Regional Environmental Change (2025) 25:142
https://doi.org/10.1007/s10113-025-02477-8

ORIGINAL ARTICLE

False spring disrupted the life cycles of *Pinus cembra* and *Vaccinium myrtillus* at the alpine treeline ecotone in the High Tatras (Western Carpathians)

Veronika Lukasová[1] · Svetlana Varšová[1] · Ivan Mrekaj[2] · Dušan Bilčík[1] · Ján Krempaský[1,2] · Milan Onderka[3]

Received: 24 March 2025 / Accepted: 15 October 2025 / Published online: 24 November 2025
© The Author(s) 2025

Abstract
This study examines the impact of extreme weather events driven by global warming on the growth and distribution limits of high-elevation vegetation by analysing the effects of frost following an exceptionally early onset of spring phenological phases. Climate data from the Skalnaté Pleso Observatory in the High Tatras indicate that the winter of 2023/24 was unusually warm, with January–April temperatures exceeding the 1961–1990 climate normal by 3.8 K for average temperature and 4.4 K for maximum. Despite increased winter precipitation, snowmelt in 2024 occurred significantly earlier and more rapidly than in previous years. Consequently, bud development in *Pinus cembra* and *Vaccinium myrtillus*, as well as leafing in *Calluna vulgaris*, began unusually early. This early onset of phenophases was interrupted by an 11-day cold spell, with minimum temperatures reaching as low as −8.3 °C and an average daily air temperature of −2.0 °C. This episode led to the frost damage of buds during the sensitive development stages, indicating a so-called false spring. *V. myrtillus* buds were visibly damaged immediately. In *P. cembra*, needle yellowing and defoliation appeared in the next weeks, while reproductive organs damage became evident later during flowering when male flowers were undeveloped and did not pollinate. Frost damage to high-elevation vegetation can disrupt plant growth, competition, and food chains, especially when phenological advances outpace the retreat of late spring frosts.

Keywords Mountains · Climate change · Extreme temperature · Late frost · Phenology

Introduction

Ongoing climate change has increased the frequency, intensity, and duration of extreme events (IPCC 2023) linked to negative vegetation anomalies, including reduced growth, shifts in species abundance, increased turnover rates, localised extinctions, and ecosystem disruptions (Gibson-Reinemer et al. 2015; Škvareninová et al. 2022; Leake 2023). High mountain environments are particularly sensitive to climate change. Many species inhabiting these regions are ecologically narrowly specialised (Stewart 2009; Hlásny et al. 2015; Werners et al. 2016) and thus prone to gradual retreat (Ernakovich et al. 2014); Verrall and Pickering 2020).

Ecosystem responses to climate change are often preceded by shifts in species phenology. In the temperate and boreal zones, the onset of spring phenological phases is closely linked to weather conditions, particularly temperature and photoperiod (Keller and Körner 2003; Basler and Körner 2012; Zohner and Renner 2015). The effect of temperature is dual, since buds go through a state of endodormancy and ecodormancy from mid-autumn to mid-spring. During this period, bud cell growth is inhibited by low temperatures or a too short photoperiod, which also promotes cell frost hardening. On the other hand, higher temperatures are necessary to promote bud growth after dormancy is broken (Chuine et al. 2016). The thermal growing season is typically defined by the period when average daily temperatures exceed 5 °C (Carter 1998; Fu et al. 2023; Koźmiński

Communicated by Wolfgang Cramer

✉ Veronika Lukasová
geofluka@savba.sk

[1] Earth Science Institute, Slovak Academy of Sciences, Dúbravská Cesta 9, Bratislava 840 05, Slovakia

[2] Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, T.G. Masaryka 24, Zvolen 96001, Slovakia

[3] Slovak Hydrometeorological Institute, Jeséniova 17, Bratislava 833 15, Slovakia

et al. 2023). However, for rather cool-adapted species, it starts when the weekly mean air temperature reaches 0 °C, including numerous warm hours that suffice to induce cambial activity (Körner and Paulsen 2004; Paulsen and Körner 2014; Körner et al. 2023). Fu et al. (2023) found that the phenological growing season, also known as the green season, lags behind the thermal season. Regardless of earlier increases in air temperature or photoperiod, snow cover dampens their signals while keeping the soil temperature and freezing depth stable. Therefore, vegetation under the snow cover remains inactive until the snow recedes (Körner 2003, Wipf and Rixen 2010; Vitasse et al. 2017). Earlier snowmelt dates, decreased snow depths, and an increasing proportion of winter precipitation falling as rain instead of snow have been recorded in mountain areas in Europe (Marty 2008; Gobiet et al. 2014) as climate change accelerates. Initiating the phenological phases earlier due to rising temperatures and advanced snowmelt may have significant implications for plant species growing at high elevations (Inouye 2008; Inouye and Wielgolaski 2024).

The time of bud burst is a particularly critical period, as it affects vegetation development and reproductive success (Zohner et al. 2018). In the alpine treeline ecotone (ATE), a species' ability to grow and reproduce under harsh climatic conditions provides a competitive advantage and potential for expansion. However, advancing spring phenology increases the risk of late frost damage (Škvareninová et al. 2022; Zahradníček et al. 2024). A hard freeze occurring after the growing season has begun in late winter or early spring is referred to as a 'false spring' (Martinuzzi et al. 2019). Although definitions vary, it generally describes a mild and prolonged period in late winter or early spring that prematurely brings vegetation out of dormancy, leaving it vulnerable to late frost and drought (Ault et al. 2013). Many temperate plant species have evolved chilling requirements to avoid leafing out during warm snaps in the middle of the winter. However, with climate change, chilling requirements may not be met, increasing the risk of adverse effects from late spring frosts (Chamberlain and Wolkovich 2021).

In temperate regions, trees have evolved to withstand extreme winter freezes, often reaching −10 to −40 °C, through dormancy and frost-avoidance mechanisms such as supercooling, extracellular ice tolerance, cold hardening, cryoprotectants, and structural adaptations like compact growth or underground organs (Sakai and Larcher 1987; Quamme 1995; Larcher 2005; Körner 2016). However, frost events during the growing season pose a greater risk, as ice crystals can damage sensitive tissues (Pardee et al. 2017; Škvareninová et al. 2021, 2022). Plant susceptibility to frost damage depends on the phenological stage (Murray 2020). To protect developing tissues from late spring frost, temperate trees synchronise their spring phenology with rising temperatures and photoperiods (Vitasse et al. 2014; Lenz et al. 2016); however, delaying phenology at high elevations reduces time for tissue maturation (Körner et al. 2016). Buds are initially protected by floral structures enabling them to tolerate sub-zero temperatures (Szalay et al. 2019), but during bud burst and flowering, flowers are directly exposed to frost and other weather conditions, which can cause their temperature to be even lower than the actual air temperature (Litschmann and Středa 2019). Freezing resistance declines as spring advances, reaching its minimum during leafing and flowering (Snyder and Melo-Abreu 2005; CaraDonna and Bain 2016; Vitra et al. 2017). Consequently, the timing of phenology, rather than winter freezing resistance, may play a crucial role in determining the cold range limits of temperate trees (Lenz et al. 2013; Vitasse et al. 2014).

This study aimed to analyse the impact of extreme frost events on the life cycles of naturally distributed shrub and tree species in the alpine treeline ecotone (ATE) in the High Tatra Mountains (Slovakia): *Pinus cembra* L., *Pinus mugo Turra* L., *Vaccinium myrtillus*, and *Calluna vulgaris* Hull. We analysed climate and snow conditions during the winters of 2021/22, 2022/23, and 2023/24 to identify the causes and consequences of the extraordinarily early onset of phenological phases in 2024. We expected that a late frost occurring after the initiation of spring phenological phases could damage plant organs; however, which organs, to what extent, and in which species remained open questions. Plant responses to environmental risks such as late frosts play a crucial role in determining which species gain a competitive advantage in forming the ATE in the High Tatra Mts in a changing climate. This study explores which of the studied species are most endangered if phenology shifts faster than the timing of late frost, also considering the effect of snowmelt date on low-growing species.

Material and methods

Study area and sites

The study area is located in the ATE on the southeast slope of the High Tatra Mountains, near the Skalnaté Pleso Observatory (SPO: 49.18928°N; 20.23410°E, Fig. 1) in the National Nature Preserve Skalnatá dolina valley (Tatra National Park). SPO is the only meteorological observatory in the High Tatra Mountains conducting long-term observations at the ATE. Measurements at the observatory, situated at 1778 m a.s.l., began in 1943 and cover two complete climate normal periods: 1961–1990 and 1991–2020 (Lukasová et al. 2023). The only exception is the snow depth measurement, which underwent a positional change within the observatory area in 1979. For this study, we utilised long-term data on air temperature, precipitation, and snow depth from a database of manual measurements at SPO, supplemented

