for periods spanning from 16-132 years in length (median 45 years) and found that 62% of those species had shown some change in their phenologies, and that 87% of phenological shifts were in the direction expected due to climate change. For plants, they found that spring events such as bud break (first date of leaf emergence) and flowering are advancing at an average rate of 2.3 days per decade.

Models developed to predict the effects of climate warming on biodiversity are often based on regional climate projections, which are too coarse ($>50\text{km}^2$) to predict the variation in local climate (microclimate) that organisms experience (Peterson et al. 1997, Lookingbill and Urban 2003, Luoto and Heikkinen 2008, Daly et al. 2010, Pepin et al.

2011, Potter et al. 2013, Frey et al. 2016b). Physical factors such as topography, snowpack accumulation and ablation, and forest cover can have significant effects on local climate, and in turn affect the timing of phenological events (Hwang et al. 2011). These microclimates can be significantly different from regional climate patterns and downscaling regional models may result in overgeneralization when projecting the effects of climate change (Daly et al. 2010, Franklin et al. 2013, Frenne et al. 2013). Mountainous regions—which make up 12.3% of the terrestrial surface on earth, excepting Antarctica (Körner et al. 2011)—are especially overgeneralized in regional models, due to the high degree of topographic heterogeneity (Luoto and Heikkinen 2008). Additionally, climate stations are often biased towards lower elevation, accessible sites, resulting in higher incidences of estimated data for remote upper elevation sites (Pepin et al. 2011). Steep mountainous terrain often leads to persistent cold air pooling events (temperature inversions) where cold air drains down mountain slopes into valleys and other areas of low topographic relief and is trapped by a layer of warmer air above and the local climate is decoupled from the regional atmospheric conditions. These events are a major driver of microclimate in mountainous regions, especially during winter months and they are largely driven regional weather patterns (Daly et al. 2010, Pepin et al. 2011, Novick et al. 2016). Some studies suggest that microclimates created by topography, canopy cover and local decoupling from regional weather patterns may mitigate the effects of regional warming, and have the potential to buffer temperatures and minimize advanced phenological events (Peterson et al. 1997, Daly et al. 2010, Dobrowski 2011, Frey et al. 2016b, Lenoir et al. 2017)

Here we report results of an eight-year study involving weekly spring phenology observations of 18 species of plants across a diverse range of fixed sites in the H.J. Andrews experimental forest on the west slope of the Oregon Cascades. We were interested in how microclimates vary across a watershed, and how regional climate variability and microclimate processes interact to influence the timing of spring phenology of native herbs, shrubs, and trees. In general, we expected that warm years with less snow pack would result in advancement of bud break and flowering, especially for the higher elevation, exposed ridgelines, and vice versa for cooler years with deeper and more persistent snowpack. Specifically, we expected to see the effects of cold air

pooling across the landscape reflected in the timing of phenology in two ways. First, we hypothesized that areas more susceptible to cold air pooling would experience less early-season temperature forcing and more persistent snowpack than topographically exposed sites of similar elevation, which would be reflected in relatively delayed spring phenology of forest plants. Second, we expected that interactions between regional and local processes may result in year to year variability in the relationship among sites across the elevation gradient (e.g., the timing bud break may be similar at two sites one year, and be widely different between those sites a different year).

Methods

Study area

The H.J. Andrews Experimental Forest is a 6400-hectare (15,800 acre) forest located on the west side of the Cascade Mountains around 50 miles east of Eugene, Oregon. The area is typical of the Western Cascade Range, with steep mountainous terrain, exposed ridges and sheltered valleys, and a high degree of topographic heterogeneity with elevations ranging from 410 to 1630 m. Vegetation is primarily a combination of 150-500 year old mixed conifer forests, and 40-60 year old *Pseudotsuga menziesii* (Douglas fir) plantations.

Study design

Sixteen core phenology sites were selected across a variety of elevations and aspects, with sites ranging from 460 to 1339 meters (Figure 1). Most phenology sites were co-located (11 of 16 sites) with long term temperature (Johnson and Gregory 2016, Daly and McKee 2016a, 2016b) and vegetation monitoring plots (Harmon and O'Connell 2015, Franklin 2017). This allowed for quality assurance and quality control (QAQC), and data validation using comparable temperature data. Additional sites (beyond those 11 co-located with long term monitoring plots) were added to augment distribution of study sites across elevation, aspect and topographic position and to create old growth and plantation paired sites at high, medium and low elevations. 18 species of native herbs, shrubs and trees were selected as target species (Appendix S1: Table S1). At each site, a center point was established and plants from all of the focal study species occurring in the area (due to the variety of terrain and elevation, not every target species was found at

every site) were added as encountered while inventorying a 25m radius circle around the center point until 5 individuals of each species were mapped and tagged (in the 2009 pilot season, only 3 individuals per species were tagged, the sample sizes were increased to 5 early in the 2010 season). In a few instances, plants of a given species were tagged up to 35m away from the center point to attain the target sample size. Each plant was mapped using bearing and distance from the center post. For herbaceous plants, individuals were marked using one or two pin flags with a numbered aluminum tag attached to the pin flag. Trees and shrubs were tagged using aluminum nails or zip ties depending on stem

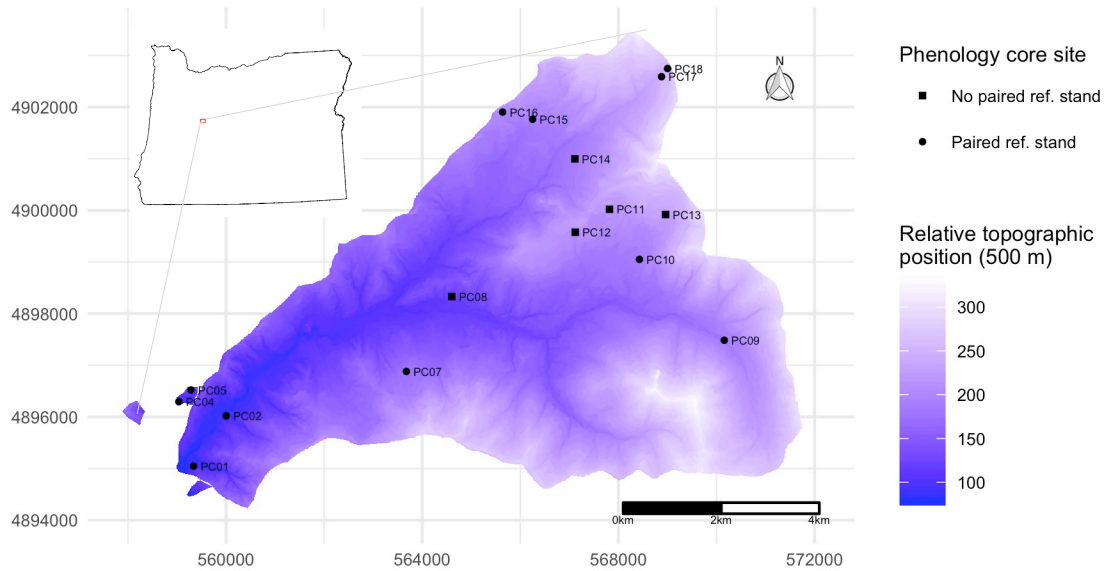


Figure 1: Map showing the location and relative topographic position of the 16 core phenology sites at the H.J. Andrews. Colors are relative topographic position, with blues showing sites of low topographic relief, and whites showing sites with high topographic relief. Purples are intermediate values. Squares indicate sites without a paired reference stand, while circles are sites with a nearby reference stand. Sites are labeled with PC (phenology core) and the site number.

diameter. If an individual died or was eaten over the course of the study, another plant was selected to maintain five individuals per site.

Understory air temperature and snow cover were the primary microclimate variables recorded. To capture the temperature of each site, HOBO (Onset Corporation, Hobo U22-001; accuracy 0.2°C) temperature sensors were placed 1.5 meters above the ground facing south in the center of each plot, and temperature data were collected every fifteen minutes. To reduce temperature spikes due to solar radiation, the sensors were placed in the shade, beneath a PVC shield (a 20.32cm long piece of 7.62 cm schedule 40 pipe split in half lengthwise). Snow data were collected via observations of depth and

percent cover made by researchers during each site visit, and partial or full burial under snow was recorded for each individual. Snow data for the winter period prior to the first phenology census were estimated using existing snow stake datasets (Schulze and Levno 2017), Andrews meteorological stations (Daly and McKee 2016b), time lapse cameras distributed across the forest, and observations from other researchers.

Surveys

We developed a species-specific scoring system for vegetative and reproductive phenophases that captured consistently observable stages between dormant buds and full leaf out/end of flowering (Schulze 2017). Over the course of each spring, the sites were visited once every 5-10 days, and each individual was scored based on its current reproductive and vegetative phenophase. In the early years of the study (2009 and 2010), visits were less consistent, due to concurrent study plot set up and early season site access limitations. From 2011-2016, sites were typically visited once every 7 days.

Observations began each year in late winter with the start date varying depending on observed winter weather, snow pack and plant condition across the elevation gradient, with the goal of initiating observations at each site prior to the onset of key phenophases (e.g., bud swell) of focal plant species. In 2015, only a subset of seven sites were visited due to budget and time limitations. To reduce bias in cross-site comparisons due to observations occurring on different days of the week (it was generally not logistically feasible to visit all sites on the same day, but visits were scheduled to occur within a one to four-day window), all observation dates were standardized to the midpoint of each week. Weeks were defined as day of year weeks rather than based on the calendar of each year, meaning regardless of what day (i.e., Monday, Tuesday) the year began on, the mid-point of the first week of the year is day of year 3, and the mid-point of week two is day of year 10. Occasionally, individuals would exhibit significant development over the course of a week, resulting in missed scores for particular phenophases. For example, a plant may be observed at bud swell one week, and have emerging leaves the subsequent week, with bud break occurring sometime in the interim. In such cases, we estimated these missed scores by splitting the difference between each observation (e.g., if bud swell was observed on day of year 30 and emerging leaves were observed on day of year 37, we interpolated that bud break occurred on day of year 33). No attempt was made to

estimate the timing of phenophases that occurred prior to the first visit of each year, or after the last summer visit.

Data processing

QAQC was conducted on all temperature data collected. All data were averaged into hourly segments and run through python (Frey et al. 2016b, Johnson and Hadley 2017) to identify and flag impossible values, periods of missing data, and when sensors were buried by snow. We then further checked the data via manual QAQC and compared values to those from nearby temperature stations to identify any erroneous snow flags (i.e. data flagged as snow burial when there was no snow at that site), as well as temperature spikes, missing data, and other questionable values not identified by automated QAQC. To produce cumulative measures of temperature forcing, all data flagged for removal (sensor error, impossible values, missing data, snow burial), were filled via regressions using nearby long-term temperature stations (Daly and McKee 2016a, 2016b) (Appendix S1: Table S2). All regressions used to interpolate temperature data had an adjusted R^2 of 0.97 or greater, and most (11 of 16) came from stations 25-200 m from the phenology plot. Growing degree days were calculated by summing all degree hours greater than 5° C accumulated over a 24-hour period and dividing that sum by 24 to get the average daily accumulation of growing degree days for a given microclimate (Murray et al. 1989, Heide 1993). Starting from December 1, we added each subsequent daily accumulation of degree days. This allowed us to estimate the total growing degree days accumulated on April 1 as an indicator of winter and spring temperature forcing. We also used the winter anticyclonic-cyclonic index (A-C index) developed by Daly et al. (2010 and unpublished) as an indicator of year to year variability in regional winter (Dec 1 – Mar 31) weather patterns. This index, calculated by subtracting the number of cyclonic (stormy/low pressure) days from the anticyclonic (clear/high pressure) days, has been shown to correlate strongly with patterns of cold air pooling and temperature inversions using methods described by Daly et al. (2010). We used data from two permanent meteorological stations on the Andrews to compare temperatures at high elevations (out of temperature inversions) and low elevations (typically beneath winter temperature inversions) to confirm the presence of winter cold air pooling events. Our assumption was that cold air pools were likely present if the lower elevation sites

deviated from normal at a lesser rate than higher elevation sites, meaning that the lower sites had temperatures that were decoupled from the regional conditions while the higher sites were not.

Analysis

Data analysis was conducted using R statistical software (version 3.3.2) and R studio (version 1.0.153) (Appendix S3). For microclimate analysis, we compared local and regional climate with a variety of temperature and climate metrics. We created linear models to regress elevation against bud break and flowering; the assumptions of linear models were checked for each model, and data were transformed where necessary to meet assumptions of normality. Additionally, collinear temperature variables (Appendix S1: Table S3) were condensed using principle components analysis (PCA) to compare microclimates between years and across sites; all assumptions of a PCA were tested.

Results

Microclimate

From 2009 to 2016, there was a large amount inter-annual variability both within and across sites. To see how the climate during phenology years compared to other years at the Andrews, we looked at temperature data from two historic reference stands with contrasting elevations and topographic positions (RS02, 478m and RS04, 1300m) associated with phenology sites. We found that from 1970 until 2015, growing degree days (GDD) accumulated between December 1 and March 31 (hereafter, winter) fluctuated greatly between years (Figure 2a), as did the winter A-C index (Figure 2b). 1982 had the lowest A-C index (-7) and the winter GDD at both the high and low elevation sites is nearly 0, with little difference between the two sites. In contrast, 2015 had an A-C index of 44 and growing degree days at both sites are well above 100. That year, RS04 (the high elevation site) accumulated more GDD than any other year in the 46-year record. Data from all 16 phenology sites over the course of this study also showed this strong inter-annual variation in climate (Figure 3a, Appendix S1: Table S4, S5).

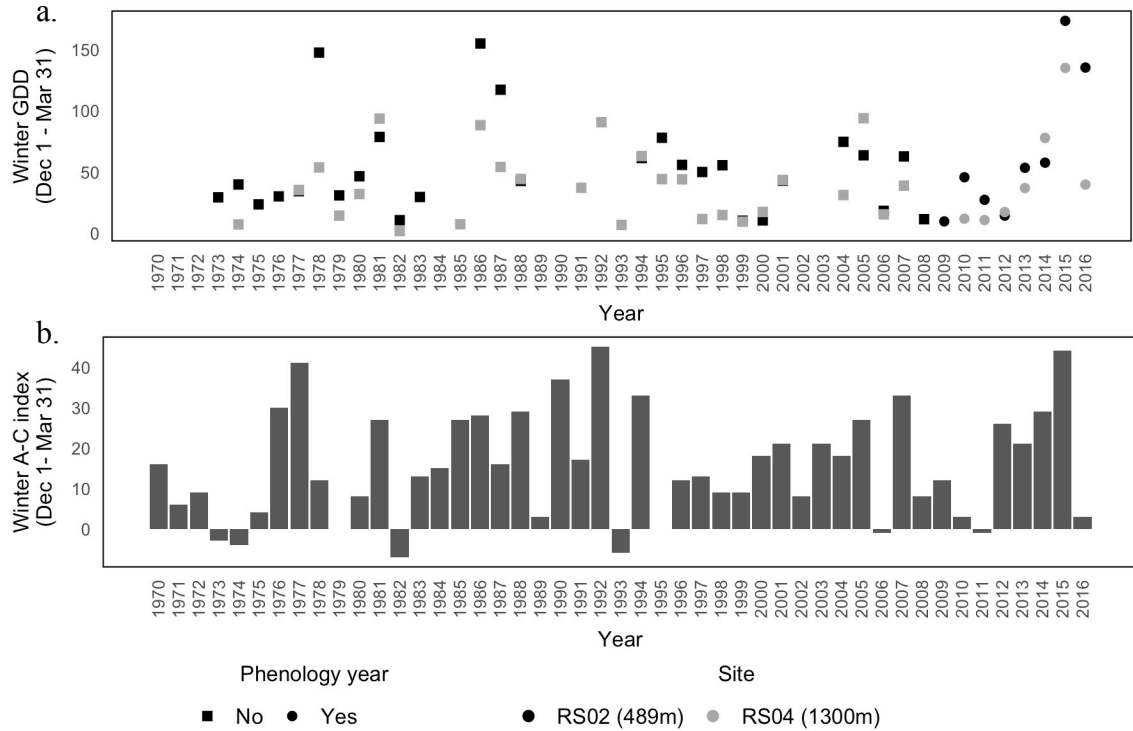


Figure 2: Historic winter climate at high and low elevation sites at the H.J. Andrews. (a) Winter A-C index values for the entire Andrews watershed from 1970 until 2016. (b) Winter growing degree days between 1970 - 2016 from two reference stands at the H.J. Andrews. In figure (a), squares indicate years without phenology surveys, and circles indicate years included in the phenology dataset. For both figures, grey indicates data from reference stand 2 (RS02), which is located at 489 m in an old-growth forest. Black indicates data from reference stand 4 (RS04), which also located in an old-growth stand, but at 1300 m. Years with incomplete data were not included in either figure.

