

A 250-year reconstruction of average July air temperatures (1775–2024): A key climate indicator of vegetation growth in the alpine treeline ecotone of the High Tatra Mts, Slovakia

Svetlana VARŠOVÁ^{1,*} , Veronika LUKASOVÁ¹ ,
Milan ONDERKA² , Jiří KOPÁČEK^{3,4} , Dušan BILČÍK¹ ,
Ján KREMPASKÝ^{1,5} 

¹ Earth Science Institute of the Slovak Academy of Sciences,
Dúbravská cesta 9, Bratislava, SK-840 05, Slovak Republic

² Slovak Hydrometeorological Institute,
Jeséniova 17, Bratislava, SK-833 151, Slovak Republic

³ Biology Centre CAS, Institute of Hydrobiology,
České Budějovice, CZ-370 05, Czech Republic

⁴ University of South Bohemia, Faculty of Science,
České Budějovice, CZ-370 05, Czech Republic

⁵ Technical University in Zvolen, Faculty of Ecology and Environmental Sciences,
Zvolen SK-960 01, Slovak Republic

Abstract: The reconstruction of historical air temperatures over the past 250 years (1775–2024) in the alpine treeline ecotone (ATE) of the High Tatra Mts, Slovakia, provides insights into long-term climate variability. As a high-elevation region sensitive to climatic fluctuations, the alpine treeline is a key indicator of environmental change. A model-based approach allows estimation of air temperature where direct measurements are lacking, offering a tool for assessing long-term climate impacts in high mountains. This study models the July monthly average air temperature (JL-Tavg) and the 10 °C July isotherm, a climatic threshold for vegetation growth. The regression model is based on the environmental temperature lapse rate (ETL), assuming a systematic decrease in temperature with altitude ($\sim 0.65^\circ\text{C}$ per 100 m). Using air temperature data from European stations spanning 191–3109 m a.s.l., the model estimated ETL, which was then applied to reconstruct JL-Tavg and track the 10 °C isotherm across the Skalná dolina ATE profile. The regression model showed a good fit between observed and predicted values, with root mean square error lower than the standard deviation of average JL-Tavg. Reconstructed data indicate that the 10 °C July isotherm fluctuated markedly between

*corresponding author, e-mail: geofsvet@savba.sk

1775 and 2024. The alpine treeline, defined as the elevation with zero probability of tree growth, varied from ≈ 2000 m a.s.l. during the cooler phase (1875–1974) to ≈ 2300 m a.s.l. in the warmer phase (1775–1874). Since 1975, accelerated warming has shifted this thermal boundary upward to ≈ 2400 m a.s.l., now representing the upper cold limit for alpine tree growth in the southern High Tatra Mts. Future work should integrate field monitoring, such as mapping dwarf pine above 2000 m a.s.l., to evaluate current distributional limits under ongoing warming.

Key words: cold limit, alpine treeline, average monthly air temperature, July isotherm, ETL model

1. Introduction

Mountain regions are highly sensitive to warming, and long-term reconstruction of air temperature is essential for evaluating its ecological impacts. The alpine treeline ecotone (ATE) represents a critical transitional zone where the thermal limits of tree growth are reached. This boundary defines the uppermost elevation at which trees can persist, primarily constrained by low temperatures and short growing seasons (Körner, 2003).

The cold climate of alpine zones limits tree growth by suppressing photosynthetic CO_2 assimilation and constraining the formation of new cells (Lehner and Lütz, 2003; Feng et al., 2022). It is now well-established that plant tissue formation ceases near 0°C , and growth in both cambial and apical meristems, above and below ground, is minimal up to temperatures around $+5^\circ\text{C}$. These thermal thresholds align with long-standing physiological limits observed in winter crops and forest trees (Körner, 2012). At high elevations or latitudes, trees encounter their lower thermal range limits, which is generally defined by the mean July temperature (or warmest-month isotherm) of 10°C , although this value does not universally apply to all regions (Körner and Paulsen, 2004). This climatically driven limit is referred to as the alpine treeline and represents the bioclimatic boundary beyond which the tree life-form cannot be sustained due to thermal constraints (Körner, 2021).

In the Tatra Mts, the treeline defined as the highest occurrence of tree groups, was observed at elevations ranging from 1777 m a.s.l. in the Low Tatras to 1806 m a.s.l. in the Western Tatras at the end of the 20th century (Kašpar and Tremel, 2016). In the High Tatras, research on ATE confirmed an upward shift of the treeline in the early 21st century in locations such

as the Mengusovská Valley (Slovakia) and Rybí Potok Valley (Poland), primarily attributed to reduced human land use, regional climate warming, and inactive avalanche paths (Kaczka *et al.*, 2015). An expansion of dwarf pine (*Pinus mugo* Turra) area has been observed due to longer growing seasons, milder winters, and reduced snow cover (Švajda *et al.*, 2011; Solár and Janiga, 2013; Lukasová *et al.*, 2021; Lukasová *et al.*, 2022). Dwarf pine is considered a sensitive bioindicator of ATE changes, responding to air temperature, snow cover, precipitation patterns, and other climatic factors. It is a widespread component of mountain tree vegetation globally.

Although increase temperatures linked to climate change remain a primary driver of alpine treeline advance, treeline dynamics are shaped by a complex interplay of factors, including land use, natural disturbances, climate stressors, tree population dynamics, and biotic interactions (Kulakowski *et al.*, 2016). To understand these complex dynamics, it is essential to integrate diverse scientific disciplines such as plant ecology, dendroecology, ecophysiology, and remote sensing (Bader *et al.*, 2021). Reliable assessments require comprehensive, complex long-term studies such as the Stillberg ecological treeline research site in the Swiss Alps (Lechler *et al.*, 2024). However, long-term trends in growth and year-to-year responses of many mountain tree and shrub species to climate change remain poorly documented.

The lack of historical instrumental data from high-elevation sites complicates efforts to reconstruct past air temperature in mountain environments. Consequently, researchers rely on a combination of natural proxy data (Büntgen *et al.*, 2015; Esper *et al.*, 2018; Žatková *et al.*, 2023) and statistical models (Dobrovolný *et al.*, 2010; Jones, 2016; Neukom *et al.*, 2019). Global reanalysis products, such as the 20th Century Reanalysis (Compo *et al.*, 2011), provide physically consistent climate fields, although their spatial resolution and accuracy in mountainous regions remain limited.

This study aims to reconstruct the July average air temperature (JLTavg) for the ATE zone of the High Tatra Mts using historical climate datasets (1775–2024) from observatories across Europe.

The specific objectives are:

1. To develop a regression model based on the environmental temperature lapse rate (ETL), using lowland and sparse high-elevation observations to estimate ATE air temperatures during periods without direct measurements.

2. To analyse the probability of occurrence of the cold limit for mountain tree growth in the High Tatra Mts related to the altitude of the 10 °C July isotherm across the ATE zone (1500–2600 m a.s.l.) in the Skalná dolina study area.

