

A long-term perspective on microclimate and spring plant phenology in the Western Cascades

SARAH E. WARD,^{1,†} MARK SCHULZE,² AND BITTY ROY¹

¹*Institute of Ecology and Evolution, 335 Pacific Hall, 5289 University of Oregon, Eugene, Oregon 97403 USA*

²*H.J. Andrews Experimental Forest, P.O. Box 300, 91991 Blue River Reservoir Road, Blue River, Oregon 97413 USA*

Citation: Ward, S. E., M. Schulze, and B. Roy. 2018. A long-term perspective on microclimate and spring plant phenology in the Western Cascades. *Ecosphere* 9(10):e02451. 10.1002/ecs2.2451

Abstract. Phenology—recurring seasonal events in an organism’s life cycle—is largely driven by local climates <1 km² (microclimates), and changes in phenology are frequently used to indicate a species’ or community response to climate change. Phenological shifts can result in trophic asynchrony, population declines of higher-level consumers, and reduction of plant fitness. While timing of phenological events is often correlated with elevation, studies have shown that microclimates created by areas of heterogeneous topography can be decoupled from regional climate patterns and that the distribution of microclimates does not always follow the elevation gradient. To examine the interaction between regional weather patterns and microclimate, and the subsequent effect of microclimate on phenology, we conducted standardized weekly spring phenology surveys of 18 native forest plants at the H.J. Andrews Experimental Forest in the Western Cascades from 2009 to 2016. We saw a high degree of inter-annual variability of microclimate within and across sites, resulting in a changing pattern of microclimate diversity across the landscape from year to year. Most importantly, we saw that years with regional conditions predicted by continued climate change showed a loss of diversity in both microclimate and phenological events, with a more rapid advancement in bud break occurring at higher elevation sites. This study highlights the importance of understanding the interactions between regional and local processes that determine microclimate conditions and how those conditions influence patterns of plant phenology within forest communities, across mountain landscapes and over time, with implications for the capacity of mountainous regions to buffer local communities against the effects of climate change.

Key words: bud break; climate variability; H.J. Andrews; long-term ecological research (LTER); microclimate; microclimate heterogeneity; topoclimate; vegetation phenology; Western Cascades.

Received 15 April 2018; revised 15 August 2018; accepted 22 August 2018. Corresponding Editor: Theresa M. Crimmins.

Copyright: © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** sward7@uoregon.edu

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, as many species have phenologies driven by

temperature cues, and phenological shifts can have significant impacts on the dynamics of an ecosystem (Walther et al. 2002, Parmesan 2006, Both et al. 2009, Fu et al. 2015). For example, 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). Thackeray et al. (2016) found that primary producers consistently have more advanced phenologies in response to seasonal warming than secondary consumers (-4.1 vs. -1.9 d/°C).

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 (Billings and Bliss 1959, Hwang et al. 2011, Lundquist et al. 2013, Sherwood et al. 2017, O'Leary et al. 2018). These microclimates can be significantly different from regional climate patterns, and for this reason, downscaling regional models may result in overgeneralization when projecting the effects of climate change (Daly et al. 2010, De Frenne et al. 2013, Franklin 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 toward lower elevation, accessible sites, leading to underrepresentation of remote mountainous sites as inputs into climatic models (Pepin et al. 2011).

Steep mountainous terrain often leads to persistent cold air pooling events 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, creating temperature inversions. These events, which can decouple valleys from regional atmospheric conditions for many days at a time, are a major driver of microclimate in mountainous regions, especially during winter months, and they are largely driven by interactions between topography, radiative cooling, and regional weather patterns (Daly et al. 2010, Pepin et al. 2011, Novick et al. 2016). In the study region, anticyclonic weather systems promote formation of cold air pools, especially in winter, while cyclonic systems result in well-mixed atmospheric conditions under which temperatures across the elevation gradient largely conform with expectations based on moist adiabatic lapse rates; Daly et al. (2010) derived an anticyclonic–cyclonic index (A–C index) as an indicator of the relative frequency of these regional weather systems. 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 in plant communities (i.e., earlier bud break or flowering; 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 (O'Leary et al. 2018). 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 (December–March) 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-ha (15,800 acre) forest located on the west side of the Cascade Mountains approximately 50 miles east of Eugene, Oregon, USA. 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. Snow is infrequent below 500 m, and intermittent snow occurs between 500 and 900 m, indicating average land surface temperatures above freezing in those elevation ranges (Moore et al. 2015). Above 900 m, substantial winter snowpack typically accumulates (Daly et al. 2010). Vegetation is primarily a combination of 150- to 500-yr-old mixed conifer forests and 40- to 60-yr-old *Pseudotsuga menziesii* (Douglas fir) plantations (Pelt and Franklin 2000).

Study design

Temperature and phenology data were collected from 16 core phenology sites (PC) across a variety of elevations and aspects, with sites

ranging from 460 to 1339 m (Fig. 1). Eleven of 16 sites were selected to be co-located with long-term temperature (Daly and McKee 2016a, b, Johnson and Gregory 2016) 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, and to relate microclimate measurements during the phenology study to long-term climate records. Five 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. Eighteen species of native herbs, shrubs, and trees were selected as target species (Appendix S1: Table S1). At each site, a center point was

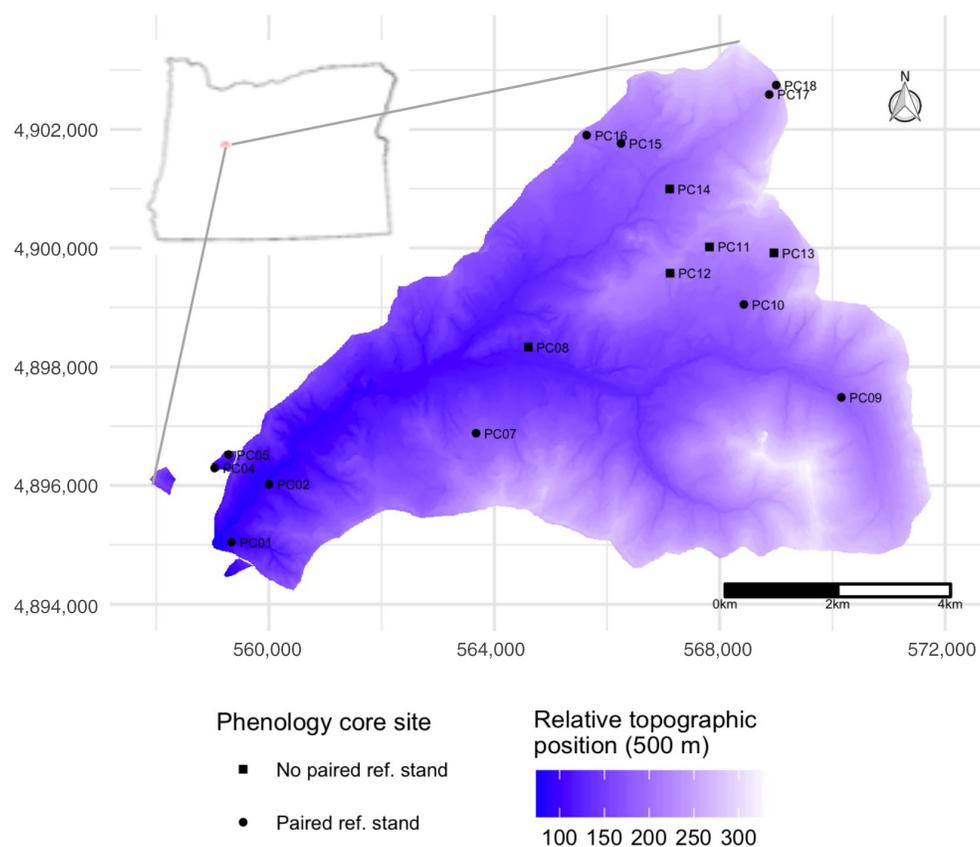


Fig. 1. Map showing the location and relative topographic position of the 16 core phenology sites at the H.J. Andrews. Colors are relative topographic position, with blues showing sites of low topographic relief, and whites showing sites with high topographic relief. Purples are intermediate values. 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. Map projection is NAD83.