To confirm the presence of winter temperature inversions, we compared data from two permanent meteorological stations (PRIMET 436m, UPLO 1284 m) to the 30 year average (179 – 2008), and found that years with lower AC indices (2010, 2011, 2016) tended to have winter temperatures that deviated similarly from normal at both high and low elevation sites (Figure 3b). In 2011 and 2016 (low AC indices), the high elevation site deviated only 0.35 and 0.35 more from normal than the low elevation site. In 2014 and 2015 (high AC indices), the mean winter temperature at the high elevation site deviated 0.07 and 3.35 degrees above normal while the low elevation site was 0.8 degrees below normal in 2014 and 2.1 degrees above normal in 2015 (a difference of 0.87 and 1.25 between high and low sites). This is likely due to cold air pooling events buffering temperatures low elevation sites during years with high AC indices. Sites with high

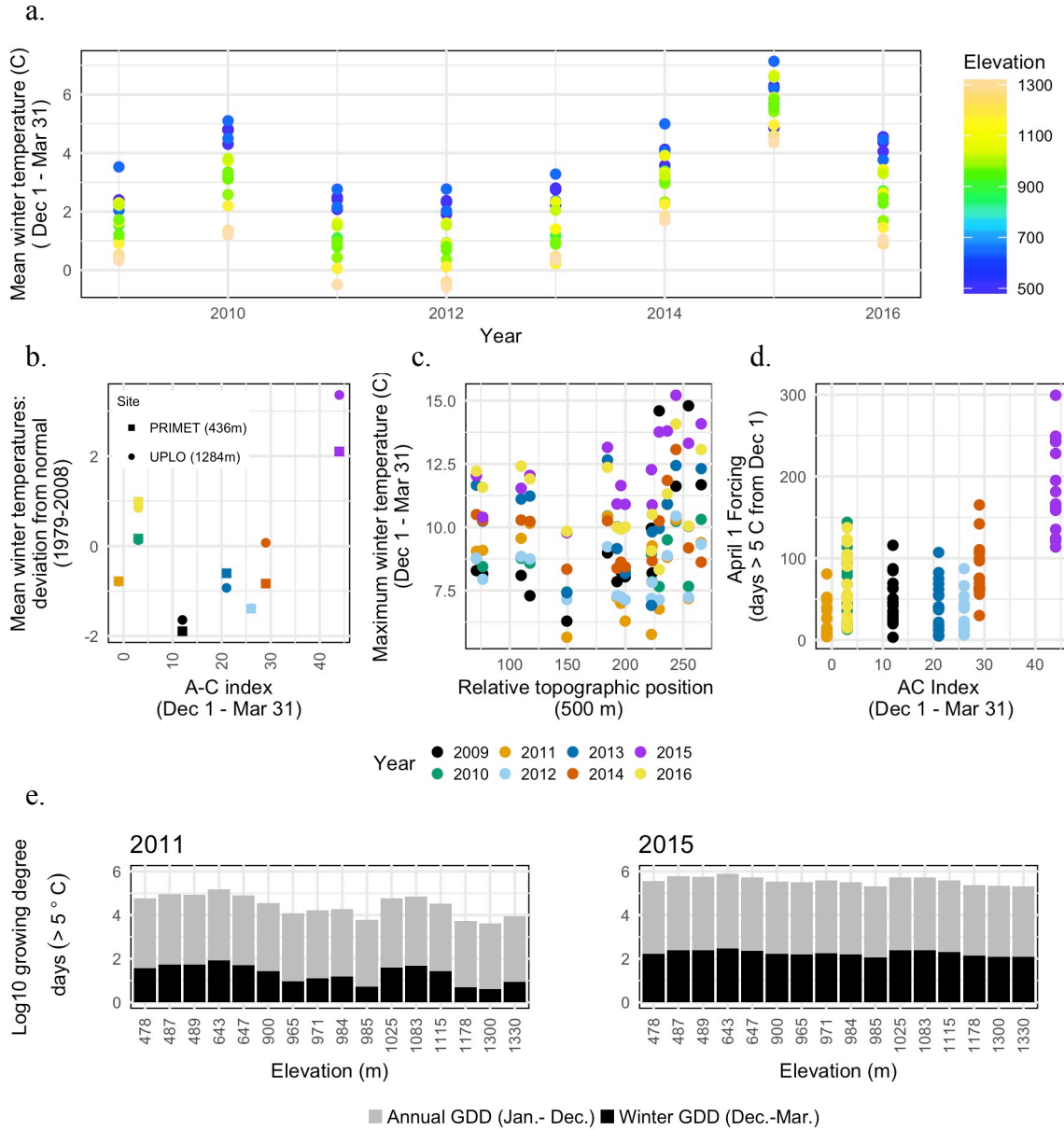


Figure 3: Microclimate patterns between 2009-2016. (a) Mean winter temperatures at all sites. Colors represent elevation, with low elevation sites in blue, high elevation sites in yellow. Intermediate elevations are in green. (b) Difference from the 30-year average (1979-2008) of mean winter temperatures at two permanent meteorological station at the HJA relative to the winter AC index. PRIMET is a station near the Andrews headquarters and is at 436 meters; it is represented by filled squares. UPLO is a high elevation site at 1284 meters and is represented by circles. (c) Maximum winter temperature relative to topographic position. Colors represent year while each point is a site during a given year. (d) GDD accumulated on April 1 at each site relative to the winter AC index. Colors are different years, while each colored point represents a different site during a given year. e.) Winter and annual GDD at all sites in 2011 and 2015. Grey bars are GDD accumulated between January 1 and December 31 at each site, while black bars are GDD accumulated between December 1 and March 31 at each site.

relative topographic position also saw greater variability in maximum winter temperature than sites with low topographic position (Figure 3c), another indicator that cold air pooling buffered winter temperatures from regional warming. In the eight years when phenology surveys occurred, 2011 and 2015 represent the coolest and warmest years respectively. We used a two tailed, unpaired t-test to compare 2011 and 2015 conditions and found that in 2015 all sites accumulated significantly more growing degree days by April 1 ($p < 0.001$, $t = -10.62_{(df=19,865)}$) than in years with a lower A-C index like 2011 and there was less difference in winter growing degree day accumulation between high and low elevation sites in 2015 compared to 2011 (Figure 3d). In 2015, sites 500 meters apart in elevation accumulated the same amount of growing degree days (242.6 and 242.7) between Dec 1 and Mar 31.

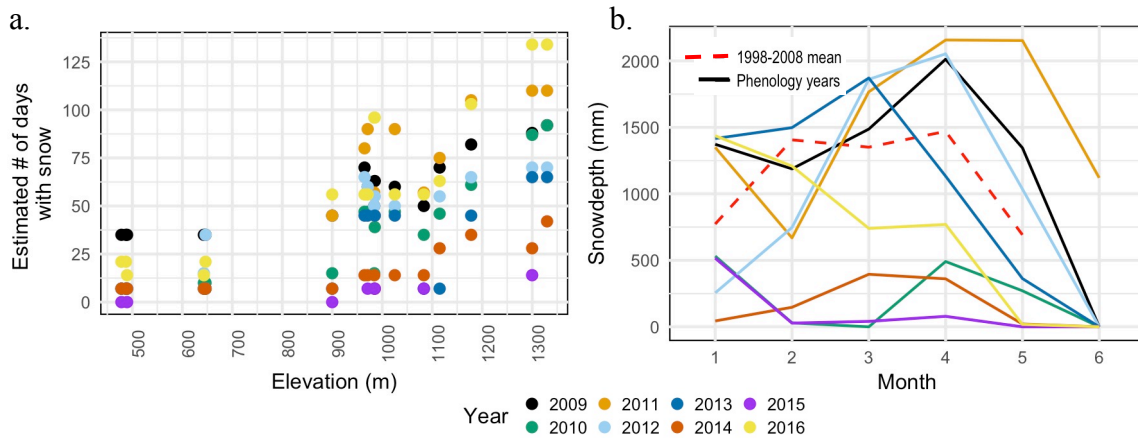


Figure 4: Snow depth during the phenology years. (a) Estimated number of days of snow at each phenology site in a given year. Data was estimated using observations and nearby meteorological stations and snow stakes. Colors represent years, while each point is a site in a given year. **(b) Snow depth at a high elevation meteorological station (VANMET, 1285 m) on the first of each month between January and June.** The red dashed line is the 10-year average from 1998 to 2008, and the solid lines are phenology years. Colors are different years.

Snow was highly variable across all year (Figure 4). In 2015, most precipitation fell as rain, resulting in minimal snowpack even at the highest elevations on the Andrews (Sproles et al. 2017). In 2011, snow persisted well into June at the 1284 m meteorological station, while all of the other years had little to no snow by June 1. The first date where 0% of plants were buried under snow was on average 94 days earlier in 2015 than 2011 (Appendix S1: Table S6). One mid-elevation site (PC15, 971m) had all plants exposed at least 144 days earlier in 2015 than in 2011.

Finally, we used a principle components analysis to compare collinear temperature variables (Figure 5). The first two principle components of the microclimate PCA explained 73.3% of the variance in microclimates between sites and years. The first principle component explained 63.0% of the variation among sites and years, and primarily separated sites by mean seasonal (Fall: Oct-Dec, winter: Jan-Mar, spring: Apr-Jun and summer: Jul-Sept) mean annual (November 1 to October 31) temperature and April 1 GDD (from Dec 1). The second principle component explained 10.3% of the variance between site microclimates, and primarily separated sites by fall average (89.4% of the axis). We used best subsets to select a model using physical variables to predict principle component 1 (Appendix S1: Table S9), and were able to predict 73.1% of the variance in PC1 using aspect, slope, elevation, topographic index and winter AC index ($F_{(5,122)} = 66.39$, $p < 2.2e-16$). Winter AC index alone explained 23.3% of the variance ($F_{(1,126)} = 38.19$, $p = 8.2e-9$) and elevation explained 38.3% of the variance in PC1 ($F_{(1,126)} = 78.24$, $p = 6.9e-15$).

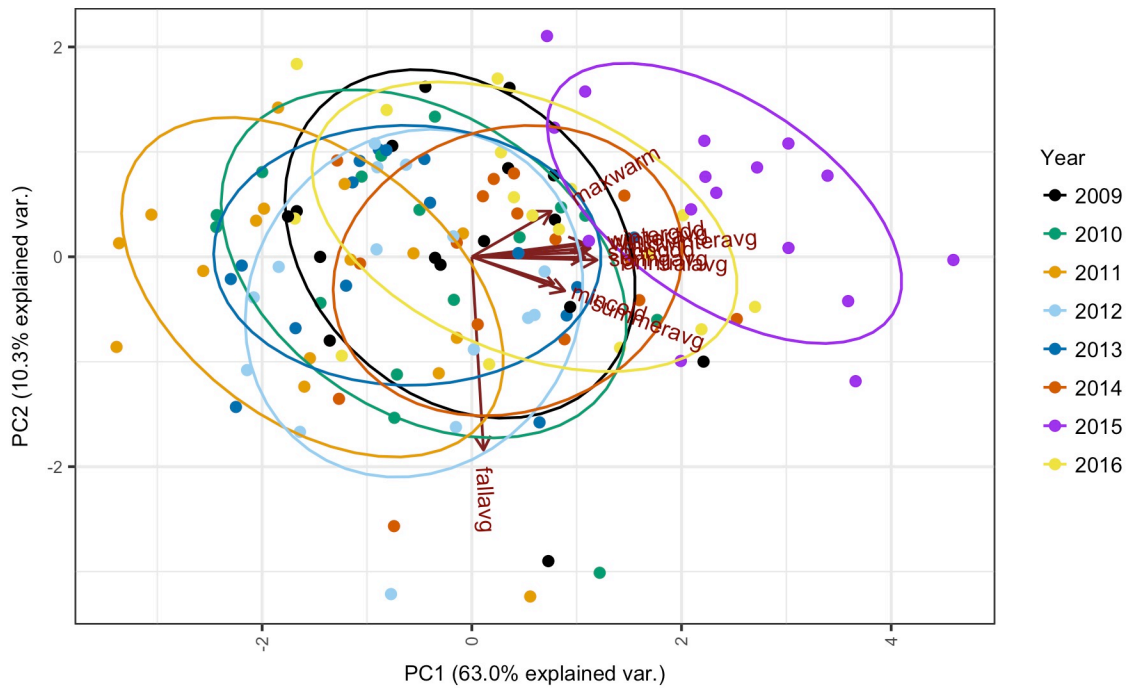


Figure 5: A principle components analysis of temperature variables at all 16 sites between 2009 and 2016. Ellipses represent 95% confidence intervals. Colors represent years and each point is a site during a given year.

Phenology

Plant phenology generally tracked the inter-annual variability of microclimates, although individual species varied in their responses to microclimate differences. The general pattern of relatively early bud break in warm years and late bud break in cold years was consistent across all focal species and sites (Figure 6; Appendix S1: Fig S1). We saw a loss of diversity in the timing of bud break in years with a higher AC index

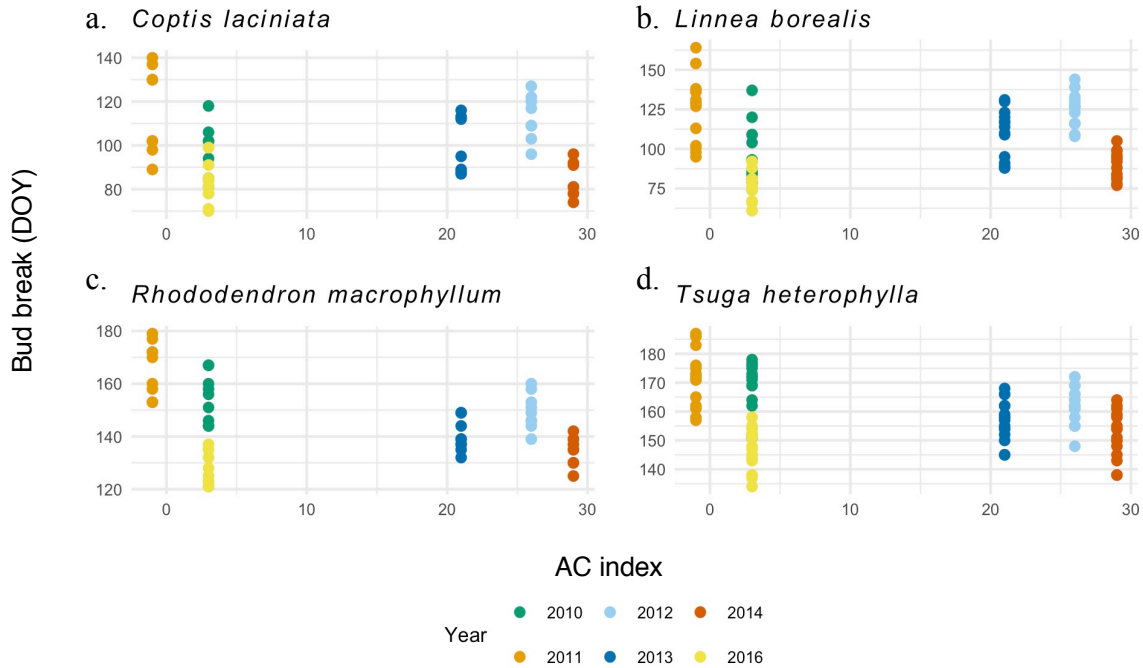


Figure 6: Day of year of bud break relative to AC index. (a) *C. laciniata* (b) *L. borealis* (c) *R. macrophyllum* and (d) *T. heterophylla*. Colors are year. 2009 and 2015 are not included due to limited sample sizes for a visual comparison of the diversity of bud break.

especially in herbs and shrubs. *Coptis laciniata* and *Linnea borealis* are both herbs, *Rhododendron macrophyllum* is an understory shrub and *Tsuga heterophylla* is a mid-canopy tree.

We explored how elevation affected bud break among individual species across sites and years, by regressing bud break against elevation, and found that in 2015, elevation was a non-significant predictor of bud break in 10 of 14 species (Appendix S1: Table S10). For example, in 2009-2014, and in 2016, elevation predicted between 52% and 86% of the variance in the timing of bud break for *A. circinatum*, but there was no relationship in 2015 (Figure 7a). In contrast, elevation was a significant predictor of bud break for all years for the conifer *Pseudotsuga menziesii* (Douglas fir), and elevation

predicted 94% ($F_{(1,5)}=87.73$, $p < 2.3e-4$) of the variance in bud break during 2015, the highest adjusted R^2 of any year for that species (Figure 7b). This retention of the elevational gradient in the timing of bud break in 2015 was seen in only 4 of 14 species modeled including *Trillium ovatum* (Figure 7c), while 10 of 14 species (including *Vaccinium parvifolium*) saw a complete loss of elevational gradient in bud break (Figure 7d; Appendix S1: Fig S1).

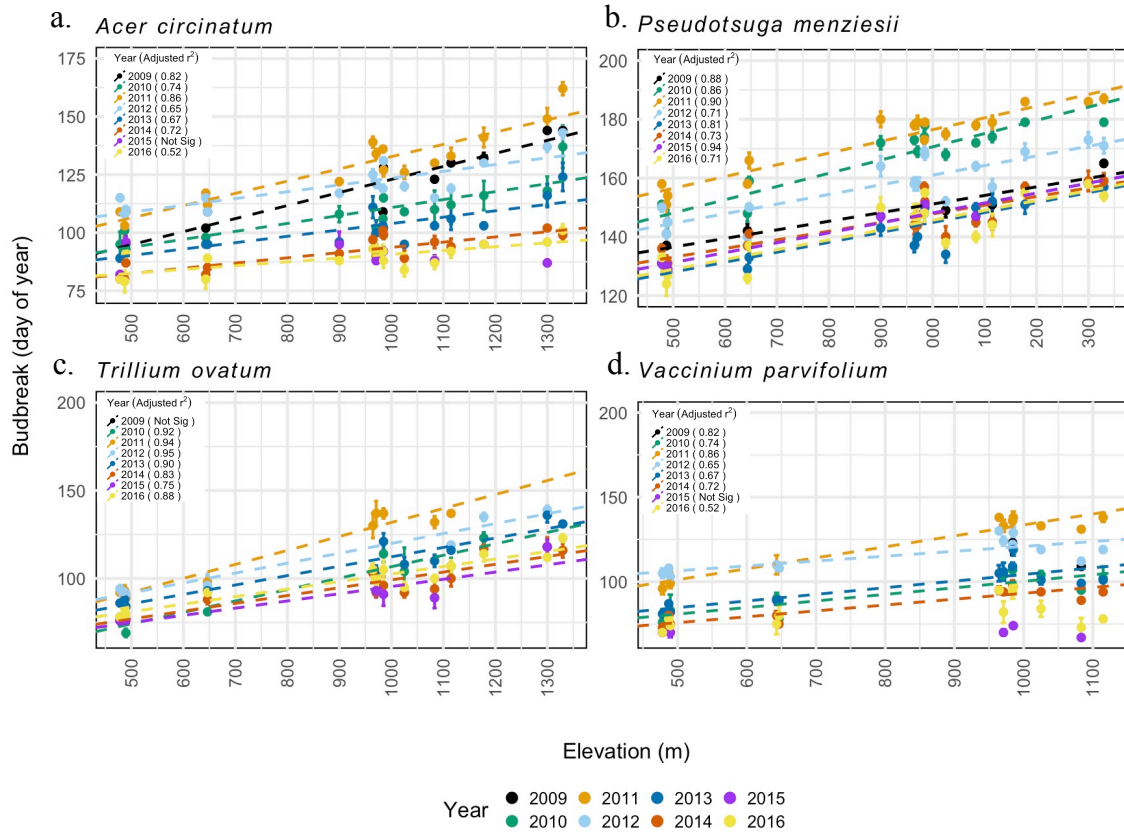


Figure 7: Elevation as a predictor of the timing of bud break. (a) *A. circinatum* (b) *P. menziesii* (c) *T. ovatum* and (d) *V. parvifolium*. Error bars are \pm SE, colors are year.

Because 2011 and 2015 represented the extremes in terms of winter climate conditions, we contrast patterns in these two years in many of the figures that follow to illustrate the magnitude of phenological response and variability across the elevational gradient. We saw a median advance of bud break for all species of 37.5 days in 2015 when compared to 2011. The most extreme advancement in bud break occurred at PC09 (984m), where *Viola sempervirens* (violet) broke bud 85 days earlier in 2015 than in 2011 (Appendix S1: Table S7). However, the degree of advancement of bud break was

both species and site specific; e.g., *V. sempervirens* showed as little as 15 days difference between years at a low elevation site (PC01).

Flowering data were limited to those species that regularly flowered over the course of the study, and many of the individuals grow in dense, heavily shaded stands with little opportunity for major reproductive output. Sufficient data (three or more observations at each site, and three or more sites per year) exist for *A. circinatum*, *Vaccinium parvifolium* (red huckleberry), and *Trillium ovatum* (trillium) to regress the date of peak flower against elevation. Elevation was an inconsistent predictor of variance in the flowering time of *A. circinatum*. We often observed *A. circinatum* flowers aborting/dying prior to reaching peak flowering, which tended to result in low sample sizes and may explain the inconsistent effect of elevation. Elevation explains a large amount of variance in the date of peak flower for *V. parvifolium* during years with typical winter weather, but the elevational gradient is lost in years with low snow like 2015. (Figure 8a). The elevation gradient appears to remain a powerful signal regardless of snowpack for *T. ovatum* (Figure 8b). Both of these species have flowers emerge from rolled leaves, and both species appear to have synced bud break and flowering trends.

