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LIMITED ALPINE CLIMATIC WARMING AND MODELED PHENOLOGY ADVANCEMENT FOR THREE ALPINE SPECIES IN THE NORTHEAST UNITED STATES¹

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- *Premise of the study:* Most alpine plants in the Northeast United States are perennial and flower early in the growing season, extending their limited growing season. Concurrently, they risk the loss of reproductive efforts to late frosts. Quantifying long-term trends in northeastern alpine flower phenology and late-spring/early-summer frost risk is limited by a dearth of phenology and climate data, except for Mount Washington, New Hampshire (1916 m a.s.l.).
- *Methods:* Logistic phenology models for three northeastern US alpine species (*Diapensia lapponica*, *Carex bigelowii* and *Vaccinium vitis-idaea*) were developed from 4 yr (2008–2011) of phenology and air temperature measurements from 12 plots proximate to Mount Washington's long-term summit meteorological station. Plot-level air temperature, the logistic phenology models, and Mount Washington's climate data were used to hindcast model yearly (1935–2011) floral phenology and frost damage risk for the focal species.
- *Key results:* Day of year and air growing degree-days with threshold temperatures of -4°C (*D. lapponica* and *C. bigelowii*) and -2°C (*V. vitis-idaea*) best predicted flowering. Modeled historic flowering dates trended significantly earlier but the 77-yr change was small (1.2–2.1 d) and did not significantly increase early-flowering risk from late-spring/early-summer frost damage.
- *Conclusions:* Modeled trends in phenological advancement and sensitivity for three northeastern alpine species are less pronounced compared with lower elevations in the region, and this small shift in flower timing did not increase risk of frost damage. Potential reasons for limited earlier phenological advancement at higher elevations include a slower warming trend and increased cloud exposure with elevation and/or inadequate chilling requirements.

Key words: alpine plants; climate change; *Carex bigelowii*; *Diapensia lapponica*; floral phenology; frost risk; long-term record; Mount Washington; New Hampshire; *Vaccinium vitis-idaea*.

Mid-latitude alpine ecosystems are typically characterized by short growing seasons and harsh environmental conditions; consequently, they are considered sensitive bellwethers of environmental change (Pauli et al., 2003; Löffler et al., 2011). Alpine ecosystems of the Northeast United States (here after, Northeast) are now scattered relict biogeographic islands occupying $\sim 34\text{ km}^2$, with the Presidential Range, New Hampshire being the largest ($\sim 11.3\text{ km}^2$), highest (1917 m a.s.l.), and most southern major unit (Kimball and Weihrauch, 2000). They

could be more susceptible to extirpation due to range shifts and community changes resulting from ongoing warming trends. These small “islands in the sky” are at relatively low elevations compared with alpine ecosystems at similar latitudes, and they occupy the highest available habitat within their range. They cannot migrate upslope farther and today are geographically distant and isolated from their postglacial tundra origin.

Plant phenology, the study of the timing of plant life cycle events, is an important component in understanding the degree of threat to Northeast alpine ecosystems in response to changing environmental conditions (Inouye, 2008; Chuine, 2010). We use phenology and long-term weather records to assess how sensitive three major species of these alpine ecosystems may be to ongoing regional warming trends. Each year, alpine plants face a trade-off between the advantages of earlier flowering and the risk of a late-spring/early-summer frost. Earlier phenological activity increases the likelihood that developing fruit will reach full maturity (Galen and Stanton, 1991; Kudo, 1991; Stenström, 1999) and provides a longer growing season to build reserves for the following years' reproductive and vegetative capacity (Mooney and Billings, 1960; Bliss, 1962), but floral damage due to a late frost would destroy that year's potential seed production (Fonda and Bliss, 1966; Inouye and McGuire, 1991; Kudo, 1993; Bannister et al., 2005; Inouye, 2008).

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At lower elevations in the Northeast, earlier flowering in concert with warming temperatures has been reported (Bertin, 2008; Miller-Rushing and Primack, 2008). Whether similar trends are happening in the region's alpine ecosystems has not been determined, and if present, the potential impacts of any changes in phenological timing remain unknown. Effects observed elsewhere, like temporal asynchrony for specialized pollinators (Aldridge et al., 2011; Inouye, 2008; Forrest et al., 2010), may be less of a factor for Northeast alpine plants because they appear to host a variety of more generalist pollinators (Levesque and Burger, 1982; McCall and Primack, 1992). Many alpine species are also long-lived perennials with life expectancies up to a couple of centuries (Molau, 1997; de Witte et al., 2012), which may buffer these populations from the impacts of climatic variability and related demographic stochasticity, such as periodic loss of seed production and seedling recruitment.

Studies on environmental factors that trigger the various reproductive phenophases for alpine plants frequently focus on temperature and recent climate warming trends, along with the somewhat related date of snowmelt (Totland and Alatalo, 2002; Molau et al., 2005). However, other factors can play a role including photoperiod, changes in precipitation, nitrogen deposition, and the interactions between all of these factors (Keller and Körner, 2003; Lambert et al., 2010; Smith et al., 2012), but vary in importance between different alpine ecosystems. Research on phenological drivers for Northeast alpine plants are lacking, and findings from better-studied alpine and arctic ecosystems may be questionable surrogates. The Northeast alpine flora and climate are considered more similar to arctic tundra than to the western Rocky Mountains of the United States (Bliss, 1963; LeDrew and Weller, 1978; Greenland et al., 1984). Comparisons to the arctic tundra, however, have limitations; for example, the photoperiods differ, and Northeast soils remain quite moist because of the high incidence of clouds and precipitation, but are generally better drained than arctic tundra soils due to greater slope (Hadley and Bliss, 1964; Billings, 1973).

Changing climate trends are not universal across different alpine ecosystems (Diaz and Bradley, 1997; Weber et al., 1997) since mountain climate is determined by latitude, altitude, distance to large water bodies, and exposure to circulation patterns. Warming trends have been reported from mountains in the western United States (Pederson et al., 2010) and some in Europe (Pauli et al., 2003). Low elevations in the Northeast also exhibit significant, but heterogeneous warming and changes in precipitation patterns (Huntington et al., 2004; Hayhoe et al., 2007). Although the region's mountains are not high in elevation (max. = 1917 m a.s.l.), our research on Northeast alpine ecosystems suggests reduced warming trends compared with mid-elevations (Seidel et al., 2009). We attribute this more moderate warming to thermal inversions, close proximity to oceanic water and subsequent, frequent cloud immersion that impedes long-wave, outgoing radiation, and the periodic uncoupling of air masses with elevation due to planetary boundary-layer dynamics. Further evidence of local resistance to warming at higher elevations in the Northeast is the paleoecological record for New Hampshire's Presidential Ranges. The alpine zone overall resisted tree invasion and persisted through the warmer than present Holocene Climate Optimum (Hypsithermal) period nine to five thousand years ago, whereas regional lower-elevation forests showed demonstrable shifts in species composition (Spear, 1989; Miller and Spear, 1999).