2. Materials and methods

2.1. Data sources

Long-term series of JL-Tavg data were collected from 12 European meteorological observatories (Fig. 1 left) situated in an elevation profile from 191 to 3109 m (Table 1). The reconstruction of historical JL-Tavg data (1775–2024) for ATE in the High Tatra Mts (Fig. 1 right) was primarily based on records from the Klementinum observatory in Prague (CZ-KLE), the oldest continuously operating climate observatory in Central Europe. Despite certain limitations, such as its location in the city centre and the placement of instruments within a building complex, this site provides a unique and highly valuable source of historical weather and climate data (*CHMI, 2025*). To complement this lowland dataset, temperature records were obtained from several mountain observatories, including the world's oldest mountain meteorological station at Hohenpeissenberg (DE-HOP) (*Winkler, 2006*), as well as summit stations at Zugspitze (DE-ZUG) and Sonnblick (AT-SON) in the Alpine region. Monthly homogenized temperature records for these Alpine sites are available through the HISTALP database, which provides historical instrumental climatological surface time series for the Greater Alpine Region (*HISTALP, 2025*). Additional data were sourced from the European Climate Assessment & Dataset (ECA&D) (*Klein Tank et al., 2002*), which includes records from two high-elevation Romanian Carpathian stations: Ceauhlau Toaca (RO-CEA) and Vârful Omu (RO-VAR). Within the Western Carpathians, the ECA&D database also includes Kasprowy Wierch (PL-KAW), a station situated on the border between Poland and Slovakia.

Temperature records from other Slovak climate stations were obtained from the database of the Slovak Hydrometeorological Institute (SHMI). Selected stations form an elevation transect from the foothill site at Tatranská Lomnica (SK-TAL), through the forest belt at Štrbské Pleso (SK-STP), to the ATE zone at Skalná dolina (SK-SKP), and up to the summit station at

Lomnický štít (SK-LOS). The SK-SKP observatory, which began operation in 1943, provides the longest continuous series of high-quality temperature observations within the ATE zone. At this site, air temperature has been recorded by qualified observers using a calibrated mercury-in-glass thermometer placed in a standard wooden meteorological shelter, located 2 m above the ground. Observations are conducted at standard times (7:00 AM, 2:00 PM, and 9:00 PM). Monthly average temperatures were calculated by averaging daily mean values. A similar methodology was used at the other observatories included in this study.

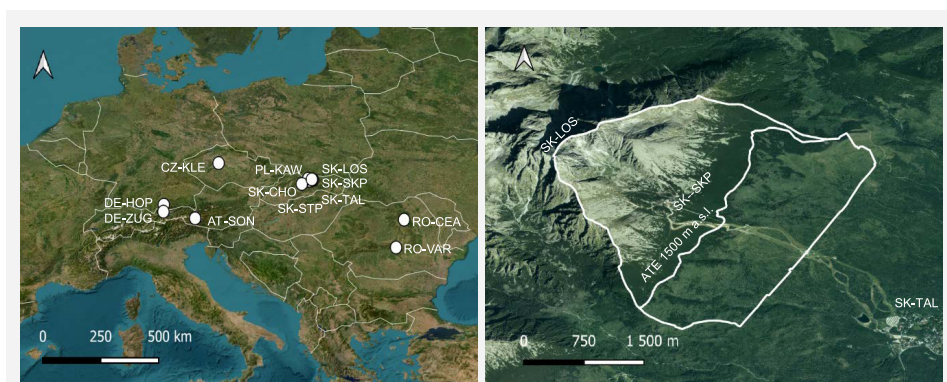


Fig. 1. Left: Locations of climate observation sites across Europe. Right: ATE study area in the High Tatra Mountains, Slovakia, located within the Skalná dolina National Nature Reserve (site abbreviations provided in Table 1).

2.2. ATE study area in the High Tatra Mts

The study area encompasses the ATE of Skalná dolina within Tatra National Park, located in the Slovak Tatra Mountains, part of the Western Carpathians (Fig. 1). Skalná dolina, or “Rocky Valley”, is a national nature reserve designated under IUCN Category Ia, indicating strict protection. The valley was shaped by Pleistocene glaciation, with preserved lateral moraines, a glacial lake, and Quaternary slope deposits. The bedrock is dominated by grey two-mica granodiorite, with pink-red K-feldspar granites near Svišťovka and fault-mylonite zones exposed in adjacent peaks (*Bezák and Majcin, 2013*). Near a glacial lake beneath the southern cliffs of Lomnický štít (2635 m a.s.l.), the Skalnaté Pleso Observatory lies at an altitude

Table 1. European meteorological observatories with long-term air temperature records, listed in ascending order of altitude.

	Observatory	Location	Abbr.	Latitude Longitude	Alt. H m a.s.l.	Observ. period
1	Klementinum	Praque	CZ-KLE	50°05′11″N 14°24′59″E	191	1775–2024
2	Tatranská Lomnica	High Tatra Mts	SK-TAL	49°09′52″N 20°17′17″E	839	1897–2024
3	Hohenpeißenberg	Mount Hohenpeißenberg	DE-HOP	47°48′05″N 11°00′35″E	986	1781–2024
4	Štrbské Pleso	High Tatra Mts	SK-STP	49°07′10″N 20°03′48″E	1323	1931–2024
5	Skalnaté Pleso	High Tatra Mts	SK-SKP	49°11′29″N 20°12′54″E	1778	1941–2024
6	Ceahlău Toaca	Ceahlău Massif	RO-CEA	46°55′47″N 25°55′11″E	1897	1964–2024
7	Kasprowy wierch	High Tatra Mts	PL-KAW	49°13′57″N 19°58′55″E	1988	1951–2024
8	Chopok	Low Tatra Mts	SK-CHO	48°56′38″N 19°35′32″E	2005	1955–2024
9	Varfu Omul	Bucegi Mts	RO-VAR	45°26′59″N 25°27′00″E	2504	1961–2024
10	Lomnický štít	High Tatra Mts	SK-LOS	49°11′43″N 20°12′54″E	2635	1951–2024
11	Zugspitze	Wetterstein Mts	DE-ZUG	47°25′20″N 10°59′12″E	2964	1901–2024
12	Sonnblick	Hohe Tauern	AT-SON	47°03′15″N 12°57′27″E	3109	1887–2024

of 1778 m a.s.l. Meteorological data from this observatory provide characterization of climatic conditions approximately at the 1800 m contour line. At this elevation, permanent snow cover typically persists for 35 to 200 days between October and May (*Ustrnul et al., 2015*), while the growing season generally spans from May to September, when average monthly air temperatures exceed 5 °C (*Žmudzka et al., 2015*). Recent climate trends in the ATE are reflected in a rise in mean annual temperature from 1.7 °C to 2.8 °C and an increase in annual precipitation from 1282 mm to 1477 mm between the periods 1961–1990 and 1991–2020 (*Lukasová et al., 2023*). The lower

part of the ATE, between 1500 and 1800 m a.s.l., is almost entirely covered by dwarf pine, with a continuous distribution reaching up to approximately 1800–1900 m a.s.l. (Krippel, 1986). The absence of conifer biomarkers from the late pleistocene (16,247 BP) to the holocene (4420 BP) suggests that this upper limit has never exceeded 1880 m a.s.l. in the past (Žatková *et al.*, 2023). At higher elevations, harsh climatic conditions, strong winds, and nutrient-poor soils restrict dwarf pine to scattered patches. The uppermost part of the ATE, the alpine zone, is characterized by sparse alpine meadows and rocky terrain. Vegetation in these areas is dominated by grass communities such as the *Juncus trifidus* community.