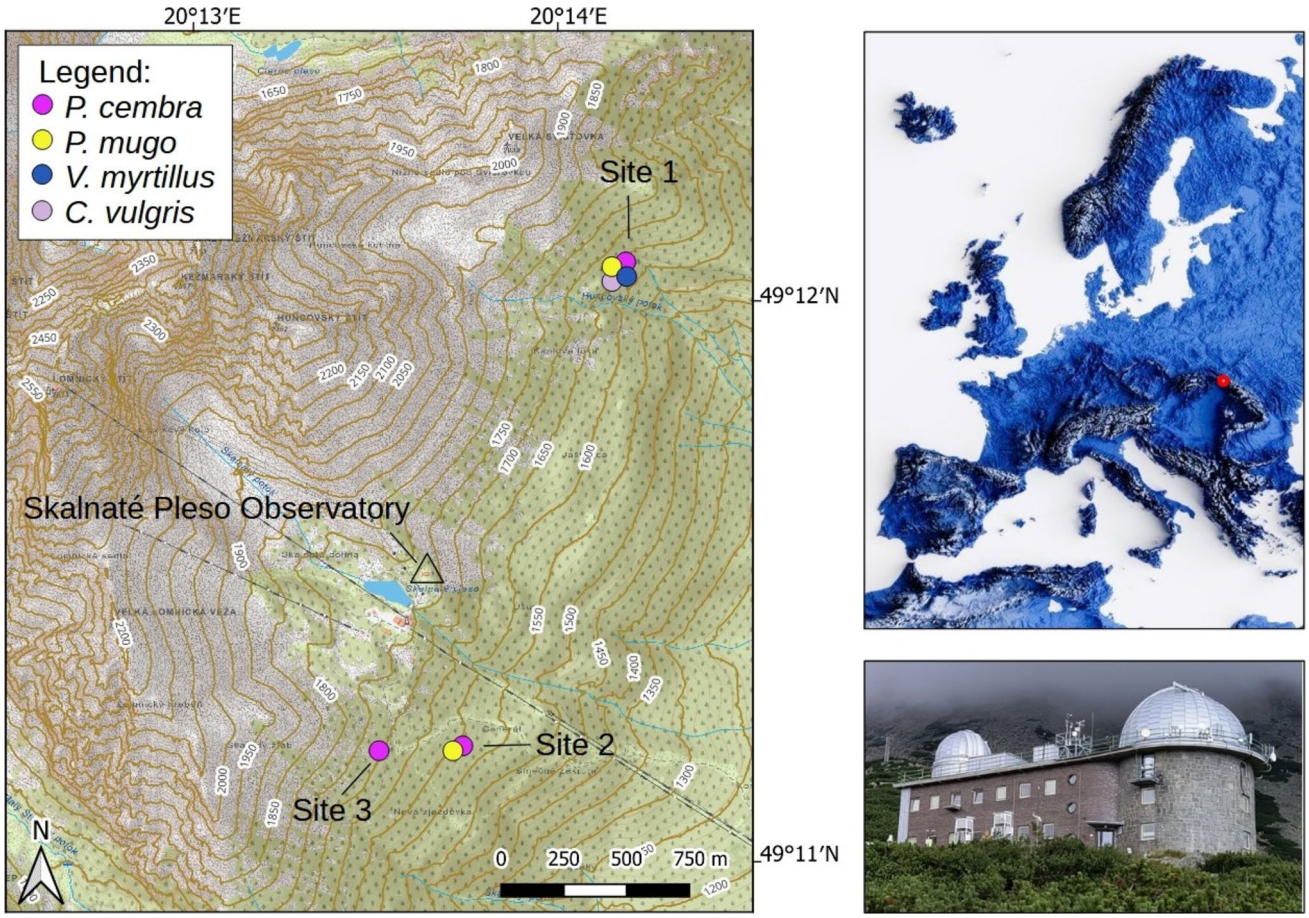


Fig. 1 Locations of in situ observational sites (left), indicating the occurrence of studied species and their spatial relationship to Skalnaté Pleso Observatory (lower right). The study area is situated on the southeast slope of the High Tatras and is highlighted in red on the map of Europe (upper right)

by time-lapse photography of the ATE and data from in situ assessments at observational sites.

In situ observational sites were established following area inspections in 2021. The sites are located on south-east-facing slopes of the High Tatra Mountains near SPO, at elevations ranging from 1600 to 1700 m a.s.l., and within a horizontal distance of 2 km. We established three observational sites (Fig. 1), where *Pinus cembra* L. (at all three sites), *Pinus mugo Turra* L. (at two sites), and *Vaccinium myrtillus* L. and *Calluna vulgaris* Hull. (at one site) naturally occur. *P. mugo* is the dominant woody plant species in the study area, whereas the other species are present in clusters or small groups. To ensure microtopographic homogeneity and minimise orographic effects (Lenoir et al. 2013; Laigle et al. 2022), we avoided terrain depressions where snow could accumulate, as well as gullies and side valleys. This approach was taken to ensure the representativeness of meteorological data measured at SPO. Microclimatic variations in the study area are primarily due to differences in site elevation relative to SPO. The soil type is relatively uniform and dominated by Lithic and other (non-rendzic) Leptosols, often associated with Cambic Podzols. These soils are shallow, highly skeletal (containing more than 50% coarse fragments), and very acidic (pH/KCl < 4.5) (Hraško et al. n.d.).

Measurements of air temperatures

Air temperatures analysed in this study were measured at SPO by a calibrated mercury-in-glass thermometer, a maximum mercury-in-glass thermometer, and a minimum spirit thermometer, for average (Tavg), maximum (Tmax), and minimum (Tmin) temperatures, respectively. The thermometers are housed in a wooden meteorological shelter positioned 2 m above ground level (a.g.l.). Temperature data, including daily and monthly averages and maxima, were compared to the climate normals 1961–1990 and 1991–2020. The 1961–1990 is considered a period when climate conditions, particularly temperatures, were more stable compared to the more recent warming period 1991–2020. The minimum temperatures were used to identify the

occurrence of the last hard frosts (LHF), defined as days with minimum temperatures below −2.2 °C (Marino et al. 2011).

Precipitation measurements

The amount and form of precipitation was considered an important factor influencing snowmelt dynamics. Rain-on-snow events cause rapid melting of the snowpack due to high liquid water content (Krajčí et al. 2016; Yang et al. 2023). The precipitation data analysed in this study were measured at SPO using a manual rain gauge. Continuous weather monitoring at SPO includes observations of the precipitation forms. In this study, daily precipitation totals were classified into three basic categories: snow, rain, and mixed precipitation.

Measurements of snow depth, occurrence, and coverage

At SPO, snow depth is traditionally measured using a snow stake with a precision of 1 cm. In addition to the depth of continuous snow cover (more than 1 cm), the fractional snow cover or a thin layer of sparkling snow is observed. From the snow cover measurements, three key characteristics were derived for each year from 1979 to 2024:

- Average snow depth (ASD; cm)—the average cumulative snow depth recorded during PSC days.
- Number of days with PSC (days)—the duration of continuous snow cover.
- Snowmelt date (SMD)—the day when snow completely melted.

A one-sample *t*-test was used to compare ASD and PSC measured in 2021/22, 2022/23, and 2023/24 with the long-term averages from 1979 to 2020, using a significance threshold of $p < 0.05$. The SMD was correlated with climatic characteristics: the means of Tavg and Tmax calculated for individual months (J—January, F—February, M—March, A—April) and periods (JFMA, JFM, FMA, FM, MA), as well as ASD, to identify significant effects on snowmelt at SPO.

Snow depth measured at SPO represents a point-specific value; however, in the natural environments, it can vary significantly over short distances due to wind, topography, or shading. Inspired by research where digital photography has been effectively applied to study environmental changes (Kučera et al. 2024; Okamoto et al. 2024), particularly snow cover dynamics (Parajka et al. 2012; Bongio et al. 2021), we complemented the snow cover data with analyses of time-lapse photography. The southeast slope of the ATE was monitored using a Tetrao Spromise S328 digital trail camera. The camera is permanently mounted on the roof of SPO and monitors the environment between approximately 1600 and 2000 m a.s.l. It captures two time-lapse images at 08:00 and two at 13:00 CET daily, with a 10-min interval between successive images. This setup has been operational since October 2021. For this study, we focused on the snowmelt period, analysing the percentage of snow cover using a procedure according to Salvatori et al. 2011 as applied by Portenier et al. (2020), in images from the expected onset of permanent snow cover on January 1 to its disappearance by May 31 in 2022, 2023, and 2024.

At the study sites, the snow was assessed as part of the in situ observational program; however, only the occurrence of snow, not its depth, was recorded. Site inspections began each year once snowmelt had started.

Phenological observations

Phenological monitoring included two species from the Pinaceae family: stone pine (*Pinus cembra* L.) and dwarf mountain pine (*Pinus mugo Turra* L.), and two species from the Ericaceae family: European blueberry (*Vaccinium myrtillus* L.) and common heather (*Calluna vulgaris* Hull). During the study years 2022–2024, phenological observations began with the onset of snowmelt and continued until the final phenological stage (BBCH 95) was recorded.

Visual assessments were conducted twice weekly during the onset of spring phenological phases and once weekly during the summer and autumn phases on the same day at each site. The exact timing of phenophase onset was interpolated based on the developmental stage observed on a monitoring day. For *P. cembra*, phenological phases were assessed using binoculars on ten mature individuals, and values were averaged for the site. Phenological phases of shrubby species were assessed on a continuous area of the species. Shrubby species were monitored over defined surface areas: *V. myrtillus* and *C. vulgaris*, were observed within 5 m^2 plots, and *P. mugo*, due to its polycormonal growth habit, was assessed as a shrubby species within a 100 m^2 area.

Phenological phases were assigned to the BBCH scale (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie, Meier 2001), which describes principal (macrostadia) and secondary growth stages using a two-digit decimal code system. The core principle of this scale is that similar developmental stages across different plant species are assigned the same BBCH code. Monitoring included seven phenological phases for each of two *Pinus* spp. and six phases for *C. vulgaris*. For *V. myrtillus*, a modified BBCH scale for *Vaccinium* spp. as defined by Wichura et al. (2024) was used to assess nine phenological phases (Table 1).