Predictions of Northeast alpine ecosystem responses to shifts in climatic conditions has mostly been speculative or inferred from lower-elevation climate records or other worldwide mountain trends. Confounding phenological studies for many mountain ecosystems is the paucity of appropriate climate data for analysis at higher elevations. Of the 347 active National Oceanic Atmospheric Administration (NOAA) meteorological stations in northern New York, Vermont, New Hampshire, and Maine, only two are above 650 m a.s.l.; the longest and most complete data set is from the summit of Mount Washington, New Hampshire (at 1917 m a.s.l.). Because high-elevation meteorological stations are uncommon worldwide, records from the most proximate lower-elevation sites are often employed to extrapolate climate variables using linear lapse rates or other methods, despite serious problems identified with these methods (Kimball and Keifer, 1988; Richardson et al., 2006; Wundram et al., 2010; Scherrer et al., 2011). The use of on-mountain weather data can greatly improve the understanding of the relationships between weather and phenology timing (Daly et al., 2009) and improve extrapolations of phenology trends backward in time where long-term weather records exist.

The Mount Washington Observatory (MWO), located in the Presidential Range, New Hampshire on the summit of Mount Washington, has a climate data set from 1935–2006 (Seidel et al., 2009). The MWO's almost eight decades of record is of sufficient length to encompass both multiyear warming and cooling events (Zielinski and Keim, 2003). This study takes advantage of the MWO's climate record by collocating alpine plant phenology permanent plots and in situ surface-air and soil temperature sensors within the Presidential Range. This study also provides an opportunity to compare alpine phenology trends with mid-elevation forest phenology models that correlated earlier leaf development and delayed leaf senescence for several tree species with regional warming (Richardson et al., 2006) at the nearby US Forest Service Hubbard Brook Experimental Forest (<50 km SW).

In this study, we used logistic modeling techniques (Richardson et al., 2006) for three alpine species [*Diapensia lapponica* L. var. *lapponica* (Diapensiaceae), *Carex bigelowii* Torr. ex Schwein. (Cyperaceae), and *Vaccinium vitis-idaea* L. subsp. *minus* (Lodd.) Hultén (Ericaceae)] based on 4 yr of day of year and in situ air temperature and phenology measurements from 12 plots to predict the timing of phenophases from dormant through seed dispersal. We derived and tested various environmental indices related to degree-days, snowmelt, and day of year (a proxy for photoperiod), and applied the best fit model results with the meteorological record from the MWO to hindcast 77 yr of phenology to identify potential trends in phenological timing and the frequency of overlap between early-season flowering and late floral-killing frost for these three alpine species.

MATERIALS AND METHODS

Site description—Mount Washington (44°16'N/71°18'W), the highest point (1917 m a.s.l.) in the Northeast United States, is part of the Presidential Range of the White Mountains of New Hampshire, a northern section of the Appalachian Mountains. The Presidential Range contains ~11.3 km² of contiguous alpine and subalpine vegetation surrounded by a spruce–fir boreal forest with northern hardwood species at lower elevations. Treeline occurs at relatively low elevations and ranges from 1100 to 1700 m a.s.l. (Kimball and Weihrauch, 2000). The treeline–alpine ecotone is correlated with exposure to cloud, wind and icing, slope, and aspect (Reiners and Lang, 1979; Kimball and Weihrauch, 2000).

The regional planetary boundary layer (PBL) typically extends up to 1100–1500 m a.s.l. (Freedman et al., 2001), and on Mount Washington it exhibits diurnal and vertical migration, whereby the alpine zone may be in or above the PBL for portions of the day. Dynamics of the PBL and increased incidence of orographic clouds in the alpine zone may partially explain the evidence of climate change declining with increased elevation based on temperature and snow records from 1930 to 2006 on Mount Washington (Seidel et al., 2009). We have since updated the Seidel et al. (2009) analyses through 2012 (unpublished data) and both spring minimum and maximum daily temperatures are now even stronger drivers in the mean annual warming trend at the summit.

A total of 12 phenology and in situ temperature permanent plots (of various size but large enough to include at least 10 flower buds of the target species) were established at three sites in the Presidential Range in the alpine zone surrounding the central Mt. Washington massif: Mizpah, Lakes of the Clouds, and Madison (Fig. 1, Table 1). In addition, we used the climate record from the MWO located on the highest summit (Fig. 1) for historical retrospective modeling. MWO air temperature data used for the retrospective analysis are described in Seidel et al. (2009).

Study species—Based on our 8 yr of observations, the three alpine species we selected represent a seasonal flowering continuum for the study area, ranging from the earliest flowering *D. lapponica*, (average peak flowering date of 9 June, standard error [SE] 6.5 d) and *C. bigelowii* (22 June, SE 5 d) to the relatively late flowering *V. vitis-idaea* (2 July, SE 8 d). As expected, we observed variability and overlap in the species’ phenology reflecting differences in aspect, elevation, and microtopography. *Diapensia lapponica* and *C. bigelowii* are of arctic-tundra origin and regionally occupy highly to moderately exposed alpine habitat, with the former found in habitat frequently blown free of snow and the latter most common at higher elevation sites with a NW aspect. *Vaccinium vitis-idaea* has a shrubby stature and inhabits boreal to arctic and alpine

habitats; in this alpine region, it is found in more protected areas, where wind-blown snow can accumulate (Kimball and Weihrauch, 2000).

Field phenology measurements—All phenophases present and the dominant phenophase at each plot were recorded approximately twice per week from 2004 to 2011. In 2010–2011, in-person field observations were supplemented with Wingscapes Time Lapse “phenocams” (WSCA04-00106; Alabaster, Alabama, USA) that took three automated pictures daily. These phenocam images were reviewed, and the best of the daily images was coded to indicate the phenophases observed. Image resolution made it difficult to determine late stage phenophases, or any phenophases for *C. bigelowii*, so only phenocam observations for phenophases before the completion of flowering were used for *D. lapponica* and *V. vitis-idaea*, while no phenocam observations were used in the construction of *C. bigelowii* models. The phenophases were coded using the number scheme in Table 2 and a weighted-average (the dominant phenophase was double weighted) was calculated for each observation. Resulting values from 1.5–2.5 are defined as the total period of flowering.