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 25 m radius circle around the center point until five individuals of each species were mapped and tagged; in the 2009 pilot season, only three individuals per species were tagged, and 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 35 m 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 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, Hobo U22-001; accuracy 0.2°C, Bourne, Massachusetts, USA) temperature sensors were placed 1.5 m 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 (8 inch long, 3.5 inch schedule 40 pipe split in half lengthwise; see Frey et al. 2016b, Johnson and Gregory 2016, Daly 2017 for more information on shield design). Observations of snow depth and percent cover were made by researchers during each site visit, and partial or full burial under snow was recorded for each individual plant. These and supplemental observations were made to estimate last day of snow cover, and the number of days each site had significant snow (>50% cover). For sites/years in which snowmelt may have occurred one or more times during the winter prior to the initiation of phenology site visits, we extrapolated estimates using observations from opportunistic winter visits to phenology sites, and data from long-term snow stake datasets (three-week observations 1970–2014, daily 2015–2016; Schulze and Levno 2017), Andrews meteorological stations (hourly snow depth and SWE and monthly snow

course measurements; Daly and McKee 2016b), 45 time lapse cameras distributed across the forest, and observations from other researchers. Phenology sites were related to these supplemental data sources based on elevation, aspect, and forest cover, to infer presence/absence of snow on specific winter date ranges when direct observations were not possible.

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). Plants were typically scored on a scale of 1–6 for leaf emergence, with 1 representing dormant, and 6 representing full leaf size. Some plants have further stem elongation after full leaf out and have a score of 7, while other plants have intermediate stages. For example, *Pseudotsuga menziesii* (Douglas fir) has an intermediate stage between bud break (3) and emerging leaves (4) and has an additional score of 3.5. The same system was followed for reproductive phases, with 1 representing dormancy and 10 representing seed dispersal. See Schulze (2017) for the full list of species scores.

Over the course of each spring, the sites were visited once every 5–10 d, 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 to 2016, sites were typically visited once every 7 d. Observations began each year in late winter (mid-February to early April) 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 [DOY] weeks rather than based on the calendar of each year). For example, regardless of what day (Monday, Tuesday, etc.) 1 January falls on, the first DOY week begins on 1 January (DOY 1), and the midpoint is 4 January (DOY 4). Thus, any survey that occurs between DOY 1 and DOY 7 is standardized to DOY 4, and any survey that occurs between DOY 8 and DOY 14 is standardized to DOY 11, and so on. This way we could compare sites surveyed within the same week, but not on the same day without introducing bias from different survey dates. The median offset (error) between adjusted DOY and observed DOY was 2 d, with a maximum offset of 5 d. 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 has 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 DOY 30 and emerging leaves were observed on DOY 37, we interpolated that bud break occurred on DOY 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

Quality assurance and quality control was conducted on all temperature data collected. All data were averaged into hourly segments and run through a Python script (see Frey et al. 2016b, and Johnson and Hadley 2017 for script details) 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, b; 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 (GDD) were calculated by summing all degree hours $>5^\circ\text{C}$ accumulated over a 24-h period and dividing that sum by 24 to get the average daily accumulation of GDD for a given plot (Perry 1971, Murray et al. 1989, Heide 1993, Polgar and Primack 2011). As a general metric of temperature forcing across sites and years, we chose 1 December as the start date for accumulation of GDD and 1 April and 1 June as the end point for winter and spring cumulative GDD. Starting from 1 December, we added each subsequent daily accumulation of degree-days. Past studies have used a variety of dates to begin GDD accumulation; 1 November has been used for chilling and forcing phenology models for species such as Douglas fir (*P. menziesii*), while other studies have suggested 1 January as a start date for GDD accumulation (Harrington et al. 2010, Forrest and Thomson 2011). The first day of frost in some portions of our landscape can occur as late as end of November (Daly 2017), yet some of the species in our study were observed flowering or with bud swell in early January, indicating early winter forcing can be important. We recognize that herbaceous species growing above snow line are likely insulated from winter/early spring forcing; however, we chose this metric as an indicator of inter-annual variability in winter and early spring temperatures.

We compared April GDD accumulation to the winter A–C index developed by Daly et al. (2010 and Daly *unpublished data*), which is an indicator of year-to-year variability in regional winter (1 December–31 March) weather patterns (Appendix S1: Table S3). 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 calculated the relative topographic position index (TPI) of each site using R package *spatialEco* (function *tpi*) and used a 500 m radius around the phenology site. This function calculates the position of a given site relative to the topography within a 500 m radius, allowing for comparison of two sites regardless of elevation. Topographic Position Index

has been found to be a useful indicator (lower scores) of places on the landscape subject to cold air pooling (Daly et al. 2010). Slope, aspect, and elevation were derived from existing raster layers in the Andrews database (Valentine and Lienkaemper 2005, Spies 2016; Appendix S1: Table S4).

Analysis

Data analysis was conducted using R statistical software (version 3.3.2; R Core Team 2017) and R studio (version 1.0.153; RStudio Team 2016), with packages MASS, sp, Lattice, ggplot2, car, ggbiplot, plyr, Rmisc, permute, gridExtra, maps, maptools, rgdal, raster, leaps, vegan, ggsn, scales, devtools, and DescTools (Venables and Ripley 2002, Pebesma and Bivand 2005, Sarkar 2008, Wickham 2009, Fox and Weisberg 2011, Vu 2011, Wickham 2011, 2017, Bivand et al. 2013, Hope 2013, Simpson 2016, Auguie 2017, Baquero 2017, Becker and Deckmyn 2017, Bivand and Lewinkoh 2017, Bivand et al. 2017, Hijmans 2017, Miller 2017, Oksanen et al. 2017, Wickham and Chang 2017, Signorell et al. 2018). To compare the 8 yr of phenology to historic temperature patterns, we looked at temperature data between 1974 and 2016 from two permanent meteorological reference stands (RS) on the Andrews, one on a high-elevation ridge with a high relative topographic position (RS04, 1307 m, TPI = 232.49) and one in a low-elevation valley (RS02, 489 m, TPI = 53.58). To see the relationship between A–C index and temperature inversions (where temperatures are lower at lower elevations than higher elevations), we looked at two metrics; we used linear regression to compare how the maximum winter temperature at each site deviated from the average maximum (1974–2016) at a given A–C index. We also used linear regression to see how well A–C index predicted the percentage of winter days when the daily temperature of RS04 exceeded RS02 (e.g., in 1974 on 19 of 121 winter days, or 15.7% of the winter, RS04 was warmer than RS02). For the 8 yr of phenology data, we conducted the same analysis as above using two phenology core (PC) sites located within 250 m of RS02 (PC02, 478 m, TPI = 76.65) and RS04 (PC17, 1300 m, TPI = 229.10). We looked at the relationship between winter A–C index and winter GDD accumulation, as well as how TPI affected the maximum winter temperature at each site.

To see how each year varied across all sites, we looked at GDD accumulation between January and June (Appendix S1: Table S5), and we also looked at estimated snow depth at each PC site (Appendix S1: Table S6) and snow depth at a permanent meteorological station (VANMET, 1285; m; Daly and McKee 2016b). As herbaceous species are likely insulated by snowpack and thus do not experience forcing until after snowmelt, we also compared 1 April and 1 June GDD accumulated from 1 December vs. GDD accumulated after snowmelt. Additionally, collinear temperature variables (Appendix S1: Table S7) were condensed using principal components analysis (PCA) to compare microclimates between years and across sites; all assumptions of a PCA were tested. We used the first principal component to derive a multiple linear regression with physical variables predicting differences in temperature metrics across sites. We used best subsets (rpackage Leaps, function leaps()) to select a model with the fewest variables and most predictive power. The function outputs a mallows C_p score (models are penalized for each additional variable) and an adjusted R^2 for each potential model. We selected the model that met all assumptions of a linear regression (i.e., no collinearity (function vif(), values >0.2 and <5), normal residuals, and homogeneity of variance), and had the lowest C_p score and highest predictive power.

Although we collected data on all stages of leaf expansion and flowering, we focused this analysis on the timing of bud break and peak flowering as these are well-documented metrics of plant phenology (Parmesan 2006). To see how variability in regional weather patterns affected bud break, we compared inter-annual variability in the timing of bud break across the PC sites. We subtracted the difference between the earliest and latest phenology years to find the maximum difference in bud break dates (Appendix S1: Table S8). Additionally, we used linear regression to test elevation, as a proxy for microclimate, as a predictor of bud break and flowering in each year of the study; if inter-annual variability in weather patterns is altering microclimate diversity in a way that is meaningful for plant phenology, we expected the slope and strength of the elevation relationship to vary by year. The assumptions of linear models were checked for each model (Appendix S1:

Tables S9, S10). See supporting information (Data S1) for data files and R code.