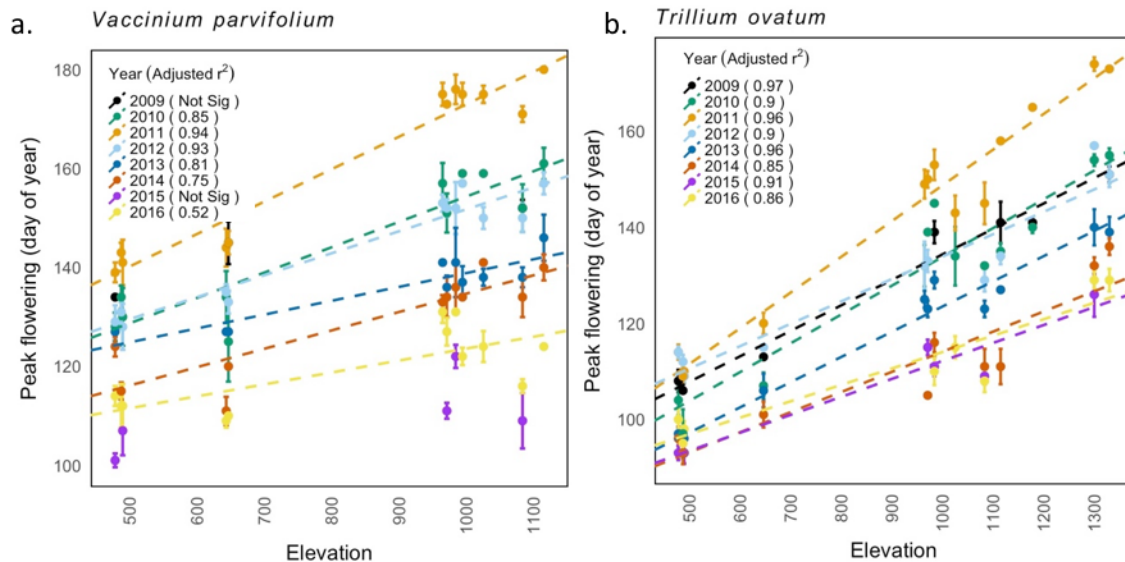


Figure 8: Elevation as a predictor of the timing of peak flowering. (a) *V. parvifolium* and (b) *T. ovatum*. Error bars are \pm SE.

Discussion

Microclimate is a strong driver of local plant phenology. We found that the combination of unusually warm and dry conditions and the decoupling of areas of low topographic relief from the regional climate patterns can lead to a homogenization of microclimate and spring phenology events in mountainous regions like the Western Cascades. A small number of physical variables explained variation in temperature, especially during winter and spring. Each plant species had a unique response to microclimate variability, and there was considerable variation across and within years. Relatively cool, snowy conditions during winter and early spring led to delayed onset of spring plant phenology (bud break), while relatively warm and dry winter and spring conditions led to an advancement in the onset of spring phenology, especially at upper elevations. In the future, winter and springs with fewer storms, less snowpack, and warm temperatures will likely have advanced bud break across most, if not all species. If areas of low topographic relief are consistently decoupled from regional conditions, and high elevation sites have limited snowpack, there will likely be a homogenization of spring phenology events across the elevation gradient, mainly due to extreme advances at upper elevation sites, especially for herbs and shrubs. A recent study that found similar results where bud break of four European trees advanced ~ 1.9 days per decade from 1960 to 2016 at high elevations (>808 m), and only ~ 0.4 days per decade at low elevations (<522 m) (Vitasse et al. 2018).

Tradeoffs exist for an individual experiencing advanced or delayed bud break (Lockhart 1983, Saxe et al. 2001). Plants that break bud early are subject to a lower solar angle and fewer overall day light hours. This means that primary productivity is limited, and the plant is at risk for frost damage and snow burial, especially at higher elevations (Inouye 2008). We often observed individuals with frost damage on new leaves during years of advanced bud break. If frost damage does not occur, a plant that breaks bud early has a longer growing season, which may result in increased fitness due to greater resource storage, or the plant may be more susceptible to early season drought due to the relatively warm conditions that initiated advanced bud break. In 2015, the warm and dry winter and spring and extraordinarily low snow pack (Sproles et al. 2017) led to early and prolonged drought conditions, reflected in some of the lowest summer flows on record in

Lookout Creek (Johnson and Rothacher 2016). Later bud break and flowering may also result in fewer incidences of fruit set due to less pollination, or less resource allocation towards reserve storage for the winter dormancy period and the following growing season (Rathcke and Lacey 1985, Chapin III et al. 1990, Kreyling 2010).

While our study focused on the herbs, shrubs and trees of the Western Cascades, the effect of advanced phenology is not limited to a single trophic level, and the negative effects of trophic asynchronies have been documented around the world (Parmesan 2006). Insects that depend on new fragile leaves for easy meals may emerge after peak leaf expansion, or after frost damages newly emerged leaves, and find themselves with limited food sources (Visser and Both 2005). Birds dependent on such insects may have less food for themselves and their young. Pollinators may emerge and become active after peak flowering, resulting in less fruit production for the plant, and less food for the pollinator. This in turn could lead to less food for birds and other animals dependent on berry producing species. Areas of topographic heterogeneity typically display a strong gradient in spring plant phenology (Hwang et al. 2011), which may mitigate the effects of regional warming and reduce for mobile organisms like birds or mammals (Gaudry et al. 2015, Frey et al. 2016a). However, in years like 2015, the timing of spring plant phenology became much less varied across microclimates, and it is possible that such loss of variation could lead to more widespread consequences and trophic asynchronies than a relatively cool (late) year in which early season microclimate and phenological diversity are maintained (e.g., 2011). A diverse spread of bud break and flowering events means a longer window of food availability for species able to move from sites with early spring phenology, to sites that begin the growing season later in the year. Losing the diversity across microclimates creates potential for fewer resources for migrants and other mobile species dependent on a varied patchwork of spring flowering and growing seasons.

Since 1979, the northern hemisphere has warmed by 0.33° C per decade (IPCC 2007), and annual average temperatures in the Pacific Northwest are projected to increase by an additional 1.8° C by the 2040s and 3.0° C by the 2080's (Mote and Salathe Jr 2010). This will likely result in more winter precipitation falling as rain and less as snow (Sproles et al. 2013, 2017), and an increase in the range of the transient snow zone, in which snowpack varies throughout the season due to repeated melting and

accumulation) (Mote 2006). Since the 1950s, 92% of snow courses in the western United States have shown negative trends in snowpack (Mote et al. 2018). Lute et al. (2015) predict a reduction of up to 60% of the April 1st snow water equivalent in the Western Cascades, and Sproles et al. (2017) suggest that patterns of snowpack seen in 2014 and 2015 are likely to become more common as warming trends continue. Some models suggest that storms may become less frequent and more severe, resulting in longer windows of clear anticyclonic weather between storms (Pepin et al. 2011). Years with long periods of clear winter weather (e.g., 2015) can lead to persistent temperature inversions in mountainous areas like the Andrews, and valleys and drainages affected by these inversions will have temperatures consistently around freezing (Daly et al. 2010, Pepin et al. 2011, Novick et al. 2016). In contrast, during the same cold air pooling events, upper elevations and ridgelines will be above the inversion and be exposed to consistently clear, sunny weather (Pepin et al. 2011). The combination of less precipitation as snow and more persistent temperature inversions will likely result in a loss of diversity in the timing of spring phenology similar to the pattern we see when comparing the distribution of phenological events in 2015 and 2011. Our data suggest that in the Western Cascades (as opposed to the higher elevation High Cascades, which may not experience a significant decrease in snow pack (Mote 2006), years with little to no snowpack like 2015, and persistent cold air pools will have much greater effects on the mountain communities situated in upper elevation sites and sites of high topographic relief than those communities situated in drainages and lower elevation valleys, and that understory species are more likely to have significant shifts in phenology than overstory trees. Additionally, because sites with less vegetation biomass are less buffered against temperature extremes than sites with old growth characteristics and high biomass (Frey et al. 2016a), understory communities in upper elevation plantations in the Western Cascades will likely have the greatest shifts in phenology due to changes in regional climate patterns. Long term, high resolution (both spatially, i.e. <1km², and temporally, i.e. > 2 years) studies such as this one are needed to capture the effects of a warming climate on forest and mountain communities, and to inform managers of vulnerable areas in need of protection. The snow pack of 2015 has been described as “extraordinarily low” (Sproles et al. 2017), and we were fortunate to capture such an

extreme year; a typical two year study would likely have missed the inter-annual variability we captured across the eight years of phenology surveys. As the effects of climate change become more severe, it will be important to understand how regional patterns affect microclimates, and how that in turn affects community dynamics. Identifying which areas across landscapes more and less susceptible to climate change, and the processes responsible for those patterns, is the first step in managing for future conditions (Lawler 2009, Morelli et al. 2016, Lenoir et al. 2017).

CHAPTER III

BRIDGE

The first half of this thesis explained the nuances of inter-annual variability and showed that changes in regional climate patterns (i.e., AC index) have a strong effect on the distribution of microclimate and spring phenology events across the Andrews. I wished to further explore the connection between microclimate and spring phenology and chose four species from the original 18 to develop models with the capacity to predict bud break. I had two goals with this second chapter: 1) to create models that could accurately predict observed bud break using only microclimate variables (i.e., no physical drivers like elevation); and 2) to upscale those models to the landscape level to remotely predict bud break across a wide region.

CHAPTER IV

MODELING BUD BREAK AND MICROCLIMATE

Acknowledgements

This chapter contains co-authored material written by Sarah Ward, Mark Schulze, Bitty Roy.

Introduction

The timing of seasonal plant activity (phenology) is often used as an indicator of a community's response to changes in climate, and in particular, the timing of bud break in plants is a simple and common metric of the onset of spring (Walther et al. 2002). Many studies have found a relationship between rising global temperatures and an advancement in the timing of spring bud break (Parmesan and Yohe 2003, Visser and Both 2005, Parmesan 2006, Menzel et al. 2006, Thackeray et al. 2016), however modeling the effect of climate change on communities across a landscape can be difficult due to the species-specific climatic requirements needed to initiate bud break (Kramer 1994, Chuine et al. 1998, 2000, Cleland et al. 2007). Inter-annual climate variability is a constant for nearly every terrestrial plant in the temperate region, and plants have adapted numerous strategies to avoid breaking bud too early or too late (Kreyling 2010). It is well established that bud break for most species is sensitive to temperature forcing (typically measured as the sum hours above a set temperature threshold, typically 5° C, starting in early winter) (Perry 1971, Polgar and Primack 2011). Many temperate species are also known to require a set amount of chilling units (often defined as degree hours between 0 and 5° C), in addition to accumulating forcing units (degree hours above a set threshold, typically 5° C) that will initiate for the onset of bud break (Hänninen 1995, Bailey and Harrington 2006). This strategy requires a certain period of cold weather before warm weather has an effect on the plant, which prevents the onset of bud break during mid-winter warm spells and mitigates the risk of frost damage to leaves (Heide 2003). However, while recent advances in phenology research have improved our understanding of species-specific bud break requirements (Chiune 2000), the exact physiological requirements of the majority of plants are still unknown (Fitter et al. 1995). Additionally,

even well studied species like *Pseudotsuga menziesii* (Douglas fir) could have local adaptations that lead to physiological differences from what is established in the literature (Bennie et al. 2010).

Advances in remote sensing and modeling techniques have led to an increase in predictions of future phenological shifts due to climate change (Chuine et al. 2000, Reed et al. 2003, Cleland et al. 2007, Buitenwerf et al. 2015). However, the climate a plant experiences is generally at a scale of less than 100m (microclimate), and is strongly affected by local topography and other physical features (Potter et al. 2013, Frenne et al. 2013, Morelli et al. 2016, Frey et al. 2016a). These microclimates can be divergent, or even decoupled from regional weather patterns (especially in winter and early spring) and can make it difficult to predict localized patterns of bud break using low resolution (i.e. >1km) spatial and climate data (Daly et al. 2010, Pepin et al. 2011, Novick et al. 2016, Lenoir et al. 2017).

We were interested in whether we could use microclimate variables to develop species-specific models of bud break for four species native to the Western Cascades using nine years of phenological observations from sixteen sites. Douglas fir, *Acer circinatum* (vine maple), *Vaccinium parvifolium* (red huckleberry) and *Trillium ovatum* (Pacific trillium), are all common native species found in the Western Cascades. Douglas fir is an over story tree that is the dominant species in much of the region (Spies et al. 1990). Vine maple and red huckleberry are both common shrubs that are typical in the understory of both old growth and second growth forests (Brown 1969, Gholz et al. 1976, Agee and Kertis 1987, Kerns et al. 2004), and Pacific trillium is a common herb found across a variety of elevations in the Western Cascades (Brockway et al. 1983). We hypothesized that species-specific models developed at the local scale could be applied to predict bud break across the landscape (Chuine et al. 2000). We hoped to develop models could be used to investigate the local effects of potential shifts in regional climates, such as reduced snow pack, increased temperatures and fewer days of precipitation and cloud cover (Mote 2006, Mote and Salathe Jr 2010, Sproles et al. 2013, Lute et al. 2015).

Areas of heterogeneous topography are known to have a diversity of microclimates (Pepin et al. 2011), which result in a diversity in the timing of

phenological events (Vitasse et al. 2018). These microclimates allow for a longer period of resource availability for organisms that can move with the phenology gradient (Frey et al. 2016a). Additionally, numerous studies have suggested that the microclimate diversity within mountainous areas can buffer against the effects of climate change and that during the glacial and interglacial periods, these buffered areas acted as micro-refugia for biodiversity (Peterson et al. 1997, Dobrowski 2011, Lenoir et al. 2017). While it is uncertain that such buffers will remain stable enough to act as micro-refugia in the future, evidence is mounting that certain microclimatic features maintain cooler conditions despite current patterns of regional warming (Pepin et al. 2011, Frenne et al. 2013, Frey et al. 2016b, Morelli et al. 2016, Frey et al. 2016a). Frey et al. (2016b) found that while high elevation sites in the Western Cascades are typically cooler, and accumulate fewer growing degree days between January and March, vegetation and topography were the dominant factors driving growing degree day accumulation during that part of the year. They also found that old growth stands in the Cascade region reduced both the maximum temperature of the warmest month and the average maximum monthly temperature from April to June when compared to closed-canopied plantations (40-60 years old). Given that the phenology of many plant species responds to late winter and early spring temperature forcing (Lavender 1991), this microclimatic buffering of temperature (driven by topography and vegetation) has the potential to mitigate the advancement of phenological events due to regional warming. Models that are developed at the local and landscape scale (rather than downscaling regional models) will be more accurate when identifying microclimates that may be less susceptible to future shifts in regional climate patterns.

Methods

Study area

The H.J. Andrews Experimental Forest is a 6400-hectare (15,800 acre) forest located on the west side of the Cascade Mountains in central Oregon. The area is representative of the Cascade Range, with steep mountainous terrain, exposed ridges and sheltered valleys, and a high degree of topographic heterogeneity with elevations ranging

from 410 to 1630 m. Vegetation is primarily a combination of 150-500 year old mixed conifer forests, and 40-60 year old *Pseudotsuga menziesii* (Douglas fir) plantations.

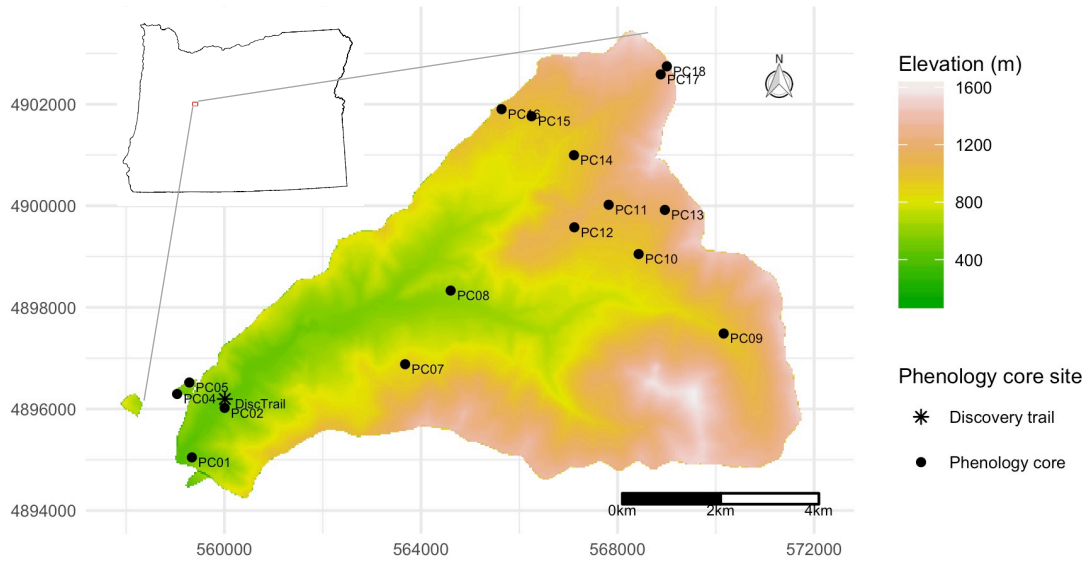


Figure 1: A digital elevation map (dem) of the H.J. Andrews Experimental Forest. Circles triangles are the 16 core phenology sites and the asterisk is the location of the Discovery trail. Phenology core sites are labeled with PC and the site number. Color represents elevation, with greens as low elevation sites and light browns as upper elevation sites. Yellows are intermediate elevations

Study design

For the initial phenology study, sixteen sites (core phenology sites) were selected across a variety of elevations and aspects, with sites ranging from 460 to 1339 meters (Appendix S2: Table S1). An additional site (discovery trail) was later added as part of an educational trail, and we used this site, along with 2017 data from the core phenology sites, to validate the bud break models we discuss below (Figure 1). Eighteen species of native herbs, shrubs and trees were permanently marked as target species, and individuals were typically located within 25 m of a center post (occasionally one or two were located up to 35m away to have 5 representatives of each species within a plot). This paper focuses only on four of those species: *Acer circinatum* (Vine maple), *Pseudotsuga menziesii* (Douglas fir), *Trillium ovatum* (Trillium) and *Vaccinium parvifolium* (Red huckleberry). We chose these four species because they are common representatives of three functional groups (trees, herbs and shrubs) at the Andrews, and we had a large number of observations of bud break for each species across the study area. Additionally, vine maple and other deciduous shrubs have been shown to support higher levels of

animal and insect diversity and are key factors in within year avian occupancy at the Andrews (Hagar 2007, Ellis and Betts 2011, Frey et al. 2016a).

Understory air temperature was the primary microclimate variable recorded. To capture the temperature of each site, HOBO (Onset Corporation, Hobo U22-001; accuracy 0.2°C) temperature sensors were placed 1.5 meters above the ground facing south in the center of each plot, and temperature data were collected every fifteen minutes. To reduce temperature spikes due to solar radiation, the sensors were placed in the shade, beneath a PVC shield (20.32cm long piece of 7.62 cm schedule 40 pipe split in half lengthwise). Temperature data were assessed for accuracy by comparing phenology data to nearby permanent monitoring sites (Daly and McKee 2016a, 2016b) with long term temperature records. Erroneous data was replaced with data regressed from permanent monitoring sites (Appendix 1, Table S2). Observations of snow depth were made during each visit, however, depth was estimated so only presence or absence data can be used reliably.

Surveys

We developed a species-specific scoring system for vegetative and reproductive phenophases (Schulze 2017). During each spring, sites were typically visited once per week, and each marked individual was scored for vegetative and reproductive growth. In the early years of the study (2009 and 2010), visitations were less consistent, due to concurrent study plot set up and early season site access limitations. From 2011-2017, sites were typically visited once every 7 days. Observations began each year in late winter with the start date varying depending on observed winter weather, snow pack and plant condition across the elevation gradient, with the goal of initiating observations at each site prior to the onset of key phenophases (e.g., bud swell) of focal plant species. In 2015, only a subset of seven sites were visited due to budget and time limitations. To reduce bias (surveys did not always occur on the same day of year each year), all observation dates were standardized to the midpoint of each week, and weeks were defined as day of year weeks (i.e. week three in January begins on 1/15 each year). Occasionally, individuals would exhibit significant development over the course of a week, resulting in missed scores for particular phenophases. For example, a plant may be observed at bud swell one week, and have emerging leaves the subsequent week, with

bud break occurring sometime in the interim. In such cases, we estimated these missed scores by splitting the difference between each observation (e.g., if bud swell was observed on day of year 30 and emerging leaves were observed on day of year 37, we interpolated that bud break occurred on day of year 33). No attempt was made to estimate the timing of phenophases that occurred prior to the first visit of each year, or after the last summer visit.