In situ temperature measurements—Onset temperature data loggers (HOBO models U23-003 and U23-004; Bourne, Massachusetts, USA) recorded hourly surface-air and soil temperatures (at 1 cm above, and 10 cm depth, respectively) at each study plot, year round from 2008 to 2011. Degree-day accumulations for the surface-air (airGDD) and soil (soilTDD) temperature data were calculated in HOBOWare software using the single sine no cut-off method (Roltsch et al., 1999; Onset Computer Corp., 2012). When a temperature sensor malfunctioned for less than 12 h, we interpolated the data as an average of the previous and following hours equal to the number of missing hours; if gaps were larger than 12 h no further accumulated degree-days were calculated for the season. Freeze–thaw soil movement of probes, and other causes, resulted in considerable soil data loss, which confounded our ability to use this parameter effectively in our phenology models.

MWO temperature measurement—Hourly air temperature data taken at the summit of Mount Washington by the MWO from 1935 to 2011 (see Seidel et al., 2009 for MWO methods) were used to generate summitGDD using methods similar to those in the previous section to calculate airGDD, with the following exceptions. For gaps 12 to 24 h long, the averages of the same hours from 2 d before and after were used. The data sets for four of the 77 yr (1938, 1939, 1948, and 1951) contained larger data gaps and were truncated to exclude those periods.

Days from snow melt (DFSM) and day of year (DOY)—Surface-air temperature readings during snow cover remain steady at or below freezing; therefore, a diurnal fluctuating pattern above freezing is a good signal of snow melt. Days from snow melt (DFSM) was calculated as the number of days from when the daily maximum surface-air temperature first was $\geq 0.1^\circ\text{C}$ for at least four consecutive days and the rolling total number of subsequent days with a maximum temperature $< 0.1^\circ\text{C}$ never exceeded the number of days $\geq 0.1^\circ\text{C}$. The variable day of year (DOY) was used as a surrogate for length of time from photoperiod-driven phenophase initiation (Richardson et al., 2006; Fisher et al., 2007).

Statistical analysis—Phenophases for our three target species were modeled using a modified two-parameter logistic curve similar to Richardson et al. (2006),

$$\frac{5}{1 + \exp(b - c_1x_1 - \dots - c_nx_n)} \tag{1}$$

where $x_1 \dots x_n$ are explanatory variables and b and $c_1 \dots c_n$ are model constants. Although less commonly used than single phenophase models, logistic models incorporate a larger data set by including all phenophases, which can be beneficial when analyzing data sets from a short time period, such as our 4-yr record. Models were fit using nonlinear least squares in the statistical package R (R Development Core Team, 2011). Seven competing models were fit for each species using airGDD, DOY, and DFSM as explanatory variables singly or in combination. Because the threshold temperature used for degree-day calculations affects the fit of models where accumulated degree-days are used as an explanatory variable, airGDD models using threshold temperatures from -6°C to 8°C in 2°C increments were first fit for each species to pick the best threshold

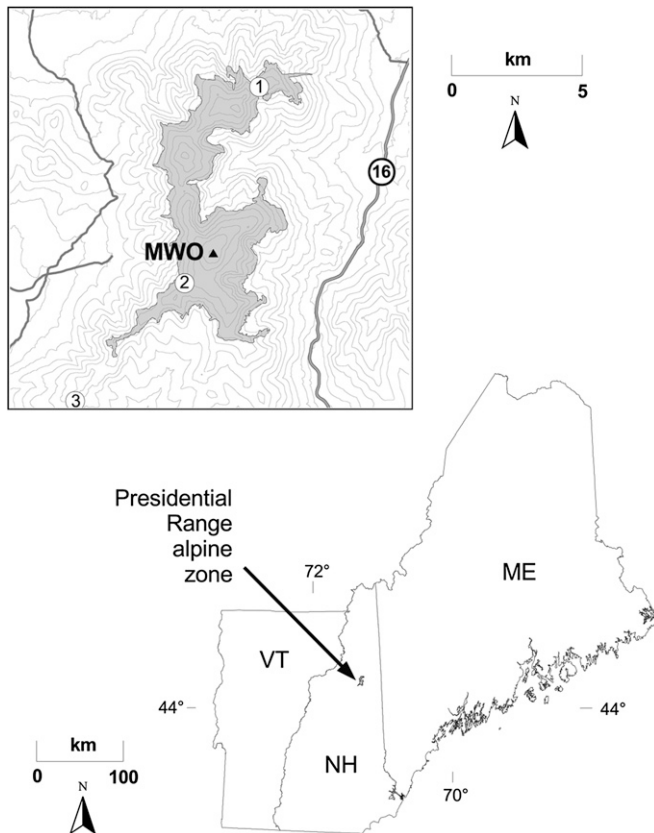


Fig. 1. The contiguous alpine zone (shaded area) and phenology plot sites of Madison (1), Lakes of the Clouds (2), Mizpah (3), and the Mount Washington Observatory (MWO) in the Presidential Range, New Hampshire, USA.

TABLE 1. Alpine phenology plots, latitude/longitude, elevation, and species present (+), Presidential Range, New Hampshire, USA.

Site	Plot	Latitude / Longitude	Elevation (m a.s.l.)	<i>Diapensia lapponica</i>	<i>Carex bigelowii</i>	<i>Vaccinium vitis-idaea</i>
Mizpah	Miz 1	44°13'17.93" / -71°22'11.83"	1258			+
	Miz 2	44°13'21.26" / -71°22'12.82"	1271	+		+
	Miz 3	44°13'22.29" / -71°22'11.73"	1271	+		+
Lakes of the Clouds	LOC 1	44°15'20.17" / -71°19'6.48"	1534	+	+	+
	LOC 2	44°15'27.17" / -71°19'8.17"	1545	+	+	+
	LOC 3	44°15'30.88" / -71°19'6.82"	1528	+	+	+
	LOC 4	44°15'30.18" / -71°19'5.36"	1528	+	+	+
	LOC 5	44°15'31.91" / -71°19'4.36"	1541			+
Madison	Mad 1	44°19'32.29" / -71°17'1.98"	1493	+	+	+
	Mad 2	44°19'32.72" / -71°17'1.17"	1495	+	+	+
	Mad 3	44°19'41.15" / -71°16'58.96"	1474	+		+
	Mad 4	44°19'40.94" / -71°17'0.89"	1466	+	+	+

temperature for calculating airGDD for a particular species. All logistic models were parameterized using nonlinear least squares. Model selection at all steps was based on Akaike's information criterion (AIC) (Anderson and Burnham, 2002; Burnham and Anderson, 2002). Predicted vs. observed values were compared for the best model for each species to ensure that no directional bias was present.