RESULTS

Microclimate

From 2009 to 2016, there was a large amount of inter-annual variability both within and across sites. To see how the climate during the phenology study compared to other years at the Andrews, we looked at temperature data from two historic reference stands (RS) with contrasting elevations and topographic positions (RS02, 489 m valley and RS04, 1307 m slope) associated with phenology sites. We found that from 1974

until 2016, the A–C index between 1 December and 31 March (hereafter, winter) fluctuated greatly between years, with a range from -7 to 45 (Fig. 2a). Winter GDD varied substantially over this time period, with a range from 2.5 to 165.5 GDD at RS04 and a range between 11 and 230.2 at RS02 (Fig. 2b). 1982 had the lowest A–C index (-7) and the winter GDD at both the high- and low-elevation sites were nearly 0, with little difference between the two sites. In contrast, 2015 had an A–C index of 44 and winter GDD were 165.5 and 230.2 at RS04 and RS02, respectively. That year, both RS02 and RS04 accumulated more GDD than any other year in the 46-yr record, and that year the GDD at RS04 exceeded all but 4 yr

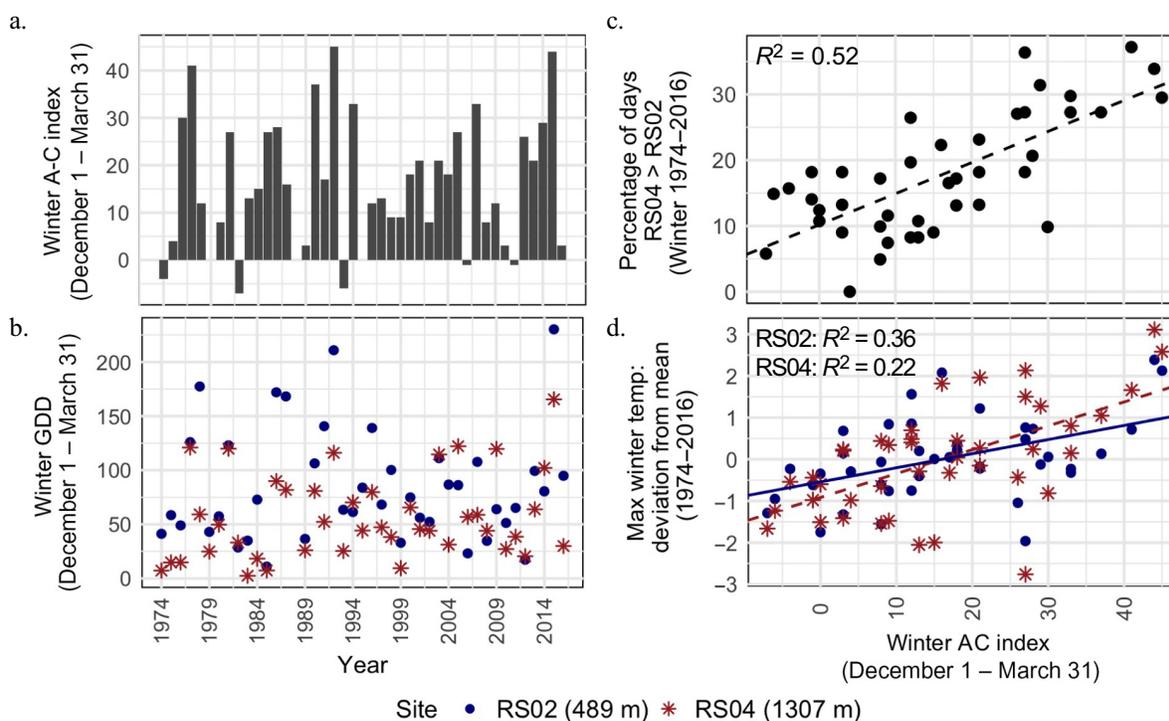


Fig. 2. (a) Historic winter anticyclonic–cyclonic (A–C) index values for the entire Andrews watershed from 1974 until 2016. (b) Winter growing degree-days between 1974 and 2016 from two reference stands at the H.J. Andrews. Red asterisks indicate data from reference stand 2 (RS02), which is located at 489 m in an old-growth forest in Lookout Creek valley. Blue circles indicate data from reference stand 4 (RS04), which also located in an old-growth stand, but at 1307 m on the upper 1/3 of the east bounding ridge of Lookout watershed. (c) The percentage of days where daily winter temperature at RS04 exceeded RS02 relative to the winter A–C index. Each point represents a year between 1974 and 2016, while the dashed line is a line of best fit, with an R^2 of 0.52. (d) The deviation of maximum winter (1 December–31 March) temperature from the mean (1974–2016) at RS02 and RS04 from 1974 to 2016 relative to A–C index. Blue circles represent RS04, and red asterisks represent RS02. Lines (dashed red for RS02 and solid blue for RS04) are lines of best fit, which explain 0.36% and 0.22% of the variation in the data, respectively.

of GDD at RS02. We found across both sites, the A–C index had a correlation coefficient of 0.53 with winter GDD; however, when we looked at each site individually, the A–C index had a stronger effect on winter GDD at the higher elevation site, with a correlation of 0.61 with winter GDD at RS04 vs. 0.54 at RS02. Anticyclonic–cyclonic index explained 52% of the variance in the number of days where mean daily temperature at RS04 exceeded RS02 ($F = 42.47_{(1,40)}$, $P = 8.87 \times 10^{-8}$; Fig. 2c). We also found that in years with high winter A–C index values, the maximum winter temperature at RS04 deviates more from the average (1974–2016) than RS02, while in years with low winter A–C index values, the opposite is true (Fig. 2d). This is likely due to cold air pooling events buffering temperatures at low-elevation sites during years with high A–C indices.

The eight years when phenology surveys occurred also displayed extreme inter-annual variability within and across sites, especially during winter months (Fig. 3a). We compared the number of winter days where daily temperatures at PC17 (<100 m from RS04) exceeded PC02 (<250 m from RS02), and found that the A–C index explained 81.2% of the variance in the data ($F = 25.82_{(1,6)}$, $P = 0.002$; Fig. 3b), suggesting that during the phenology study, cold air pooling events had a strong effect on microclimate variation across the elevation gradient. We also see that temperature differentials between high- and low-elevation sites vary greatly based on daily A–C conditions and that this effect is largely diminished as spring progresses (typically after early to mid-April; Appendix S1: Fig. S1). Anticyclonic–cyclonic index was positively correlated (0.42) with winter GDD accumulation, and years with low A–C indices had a greater variation across sites in the rate of GDD accumulation than years with high A–C indices (Spearman rank correlation of -0.47 between the winter A–C index and the annual range of 1 April GDD; Fig. 3c).

In 2015, the year with the highest A–C index, we saw a homogenization of GDD accumulation across the elevation gradient. That year, sites 500 m apart in elevation (PC01 and PC16) accumulated the same amount of GDD (242.6 and 242.7) between 1 December and 31 March. Sites with high relative topographic position saw greater inter-annual variability in maximum winter temperature than sites with low topographic

position during phenology years (Fig. 3d), which likely contributed to the rapid accumulation of winter GDD at higher elevation sites. 2015 had the highest A–C index and was the warmest year at all sites, and the rate of GDD accumulation was nearly linear at PC12 and PC17, both sites with a relatively high topographic position (243.6 and 229.1 respectively; Fig. 3e). In contrast, PC02 is a site with a topographic position of 76.7, and GDD accumulation followed a more logarithmic pattern in 2015, likely due to frequent winter cold air pooling and a lack of persistent cold air pools in the spring.

Snow was highly variable across all phenology years, and early winter snow accumulation was not a good indication of the persistence of snow cover into the spring. 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 VANMET (a meteorological station at 1285 m), while all of the other years had little to no snow by 1 June (Fig. 4a). The phenology sites maintained a similar pattern, with the number of days with snow cover varying by more than 100 d across years at PC17 (Fig. 4b). 2016 had the most days with snow; however, most of that snow fell in the early winter, and by February, the snow pack at VANMET was below the 10-yr average and snowmelted by early May. 2015 had nearly no snow by February but had more snow in January at VANMET than 2012, which had a snow pack 500 mm above average on 1 April. In terms of late winter/early spring snow pack, 2011 and 2015 again represent the extremes in inter-annual snow variability, with over a meter of snow at VANMET on 1 June 2011, and no snow on the same date in 2015. The first date where 0% of plants were buried under snow was on average 94 d earlier in 2015 than in 2011 (Appendix S1: Table S6). One mid-elevation site (PC15, 971 m) had all plants exposed 144 d earlier in 2015 than in 2011.