Table 1 Phenological phases observed in the studied species (*Pinus cembra* and *Pinus mugo* as *Pinus* spp., *Vaccinium myrtillus*, *Calluna vulgaris*) described according to the BBCH scale

Phenological phases		Species		
BBCH	Description	*C. vulgaris*	*V. myrtillus*	*Pinus* spp.
01	Beginning of vegetative bud swelling		x	
07	Beginning of vegetative bud break: first green leaf tips visible		x	x
10	Leaf tips are about 10 mm above bud scales			x
11	First leaves are unfolded	x	x	
19	First leaves are fully expanded	x	x	x
31	Beginning of shoot growth			x
51	Inflorescence or flower buds visible	x	x	x
61	Beginning of flowering	x	x	x
67	Flowering finishing: majority of petals fallen or dry	x		x
69	End of flowering, green fruits become visible	x		
71	Green fruits begin to increase in size		x	
89	First fruits are fully ripe, successive fruit ripening		x	
95	50% of leaves discoloured or fallen		x	

Growing degree days

To compare the temperature requirements for the initiation of phenological phases among the studied species, we calculated growing degree days (GDD). Given the elevation difference between SPO (1778 m a.s.l.) and the average elevation of phenological observation sites (1650 m a.s.l.), which is 128 m, we estimated the temperatures at the lower elevation using a standard lapse rate of 0.6 °C per 100 m. Accordingly, 0.8 °C was added to the daily temperatures measured at SPO to approximate conditions at 1650 m a.s.l. GDD for each species was then calculated using these adjusted values (Eq. 1):

$$\mathrm{GDD} = \sum \frac{T_{\max} + T_{\min}}{2} - T_{\mathrm{base}} \quad (1)$$

where $T_{\max}$ and $T_{\min}$ are the daily maximum and minimum temperatures, respectively, and T_{base} is the base temperature. Two base thresholds were applied: 0 °C (GDD_0) and 5 °C (GDD_5). If the daily mean temperature was below the base threshold, GDD was set to 0 for that day. We also calculated active growing days (AGD), defined as days with positive GDD contribution: AGD_0 and AGD_5 for $\mathrm{GDD}_0 > 0$ and $\mathrm{GDD}_5 > 0$. To exclude contributions from winter warm spells or anomalous weather, GDD accumulation began on the first day of the last month with a negative average monthly air temperature.

The day of year (DOY) on which the average GDD_5 for a given species was reached was used to estimate the potential timing of phenological phase initiation. For species that showed frost damage, trends and shifts in GDD_5 calculated for the first vegetative phenological phase were analysed using the Mann-Kendall non-parametric test and Theil-Sen's slope estimator. These trends were then compared with the last hard frost (LHF) trend and, for low-stature shrubs such as *V. myrtillus* and *C. vulgaris*, also with the snowmelt date (SMD). Because the snow depth measurement site at SPO was relocated in 1979, the analysis of GDD_5, LHF, and SMD trends was restricted to the period 1979–2024.

Results

Climatic conditions preceding the false spring of 2024

Exceptionally high air temperatures

The snowmelt period in 2024 was associated with abnormally high temperatures recorded during winter. Between January 1 and April 30 (JFMA), the daily mean air temperatures (Tavg) exceeded the 1961–1990 climate normal on 93 days (Fig. 2a), with an average difference of +3.8 K. Compared to the 1991–2020 climate normal (Fig. 2c), Tavg exceeded the normal on 87 days, with an average deviation of +2.8 K. Until late March, Tavg fluctuated near 0 °C before rising sharply above freezing. The most pronounced anomalies were observed in the daily maximum temperatures (Tmax). Compared to the 1961–2020 climate normal (Fig. 2b), Tmax of JFMA was on average 4.4 K higher, with 99 abnormally warm days. Against the 1991–2020 climate normal (Fig. 2d), the average anomaly in Tmax was +3.3 K, with 94 days above normal. Tmax remained above 0 °C for almost the entire JFMA period, indicating an exceptionally

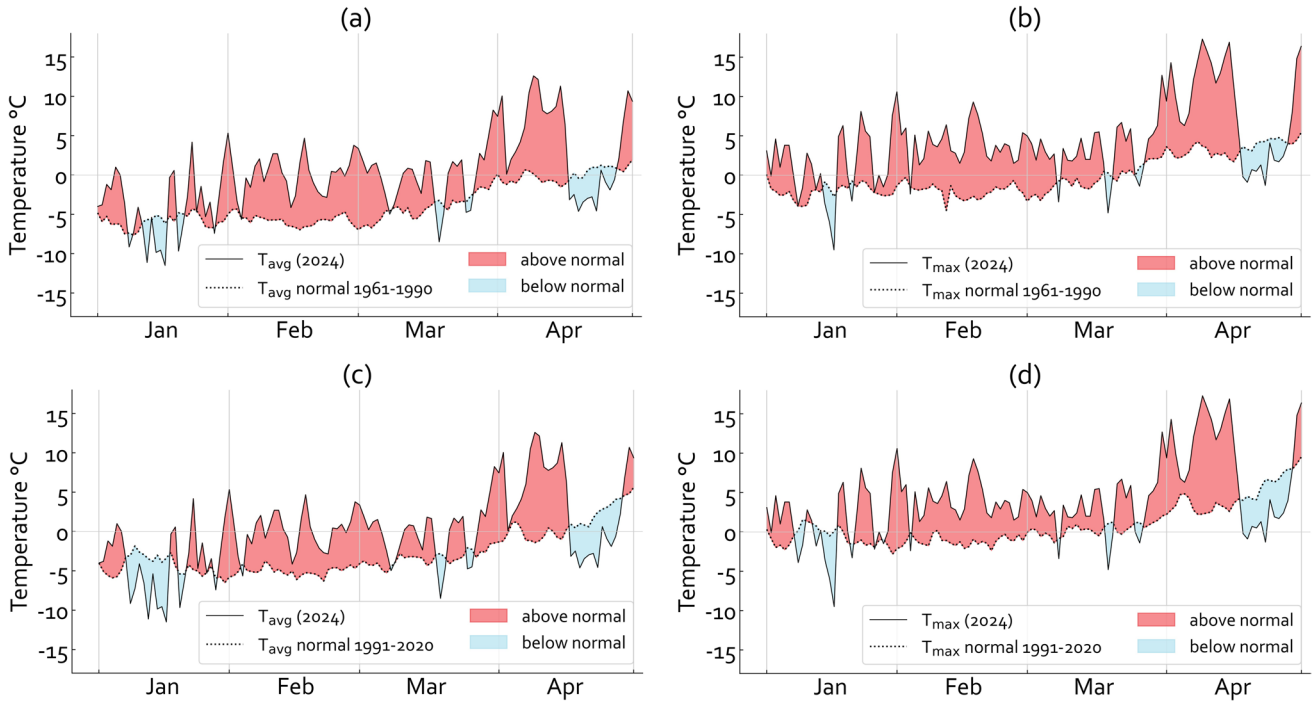


Fig. 2 Daily courses of average (**a**, **c**) and maximum (**b**, **d**) air temperatures from January to April 2024 compared to climatic normals for 1961–1990 (**a**, **b**) and 1991–2020 (**c**, **d**), indicating an exceptionally warm winter

warm winter. In comparison to the preceding years 2022 and 2023, JFMA temperatures in 2024 were more than 2 K higher. By late March and early April 2024, daily Tmax peaked between 15 and 17 °C, with Tavg reaching 10–12 °C on multiple days. Such high temperatures are rarely observed at this altitude during this period.

Snow cover

Long-term snow depth measurements at SPO from 1979 to 2024 indicate that the ASD is 31 cm (standard deviation, Sd = 13 cm), and the average duration of PSC is 164 days (Sd = 18 days). A comparison with the winters of 2021/22, 2022/23, and 2023/24 shows that the PSC duration was near the long-term average, lasting 164, 159, and 154 days, respectively. The primary interannual difference was a temporal shift in the PSC season in 2023/24, which began on November 6, 2023—earlier than in 2021/22 (November 27) and 2022/23 (November 18). The ASD in 2023/24 reached 45 cm, which was significantly higher ($p < 0.05$) than the long-term average and also exceeded values observed in the two previous winters. The total precipitation from all forms between November and March amounted to 526.4 mm in the 2021/22 season, 477.6 mm in 2022/23, and 679.3 mm in 2023/24. Despite the highest snowfall total being recorded in 2023/24 (498.0 mm), snow cover persisted longer in the preceding seasons, with 371.9 mm of snowfall in 2021/22 and 378.8 mm in 2022/23, lasting into May (Fig. 3).

Time-lapse imagery revealed a notably early and rapid snowmelt in 2024 across the ATE. On DOY 105 (April 14), only scattered patches of snow remained, whereas in 2022 and 2023, continuous snow cover was still present. Image analysis indicated that just 10% of the monitored area remained snow-covered on DOY 105 in 2024, and the snowmelt period lasted only 17 days. Comparatively, a similar extent of snow cover was not reached until DOY 140 in 2022 and DOY 143 in 2023 (Fig. 3).