1935–2011 Retrospective modeling—Historical retrospective modeling was focused on phenophases 1.5 (early flowering), 2 (peak flowering), and 2.5 (late flowering) to examine trends in the overall flowering period. The permanent plots are 371 to 658 m lower than the conical summit peak location of the MWO, but to avoid relying on simple adiabatic lapse rates, Gaussian linear regressions were employed to model the relationship between the 2008–2011 average daily airGDD values (computed from all available study plot airGDD records) and the MWO daily summitGDD values for both -4°C and -2°C threshold temperatures. The resulting models ($\text{airGDD}_{-4} = 1.55 \cdot \text{summitGDD}_{-4} + 66.73$, $R^2 = 0.99$; $\text{airGDD}_{-2} = 1.63 \cdot \text{summitGDD}_{-2} + 18.57$, $R^2 = 0.99$) were used to predict average daily airGDD₋₄ and airGDD₋₂ from the 1935–2011 MWO record. These hindcasted airGDD values and DOY for the 1935–2011 period were input into the logistic models for each species to determine the predicted phenophase for each species for a given airGDD and DOY combination. A Gaussian linear model was next used to establish the relationship between DOY and predicted phenophase for each species in each year to determine the average DOY for a given species in a given year that phenophases 1.5 (early flowering), 2 (peak flowering), and 2.5 (late flowering) were reached. Upper and lower predicted DOY ranges were also hindcast for phenophase 2 for each species for the 1935–2011 period by adding and subtracting coefficient standard errors to the models. To account for year to year temporal autocorrelation, we used generalized least squares (GLS) models to evaluate modeled phenology trends for phenophases 1.5, 2, and 2.5 in each species.

Annual frost damage hours ($\leq -2^{\circ}\text{C}$) for the period from 1 May to 31 July were totaled for each year of the MWO record; trends in total annual May–July frost damage hours were evaluated with a GLS model to account for year to year temporal autocorrelation. Annual frost damage hours that occurred during the predicted period of flowering were totaled for each species; trends in annual frost damage hours for each species were analyzed via the nonparametric Sen's slope estimator. The significance of the Sen's slope estimate for each species was evaluated via the Mann–Kendall test. This methodology was chosen due to the high number of years in which no frost damage hours were experienced, leading to over dispersion of the data. All statistical analyses were carried out in R (R Development Core Team, 2011).

TABLE 2. Phenophases and numeric model equivalents.

Numeric	Phenophase
0	Dormant
1	Bud swelling
2	Flowering
3	Post flowering
4	Fruit ripe
5	Seed dispersal

RESULTS

Logistic model selection—The interannual variability of monthly mean surface-air and soil temperatures for our 12 phenology plots (Table 3) ranged from 1.0 to 5.4°C and 0.8 to 5.7°C, respectively, suggesting that this 4-yr sample period included a broad spectrum of weather conditions. Surface-air and soil temperatures were quite similar in actual temperature and interannual variability by month (2008 $R = 0.94$; 2009, 2010, 2011 $R = 0.96$). These alpine soils are frequently exposed to clouds and precipitation (Babrauckas and Schmidlin, 1997) and moist conditions favorable to heat conduction. Therefore, it is not surprising that the surface-air and soil temperatures track as closely as they do.

Threshold temperatures of -4°C (*D. lapponica* and *C. bigelowii*) and -2°C (*V. vitis-idaea*) were chosen for use in all subsequent phenology models based on the AIC model comparison of airGDD logistic models. For each species, DOY alone provided a better model fit than did airGDD alone; however, DOY+airGDD (e.g., Fig. 2 for *D. lapponica*) provided the best model fit for *D. lapponica* and *C. bigelowii* (Table 4). The addition of DFSM improved model fit for *V. vitis-idaea*, but could not be used further in the modeling process due to the inability to accurately hindcast DFSM from the relationship between MWO snowmelt records and alpine HOBO temperatures. DFSM is likely to be an important variable in determining phenology for many alpine species that inhabit snowbank communities and less exposed sites such as *V. vitis-idaea*; it is understandable that DFSM did not improve model fit for *D. lapponica* and contributed minimally to *C. bigelowii* considering their more exposed, snow blown-off habitat preference. SoilTDD was included in preliminary modeling runs, but was dropped for several reasons. Improved model fits using soilTDD were possibly being masked due to soil temperature data loss, which in return truncated the available concurrent data for the other variables. And airGDD and soilTDD were highly correlated. DOY+airGDD model coefficients \pm their standard errors did not overlap zero in any case.

Logistic model results compared with 2008–2011 field observations predicted time of flowering best for the earlier flowering *D. lapponica* (the same day) and *C. bigelowii* flowering (within 1 d of mean observed peak flowering) than the later flowering *V. vitis-idaea* (within 5 d of mean observed peak flowering) (Table 5). Except for the late-flowering *V. vitis-idaea*, bud swelling and flowering (phenophases 1 and 2, respectively) were more accurately predicted than was post flowering and fruit ripe (phenophases 3 and 4). This reduced

TABLE 3. Alpine permanent plots monthly mean (and standard deviation) surface-air and soil temperatures (°C), 2008–2011, Presidential Range, New Hampshire, US.