In 62 of 128 (48%) site/year combinations, 0 GDD accumulated by 1 April when date of snowmelt was the starting point, vs. no sites/years with 0 GDD by 1 April with 1 December as a starting date. In these circumstances, early season air temperature forcing is likely lost on those plants buried by snow. For example, in 2012, deep and persistent snowpack at mid- to high-elevation sites despite a relatively warm spring

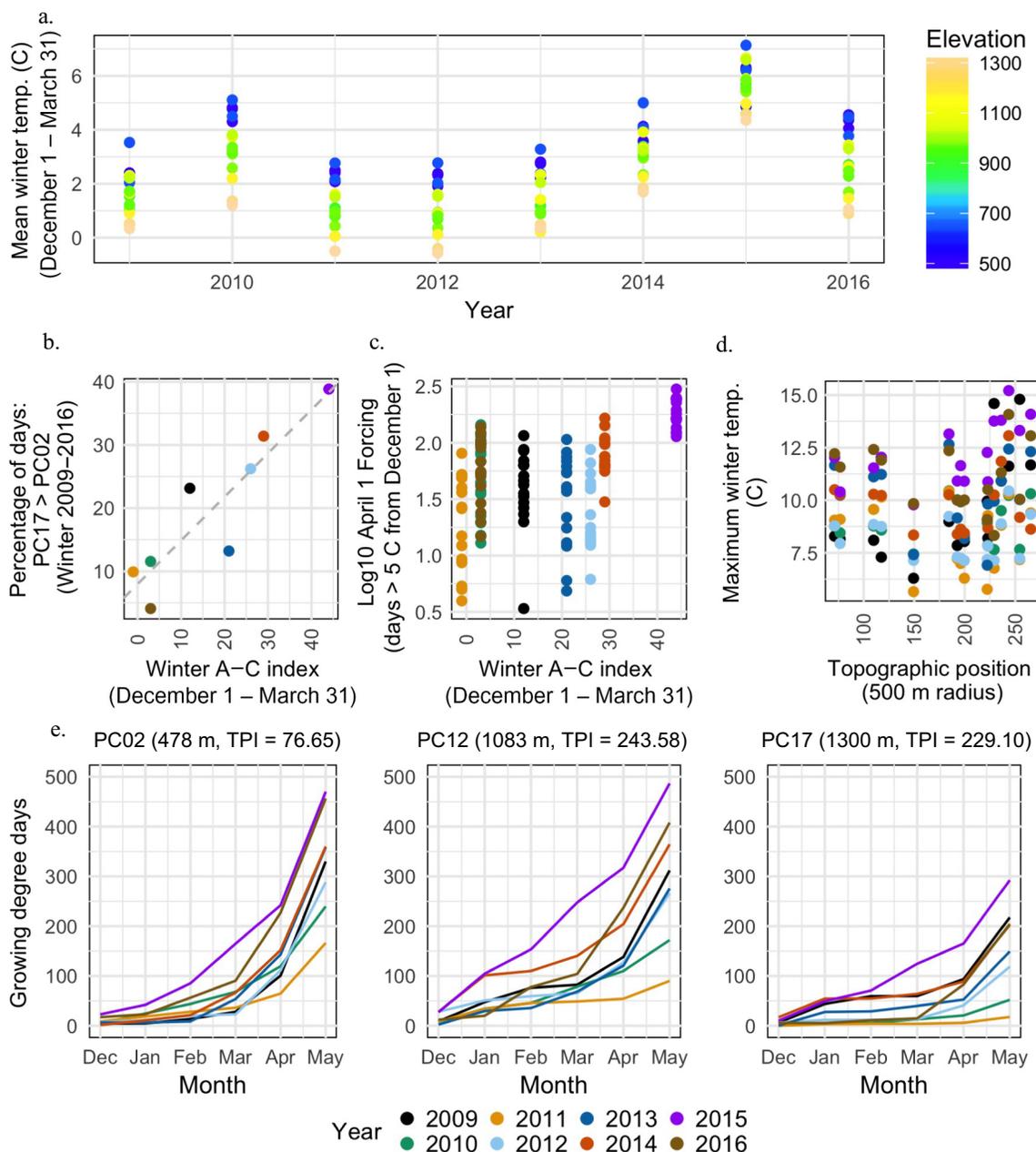


Fig. 3. Microclimate patterns 2009–2016. (a) Mean winter temperatures at all sites. Colors represent elevation, with low-elevation sites in blue, high-elevation sites in yellow. Intermediate elevations are in green. (b) Percentage of days where daily winter temperature at PC17 (1300 m) exceeds PC02 (478 m) relative to the winter anticyclonic-cyclonic (A–C) index. The dashed line is a line of best fit that explains 81% of the variance in the data and color represents year. (c) Growing degree-days accumulated on 1 April at each site relative to the winter A–C index. Growing degree-days are on a log (base 10) scale, colors are different years, with each colored point representing a different site during a given year. (d) Maximum winter temperature at a given topographic position (from a 500 m radius). Colors are different years, with each colored point representing a different site during a given year. (e) Growing degree day accumulation curves for a low (PC02)-, mid (PC12)-, and high (PC17)-elevation site from 2009 to 2016. Colors represent years, and topographic position index (TPI) is noted at the top of each panel.

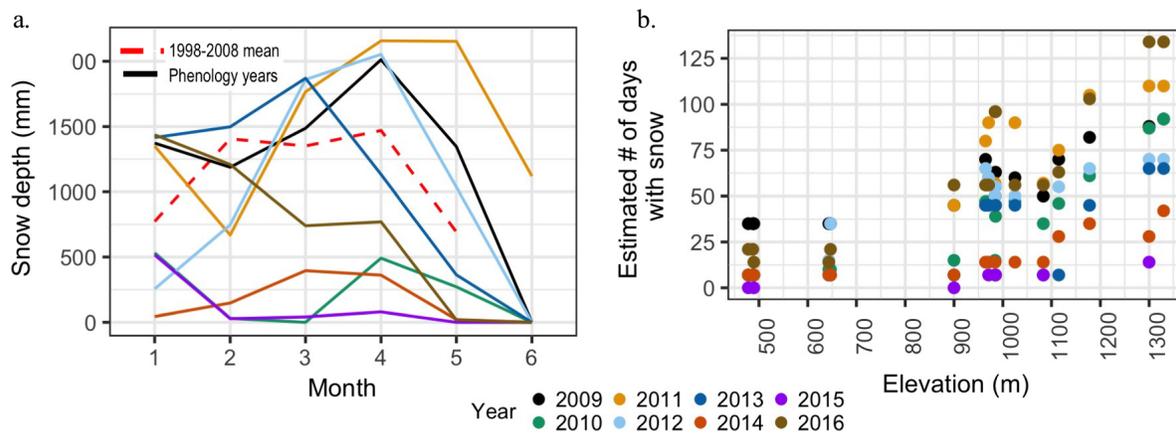


Fig. 4. Snow cover during the phenology years. (a) Snow depth at a high-elevation meteorological station (VANMET, 1268 m) on the first of each month between January and June. The red dashed line is the 10-yr average from 1998 to 2008, and the solid lines are phenology years. Colors are different years. (b) Estimated number of days of snow at each phenology site in a given year from 1 December. Data were estimated using observations and nearby meteorological stations and snow stakes. Colors represent years, while each point is a site in a given year.

resulted in large difference between early season GDD accumulation above the snowpack and temperatures herbs and shrubs experienced during this period, as well as a greater range in microclimate conditions across the elevation gradient than is apparent from GDD values alone (Appendix S1: Fig. S2). In contrast, years like 2014, 2015, and 2016 with minimal snow by 1 April, there appears to be little difference between 1 April GDD accumulated after snowmelt and 1 April GDD accumulated beginning 1 December.

Principal components analysis illustrated that A–C index, in addition to fixed topographic characteristics, was an important predictor of variability across sites/years in temperature variables and snowmelt date (Fig. 5; Appendix S1: Table S11). The first two principal components of the microclimate PCA explained 73.3% of the variance in microclimates among sites and years. The first principal component explained 63.0% of the variation among sites and years, and primarily separated sites by mean seasonal temperature (Fall: October–December, winter: January–March, spring: April–June and summer: July–September) mean annual temperature (1 November–31 October) and 1 April GDD (from 1 December). The second principal component explained 10.3% of the variance between site microclimates, and

primarily separated sites by fall average temperature (89.4% of the axis). We used best subsets (rfunction leaps) to select a linear model using physical variables to predict principal component 1 and were able to predict 73.1% of the variance in PC1 using aspect, slope, elevation, TPI, and winter A–C index ($F_{(5, 122)} = 66.39$, $P < 2.2 \times 10^{-16}$). Winter A–C index alone explained 23.3% of the variance ($F_{(1, 126)} = 38.19$, $P = 8.2 \times 10^{-9}$) and elevation explained 38.3% of the variance in PC1 ($F_{(1, 126)} = 78.24$, $P = 6.9 \times 10^{-15}$). We used the same method of model selection to investigate how physical variables plus the A–C index affect snowmelt; elevation, TPI, and the winter A–C index predicted 41.6% of the variance in the last date of snowmelt ($F_{(3, 115)} = 27.31$, $P = 2.08 \times 10^{-13}$).