The Mann-Kendall trend test and Theil-Sen's slope analysis revealed a statistically significant trend toward earlier snowmelt dates over the period 1979–2024, with a shift of −3.6 days per decade ($p = 0.03$). Correlation analyses between snowmelt date (SMD), temperature, and average snow depth (ASD) for the same period showed a significant relationship ($p < 0.01$) between SMD and both average (Tavg) and maximum (Tmax) air temperatures during March and April. The coefficients of determination were $R^2 = 0.29$ for Tavg and $R^2 = 0.30$ for Tmax. According to the regression models, a 1 °C increase in temperature during this period corresponded to a snowmelt date shift of 5.0 days earlier for Tmax and 5.4 days earlier for Tavg. Weaker but still significant correlations ($p < 0.05$; $R^2 < 0.15$) were also found for March and April temperatures considered individually, and for the February–April period. Correlations between SMD

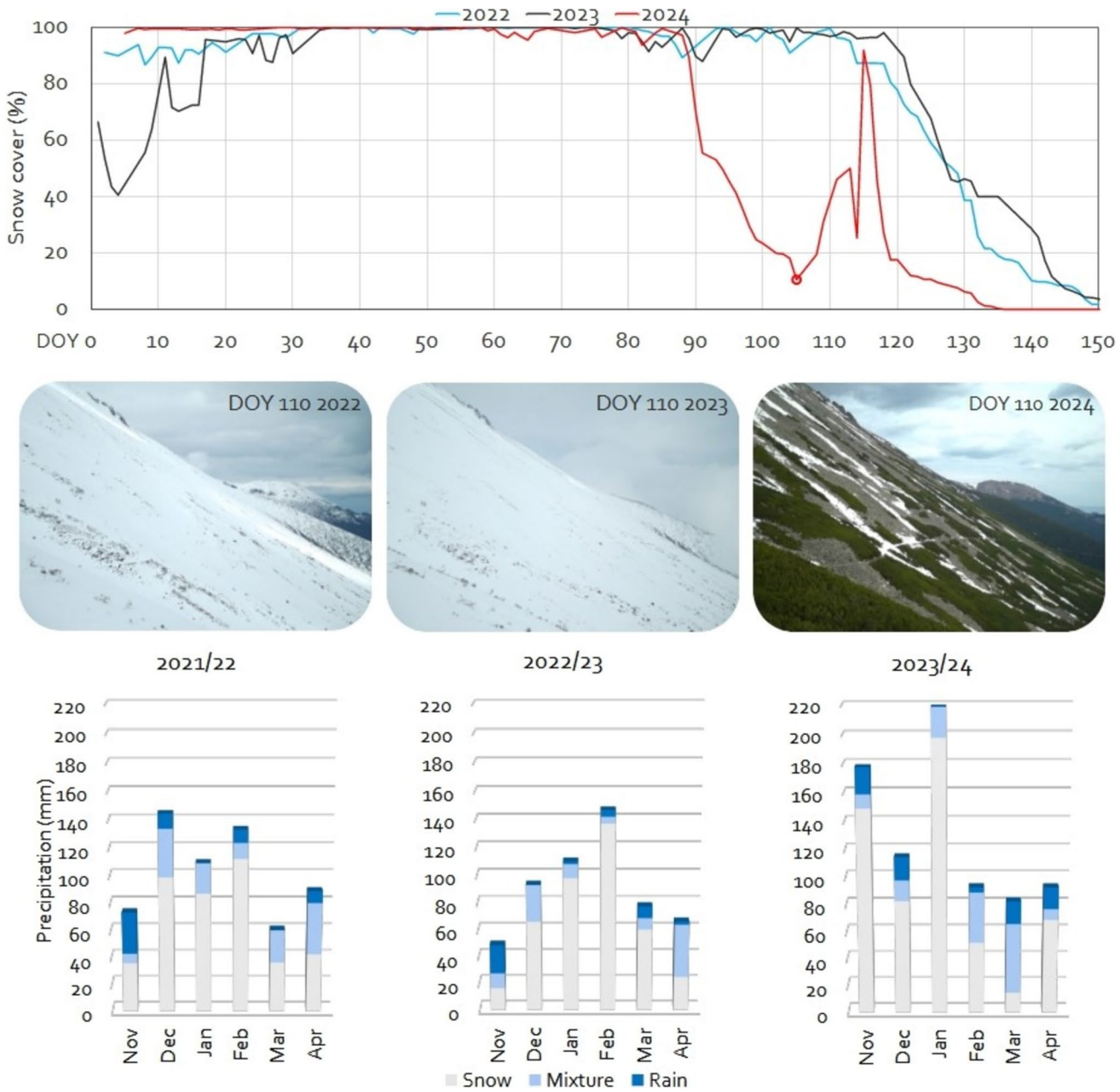


Fig. 3 Snowmelt progression based on time-lapse photography from 2022, 2023, and 2024, highlighting the state of snow cover on day of year (DOY) 105 for each year. The distribution of precipitation from November to March, categorised into snow, mixed precipitation, and rain, is shown below

and temperatures of other individual months or alternative multi-month periods were not statistically significant. Additionally, no significant relationship was found between SMD and ASD.

In addition to air temperature, the role of snow precipitation distribution throughout winter and the occurrence of rain-on-snow events in determining the snowmelt date (SMD) was also analysed. The highest snow totals in the 2023/24 season were recorded in January, when monthly maximum and average temperatures reached 1.4 °C and −2.0 °C, respectively. In contrast, February, the month with the highest snowfall in 2022 and 2023, was marked by minimal snow precipitation in 2024. February is historically the coldest month at SPO, with Tmax averages of −2.0 °C and −1.1 °C and Tavg of −5.8 °C and −5.0 °C for the 1961–1990 and 1991–2020 climate normals, respectively (Lukasová et al. 2023). Despite a Tavg of −2.1 °C in February 2024, the monthly Tmax reached 3.9 °C, contributing to

an increased occurrence of mixed precipitation and a snow cover loss of 23 cm. By March 2024, a substantial portion of precipitation fell as rain or mixed precipitation, in contrast to predominantly snow precipitation in the same month in 2022 and 2023 (Fig. 3). From late March to early April 2024, the snow cover at SPO melted entirely, with a recorded snow depth loss of 52 cm over 2 weeks. In summary, reduced snowfall and the occurrence of rain-on-snow events, together with elevated temperatures in February but mainly in March and April, contributed to accelerated snowmelt, a key limiting factor for the phenological development of low-growing alpine species.

False spring in 2024

Between March 29 and April 1, 2024, the first sustained period of four consecutive days with daily Tavg exceeding 5 °C was recorded. Subsequently, from April 6 to April 15, daily Tavg surpassed 5 °C (mean = 9.2 °C), while Tmax remained consistently above 10 °C (mean = 14.2 °C) for ten consecutive days. This period qualified as an intense heatwave, with all 10 days surpassing the 90th percentile of both the 1961–1990 and 1991–2020 climate normals. During this warm spell, the first visible signs of phenological activity were observed. On DOY 97 (April 7), the onset of vegetative bud swelling (BBCH01) in *V. myrtillus* (Fig. 4a) and the first leaf unfolding (BBCH11) in *C. vulgaris* (Fig. 4b) were recorded at site 1 (1650 m a.s.l.). On the same day, the beginning of vegetative bud break (BBCH07) in *Pinus cembra* was observed at site 2 (1600 m a.s.l.). Subsequently, BBCH07 in *Pinus cembra* was recorded on DOY 100 at site 1 and on DOY 104 at site 3 (1700 m a.s.l.). On DOY 104, BBCH07 was also observed in *V. myrtillus* at site 1 (Fig. 4a). At this site, the snow cover melted between site inspections on DOY 90 and 95, enabling the onset of phenological phases in low-growing species. During this period, approximately 50% of the studied ATE area remained snow-covered in 2024 (Fig. 3). In contrast, a comparable snow coverage (50%) was reached on DOY 127 in both 2022 and 2023, with complete snowmelt at site 1 occurring between DOY 120–125 in 2022 and DOY 122–126 in 2023. In those years, the first phenophases were recorded after DOY 130, during the second half of May (Fig. 4), indicating a delay of more than one month compared to 2024.

The early phenological development was abruptly interrupted by a significant synoptic shift starting on April 16, 2024 (https://www.wetterzentrale.de/reanalysis.php?map=1&model=era&var=2&jaar=2024&maand=4&dag=16&h=0&nmaps=24#google_vignette), when an Arctic air mass penetrated deep into Central Europe, triggering an exceptionally severe cold spell lasting 11 days. During this cold spell,

- the mean daily Tmax dropped to approximately 1.3 °C, with three ice days (Tmax < 0 °C)
- the mean daily Tavg was −2.0 °C, with a minimum daily Tavg of −5.3 °C.
- the lowest Tmin reached −8.3 °C (Fig. 5).

The most pronounced impacts of the hard frost were observed on *V. myrtillus* and *P. cembra* (Fig. 5). In contrast to 2024, the LHF in 2022 and 2023 occurred prior to the onset of the first phenological phases, allowing vegetation to avoid exposure to frost damage. In both years, phenological development proceeded under typical conditions, with no visible damage to vegetative or reproductive organs during the spring phenophases (Fig. S1).

Vaccinium myrtillus

In *V. myrtillus*, green vegetative buds in the bursting phase (Fig. 4a) were damaged by frost, turning black, desiccated, and necrotic (Fig. 5). Later, during generative phenological phases, we observed the development of degenerated flowers and fruits. Only a small proportion of the fruit matured in good condition. Among the studied species, *V. myrtillus* exhibited the lowest thermal requirements for initiating the first phenological phase. It required a mean GDD_0 of 100.7 °C accumulated over 28 AGD_0, and a GDD_5 of only 13 °C accumulated over 7 AGD_5 (Table 2).

Pinus cembra

P. cembra required a mean GDD_0 of 130.1 °C and GDD_5 of 29.0 °C, with an AGD_0 of 31 days and AGD_5 of 9 days to initiate BBCH07. After the false spring ended, the phenological development of *P. cembra* continued with some delay, although it still proceeded slightly earlier than in previous years (Fig. 4c). During May, the needle condition deteriorated, with approximately one-third turning yellow and subsequently falling off. However, no visible frost injury was detected on the buds at that time. Damage caused by frost during the bud bursting phase became apparent later, during flowering. Frost-affected tissues led to the development of malformed male flowers, which remained enclosed within the bud scales and failed to release pollen (Fig. 5). Instead of normal pollination, the degenerated male flowers dried out and were shed from the bud scales, which remained temporarily attached to the tree. In unaffected development, male flowers mature inside the bud scales, which then fell off, allowing the flowers to release pollen (Fig. S1, above).