2.3. Modelling of JL-Tavg and changes of alpine treeline altitude for ATE of the High Tatra Mts over the historical period (1775–2024)

Modelling of JL-Tavg in the ATE zone of the High Tatra Mts was primarily based on historical data from CZ-KLE, supplemented by observations from multiple European sites spanning a broad elevation range (191–3109 m). The regression model estimates the ETL, assuming a systematic and approximately linear decrease in air temperature with increasing elevation. While the commonly cited average environmental lapse rate (ELR) in the troposphere is around 6.5°C per kilometre (or 0.65°C per 100 metres), this value can vary depending on local climatic and geographic conditions (Barry, 2008; Barry and Chorley, 2009). Calibration of ETL regression coefficients to reconstruct JL-Tavg over the historical period (1775–2024) in the MATLAB programming environment was conducted, following six main steps:

1. ETL regression analysis of gap-free data (1964–2024) performed separately for each year to examine the relationship between altitude and the observed JL-Tavg values across all 12 sites (Table 1).
2. Evaluation of the relationship between the regression coefficients from the ETL analysis (Step 1) and the observed JL-Tavg data from the CZ-KLE site, in order to extend the ETL regression model from the 1964–2024 period to the full 1775–2024 period.
3. Model validation through differences between modelled and observed JL-Tavg values, with the root mean square error (RMSE) calculated for all 12 sites (Table 1).

4. Generate JL-Tavg values for the period 1775–2024 across elevation profile from 1500 to 2600 m, at 100-meter intervals, corresponding to the elevation profile in the ATE of Skalná dolina study area.
5. Model simulation of alpine treeline altitude changes related to the thermal criteria of the July isotherm using Regression Learner, an interactive app of Matlab for training, comparing, and optimizing regression models with support for multiple algorithms, including Linear Regression, Support Vector Machines (SVM), Gaussian Process Regression (GPR), Decision Trees, and Ensemble methods.
6. To assess the probability of meeting the 10°C July isotherm thermal criterion along the ATE elevation profile of Skalná dolina study area over the last five half-century periods.

3. Results

3.1. Modelling JL-Tavg and tree growth cold limit in the ATE zone of the High Tatra Mts

The results of the model processing, following the six-step methodology (steps 1–6), are presented in Figs. 2–7 and Tables 2–4.

Processing the complete JL-Tavg data series from all 12 stations (Table 1) over a period exceeding six decades (1964–2024) yielded the ETL linear regression coefficients (a_1 , b_1), shown in Fig. 2 (step 1). Recalculated slope (a_2) and intercept (b_2) values for the extended historical period (1775–2024), based on the relationship between regression coefficients (a_1 , b_1) and JL-Tavg from the longest dataset at CZ-KLE (Fig. 3), are presented in Fig. 4 (step 2). In the first case (Fig. 2), the most frequent a_1 values ranged from -0.0065 to -0.0061 ; in the second case (Fig. 4), a_2 values were between -0.0063 and -0.0062 . Both are close to the expected environmental lapse rate of $6.5^\circ\text{C}/\text{km}$ ($0.65^\circ\text{C}/100\text{ m}$).

Model accuracy (step 3) is supported by statistical error metrics (Table 2) indicates a good fit of the ETL model across all 12 sites, with RMSE being lower than the STD of the average values. The highest RMSE values (>1.00) showed sites RO-VAR and RO-CEA in the Romanian Carpathians. The weaker correlation with the meteorological stations in Romania (Table 2) may arise from a stronger continental influence, different air circu-

lation, and distinct topography in comparison to the High Tatras. The Alps and the Tatras have a similar orographic orientation (mostly west–east), which makes the capture and distribution of air masses more comparable. The Romanian Carpathians, on the other hand, have a more complex and arcuate structure, which leads to different regional patterns of precipitation, cloudiness, and consequently temperature (*Popa and Bouriaud, 2014*). A comparison of observed and modelled JL-Tavg at the SK-TAL, SK-SKP, and SK-LOS sites along the elevation profile of the Skalná dolina study area (Fig. 5) reveals a similar temporal course, with acceptable RMSE values ranging from 0.74 to 0.82 limits.

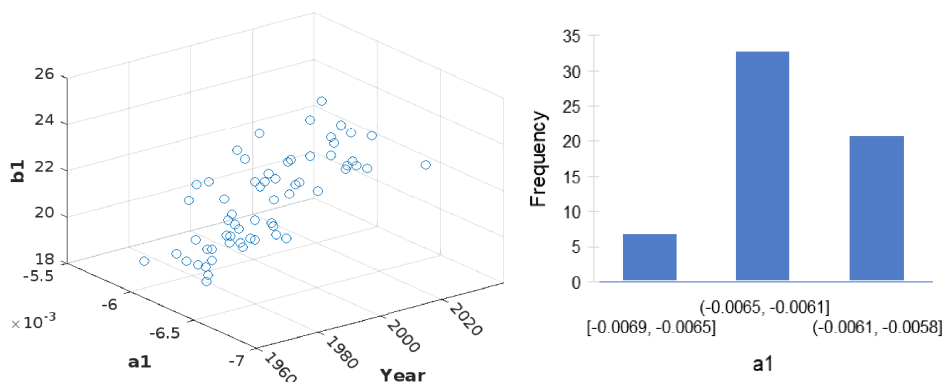


Fig. 2. Annual linear regression coefficients (a_1 : slope, b_1 : intercept) describing the relationship between JL-Tavg and altitude across the 12 study sites listed in Table 1 (left), along with the frequency distribution of a_1 values (right), based on data from the period 1964–2024.

Figure 6 (step 4) visualizes year-to-year changes in JL-Tavg over the historical period (1775–2024) along the elevation profile of the Skalná dolina study area (1500–2600 m), with colour shading applied using locally weighted linear smoothing. The figure confirms the expected decrease in JL-Tavg with altitude, accelerated warming over the past five decades, and shift of 10°C isotherm to altitudes above 2000 m a.s.l. This modelled JL-Tavg time series served as the basis for reconstructing the altitude of the 10°C isotherm using multiple regression models (Fig. 7, step 5). Despite variations in model outputs, all simulations indicate an upward shift in the cold limit for tree growth with RMSE of approximately 200 m (Table 3).

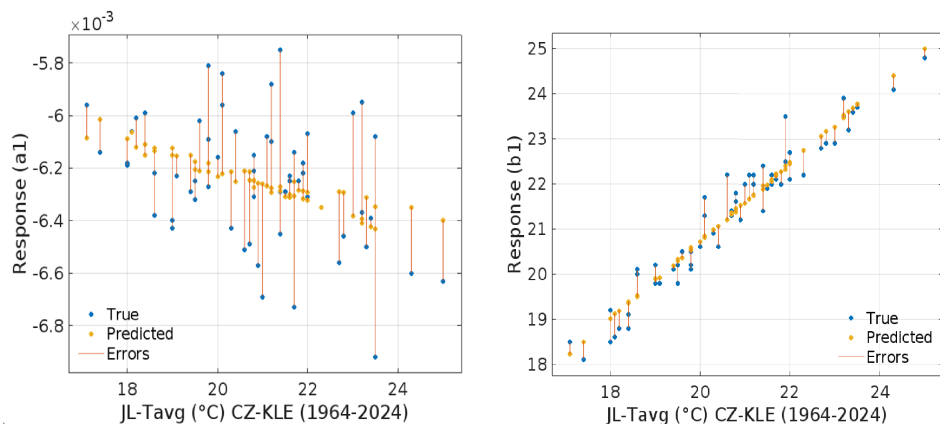


Fig. 3. Response plots for the prediction of ETL linear regression coefficients: slope (left) and intercept (right).

Finally, Table 4 (step 6) presents the results of a probability-based analysis tracking the altitude of the cold limit for tree growth, defined as the elevation at which the probability of the 10 °C July isotherm occurrence is zero. This thermal boundary varied from approximately 2000 m a.s.l. during the relatively cooler period (1875–1974) to about 2300 m a.s.l. in the warmer phase (1775–1874). From 1975, the cold limit driven by accelerated warming has shifted upward to altitude of 2400 m a.s.l.

Step 1: ETL regression using complete JL-Tavg dataset (1964–2024, 12 sites) (Fig. 2).