Phenology

Plant phenology tracked inter-annual climate variability. 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 (Appendix S1: Fig. S3). However, for most species, the relationship among sites in timing of bud break was not consistent across all years. We saw a loss of diversity in the timing of bud break across the elevation gradient in years with a higher A–C index especially in herbs and

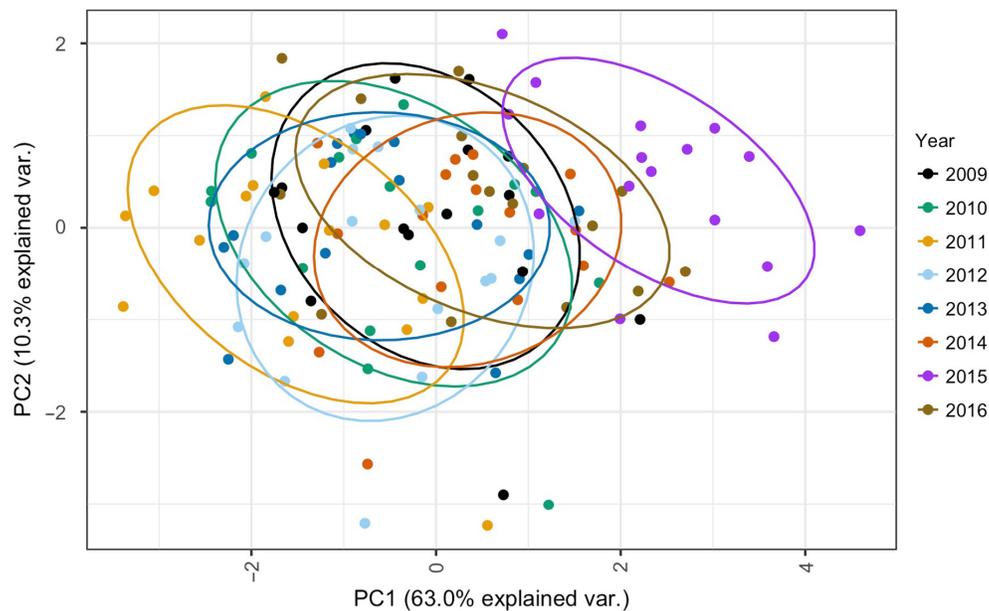


Fig. 5. A principal components analysis of temperature variables at all 16 sites across 8 yr of phenology data (2009–2016). Principal component 1 is on the x-axis, while principal component two is on the y-axis. Ellipses represent a 95% confidence interval. See Appendix S1: Table S11 for variable contributions and loadings.

shrubs (Fig. 6; *Coptis laciniata* and *Linnaea borealis* are both herbs, *Rhododendron macrophyllum* is an understory shrub, and *Tsuga heterophylla* is a mid-canopy tree).

We regressed bud break against elevation to explore how closely timing of bud break of individual species across sites in each year of the study related to the elevation gradient, as an indicator of the degree to which plant phenology was sensitive to the effect of the A–C index on microclimate (high A–C index years reducing winter microclimate differentiation across elevations). Although elevation, as a proxy for temperature and snowmelt patterns that drive spring phenology, was a significant predictor in models for most species in most years, the pattern broke down in the year with the highest A–C index and lowest snowpack; in 2015, elevation was a non-significant predictor of bud break in 10 of 14 species (Fig. 7; Appendix S1: Fig. S3, Table S9). For example, in 2009–2014, and in 2016, elevation predicted between 52% and 86% of the variance in the timing of bud break for *Acer circinatum*, but there was no relationship in 2015 (Fig. 7a). In contrast, elevation was a significant predictor of bud break for all years for the conifer *P. menziesii* (Douglas fir),

and elevation predicted 94% ($F_{(1,5)} = 87.73$, $P < 2.3 \times 10^{-4}$) of the variance in bud break during 2015, the highest adjusted R^2 of any year for that species (Fig. 7b). All 12 species with a wide distribution across microclimates show a strong positive relationship among bud break and snow regardless of year (Appendix S1: Fig. S4), while the relationship between GDD and bud break has more variability among years and species (Appendix S1: Fig. S5). The variation in the relationship between bud break and GDD suggests that it is an interaction among snow, temperatures, and regional weather (i.e., A–C index) that drives the onset of spring plant growth.

Since 2011 and 2015 represented the extremes in terms of winter climate conditions in our sample, we contrast patterns in these two years 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 d in 2015 when compared to 2011. The most extreme advancement in bud break occurred at PC09 (984 m), where *Viola sempervirens* (violet) broke bud 85 d earlier in 2015 than in 2011 (Appendix S1: Table S8). However, the degree of advancement of bud break was

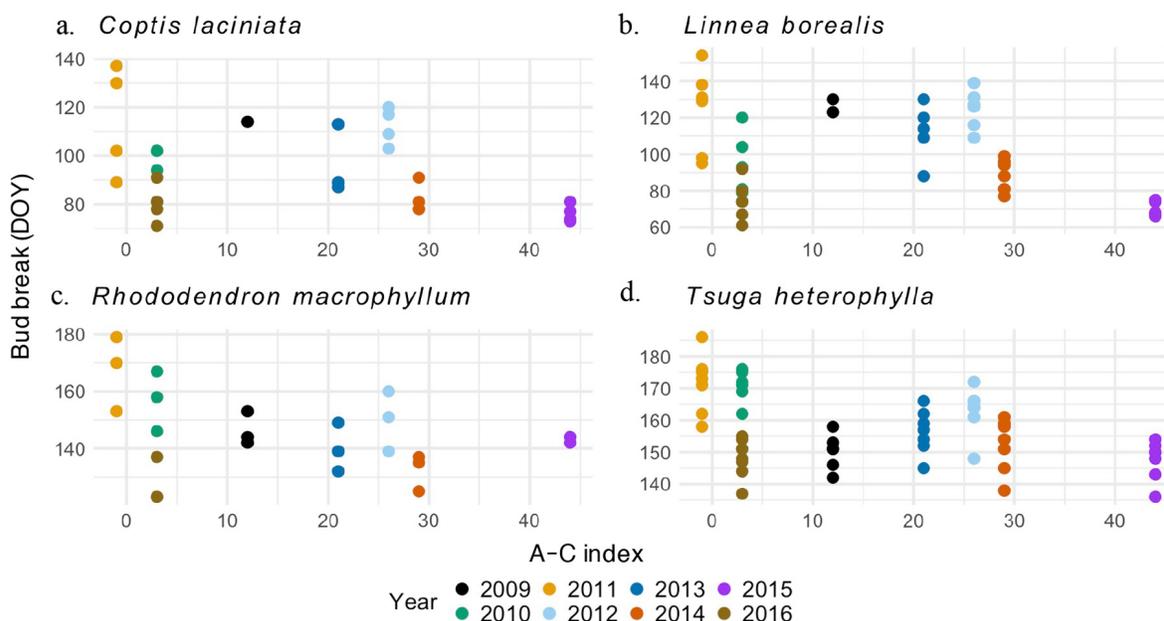


Fig. 6. Day of year of bud break relative to anticyclonic–cyclonic index for (a) *Coptis laciniata*, (b) *Linnea borealis*, (c) *Rhododendron macrophyllum*, and (d) *Tsuga heterophylla*. Colors are year, with each point representing a site in a given year.

both species and site specific; for example, *V. sempervirens* showed as little as 15-d difference between years at a low-elevation site (PC01).

Flowering

Flowering data were limited to those species that regularly flowered over the course of the study. These data are spotty because many of the individuals grew in dense, heavily shaded stands and thus rarely flowered. 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* in all years except 2015 (Fig. 8a). While both 2014 and 2015 have both been classified as below average snow years (Sproles et al. 2017), Fig. 4a shows that in 2014 there was between a

quarter and half meter of snow at the highest (1285 m) sites between February and May, while in 2015 there was effectively no snow during that period. This suggests that even below average snow pack can be enough to maintain an elevation gradient in flowering, and it may require a total loss of winter snow to stimulate early flowering at the sites that typically experience persistent snow pack. In contrast, the elevation gradient appears to remain a powerful signal regardless of snowpack for *T. ovatum*, similar to the pattern of bud break seen in that species (Fig. 8b). Both *V. parvifolium* and *T. ovatum* have flowers emerge from rolled leaves, and both species appear to have synced bud break and flowering trends.