In contrast, the new shoots developed normally, without visible needle or growth abnormalities, and female flowers were formed at their tips. Several cones from 2024 were observed on one of the ten monitored trees. However, whether pollination occurred via distant *P. cembra*

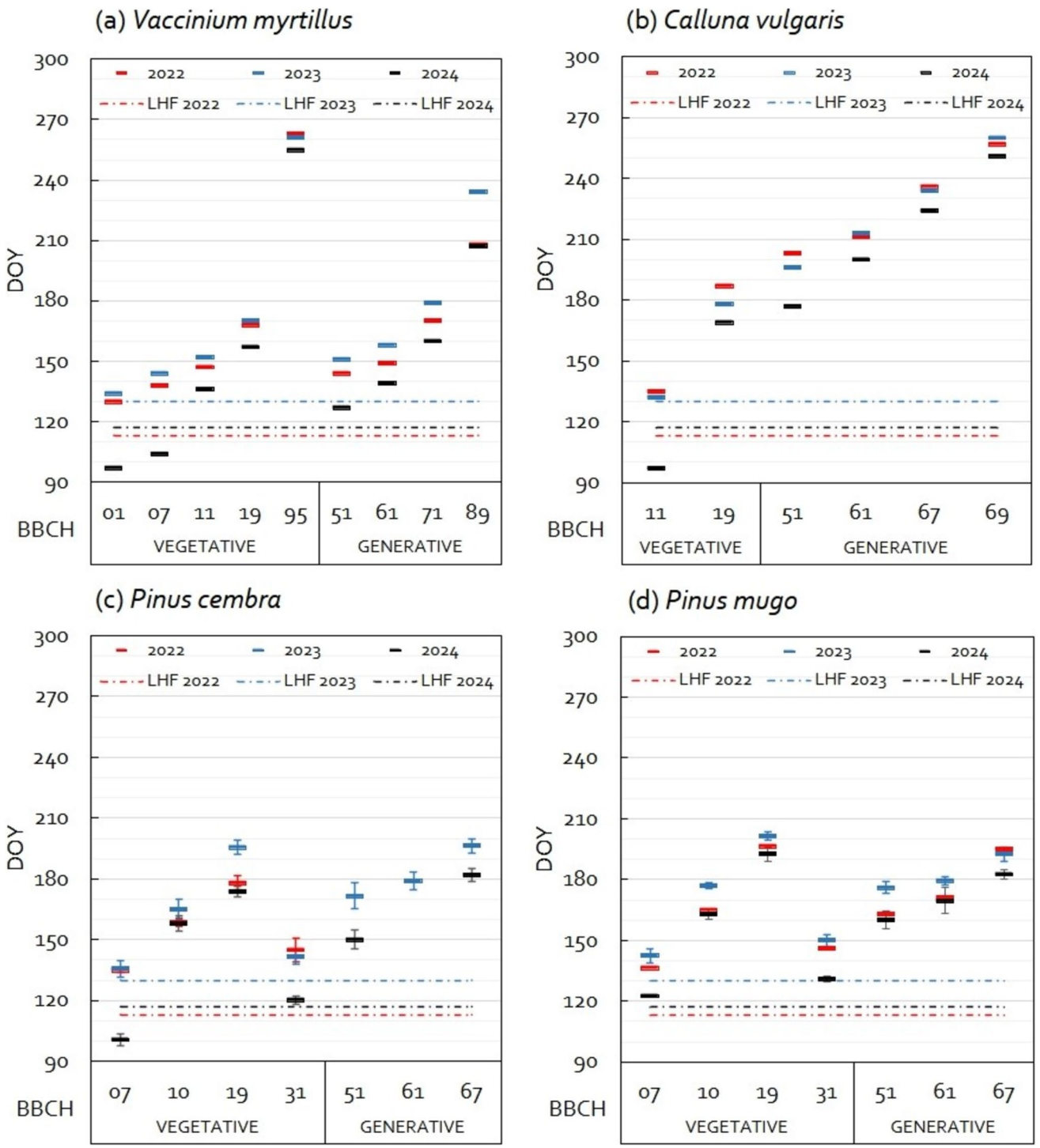


Fig. 4 Onset dates (day of year, DOY) of phenological phases for vegetative and generative organs of the studied species in 2022, 2023, and 2024, based on the BBCH scale (Table 1). Vertical lines indicate the timing of the last hard frost events in the alpine treeline ecotone of the High Tatras. Error bars in panels (**c**) and (**d**) represent the standard deviation of average onset dates across observational sites

individuals remains uncertain, since malformed male flowers were also observed at a foothill phenological site at 800 m a.s.l., where *P. cembra* was at the BBCH31 stage during the frost event (unpublished data).

Calluna vulgaris

Similar to *V. myrtillus*, *C. vulgaris* initiates the BBCH11 phase immediately after snowmelt, requiring a mean GDD_0

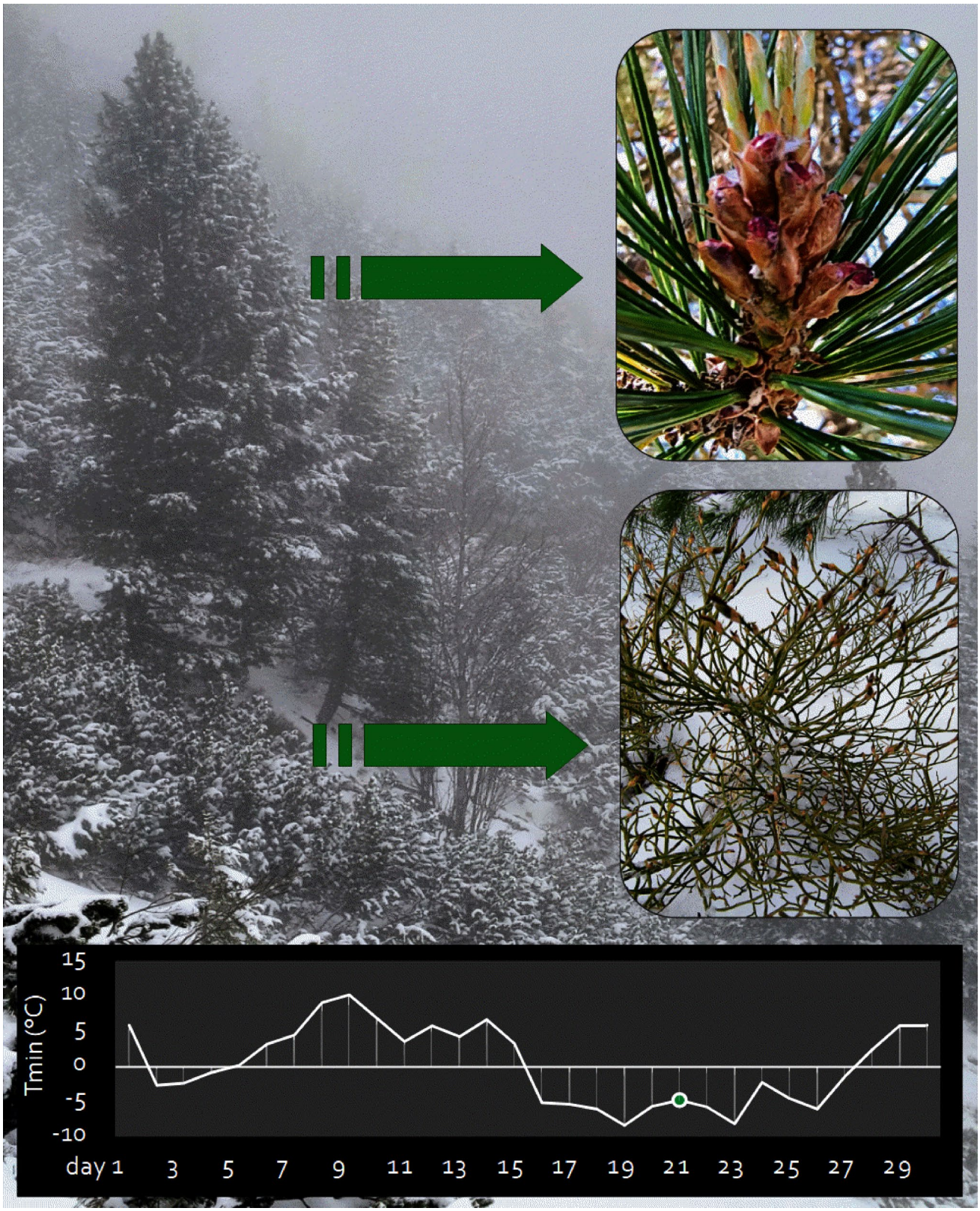


Fig. 5 Phenological site 1 with *P. cembra* and *V. myrtillus* on April 21, 2024 (DOY 112), during the cold spell. The accompanying graph shows daily minimum air temperatures (Tmin, °C) in April 2024. The right panel illustrates damage attributed to the false spring, with visible injury symptoms on *P. cembra* (upper image) and *V. myrtillus* (lower image)

Table 2 Growing degree days (GDD) in °C and the number of active growing days (AGD, in brackets) associated with the first observed vegetative and generative phenological phases of the analysed species, calculated for temperature bases of 0 °C (GDD_0, AGD_0) and 5 °C (GDD_5, AGD_5)