Step 2: The relationship between ETL regression coefficients (a1 and b1, step 1) and JL-Tavg at the CZ-KLE site, used to extend the model from the observed period (1964–2024) to the reconstruction period (1775–2024) (Figs. 3–4).

Step 3: Model validation (Fig. 5, Table 2).

Step 4: JL-Tavg reconstruction (1775–2024) across the 1500–2600 m a.s.l. elevation profile (Fig. 6, Table 3).

Step 5: Simulation of alpine treeline altitude changes (Fig. 7).

Step 6: Probability of meeting the 10 °C thermal criterion according to JL-Tavg values (Table 4).

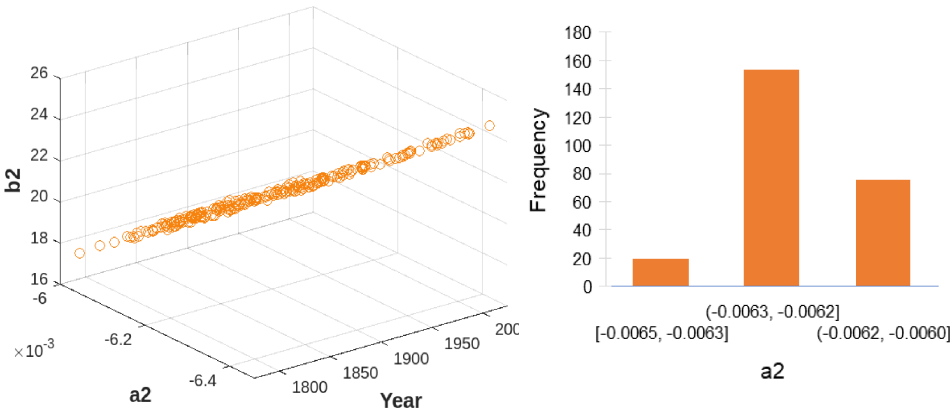


Fig. 4. Annual linear regression coefficients (a2: slope, b2: intercept) describing the relationship between JL-Tavg and altitude across the 12 sites listed in Table 1 (left), along with the frequency distribution of a2 values (right), based on data JL-Tavg from the CZ-KLE for the period 1775–2024.

Table 2. Comparison of average July air temperature (AVG) and standard deviation (STD) based on observed (o) and modelled (m) data for both the observed (Table 1) and the modelled (1775–2024) periods, along with goodness-of-fit metrics for ETL model: SSE – Sum of Squares due to Error, R^2 – Coefficient of Determination, DFE – Degrees of Freedom for Error, Adj R^2 – Adjusted R-square, RMSE – Root Mean Square Error.

	Location	AVG-o	STD-o	AVGg-m	STD-m	SSE	R^2	DFE	Ad R^2	RMSE
1	CZ-KLE	19.9	1.6	19.5	1.4	0.2	1.00	248	1.00	0.03
2	SK-TAL	15.4	1.3	15.4	1.3	77.5	0.64	115	0.64	0.82
3	DE-HOP	15.0	1.8	14.5	1.3	111.7	0.74	242	0.74	0.68
4	SK-STP	12.9	1.5	12.4	1.3	52.2	0.67	92	0.67	0.75
5	SK-SKP	10.3	1.6	9.6	1.3	32.2	0.78	81	0.78	0.63
6	RO-CEA	10.1	1.7	8.9	1.2	76.3	0.33	59	0.32	1.14
7	PL-KAW	7.8	1.7	8.4	1.2	31.4	0.77	72	0.77	0.66
8	SK-CHO	7.8	1.7	8.2	1.2	24.9	0.80	68	0.80	0.60
9	RO-VAR	6.1	1.5	5.1	1.2	84.0	0.27	62	0.26	1.16
10	SK-LOS	4.5	1.7	4.3	1.2	39.4	0.68	72	0.68	0.74
11	DE-ZUG	2.5	1.6	2.3	1.2	26.2	0.85	120	0.85	0.47
12	AT-SON	1.9	1.7	1.4	1.1	35.5	0.81	136	0.81	0.51

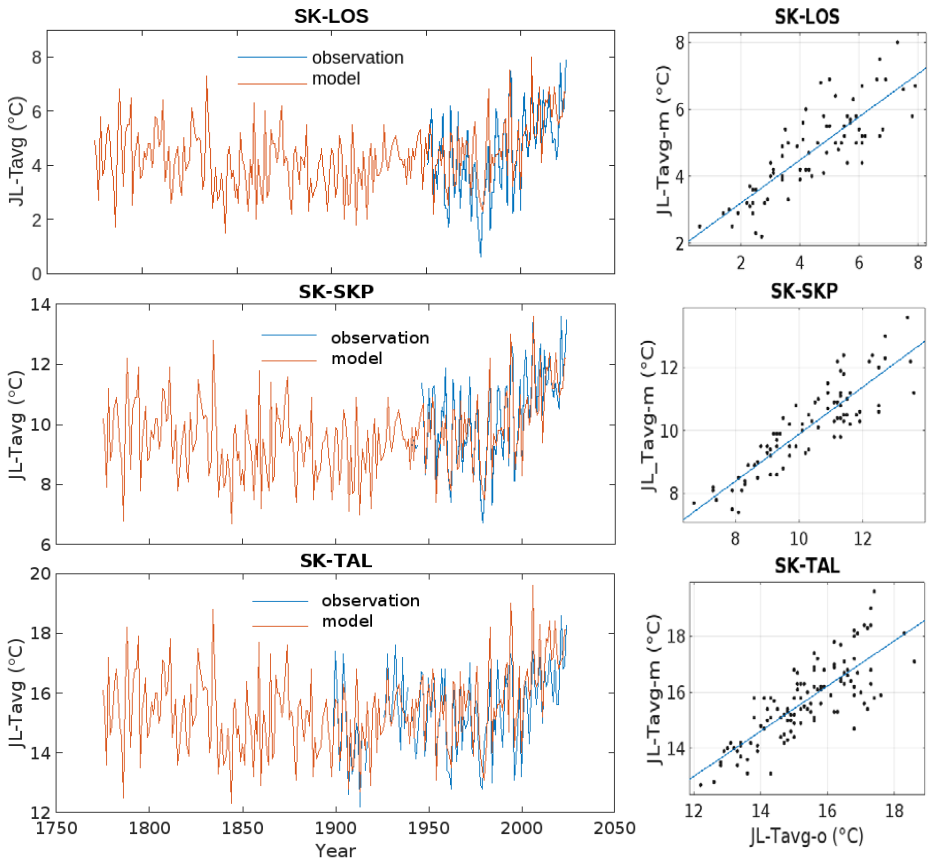


Fig. 5. Comparison of modelled (m) and observed (o) JL-Tavg values for stations located along the Skalná dolina elevation profile over the period 1775–2024.