Modeling bud break:

Final models of bud break were validated using data from the core phenology sites collected in 2017 (not included in the initial model development) and against three years of observations from the discovery trail. These data represent external conditions independent of the original data (internal conditions) used to develop the models. The discovery trail data did not include observations of bud break for Douglas fir, and was not included in the validation of that model. To develop the initial models, we used temperature data (Johnson and Hadley 2017) at each site to calculate forcing, chilling, and frost variables. The two frost variables included were the last day of year when the mean daily temperature was below zero, and the number of days between November 1 and the end of June where the mean daily temperature was below zero. Forcing and chilling units were calculated using models from Harrington et al. (2010), and the chilling variable we included was the day of year at which chilling units reached 1200 (Bailey and Harrington 2006). We calculated two forcing variables, one where forcing units were accumulated beginning on November 1 (in concert with chilling variables) and one where the forcing did not begin to accumulate until the chilling units were greater than or equal to 1200. While the forcing model was developed for Douglas fir trees, we found little literature on appropriate units for the other species, and after initial testing with other established forcing units (namely growing degree days above 5 degrees C and growing degree days above 10 degrees C from January 1), we found both versions of the Harrington forcing model (i.e. simultaneous accumulation and accumulation after a set threshold) to have the most predictive power. We included forcing accumulated on the first of April, May and June from November 1st and after 1200 hours of chilling were accumulated. We also calculated mean April temperature, as an indicator of the relative warmth of the spring regardless of the earlier winter conditions. We used presence or

absence of snow observed during the closet visit to the first of April and the first of May as snow metrics. All data was examined prior to modeling and transformed to reduce skew where necessary.

For vine maple, red huckleberry and trillium, we tested two initial sets of variables (Table 1). We chose to test one model that included simultaneous forcing and chilling, and another that included forcing after chilling, we did not know whether these plants respond to forcing accumulated at the same time as chilling or forcing that does not begin accumulating until after a set chilling unit was reached. For Douglas fir, we included both types of forcing variables in one model, as we only included forcing on June 1, and assumed the model selection would select one of the two forcing metrics.

Table 1: Variables included initial bud break models.

| Vine maple, Red huckleberry and Trillium : Forcing⁺ | Vine maple, Red huckleberry and Trillium : Chilling⁺ | Douglas fir |
|--|--|--|
| Days below 0 | Days below 0 | Days below 0 |
| Last day of year below 0 | Last day of year below 0 | Last day of year below 0 |
| April 1 snow (0 or 1) | April 1 snow (0 or 1) | April 1 snow (0 or 1) |
| May 1 snow (0 or 1) | May 1 snow (0 or 1) | Mean April temperature |
| Mean April temperature | Mean April temperature | June forcing (from Nov. 1) |
| Day of year when chilling units = 1200 | May 1 forcing.chilling x April 1 snow | June forcing (after 1200 chilling units) |
| May 1 forcing ⁺ x April 1 snow | OR | Day of year when chilling units = 1200 |
| OR | April 1 forcing.chilling x April 1 snow | |
| April 1 forcing ⁺ x April 1 snow | | |
| +For vine maple, red huckleberry and trillium four versions of the model were tested: Forcing from November 1 to April 1; forcing after chilling to April 1; forcing from November 1 to May 1; forcing after chilling to May 1. This was due to high correlation between the two months. | | |

All species models were initially reduced using best subsets (rpackage leaps, Appendix S3) which gives two potential models for each number of available variables (i.e., if there are 3 variables, leaps outputs two models with one variable, two with two variables etc.) and a Mallows CP score and an adjusted R² value for each model. We always tested the model with the highest adjusted R² and the lowest Cp score; however if that model had significant multicollinearity (variance inflation factors identified via r base function vif(), Appendix S3), we removed the variable with the highest vif score and tested the reduced model. See Appendix S2: Table S3 for all tested models. We selected

the final model based on the prediction accuracy of observed validation data (Appendix S2: Table S4). Accuracy was determined via the coefficient of determination (R^2) from a linear regression of observed versus predicted dates of bud break. If two models were nearly identical in their predictive power, we favored models that most accurately predicted the discovery trail data, as it was completely independent of the original model development. Assumptions of linear models were checked for each model.

Modeling microclimate

To upscale the models at the landscape level, we needed to predict the temperature variables included in each species model. We used available spatial data (Valentine and Lienkaemper 2005, Valentine and DeSilva 2014, Spies 2015, 2016), to predict all of the microclimate included in each species model and created 30m resolution rasters with each temperature variable across the Andrews for 2009-2016. To model snow, we used snow depth data from an existing network of snow stakes that have been visited approximately once every three weeks during the winter from 1998 to 2014 (Schulze and Levno 2017) and created a binary presence absence variable for the first of each month between December and June. Because the sites were not always visited precisely on the first of each month, we considered any survey that occurred within four days on either side of the first to be representative of the snow depth on the first of the month. We used stepwise logistic regression to select the snow model (rpackage MASS, Appendix S3) with AIC as the selection criteria, and initially included the depth of snow on the date of interest at two permanent meteorological stations (CENMET and UPLMET, 1028 m and 1284 m respectively), aspect, biomass and elevation, and mean monthly air temperature at one low and high elevation meteorological stations (PRIMET, 436 m; UPLMET 1284m) (Daly and McKee 2016b). For all variables except snow, we used multiple linear regression and stepwise model selection. The initial models included observed temperature metrics from the phenology sites as predicted by relative topographic position (i.e. ridge or valley), biomass, slope and elevation, mean temperature at PRIMET and two anticyclonic-cyclonic indices (AC index) (Table S5). The AC index is a metric used by Daly et al (2010) (data courtesy of Chris Daly) and can indicate the frequency anticyclonic versus cyclonic weather systems over a given period of interest and thereby the frequency of temperature inversions. Anticyclonic weather

patterns result in cold air pooling and decoupling of valleys and depressions from regional weather, particularly in winter and early spring. With cyclonic weather systems, temperatures across the Andrews Forest elevation gradient typically conform to expectations based on moist adiabatic lapse rates, whereas in periods with anticyclonic systems, valleys maintain temperatures near freezing, and ridges and slopes are exposed to clear weather and higher daily temperatures due to increased irradiation (Daly et al. 2010, Pepin et al. 2011). Hence, a relatively warm winter with no shift in the AC index would be expected to preserve a strong elevational gradient in average air temperature, whereas a shift in the AC index could result in homogenization of mean or cumulative temperature metrics such as forcing units. We used the AC index from November to May (for June forcing, chilling) and from November to March (for April forcing/April forcing, chilling) as an annual constant that represents the inter-annual variability of regional climate and is an indicator of local climatic decoupling due to cold air pooling. We also included two mean temperature variables (mean April temperature and mean temperature between November 1 and May 31) from the low elevation meteorological station (PRIMET, 436 m), and a snow depth variable for the first of the month for April and May from a mid and a high elevation meteorological station (CENMET, 1025 m; UPLMET 1284 m, MS001) as indicators of the annual conditions (Daly and McKee 2016b). We tested the predicted climate models against four years (2011-2014) of data from 180 sites across the Andrews (Johnson and Hadley 2017). While this validation data set is more spatially robust, we chose to model the phenology temperature data as it is more temporally robust and includes data from all of the phenology survey years. We do not have AC index data for 2017, and so we tested the upscaled landscape models against the observed 2009-2016 phenology core data and discovery trail data.

Results

Bud break models

We successfully developed bud break models for all four species with a range of predictive success, both for internal (original 2009 to 2016 data) and external (2017 and Discovery trail validation data) conditions (Figure 2, Table 2). All four models were quite accurate when predicting the original phenology data and the validation data (Table

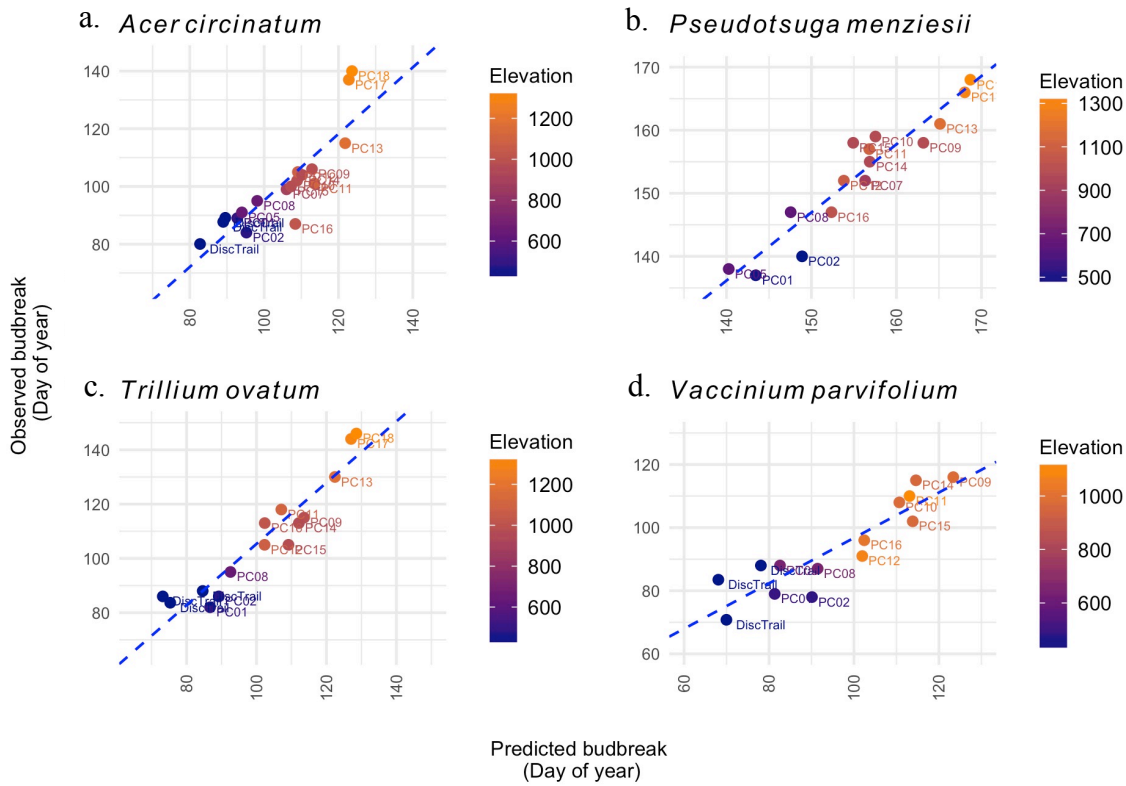


Figure 2: Observed bud break for 2017 and discovery trail data versus bud break predicted by species models. (a) *Acer circinatum*; (b) *Pseudotsuga menziesii*; (c) *Trillium ovatum*; (d) *Vaccinium parvifolium*. Colors are elevation, with oranges indicating high elevation sites, and blues indicating low elevation sites, with reds as intermediate values. Sites are labeled as PC and the site number for phenology core sites or Disc. Trail for the discovery trail.

3). The vine maple model included mean April temperature, total days below and the first day of year where chilling units were greater than 1200. The model explained 73% of the variance in the 2009-2016 data and 74% of the variance in the validation data. The model for Douglas fir was surprisingly simple and only included June 1 forcing after chilling as a predictive variable. The model explained 83% of the variance in the original dataset 90% of the variance in the validation data. The trillium model was also highly successful and included observed presence or absence of snow on April 1, total days below 0 and mean April temperature; the model explained 85% of the variance in the original dataset and 90% of the variance in the validation data. Finally, the model for red huckleberry explained 82% of the variance in the original data, and 81% of the variance in the validation data. This included mean April temperature, the last day of year below freezing and April 1 forcing after chilling.

Table 2: Variables included in each bud break model

| Species | Model variables and coefficients ⁺ | Cp Score | R ² | F-stat | P-value |
|--|---|----------------------|----------------|--------------------------|---------|
| <i>Acer circinatum</i> | Budbreak (DOY) = $e^{(4.67 - 0.04 \times \text{MAT} + 0.04 \times (\sqrt{\text{DB0}}) - 0.03 \times (\sqrt{\text{DOY@1200}}))}$ | 2.79 | 0.73 | 94.72 _(3,107) | *** |
| <i>Pseudotsuga menziesii</i> | Budbreak (DOY) = $179.68 - 0.09 \times \text{JFC}$ | 18.55 ⁺⁺⁺ | 0.83 | 510 _(1,105) | *** |
| <i>Trillium ovatum</i> ⁺⁺ | Budbreak (DOY) = $(10.05 + 0.20 \times \text{A.snow} + 0.48 \times (\sqrt{\text{DB0}}) - 0.25 \times (\text{MAT}))^2$ | 5.42 | 0.85 | 125.1 _(3,64) | *** |
| <i>Vaccinium parvifolium</i> ⁺⁺ | Budbreak (DOY) = $(9.86 + 0.20 \times \text{LD0} - 0.30 \times \text{MAT} - 0.52 \times \ln(\text{AFC}))^2$ | 0.09 | 0.82 | 110.6 _(3,73) | *** |

+ AF = April forcing (from Nov.1); AFC = April forcing after chilling; A.snow = April 1 snow; DB0 = Number of days below 0 between November 1 and June 1; DOY@1200 = First day of year where 1200 chilling hours are accumulated; JFC = June forcing after chilling; LD0 = Last day of year below 0; MAT = Mean April temperature

++ Predictor variables scaled (mean centered) using r function scale() to reduce collinearity; scaling occurred after any transformation of data.

+++ Despite a high CP score, all other potential models had highly correlated variables and R² values that differed only by around 0.01.

Table 3: Model statistics for the 2017 and discovery trail validation data

| Species | R ₂ | F-stat _(df) | p-value |
|------------------------------|----------------|-------------------------|---------|
| <i>Acer circinatum</i> | 0.74 | 45.91 _(1,16) | *** |
| <i>Pseudotsuga menziesii</i> | 0.90 | 112.1 _(1,13) | *** |
| <i>Trillium ovatum</i> | 0.90 | 110.5 _(1,13) | *** |
| <i>Vaccinium parvifolium</i> | 0.81 | 50.78 _(1,12) | *** |

Microclimate models

We were able to successfully model all of the predictive climate variables across the Andrews watershed (Appendix S2: Table S6). The microclimate models explained between 63% and 81% of the variance in the validation data for all variables except for April forcing after chilling (Table 4). The model for April forcing after chilling

explained 35% of the variance in the validation data. For snow, we used a logistic regression, and compared observed snow at snow stake sites between 2014 and 2015 and found that sites with observed presence of snow had a mean probability of 0.64, and sites with no snow had a mean probability of 0.27 (Table S8). We applied the bud break models to the new microclimate rasters and predicted bud break across the entire Andrews watershed, and tested the validity against the 2009 to 2016 observed phenology data (Table S9, Figure S1).

Table 4: Model statistics from validation of microclimate variables.

| Microclimate variable | F-stat _(df) | R ² | p-value |
|------------------------------|--------------------------|----------------|---------|
| April chilling after forcing | 282.6 _(1,533) | 0.35 | *** |
| DOY chilling above 1200 | 889.4 _(1,533) | 0.63 | *** |
| Mean April temperature | 2325 _(1,533) | 0.81 | *** |
| Days below 0 | 891.3 _(1,533) | 0.63 | *** |
| Last day of year below 0 | 1023 _(1,533) | 0.66 | *** |
| June forcing after chilling | 1162 _(1,533) | 0.69 | *** |

To explore the possibility of identifying microclimates less susceptible to warming trends, we compared the two years with the highest and lowest values of each predicted microclimate variable. June forcing after chilling, the day of year where 1200 chilling units are accumulated, number of days below 0 and April forcing after chilling all had distinct patterns of microclimate distribution, with some areas experiencing a much greater range of values than others (Figure 3). High elevation sites saw much greater ranges in both the day of year where chilling reached 1200 and the last day of year where the temperature dropped below 0. Low elevation sites tended to see greater ranges in forcing metrics, although the April 1 forcing appears to be buffered near the stream channels, even when nearby areas show extreme ranges in April 1 forcing units.

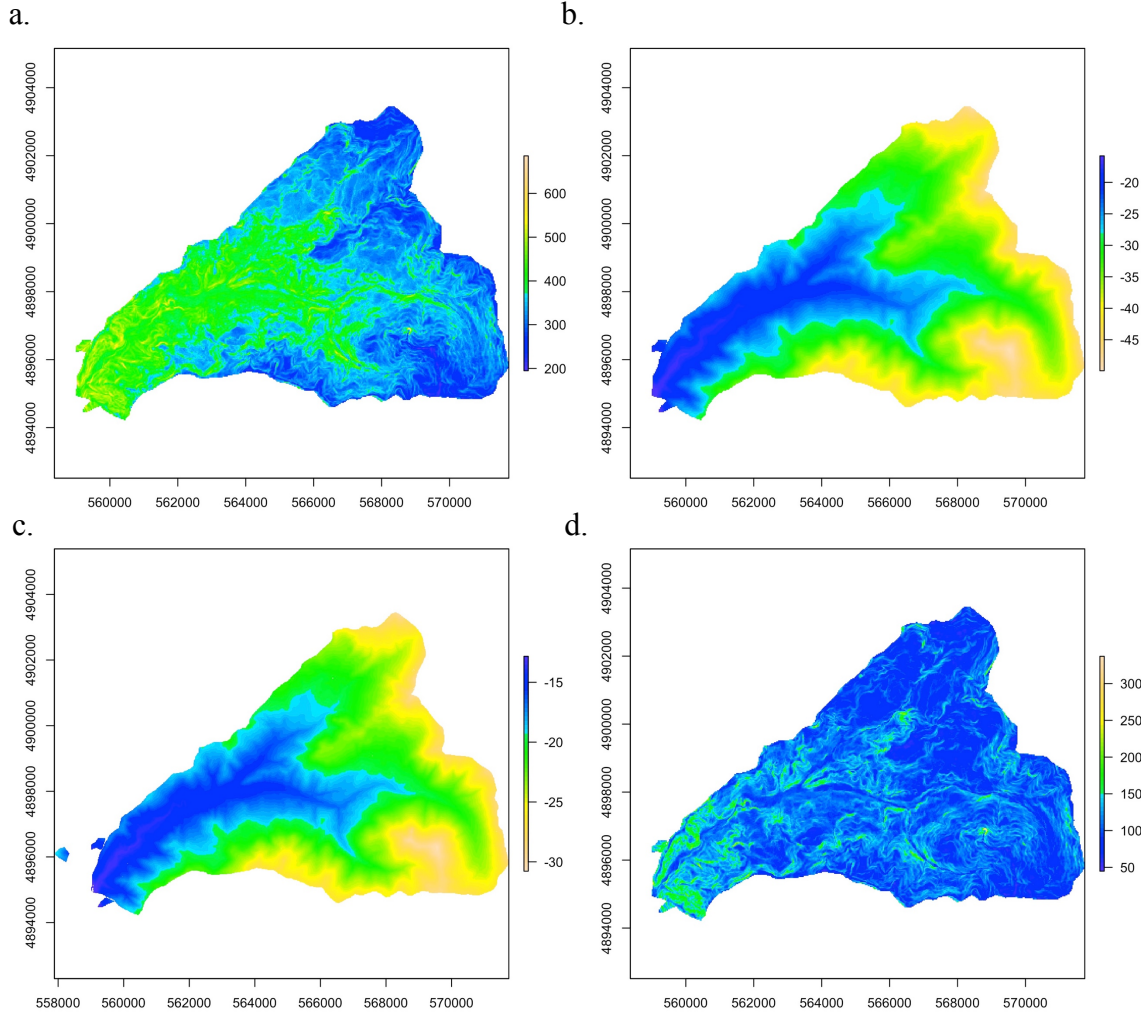


Figure 3: Range in microclimate variables across the Andrews between the warmest (2015) and coolest (2011) years in the phenology record. (a) June forcing after chilling. (b) Number of days below 0. (c) First day of year above 1200 chilling units. (d) April forcing after chilling. All colors represent the range between 2011 and 2015 values (2015 was the warmest year in the phenology record while 2011 was the coolest). Blues represent regions with the least range in the given variable, while yellows are the areas with the greatest range between the two years. Greens are intermediate.