Sp	Year	BBCH	GDD_0 (AGD_0)	GDD_5 (AGD_5)	BBCH	GDD_0 (AGD_0)	GDD_5 (AGD_5)
C. vulgaris	2022	11	167.4 (31)	45.5 (15)	51	964.0 (99)	504.0 (82)
	2023		92.8 (29)	5.1 (6)		672.9 (93)	277.0 (62)
	2024		89.7 (27)	16.7 (4)		784.2 (98)	367.4 (70)
	Mean		116.6 (29)	22.4 (8)		807.0 (97)	382.8 (71)
	Sd		35.9 (2)	17.0 (5)		119.9 (3)	93.3 (8)
V. myrtillus	2022	01	114.1 (26)	17.2 (10)	51	243.7 (40)	76.8 (24)
	2023		98.5 (31)	5.1 (6)		250.4 (48)	72.6 (22)
	2024		89.7 (27)	16.7 (4)		284.0 (48)	117.2 (22)
	Mean		100.7 (28)	13.0 (7)		259.3 (45)	88.9 (23)
	Sd		10.1 (2)	5.6 (2)		17.6 (4)	20.1 (1)
P.mugo	2022	07	183.9 (33)	52.0 (17)	51	436.9 (59)	176.9 (42)
	2023		163.7 (40)	31.0 (14)		458.0 (73)	162.1 (42)
	2024		239.4 (44)	92.6 (18)		582.3 (81)	250.5 (54)
	Mean		195.7 (39)	58.5 (16)		492.4 (71)	196.5 (46)
	Sd		32.0 (5)	25.6 (2)		64.1 (9)	38.7 (6)
P.cembra	2022	07	158.0 (30)	41.1 (14)	51	-	-
	2023		104.5 (32)	6.1 (7)		458.0 (73)	162.1 (42)
	2024		127.9 (30)	39.9 (7)		463.7 (70)	186.9 (42)
	Mean		130.1 (31)	29.0 (9)		460.8 (72)	174.4 (42)
	Sd		21.9 (1)	16.2 (3)		2.8 (2)	12.4 (0)

of 116.6 °C and GDD_5 of 22.4 °C, as well as 29 AGD_0 and 8 AGD_5. Compared to other species, *C. vulgaris*, which was in the leaf development phase when the hard frost occurred (Fig. 4b), showed no visible signs of damage. The newly developed leaves tolerated the frost, likely because the snowfall during the cold spell created a fresh snow cover that protected this low-growing shrub (less than 20 cm in height at the observation site). During the site inspection on April 21 (DOY 112), the species was found completely covered by snow. Snow depth measurements from SPO indicated a maximum of 22 cm during this episode, and snow cover persisted for 13 days. Based on our observations, *C. vulgaris* has the highest temperature requirements to initiate the generative phenophase BBCH51 (Table 2). Flowering usually occurs between late June and late July (Fig. 4b); therefore, the risk of frost damage to its flowers is very low.

Pinus mugo Turra

Both vegetative and generative organs of *P. mugo* remained undamaged after the cold snap, as its phenological growing season began only after the late frosts had ended (Fig. 4d). The delayed phenology of *P. mugo* compared to *P. cembra* and the other studied species is related to its higher temperature requirements and/or the need for more active growing days to initiate its vegetative and generative phenological phases (Table 2). Compared to *P. cembra*, the temperature requirements of *P. mugo* were 1.5 to 2 times higher. Following the false spring of 2024, *P. mugo* required only a few warm days to initiate bud break (BBCH07); however, GDD were considerably higher compared to previous years. Similarly, the onset of the flower buds (BBCH51) was delayed by 12 AGD_5 in this species in 2024, while in other species, the timing of BBCH51 relative to GDD and AGD showed no substantial differences (Table 2).

Shifts in growing degree days, snowmelt date, and last hard frost

The average GDD_5 values from Table 2 were used to calculate trends in potential onset days of BBCH07 for *P. cembra* and BBCH01 for *V. myrtillus* over the period 1979–2024. The average potential onset day was DOY 130 (Sd = 13.2 days) for *P. cembra* and DOY 121 (Sd = 13.8 days) for *V. myrtillus*. During the 46-year-long period, the Mann-Kendall test indicated a significant trend toward earlier potential onset dates for both BBCH07 ($p = 0.003$) by −4.7 days per decade in *P. cembra* and BBCH01 ($p = 0.002$) by −4.8 days per decade in *V. myrtillus*.

The key factor in the occurrence of false spring is the timing of the LHF, which poses a risk of damage when the phenological phases begin before the LHF. The trend in LHF was not statistically significant ($p = 0.09$), with the shift of −3.7 days per decade. This indicates a faster advance

in GDD_5 accumulation for both species than in LHF. Unlike *P. cembra*, the phenology of *V. myrtillus* is also influenced by the snow cover; thus, even when GDD_5 for BBCH01 is reached, the phenological development is delayed until the snow melts.

The significant trend in SMD, advancing by −3.6 days per decade, is slower than the trend in GDD_5 for *V. myrtillus*, but similar to that of the LHF. These results suggest that snowmelt may continue to play a critical role in protecting *V. myrtillus* from frost damage in the future. In contrast, *P. cembra*, whose phenology is not constrained by snow cover, may increasingly face damage as GDD_5 advances more rapidly than the occurrence of the LHF.

Discussion

The studied species are well adapted to harsh climate conditions of the alpine treeline ecotone. However, in 2024, severe frost during sensitive developmental phases disrupted the vegetation cycles of some species. Our results indicated that the most pronounced damage occurred in *P. cembra* and *V. myrtillus*. In both species, only vegetative buds were visibly initiated development at the time of the frost event; however, the freezing temperatures disrupted not only vegetative growth but also the development of generative organs. In contrast, *P. mugo* and *C. vulgaris* showed no signs of injury or disruption in phenological development following the 2024 false spring in the ATE of the High Tatras. In the case of *C. vulgaris*, frost resistance was likely enhanced by the presence of temporary snow cover, which can buffer extreme temperature minima and reduce the rate of temperature change experienced by plants (Neuner 2014). However, such thermal insulation was only effective for this low-growing shrub. A snow depth of up to 22 cm was insufficient to protect *V. myrtillus*, which reaches approximately 0.4 m in height, or the taller *P. cembra* trees. During the hard frost period, buds of *P. mugo* remained closed. When this species later initiated shoot and needle development and reached the flowering stage, no visible frost damage signs were visible at our study sites. Nevertheless, frost rings, caused by the collapse of xylem vessels during freezing events, may still form within the annual growth rings, as has been observed in *Pinus mugo* subsp. uncinata (Rixen et al. 2012).

Late spring frost damage typically results from a complex interaction between biological factors, frost events, and other abiotic influences (Körner 2021; Lamichhane 2021); therefore, frost risk is highly variable and difficult to predict. Spring development in plants is commonly controlled by three factors, interacting in a non-linear fashion: (1) the fulfilment of chill demand to ensure winter has passed, (2) a photoperiod signal 'opening' the window for final release from dormancy, and (3) actual weather conditions, particularly temperature (Körner 2006). In the studied ATE, the winters remain sufficiently cold (Lukasová et al. 2023) to fulfil chill requirements, and the increasing length of photoperiod permits the shift in phenological phases to earlier dates. Our findings indicate that Tavg fluctuating around 0 °C during winter 2024 was adequate to meet chilling requirements, while the photoperiod signalled a 'save' date in early April. A significant increase in temperature then rapidly advanced phenology in the observed species. However, these evolutionary adaptations, chill control, and photoperiodism (Körner 2012) proved insufficient to prevent early development during the false spring, allowing for reduced dormancy depth and an earlier increase in bud vitality (Baumgarten et al. 2021). In conifers such as *P. cembra*, the buds overwinter through extracellular ice tolerance. *P. cembra* belongs to a species with high winter frost resistance of leaves and buds; however, warm spells in late winter led to premature frost de-hardening, leading to significantly earlier bud swelling and burst (Buchner and Neuner 2011). Similarly, in *Vaccinium myrtillus*, Taulavuori et al. (1996) demonstrated that even a moderate temperature increase of 2–3 K during the overwintering period can significantly accelerate de-hardening and advance bud burst.

Dwarf shrubs are the species group with the greatest phenological sensitivity to changes in snowmelt (Wipf and Rixen 2010). Snow cover data, obtained through a combination of manual point measurements with a snow stake at SPO, time-lapse photography using a trail camera, and in situ observations, enabled a more comprehensive analysis of snow cover dynamics in the ATE. The measurements indicated that snow depth was significantly higher compared to the 2021/22 and 2022/23 seasons, and also higher than the long-term average. However, the distribution and form of prevailing precipitation, particularly rain-on-snow events, in combination with higher temperatures, accelerate snowmelt (Dong and Menzel 2019; Hotovy et al. 2023). In February 2024, only minimal snowfall was recorded, while the proportion of mixed precipitation increased and by March, a large share of precipitation fell as rain or mixed forms, accelerating the reduction of snow which enabled the onset of phenological phases in *V. myrtillus* and *C. vulgaris*. Our analyses revealed that, in the absence of snow cover, *V. myrtillus* followed by *C. vulgaris* required the lowest GDD to initiate bud swelling and leafing, respectively. In contrast, *P. mugo* showed the highest thermal requirements, needing 1.5 to 2 times higher GDD than *P. cembra* to initiate bud bursting.

The consequences of a false spring may disrupt food chains, as the flowers and fruits of *V. myrtillus* and the seeds of *P. cembra* are essential food sources for primary consumers, ranging from insects to large mammals and

birds inhabiting the ATE of the High Tatras. In *V. myrtillus*, the impact of damage was already evident in 2024 through a poor fruit harvest. The effect on seed production in *P. cembra* will become apparent in subsequent seasons. If the unpollinated female flowers do not abscise in the first growing season, malformed shapes, stunted growth, and cone loss are typical symptoms of low or unsuccessful pollination, generally visible after the cones complete their development at the end of the second growing season (Oppitz 1971). Due to the rocky terrain and dense understory thickets, primarily formed by *P. mugo*, early cone drop following potential imperfect fertilisation was difficult to observe. The quality and presence of cones will be monitored at the end of the 2025 growing season, and subsequently in 2026, when the cones are expected to complete their life cycle.

