

# Climate drives phenological reassembly of a mountain wildflower meadow community

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**Abstract.** Spatial community reassembly driven by changes in species abundances or habitat occupancy is a well-documented response to anthropogenic global change, but communities can also reassemble temporally if the environment drives differential shifts in the timing of life events across community members. Much like spatial community reassembly, temporal reassembly could be particularly important when critical species interactions are temporally concentrated (e.g., plant-pollinator dynamics during flowering). Previous studies have documented species-specific shifts in phenology driven by climate change, implying that temporal reassembly, a process we term “phenological reassembly,” is likely. However, few studies have documented changes in the temporal co-occurrence of community members driven by environmental change, likely because few datasets of entire communities exist. We addressed this gap by quantifying the relationship between flowering phenology and climate for 48 co-occurring subalpine wildflower species at Mount Rainier (Washington, USA) in a large network of plots distributed across Mt. Rainier’s steep environmental gradients; large spatio-temporal variability in climate over the 6 yr of our study (including the earliest and latest snowmelt year on record) provided robust estimates of climate-phenology relationships for individual species. We used these relationships to examine changes to community co-flowering composition driven by ‘climate change analog’ conditions experienced at our sites in 2015. We found that both the timing and duration of flowering of focal species was strongly sensitive to multiple climatic factors (snowmelt, temperature, and soil moisture). Some consistent responses emerged, including earlier snowmelt and warmer growing seasons driving flowering phenology earlier for all focal species. However, variation among species in their phenological sensitivities to these climate drivers was large enough that phenological reassembly occurred in the climate change analog conditions of 2015. An unexpected driver of phenological reassembly was fine-scale variation in the direction and magnitude of climatic change, causing phenological reassembly to be most apparent early and late in the season and in topographic locations where snow duration was shortest (i.e., at low elevations and on ridges in the landscape). Because phenological reassembly may have implications for many types of ecological interactions, failing to monitor community-level repercussions of species-specific phenological shifts could underestimate climate change impacts.

**Key words:** *climate change; community shifts; disassembly; elevation gradient; global change; mutualisms; phenological synchrony.*

## INTRODUCTION

Accelerating environmental change, including anthropogenic climate change, is reshaping ecological communities through changes in species abundance (Elmendorf et al. 2015, McIntyre et al. 2015), site occupancy (Comte and Grenouillet 2013, Rowe et al. 2015, Stevens et al. 2015), and species interactions (Visser et al. 2006, Ockendon et al. 2014). This process of spatial “community reassembly” (Schaefer et al. 2008) has been well-documented throughout terrestrial and marine ecosystems, and represents a coherent fingerprint of humanity on the global biosphere (Parmesan 2006, Poloczanska et al.

2013). Despite this global-scale coherence, our efforts to forecast the trajectory of community reassembly in response to environmental change have met limited success, as only a slim majority of species have shifted their distribution to track changes in climate (Chen et al. 2011, Serra-Diaz et al. 2016), and interactions between species have produced surprising ecological outcomes (Parmesan and Hanley 2015).

In contrast to the spatial diversity of observed changes in abundance and occupancy, changes in plant flowering phenology in response to climate warming have been remarkably consistent across species and systems (Thackeray et al. 2016) – consistent in that the vast majority of plant species advance their phenologies in response to warming. These consistent relationships facilitate the use of annual variation in climate to gain insight into community-level changes in phenology. We term these community-level phenological changes “phenological reassembly”:

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changes in temporal co-occurrence driven by species-specific exposure and responses to changes in the environment. In this work, we develop the phenological reassembly concept, define criteria for measuring it, and demonstrate phenological reassembly of a mountain wildflower community driven by extreme climate conditions analogous to those expected by the late 21st century under unabated climate change.

Ecologically relevant, climate-induced phenological reassembly in plant communities is contingent on three conditions. First, flowering species must be sensitive to the key climate drivers that are changing. Second, species must differ in their sensitivities to these climate drivers, either by having different sensitivities to the same climate drivers or by being sensitive to different climate drivers. Finally, species with different responses to climate must occur together in relative proximity. Phenological reassembly is then characterized by species co-flowering in new ways, for example, through increased or decreased overlap in flowering (Fig. 1). These changes in overlap can be caused by shifts in the timing of flowering or in changes in the duration of flowering, which are dictated by each species' sensitivity to climate. In turn, these new co-flowering patterns, or the degree of phenological reassembly, can be measured by changes in richness of concurrently flowering species, occurrence of novel co-flowering patterns, changes in lag of the timing of first flower, and changes in the flowering season duration. Fig. 1 graphically represents community reassembly: how it happens and how it is measured.

Phenological reassembly is likely: numerous studies have documented earlier plant flowering coinciding with warming trends in regional climate (e.g., Fitter and Fitter 2002, Inouye 2008), but not all plant species are shifting their reproductive phenologies identically (Parmesan and Yohe 2003, Parmesan 2007, Thackeray et al. 2010, 2016). Such species-specific phenological shifts likely arise because species are differentially sensitive to key climatic drivers (e.g., growing season temperature vs. precipitation: Diez et al. 2012) and/or are distributed in areas exposed to different magnitudes of changes in those drivers (e.g., uplands vs. lowlands: Crimmins et al. 2010). Regardless of the cause, these species-specific shifts in phenology are likely to cause phenological reassembly.

Surprisingly, few studies have examined how climate reshapes co-flowering relationships within communities at small spatial scales. Multi-species studies exist, but most attempt to explain species-specific differences in phenological sensitivity to climate change by examining how trophic levels (Voigt et al. 2003, Parmesan 2007, Thackeray et al. 2010, 2016), traits (e.g., Miller-Rushing and Primack 2008, Molnár et al. 2012, Cortés-flores et al. 2015), phylogenetic relatedness (CaraDonna and Inouye 2015), or identity of climate variables (e.g., Diez et al. 2012, Wolkovich et al. 2012) drive species-specific phenological responses. Others have attempted to assess community-level responses from the perspective of impacts on a subset of species in communities (e.g., Forrest et al.