DISCUSSION

Microclimate is a strong driver of local plant phenology, and all of the focal plant species in this study displayed a high degree of phenological plasticity in response to inter-annual climate variability. A small number of physical variables explained spatial variation in temperature, especially during winter and spring. As expected, relatively cool, snowy conditions during winter and

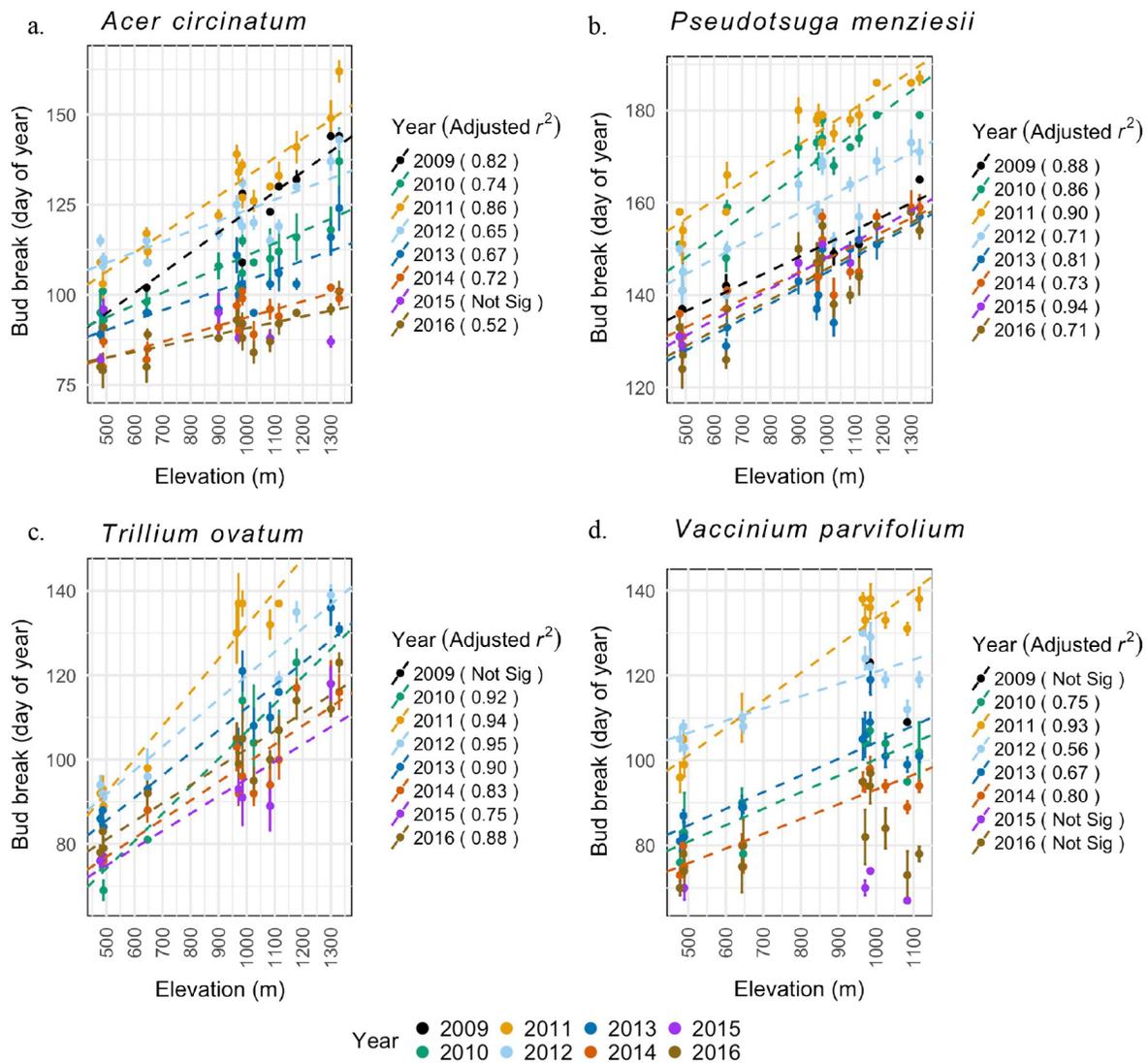


Fig. 7. Elevation as a predictor of the timing of bud break for (a) *A. circinatum*, (b) *Pseudotsuga menziesii*, (c) *Trillium ovatum*, and (d) *Vaccinium parvifolium*. Error bars are \pm SE; colors are year.

early spring led to delayed onset of spring plant phenology (bud break), while relatively warm winter and spring conditions with below normal snowpack led to an advancement in the onset of spring phenology, especially at upper elevations. Less intuitive was the loss of early season microclimate diversity and homogenization of plant phenology across the landscape when low snowpack coincided with high frequencies of anticyclonic weather systems.

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 2080s (Mote and Salathe 2010). This will likely result in more winter precipitation falling as rain and less as snow (Stewart 2009, 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.

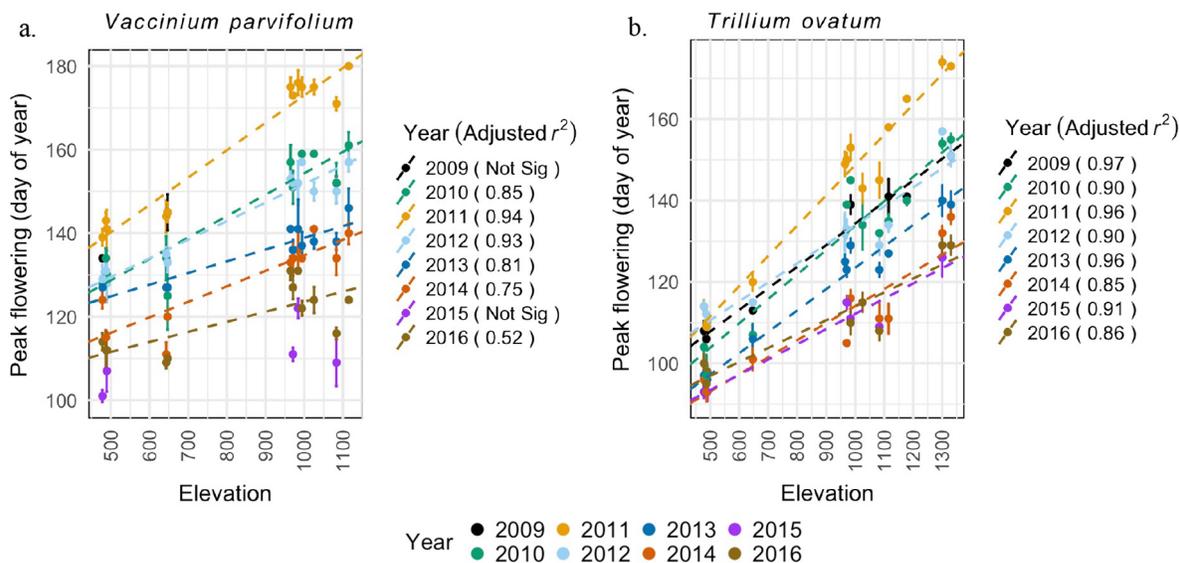


Fig. 8. Elevation as a predictor of the timing of peak flowering for (a) *Vaccinium parvifolium* and (b) *Trillium ovatum*. Error bars are \pm SE; colors are year.

2018). Lute et al. (2015) predict a reduction of up to 60% of the 1 April 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 net result of these predicted changes in snowpack and winter weather patterns would likely be a homogenization of spring phenology events across the elevation gradient. Our data suggest that in the Western Cascades (as opposed to the higher elevation High Cascades, which may not experience as great of a decrease in snowpack, Mote 2006, Mote et al. 2018), years with snowpack well below average (Sproles et al.

2017), and frequent anticyclonic weather patterns will have much greater effects on the mountain communities situated in upper elevation sites and sites of high topographic relief due to increased daily maxima (Appendix S1: Fig. S1). Understory species are more likely to have significant shifts in phenology than overstory trees, and 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 (i.e., replanted second-growth timber stands) in the Western Cascades will likely have the greatest shifts in phenology due to changes in regional climate patterns. A recent study in the European Alps found a similar homogenization of phenological events, where bud break of four European trees advanced \sim 1.9 d per decade from 1960 to 2016 at high elevations ($>$ 808 m), and only \sim 0.4 d per decade at low elevations ($<$ 522 m; Vitasse et al. 2018).

Trade-offs 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 daylight 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). At sites above 1200 m, we

observed individuals of *Vaccinium* spp., *T. ovatum* and *V. sempervirens* with frost damage on new leaves during years (2014, 2015, and 2016) of advanced bud break (Schulze 2017). If frost damage does not occur, a plant that breaks bud early has a longer growing season (and in some circumstances a competitive advantage, through shading, over other plants that break bud later), which may result in increased fitness due to greater resource storage, or the plant may be more susceptible to early onset of summer drought due to the relatively warm conditions that initiated advanced bud break and the Mediterranean climate. 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) and observations of early growth cessation in lower elevations of the *P. menziesii* range in the Pacific Northwest (Ford et al. 2016).

While our study focused on herbs, shrubs, and trees native to 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 (Walther et al. 2002, Parmesan and Yohe 2003, Visser and Both 2005, Both et al. 2009, Aldridge et al. 2011, Forrest and Thomson 2011). 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 for mobile organisms like birds or mammals (Gaudry et al. 2015, Frey et al. 2016a). However, in 2015, a potential analogue of future winter weather and snowpack dynamics, the timing of spring plant phenology became much less varied across the landscape; it is possible that such loss of variation could lead to more widespread consequences and trophic asynchronies than in years 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 diversity in the timing of bud break and flowering across microclimates creates potential for fewer resources for migrants and other mobile

species dependent on a varied patchwork of spring flowering and growing seasons.