The risk of frost damage is not necessarily diminished in a warmer climate, as earlier spring phenology may offset the benefits of fewer late frost events by increasing plant exposure during vulnerable developmental stages (Chamberlain and Wolkovich 2021). Trends analyses of GDD_5 for the first observed phenophases in two frost-damaged species (*P. cembra* and *V. myrtillus*) showed that GDD_5 is shifting to earlier dates more rapidly than the last hard frost (LHF). This suggests a rising risk of frost damage in the future, especially for *P. cembra*, which, unlike *V. myrtillus*, is not affected by snowmelt date. With shifting growing seasons leading to phenological mismatches and increased environmental risk, species-specific responses to climate change will be crucial in determining which species gain a competitive advantage in future climate conditions (Cleland et al. 2012; Jaroszynska et al. 2023; Dawson-Glass et al. 2025) since the reproductive success and competitive ability of subalpine and alpine plants may be weakened under such conditions (Rixen et al. 2012). While the trend in SMD is advancing, it lags behind that of GDD_5, implying that the earlier onset of BBCH01 in *V. myrtillus* may still be delayed by persistent snow. However, it remains uncertain how long dwarf shrub species will continue to benefit from snow cover as a regulator of life cycle timing. Projections suggest that snowpacks in mountain regions will become increasingly shallow, short-persistent, and subject to earlier melt if greenhouse gas emissions continue along current trajectories (Siirila-Woodburn et al. 2021); Notarnicola 2022).

Conclusions

Our study demonstrates the increasing vulnerability of alpine and subalpine species in the High Tatra Mountains to false spring events under ongoing climate change. In 2024, a mid-April cold spell following an exceptionally warm winter and spring caused severe frost damage to *Pinus cembra* and *Vaccinium myrtillus* during sensitive phenological stages, affecting both vegetative and reproductive organs. In contrast, *Pinus mugo* exhibited delayed phenology, and *Calluna vulgaris* was protected by snow cover, avoiding frost injury. We found that the advancement of growing degree days accumulation is outpacing the retreat of the last hard frost, particularly in those early-developing species. Although snow cover still offers protection to low-stature shrubs, its diminishing duration may increasingly limit this protective effect in the future. The increasing decoupling between climatic cues and frost risk heightens the likelihood of phenological mismatches, with potential consequences for reproductive success, competitive relationships, and food web interactions. While our phenological dataset is currently too short for robust climate-phenology correlations, continued observations will enable stronger inference on species responses under accelerating climate change.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10113-025-02477-8.

Funding Open access funding provided by The Ministry of Education, Science, Research and Sport of the Slovak Republic in cooperation with Centre for Scientific and Technical Information of the Slovak Republic. This study was funded by the VEGA 2/0048/25 project.

Data availability Data are available from the authors upon reasonable request.

Declarations

Human and animal rights No humans or animals were involved in the research.

Conflict of interest The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Ault TR, Henebry GM, Schwartz MD, Betancourt JL, Moore D (2013) The false spring of 2012, earliest in North American

record. Eos Trans Am Geophys Union 94(20):181–182. https://doi.org/10.1002/2013EO200001
Basler D, Körner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. Agric for Meteorol 165:73–81. https://doi.org/10.1016/j.agrformet.2012.06.001
Baumgarten F, Zohner CM, Gessler A, Vitasse Y (2021) Chilled to be forced: the best dose to wake up buds from winter dormancy. New Phytol 230:1366–1377. https://doi.org/10.1111/nph.17270
Bongio M, Arslan AN, Tanis CM, De Michele C (2021) Snow depth time series retrieval by time-lapse photography: Finnish and Italian case studies. Cryosphere 15:369–387. https://doi.org/10.5194/tc-15-369-2021
Buchner O, Neuner G (2011) Winter frost resistance of *Pinus cembra* measured in situ at the alpine timberline as affected by temperature conditions. Tree Physiol 31(11):1217–1227. https://doi.org/10.1093/treephys/tpr103
CaraDonna PJ, Bain JA (2016) Frost sensitivity of leaves and flowers of subalpine plants is related to tissue type and phenology. J Ecol 104(1):55–64. https://doi.org/10.1111/1365-2745.12482
Carter TR (1998) Changes in the thermal growing season in Nordic countries during the past century and prospects for the future. Agri Food Sci 7(2):161–179. https://doi.org/10.23986/afsci.72857
Chamberlain CJ, Wolkovich EM (2021) Late spring freezes coupled with warming winters alter temperate tree phenology and growth. New Phytol 231(3):987–995. https://doi.org/10.1111/nph.17416
Chuine I, Bonhomme M, Legave J-M, García de Cortázar-Atauri I, Charrier G et al (2016) Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. Glob Chang Biol 22:3444–3460. https://doi.org/10.1111/gcb.13383
Cleland EE, Allen JM, Crimmins TM, Dunne JA, Pau S et al (2012) Phenological tracking enables positive species responses to climate change. Ecology 93:1765–1771. https://doi.org/10.1890/11-1912.1
Dawson-Glass E, Schiafo R, Miller CN, Kuebbing SE, Stuble KL (2025) Toward a comprehensive understanding of the phenological responses of non-native plants to climate warming: a review. Ann Bot. https://doi.org/10.1093/aob/mcaf008
Dong C, Menzel L (2019) Recent snow cover changes over central European low mountain ranges. Hydrol Process 34(2):321–338. https://doi.org/10.1002/hyp.13586
Ernakovich JG, Hopping KA, Berdanier AB, Simpson RT, Kachergis EJ, Steltzer H, Wallenstein MD (2014) Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. Glob Chang Biol 20(10):3256–3269. https://doi.org/10.1111/gcb.12568
Fu YH, Geng X, Chen S, Wu H, Hao F (2023) Global warming is increasing the discrepancy between green (actual) and thermal (potential) seasons of temperate trees. Glob Change Biol 29(5):1377–1389. https://doi.org/10.1111/gcb.16545
Gibson-Reinemer DK, Sheldon KS, Rahel FJ (2015) Climate change creates rapid species turnover in montane communities. Ecol Evol 5(12):2340–2347. https://doi.org/10.1002/ece3.1518
Gobiet A, Kotlarski S, Beniston M, Heinrich G, Rajczak J et al (2014) 21st century climate change in the European Alps—a review. Sci Total Environ 493:1138–1151. https://doi.org/10.1016/j.scitotenv.2013.07.050
Hlásny T, Trombik J, Dobor L, Barcza Z, Barka I (2015) Future climate of the Carpathians: climate change hot-spots and implications for ecosystems. Reg Environ Change 16:1495–1506. https://doi.org/10.1007/s10113-015-0890-2
Hotovy O, Nedelcev O, Jenicek M (2023) Changes in rain-on-snow events in mountain catchments in the rain–snow transition zone. Hydrol Sci J 68(4):572–584. https://doi.org/10.1080/02626667.2023.2177544
Hraško J, Linkeš V, Šály R, Šurina B (n.d.). Pôdna mapa Slovenska 1:400 000. http://www.podnemapy.sk/portal/prave_menu/podna_mapa/podna_mapa.aspx. Accessed 6 Jun 2025
Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecol 89(2):353–362. https://doi.org/10.1890/06-2128.1
Inouye DW, Wielgolaski FE (2024) Phenology at high altitudes. In: Schwartz MD (ed) Phenology: an integrative environmental science. Springer, Cham, pp 281–311. https://doi.org/10.1007/978-3-031-75027-4_13
IPCC (2023) Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, 184. https://doi.org/10.59327/IPCC/AR6-9789291691647
Jaroszynska F, Rixen C, Woodin S, Lenoir J, Wipf S (2023) Resampling alpine herbarium records reveals changes in plant traits over space and time. J Ecol 111(2):338–355. https://doi.org/10.1111/1365-2745.14062
Keller F, Körner C (2003) The role of photoperiodism in alpine plant development. Arct Antarct Alp Res 35:361–368. https://doi.org/10.1657/1523-0430(2003)035[0361:tropia]2.0.co;2
Körner C (2003) Alpine plant life. Springer, Berlin Heidelberg, p 349. https://doi.org/10.1007/978-3-642-18970-8
Körner C (2006) Significance of temperature in plant life. In: Morison JIL, Morecroft MD (eds) Plant growth and climate change. Blackwell, Oxford, pp 48–69. https://doi.org/10.1002/9780470988695.ch3
Körner C (2012) Alpine treelines: functional ecology of the global high elevation tree limits. Springer, 220. https://doi.org/10.1007/978-3-0348-0396-0
Körner C (2016) Plant adaptation to cold climates. F1000Res. https://doi.org/10.12688/f1000research.9107.1
Körner C (2021). Alpine Plant Life: Functional plant ecology of high mountain ecosystems, 3rd edn. Cham. Springer, Switzerland, p 500
Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. J Biogeogr 31:713–732. https://doi.org/10.1111/j.1365-2699.2003.01043.x
Körner C, Basler D, Hoch G, Kollas C, Lenz A et al (2016) Where, why and how? Explaining the low-temperature range limits of temperate tree species. J Ecol 104:1076–1088. https://doi.org/10.1111/1365-2745.12574
Körner C, Möhl P, Hiltbrunner E (2023) Four ways to define the growing season. Ecol Lett 26(8):1277–1292. https://doi.org/10.1111/ele.14260
Koźmiński C, Mąkosza A, Michalska B (2023) Air frosts in Poland in the thermal growing season (AT > 5 °C). Agriculture (Basel) 13(6):1228. https://doi.org/10.3390/agriculture13061228
Krajčí P, Danko M, Hlavčo J, Kostka Z, Holko L (2016) Experimental measurements for improved understanding and simulation of snowmelt events in the Western Tatra Mountains. J Hydrol Hydromech 64(4):316–328. https://doi.org/10.1515/johh-2016-0038
Kučera J, Podhrázská J, Středa T, Středová H, Fukalová P et al (2024) New methods of assessing wind erosion risk: innovative approach to soil protection respecting windbreak effect. Contrib Geophys Geod 54(4):371–388. https://doi.org/10.31577/congeo.2024.54.4.4
Laigle I, Carlson BZ, Delestrade A, Bison M, Van Reeth C et al (2022) In-situ temperature stations elucidate species' phenological responses to climate in the Alps, but meteorological and snow reanalysis facilitates broad scale and long-term studies. Front Earth Sci 10:912048. https://doi.org/10.3389/feart.2022.912048

Lamichhane JR (2021) Rising risks of late-spring frosts in a changing climate. Nat Clim Chang 11:554–555. https://doi.org/10.1038/s41558-021-01090-x