Year: site	January	February	March	April	May	June	July	August	September	October	November	December
2008: surface-air	-4.7 (4.2)	-4.1 (3.3)	-3.7 (2.8)	3.4 (8.5)	12.3 (10.9)	17.7 (8.7)	19.4 (6.5)	16.1 (6.5)	15.2 (7.1)	5.2 (7.1)	-0.8 (5.3)	-2.3 (3.1)
2008: soil	-4.3 (3.2)	-3.8 (2.5)	-3.6 (2.5)	-0.9 (1.8)	1.9 (2.2)	8.3 (3.0)	11.9 (1.7)	10.9 (1.6)	9.7 (2.1)	3.8 (2.2)	0.9 (1.9)	-0.9 (1.6)
2009: surface-air	-6.8 (4.8)	-5.6 (3.9)	-3.3 (3.4)	1.7 (6.3)	10.1 (7.7)	16.4 (7.2)	15.3 (5.2)	19.5 (7.1)	15.8 (8.7)	2.9 (4.7)	2.5 (4.9)	-3.3 (3.8)
2009: soil	-5.8 (4.0)	-5.8 (3.7)	-4.0 (3.2)	-0.9 (1.4)	2.4 (2.3)	7.4 (3.2)	9.9 (1.8)	12.3 (2.0)	9.2 (2.1)	2.9 (2.0)	1.1 (1.0)	-0.6 (1.4)
2010: surface-air	-1.4 (2.1)	-2.2 (2.6)	-0.5 (1.1)	2.2 (4.1)	12.9 (10.1)	15.6 (5.3)	19.9 (5.7)	18.8 (5.7)	14.4 (6.6)	5.3 (5.3)	0.3 (4.0)	-2.8 (2.6)
2010: soil	-0.1 (2.1)	-0.9 (2.8)	-0.1 (1.4)	0.9 (1.4)	5.0 (4.2)	10.2 (3.3)	14.2 (3.2)	13.8 (2.6)	11.8 (3.2)	5.6 (3.1)	1.7 (1.5)	-0.1 (1.1)
2011: surface-air	-2.6 (3.0)	-2.6 (3.3)	-1.3 (2.3)	0.2 (3.1)	12.4 (8.1)	16.7 (7.5)	19.9 (5.7)	17.9 (4.9)	15.9 (5.3)	NA	NA	NA
2011: soil	-1.3 (2.6)	-1.8 (3.2)	-0.9 (2.2)	-0.2 (1.3)	4.9 (4.3)	9.7 (2.9)	12.8 (2.1)	13.6 (3.1)	12.5 (3.6)	NA	NA	NA

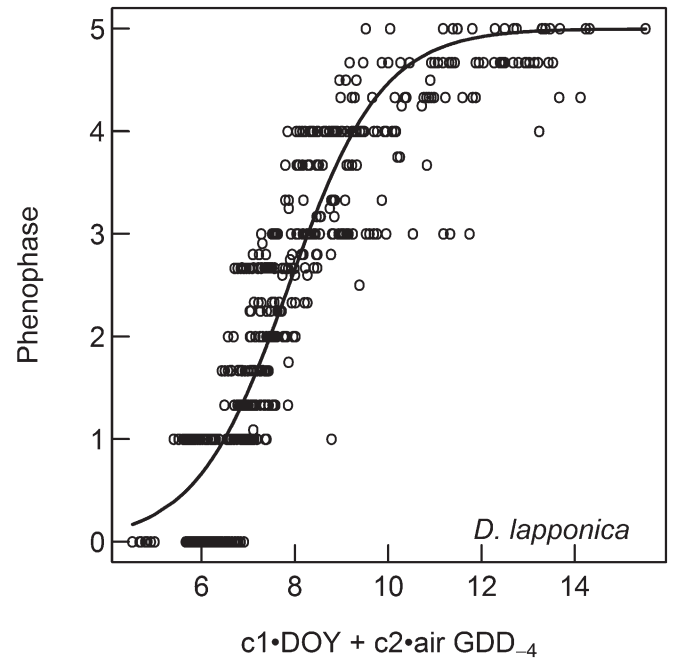


Fig. 2. Logistic phenology model for *Diapensia lapponica* constructed from day of year (DOY) and growing degree-day (airGDD₄). The x-axis is a linear combination of $c_1 \cdot \text{DOY} + c_2 \cdot \text{airGDD}_4$ where c_1 and c_2 are the best-fit model coefficients.

accuracy in large part reflects the longer duration of pre and post flowering periods as compared with the relatively narrow flowering window and relative paucity of later season post flowering data. Values for phenophases 0 and 5 (dormant and seed dispersal) are not presented due to the asymptotic nature of the logistic models, which are poor predictors for beginning and ending phenophases.

Historic phenology modeling and frost damage trends—Over the 77-yr period of record, mean annual and spring summit temperatures increased significantly 0.009 ($P = 0.010$) and 0.015 ($P = 0.022$) °C/yr, respectively (Seidel et al., 2009; updated to reflect 1935–2011: G. L. D. Murray, unpublished data). DOY+airGDD models were run using the hindcasted airGDD values to predict annual alpine floral phenology timing. Interannual and plot to plot variability were large for all species and closely matched trends in the MWO temperature record. Each species showed significant earlier trends in flowering time (*D. lapponica*: slope = -0.027 d/yr; $t = -3.11$, $df = 75$, $P = 0.003$; *C. bigelowii*: slope = -0.017 d/yr; $t = -3.21$, $df = 75$, $P = 0.002$; *V. vitis-idaea*: slope = -0.016 d/yr; $t = -2.88$, $df = 75$, $P = 0.005$), although the magnitude of the shifts was small (≤ 2.1 d earlier) compared with observed and modeled variability (Table 6, Fig. 3).

The number of hours from May to July that were $\leq -2^\circ\text{C}$ did not change significantly over the MWO period of record (slope = -0.726 frost damage h/yr; $t = -1.816$, $df = 75$, $P = 0.073$) (Fig. 4). Despite the lack of a statistically significant change in the number of hours $\leq -2^\circ\text{C}$ in the early growing season, combined with the small but significant shift toward earlier flowering phenology, there were no significant trends in the number of hours $\leq -2^\circ\text{C}$ experienced by alpine species during the modeled flowering period (*D. lapponica*: slope = 0 frost damage hours/yr;

TABLE 4. AIC model selection values and model coefficients (± 1 SE) for logistic phenology models for three alpine species based on 2008–2011 data from the Presidential Range, New Hampshire, US. Explanatory variables include day of year (DOY), accumulated surface-air degree-days (airGDD), days from snow melt (DFSM), and their interactions, with best-fit models based on AIC values highlighted in gray. Because DFSM could not be calculated for Mount Washington Observatory meteorological data, best-fit models without DFSM were selected for testing and hindcasting (in bold).