Long-term, high-resolution (both spatially, i.e., $<1 \text{ km}^2$, and temporally, i.e., $>5 \text{ yr}$) studies such as this one are needed to capture the effects of a warming climate on forest and mountain communities. There is a need to further explore the interaction between microclimate and phenology and to develop species-specific models of bud break using microclimate variables, with the goal of developing high-resolution predictive models of bud break across a landscape (Ault et al. 2011, 2015). 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.

Homogenization of microclimate and phenology has been documented in other recent studies from mountainous regions. Maclean et al. (2017) found that between 1977 and 2014, higher altitude areas had significantly faster rates of warming than valley bottoms and northeast slopes. Additionally, Vitasse et al. (2018) show that warmer winter and spring temperatures result in a homogenization of phenological diversity across a mountainous landscape; similarly, this study provides evidence that years with long periods of anticyclonic winter weather result in a more rapid advancement of phenology at higher elevation ridge sites and a reduction in diversity of phenological events across a landscape. All three studies occurred in areas of heterogeneous topography, although the magnitude of variation was different at each site. Given the differences in site characteristics and site location (Western Cascades of North America, southern Britain and the European Alps), it is possible that this phenomenon of heterogeneous warming across a landscape (and thus a homogenization of phenology) is occurring at areas of variable topography around the world. Trophic asynchronies and community shifts due to altered phenologies have already resulted in declines in species populations (Parmesan 2006, Both et al. 2009). Identifying which areas across landscapes are more and less susceptible to climate change, and the processes responsible for those patterns, is the first step in managing for future conditions and mitigating future population declines due to climate change (Lawler 2009, Morelli et al. 2016, Lenoir et al. 2017).

ACKNOWLEDGMENTS

This work was funded by the NSF LTER program (DEB 1440409). Data and facilities were provided by the HJ Andrews Experimental Forest and Long Term Ecological Research program, administered cooperatively by the USDA Forest Service Pacific Northwest Research Station, Oregon State University, and the Willamette National Forest. Special thanks to Dan Gavin, Jay Sexton, and to all of the people who assisted with data collection in one or more seasons.

LITERATURE CITED

- Aldridge, G., D. W. Inouye, J. R. K. Forrest, W. A. Barr, and A. J. Miller-Rushing. 2011. Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *Journal of Ecology* 99:905–913.
- Auguie, B. 2017. gridExtra: miscellaneous functions for “Grid” graphics. R package version 2.3. <https://CRAN.R-project.org/package=gridExtra>
- Ault, T. R., A. K. Macalady, G. T. Pederson, J. L. Betancourt, and M. D. Schwartz. 2011. Northern hemisphere modes of variability and the timing of spring in Western North America. *Journal of Climate* 24:4003–4014.
- Ault, T. R., M. D. Schwartz, R. Zurita-Milla, J. F. Weltzin, and J. L. Betancourt. 2015. Trends and natural variability of spring onset in the coterminous United States as evaluated by a new gridded dataset of spring indices. *Journal of Climate* 28:8363–8378.
- Baquero, O. S. 2017. ggsm: north symbols and scale bars for maps created with ‘ggplot2’ or ‘ggmap’. R package version 0.4.0. <https://CRAN.R-project.org/package=ggsm>
- Becker, M., and A. Deckmyn. 2017. maps: draw geographical maps. R package version 3.2.0. <https://CRAN.R-project.org/package=maps>
- Billings, W. D., and L. C. Bliss. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology* 40:388–397.
- Bivand, R., T. Keitt, and B. Rowlingson. 2017. rgdal: bindings for the ‘Geospatial’ data abstraction library. R package version 1.2-16. <https://CRAN.R-project.org/package=rgdal>
- Bivand, R., and N. Lewin-Koh. 2017. mapproj: tools for reading and handling spatial objects. R package version 0.9-2. <https://CRAN.R-project.org/package=mapproj>
- Bivand, R., E. Pebesma, and V. Gomez-Rubio. 2013. *sp: applied spatial data analysis with R*. Second edition. Springer, New York, New York, USA. <http://www.asdar-book.org/>
- Both, C., C. A. M. V. Turnhout, R. G. Bijlsma, H. Siepel, A. J. V. Strien, and R. P. B. Foppen. 2009. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London B: Biological Sciences* 277:1259–1266.
- Daly, C. 2017. Cold air drainage transect studies at the Andrews Experimental Forest, 2002 to Present. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, Oregon, USA. <http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=MS036>
- Daly, C., D. R. Conklin, and M. H. Unsworth. 2010. Local atmospheric decoupling in complex topography alters climate change impacts. *International Journal of Climatology* 30:1857–1864.
- Daly, C., and W. McKee. 2016a. Air and soil temperature data from the reference stand network at the Andrews Experimental Forest, 1971 to present. Forest Science Data Bank, Corvallis, Oregon, USA. <https://doi.org/10.6073/pasta/75d4bffa8a8824977126c25f7763d8ae3>
- Daly, C., and W. McKee. 2016b. Meteorological data from benchmark stations at the Andrews Experimental Forest, 1957 to present. Forest Science Data Bank, Corvallis, Oregon, USA. <https://doi.org/10.6073/pasta/c96875918bb9c86d330a457bf4295cd9>
- De Frenne, P., et al. 2013. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences USA* 110:18561–18565.
- Dobrowski, S. Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* 17:1022–1035.
- Ford, K. R., C. A. Harrington, S. Bansal, P. J. Gould, and J. B. St. Clair. 2016. Will changes in phenology track climate change? A study of growth initiation timing in coast Douglas-fir. *Global Change Biology* 22:3712–3723.
- Forrest, J. R. K., and J. D. Thomson. 2011. An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecological Monographs* 81:469–491.
- Fox, J., and S. Weisberg. 2011. *car: an R companion to applied regression*. Second edition. Sage, Thousand Oaks, California, USA. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- Franklin, J., F. W. Davis, M. Ikegami, A. D. Syphard, L. E. Flint, A. L. Flint and L. Hannah. 2013. Modeling plant species distributions under future climates: how fine scale do climate projections need to be? *Global Change Biology* 19:473–483.
- Franklin, J. F. 2017. Long-term growth, mortality and regeneration of trees in permanent vegetation plots in the Pacific Northwest, 1910 to present. Long-

- Term Ecological Research. Forest Science Data Bank, Corvallis, Oregon, USA. <https://doi.org/10.6073/pasta/2315afa15ad0a2317b49565da6258c47>
- Frey, S. J. K., A. S. Hadley, and M. G. Betts. 2016a. Microclimate predicts within-season distribution dynamics of montane forest birds. *Diversity and Distributions* 22:944–959.
- Frey, S. J. K., A. S. Hadley, S. L. Johnson, M. Schulze, J. A. Jones, and M. G. Betts. 2016b. Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances* 2:e1501392.
- Fu, Y. H., S. Piao, Y. Vitasse, H. Zhao, H. J. De Boeck, Q. Liu, H. Yang, U. Weber, H. Hänninen, and I. A. Janssens. 2015. Increased heat requirement for leaf flushing in temperate woody species over 1980–2012: effects of chilling, precipitation and insolation. *Global Change Biology* 21:2687–2697.
- Gaudry, W., S. Saïd, J.-M. Gaillard, T. Chevrièr, A. Loison, D. Maillard, and C. Bonenfant. 2015. Partial migration or just habitat selection? Seasonal movements of roe deer in an Alpine population. *Journal of Mammalogy* 96:502–510.
- Grimm, N. B., P. Groffman, M. Staudinger, and H. Tallis. 2016. Climate change impacts on ecosystems and ecosystem services in the United States: process and prospects for sustained assessment. *Climatic Change* 135:97–109.
- Harmon, M., and K. O’Connell. 2015. Plant biomass dynamics following logging, burning, and thinning in Watersheds 6 and 7, Andrews Experimental Forest, 1979 to present. Forest Science Data Bank, Corvallis, Oregon, USA. <https://doi.org/10.6073/pasta/f45b3280ab4fab12ff879813495cb869>
- Harrington, C. A., P. J. Gould, and J. B. St. Clair. 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. *Forest Ecology and Management* 259:798–808.
- Harrington, R., I. Woiwod, and T. Sparks. 1999. Climate change and trophic interactions. *Trends in Ecology & Evolution* 14:146–150.
- Heide, O. M. 1993. Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* 88:531–540.
- Hijmans, R. 2017. raster: geographic data analysis and modeling. R package version 2.6-7. <https://CRAN.R-project.org/package=raster>
- Hope, R. M. 2013. Rmisc: Rmisc: Ryan miscellaneous. R package version 1.5. <https://CRAN.R-project.org/package=Rmisc>
- Hwang, T., C. Song, J. M. Vose, and L. E. Band. 2011. Topography-mediated controls on local vegetation phenology estimated from MODIS vegetation index. *Landscape Ecology* 26:541–556.
- Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.
- IPCC 2007. Climate Change 2007: The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge, UK.
- Johnson, S., and S. Gregory. 2016. Stream and air temperature data from stream gages and stream confluences in the Andrews Experimental Forest, 1950 to present. Forest Science Data Bank, Corvallis, Oregon, USA. <https://doi.org/10.6073/pasta/11cf1a8de0b8d23cf482a110c77be191>
- Johnson, S., and S. Hadley. 2017. Air temperature at core phenology sites and additional bird monitoring sites in the Andrews Experimental Forest, 2009-Present. Forest Science Data Bank, Corvallis, Oregon, USA. <http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=MS045>
- Johnson, S., and J. Rothacher. 2016. Stream discharge in gaged watersheds at the Andrews Experimental Forest, 1949 to present. Long-Term Ecological Research. <http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=HF004>
- Körner, C., J. Paulsen, and E. M. Spehn. 2011. A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany* 121:73.
- Lawler, J. J. 2009. Climate change adaptation strategies for resource management and conservation planning. *Annals of the New York Academy of Sciences* 1162:79–98.
- Lenoir, J., T. Hattab, and G. Pierre. 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography* 40:253–266.
- Lockhart, J. A. 1983. Optimum growth initiation time for shoot buds of deciduous plants in a temperate climate. *Oecologia* 60:34–37.
- Lundquist, J. D., S. E. Dickerson-Lange, J. A. Lutz, and N. C. Cristea. 2013. Lower forest density enhances snow retention in regions with warmer winters: a global framework developed from plot-scale observations and modeling. *Water Resources Research* 49:6356–6370.
- Luoto, M., and R. K. Heikkinen. 2008. Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biology* 14:483–494.
- Lute, A. C., J. T. Abatzoglou, and K. C. Hegewisch. 2015. Projected changes in snowfall extremes and interannual variability of snowfall in the western United States. *Water Resources Research* 51:960–972.