Discussion

We were able to create species-specific models of bud break that were robust for predicting both internal and external (validation) data. The Douglas fir model was highly accurate across all elevations, with a median difference of 2.26 days, and a maximum difference between observed and predicted data of 8.9 days (Table S11). Interestingly, the model for Douglas fir included the forcing variable that accumulated

after 1200 chilling units rather than a forcing variable that accumulates simultaneously with chilling (parallel model). This is counter to Harrington et al. (2010), whose models of forcing and chilling units we used. They modeled Douglas fir bud break possibility lines using chilling and forcing units that accumulated simultaneously. However, other studies have supported temperate trees requiring a certain number of chilling units prior to forcing accumulation (sequential model) (Landsberg 1974, Hänninen 1995, Bailey and Harrington 2006). Because the Harrington *et al.* models were developed using seed sources that had a maximum elevation of 880m, it is possible that the individuals from our study have a more rigid chilling requirement as individuals that break bud too early at higher elevations will more likely be subject to frost damage. Red huckleberry also included forcing after chilling, which was surprising. We tend to (anecdotally) observe huckleberry rapidly breaking bud as soon as daily temperatures begin to warm up. It's possible that the day of year when chilling is near 1200 units is also closely timed with snow melt, and the variable is a stand in for the more direct effect of snow. Neither models for vine maple or trillium had any forcing metrics included, and both included mean April temperature and the number of days below 0. Because both species are subject to snow burial and persistent freezing temperatures beneath temperature inversions, it is possible that mean April temperature captures the late season forcing that occurs after snow melts and the number of days below 0 indicate the persistence of cold air pooling events.

The models for trillium and vine maple were both the least accurate when predicting bud break at the two highest elevation sites (PC17 at 1300 m and PC18 at 1330 m) (Table S4). Both of these species are subject to winter snow burial, and it is likely that our snow variable (presence or absence at the site) does not capture the fine scale nuances of snow pack (and snow melt) that affect an individual plant, and thus the bud break models fail to capture as much variance as the other species less affected by snow (i.e. Douglas fir). The vine maple model also predicted a later bud break at PC16. This site is a mid to high elevation site (1025m) that is situated at the top of a south facing ridge that is often much more advanced than other sites at the same elevation. The model predicted bud break 17 days later than the observed value and as there is rarely a late

season snow pack at this site, it is likely that some of the finer nuances of microclimate are not captured in the overall model.

We were able to accurately predict microclimate across the landscape using only a few sites. When comparing the two extreme years, we found that the low elevation stream sites were buffered against extreme variability in freezing events and the rate of chilling accumulation, while high elevation sites were buffered against extreme ranges in June forcing metrics. The range in April forcing after chilling was particularly interesting, as the low elevation stream valleys showed little variability while sites only a few hundred meters up the hillsides showed extreme ranges in April forcing accumulation. Further exploration of historic data may indicate sites that are consistently buffered against extreme climate variability.

Conclusions

Vegetation and topography are the dominant factors driving winter and spring temperature in the Western Cascades, and areas of heterogeneous topography and high biomass (i.e., old growth forests) have the potential to buffer species from regional increases in winter and spring temperature (Pepin et al. 2011, Frenne et al. 2013, Frey et al. 2016b, Morelli et al. 2016, Frey et al. 2016a). However, identifying potential microclimates is difficult due to the highly variable physiologies of individual species. We found that physical variables and temperature metrics from a few local sites can be used to accurately predict microclimate across a landscape, and species-specific models can then be applied to a broad area. Upscaling species-specific bud break models derived from a local scale has the potential both explore the effects of future climate scenarios, and to identify sites that may continue to maintain microclimatic diversity in the future. These sites could benefit or protect those species most susceptible to a homogenization of microclimates and phenologies driven by warming climate trends.

CHAPTER V

CONCLUSION

In summary, we found that during the eight year phenology study, years with a decline in winter snow pack, and an increase in cold air pooling events resulted in a more similar distribution of microclimates across a watershed. This homogenization of microclimates led to a less diverse range of spring phenology events, especially in herbs and shrubs. Microclimate is a significant driver of spring plant phenology, and local temperature metrics can be used to accurately predict phenology across a wide range of microclimates. Snow is likely the most limiting factor in modeling plant phenology, especially for herbs and shrubs, as it is difficult to measure at a high enough resolution. The models we developed tended to predict bud break early than observed at sites with persistent snow pack. Finally, physical variables can be used to accurately predict microclimate across a landscape, using observed data from only a few sites. These up scaled microclimate variables can be used to accurately predict bud break across the landscape and have the potential to help identify local zones that are protected from the predicted changes in regional climate.

APPENDIX A

APPENDIX S1

Table S1: Species list for plants included in phenology study.

| Species | Common name | Species code |
|----------------------------------|----------------------|--------------|
| <i>Abies amabilis</i> | Pacific silver fir | ABAM |
| <i>Abies procera</i> | Noble fir | ABPR |
| <i>Acer circinatum</i> | Vine maple | ACCI |
| <i>Acer macrophyllum</i> | Big leaf maple | ACMA3 |
| <i>Chimaphila umbellata</i> | Princes pine | CHUM |
| <i>Coptis laciniata</i> | Cut-leaf goldthread | COLA3 |
| <i>Cornus canadensis</i> | Bunchberry | COCA13 |
| <i>Cornus nutalii</i> | Pacific dogwood | CONU4 |
| <i>Linnaea borealis</i> | Twinflower | LIBO3 |
| <i>Pseudotsuga menziesii</i> | Douglas fir | PSME |
| <i>Rhododendron macrophyllum</i> | Pacific rhododendron | RHMA |
| <i>Rubus ursinus</i> | Creeping blackberry | RUUR |
| <i>Synthyris reniformis</i> | Snow queen | SYRE |
| <i>Trillium ovatum</i> | Trillium | TROV2 |
| <i>Tsuga heterophylla</i> | Western hemlock | TSHE |
| <i>Vaccinium membranaceum</i> | Mountain huckleberry | VAME |
| <i>Vaccinium parvifolium</i> | Red huckleberry | VAPA |
| <i>Viola sempervirens</i> | Violet | WISE3 |

Table S2: Regression equations used to fill in any missing or erroneous temperature data.

| Site | Equation | Adjusted R ² | df | F-stat | P-value |
|------|-------------------------------|-------------------------|---------|---------|---------|
| PC01 | PC01 = RS02 x 0.941 + 0.649 | 0.989 | 1,45215 | 425924 | *** |
| PC02 | PC02 = CS2met x 0.933 + 1.074 | 0.986 | 1,49115 | 354185 | *** |
| PC04 | PC04 = RS89 x 0.985 + 0.632 | 0.994 | 1,54915 | 979041 | *** |
| PC05 | PC05 = RS86 x 0.992 + 0.430 | 0.994 | 1,44049 | 706341 | *** |
| PC07 | PC07 = RS05 x 0.987 - 0.075 | 0.996 | 1,55057 | 1271158 | *** |
| PC08 | PC08 = RS10 x 1.000 + 0.115 | 0.997 | 1,54568 | 1571495 | *** |
| PC09 | PC09 = RS12 x 1.001 + 0.381 | 0.992 | 1,53536 | 647952 | *** |
| PC10 | PC10 = RS05 x 1.003 - 0.568 | 0.986 | 1,54745 | 376250 | *** |
| PC11 | PC11 = RS26 x 0.975 - 0.554 | 0.991 | 1,47045 | 495211 | *** |
| PC12 | PC12 = RS26 x 0.979 + 0.107 | 0.996 | 1,54593 | 1402571 | *** |
| PC13 | PC13 = RS26 x 0.952 - 1.235 | 0.971 | 1,54196 | 181439 | *** |
| PC14 | PC14 = RS05 x 1.016 - 0.454 | 0.989 | 1,55067 | 485521 | *** |
| PC15 | PC15 = HI15 x 0.984 + 0.386 | 0.985 | 1,48635 | 320198 | *** |
| PC16 | PC16 = RS26 x 0.996 - 0.026 | 0.986 | 1,54059 | 372480 | *** |
| PC17 | PC17 = RS04 x 0.977 + 0.014 | 0.992 | 1,47550 | 595117 | *** |
| PC18 | PC18 = RS04 x 1.001 - 0.203 | 0.984 | 1,48787 | 308451 | *** |

Notes
 -- Non Significant; * P<0.05; ** P<0.01; ***P<0.001; In the site column, PC represents “phenology core”; In the equation column, all abbreviations following = are representative of reference stands (RS) or other climate stations (HI15 and CS2met); df, degrees of freedom.

Table S3: Variables included in principle component analysis of temperature data.

| Temperature PCA Variables | Description: |
|---------------------------|--|
| Winter average | Mean temp between January 1 and March 31 |
| Spring average | Mean temperature between April 1 and June 30 |
| Summer average | Mean temperature between July 1 and September 30 |
| Fall average | Mean temperature between October 1 and December 31 |
| Annual average | Mean temperature between January 1 and December 31 |
| Winter GDD | Accumulated growing degree days above 5° C between December 1 and March 31 |
| Spring GDD | Accumulated growing degree days above 5° C between April 1 and June 30 |
| Minimum: coldest month | Minimum temperature (°C) of the coldest month per year (Nov 1 – Oct 31) |
| Maximum: warmest month | Maximum temperature (°C) of the warmest month per year (Nov 1 – Oct 31) |
| Mid winter average | Mean temperature between December 1 and March 31 |

Table S4: Variable contributions to each principle component in Figures 2a and 2b

| Variable | PC1 | PC2 |
|--------------------------------|-------|-------|
| Winter average (Jan – Mar) | 12.84 | 0.36 |
| Spring average (Apr – Jun) | 12.40 | 0.00 |
| Summer average (Jul – Sept) | 8.39 | 2.78 |
| Fall average (Oct – Dec) | 0.13 | 89.44 |
| Annual average (Jan – Dec) | 15.24 | 0.03 |
| Winter GDD (Dec – Mar31) | 11.99 | 0.46 |
| Spring GDD (Apr 1- Jun 30) | 12.70 | 0.05 |
| Minimum temp (Jan – Dec) | 6.54 | 1.73 |
| Maximum temp (Jan – Dec) | 6.14 | 4.97 |
| Mid winter average (Dec-Mar31) | 13.62 | 0.17 |

Table S5: Growing degree days for all sites and all years for the first six months of each year (January 1 to June 30), and for winter (December 1 – March 31).

| Plot | Elevation | 2009 | 2010 | 2011 | 2012 | 201 | 2014 | 2015 | 2016 |
|---|-----------|--------------------|--------------------|-------------------|-------------------|--------------------|--------------------|---------------------|--------------------|
| PC01 | 489.47 | 635.33 (35.52) | 528.07 (104.32) | 428.98 (52.35) | 548.37 (41.67) | 697.21 (74.8) | 705.31 (96.82) | 939.72 (242.63) | 830.28 (123.19) |
| PC02 | 478.21 | 627.46 (29.47) | 478.48 (68.18) | 399.52 (36.3) | 502.08 (23) | 649.05 (55.17) | 625.31 (69.21) | 833.7 (164.8) | 745.66 (90.4) |
| PC04 | 487.25 | 666.87 (42.28) | 555.44 (113.95) | 443.25 (51.98) | 571.56 (44.53) | 720.77 (82.47) | 713.32 (106.5) | 950.91 (249.18) | 829.44 (120.07) |
| PC05 | 643.14 | 764.49 (115.82) | 586.08 (144.05) | 472.97 (80.73) | 614.53 (87.3) | 770.96 (107.09) | 794.44 (165.14) | 1051.37 (299.24) | 887.67 (137.31) |
| PC07 | 899.88 | 474.95 (26.44) | 304.89 (37.22) | 245.99 (26.06) | 357.03 (14.93) | 484.7 (21.72) | 494.08 (64.38) | 748.45 (166.4) | 607.17 (55.57) |
| PC08 | 646.51 | 624.44 (46.01) | 480.94 (94.98) | 381.69 (49.4) | 510.61 (39.08) | 654.04 (61.66) | 667.99 (99.92) | 909.35 (228.03) | 775.86 (98.68) |
| PC09 | 985 | 389.81 (3.38) | 258.79 (19.48) | 176.47 (5.35) | 286.41 (6.15) | 398.86 (6) | 416.36 (29.89) | 649.12 (113.67) | 501.49 (23.95) |
| PC10 | 984 | 446.6 (19.88) | 294.39 (44.85) | 207.96 (14.89) | 330.2 (17.71) | 439.42 (17.53) | 468.12 (60.46) | 711.66 (161.27) | 584.08 (52.65) |
| PC11 | 1114.83 | 473.86 (69.35) | 287.82 (54.18) | 205.4 (26.87) | 339.29 (39.58) | 442.84 (37.09) | 486.77 (110.42) | 734.98 (195.11) | 574.76 (68.29) |
| PC12 | 1083.18 | 524.94 (87.2) | 330.67 (78.65) | 245.1 (48.7) | 389.3 (66.34) | 508.25 (68.73) | 540.42 (141.98) | 821.81 (247.79) | 650.93 (104.68) |
| PC13 | 1177.89 | 402.41 (50.84) | 203.68 (22.34) | 116.31 (5.02) | 233.58 (13.97) | 338.42 (4.85) | 371.35 (55.98) | 619.73 (135.36) | 446.32 (19.84) |
| PC14 | 964.54 | 469.42 (23.21) | 291.9 (35.14) | 210.11 (9.29) | 335.93 (12.37) | 458.43 (12.13) | 486.75 (62.98) | 744.67 (158.55) | 590.56 (41.28) |
| PC15 | 970.83 | 500.57 (33.44) | 317.48 (43.2) | 225.63 (12.25) | 360.79 (15.95) | 483.95 (12.96) | 523.3 (75.55) | 814.07 (181.33) | 634.39 (50.34) |
| PC16 | 1025.07 | 546.23 (84.86) | 373.03 (83.01) | 266.9 (40.1) | 410.94 (53.53) | 524.65 (54.23) | 523.3 (75.55) | 838.41 (242.65) | 668.02 (97.45) |
| PC17 | 1299.86 | 386.89 (63.08) | 176.65 (12.91) | 96.61 (3.96) | 225.45 (13.28) | 340.02 (39.81) | 347.68 (64.39) | 601.68 (124.5) | 408.91 (14.74) |
| PC18 | 1329.72 | 392.32 (63.5) | 191.38 (15.09) | 111.75 (8.65) | 231.67 (13.16) | 342.39 (40.68) | 355.88 (60.88) | 602 (121.24) | 417.97 (29.09) |
| Notes | | | | | | | | | |
| Data outside the parentheses is January 1 – June 30 growing degree day accumulation, while data within parentheses is winter growing degree days (December 1 – March 31). | | | | | | | | | |

Table S6: A-C index values between December 1- March 31 from 2009 to 2016.

| Year | AC index |
|------|----------|
| 2009 | 12 |
| 2010 | 3 |
| 2011 | -1 |
| 2012 | 26 |
| 2013 | 21 |
| 2014 | 29 |
| 2015 | 44 |
| 2016 | 3 |

Table S7: Snow data for all sites and years.

| Plot | Elevation (m) | Year | Estimated last DOY with patchy snow | Estimated max days of snow (Dec 1 – Mar 31) | DOY with no buried plants observed |
|------|---------------|------|---|---|---------------------------------------|
| PC01 | 489.47 | 2009 | 96 | 35 | NA |
| PC02 | 478.21 | 2009 | 96 | 35 | NA |
| PC04 | 487.25 | 2009 | 96 | 35 | NA |
| PC05 | 643.14 | 2009 | 105 | 35 | NA |
| PC07 | 899.88 | 2009 | 105 | 45 | NA |
| PC08 | 646.51 | 2009 | 105 | 35 | NA |
| PC09 | 985 | 2009 | 120 | 63 | NA |
| PC10 | 984 | 2009 | 110 | 50 | NA |
| PC11 | 1114.83 | 2009 | 133 | 70 | NA |
| PC12 | 1083.18 | 2009 | 132 | 50 | NA |
| PC13 | 1177.89 | 2009 | 141 | 82 | NA |
| PC14 | 964.54 | 2009 | 125 | 70 | NA |
| PC15 | 970.83 | 2009 | 110 | 60 | NA |
| PC16 | 1025.07 | 2009 | 110 | 60 | NA |
| PC17 | 1299.86 | 2009 | 145 | 88 | NA |
| PC18 | 1329.72 | 2009 | 150 | 92 | NA |
| PC01 | 489.47 | 2010 | 91 | 7 | 62 |
| PC02 | 478.21 | 2010 | 91 | 7 | 48 |
| PC04 | 487.25 | 2010 | 91 | 7 | 55 |
| PC05 | 643.14 | 2010 | 95 | 10 | 55 |
| PC07 | 899.88 | 2010 | 105 | 15 | 62 |
| PC08 | 646.51 | 2010 | 95 | 10 | 48 |
| PC09 | 985 | 2010 | 123 | 39 | 125 |
| PC10 | 984 | 2010 | 102 | 15 | 48 |
| PC11 | 1114.83 | 2010 | 139 | 46 | 132 |
| PC12 | 1083.18 | 2010 | 127 | 35 | 48 |
| PC13 | 1177.89 | 2010 | 137 | 61 | 132 |
| PC14 | 964.54 | 2010 | 121 | 47 | 125 |