4. Discussion

Reconstructing past air temperatures is a critical tool in climate science and meteorology for analysing long-term climate trends, particularly in the context of projections indicating a global temperature rise of 1.4 to 4.4°C by 2100 (IPCC, 2023). Continued warming has significant impacts on vulnerable mountain regions, which face transboundary, multi-hazard risks (Pittore et al., 2023). The occurrence of extreme events is closely associated with permafrost degradation (Krautblatter et al., 2018), slope desta-

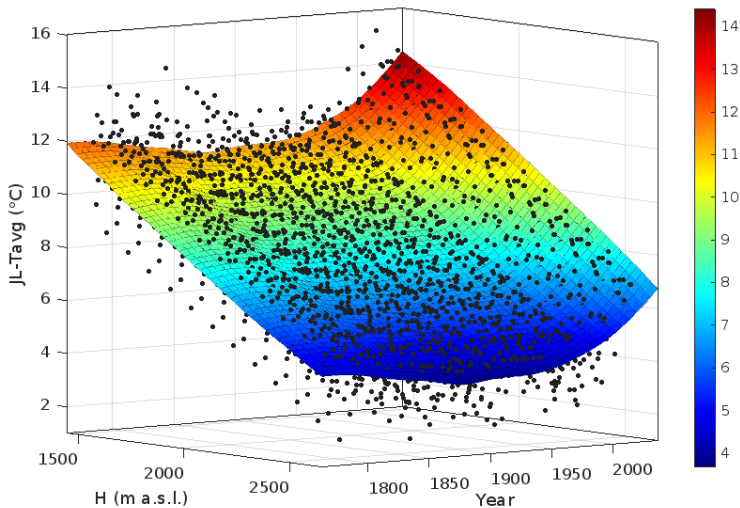


Fig. 6. Model visualization of reconstructed JL-Tavg across ATE-zone elevations in the Skalná dolina study area.

Table 3. Goodness-of-fit metrics for ETL model.

N.	Model Type	RMSE	MSE	RSquared	MAE
1	Linear Regression	199	39621	0.03	159
2	Cubic SVM	182	33161	0.19	145
3	Exponential GPR	183	33343	0.19	144
4	Least Squares Regression Kernel	182	32948	0.20	143
5	Medium Neural Network	184	33839	0.17	145
6	Medium Tree	187	34864	0.15	149

bilization and rockfalls (*Jacobs et al., 2020*) intensified erosion from mud and debris flows (*Stammberger et al., 2025*), landslides (*Kincey et al., 2024*), and negative glacier mass balances leading to increased runoff (*Hofmeister, 2025*). Changes in the cryosphere further affect landscapes, hydrological regimes, water resources, and infrastructure (*Beniston et al., 2018*). Effectively addressing these challenges requires an integrated understanding of historical and ongoing climate trends, their links to natural hazards, the underlying physical processes, and their likely future developments (*Crespi, 2025*).

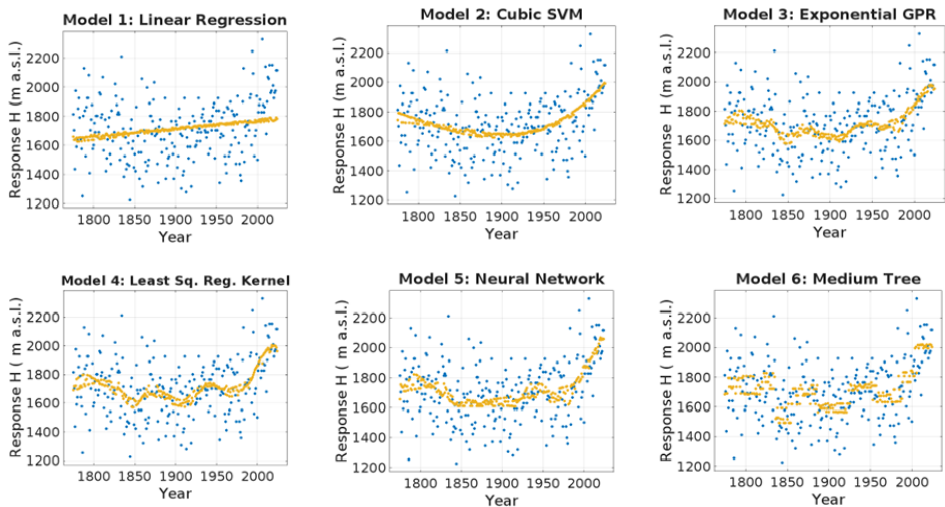


Fig. 7. Changes in alpine treeline altitude based on various regression modelling approaches.

Table 4. Probability (%) of cold-limit tree growth across ATE elevations (H m a.s.l.) in the High Tatra Mts over the last five half-centuries (1775–2024).

N.	Period	H (m a.s.l.)											
		1500	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500	2600
1	1775–1824	90%	76%	56%	38%	18%	6%	2%	0%	0%	0%	0%	0%
2	1825–1874	77%	62%	42%	27%	13%	7%	2%	2%	0%	0%	0%	0%
3	1875–1924	75%	50%	35%	10%	5%	0%	0%	0%	0%	0%	0%	0%
4	1925–1974	92%	80%	54%	32%	6%	0%	0%	0%	0%	0%	0%	0%
5	1975–2024	92%	86%	76%	62%	48%	24%	16%	4%	2%	0%	0%	0%

In addition to natural hazard risk, climate-driven ecological changes can profoundly impact biodiverse montane ecosystems, with effects varying by elevation due to species traits that shift along mountain gradients (Mamantov *et al.*, 2021). This shift is particularly evident in treelines, while the influence of climate change on treeline dynamics is regarded as a key indicator of global change affecting terrestrial ecosystems (Wang and Liang, 2019). The alpine treeline is typically defined by a mean July temperature of around 10 °C, though this threshold is not universal (Körner and Paulsen, 2004). Globally, the alpine treeline occurs where the seasonal mean temperature is around 6 °C, with a growing season of at least three months (Körner,

2020; 2021). The elevational range of naturally occurring mountain tree vegetation varies markedly among regions: 1134–1806 m in the Central European mountain ranges (*Kašpar and Tremł, 2016*), 1400–2010 m in the Ukrainian Eastern Carpathians (*Tsaryk et al., 2006*), 1221–2640 m in the Central Apennines (*Dai et al., 2017*), 1282–373 m across the western United States (*Weiss et al., 2015*), up to approximately 4000 m in the Hengduan Mountains, China (*Tian et al., 2022*), and reaching nearly 4900 m in the Himalayas, the highest known upper treelines in the Northern Hemisphere (*Singh et al., 2019*).

The reconstruction of alpine treeline altitude in the High Tatra Mts indicates an upward shift of the cold limit for tree growth to approximately 2400 m a.s.l. over the past half-century (1975–2024). This altitude corresponds to a zero probability of meeting the thermal criterion of a 10 °C mean July temperature (Table 4). Above 2000 m a.s.l., the probability remains low but increases steadily with decreasing altitude, reaching nearly 100% close to 1500 m a.s.l. The mentioned cold limit estimate is considerably higher than those reported elsewhere, *Kašpar and Tremł (2016)*. However, their definition of the treeline corresponds to the uppermost boundary of dwarf pine group occurrence, whereas smaller individuals and isolated clusters may occur at higher elevations. Small individuals of dwarf pine intrude into fragmented grass-herb stands on scree cones, which is related to edaphic conditions – accumulated organic matter, humus and other small-debris-like weathering materials with an elevated availability of nutrients. Further, they spread along the paths (grooves) of former but also current debris flows, avalanche paths and other disturbed surfaces of the soil-wind mantle, or on the backs and mounds of moraines, but also stone glaciers and forms of the so-called snowbanks (*Bolțižiar, 2007; Hreško et al., 2012*). Consequently, future research should prioritize monitoring dwarf pine individuals in areas with a low probability of occurrence, particularly at altitudes above 2000 m a.s.l.