- Maclean, I. M. D., A. J. Suggitt, R. J. Wilson, J. P. Duffy, and J. J. Bennie. 2017. Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Global Change Biology* 23:256–268.
- Miller, T. 2017. leaps: regression subset selection. R package version 3.0. <https://CRAN.R-project.org/package=leaps>
- Moore, C., S. Kampf, B. Stone, and E. Richer. 2015. A GIS-based method for defining snow zones: application to the western United States. *Geocarto International* 30:62–81.
- Morelli, T. L., et al. 2016. Managing climate change refugia for climate adaptation. *PLoS ONE* 11:e0159909.
- Mote, P. W. 2006. Climate-driven variability and trends in mountain snowpack in Western North America. *Journal of Climate* 19:6209–6220.
- Mote, P. W., S. Li, D. P. Lettenmaier, M. Xiao, and R. Engel. 2018. Dramatic declines in snowpack in the western US. *npj Climate and Atmospheric Science* 1:2.
- Mote, P. W., and E. P. Salathe Jr. 2010. Future climate in the Pacific Northwest. *Climatic Change* 102:29–50.
- Murray, M. B., M. G. R. Cannell, and R. I. Smith. 1989. Date of budburst of fifteen tree species in Britain following climatic warming. *Journal of Applied Ecology* 26:693–700.
- Novick, K. A., A. C. Oishi, and C. F. Miniat. 2016. Cold air drainage flows subsidize montane valley ecosystem productivity. *Global Change Biology* 22:4014–4027.
- Oksanen, J., et al. 2017. vegan: community ecology package. R package version 2.4-4. <https://CRAN.R-project.org/package=vegan>
- O’Leary, D. S., J. L. Kellermann, and C. Wayne. 2018. Snowmelt timing, phenology, and growing season length in conifer forests of Crater Lake National Park, USA. *International Journal of Biometeorology* 62:273–285.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637–669.
- Parnesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Pebesma, E. J., and R. S. Bivand. 2005. sp: “classes and methods for spatial data in R”. *R News* 5:9–13.
- Pelt, R. V. and J. F. Franklin. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Canadian Journal of Forest Research* 30:1231–1245.
- Pepin, N. C., C. Daly, and J. Lundquist. 2011. The influence of surface versus free-air decoupling on temperature trend patterns in the western United States. *Journal of Geophysical Research: Atmospheres* 116:D10109.
- Perry, T. O. 1971. Dormancy of trees in winter. *Science* 171:29–36.
- Peterson, D. L., E. G. Schreiner, and N. M. Buckingham. 1997. Gradients, vegetation and climate: spatial and temporal dynamics in the Olympic Mountains, U.S.A. *Global Ecology and Biogeography Letters* 6:7–17.
- Polgar, C. A., and R. B. Primack. 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist* 191:926–941.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RStudio Team. 2016. RStudio: integrated development environment for R. RStudio, Inc., Boston, Massachusetts, USA. <http://www.rstudio.com/>
- Sarkar, D. 2008. Lattice: multivariate data visualization with R. Springer, New York, New York, USA. <http://lmdvr.r-forge.r-project.org>
- Saxe, H., M. G. R. Cannell, Ø. Johnsen, M. G. Ryan, and G. Vourlitis. 2001. Tree and forest functioning in response to global warming. *New Phytologist* 149:369–399.
- Schulze, M. 2017. Vegetative phenology observations at the Andrews Experimental Forest, 2009–present. Ecological Research. Forest Science Data Bank, Corvallis, Oregon, USA. <http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TV075>
- Schulze, M., and A. Levno. 2017. Snow depth and snow water equivalent measurements along a road course and historic snow course in the Andrews Experimental Forest, 1978 to present. Forest Science Data Bank, Corvallis, Oregon, USA. <https://doi.org/10.6073/pasta/249eba042fd7bbbe9fc a1d8b36dc7869>
- Sherwood, J. A., D. M. Debinski, P. C. Caragea, and M. J. Germino. 2017. Effects of experimentally reduced snowpack and passive warming on montane meadow plant phenology and floral resources. *Ecosphere* 8:e01745.
- Signorell, A., et al. 2018. DescTools: tools for descriptive statistics. R package version 0.99.25. <https://cran.r-project.org/web/packages/DescTools/index.html>
- Simpson, G. 2016. permute: functions for generating restricted permutations of data. R package version 0.9-4. <https://CRAN.R-project.org/package=permute>
- Spies, T. 2016. LiDAR data (August 2008) for the Andrews Experimental Forest and Willamette National Forest study areas. Forest Science Data Bank, Corvallis, Oregon, USA. <https://doi.org/10.6073/pasta/c47128d6c63dff39ee48604ecc6fabfc>

- Sproles, E. A., A. W. Nolin, K. Rittger, and T. H. Painter. 2013. Climate change impacts on maritime mountain snowpack in the Oregon Cascades. *Hydrology and Earth System Sciences* 17:2581–2597.
- Sproles, E. A., T. R. Roth, and A. W. Nolin. 2017. Future snow? A spatial-probabilistic assessment of the extraordinarily low snowpacks of 2014 and 2015 in the Oregon Cascades Cryosphere; *Katlenburg-Lindau* 11:331–341.
- Stewart, I. T. 2009. Changes in snowpack and snowmelt runoff for key mountain regions. *Hydrological Processes* 23:78–94.
- Thackeray, S. J., et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535:241–245.
- Valentine, T., and G. Lienkaemper. 2005. 30 meter digital elevation model (DEM) clipped to the Andrews Experimental Forest, 1996. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, Oregon, USA. <https://doi.org/10.6073/pasta/283ce7118c4c11b4f222896d46be81bd>
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. Fourth edition. Springer, New York, New York, USA. <http://www.stats.ox.ac.uk/pub/MASS4>
- Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London B: Biological Sciences* 272:2561–2569.
- Visser, M. E., C. Both and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research* 35:89–110.
- Vitasse, Y., C. Signarbieux, and Y. H. Fu. 2018. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences USA* 115:1004–1008.
- Vu, V. Q. 2011. ggbiplot: a ggplot2 based biplot. R package version 0.55. <http://github.com/vqv/ggbiplot>
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York, New York, USA. <http://ggplot2.org>
- Wickham, H.. 2011. plyr: “the Split-Apply-Combine Strategy for Data Analysis”. *Journal of Statistical Software* 40:1–29.
- Wickham, H. 2017. scales: scale functions for visualization. R package version 0.5.0. <https://CRAN.R-project.org/package=scales>
- Wickham, H., and W. Chang. 2017. devtools: tools to make developing R packages easier. R package version 1.13.4. <https://CRAN.R-project.org/package=devtools>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2451/full>