| | | | | | |
|------|---------|------|-----|-----|-----|
| PC15 | 970.83 | 2010 | 121 | 47 | 125 |
| PC16 | 1025.07 | 2010 | 121 | 47 | 132 |
| PC17 | 1299.86 | 2010 | 149 | 87 | 153 |
| PC18 | 1329.72 | 2010 | 149 | 92 | 153 |
| PC01 | 489.47 | 2011 | 91 | 7 | 75 |
| PC02 | 478.21 | 2011 | 118 | 7 | 75 |
| PC04 | 487.25 | 2011 | 91 | 7 | 75 |
| PC05 | 643.14 | 2011 | 82 | 7 | 82 |
| PC07 | 899.88 | 2011 | 116 | 45 | 103 |
| PC08 | 646.51 | 2011 | 105 | 7 | 103 |
| PC09 | 985 | 2011 | 137 | 45 | 152 |
| PC10 | 984 | 2011 | 128 | 57 | 131 |
| PC11 | 1114.83 | 2011 | 150 | 75 | 152 |
| PC12 | 1083.18 | 2011 | 132 | 57 | 138 |
| PC13 | 1177.89 | 2011 | 158 | 105 | 159 |
| PC14 | 964.54 | 2011 | 147 | 80 | 145 |
| PC15 | 970.83 | 2011 | 137 | 90 | 145 |
| PC16 | 1025.07 | 2011 | 137 | 90 | 131 |
| PC17 | 1299.86 | 2011 | 166 | 110 | 173 |
| PC18 | 1329.72 | 2011 | 166 | 110 | 180 |
| PC01 | 489.47 | 2012 | 87 | 7 | 88 |
| PC02 | 478.21 | 2012 | 87 | 7 | 88 |
| PC04 | 487.25 | 2012 | 87 | 7 | 81 |
| PC05 | 643.14 | 2012 | 99 | 15 | 102 |
| PC07 | 899.88 | 2012 | 92 | 7 | 109 |
| PC08 | 646.51 | 2012 | 96 | 35 | 88 |
| PC09 | 985 | 2012 | 152 | 55 | 130 |
| PC10 | 984 | 2012 | 116 | 50 | 116 |
| PC11 | 1114.83 | 2012 | 122 | 55 | 116 |
| PC12 | 1083.18 | 2012 | 107 | 7 | 116 |
| PC13 | 1177.89 | 2012 | 126 | 65 | 137 |
| PC14 | 964.54 | 2012 | 126 | 65 | 123 |
| PC15 | 970.83 | 2012 | 121 | 60 | 123 |
| PC16 | 1025.07 | 2012 | 108 | 50 | 116 |
| PC17 | 1299.86 | 2012 | 144 | 70 | 144 |
| PC18 | 1329.72 | 2012 | 146 | 70 | 165 |
| PC01 | 489.47 | 2013 | 91 | 7 | 72 |
| PC02 | 478.21 | 2013 | 91 | 7 | 72 |
| PC04 | 487.25 | 2013 | 91 | 7 | 72 |
| PC05 | 643.14 | 2013 | 91 | 7 | 72 |
| PC07 | 899.88 | 2013 | 104 | 7 | 93 |
| PC08 | 646.51 | 2013 | 91 | 7 | 79 |
| PC09 | 985 | 2013 | 120 | 45 | 121 |

| | | | | | |
|------|---------|------|-----|-----|-----|
| PC10 | 984 | 2013 | 112 | 7 | 107 |
| PC11 | 1114.83 | 2013 | 112 | 7 | 114 |
| PC12 | 1083.18 | 2013 | 110 | 7 | 114 |
| PC13 | 1177.89 | 2013 | 112 | 45 | 121 |
| PC14 | 964.54 | 2013 | 112 | 45 | 114 |
| PC15 | 970.83 | 2013 | 112 | 45 | 114 |
| PC16 | 1025.07 | 2013 | 112 | 45 | 114 |
| PC17 | 1299.86 | 2013 | 130 | 65 | 128 |
| PC18 | 1329.72 | 2013 | 130 | 65 | 135 |
| PC01 | 489.47 | 2014 | 91 | 7 | 57 |
| PC02 | 478.21 | 2014 | 91 | 7 | 57 |
| PC04 | 487.25 | 2014 | 91 | 7 | 57 |
| PC05 | 643.14 | 2014 | 91 | 7 | 57 |
| PC07 | 899.88 | 2014 | 91 | 7 | 71 |
| PC08 | 646.51 | 2014 | 91 | 7 | 71 |
| PC09 | 985 | 2014 | 91 | 7 | 120 |
| PC10 | 984 | 2014 | 119 | 14 | 99 |
| PC11 | 1114.83 | 2014 | 119 | 28 | 120 |
| PC12 | 1083.18 | 2014 | 96 | 14 | 120 |
| PC13 | 1177.89 | 2014 | 126 | 35 | 120 |
| PC14 | 964.54 | 2014 | 119 | 14 | 99 |
| PC15 | 970.83 | 2014 | 118 | 14 | 120 |
| PC16 | 1025.07 | 2014 | 118 | 14 | 99 |
| PC17 | 1299.86 | 2014 | 119 | 28 | 127 |
| PC18 | 1329.72 | 2014 | 126 | 42 | 127 |
| PC01 | 489.47 | 2015 | 1 | 0 | 1 |
| PC02 | 478.21 | 2015 | 1 | 0 | 1 |
| PC07 | 899.88 | 2015 | 1 | 0 | 1 |
| PC09 | 985 | 2015 | 1 | 7 | 47 |
| PC12 | 1083.18 | 2015 | 102 | 7 | 47 |
| PC15 | 970.83 | 2015 | 1 | 7 | 1 |
| PC17 | 1299.86 | 2015 | 117 | 14 | 102 |
| PC01 | 489.47 | 2016 | 40 | 14 | 47 |
| PC02 | 478.21 | 2016 | 75 | 21 | 83 |
| PC04 | 487.25 | 2016 | 75 | 21 | 83 |
| PC05 | 643.14 | 2016 | 40 | 14 | 47 |
| PC07 | 899.88 | 2016 | 83 | 56 | 89 |
| PC08 | 646.51 | 2016 | 75 | 21 | 83 |
| PC09 | 985 | 2016 | 92 | 96 | 96 |
| PC10 | 984 | 2016 | 83 | 96 | 89 |
| PC11 | 1114.83 | 2016 | 91 | 63 | 96 |
| PC12 | 1083.18 | 2016 | 80 | 56 | 90 |
| PC13 | 1177.89 | 2016 | 91 | 103 | 96 |

| | | | | | |
|--|---------|------|----|-----|-----|
| PC14 | 964.54 | 2016 | 89 | 56 | 96 |
| PC15 | 970.83 | 2016 | 89 | 56 | 96 |
| PC16 | 1025.07 | 2016 | 89 | 56 | 93 |
| PC17 | 1299.86 | 2016 | 97 | 134 | 124 |
| PC18 | 1329.72 | 2016 | 97 | 134 | 124 |
| Notes | | | | | |
| In 2009, sites were not visited prior to snowmelt. | | | | | |

Table S8: Difference in average bud break date from 2011 to 2015.

| Plot | Species | 2011 | 2015 | 2011-2015 |
|------|---------|------|------|-----------|
| PC01 | ACCI | 109 | 96 | 13 |
| PC01 | ACMA3 | 135 | 86 | 49 |
| PC01 | COLA3 | 89 | 74 | 15 |
| PC01 | LIBO3 | 95 | 68 | 27 |
| PC01 | PSME | 154 | 129 | 25 |
| PC01 | RUUR | 110 | 81 | 29 |
| PC01 | TROV2 | 89 | 77 | 12 |
| PC01 | TSHE | 158 | 136 | 22 |
| PC01 | VAPA | 99 | 70 | 29 |
| PC01 | VISE3 | 81 | 66 | 15 |
| PC02 | ACCI | 109 | 82 | 27 |
| PC02 | CHUM | 137 | 96 | 41 |
| PC02 | COLA3 | 102 | 77 | 25 |
| PC02 | CONU4 | 107 | 79 | 28 |
| PC02 | LIBO3 | 98 | 74 | 24 |
| PC02 | PSME | 158 | 131 | 27 |
| PC02 | RHMA | 153 | 144 | 9 |
| PC02 | RUUR | 131 | 91 | 40 |
| PC02 | TROV2 | 92 | 76 | 16 |
| PC02 | TSHE | 162 | 143 | 19 |
| PC02 | VAPA | 96 | 70 | 26 |
| PC02 | VISE3 | 95 | 61 | 34 |
| PC04 | ACCI | 103 | NA | NA |
| PC04 | COLA3 | 98 | NA | NA |
| PC04 | LIBO3 | 101 | NA | NA |
| PC04 | PSME | 151 | NA | NA |
| PC04 | RHMA | 153 | NA | NA |
| PC04 | RUUR | 112 | NA | NA |
| PC04 | SYRE | 90 | NA | NA |

| | | | | |
|-------------|--------------|------------|-----------|-----------|
| PC04 | TROV2 | 93 | NA | NA |
| PC04 | TSHE | 157 | NA | NA |
| PC04 | VAPA | 105 | NA | NA |
| PC04 | WISE3 | 85 | NA | NA |
| PC05 | ACCI | 117 | NA | NA |
| PC05 | CONU4 | 102 | NA | NA |
| PC05 | LIBO3 | 102 | NA | NA |
| PC05 | PSME | 158 | NA | NA |
| PC05 | RHMA | 160 | NA | NA |
| PC05 | RUUR | 119 | NA | NA |
| PC05 | TSHE | 161 | NA | NA |
| PC05 | VAPA | 110 | NA | NA |
| PC05 | WISE3 | 85 | NA | NA |
| PC07 | ACCI | 122 | 95 | 27 |
| PC07 | CHUM | 161 | 116 | 45 |
| PC07 | LIBO3 | 129 | 67 | 62 |
| PC07 | PSME | 180 | 147 | 33 |
| PC07 | RHMA | 170 | 142 | 28 |
| PC07 | TSHE | 171 | 154 | 17 |
| PC08 | ACCI | 112 | NA | NA |
| PC08 | CHUM | 133 | NA | NA |
| PC08 | COLA3 | 102 | NA | NA |
| PC08 | LIBO3 | 113 | NA | NA |
| PC08 | PSME | 166 | NA | NA |
| PC08 | RHMA | 158 | NA | NA |
| PC08 | RUUR | 130 | NA | NA |
| PC08 | SYRE | 105 | NA | NA |
| PC08 | TROV2 | 98 | NA | NA |
| PC08 | TSHE | 165 | NA | NA |
| PC08 | VAPA | 108 | NA | NA |
| PC08 | WISE3 | 88 | NA | NA |
| PC09 | ABAM | 174 | 149 | 25 |
| PC09 | ACCI | 127 | 92 | 35 |
| PC09 | CHUM | 169 | 117 | 52 |
| PC09 | COCA13 | 145 | 81 | 64 |
| PC09 | LIBO3 | 154 | 75 | 79 |
| PC09 | PSME | 179 | 151 | 28 |
| PC09 | RHMA | 179 | 144 | 35 |
| PC09 | RUUR | 155 | 84 | 71 |
| PC09 | TROV2 | 137 | 91 | 46 |
| PC09 | TSHE | 176 | 150 | 26 |
| PC09 | VAPA | 138 | 74 | 64 |
| PC09 | WISE3 | 144 | 59 | 85 |

| | | | | |
|------|--------|-----|-----|----|
| PC10 | ABAM | 177 | NA | NA |
| PC10 | ACCI | 136 | NA | NA |
| PC10 | CHUM | 154 | NA | NA |
| PC10 | COCA13 | 140 | NA | NA |
| PC10 | COLA3 | 130 | NA | NA |
| PC10 | LIBO3 | 129 | NA | NA |
| PC10 | PSME | 173 | NA | NA |
| PC10 | RHMA | 172 | NA | NA |
| PC10 | RUUR | 146 | NA | NA |
| PC10 | TSHE | 172 | NA | NA |
| PC10 | VAPA | 136 | NA | NA |
| PC10 | WISE3 | 119 | NA | NA |
| PC11 | ABPR | 174 | NA | NA |
| PC11 | ACCI | 133 | NA | NA |
| PC11 | CHUM | 157 | NA | NA |
| PC11 | COCA13 | 147 | NA | NA |
| PC11 | LIBO3 | 136 | NA | NA |
| PC11 | PSME | 179 | NA | NA |
| PC11 | RUUR | 162 | NA | NA |
| PC11 | SYRE | 144 | NA | NA |
| PC11 | TROV2 | 137 | NA | NA |
| PC11 | TSHE | 173 | NA | NA |
| PC11 | VAPA | 138 | NA | NA |
| PC11 | WISE3 | 133 | NA | NA |
| PC12 | ACCI | 130 | 88 | 42 |
| PC12 | CHUM | 150 | 110 | 40 |
| PC12 | COLA3 | 137 | 73 | 64 |
| PC12 | LIBO3 | 131 | 66 | 65 |
| PC12 | PSME | 178 | 147 | 31 |
| PC12 | RUUR | 152 | 70 | 82 |
| PC12 | SYRE | 137 | 56 | 81 |
| PC12 | TROV2 | 132 | 89 | 43 |
| PC12 | TSHE | 173 | 150 | 23 |
| PC12 | VAPA | 131 | 67 | 64 |
| PC12 | WISE3 | 133 | 60 | 73 |
| PC13 | ABAM | 181 | NA | NA |
| PC13 | ACCI | 141 | NA | NA |
| PC13 | CHUM | 172 | NA | NA |
| PC13 | COCA13 | 165 | NA | NA |
| PC13 | LIBO3 | 164 | NA | NA |
| PC13 | PSME | 186 | NA | NA |
| PC13 | RUUR | 175 | NA | NA |
| PC13 | TSHE | 183 | NA | NA |

| | | | | |
|------|--------|-----|-----|----|
| PC13 | WISE3 | 159 | NA | NA |
| PC14 | ACCI | 139 | NA | NA |
| PC14 | CHUM | 159 | NA | NA |
| PC14 | COCA13 | 140 | NA | NA |
| PC14 | COLA3 | 140 | NA | NA |
| PC14 | LIBO3 | 137 | NA | NA |
| PC14 | PSME | 178 | NA | NA |
| PC14 | RHMA | 177 | NA | NA |
| PC14 | RUUR | 162 | NA | NA |
| PC14 | TROV2 | 130 | NA | NA |
| PC14 | TSHE | 171 | NA | NA |
| PC14 | VAPA | 138 | NA | NA |
| PC14 | WISE3 | 129 | NA | NA |
| PC15 | ABAM | 179 | 151 | 28 |
| PC15 | ACCI | 134 | 88 | 46 |
| PC15 | CHUM | 152 | 103 | 49 |
| PC15 | COCA13 | 148 | 87 | 61 |
| PC15 | COLA3 | 130 | 81 | 49 |
| PC15 | LIBO3 | 138 | 67 | 71 |
| PC15 | PSME | 179 | 147 | 32 |
| PC15 | RUUR | 164 | 92 | 72 |
| PC15 | SYRE | 137 | 68 | 69 |
| PC15 | TROV2 | 137 | 93 | 44 |
| PC15 | TSHE | 175 | 148 | 27 |
| PC15 | VAPA | 133 | 70 | 63 |
| PC15 | WISE3 | 130 | 54 | 76 |
| PC16 | ACCI | 126 | NA | NA |
| PC16 | CHUM | 150 | NA | NA |
| PC16 | LIBO3 | 127 | NA | NA |
| PC16 | PSME | 175 | NA | NA |
| PC16 | RHMA | 172 | NA | NA |
| PC16 | RUUR | 154 | NA | NA |
| PC16 | TSHE | 171 | NA | NA |
| PC16 | VAPA | 133 | NA | NA |
| PC16 | WISE3 | 130 | NA | NA |
| PC17 | ABAM | 181 | 151 | 30 |
| PC17 | ACCI | 149 | 87 | 62 |
| PC17 | CHUM | 190 | 132 | 58 |
| PC17 | COCA13 | 174 | 108 | 66 |
| PC17 | PSME | 186 | 158 | 28 |
| PC17 | RUUR | 186 | 113 | 73 |
| PC17 | TROV2 | NA | 118 | NA |
| PC17 | TSHE | 186 | 152 | 34 |

| | | | | |
|---|--------|-----|----|----|
| PC17 | VAME | NA | 74 | NA |
| PC17 | WISE3 | 169 | 97 | 72 |
| PC18 | ABPR | 181 | NA | NA |
| PC18 | ACCI | 162 | NA | NA |
| PC18 | CHUM | 191 | NA | NA |
| PC18 | COCA13 | 174 | NA | NA |
| PC18 | PSME | 187 | NA | NA |
| PC18 | RUUR | 179 | NA | NA |
| PC18 | TSHE | 187 | NA | NA |
| PC18 | WISE3 | 172 | NA | NA |
| <p>Notes</p> <p>Mean bud break from 2011 was subtracted from 2015 to find the most extreme advancement of bud break between those two years.</p> | | | | |

Table S9: Physical variables included in microclimate model

| Plot | Elevation (m) | Slope (25m radius) | Aspect (25 m radius) | Relative topographic position (500 m radius) |
|-------|------------------|-----------------------|-------------------------|--|
| PC001 | 489.47 | 61.484 | 0.917 | 109.852 |
| PC002 | 478.21 | 21.826 | 0.480 | 76.648 |
| PC004 | 487.25 | 66.114 | -0.966 | 71.178 |
| PC005 | 643.14 | 64.593 | -0.983 | 184.431 |
| PC007 | 899.88 | 14.373 | 0.425 | 222.997 |
| PC008 | 646.51 | 48.223 | -0.784 | 117.416 |
| PC009 | 984.48 | 32.431 | -0.214 | 149.310 |
| PC010 | 983.62 | 18.496 | -0.873 | 192.657 |
| PC011 | 1114.83 | 28.690 | -0.360 | 236.108 |
| PC012 | 1083.18 | 39.696 | -0.973 | 243.581 |
| PC013 | 1177.89 | 18.772 | -0.402 | 222.385 |
| PC014 | 964.54 | 20.847 | 0.215 | 199.705 |
| PC015 | 970.82 | 14.109 | -0.541 | 196.015 |
| PC016 | 1025.07 | 34.904 | -0.924 | 265.403 |
| PC017 | 1299.86 | 41.105 | 0.473 | 229.104 |
| PC018 | 1329.72 | 45.493 | -0.017 | 254.462 |

Table S10: Elevation as a predictor of bud break for each species and year.