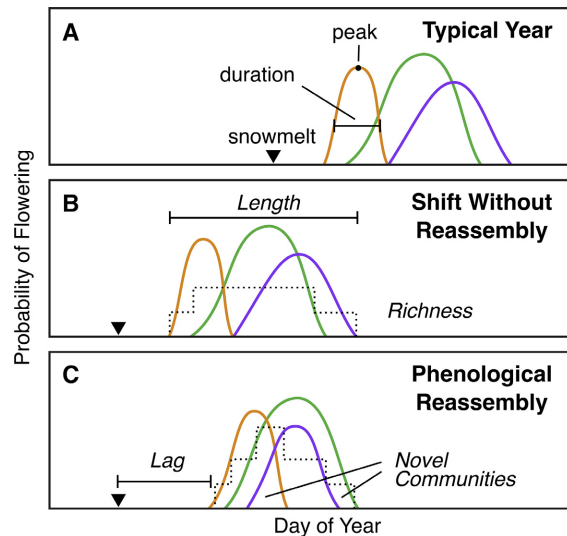


FIG. 1. By modeling peak flowering and duration of each species in the flowering community, we demonstrate under which conditions phenological community reassembly will occur. For three representative flowering species (yellow, green, and purple curves), the top panel (A) shows seasonal phenological progressions in typical years, the second panel (B), and the bottom panel (C) show seasonal phenological progressions in climate-change-like years when phenology shifts earlier but communities do not reassemble (B), and when phenology shifts and communities do reassemble (C). Community reassembly (C) occurs when the three species have differential sensitivities to climate, resulting in differential shifts in their phenologies (e.g., the yellow species advances its peak (flower) less than the purple species, and the yellow species lengthens its flowering duration while the purple species shortens its flowering duration). Phenological community reassembly can manifest itself in four measurable ways: change in the lag (the time between snowmelt and first flower; indicated in C), change in flowering season length (indicated in B), change in seasonal richness (black dashed line in B and C), and presence of novel communities (indicated in C). In this hypothetical example (C), flowering occurs later after snowmelt (i.e. longer lag), reaches higher richness (peak richness = 3), and exhibits a novel co-flowering pattern (novel community) and a slightly shorter flowering season length relative to typical years (A) or climate-change years without reassembly (B).

2010). The few community-wide studies we are familiar with document changes in first-flower dates (Diez et al. 2012), or broad-scale pairwise co-flowering within communities (CaraDonna et al. 2014), without determining whether species with different sensitivities to climate co-occur at plot scales, or directly attributing changes in co-flowering to changes in climate (Fig. 1; but see Hua et al. 2016 for an example in a vertebrate system).

Understanding if, where, and how phenological reassembly happens is critical, because such shifts are likely to influence the nature and strength of ecological interactions that often are shaped by their community context. For example, the majority of angiosperm plant species rely on animal pollinators for sexual reproduction (Ollerton et al. 2011), implying that changes in

community-wide flowering phenology under climate change may result both in the loss and the gain of interactions between plant species and their pollinators. This will also alter plant-plant interactions, by changing both competitive and facilitative interactions mediated by shared pollinators (Pauw 2013). Thus, phenological reassembly could have trophic implications and conservation repercussions (Morellato et al. 2016).

To understand the potential for floral phenological reassembly and its causes, we studied the flowering phenology of a community of 48 species observed over 6 yr at 70 spatially heterogeneous locations in the subalpine meadows of Mount Rainier National Park. Specifically, we (1) estimated species-specific sensitivities to three climate drivers (the timing of snowmelt, growing degree day accumulation, and soil moisture duration) in terms of species-specific timing of peak flower and flowering duration, and (2) used these estimates and a ‘‘natural experiment’’: a year mimicking conditions projected to be typical in the late 21st century (Figs. 2, Appendix S1: Figs. S1, S2, Mauger et al. 2015) to calculate the degree to which species-specific climate sensitivities resulted in floral phenological reassembly (measured by changes in richness, novelty, lag, and season length; Fig. 1). We then dissected this phenological reassembly to determine when (early or late in the season) and where (which locations across elevation bands as well as across topographic positions in the landscape) phenological reassembly was most prevalent. We hypothesized that species in our study have individualistic sensitivities to the three climate drivers that would affect both the timing of flowering and the duration of flowering. We expected that these species-specific sensitivities would cause phenological reassembly with warming. However, because the magnitude of changes in climate drivers varied across microenvironments in our study, we also expected that the magnitude and temporal progression of phenological reassembly might vary across space.

## METHODS

### *Data collection*

We collected phenology data in the subalpine wildflower meadows of Mount Rainier National Park for six summers (2010–2015). Mount Rainier (46.8529° N, 121.7604° W) is a 4,392 m volcano in the Cascade mountain range in western Washington State, USA. The region experiences a maritime climate with dry summers and wet winters, with the majority of winter precipitation falling as snow (Franklin et al. 1988). Mt. Rainier’s environments are characterized by coniferous forests at lower elevations (<1,450 m), subalpine wildflower meadows at mid-elevations (1,450–1,900 m), and bare ground, rock, and ice at the highest elevations (1,900 m and above; Franklin et al. 1988).

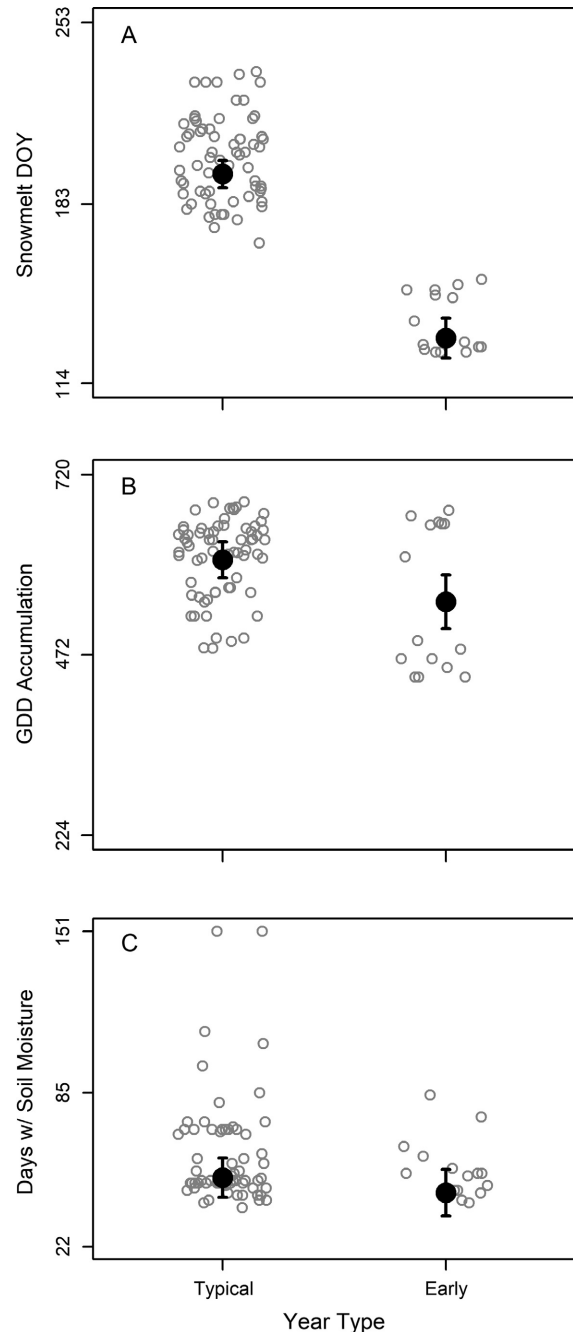


FIG. 2. Climate in typical (2010–2014) compared to the climate-change analog year early (2015). Filled points represent modeled mean conditions at middle-elevation slope sites (1,680 m). Open points show distribution of values in plots spanning all micro-topographic positions at this site. (A) Date of snowmelt; for reference, DOY 130 is May 10th, DOY 190 is July 9th in non-leap years. (B) Growing degree days accumulated for 50 d after snowmelt at each site in typical- and early-snowmelt years. (C) Number of days where soil moisture is >5% of total recorded at each site. The y-axis brackets the range of observed data for all sites. Error bars show 95% credible intervals around the estimated mean.