Larcher W (2005) Climatic constraints drive the evolution of low temperature resistance in woody plants. J Agric Meteorol 61:189–202. https://doi.org/10.2480/agrmet.61.189

Leake I (2023) Climate extremes drive negative vegetation growth. Nat Rev Earth Environ 4:68. https://doi.org/10.1038/s43017-023-00392-2

Lenoir J, Graae BJ, Aarrestad PA et al (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. Glob Change Biol 19(5):1470–1481. https://doi.org/10.1111/gcb.12129

Lenz A, Hoch G, Vitasse Y, Körner C (2013) European deciduous trees exhibit similar safety margins against damage by spring freeze events along elevational gradients. New Phytol 200:1166–1175. https://doi.org/10.1111/nph.12452

Lenz A, Hoch G, Körner C, Vitasse Y (2016) Convergence of leaf-out towards minimum risk of freezing damage in temperate trees. Funct Ecol 30:1480–1490. https://doi.org/10.1111/1365-2435.12623

Litschmann T, Středa T (2019) The surface temperature of plant tissues. Which method of air temperature measurement fits best? Contrib Geophys Geodesy 49:11–23. https://doi.org/10.2478/congeo-2019-0002

Lukasová V, Varšová S, Buchholcerová A, Onderka M, Bilčík D (2023) Changes in the high-altitude climate of High Tatra Mts. evaluated by climatic normals from the Skalnaté pleso observatory. Met J (Meteorologický Časipis) 26(1):47–52

Marino GP, Kaiser DP, Gu L, Ricciuto DM (2011) Reconstruction of false spring occurrences over the southeastern United States, 1901–2007: an increasing risk of spring freeze damage? Environ Res Lett 6:024015. https://doi.org/10.1088/1748-9326/6/2/024015

Martinuzzi S, Allstadt AJ, Pidgeon AM, Flather CH, Jolly WM et al (2019) Future changes in fire weather, spring droughts, and false springs across U.S. national forests and grasslands. Ecol Appl 29(5):e01904. https://doi.org/10.1002/eap.1904

Marty C (2008) Regime shift of snow days in Switzerland. Geophys Res Lett 35(12):L12501 https://doi.org/10.1029/2008GL033998

Meier U (2001) Growth stages of mono- and dicotyledonous plants. BBCH Monograph, 2nd edn. Federal Biological Research Centre for Agriculture and Forestry: Quedlinburg, Germany, p 158

Murray M (2020) Critical temperatures for frost damage on fruit trees.https://www.chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/https://extension.usu.edu/productionhort/files/CriticalTemperaturesFrostDamageFruitTrees.pdf. Accessed 12 Mar 2025

Neuner G (2014) Frost resistance in alpine woody plants. Front Plant Sci 5:117002. https://doi.org/10.3389/fpls.2014.00654

Notarnicola C (2022) Overall negative trends for snow cover extent and duration in global mountain regions over 1982–2020. Sci Rep 12(1):1–16. https://doi.org/10.1038/s41598-022-16743-w

Okamoto R, Ide R, Oguma H (2024) Automatically drawing vegetation classification maps using digital time-lapse cameras in alpine ecosystems. Remote Sens Ecol Conserv 10(2):188–202. https://doi.org/10.1002/rse2.364

Oppitz H (1971) Pokusný semenný sad borovice limby (Pinus cembra L.) v Javorine v rokoch 1964–1967. Zborník Prác o Tatranskom Národnom Parku 13:183–242 (In Slovak)

Parajka J, Haas P, Kirnbauer R, Jansa J, Blöschl G (2012) Potential of time-lapse photography of snow for hydrological purposes at the small catchment scale. Hydrol Process 26:3327–3337. https://doi.org/10.1002/hyp.8389

Pardee GL, Inouye DW, Irwin RW (2017) Direct and indirect effects of episodic frost on plant growth and reproduction in subalpine wildflowers. Glob Change Biol 24(2):848–857. https://doi.org/10.1111/gcb.13865

Paulsen J, Körner C (2014) A climate-based model to predict potential treeline position around the globe. Alpine Bot 124:1–12. https://doi.org/10.1007/s00035-014-0124-0

Portenier C, Hüsler F, Härer S, Wunderle S (2020) Towards a webcam-based snow cover monitoring network: methodology and evaluation. Cryosphere 14(4):1409–1423. https://doi.org/10.5194/tc-14-1409-2020

Quamme HA (1995) Deep supercooling in buds of woody plants. In: Lee RE, Warren GJ, Gusta LV (eds) Biological ice nucleation and its application. APS Press, St. Paul, pp 183–200

Rixen C, Dawes MA, Wipf S, Hagedorn F (2012) Evidence of enhanced freezing damage in treeline plants during six years of CO2 enrichment and soil warming. Oikos 121:1532–1543. https://doi.org/10.1111/j.1600-0706.2011.20031.x

Sakai A, Larcher W (1987) Frost survival of plants: responses and adaptation to freezing stress. Springer, Berlin

Salvatori R, Plini P, Giusto M, Valt M, Salzano R et al (2011) Snow cover monitoring with images from digital camera systems. Ital J Rem Sens 43:137–145. https://doi.org/10.5721/ItJRS201143211

Siirila-Woodburn ER, Rhoades AM, Hatchett BJ, Huning LS, Szinai J, Tague C, Nico PS, Feldman DR, Jones AD, Collins WD, Kaatz LA (2021) A low-to-no snow future and its impacts on water resources in the western United States. Nat Rev Earth Environ 2:800–819. https://doi.org/10.1038/s43017-021-00219-y

Škvareninová J, Sitárová Z, Kvas A, Kijovský P (2021) Occurrence of spring frosts and their influence on flowering of pedunculate oak (Quercus robur L.) in Slovakia. Zprávy lesnického výzkumu 66(3):155–163 (in Slovak, English abstract)

Škvareninová J, Lukasová V, Borsányi P, Kvas A, Vido J et al (2022) The effect of climate change on spring frosts and flowering of Crataegus laevigata – the indicator of the validity of the weather lore about "The Ice Saints." Ecol Indic 145:109688. https://doi.org/10.1016/j.ecolind.2022.109688

Snyder RL, Melo-Abreu JP (2005) Frost protection: fundamentals, practice and economics. FAO Environment and Natural Resources Service Series 1:241

Stewart JR (2009) The evolutionary consequence of the individualistic response to climate change. J Evol Biol 22(12):2363–2375. https://doi.org/10.1111/j.1420-9101.2009.01859.x

Szalay L, Gyorgy Z, Tóth M (2019) Frost hardiness of apple (*Malus X domestica*) flowers in different phenological phases. Sci Horticult 253:309–315. https://doi.org/10.1016/j.scienta.2019.04.055

Taulavuori K, Laine K, Taulavuori E, Pakonen T, Saari E (1996) Accelerated dehardening in bilberry (Vaccinium myrtillus L.) induced by a small elevation in air temperature. Environ Pollut 98(1):91–95. https://doi.org/10.1016/S0269-7491(97)00115-2

Verrall B, Pickering CM (2020) Alpine vegetation in the context of climate change: a global review of past research and future directions. Sci Total Environ 748:141344. https://doi.org/10.1016/j.scitotenv.2020.141344

Vitasse Y, Lenz A, Hoch G, Körner C (2014) Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. J Ecol 102:981–988. https://doi.org/10.1111/1365-2745.12251

Vitasse Y, Rebetez M, Filippa G, Cremonese E, Klein G et al (2017) 'Hearing' alpine plants growing after snowmelt: ultrasonic snow sensors provide long-term series of alpine plant phenology. Int J Biometeorol 61:349–361. https://doi.org/10.1007/s00484-016-1216-x

Vitra A, Lenz A, Vitasse Y (2017) Frost hardening and dehardening potential in temperate trees from winter to budburst. New Phytol 216(1):113–123. https://doi.org/10.1111/nph.14698

Werners SE, Szalai S, Zingstra H, Kőpataki É, Beckmannet A al (2016) Climate change adaptation in the Carpathian Mountain Region. In: Salzmann N, Huggel C, Nussbaumer SU, Ziervogel G (eds) Climate change adaptation strategies: an upstream-downstream

perspective. Springer International Publishing Switzerland, pp 79–99. https://doi.org/10.1007/978-3-319-40773-9_5

Weterzentrale.de. https://www.wetterzentrale.de/reanalysis.php?map=1&model=era&var=2&jaar=2024&maand=4&dag=16&h=0&nmaps=24#google_vignette. Accessed 12 Mar 2025

Wichura MA, Koschnick F, Jung J, Bauer S, Wichura A (2024) Phenological growth stages of highbush blueberries (*Vaccinium* spp.): codification and description according to the BBCH scale. Bot 102(11):428–437. https://doi.org/10.1139/cjb-2024-0036

Wipf S, Rixen C (2010) A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Res 29(1):95–109. https://doi.org/10.1111/j.1751-8369.2010.00153.x

Yang Z, Chen R, Liu Y, Zhao Y, Liu Z, Liu J (2023) The impact of rain-on-snow events on the snowmelt process: a field study. Hydrol Process 37(11):e15019. https://doi.org/10.1002/hyp.15019

Zahradníček P, Brázdil R, Řehoř J, Trnka M, Bartošová L (2024) Past and present risk of spring frosts for fruit trees in the Czech Republic. Theor Appl Climatol 155:965–984. https://doi.org/10.1007/s00704-023-04671-2

Zohner CM, Renner SS (2015) Perception of photoperiod in individual buds of mature trees regulates leaf-out. New Phytol 208:1023–1030. https://doi.org/10.1111/nph.13510

Zohner CM, Mo LD, Renner SS (2018) Global warming reduces leaf-out and flowering synchrony among individuals. Elife 7:e40214. https://doi.org/10.7554/eLife.40214

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.