Model	Variable	<i>Diapensia lapponica</i>	<i>Carex bigelowii</i>	<i>Vaccinium vitis-idaea</i>
DOY				
AIC (Δ AIC)		925.7 (30.2)	782.8 (8.5)	1161.4 (43.4)
<i>b</i>		10.37 \pm 0.41	13.79 \pm 0.78	10.57 \pm 0.29
<i>c</i> ₁	DOY	0.0641 \pm 0.0025	0.078 \pm 0.0045	0.0543 \pm 0.0016
AirGDD				
AIC (Δ AIC)		957.3 (61.8)	842.0 (67.7)	1364.8 (246.8)
<i>b</i>		3.20 \pm 0.13	4.11 \pm 0.25	3.48 \pm 0.099
<i>c</i> ₁	airGDD	0.0032 \pm 0.00013	0.00359 \pm 0.00023	0.00252 \pm 0.000081
DFSM				
AIC (Δ AIC)		957.2 (61.7)	971.1 (196.8)	1426.6 (308.5)
<i>b</i>		2.21 \pm 0.12	3.26 \pm 0.23	3.64 \pm 0.11
<i>c</i> ₁	DFSM	0.0402 \pm 0.0021	0.0517 \pm 0.0038	0.0408 \pm 0.0013
DOY+airGDD				
AIC (Δ AIC)		895.5 (0.0)	774.9 (0.6^a)	1125.3 (7.3)
<i>b</i>		7.87 \pm 0.60	11.57 \pm 1.00	8.88 \pm 0.38
<i>c</i> ₁	DOY	0.00136 \pm 0.00023	0.00101 \pm 0.00031	0.00074 \pm 0.00012
<i>c</i> ₂	airGDD	0.0393 \pm 0.0048	0.0593 \pm 0.0072	0.0406 \pm 0.0026
DOY+DFSM				
AIC (Δ AIC)		927.6 (32.1)	784.1 (9.8)	1137.6 (19.5)
<i>b</i>		10.52 \pm 0.54	14.22 \pm 0.94	9.29 \pm 0.35
<i>c</i> ₁	DOY	0.0631 \pm 0.0039	0.082 \pm 0.0063	0.0433 \pm 0.0025
<i>c</i> ₂	DFSM	0.000833 \pm 0.0026	-0.0035 \pm 0.042	0.0101 \pm 0.002
AirGDD+DFSM				
AIC (Δ AIC)		957.2 (61.7)	840.2 (65.9)	1278.0 (160.0)
<i>b</i>		3.17 \pm 0.13	4.13 \pm 0.25	3.74 \pm 0.10
<i>c</i> ₁	airGDD	0.00296 \pm 0.00019	0.00317 \pm 0.00028	0.0015 \pm 0.00012
<i>c</i> ₂	DFSM	0.00381 \pm 0.0025	0.00837 \pm 0.0043	0.0191 \pm 0.002
DOY+airGDD+DFSM				
AIC (Δ AIC)		895.7 (0.2)	774.3 (0.0)	1118.0 (0.0)
<i>b</i>		8.19 \pm 0.65	12.16 \pm 1.07	8.43 \pm 0.4
<i>c</i> ₁	DOY	-0.0036 \pm 0.0026	-0.0071 \pm 0.0043	0.00641 \pm 0.0021
<i>c</i> ₂	airGDD	0.00146 \pm 0.0024	0.00114 \pm 0.00032	0.000594 \pm 0.00013
<i>c</i> ₃	DFSM	0.0418 \pm 0.0052	0.0642 \pm 0.0078	0.0364 \pm 0.0029

^a When more than one of the competing models have substantial support (Δ AIC \leq 2), the model with fewer variables is considered the best-fit model (Burnham and Anderson, 2002, 2004).

$t = -0.140$, $N = 77$, $P = 0.091$; *C. bigelowii*: slope = 0 frost damage hours/yr; $t = -0.138$, $N = 77$, $P = 0.13$; *V. vitis-idaea*: slope = 0 frost damage hours/yr; $t = -0.029$, $N = 77$, $P = 0.77$) (Fig. 5).

DISCUSSION

We predicted phenology timing for three alpine plant species using logistic modeling. Our modeled trends for the annual

flowering dates from 1935–2011 exhibited significantly earlier flowering dates for all three species, but the 77 yr period of record change was small (\leq 2.1 d earlier; 0.016 to 0.028 d/yr; Table 6). Our methodology is similar to that used by Richardson et al. (2006) for mid-elevation (250–825 m a.s.l.) tree leaf out and senescence at the nearby US Forest Service Hubbard Brook Experimental Forest. Compared with our 77-yr retrospective modeling period, their shorter 1957–2004 retrospective modeling period shows an order of magnitude faster leaf out rates of change (\sim 0.18 d/yr earlier) for sugar maple (*Acer saccharum*

TABLE 5. Comparison of mean observed (and standard deviation) and predicted day of year of bud swelling, flowering, post flowering, and fruit ripe phenophases for three alpine species, Presidential Range, New Hampshire, US. Alpine growing degree days for 2008–2011 as modeled from the relationship between summit and alpine plot growing degree days were used with the logistic phenology models for each species to estimate the average day of year each phenological stage was reached. The following numbers contain model levels used to hindcast phenological predictions and illustrate the bounds of accuracy arising from the model process.

Phenophase	<i>Diapensia lapponica</i>		<i>Carex bigelowii</i>		<i>Vaccinium vitis-idaea</i>	
	Observed ($N = 660$)	Predicted	Observed ($N = 333$)	Predicted	Observed ($N = 691$)	Predicted
1 (bud swelling)	143.67 (11.25)	145.28	159.81 (26.12)	159.52	164.39 (11.85)	169.35
2 (flowering)	160.27 (6.54)	160.60	171.33 (5.31)	172.39	183.19 (8.11)	188.08
3 (post flowering)	178.95 (14.68)	168.47	176.35 (8.53)	177.21	201.04 (14.7)	198.55
4 (fruit ripe)	182.87 (13.80)	186.85	192.6 (15.09)	193.18	220.09 (18.9)	218.52

TABLE 6. Total change in days taken to reach phenophases 1.5 (early flowering), 2 (peak flowering), and 2.5 (late flowering) for the 77-yr period from 1935–2011 for three alpine species, as estimated from logistic phenology models. Confidence intervals for all trends were 0.009 or less; these confidence intervals are for generalized least squares trends only and do not reflect the multiple levels of uncertainty inherent in hindcasting phenological trends.

Phenophase	<i>Diapensia lapponica</i>	<i>Carex bigelowii</i>	<i>Vaccinium vitis-idaea</i>
1.5 (early flowering)	-2.09	-1.27	-1.18
2 (peak flowering)	-2.12	-1.29	-1.21
2.5 (late flowering)	-2.15	-1.32	-1.24

Marsh.) and that green canopy duration increased by 0.21 d/yr longer over their period of study. Other regional studies of spring phenology events also found rates of change 2–10 times faster than our results (Bradley et al., 1999; Wolfe et al., 2005). The period of record used in any such analysis can strongly influence rates of change, as Richardson et al. (2006) demonstrated, making comparisons between studies using different time periods problematic. There are few paired, long-term phenological and climate records in existence, and studies using more recent years tend to increase the rate of change for warmer responses. The 77-yr climate record in our study is less sensitive to annual variation and the more recent increase in warming rates.