On the southern slope of Mt. Rainier we identified five sites spaced approximately 100 m apart in elevation. Collectively, these sites spanned the distribution of sub-alpine meadows at Mt. Rainier (1,490–1,901 m). At each site we selected and permanently marked 12–16 1 m<sup>2</sup> plots within which we quantified floral phenology. Plots were stratified to sample natural topographic variation in the landscape at each site, with an equal number of plots situated on small-scale ridges, slopes, and coves (or depressions) at each site. Because snow accumulates in coves and first melts from ridges (Ford et al. 2013), this sampling design meant that the plots fully captured the natural variation in date of snowmelt driven by insolation and topography at each site. In fact, there was as much variation in snowmelt date between plots within sites as there was between sites (Appendix S1: Fig. S2; Ford et al. 2013).

At each plot we measured the date of snowmelt, known to be an important control of flowering in snow-dominated ecosystems (Inouye 2008, Hülber et al. 2010, Lambert et al. 2010), as well as two other climate covariates that we suspected influence flowering phenology because of their impact on plant physiology: post-snow air temperature growing degree days (Pau et al. 2011), and post-snow soil moisture duration (Chaves et al. 2003). These three environmental variables are described in more detail in subsequent paragraphs and are not strongly correlated with each other at our sites (Appendix S1: Fig. S3). We monitored snow using data-logging microclimate sensors (HOBO Pendants made by Onset Computer Corporation or iButtons made by Maxim) buried approximately 4 cm below the soil surface and programmed to measure soil temperature in 4-h intervals. Date of snowmelt was identified in these time series of soil temperatures as the day where surface soil temperature changes from a near constant measurement of <1°C to diurnally fluctuating with measurements above this temperature (Lundquist and Lott 2008, Raleigh et al. 2013). In the 6 yr of data collection, 9.5% of our sensors failed, in which cases date of snowmelt was interpolated using a linear regression model applied to all sensors (as plot-level differences in snowmelt date were extremely consistent from year to year – model  $R^2$  were >90%; Kroiss and HilleRisLambers 2015).

Each site was also instrumented with two air temperature sensors (HOBO Pendants or iButtons) suspended under white plastic funnels approximately 5 m above the soil surface in nearby trees (this height was necessary so that the air sensors were never covered by snow). These sensors recorded air temperatures at 2-h intervals, and data were downloaded twice yearly. We used these sensors to calculate a plot-specific growing degree days (GDD) as the daily temperature sum above a 0°C temperature threshold that each plot experienced in the 50 d after snow melted at that precise location (i.e., plot). We chose a 50-d post-snow window to calculate GDD because it integrated climate over the period most critical to plant growth and development.

We measured soil moisture in each plot weekly using a ProCheck reader (Decagon Devices, Pullman, Washington, USA) and a EC-5 or GS-3 Soil Moisture Sensor (Decagon Devices). In each week after snowmelt at each plot, we took point measurements roughly 4 cm below the soil surface at 1–3 representative locations within the plot and averaged the readings if multiple were taken. As volumetric soil moisture itself does not reflect the soil moisture available to plants (Kramer and Boyer 1995), raw measurements were converted to seasonal estimates of the number of days between snowmelt and soil drying to 5% volumetric water content (considered stressful to plants) at each plot in each year. This conversion was done by fitting a log-linear drawdown curve for each site and year in a linear mixed-model with intercept fixed at 1 and plot and year as random slope effects. Estimates were computed using the R package lme4 (Bates et al. 2013).

Finally, at each 1-by-1 m plot we monitored the flowering phenology of all of the animal-pollinated angiosperms present, totaling 48 species across our sites. To monitor flowering, we visited each of the plots weekly, from approximately the time of snow disappearance to the time of each species' fruit dispersal or the time of snow fall (between 9 and 13 total weeks, depending on the year), and recorded whether the species had flowers (flowers present) or not (flowers absent). For a small number of plot-species combinations (~3%), flowering was also recorded on individuals up to 1 m away from the focal plot to increase the number of monitored individuals (targeting rare species), and thus increasing the reliability of estimates. The full observational dataset (2010–2015) included 29,420 observations.

### Data analysis

*Flowering sensitivity to snowmelt, soil moisture, and growing degree days.—Model structure.*—To quantify species-specific flowering sensitivity to snowmelt, growing degree days and days with soil moisture, we fit flowering observations as a function of these climate covariates for all species simultaneously in a generalized non-linear mixed effects model implemented in a hierarchical Bayesian framework. Specifically, we modeled the relationship between the observed presence/absence of flowers  $y$  of species  $i$ , in plot  $j$ , year  $k$ , and on day of year  $m$  and plot- and year-specific climate covariates. We treated our flower presence/absence data as a Bernoulli distributed random variable:

$$y_{ijkm} \sim \text{Bernoulli}(\alpha_{ijkm}) \quad (1)$$

The Bernoulli mean probability  $\alpha$  was related to covariates via a logit link function, and a unimodal curve relating flowering probability to day of year (DOY) described by three parameters that varied by species: these parameters were related to the time of peak flowering (peak), the duration of flowering (duration),



and the maximum probability of observing a flower (height; see Fig. 1):

$$\text{logit}(\alpha_{ijkm}) = \text{duration}_{ijk} \times (\text{DOY}_{ijkm} - \text{peak}_{ijk})^2 + \text{height}_{ijk} \quad (2)$$

We allowed peak flowering and duration parameters to vary as functions of the environmental covariates snow disappearance date (SDD), growing degree days (GDD), and soil moisture duration (SoilMoist). Height was allowed to vary as a function of SDD. Specifically, environmental responses for each species within each plot were the following:

$$\text{peak}_{ijk} = \beta_{1i} \times \text{SDD}_{ijk} + \beta_{2i} \times \text{SoilMoist}_{ijk} + \beta_{3i} \times \text{GDD}_{ijk} + \beta_{0i} + \beta_{0jkm} \quad (3)$$

$$\text{width}_{ijk} = \exp(\delta_{1i} \times \text{SDD}_{ijk} + \delta_{2i} \times \text{SoilMoist}_{ijk} + \delta_{3i} \times \text{GDD}_{ijk} + \delta_{0i}) \times -1 \quad (4)$$

$$\text{height}_{ijk} = \gamma_{1i} \times \text{SDD}_{ijk} + \gamma_{0i} + \gamma_{0jkm} \quad (5)$$

In combination, Eqs. 2–5 allowed each species to be influenced by each environmental variable in different ways. Parameters  $\beta_{1i} - \beta_{3i}$  represent the sensitivity of peak flowering to year and plot-specific climatic covariates, parameters  $\delta_{1i} - \delta_{3i}$  represent estimates of the sensitivity of the duration of flowering to climatic covariates, and parameter  $\gamma_{1i}$  represents the response of the maximum probability of flowering to changes in snow. For example, a species experiencing no phenological shifts with changes in snow disappearance date would be indicated by a  $\beta_{1i}$  of zero; values of 1 would indicate a consistent lag (i.e., number of days) between SDD and peak flowering, regardless of date of snowmelt. Species whose flowering duration lengthened with earlier snowmelt would have a negative  $\delta_{1i}$ , and species whose flowers are less likely to be observed in early snowmelt conditions would have a negative  $\gamma_{1i}$ . Finally, the  $\beta_0$ ,  $\gamma_0$  and  $\delta_0$ , parameters represent plot- and species-specific intercepts. Large changes in the height of the fit curve also affect the curve duration, but this effect was small for the parameter ranges that fit our data. Covariates SoilMoist and GDD were scaled to a mean of zero and standard deviation of one to improve model fitting, and covariates DOY and SDD were approximately scaled and centered by dividing by 10 and subtracting 1.7.