An afforestation experiment in the Alpine Treeline Ecotone (ATE) at the Stillberg treeline research site demonstrated that dwarf pine can survive at and above the current 2100 m treeline in the transitional region between the relatively humid Northern Alps and the more continental Central Alps. However, a marked increase in mortality at higher elevations was linked to snow fungal pathogens, driven by microclimatic factors such as snow cover

duration, solar radiation, and wind exposure (Lechler et al., 2024). In this region, the treeline has advanced by an average of 40 m over the past 40 years, with pine trees favouring ridges and north-facing slopes (Frei et al., 2023). A comparable upward shift of the treeline has been documented in the Central Apennines (Dai et al., 2017), the Carpathian Mountains (Weisberg et al., 2013), and in the Central and the Hengduan Mountains in China, where it is primarily determined by growing season temperature and precipitation (Tian et al., 2022). In the Polish Carpathians, vertical climate zones shifted upward approximately by 350 metres over 1851–2010 (Wypych et al., 2018). The effect of increasing air temperatures during the growing season and earlier snow melt-out dates is considered to be the reason for enhanced growth of alpine shrubs in French Pyrenees over at least the last century (Francon et al., 2023). A slight upward shift in the boundaries of coniferous forests, shrublands, and alpine meadows was observed in the High Tatra Mts over more than 50 years (1956–2010), (Solár and Solár, 2020). The most pronounced shift was documented for dwarf pine, which expanded to higher altitudes, primarily on sunny and gently sloping sites (Piscová et al., 2023).

These observed changes are consistent with the modelled trend in historical treeline altitude (Fig. 7), based on reconstructed JL-Tavg (Figs. 5–6), which indicates an upward shift over the past five decades (1975–2024). This trend is further supported by data from the Skalnaté Pleso Observatory, where mean annual temperature increased by 1.1 °C and JL-Tavg by 1.7 °C between the periods 1961–1990 and 1991–2020 (Lukasová et al., 2023). The applied ETL model showed satisfactory performance, with RMSE values lower than the standard deviation of observed means, suggesting that model predictions fall within the natural variability of the data (Table 2).

Given its performance, the ETL model offers potential for reconstructing the historical position of the alpine treeline based on the global thermal criterion of a mean seasonal air temperature ≈ 6 °C sustained over a minimum three-month growing season (Körner, 2020). For the High Tatra Mts, mean air temperatures from the warmest months (June–August) should be used. To complement the modelling, field-based monitoring should be conducted, including systematic mapping of dwarf pine at elevations above 2000 meters, in order to assess its current distribution limits in relation to thermal constraints.

5. Conclusion

This study provides a 250-year reconstruction (1775–2024) of July average air temperatures (JL-Tavg) in the Alpine Treeline Ecotone (ATE) of the High Tatra Mts, using a regression model based on the environmental temperature lapse rate (ETL) derived from 12 European meteorological observatories across a wide elevation range (191–3109 m). The model accurately estimated JL-Tavg and enabled the delineation of the 10 °C isotherm, critical for alpine vegetation growth, along the ATE profile in the Skalná dolina study area.

Findings indicate that the modelled alpine treeline, defined as the altitude with zero probability of tree growth, varied across different time intervals of the historical period. During the relatively warm phase of 1775–1874, it reached elevations of approximately 2200–2300 m, while in the cooler period of 1875–1974, it declined to level around 2000 m. Over the past 50 years, the alpine treeline has shifted upward to about 2400 m, representing the current upper cold limit for alpine tree growth in the southern part of the High Tatra Mountains.

These results emphasize the sensitivity of high-mountain ecosystems to ongoing climate warming and underscore the importance of targeted field monitoring. Future research should focus on field monitoring of dwarf pine and alpine vegetation dynamics within the ATE zone between 2000 and 2400 m, where climate-induced shifts in the bioclimatic boundary for vegetation growth are anticipated. Research on these topics is essential for developing adaptive management strategies, informing conservation efforts, and predicting future ecological shifts in the biodiversity-sensitive ATE zones of high-mountain regions in Central and Eastern Europe.

Acknowledgements. This work was supported by the Scientific Grant Agency of the Slovak Republic, VEGA project 2/0048/25.

References

- Bader M. Y., Llambí L. D., Case B. S., Buckley H. L., Toivonen J. M., Camarero J. J., Cairns D. M., Brown C. D., Wiegand T., Resler L. M., 2021: A global framework for linking alpine-treeline ecotone patterns to underlying processes. *Ecography*, **44**, 2, 265–292, doi: 10.1111/ecog.05285.
- Barry R. G., 2008: *Mountain Weather and Climate* (3rd ed.). Cambridge, UK, Cambridge University Press.

- Barry R. G., Chorley R. J., 2009: Atmosphere, Weather and Climate. Routledge, London, 536 p., doi: 10.4324/9780203871027.
- Beniston M., Farinotti D., Stoffel M., Andreassen L. M., Coppola E., Eckert N., Fantini A., Giacona F., Hauck C., Huss M., Huwald H., Lehning M., López-Moreno J.-I., Magnusson J., Marty C., Morán-Tejeda E., Morin S., Naaïm M., Provenzale A., Rabatel A., Six D., Stötter J., Strasser U., Terzago S., Vincent C., 2018: The European mountain cryosphere: a review of its current state, trends, and future challenges. *Cryosphere*, **12**, 2, 759–794, doi: 10.5194/tc-12-759-2018.
- Bezák V., Majcin D., 2013: Brief description of geological and geomorphological features in the vicinity of the Skalanatá dolina valley. In: Bičárová S. (Ed.): Observatory of SAS at Skalná Pleso – 70 Years of Meteorological Measurements. Geophysical Institute SAS: Stará Lesná, Slovakia, 63 p., http://gpi.savba.sk/GPIweb/ofa/images/slovak/Publikacie/Manuscript_70SkP.pdf (in Slovak with English summary).
- Boltíziar M., 2007: Structure of high mountain landscape of Tatra Mountains – Largescale mapping, analysis and evaluation of changes by application of data from Earth remote survey (Štruktúra vysokohorskej krajiny Tatier – Veľkomierkové mapovanie, analýza a hodnotenie zmien aplikáciou údajov diaľkového prieskumu Zeme). Nitra, Slovakia. CPU, ILE, SAS, 248 p., ISBN 978-80-8094-197-0 (in Slovak).
- Büntgen U., Trnka M., Krusic P. J., Kyncl T., Kyncl J., Luterbacher J., Zorita E., Ljungqvist F. C., Auer I., Konter O., Schneider L., Tegel W., Štěpánek P., Brönnimann S., Hellmann L., Nievergelt D., Esper J., 2015: Tree-ring amplification of the early nineteenth-century summer cooling in central Europe. *J. Clim.*, **28**, 13, 5272–5288, doi: 10.1175/JCLI-D-14-00673.1.
- CHMI (Czech Hydrometeorological Institute), 2025: Prague Clementinum. <https://www.chmi.cz/historicka-data/pocasi/praha-klementinum?l=en>.
- Compo G. P., Whitaker J. S., Sardeshmukh P. D., Matsui N., Allan R. J., Yin X., Gleason B. E., Vose R. S., Rutledge G., Bessemoulin P., Brönnimann S., Brunet M., Crouthamel R. I., Grant A. N., Groisman P. Y., Jones P. D., Kruk M. C., Kruger A. C., Marshall G. J., Maugeri M., Mok H. Y., Nordli Ø., Ross T. F., Trigo R. M., Wang X. L., Woodruff S. D., Worley S. J., 2011: The twentieth century reanalysis project. *Q. J. R. Meteorol. Soc.*, **137**, 654, 1–28, doi: 10.1002/qj.776.
- Crespi A., 2025: combining climate, hazard and impact analyses to explore future local risk scenarios in the Alpine region: Insights from the X-RISK-CC project. VAO Symposium 2025, Kaprun, 02.-04. April 2025, https://www.vao.bayern.de/events/symposium_2025.html.
- Dai L., Palombo C., van Gils H., Rossiter D. G., Tognetti R., Luo G., 2017: *Pinus mugo* krummholz dynamics during concomitant change in pastoralism and climate in the central Apennines. *Mt. Res. Dev.*, **37**, 1, 75–86, doi: 10.1659/MRD-JOURNAL-D-14-00104.1.
- Dobrovolný P., Moberg A., Brázdil R., Pfister C., Glaser R., Wilson R., van Engelen A., Limanówka D., Kiss A., Halíčková M., Macková J., Riemann D., Luterbacher J., Böhm R., 2010: Monthly, seasonal and annual temperature reconstructions for Central Europe derived from documentary evidence and instrumental records since AD 1500. *Clim. Change*, **101**, 1–2, 69–107, doi: 10.1007/s10584-009-9724-x.