| Year | Species code | Adj R ² | P-value | F-stat | df1 | df2 | Intercept | Slope |
|------|--------------|--------------------|----------|--------|-----|-----|-----------|-------|
| 2009 | ABAM | 0.83 | 1.99E-02 | 20.68 | 1 | 2 | 123.35 | 0.03 |
| 2010 | ABAM | Not Sig | 2.19E-01 | 2.40 | 1 | 2 | 0.00 | 0.00 |
| 2011 | ABAM | Not Sig | 1.48E-01 | 3.76 | 1 | 2 | 0.00 | 0.00 |
| 2012 | ABAM | Not Sig | 1.98E-01 | 2.72 | 1 | 2 | 0.00 | 0.00 |
| 2013 | ABAM | Not Sig | 8.44E-01 | 0.05 | 1 | 2 | 0.00 | 0.00 |
| 2014 | ABAM | Not Sig | 3.37E-01 | 1.30 | 1 | 2 | 0.00 | 0.00 |
| 2015 | ABAM | Not Sig | 6.91E-01 | 0.28 | 1 | 1 | 0.00 | 0.00 |
| 2016 | ABAM | Not Sig | 4.91E-01 | 0.61 | 1 | 2 | 0.00 | 0.00 |
| 2009 | ACCI | 0.82 | 4.61E-04 | 38.01 | 1 | 6 | 66.78 | 0.06 |
| 2010 | ACCI | 0.74 | 2.37E-05 | 40.88 | 1 | 3 | 76.61 | 0.03 |
| 2011 | ACCI | 0.86 | 1.22E-07 | 95.72 | 1 | 4 | 80.00 | 0.05 |
| 2012 | ACCI | 0.65 | 9.77E-05 | 28.91 | 1 | 4 | 94.24 | 0.03 |
| 2013 | ACCI | 0.67 | 7.14E-05 | 30.82 | 1 | 4 | 76.46 | 0.03 |
| 2014 | ACCI | 0.72 | 1.89E-05 | 39.96 | 1 | 4 | 71.22 | 0.02 |
| 2015 | ACCI | Not Sig | 8.76E-01 | 0.03 | 1 | 5 | 0.00 | 0.00 |
| 2016 | ACCI | 0.52 | 1.02E-03 | 17.07 | 1 | 4 | 74.38 | 0.02 |
| 2009 | CHUM | 0.72 | 3.19E-04 | 28.73 | 1 | 7 | 90.57 | 0.05 |
| 2010 | CHUM | 0.71 | 2.01E-04 | 29.70 | 1 | 8 | 88.36 | 0.06 |
| 2011 | CHUM | 0.69 | 2.64E-04 | 27.79 | 1 | 8 | 96.87 | 0.06 |
| 2012 | CHUM | 0.74 | 1.07E-04 | 34.52 | 1 | 8 | 91.44 | 0.06 |
| 2013 | CHUM | 0.68 | 3.06E-04 | 26.78 | 1 | 8 | 88.10 | 0.05 |
| 2014 | CHUM | 0.51 | 3.59E-03 | 13.58 | 1 | 8 | 81.96 | 0.04 |
| 2015 | CHUM | 0.61 | 4.06E-02 | 8.89 | 1 | 9 | 75.81 | 0.04 |
| 2016 | CHUM | Not Sig | 2.14E-01 | 1.74 | 1 | 8 | 0.00 | 0.00 |
| 2009 | COCA | Not Sig | 4.29E-01 | 0.83 | 1 | 2 | 0.00 | 0.00 |
| 2010 | COCA | 0.81 | 1.34E-03 | 31.71 | 1 | 10 | 4.83 | 0.11 |
| 2011 | COCA | 0.89 | 2.68E-04 | 57.94 | 1 | 10 | 53.35 | 0.09 |
| 2012 | COCA | 0.77 | 2.66E-03 | 24.20 | 1 | 10 | 66.43 | 0.07 |
| 2013 | COCA | 0.92 | 1.00E-04 | 82.47 | 1 | 10 | 47.10 | 0.07 |
| 2014 | COCA | Not Sig | 1.80E-01 | 2.30 | 1 | 10 | 0.00 | 0.00 |
| 2015 | COCA | Not Sig | 1.60E-01 | 15.17 | 1 | 1 | 0.00 | 0.00 |

| | | | | | | | | |
|------|------|---------|----------|--------|---|----|--------|------|
| 2016 | COCA | 0.78 | 2.35E-03 | 25.44 | 1 | 10 | 42.06 | 0.06 |
| 2009 | COLA | Not Sig | 4.33E-01 | 1.53 | 1 | 1 | 0.00 | 0.00 |
| 2010 | COLA | 0.52 | 4.08E-02 | 7.50 | 1 | 5 | 67.45 | 0.04 |
| 2011 | COLA | 0.91 | 1.64E-04 | 69.20 | 1 | 10 | 59.60 | 0.07 |
| 2012 | COLA | 0.71 | 5.48E-03 | 17.91 | 1 | 10 | 86.57 | 0.03 |
| 2013 | COLA | 0.96 | 1.72E-05 | 152.61 | 1 | 10 | 64.61 | 0.05 |
| 2014 | COLA | 0.65 | 9.62E-03 | 13.99 | 1 | 10 | 64.41 | 0.03 |
| 2015 | COLA | Not Sig | 8.98E-01 | 0.02 | 1 | 11 | 0.00 | 0.00 |
| 2016 | COLA | 0.44 | 4.40E-02 | 6.46 | 1 | 10 | 61.96 | 0.03 |
| 2009 | LIBO | Not Sig | 9.25E-02 | 4.85 | 1 | 9 | 0.00 | 0.00 |
| 2010 | LIBO | 0.44 | 5.54E-03 | 11.38 | 1 | 12 | 52.25 | 0.05 |
| 2011 | LIBO | 0.80 | 9.04E-06 | 53.80 | 1 | 12 | 60.40 | 0.08 |
| 2012 | LIBO | 0.73 | 5.48E-05 | 36.99 | 1 | 12 | 93.02 | 0.04 |
| 2013 | LIBO | 0.80 | 8.93E-06 | 53.93 | 1 | 12 | 60.30 | 0.06 |
| 2014 | LIBO | 0.77 | 2.55E-05 | 43.53 | 1 | 12 | 62.59 | 0.03 |
| 2015 | LIBO | Not Sig | 5.46E-01 | 0.43 | 1 | 9 | 0.00 | 0.00 |
| 2016 | LIBO | 0.63 | 3.98E-04 | 23.53 | 1 | 12 | 46.40 | 0.03 |
| 2009 | PSME | 0.88 | 1.18E-02 | 30.38 | 1 | 2 | 121.87 | 0.03 |
| 2010 | PSME | 0.86 | 4.99E-07 | 83.72 | 1 | 3 | 125.57 | 0.05 |
| 2011 | PSME | 0.90 | 1.36E-08 | 135.87 | 1 | 4 | 136.52 | 0.04 |
| 2012 | PSME | 0.71 | 2.65E-05 | 37.45 | 1 | 4 | 128.15 | 0.03 |
| 2013 | PSME | 0.81 | 1.51E-06 | 62.94 | 1 | 4 | 111.08 | 0.03 |
| 2014 | PSME | 0.73 | 1.38E-05 | 42.38 | 1 | 4 | 118.31 | 0.03 |
| 2015 | PSME | 0.94 | 2.34E-04 | 87.73 | 1 | 5 | 114.31 | 0.03 |
| 2016 | PSME | 0.71 | 2.48E-05 | 37.95 | 1 | 4 | 112.21 | 0.03 |
| 2009 | RHMA | 0.77 | 1.21E-03 | 27.38 | 1 | 6 | 132.82 | 0.02 |
| 2010 | RHMA | 0.75 | 1.56E-03 | 25.02 | 1 | 6 | 126.52 | 0.04 |
| 2011 | RHMA | 0.92 | 3.23E-05 | 88.22 | 1 | 6 | 131.83 | 0.04 |
| 2012 | RHMA | Not Sig | 5.70E-02 | 5.18 | 1 | 6 | 0.00 | 0.00 |
| 2013 | RHMA | 0.42 | 3.62E-02 | 6.69 | 1 | 6 | 125.40 | 0.02 |
| 2014 | RHMA | 0.65 | 5.56E-03 | 15.57 | 1 | 6 | 118.88 | 0.02 |
| 2015 | RHMA | Not Sig | 7.67E-01 | 0.15 | 1 | 1 | 0.00 | 0.00 |
| 2016 | RHMA | Not Sig | 5.46E-02 | 5.31 | 1 | 6 | 0.00 | 0.00 |
| 2009 | RUUR | 0.44 | 4.34E-02 | 6.51 | 1 | 10 | 119.15 | 0.02 |

| | | | | | | | | |
|------|------|---------|----------|--------|---|----|--------|------|
| 2010 | RUUR | 0.76 | 1.49E-05 | 44.76 | 1 | 3 | 64.71 | 0.07 |
| 2011 | RUUR | 0.89 | 1.08E-07 | 109.15 | 1 | 3 | 78.04 | 0.08 |
| 2012 | RUUR | 0.79 | 6.32E-06 | 52.77 | 1 | 3 | 94.73 | 0.05 |
| 2013 | RUUR | 0.83 | 1.71E-06 | 67.22 | 1 | 3 | 67.38 | 0.06 |
| 2014 | RUUR | 0.71 | 4.50E-05 | 35.91 | 1 | 3 | 64.38 | 0.04 |
| 2015 | RUUR | Not Sig | 5.00E-01 | 0.55 | 1 | 9 | 0.00 | 0.00 |
| 2016 | RUUR | 0.72 | 3.59E-05 | 37.60 | 1 | 3 | 65.02 | 0.05 |
| 2009 | SYRE | Not Sig | | | | | 0.00 | |
| 2010 | SYRE | Not Sig | 5.64E-02 | 9.17 | 1 | 2 | 0.00 | 0.00 |
| 2011 | SYRE | 0.97 | 1.28E-03 | 141.62 | 1 | 2 | 50.31 | 0.08 |
| 2012 | SYRE | Not Sig | 6.49E-02 | 8.14 | 1 | 2 | 0.00 | 0.00 |
| 2013 | SYRE | 0.76 | 3.52E-02 | 13.42 | 1 | 2 | 65.44 | 0.04 |
| 2014 | SYRE | Not Sig | 1.44E-01 | 3.88 | 1 | 2 | 0.00 | 0.00 |
| 2016 | SYRE | Not Sig | 1.64E-01 | 3.37 | 1 | 2 | 0.00 | 0.00 |
| 2009 | TROV | Not Sig | | | | | 0.00 | |
| 2010 | TROV | 0.92 | 2.42E-05 | 96.37 | 1 | 6 | 41.68 | 0.06 |
| 2011 | TROV | 0.94 | 8.66E-06 | 131.32 | 1 | 6 | 52.35 | 0.08 |
| 2012 | TROV | 0.95 | 1.29E-04 | 112.57 | 1 | 5 | 63.68 | 0.06 |
| 2013 | TROV | 0.90 | 5.35E-06 | 90.74 | 1 | 13 | 58.88 | 0.05 |
| 2014 | TROV | 0.83 | 8.31E-06 | 60.83 | 1 | 8 | 54.74 | 0.04 |
| 2015 | TROV | 0.75 | 1.57E-02 | 16.25 | 1 | 9 | 54.35 | 0.04 |
| 2016 | TROV | 0.88 | 1.15E-06 | 91.49 | 1 | 8 | 59.71 | 0.04 |
| 2009 | TSHE | 0.59 | 1.22E-03 | 18.62 | 1 | 8 | 133.90 | 0.02 |
| 2010 | TSHE | 0.79 | 2.96E-06 | 55.98 | 1 | 4 | 140.89 | 0.03 |
| 2011 | TSHE | 0.90 | 1.32E-08 | 136.43 | 1 | 4 | 143.07 | 0.03 |
| 2012 | TSHE | 0.71 | 2.55E-05 | 37.74 | 1 | 4 | 144.65 | 0.02 |
| 2013 | TSHE | 0.61 | 2.22E-04 | 24.29 | 1 | 4 | 139.02 | 0.02 |
| 2014 | TSHE | 0.59 | 3.20E-04 | 22.41 | 1 | 4 | 131.39 | 0.02 |
| 2015 | TSHE | 0.60 | 2.55E-02 | 9.91 | 1 | 5 | 132.88 | 0.02 |
| 2016 | TSHE | 0.51 | 1.19E-03 | 16.41 | 1 | 4 | 129.38 | 0.02 |
| 2009 | VAPA | Not Sig | | | | | 0.00 | |
| 2010 | VAPA | 0.75 | 7.92E-04 | 27.37 | 1 | 14 | 61.49 | 0.04 |
| 2011 | VAPA | 0.93 | 3.56E-07 | 138.08 | 1 | 7 | 68.81 | 0.06 |
| 2012 | VAPA | 0.56 | 2.93E-03 | 15.26 | 1 | 7 | 92.07 | 0.03 |

| | | | | | | | | |
|------|------|---------|----------|--------|---|---|-------|------|
| 2013 | VAPA | 0.67 | 6.68E-04 | 23.55 | 1 | 7 | 65.11 | 0.04 |
| 2014 | VAPA | 0.80 | 4.84E-05 | 46.02 | 1 | 7 | 58.44 | 0.03 |
| 2015 | VAPA | Not Sig | 9.52E-01 | 0.00 | 1 | 2 | 0.00 | 0.00 |
| 2016 | VAPA | Not Sig | 9.01E-02 | 3.52 | 1 | 7 | 0.00 | 0.00 |
| 2009 | WISE | 0.78 | 9.47E-04 | 29.80 | 1 | 6 | 72.42 | 0.05 |
| 2010 | WISE | 0.56 | 2.00E-03 | 16.19 | 1 | 8 | 35.23 | 0.07 |
| 2011 | WISE | 0.91 | 2.51E-08 | 139.65 | 1 | 3 | 31.21 | 0.10 |
| 2012 | WISE | 0.90 | 4.06E-08 | 128.85 | 1 | 3 | 37.08 | 0.08 |
| 2013 | WISE | 0.76 | 1.50E-05 | 44.74 | 1 | 3 | 46.82 | 0.06 |
| 2014 | WISE | 0.35 | 1.21E-02 | 8.49 | 1 | 3 | 49.21 | 0.04 |
| 2015 | WISE | Not Sig | 3.55E-01 | 1.09 | 1 | 9 | 0.00 | 0.00 |
| 2016 | WISE | 0.69 | 7.20E-05 | 32.58 | 1 | 3 | 27.61 | 0.06 |

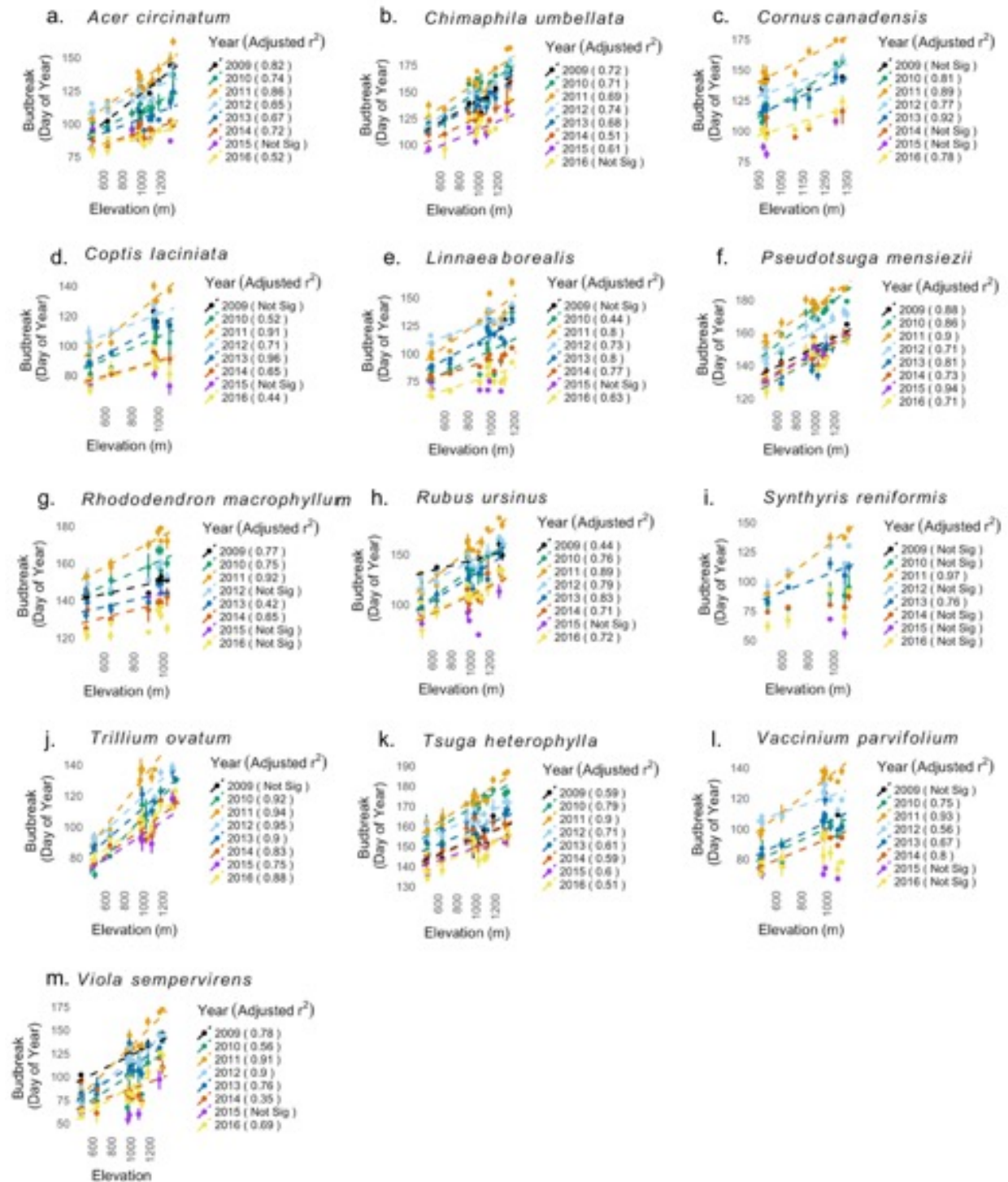


Figure S1: Elevation as a predictor of bud break for focal species from 2009-2016. Colors represent year, while dashed line is the line of best fit. Error bars are \pm SE. *Abies amabilis*, *Abies procera*, *Acer macrophyllum*, *Cornus nuttallii* and *Vaccinium membranaceum* are not included due to limited distribution and small sample sizes.

APPENDIX B

APPENDIX S2

Table S1: Location data of phenology sites

| Site Code | Site Type | UTM X (m, zone 10) | UTM Y (m, zone 10) | Latitude (dd.mmss) | Longitude (dd.mmss) | Elevation (m) |
|--------------|--------------|-----------------------|-----------------------|-----------------------|------------------------|------------------|
| PC01 | PC | 559337.35 | 4895046.44 | 44.2062254 | -122.25732 | 489 |
| PC02 | PC | 560002.77 | 4896020.61 | 44.2149409 | -122.24888 | 478 |
| PC04 | PC | 559036.61 | 4896294.35 | 44.2174841 | -122.26094 | 487 |
| PC05 | PC | 559285.46 | 4896520.5 | 44.2194998 | -122.2578 | 643 |
| PC07 | PC | 563676.24 | 4896880.81 | 44.222373 | -122.20279 | 900 |
| PC08 | PC | 564602.71 | 4898330.95 | 44.2353459 | -122.19102 | 647 |
| PC09 | PC | 570158.63 | 4897484.72 | 44.2272141 | -122.12156 | 985 |
| PC10 | PC | 568428.4 | 4899050.06 | 44.2414701 | -122.14302 | 984 |
| PC11 | PC | 567818.24 | 4900020.42 | 44.2502624 | -122.15054 | 1115 |
| PC12 | PC | 567119.53 | 4899576.57 | 44.2463316 | -122.15934 | 1083 |
| PC13 | PC | 568962.13 | 4899919.42 | 44.2492458 | -122.13622 | 1178 |
| PC14 | PC | 567112.4 | 4900996.98 | 44.259119 | -122.15925 | 965 |
| PC15 | PC | 566249.07 | 4901763.91 | 44.2661021 | -122.16997 | 971 |
| PC16 | PC | 565638.52 | 4901903.32 | 44.2674124 | -122.1776 | 1025 |
| PC17 | PC | 568878.06 | 4902587.96 | 44.2732761 | -122.13692 | 1300 |
| PC18 | PC | 569001.89 | 4902746.4 | 44.2746907 | -122.13535 | 1330 |
| DT | DT | 560008.19 | 4896195.93 | 44.216519 | -122.24879 | 436 |

Table S2 Regression equations used to fill in any missing or erroneous temperature data.

| Site | Equation | Adjusted R ² | df | F-stat | P-value |
|------|-------------------------------|-------------------------|---------|---------|---------|
| PC01 | PC01 = RS02 x 0.941 + 0.649 | 0.989 | 1,45215 | 425924 | *** |
| PC02 | PC02 = CS2met x 0.933 + 1.074 | 0.986 | 1,49115 | 354185 | *** |
| PC04 | PC04 = RS89 x 0.985 + 0.632 | 0.994 | 1,54915 | 979041 | *** |
| PC05 | PC05 = RS86 x 0.992 + 0.430 | 0.994 | 1,44049 | 706341 | *** |
| PC07 | PC07 = RS05 x 0.987 - 0.075 | 0.996 | 1,55057 | 1271158 | *** |
| PC08 | PC08 = RS10 x 1.000 + 0.115 | 0.997 | 1,54568 | 1571495 | *** |
| PC09 | PC09 = RS12 x 1.001 + 0.381 | 0.992 | 1,53536 | 647952 | *** |
| PC10 | PC10 = RS05 x 1.003 - 0.568 | 0.986 | 1,54745 | 376250 | *** |
| PC11 | PC11 = RS26 x 0.975 - 0.554 | 0.991 | 1,47045 | 495211 | *** |
| PC12 | PC12 = RS26 x 0.979 + 0.107 | 0.996 | 1,54593 | 1402571 | *** |
| PC13 | PC13 = RS26 x 0.952 - 1.235 | 0.971 | 1,54196 | 181439 | *** |
| PC14 | PC14 = RS05 x 1.016 - 0.454 | 0.989 | 1,55067 | 485521 | *** |
| PC15 | PC15 = HI15 x 0.984 + 0.386 | 0.985 | 1,48635 | 320198 | *** |
| PC16 | PC16 = RS26 x 0.996 - 0.026 | 0.986 | 1,54059 | 372480 | *** |
| PC17 | PC17 = RS04 x 0.977 + 0.014 | 0.992 | 1,47550 | 595117 | *** |
| PC18 | PC18 = RS04 x 1.001 - 0.203 | 0.984 | 1,48787 | 308451 | *** |

Notes

-- Non Significant; * P<0.05; ** P<0.01; ***P<0.001; In the site column, PC represents “phenology core”; In the equation column, all abbreviations following = are representative of reference stands (RS) or other climate stations (HI15 and CS2met); df, degrees of freedom.