We simultaneously fit all model parameters using a hierarchical Bayesian approach. We used this approach because it allowed us to estimate species-specific parameters of interest as well as community means, “borrowing strength” across species so that species with limited information (for example rare species, or extremely early-flowering species where early-season zeros were not always observed) would shrink to the mean and fit

biologically plausible relationships. We also considered this to be a conservative choice as it minimizes the influence of outlier observations and rare species on our estimates of the magnitude of community reassembly and acknowledges that the flowering time of all species is likely partly controlled by a common set of biological processes, thus making individual species not entirely independent. This decision did result in parameter estimates for rare species being shrunk towards community means (Appendix S1: Fig. S4). For comparisons between species and climatic conditions, we computed the duration of flowering numerically using each fit curve. Curves were numerically standardized to have an area of one using the R function *integrate*, and flowering durations were calculated to span 80% of the highest normalized area under each curve. Models were fit in JAGS 4.1, with all other analyses run in R version 3.2.3 (R Core Team 2015). Model fitting details (including prior distributions and random effects specifications) can be found in the supplemental methods (Appendix S1). Code and data can be found on github at: [https://github.com/ibrekhe/MORA\\_pheno\\_reassembly](https://github.com/ibrekhe/MORA_pheno_reassembly).

#### *Quantifying phenological reassembly: four measures.*

We used posterior samples of the phenology model parameters to estimate the effects of a “climate-change-like” year (i.e., 2015) on four properties of the floral community, or four metrics of phenological reassembly: (1) co-flowering species richness across the flowering season, (2) the development of novel combinations of co-flowering species, (3) the lag time between snowmelt and first flower, and (4) the total duration of the flowering season. We defined co-flowering species richness as the sum of the probabilities of flowering across all species found at each topographic band at each site, for each day of the flowering season (i.e., from snow disappearance until all flowering ceased). We quantified novelty by comparing the species composition of the flowering community on a given day relative to snowmelt in 2015 to the composition of the flowering community observed at any time point in 2010–2014 at that site/elevation. In other words, novelty measures how different the flowering community is in the ‘climate-change-like’ year 2015 from any floral community observed in “typical” years at a site. We used the Bray-Curtis distance as our measure of novelty, so values near 1 indicate that the observed combination of flowering species in 2015 are completely novel and weren’t observed at that elevation in any time in 2010–2014. We measured lag as the number of days between snowmelt and the onset of the flowering season, defined here as the first day where the summed flowering probabilities exceed 0.5 in each elevation / topographic position, indicating that an observer has a >50% chance of recording at least one species in flower. Finally, we defined the length of the flowering season as the number of days between the first and last days where the summed flowering probabilities exceeded 0.5.

For each metric of phenological reassembly, we capitalized on the climate-change-like extremely warm, low-snow, and dry conditions experienced in 2015 (Figs. 2, Appendix S1: Figs. S1, S2; Mauger et al. 2015), and compared flowering phenology in those conditions to phenology in conditions typical of 2010–2014 (which are collectively near the 20th-century average for temperature, precipitation, and snowpack at our sites). Because 2015 mimicked conditions expected to be typical in the mid to late 21st century (Appendix S1: Fig. S1; Mauger et al. 2015), any large phenological changes in flowering communities in that year may be analogous to the changes we are likely to see under continued climate change by the late 21st century.

To derive each measure of phenological reassembly, we computed mean conditions of SDD, GDD, and soil moisture duration separately for plots within each topographic position (ridges, slopes, and coves) and elevation site (1,490–1,901 m) for 2015 and the baseline period 2010–2014. Then we used parameter estimates describing species-specific phenologies (and responses to climate change) to estimate the probability of each species flowering in each topographic position within a given elevation, on every day of the growing season relative to when snow melted in these “typical” vs. “climate-change-like” years. Because each species does not occur at each topographic position or elevation and varies in overall abundance, we multiplied the estimated probability of flowering by the probability that a species occurs in a representative plot in that topographic position for all analyses of phenological reassembly. For example, if a species occurs in 2 out of 5 of the plots in a single topographic position at a single elevation, then all of the flowering probabilities are multiplied by 0.4 (2/5) for that topographic position. Thus, species that don’t occur in a topographic position don’t contribute to the assessment of reassembly, and rare species contribute less than common species. Because all four indices of phenological reassembly are transformations of the phenology model predictions, we assessed uncertainty of each index by computing posterior credible intervals using each of 1,000 posterior samples of the parameters of the fitted phenology model.

## RESULTS

### *Flowering sensitivity to climate*

Several lines of evidence indicate that the model fit our data well; see Supplemental Methods for details (Appendix S1: Fig. S5; Appendix S2). All species shifted their flowering phenology earlier in climate-change-like conditions (Fig. 3, Appendix S1: Fig. S6). However, species varied in their specific responses to climate-change-like conditions, with species shifting the timing of peak flower between 39.3 and 59.0 d earlier (mean = 49.5 d; SD = 4.52) in response to the warm, early-melt conditions in 2015 (mean melt = 58 d earlier; range = 45–63 d earlier; Appendix S1: Fig. S6).

Additionally, although phenological advance in climate-change-like conditions was ubiquitous across species, climate drivers differed in their average effects on peak sensitivities (Fig. 3, Appendix S1: Fig. S5). Because climate variables (see *Methods*) were scaled and centered, the coefficients of the model are not in easily interpretable units. Community-wide, the timing of peak flower was most sensitive to snowmelt (100% of species) and growing degree days (98% of species), but was less sensitive to soil moisture (17% of species; Fig. 3, Appendix S1: Fig. S6). Taken together, this means that species all advanced the timing of peak flower in warm, early melt conditions but did not track snowmelt perfectly. In other words, a 1-d change in snowmelt did not translate to a 1-d change in phenology (e.g., peak flowering).

Similarly, differential species-specific duration sensitivities to climate drivers led to a difference in flowering duration for individual species in climate-change-like conditions. Overall, 54% of species ( $n = 26$ ) lengthened their flowering duration whereas 46% ( $n = 22$ ) shortened their duration under earlier snowmelt conditions. Differences in individual flowering duration ranged from an 18.7 d shortening of flowering duration to a 15.0 d lengthening of flowering duration (mean lengthening 0.740 d, SD = 6.10). Flowering duration sensitivities were less consistently related to climatic covariates than sensitivity of peak flowering: flowering duration was most sensitive to GDD (35% are sensitive, all of which shortened duration in response to increased GDD, mean = 0.217, SD = 0.113; note that covariates are scaled so the units are not interpretable as days per GDD), followed by snowmelt (31% of species, mean = 0.0844, SD = 1.13) and finally soil moisture (8% of species, mean = 0.00388, SD = 0.105).