The importance of plot-to-plot variability on alpine flowering times is highlighted by the relatively large upper and lower predictions for each phenophase for a given species (Fig. 6). For example, the peak of phenophase 2 (flowering) for *D. lapponica* is predicted to occur 2.1 d earlier over the model period, but there is typically an approximately 11 d range in which phenophase 2 is predicted to have peaked in any given year as well as an average observed 11-d range in the date that phenophase 2 peaked during the 2008–2011 phenology record.

Relating climate data to alpine plant phenology generally presents an additional problem, as high-elevation climate data sets of any length are rare, and climate trends often differ from nearby lower-elevations sites (Rangwala and Miller, 2012). Many studies extrapolate climate values from lower-elevation sites, but the complexity of mountain turbulence, planetary boundary layers

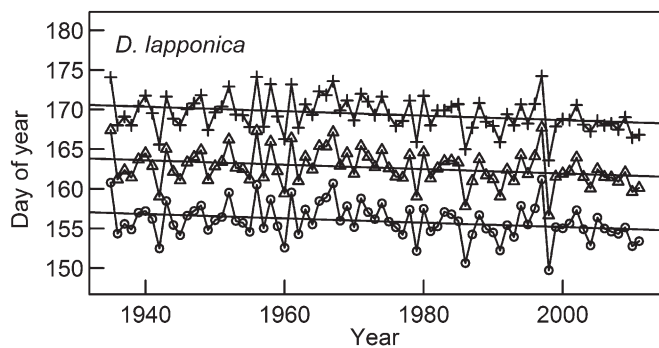


Fig. 3. Hindcasted phenological predictions for phenophases 1.5 (o), 2 (Δ), and 2.5 (+) of *Diapensia lapponica* for 1935–2011. Phenophase predictions are based on the best-fit DOY+airGDD₄ logistic model. Lines represent the best GLS model fit for each phenophase; all species showed a significant trend ($P < 0.05$) toward earlier occurrence in phenophases 1.5 (early flowering), 2 (peak flowering), and 2.5 (late flowering).

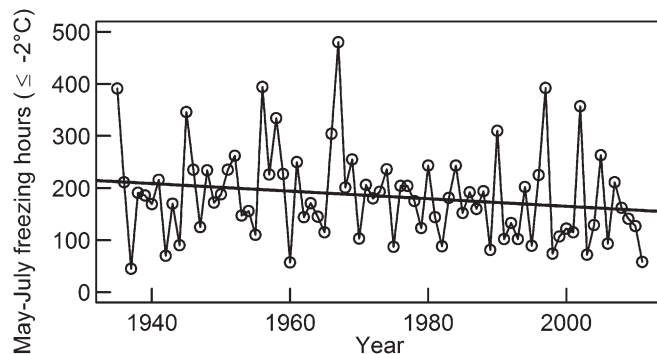


Fig. 4. Total May–July frost damage hours (hours $\leq -2^{\circ}\text{C}$) at the summit of Mount Washington, New Hampshire for 1935–2011. The regression line represents the best-fit GLS model; total May–July freezing hours for the summit trend down, but not significantly ($P = 0.073$).

and rapid shifts from saturated to unsaturated conditions make simple lapse rate calculations problematic (Pepin et al., 1999; Stahl et al., 2006). Even when climate data from a similar elevation within the region are available, these data are unlikely to precisely represent local conditions, as differences in microtopography in alpine habitats can result in large temperature differences (Scherrer and Körner, 2011). Our method improves on the application of standard lapse rates by using more biologically relevant in situ temperature data to relate standard meteorological station data to the on-site ground level conditions experienced by the generally low-growing species of the alpine biome (Davidson et al., 1990; Graae et al., 2012).

Meteorological evidence suggests that climate warming at Northeast alpine elevations is partially uncoupled from and occurring slower compared with that at mid-elevations (Seidel et al., 2009), and modeled rates of flowering phenology responses follow that pattern. Inouye et al. (2000) similarly reported a disjunct relationship for phenological trends at high elevations compared with lower elevations in the Colorado Rocky Mountains, though they attribute their results to increased winter precipitation and snow that melts out later, thereby subordinating the effects of warmer springs. Our predicted small changes in alpine floral phenology parallel Spear’s (1989) conclusion that the region’s alpine vegetation remained somewhat stable during the warmer than present Holocene Climate Optimum warming events. But the mid- and lower-elevation forest species composition changed more dramatically, a similar pattern of change reported by Richardson et al. (2006) for ongoing changes in mid-elevation forest phenology.

Ellwood et al. (2013) found that 32 species in Concord, Massachusetts showed a flowering advance of 3.2 d/°C warming of the mean spring temperature over the last 161 yr. They postulate that the species they examined had yet to show signs of physiological constraints in phenological advancement. Other studies have reported variable phenological advancements of 2 to 15 d/°C warming for other regions (Rutishauser et al., 2009). However, not all plants advance at the same rate or for the same reasons, and plants in warmer climates generally have lower rates of temperature sensitivity and may be reacting to moisture stress, photoperiod, seasonal insolation, or other factors (Cook et al., 2012a) rather than to spring warming. Results for our three alpine species suggest a low to moderate rate of phenological temperature sensitivity, each advancing less than 2.1 d/°C warming.