- Esper J., St. George S., Anchukaitis K., D'Arrigo R., Ljungqvist F. C., Luterbacher J., Schneider L., Stoffel M., Wilson R., Büntgen U., 2018: Large-scale, millennial-length temperature reconstructions from tree-rings. *Dendrochronologia*, **50**, 81–90, doi: 10.1016/j.dendro.2018.06.001.
- Feng X., Lin P., Zhao W., 2022: The physiological constraints of alpine treeline in Qilian Mountains. *For. Ecol. Manag.*, **503**, 119761, doi: 10.1016/j.foreco.2021.119761.
- Francon L., Roussel E., Lopez-Saez J., Saulnier M., Stoffel M., Corona C., 2023: Alpine shrubs have benefited more than trees from 20th century warming at a treeline ecotone site in the French Pyrenees. *Agric. For. Meteorol.*, **329**, 109284, doi: 10.1016/j.agrformet.2022.109284.
- Frei E. R., Barbeito I., Erdle L. M., Leibold E., Bebi P., 2023: Evidence for 40 years of treeline shift in a Central Alpine valley. *Forests*, **14**, 2, 412, doi: 10.3390/f14020412.
- HISTALP, 2025: Historical instrumental climatological surface time series of the Greater Alpine region (a multi element climate database). <http://www.zamg.ac.at/histalp>.
- Hofmeister F., 2025: 50 years of hydrometeorological observations at the Glacier Observatory Vernagtferner. VAO Symposium 2025, Kaprun, 2–4 April 2025, https://www.vao.bayern.de/events/symposium_2025.html.
- Hreško J., Bugár G., Petrovič F., Mačutek J., Kanášová D., 2012: Morphodynamic effects on lacustrine deposits in the High Tatra Mts. *Ekológia*, **31**, 4, 390–404, doi: 10.4149/ekol.2012.04.390.
- IPCC (Intergovernmental Panel on Climate Change), 2023: Summary for Policymakers. In: Core Writing Team, Lee H., Romero J. (Eds.): *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, pp. 1–34, https://www.ipcc.ch/report/ar6/syr/downloads/report/IPCC_AR6_SYR_SPM.pdf, doi: 10.59327/IPCC/AR6-9789291691647.001.
- Jacobs B., Grabmaier A., Krautblatter M., 2020: Benchmark rock fall hazard assessment and safety concept for touristically developed alpine gorges (Höllentalklamm, Bavarian Alps). *EGU General Assembly 2020*, online, 4–8 May 2020, EGU2020-18427, doi: 10.5194/egusphere-egu2020-18427.
- Jones P., 2016: The reliability of global and hemispheric surface temperature records. *Adv. Atmos. Sci.*, **33**, 3, 269–282, doi: 10.1007/s00376-015-5194-4.
- Kaczka R. J., Lempa M., Czajka B., Janecka K., Rączkowska Z., Hreško J., Bugar G., 2015: The recent timberline changes in the Tatra Mountains: A case study of the Mengusovská Valley (Slovakia) and the Rybi Potok Valley (Poland). *Geogr. Pol.*, **88**, 2, 71–83, doi: 10.7163/GPol.0016.
- Kašpar J., Tremml V., 2016: Thermal characteristics of alpine treelines in Central Europe north of the Alps. *Clim. Res.*, **68**, 1–12, doi: 10.3354/cr01370.
- Kincey M. E., Rosser N. J., Swirad Z. M., Robinson T. R., Shrestha R., Pujara D. S., Basyal G. K., Densmore A. L., Arrell K., Oven K. J., Dunant A., 2024: National-scale rainfall-triggered landslide susceptibility and exposure in Nepal. *Earth's Future*, **12**, 2, e2023EF004102, doi: 10.1029/2023EF004102.

- Klein Tank A. M. G., Wijngaard J. B., Können G. P., Böhm R., Demarée G., Gocheva A., Mileta M., Pashiardis S., Hejkrlik L., Kern-Hansen C., Heino R., Bessemoulin P., Müller-Westermeier G., Tzanakou M., Szalai S., Pálsdóttir T., Fitzgerald D., Rubin S., Capaldo M., Maugeri M., Leitass A., Bukantis A., Aberfeld R., van Engelen A. F. V., Forland E., Mielus M., Coelho F., Mares C., Razuvaev V., Nieplova E., Cegnar T., Antonio López J., Dahlström B., Moberg A., Kirchhofer W., Ceylan A., Pachaliuk O., Alexander L. V., Petrovic P., 2002: Daily dataset of 20th-century surface air temperature and precipitation series for the European Climate Assessment. *Int. J. Climatol.*, **22**, 12, 1441–1453, doi: 10.1002/joc.773.
- Körner C., 2003: *Alpine Plant Life (Functional Plant Ecology of High Mountain Ecosystems)*. Springer Berlin, Heidelberg, 349 p., doi: 10.1007/978-3-642-18970-8.
- Körner C., 2012: *Alpine Treelines (Functional Ecology of the Global High Elevation Tree Limits)*. Springer Basel. Springer Basel, 220 p., doi: 10.1007/978-3-0348-0396-0.
- Körner C., 2020: Climatic Controls of the Global High Elevation Treelines. In: Goldstein M. I., DellaSala D. A. (Eds.): *Encyclopedia of the World's Biomes*. Elsevier, pp. 275–281, doi: 10.1016/B978-0-12-409548-9.11998-0.
- Körner C., 2021: The cold range limit of trees. *Trends Ecol. Evol.*, **36**, 11, 979–989, doi: 10.1016/j.tree.2021.06.011.
- Körner C., Paulsen J., 2004: A world-wide study of high altitude treeline temperatures. *J. Biogeogr.*, **31**, 5, 713–732, doi: 10.1111/j.1365-2699.2003.01043.x.
- Krautblatter M., Kellerer-Pirklbauer A., Gärtner-Roer I., 2018: Permafrost in the Alps: Features, geographic spread, and future development (Permafrost in den Alpen: Erscheinungsformen, Verbreitung und zukünftige Entwicklung). *Geogr. Rundsch.*, **70**, 11, 22–29, <https://www.zora.uzh.ch/server/api/core/bitstreams/7ce7a0ea-f9d0-41e9-afdc-e3c58104b93c/content> (in German).
- Krippel E., 1986: Postglacial development of vegetation in Slovakia (Postglaciálny vývoj vegetácie Slovenska). VEDA, Bratislava, 307 p. (in Slovak).
- Kulakowski D., Barbeito I., Casteller A., Kaczka R. J., Bebi P., 2016: Not only climate: Interacting drivers of treeline change in Europe. *Geogr. Pol.*, **89**, 1, 7–15, doi: 10.7163/GPol.0042.
- Lechler L., Rixen C., Bebi P., Bavay M., Marty M., Barbeito I., Dawes M. A., Hagedorn F., Krumm F., Möhl P., Schaub M., Frei E. R., 2024: Five decades of ecological and meteorological data enhance the mechanistic understanding of global change impacts on the treeline ecotone in the European Alps. *Agric. For. Meteorol.*, **355**, 110126, doi: 10.1016/j.agrformet.2024.110126.
- Lehner G., Lütz C., 2003: Photosynthetic functions of cembran pines and dwarf pines during winter at timberline as regulated by different temperatures, snowcover and light. *J. Plant Physiol.*, **160**, 2, 153–166. doi: 10.1078/0176-1617-00798.
- Lukasová V., Bičárová S., Buchholcerová A., Adamčíková K., 2022: Low sensitivity of *Pinus mugo* to surface ozone pollution in the subalpine zone of continental Europe. *Int. J. Biometeorol.*, **66**, 11, 2311–2324, doi: 10.1007/s00484-022-02359-2.
- Lukasová V., Bucha T., Mareková E., Buchholcerová A., Bičárová S., 2021: Changes in the greenness of Mountain pine (*Pinus mugo* Turra) in the subalpine zone related to the winter climate. *Remote Sens.*, **13**, 9, 1788, doi: 10.3390/rs13091788.