There were several ways in which species responses to warming were generalizable across taxa. Species whose flowering duration lengthened in warmer, drier, earlier melt conditions (i.e., 2015) tended to also delay peak flower relative to snowmelt in 2015 ( $F = 9.14$ ,  $df = 46$ ,  $P < 0.01$ ; Appendix S1: Fig. S7). This is likely due to species experiencing different changes in GDD, with species at early-melt sites experiencing cooler conditions (decreased GDD) that delayed plant development (Appendix S1: Fig. S2). The onset of flowering (relative to snowmelt), in response to warmer, drier, earlier snowmelt conditions (i.e., 2015), shifted less for early-flowering species than for late-flowering species ( $F = 8.40$ ,  $df = 46$ ,  $P < 0.01$ ), but this pattern was not apparent for changes in peak flower or the end of flowering ( $P > 0.2$  for both relationships; Appendix S1: Fig. S8). Changes in flowering duration in 2015 were also related to the average length of flowering in typical climatic conditions, with longer-flowering species shortening their flowering period while shorter-flowering species lengthened their flowering period in 2015 ( $F = 27.64$ ,  $df = 46$ ,  $P < 0.01$ ; Appendix S1: Fig. S8).

Overall, we found strong evidence for generalizable responses to environmental conditions that closely

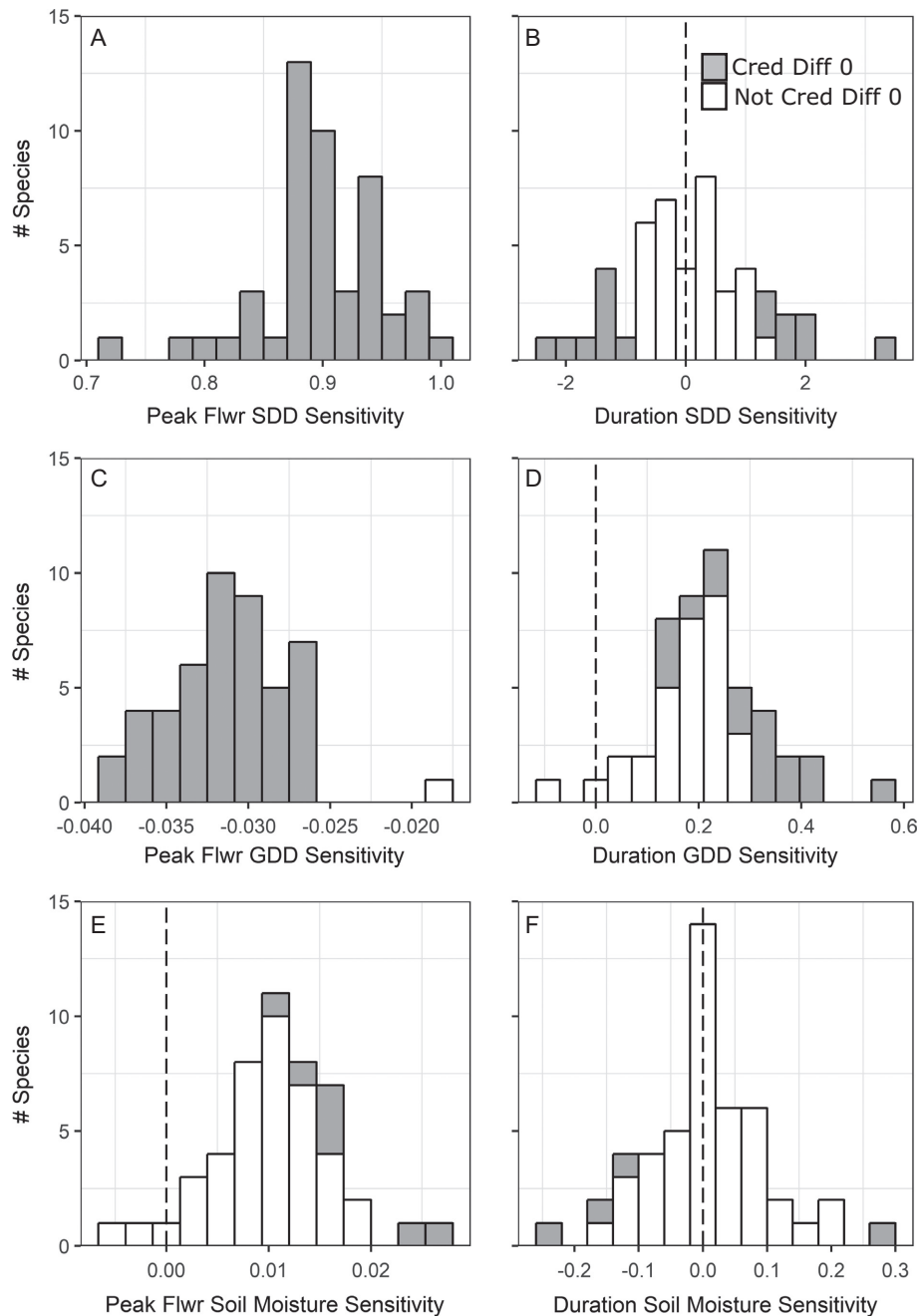


FIG. 3. Species vary in their phenological sensitivity to climate change, both in terms of (A, C, E) peak flower and (B, D, F) flowering duration (length), in response to snowmelt (A, B; SDD is snow disappearance date), growing degree days (C, D; GDD is growing degree days) and soil moisture (E, F). Each plot shows the distribution of parameter values for all species. Grey bars indicate species with sensitivities that are credibly different than zero and white bars indicate species that are not credibly different than zero. Dashed lines at zero for reference show parameter values indicating "not sensitive" species.

mirror those we expect in the late-21st century under unabated climate change (early snowmelt, warmer temperatures, and drier summer soil conditions). Earlier snowmelt drives consistently earlier flowering for all species (although the magnitude of the shifts varies), and has large but species-specific influences on flowering

durations in this system (Fig. 3). Increases in post-snow growing-degree days drive earlier flowering peaks for all species and shorter flowering periods for most species (Fig. 3). Decreases in soil moisture duration cause smaller and species-specific changes in phenology for a subset of species (Fig. 3).

### Phenological reassembly

Comparing community co-flowering richness (Fig. 4) and novelty (Fig. 5) trajectories in climate change-like conditions (2015), to trajectories in typical years (2011–2014) indicates that low-elevation ridges and slopes experienced the greatest amount of phenological reassembly in 2015. First, flowering richness changed most at low elevations and on ridges and slopes where changes in environmental drivers were most dramatic (Figs. 4, Appendix S1: Fig. S2). There was not a strong location-specific pattern in median novelty (Fig. 5). Overall, coves and high-elevation sites reassembled less in 2015, likely because they melt in the heart of the growing season when temperatures are peaking, even in the early melt conditions. In contrast, ridges and sites at lower elevations melted when conditions were cooler and wetter in 2015 than they typically are. These novel combinations of environmental conditions interacted with species-specific sensitivities to produce large differences

in phenological reassembly across the elevation gradient of subalpine meadows.