Table S3: Alternative and selected bud break models tested; final models in bold:

| Species | Model | CP | Adj R ² |
|------------------------------|---|--------------|--------------------|
| <i>Acer circinatum</i> | log(Budbreak)~ meanaprtemp + log(apr_chill.force) | 0.17 | 0.74 |
| <i>Acer circinatum</i> | log(Budbreak) ~ meanaprtemp + sqrt(days_below_0) + sqrt(DOYchilling_above_1200) | 2.09 | 0.74 |
| <i>Acer circinatum</i> | log(Budbreak) ~ meanaprtemp + sqrt(days_below_0) | 5.25 | 0.70 |
| <i>Pseudotsuga menziesii</i> | Budbreak ~ meanaprtemp + june force + lastdoybelow0 | 6.5 | 0.85 |
| <i>Pseudotsuga menziesii</i> | Budbreak ~ june force | 25.55 | 0.85 |
| <i>Pseudotsuga menziesii</i> | Budbreak ~ june_chill.force | 18.55 | 0.83 |
| <i>Vaccinium parvifolium</i> | sqrt(Budbreak)~ scale(obs_aprsnow) + scale(lastdoybelow0) + scale(meanaprtemp) + scale(sqrt(may_chill.force)) + scale(obs_aprsnow)*scale(sqrt(may_chill.force)) | 4.73 | 0.82 |
| <i>Vaccinium parvifolium</i> | sqrt(Budbreak)~ scale(lastdoybelow0) + scale(meanaprtemp) + scale(log(apr_chill.force)) | 0.09 | 0.81 |
| <i>Vaccinium parvifolium</i> | sqrt(Budbreak)~ scale(obs_aprsnow) + scale(lastdoybelow0) + scale(sqrt(mayforce)) + (obs_aprsnow)*scale(sqrt(mayforce)) | 2.69 | 0.78 |

| | | | |
|-------------------------------|--|-------------|-------------|
| <i>Vaccinium parvifolium</i> | $\text{sqrt}(\text{Budbreak}) \sim \text{scale}(\text{sqrt}(\text{days_below_0}) + \text{scale}(\text{meanaprtemp}) + \text{scale}(\log(\text{aprforce}))$ | 2.11 | 0.76 |
| <i>Trillium ovatum</i> | $\text{sqrt}(\text{Budbreak}) \sim (\text{obs_aprnsnow}) + (\text{sqrt}(\text{days_below_0})) + (\text{meanaprtemp})$ | 5.42 | 0.85 |
| <i>Trillium ovatum</i> | $\text{sqrt}(\text{Budbreak}) \sim \text{scale}(\text{sqrt}(\text{days_below_0})) + \text{scale}(\text{obs_aprnsnow}) + \text{scale}(\text{lastdoybelow0}) + \text{scale}(\text{meanaprtemp}) + \text{scale}(\text{sqrt}(\text{may_chill.force})) + \text{scale}(\text{sqrt}(\text{may_chill.force})) * \text{scale}(\text{obs_aprnsnow})$ | 6.42 | 0.86 |
| <i>Trillium ovatum</i> | $\text{sqrt}(\text{Budbreak}) \sim \text{scale}(\text{sqrt}(\text{days_below_0})) + \text{scale}(\text{obs_aprnsnow}) + \text{scale}(\text{lastdoybelow0}) + \text{scale}(\text{meanaprtemp}) + \text{scale}(\log(\text{apr_chill.force})) + \text{scale}(\log(\text{apr_chill.force})) * \text{scale}(\text{obs_aprnsnow})$ | 6.09 | 0.86 |

Table S4: Difference in observed and predicted bud break days.

| SITECODE ⁺ | Year | Species ⁺⁺ | Observed budbreak | Predicted budbreak | Difference (Days) | Elevation (m) |
|-----------------------|------|-----------------------|----------------------|-----------------------|----------------------|---------------|
| DiscTrail | 2014 | ACCI | 89 | 89.53 | -0.40 | 436 |
| DiscTrail | 2015 | ACCI | 88 | 86.29 | 1.43 | 436 |
| DiscTrail | 2016 | ACCI | 80 | 79.06 | 0.99 | 436 |
| PC02 | 2017 | ACCI | 84 | 92.00 | -8.00 | 478 |
| PC01 | 2017 | ACCI | 89 | 89.69 | -0.69 | 489 |
| PC05 | 2017 | ACCI | 91 | 90.86 | 0.14 | 643 |
| PC08 | 2017 | ACCI | 95 | 94.92 | 0.08 | 647 |
| PC07 | 2017 | ACCI | 99 | 103.07 | -4.07 | 900 |
| PC14 | 2017 | ACCI | 104 | 106.87 | -2.87 | 965 |
| PC15 | 2017 | ACCI | 100 | 104.73 | -4.73 | 971 |
| PC10 | 2017 | ACCI | 102 | 105.79 | -3.79 | 984 |
| PC09 | 2017 | ACCI | 106 | 110.65 | -4.65 | 985 |
| PC16 | 2017 | ACCI | 87 | 104.35 | -17.35 | 1025 |
| PC12 | 2017 | ACCI | 105 | 105.39 | -0.39 | 1083 |
| PC11 | 2017 | ACCI | 101 | 109.76 | -8.76 | 1115 |
| PC13 | 2017 | ACCI | 115 | 118.28 | -3.28 | 1178 |
| PC17 | 2017 | ACCI | 137 | 120.92 | 16.08 | 1300 |
| PC18 | 2017 | ACCI | 140 | 122.36 | 17.64 | 1330 |
| PC02 | 2017 | PSME | 140 | 148.89 | -8.89 | 478 |

| | | | | | | |
|-----------|------|-------|-----|--------|--------|------|
| PC01 | 2017 | PSME | 137 | 143.44 | -6.44 | 489 |
| PC05 | 2017 | PSME | 138 | 140.26 | -2.26 | 643 |
| PC08 | 2017 | PSME | 147 | 147.55 | -0.55 | 647 |
| PC07 | 2017 | PSME | 152 | 156.31 | -4.31 | 900 |
| PC14 | 2017 | PSME | 155 | 156.85 | -1.85 | 965 |
| PC15 | 2017 | PSME | 158 | 154.91 | 3.09 | 971 |
| PC10 | 2017 | PSME | 159 | 157.52 | 1.48 | 984 |
| PC09 | 2017 | PSME | 158 | 163.17 | -5.17 | 985 |
| PC16 | 2017 | PSME | 147 | 152.35 | -5.35 | 1025 |
| PC12 | 2017 | PSME | 152 | 153.81 | -1.81 | 1083 |
| PC11 | 2017 | PSME | 157 | 156.79 | 0.21 | 1115 |
| PC13 | 2017 | PSME | 161 | 165.13 | -4.13 | 1178 |
| PC17 | 2017 | PSME | 166 | 168.04 | -2.04 | 1300 |
| PC18 | 2017 | PSME | 168 | 168.70 | -0.70 | 1330 |
| DiscTrail | 2014 | TROV2 | 88 | 84.62 | 3.38 | 436 |
| DiscTrail | 2015 | TROV2 | 84 | 75.34 | 8.32 | 436 |
| DiscTrail | 2016 | TROV2 | 86 | 73.21 | 12.79 | 436 |
| PC02 | 2017 | TROV2 | 86 | 89.22 | -3.22 | 478 |
| PC01 | 2017 | TROV2 | 82 | 86.73 | -4.73 | 489 |
| PC08 | 2017 | TROV2 | 95 | 92.56 | 2.44 | 647 |
| PC14 | 2017 | TROV2 | 113 | 112.11 | 0.89 | 965 |
| PC15 | 2017 | TROV2 | 105 | 109.14 | -4.14 | 971 |
| PC09 | 2017 | TROV2 | 115 | 113.58 | 1.42 | 985 |
| PC16 | 2017 | TROV2 | 113 | 102.35 | 10.65 | 1025 |
| PC12 | 2017 | TROV2 | 105 | 102.31 | 2.69 | 1083 |
| PC11 | 2017 | TROV2 | 118 | 107.09 | 10.91 | 1115 |
| PC13 | 2017 | TROV2 | 130 | 122.41 | 7.59 | 1178 |
| PC17 | 2017 | TROV2 | 144 | 127.03 | 16.97 | 1300 |
| PC18 | 2017 | TROV2 | 146 | 128.55 | 17.45 | 1330 |
| DiscTrail | 2014 | VAPA | 88 | 79.14 | 8.86 | 436 |
| DiscTrail | 2015 | VAPA | 84 | 70.19 | 13.31 | 436 |
| DiscTrail | 2016 | VAPA | 71 | 66.47 | 4.33 | 436 |
| PC02 | 2017 | VAPA | 78 | 92.39 | -14.39 | 478 |
| PC01 | 2017 | VAPA | 79 | 83.23 | -4.23 | 489 |

| | | | | | | |
|--|------|------|-----|--------|--------|------|
| PC05 | 2017 | VAPA | 88 | 85.36 | 2.64 | 643 |
| PC08 | 2017 | VAPA | 87 | 92.35 | -5.35 | 647 |
| PC14 | 2017 | VAPA | 115 | 117.09 | -2.09 | 965 |
| PC15 | 2017 | VAPA | 102 | 115.71 | -13.71 | 971 |
| PC10 | 2017 | VAPA | 108 | 102.14 | 5.86 | 984 |
| PC09 | 2017 | VAPA | 116 | 122.99 | -6.99 | 985 |
| PC16 | 2017 | VAPA | 96 | 101.96 | -5.96 | 1025 |
| PC12 | 2017 | VAPA | 91 | 103.36 | -12.36 | 1083 |
| PC11 | 2017 | VAPA | 110 | 107.87 | 2.13 | 1115 |
| +PC = phenology core; DiscTrail = discovery trail | | | | | | |
| ++ACCI = <i>Acer circinatum</i> ; PSME = <i>Pseudotsuga menziesii</i> ; TROV2 = <i>Trillium ovatum</i> ; VAPA = <i>Vaccinium parvifolium</i> | | | | | | |

TABLE S5: Variables initially included in microclimate models.

| Microclimate variable | Predictor variables in initial models |
|------------------------------|---|
| April chilling after forcing | $\text{sqrt}(\text{apr_chill.force}) \sim \text{ELEVATION} + \text{tpi_500m} + \text{aspect} + \text{sqrt}(\text{biomass}) + \text{vegheight} + \text{Nov_Mar_acindex} + \text{Slope} + \text{mean_mar_temp_PRIMET}$ |
| DOY chilling above 1200 | $\text{sqrt}(\text{DOYchilling_above_1200}) \sim \text{ELEVATION} + \text{aspect} + \text{sqrt}(\text{biomass}) + \text{vegheight} + \text{Nov_Mar_acindex} + \text{Slope} + \text{mean_mar_temp_PRIMET}$ |
| Mean april tempearture | $\text{meanaprtemp} \sim \text{ELEVATION} + \text{tpi_500m} + \text{aspect} + \text{sqrt}(\text{biomass}) + \text{vegheight} + (\text{Nov_Mar_acindex}) + \text{mean_apr_temp_PRIMET} + \text{Slope}$ |
| Days below 0 | $\text{sqrt}(\text{days_below_0}) \sim \text{ELEVATION} + \text{tpi_500m} + \text{sqrt}(\text{biomass}) + (\text{Nov_May_acindex}) + \text{Slope} + \text{mean_temp_novmay_PRIMET}$ |
| Last day of year below 0 | $\text{lastdoybelow0} \sim \text{ELEVATION} + \text{tpi_500m} + \text{aspect} + \text{sqrt}(\text{biomass}) + (\text{Nov_May_acindex}) + \text{mean_temp_novmay_PRIMET} + \text{Slope}$ |
| June forcing after chilling | $\text{sqrt}(\text{jun_chill.force}) \sim \text{ELEVATION} + \text{tpi_500m} + \text{aspect} + \text{sqrt}(\text{biomass}) + \text{vegheight} + (\text{Nov_May_acindex}) + \text{Slope} + \text{meantemp_mar_may_PRIMET}$ |
| April 1 snow | $\text{snow_present} \sim \log(\text{biomass}) + \text{ELEVATION} + \text{sqrt}(\text{CENMET_snowdepth}) + \text{sqrt}(\text{UPLMET_snowdepth}) + \text{hja_aspect} + \text{avg_monthly_airtemp_PRIMET} + \text{avg_monthly_airtmepr_UPLMET}$ |

Table S6: Model summaries of microclimate predictions.

| Microclimate variable | Predictor variables | F-stat _(df) | R ² | p-value |
|------------------------------|---|--|----------------|---------|
| April chilling after forcing | ELEVATION + tpi_500m + sqrt(biomass) + Nov_Mar_acindex + Slope + mean_mar_temp_PRIMET | 72.3 _(6,121) | 0.78 | *** |
| DOY chilling above 1200 | Elevation + Nov_Mar_acindex | 117.8 _(2,125) | 0.65 | *** |
| Mean april tempearture | Elevation + tpi_500m + meanapriltemp_PRIMET + Slope | 464.4 _(4,123) | 0.94 | *** |
| Days below 0 | Elevation + tpi_500m + mean_temp_Nov-May_PRIMET | 138.9 _(3,124) | 0.77 | *** |
| Last day of year below 0 | Elevation + mean_temp_Nov-May_PRIMET | 169.9 _(2,125) | 0.731 | *** |
| June forcing after chilling | Elevation + tpi_500m + sqrt(biomass) + Nov_May_acindex + Slope + mean_temp_Mar-May_PRIMET | 177.8 _(6,121) | 0.90 | *** |
| April 1 snow | log(biomass) + ELEVATION + sqrt(CENMET_snowdepth) + avgUPLMET_airtemp | G2: 0.98 Deviance: 1105.326 Dispersion: 0.91 | | |

Table S7: Observed presence absence of April 1 snow versus predicted probability.

| Month | Mean | SD | Min | Max | Observations (n) |
|---------------|------|------|------|------|------------------|
| April absent | 0.27 | 0.25 | 0.02 | 0.89 | 51 |
| April present | 0.64 | 0.29 | 0.08 | 0.98 | 77 |

Table S8: Landscape model predictions of observed 2009 to 2016 bud break

| Species | R ₂ | F-stat _(df) | p-value |
|------------------------------|----------------|--------------------------|---------|
| <i>Acer circinatum</i> | 0.60 | 164.3 _(1,109) | *** |
| <i>Pseudotsuga menziesii</i> | 0.84 | 538.9 _(1,105) | *** |
| <i>Trillium ovatum</i> | 0.62 | 109.9 _(1,66) | *** |
| <i>Vaccinium parvifolium</i> | 0.19 | 17.79 _(1,75) | *** |

Figure S1

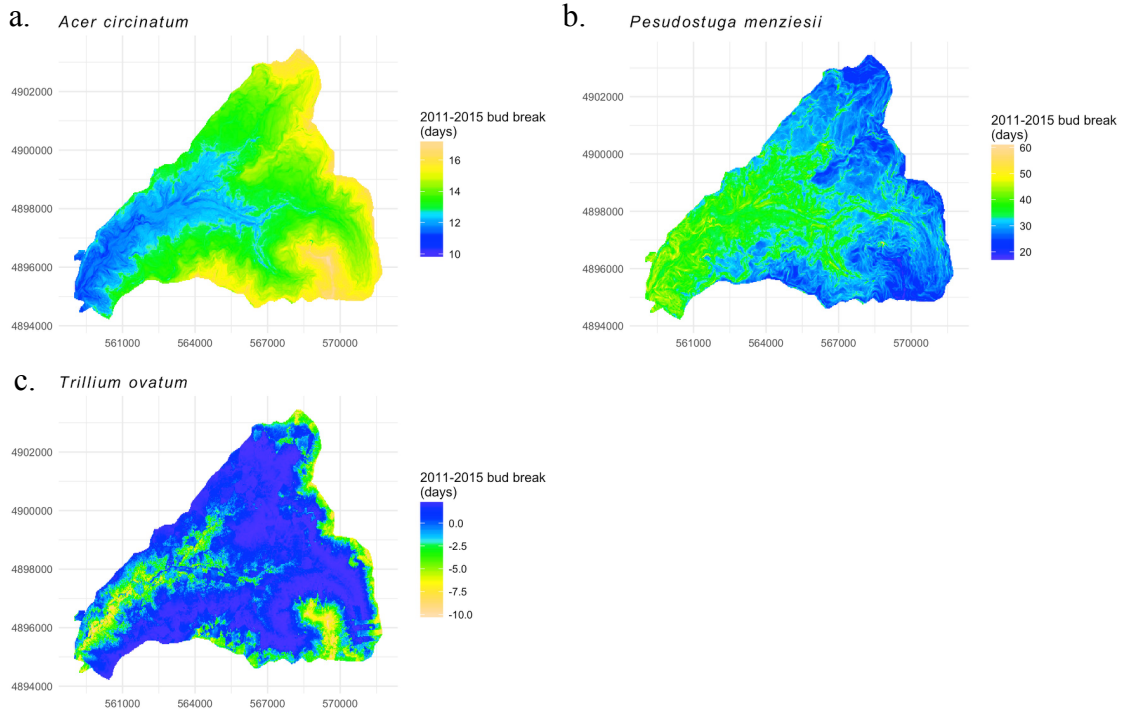


Figure 3: Range predicted bud break across the Andrews Mountains between the warmest (2015) and coolest (2011) years in the phenology record. (a) *Acer circinatum* (b) *Pseudotsuga menziesii* (c) *Trillium ovatum*. Colors represent the range between 2011 and 2015 values (2015 was the warmest year in the phenology record while 2011 was the coolest). Blues represent regions with the least range bud break, while yellows are the areas with the greatest range between the two years. Greens are intermediate. Red huckleberry is not presented due to limited accuracy of the landscape model

APPENDIX C

APPENDIX S3

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