- Lukasová V., Buchholcerová A., Onderka M., Bičárová S., Bilčík D., Nejedlík P., 2023: How can the transition from conventional to automatic measurements affect the climatological normals? – A case study from an alpine meteorological observatory at Skalnaté Pleso, Slovakia. *Meteorol. Z.*, **32**, 5, 431–444, doi: 10.1127/metz/2023/1200.
- Mamantov M. A., Gibson-Reinemer D. K., Linck E. B., Sheldon K. S., 2021: Climate-driven range shifts of montane species vary with elevation. *Glob. Ecol. Biogeogr.*, **30**, 4, 784–794, doi: 10.1111/geb.13246.
- Neukom R., Barboza L. A., Erb M. P., Shi F., Emile-Geay J., Evans M. N., Franke J., Kaufman D. S., Lücke L., Rehfeld K., Schurer A., Zhu F., Brönnimann S., Hakim G. J., Henley B. J., Ljungqvist F. C., McKay N., Valler V., von Gunten L., 2019: Consistent multidecadal variability in global temperature reconstructions and simulations over the Common Era. *Nat. Geosci.*, **12**, 8, 643–649, doi: 10.1038/s41561-019-0400-0.
- Piscová V., Hreško J., Ševčík M., Slobodová T., 2023: Impacts of human activities on the high mountain landscape of the Tatras (Example of the border area of the High and Belianske Tatras, Slovakia). In: Hufnagel L. El-Esawi M A., Summers J. K. (Eds.): *Vegetation Dynamics, Changing Ecosystems and Human Responsibility*. IntechOpen, doi: 10.5772/intechopen.105601.
- Pittore M., Campalani P., Renner K., Plörer M., Tagliavini F., 2023: Border-independent multi-functional, multi-hazard exposure modelling in Alpine regions. *Nat. Hazards*, **119**, 2, 837–858, doi: 10.1007/s11069-023-06134-3.
- Popa I., Bouriaud O., 2014: Reconstruction of summer temperatures in Eastern Carpathian Mountains (Rodna Mts, Romania) back to AD 1460 from tree-rings. *Int. J. Climatol.*, **34**, 3, 871–880, doi: 10.1002/joc.3730.
- Singh S. P., Sharma S., Dhyani P. P., 2019: Himalayan arc and treeline: distribution, climate change responses and ecosystem properties. *Biodivers. Conserv.*, **28**, 8–9, 1997–2016, doi: 10.1007/s10531-019-01777-w.
- Solár J., Janiga M., 2013: Long-term changes in Dwarf Pine (*Pinus mugo*) cover in the High Tatra Mountains, Slovakia. *Mt. Res. Dev.*, **33**, 1, 51–62, doi: 10.1659/MRD-JOURNAL-D-12-00079.1.
- Solár J., Solár V., 2020: Land-cover change in the Tatra Mountains, with a particular focus on vegetation. *eco.mont (Journal on Protected Mountain Areas Research)*, **12**, 1, 15–26, doi: 10.1553/eco.mont-12-1s15.
- Stammlberger V., Boie K., Krautblatter M., 2025: Erosive power of debris flows: predictive modelling by a simple empirical approach. *EGU General Assembly 2025*, Vienna, Austria, 27 Apr–2 May 2025, EGU25-16175, doi: 10.5194/egusphere-egu25-16175.
- Švajda J., Solár J., Janiga M., Buliak M., 2011: Dwarf Pine (*Pinus mugo*) and selected abiotic habitat conditions in the Western Tatra Mountains. *Mt. Res. Dev.*, **31**, 3, 220–228, doi: 10.1659/MRD-JOURNAL-D-09-00032.1.
- Tian L., Fu W., Tao Y., Li M., Wang L., 2022: Dynamics of the alpine timberline and its response to climate change in the Hengduan mountains over the period 1985–2015. *Ecol. Indic.*, **135**, 108589, doi: 10.1016/j.ecolind.2022.108589.

- Tsaryk I., Didukh Y. P., Tassenkevich L., Waldon B., Boratyński A., 2006: *Pinus mugo* Turra (Pinaceae) in the Ukrainian Carpathians. *Dendrobiology*, **55**, 39–49.
- Ustrnul Z., Walawender E., Czekierda D., Šťastný P., Lapin M., Mikulová K., 2015: Precipitation and snow cover. In: Dąbrowska K., Guzik M. (Eds.): *Atlas of the Tatra Mountains. Abiotic Nature*, Zakopane, Tatra National Park.
- Wang Y., Liang E., 2019: Research advances in disturbance and ecological processes of the treeline ecotone. *Chin. Sci. Bull.*, **64**, 16, 1711–1721, doi: 10.1360/N972018-01273.
- Weisberg P. J., Shandra O., Becker M. E., 2013: Landscape influences on recent timberline shifts in the Carpathian Mountains: Abiotic influences modulate effects of land-use change. *Arct. Antarct. Alp. Res.*, **45**, 3, 404–414, doi: 10.1657/1938-4246-45.3.404.
- Weiss D. J., Malanson G. P., Walsh S. J., 2015: Multiscale relationships between alpine treeline elevation and hypothesized environmental controls in the Western United States. *Ann. Am. Assoc. Geogr.*, **105**, 3, 437–453, doi: 10.1080/00045608.2015.1015096.
- Winkler P., 2006: Hohenpeißenberg 1781–2006 – the world’s oldest mountain observatory (Hohenpeißenberg 1781–2006 – das älteste Bergobservatorium der Welt). *Geschichte der Meteorologie in Deutschland*, **7**, Deutscher Wetterdienst, Offenbach am Main, 174 p. with illustrations (in German).
- Wypych A., Ustrnul Z., Schmatz D. R., 2018: Long-term variability of air temperature and precipitation conditions in the Polish Carpathians. *J. Mt. Sci.*, **15**, 2, 237–253, doi: 10.1007/s11629-017-4374-3.
- Žatková L., Milovský R., Bechtel A., Starek D., Pipík R., Šurka J., 2023: *n*-Alkane and terpenoid fingerprints of modern biomass producers unveil floral changes recorded in postglacial alpine lake sediments, Tatra Mountains, Slovakia. *Org. Geochem.*, **184**, 104672, doi: 10.1016/j.orggeochem.2023.104672.
- Žmudzka E., Nejedlík P., Mikulová K., 2015: Temperature, thermal indices. In: Dąbrowska K., Guzik M. (Eds.): *Atlas of the Tatra Mountains. Abiotic Nature*. Zakopane, Tatra National Park.