Reassembly is greatest early and late in the season (Figs. 4 and 5). This was reflected by changes in flowering richness that were greatest early and late in the season (Fig. 4), with lower richness early in the flowering season in climate-change-like years. Additionally, novel communities were also likely early in the season (Fig. 5). These patterns in novelty are largely due to early-flowering species lengthening their flowering duration in 2015, while later-flowering species shortened their flowering duration ( $F = 6.74$ ,  $df = 46$ ,  $P < 0.05$ ; Appendix S1: Fig. S8). These asymmetric shifts in duration (likely driven by cooler temperatures after snow melt and reduction in late-season soil moisture) meant that early-flowering species newly co-flower with mid-season flowers (novel flowering patterns) whereas late-flowering species truncated their flowering.

The lag between snowmelt and the onset of the flowering season increased in the climate-change-like year,

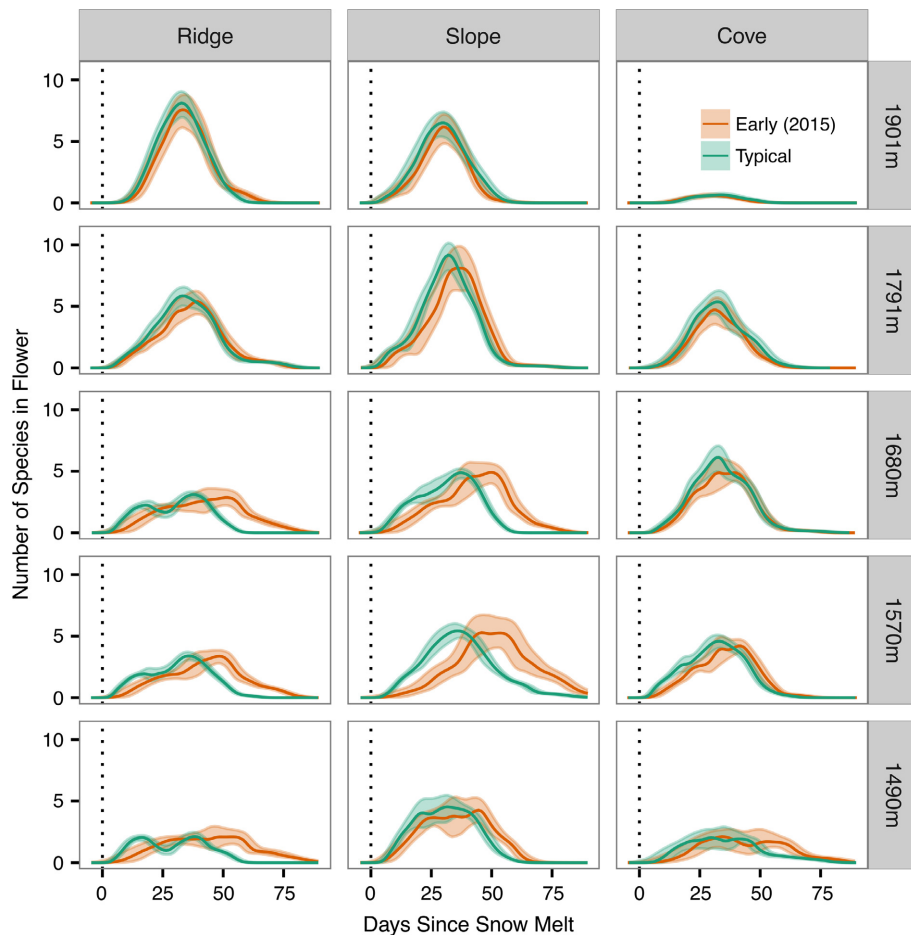


FIG. 4. Estimated species richness for each day from snowmelt (vertical dotted line) to 90 d past snowmelt at each topographic position at each elevation in 2015 (light grey) and conditions of typical snowmelt years (2010–2014, dark grey). Shading indicates 80% credible intervals. Reassembly is evident when curves do not align, primarily at lower elevations along ridges and slopes. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



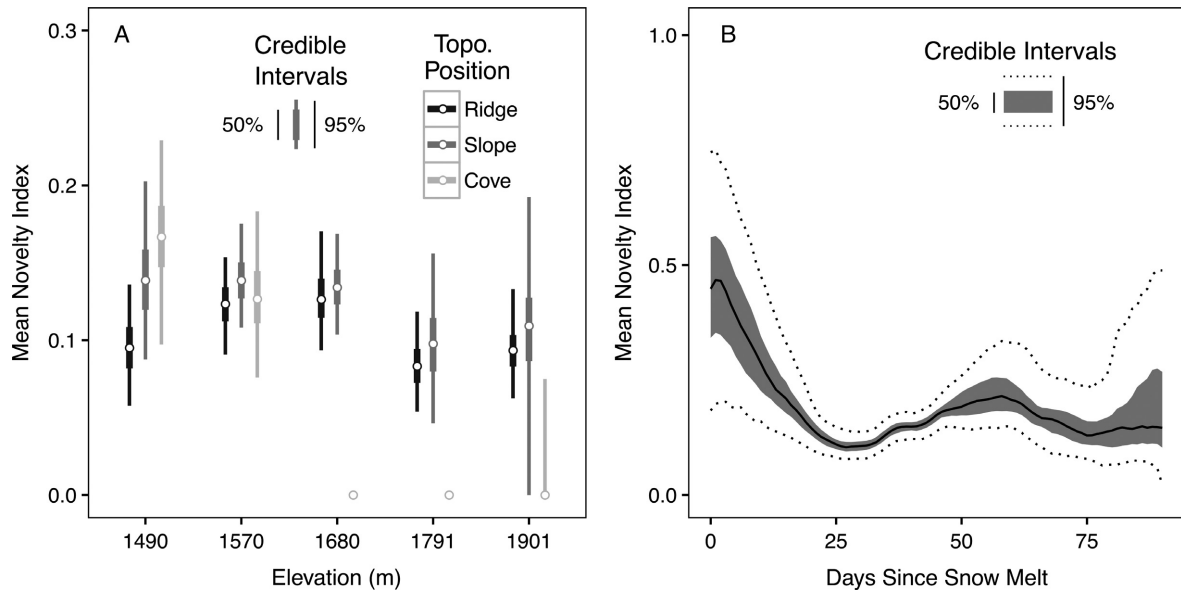


FIG. 5. Novelty of communities in early vs. typical snowmelt years. Median novelty (A) is greater at low elevations. Interestingly, trajectory of novelty through the flowering season (B) shows that novelty is most pronounced early in the season. In A, wide bars span 50% and narrow bars span 95% credible intervals, and in B shaded bands indicate 50% credible intervals and dashed lines show 95% credible intervals.

changing most dramatically at low-elevation sites that melted out early in the growing season (Fig. 6). The average increase in lag across all sites was 3.22 d (95% credible intervals 0.93–5.43 d), but was 4.61 (95% CI 0.05–7.89) days at low elevation sites (1,490–1,680 m). Changes in lag were less dramatic at cove sites at higher elevations, where both snowmelt date and post-snow temperatures also changed less dramatically in 2015.