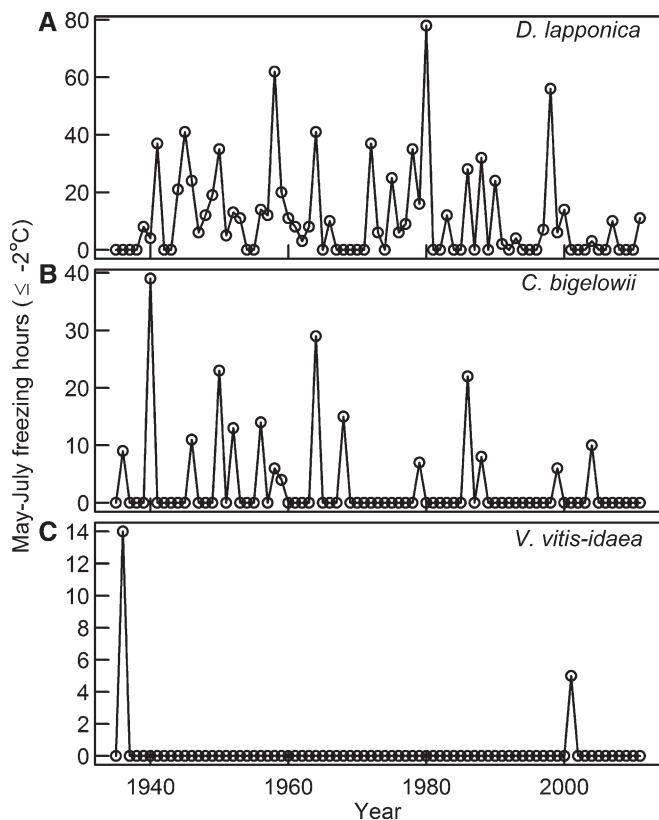


Fig. 5. Total frost damage hours (hours $\leq -2^{\circ}\text{C}$) during the modeled flowering period (phenophases 1.5-2.5) by year for (A) *Diapensia lapponica*, (B) *Carex bigelowii*, and (C) *Vaccinium vitis-idaea*. Sen's slope estimates for all species = 0; all associated Mann-Kendall tests are insignificant.

Another possible explanation for the small advance in flowering time may be related to warming in the fall and early winter, which can counteract, cancel out, or overwhelm an earlier phenological response that would otherwise be caused by spring warming. A chilling requirement (vernalization) must be met before many species are ready to break bud dormancy at the start of the next growing season, and a recent study (Cook et al., 2012b) found that many species that would otherwise be considered nonresponsive or delay phenology with climate warming are actually responding to both counteracting drivers of spring warming and vernalization (i.e., divergent responders). Cook et al. (2012b) analyzed first flower date for a set of temperate species and found that spring-only responders advanced by 0.14 d/yr, while divergent responders advanced by 0.07 d/yr on average, which is still a much greater advance than our modeled results (0.016 to 0.027 d/yr). There appears to be a relationship between increasing latitude and vernalization sensitivity (Linkosalo et al., 2006; Cook et al., 2012b), suggesting that arctic-alpine species may have a higher rate of vernalization sensitivity in comparison with other biomes. This vernalization factor has often been ignored when modeling these cold-climate systems, either because arctic-alpine or high latitude/elevation species are assumed to reach the needed chilling requirement (Chuine and Cour, 1999; Van Wijk et al., 2003; but see Yu et al., 2010), or simply because little phenological study has occurred in this biome. The inability to reach the chilling requirement needed to break bud dormancy is recognized as the

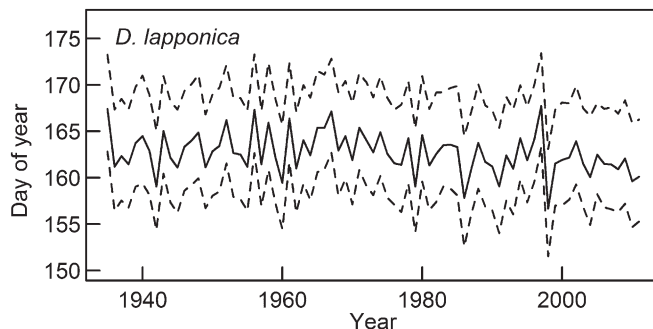


Fig. 6. Hindcasted predicted phenophase 2 (—), with upper and lower modeled range for *Diapensia lapponica* for 1935–2011. Phenological predictions are based on the best-fit DOY+airGDD₋₄ logistic model; upper and lower bound predictions were generated by adding and subtracting coefficient standard errors to the model and largely represent plot to plot phenophase variability.

primary mechanism through which phenology generally controls plant distributions at the southern end of species' ranges (Chuine, 2010) and therefore may play a larger role in the persistence of these outlier alpine populations (although at our study site, seasonal fall and winter temperatures, though trending warmer, did not change significantly; K. Kimball, unpublished data). Lesica and McCune (2004) found a decline in the abundance of alpine species at the southern margin of their range in Glacier National Park, United States, although their descriptive study could not attribute causality or mechanism of the decline. In our study with a nominal warming observed, it is not clear that vernalization is in play at the moment.

As compared with later blooming species that inhabit areas with longer snow duration, earlier-blooming species such as *D. lapponica* that use habitats frequently scoured free of snow by winds may gain longer growing seasons, similar to what Wipf et al. (2009) reported for *Loiseleuria procumbens* (L.) Desv. in the Swiss Alps. The modeled risk of late-spring/early-summer killing frost did not change significantly in our study, suggesting that earlier blooming may be beneficial with extension of the frost-free growing period, providing opportunity to build additional reserves for subsequent-year flowering for the species studied. The amount of energy reserves stored from previous seasons and the timing of flowering can influence seed productivity and success (Mondoni et al., 2012).

Late-blooming *V. vitis-idaea*, which inhabits boreal to tundra and alpine habitats in snow protected areas, was our only species responsive to modeled days from snow melt and its observed field time of flowering compared with predicted logistic model results using DOY+airGDD model coefficients was 9.2 to 4.6 times worse compared with *D. lapponica* and *C. bigelowii*, respectively. Species that do not or weakly exhibit advanced springtime phenology with warming are typically late-blooming plants (Menzel et al., 2006). Considering that Northeast alpine ecosystems contain a mix of arctic-alpine and lower elevation plant taxa (Bliss, 1963), it is possible that both spring-only and divergent-responding species exist here, with varying phenological sensitivity to advanced springtime warming.

Our plant phenology results could be applicable to other temperate or boreal zone alpine areas with similar climate in our region or beyond. Other alpine phenology studies from the region (northeastern United States and eastern Canada) are lacking,

but Kudo and Hirao (2006) found that artificial warming experiments in Japan did not cause an acceleration in flower timing among alpine plants in early snowmelt habitat.

The data used in our logistic modeling represents a span of only 4 yr, but contains reasonable and representative interannual variability. We consider our results and the magnitude of the ongoing trends we observed as helpful indicators of what may have occurred over the past almost eight decades in Northeast alpine ecosystems. To enhance our results, future research should test the importance of additional environmental cues, parse out what species may be more sensitive to early-season cumulative warming vs. post-growing season vernalization requirements, extend the period of record for the data used in the logistic models to determine whether that would influence model outcomes and investigate whether biologic responses to ongoing trends of warming are linear or nonlinear.

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