Additionally, the length of the entire flowering season increased in the climate-change-like year such that the average length of the flowering season across all sites was 64.09 d in 2015, compared to 55.67 d in ‘typical years’, an average lengthening of 8.36 d (95% CI 6.76–10.09 d; Fig. 6). This metric showed a similar pattern to the other three, with the flowering season lengthening the most at sites and topographic positions that

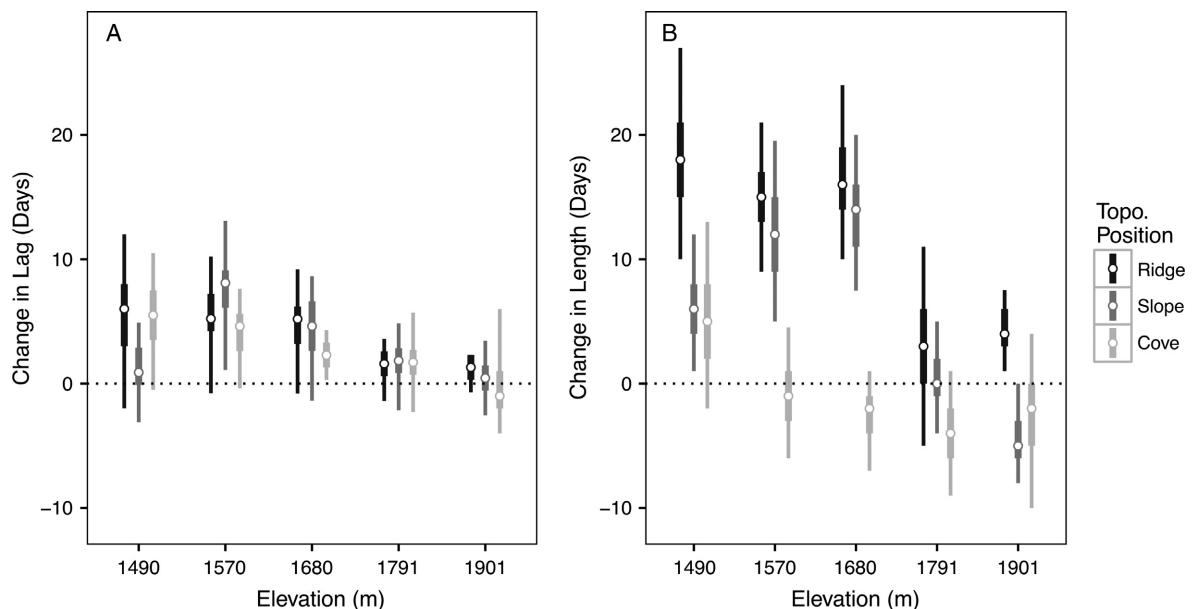


FIG. 6. Changes in lag, (A) the number of days between snowmelt and first flower, and season length, (B) in 2015 compared to average conditions from 2010–2014. Wide bars span 50% and narrow bars span 95% credible intervals.

experienced the most dramatic environmental changes in 2015 relative to typical years.

### DISCUSSION

We used our extensive dataset of community-wide flowering phenology and the natural experiment of a year with ‘climate change analog’ conditions to (1) determine whether differences in flowering phenology are likely to drive the phenological reassembly of plant communities with climate change, and (2) determine which sites and time-periods are most sensitive to phenological reassembly. To do so, we disentangled the mechanisms by which phenological reassembly would occur in three steps. Specifically, we first demonstrated that species are sensitive to the three environmental drivers we measured: timing of snowmelt, post-snow growing degree days, and soil moisture duration. Second, we determined that species-specific sensitivities to climate were unique to each species and apparent both in changes in the timing of peak flower and in flowering duration (Fig. 3). Finally, we verified that species with different sensitivities to climate co-occurred. In combination, this led to floral phenological reassembly in a year that mimicked climate conditions predicted in the 2080s under unabated climate change (Figs. 1, Appendix S1: Fig. S1 and Figs. 4–6). Below we elaborate on these results, and speculate about the causes, context, and implications of phenological reassembly in a warmer world.

#### *Phenological reassembly: causes*

Overall, phenological reassembly occurred as species differentially shifted both their timing of peak flowering and duration of flowering with changing climate drivers, although responses across species were more consistent than we originally expected. For example, although species showed individualistic shifts in peak flowering in response to earlier snowmelt, *all* species did shift their phenology earlier in response to changes in snowmelt. Similarly, species’ peak flowering shifted earlier with greater growing season temperatures (GDD), with most additionally shortening their flowering duration in response to increases in GDD (Fig. 3). Other studies have found evidence of similar climate drivers (most often snow, to a lesser extent temperature as seasonal or monthly means, and in one case previous summer’s precipitation) influencing flowering phenology in mountainous regions (Dunne et al. 2003, Inouye et al. 2003, Kudo and Hirao 2006, Crimmins et al. 2008, Inouye 2008, Hülber et al. 2010, Iler et al. 2013), but few (to our knowledge) have found complex effects of multiple climate drivers (snow, growing degree days, soil moisture) on different aspects of flowering phenology, as we did (Fig. 3).

It is not surprising that snowmelt and growing degree days were the strongest predictors of peak flowering (as opposed to flowering duration), because the snow-free

growing season is very short at in the subalpine meadows of Mount Rainier (as short as 8 weeks at high-elevation sites). Thus, strong phenological sensitivities to snowmelt in this system likely reflect strong selection for these high mountain plants to time their reproductive phenology closely to a temporally constrained growing season (Sheth and Angert 2016). Spring or growing-season temperatures (as measured by post-snow growing degree days in our system) are also known to constrain plant development, and thus strongly influence when a plant is ready for reproduction (Wahid et al. 2007). Sensitivity to growing degree days may also be an adaptive way to reduce the risk of early-season frost in this system (Inouye 2008, Forrest and Miller-Rushing 2010). Thus, for these subalpine species, flowering soon after snowmelt and when growing season temperatures are warm may be the best way to maximize reproductive opportunity in a location where climatic conditions (i.e., frost) are harsh (similar to Crimmins et al. 2010).

Our results also highlight the importance of considering multiple climate variables when calculating the phenological sensitivities of species to climate. For one, preliminary model fitting using only snow as an explanatory variable suggested that attributing all of the variation in responses to any single climate variable may over-estimate the importance of that climate variable, presumably because climatic factors often co-vary. We found less between-species variation in the sensitivity of peak flower to snowmelt and growing degree days (than we expected from most previous studies; e.g., Caradonna et al. 2014) once we fit models with multiple climate variables, complementing findings from other studies (e.g., Diez et al. 2012). Furthermore, our preliminary analyses, which only included date of snowmelt as a predictor of phenology, showed strongly non-linear phenological responses to date of snowmelt (analyses not shown). These non-linear trends disappeared in our final model incorporating multiple climate drivers; this suggests we must be cautious about interpreting non-linear phenological responses (as found by Iler et al. 2013) when demonstrated by models including only single climate drivers. More generally, because climate change will cause changes in many axes of climate to which phenology might be sensitive, incorporating multiple drivers of change is likely essential both to understanding the mechanisms by which phenology is cued, as well as to predicting potential phenological shifts in response to climate change (Diez et al. 2012, Wolkovich et al. 2012). Moreover, quantifying species’ phenological sensitivities to multiple climate drivers allows us to assess the possibility of phenological reassembly. Although our observational study cannot rule out the influence of other, unmeasured climatic or habitat effects on phenology, the out-of-sample predictive performance of our model (Appendix S1: Fig. S5, Appendix S2) suggests that there is relatively little variation in flowering phenology that is not associated with the environmental drivers we included in our analysis.

### *Phenological reassembly: context*

Phenological reassembly requires species-specific climate sensitivities (either in identity of drivers or magnitude, as we found), but also depends on the magnitude of change in the climatic drivers of phenology (Crimmins et al. 2010). In our case, we found a rather unexpected amount of fine-scale spatial variability in the amount and nature of climatic change that our sites experienced in 2015, and these patterns strongly influenced spatial patterns in reassembly. For example, reassembly was most apparent at low elevations and along ridges and slopes in the landscape (Figs. 4–6). This pattern was largely driven by the fact that these sites (low elevations and ridges and slopes) experienced larger differences in both snowmelt and growing degree day accumulation in 2015 than did high-elevation sites (Appendix S1: Fig. S2). An additional factor was that the direction of change in snowmelt and growing degree day accumulation differed at these sites relative to the broader trends across our entire study. Specifically, snow disappeared from low-elevation ridge and slope sites so early in 2015 that these sites experienced cooler, spring-like temperatures than in normal years (Appendix S1: Fig. S2), which is consistent with what is expected as the climate warms (Inouye 2000, 2008, Mauger et al. 2015). By contrast, plots in coves (across all elevations) and high elevation sites experienced both earlier snowmelt and warm and summer-like temperatures (high elevations and coves experienced virtually no change in GDD in 2015 compared to typical years; Appendix S1: Fig. S2). Thus, both the magnitude of climatic change and covariance among climatic drivers varied spatially, driving differential reassembly across elevations and topographic positions.

It is also likely that locations experiencing minimal reassembly in 2015 contained combinations of species that were either not strongly sensitive to climate drivers or that varied less in their phenological sensitivities to climate. For example, at high elevations (where snow often lingers into August) there is likely even stronger selective pressure for species to time their reproductive phenology closely to climatically favorable environments given that the growing season is predictably extremely short (Sheth and Angert 2016). Consistent with this possibility is that species found at high elevations tracked climate more closely than plants at low elevations (Appendix S1: Fig. S8), whereas low-elevation plants generally demonstrated a longer lag between snowmelt and peak flowering. For these high-elevation species, flowering soon after snowmelt is critical for maximizing reproductive opportunity (similar to Crimmins et al. 2010). It is possible that these high-elevation plants preform flowers before the dormant season, facilitating their ability to flower rapidly as conditions improve. Regardless of cause, this suggests that locations where all species are tightly cued to climate may see less overall variation in community responses to climate change, minimizing reassembly in climatically variable years.

Reassembly in 2015 also varied temporally within the flowering season. Specifically, early in the season there were large changes in flowering species richness (Fig. 4; lower richness in reassembled years) and high novelty (Fig. 5). This is likely due to early-flowering species lengthening their phenologies more than late-flowering species (Appendix S1: Fig. S8; Miller-Rushing and Primack 2008, Miller-Rushing and Inouye 2009, Munguía-Rosas et al. 2011), increasing the extent to which early-flowering species co-flower with other species, thus creating novel co-flowering patterns. By contrast, late-flowering species tended to decrease their flowering duration, possibly in response to dry conditions at these sites (Appendix S1: Fig. S8), but did not differentially shift their phenologies sufficiently to result in novel co-flowering patterns (Fig. 5).

We cannot be certain that the environmental changes experienced at our sites, or the phenological changes we observed in 2015, are representative of future conditions: the environmental forecasts are uncertain and late 21st century climates of Mt. Rainier depend on global CO<sub>2</sub> emissions, regional variability in atmospheric circulation, as well as complex interactions between climatic and hydrological processes (Salathe et al. 2013, Steinman et al. 2014). However, recent modeling studies do increase our confidence that 2015 conditions are broadly representative of the trajectory of critical climatic drivers (spring temperatures, snowmelt dates) in our system if climate change continues unabated (Mauger et al. 2015). Although the phenological responses of an extreme year might differ somewhat from responses to decadal-scale shifts in mean climate, studies in other systems have demonstrated strong relationships between phenological responses to annual climate variability and decadal-scale trends (Studer et al. 2005, Iler et al. 2016). Moreover, our spatially and temporally extensive whole-community phenological data allow us to demonstrate that all elements required for phenological reassembly are present (strong but species-specific sensitivity of co-occurring species to multiple climate drivers). Thus, despite its limitations, we believe that this natural experiment provides unique insight into the magnitude, spatial pattern, and drivers of phenological reassembly in this system driven by variation in climate (Diamond 1983, HilleRisLambers et al. 2013).

### *Phenological reassembly: implications*

Though beyond the scope of this study, floral phenological reassembly may have impacts on plant-pollinator dynamics. In this case, floral phenological reassembly may disrupt current patterns in plant-pollinator interactions if early-flowering species lengthen their phenology disproportionately compared to late-flowering species, because plant species provision different amounts of sugar (via nectar) and protein (via pollen). Over the long-term, this may impact pollinator foraging patterns (Burkle et al. 2013), and populations (Potts et al. 2010,

Vanbergen and Initiative 2013). Furthermore, these shifts have the potential to change plant-plant interactions through the dynamics of competition for and facilitation of pollinator services (e.g., Moeller 2004, Waters et al. 2014). Changes in the facilitative and competitive interactions between plant species could lead to increased or decreased plant reproduction and ultimately population success (Palmer et al. 2003). On the other hand, the existing spatial and year-to-year variability in phenology may also buffer plants and their pollinators from long-term disruptions (Bronstein et al. 2006, Alarcón et al. 2008).

Over decadal scales, we anticipate that phenological reassembly will be important in communities of long-lived organisms, like ours, where changes in abundance and distributions will be slow relative to changes in climate (Kroiss and HilleRisLambers 2015). As the speed of anticipated climate change across space is expected to exceed the dispersal rates of most organisms (Loarie et al. 2011, Dobrowski et al. 2013), measuring the in-situ responses of species and ecological communities to climate, including phenological reassembly, gives critical insight into near-term ecological change.

#### CONCLUSIONS

Assessing community-level phenological shifts is a critical, yet often overlooked, aspect of evaluating the biological impacts of climate change. Differences in species-specific climate sensitivities can have large impacts on the magnitude and direction of shifts in peak flower and on the duration of flowering, and in turn, these phenological shifts can have large impacts on the timing of flowering communities. Interestingly, we found that species-specific sensitivities to climate, as well as spatial and temporal patterns in the magnitude of change in three critical climate drivers, jointly influenced the temporal and geographic patterns of phenological reassembly. In networks of interacting species, such as plant-pollinator networks, this has the potential to alter or disrupt species interactions, with implications for both parties. Targeted efforts to determine the ecological consequences of phenological reassembly, for example, if phenological reassembly could contribute to spatial community reassembly via reduced seed production, may help identify extinction risks for species, and impacts on important ecological processes as the climate warms.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1996/supinfo>