Boulders as functional microrefugia: Quantifying a continental-like microclimate supporting *Pinus cembra* at its oceanic range margin

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Abstract: Climatic microrefugia allow some forest tree species to persist outside their main distribution range by locally decoupling site conditions from the regional climate. At its western, oceanic range margin in the Swiss Prealps, the Swiss stone pine (*Pinus cembra* L.) occurs on large boulders embedded within subalpine forests dominated by Norway spruce [*Picea abies* (L.) H. Karst.]. We hypothesised that these landforms generate a continental-like microclimate enabling *P. cembra* persistence under otherwise sub-oceanic conditions, and we aimed to quantify this phenomenon. Using high-resolution data loggers, we measured air and soil temperature, thermal amplitudes, and soil moisture on the summits and at the bases of ten limestone boulders over a two-year period. Linear mixed-effects models revealed a pronounced microclimatic decoupling between positions. Boulder summits were consistently warmer and drier during the growing season. In contrast, during winter, summits were significantly colder, while boulder bases remained thermally stable due to persistent snow insulation. The strongest microclimatic divergence occurred in spring, when temperatures at the bases remained stable near 0 °C, whereas summit temperatures were markedly warmer and more variable. This continental-like microclimate likely promotes *P. cembra* persistence. Our results highlight the importance of topographic heterogeneity for maintaining marginal tree populations.

Keywords: climatic microrefugia; microclimate measurements; relict species; subalpine forests; Swiss stone pine; thermal decoupling; topographic heterogeneity

Understanding the mechanisms that allow species to persist outside their primary distribution range has become a central focus of conservation biology (Kemppinen et al. 2024). Areas that are decoupled from the regionally dominant macroclimate, known as climatic microrefugia, allow species to survive locally in environments that would otherwise be unsuitable (Lenoir et al. 2017, Millar et al. 2018, Fragnière et al. 2024). The existence of microrefugia is fundamentally driven by topography. Terrain heterogeneity, or topodiversity, allows climatic conditions to deviate significantly from regional averages, creating a mosaic of microclimates (Dobrowski 2011; Li, Yang 2004; Körner, Spehn 2019). This is particularly evident in mountainous landscapes, where micro-relief can induce drastic variations in temperature and moisture over very short distances (Ellenberg 1988).

A prime example of a tree species restricted to such microrefugia at its range margin is the

Swiss stone pine (*Pinus cembra* L.). As a glacial relict, *P. cembra* is the European tree species best adapted to the harsh subalpine climates of the Alps and Carpathians (Ulber et al. 2004). Its distribution spans the Alpine chain, from the Maritime Alps in France to the Julian Alps in Northern Slovenia. It also occurs in isolated populations across the Tatra Massif, the Carpathians, and the Transylvanian Alps (Caudullo, De Rigo 2016). In the Swiss Prealps, the species reaches its westernmost oceanic margin.

Pinus cembra is a high-altitude specialist, capable of reaching elevations near 2 500 m a.s.l. It is characterised by its exceptional cold hardiness, withstanding temperatures as low as −40 °C without damage (Leuschner, Ellenberg 2017). While it is an edaphic generalist, thriving on both calcareous and siliceous substrates (Zieba et al. 2019), it is typically found in the Central Alps where the climate is continental, benefiting particularly from the higher summer solar radiation (Leuschner, Ellenberg 2017; Gugerli et al. 2022).

It rarely exceeds 25 m in height and is characterised by a notably slow growth rate. Taxonomically, it belongs to the five-needle pines (section *Quinquefoliae*) and is closely related to the North and East Asiatic Siberian pine (*Pinus sibirica* Du Tour) and the Siberian dwarf pine [*Pinus pumila* (Pall.) Regel] (Hao et al. 2015; Gernandt et al. 2018). While these species once shared a continuous range, they became geographically disjunct during the Holocene (Gugerli et al. 2009, 2023). Although *P. cembra* was widespread across the Alps in the early and mid-Holocene (Lotter, Birks 2003), its distribution subsequently contracted due to post-glacial warming and increasing competition from Norway spruce [*Picea abies* (L.) H. Karst.] (Höhn et al. 2009). Today, its core Swiss distribution is confined to the continental central Alps (Engadine and Valais), where high thermal amplitudes and low precipitation provide a competitive advantage over *Picea abies* (Gugerli et al. 2022).

In the Northern Prealps, particularly within the Canton of Fribourg and in the region of the study site, the climate is predominantly sub-oceanic, with annual precipitation of approximately 1 500 mm and a mean annual temperature of around 3 °C (MeteoSwiss 2023). Under these conditions, *P. abies* typically dominates the subalpine zone, while *P. cembra* is generally absent (Doutaz et al. 2006; Gugerli et al. 2022). However, natural

sporadic populations of *P. cembra* persist in this region, restricted almost exclusively to specific habitats such as wind-swept ridges, cliffs, and boulders (Rikli 1909; Fragnière et al. 2022). Notably, while *P. cembra* has been planted elsewhere in the region, these efforts have generally failed; the species successfully maintains itself only within these specific natural stations (Fragnière et al. 2022). These marginal populations possess a unique genetic diversity within the Swiss context (Sonnenwyl et al. 2024), a phenomenon often observed at the edge of a species' range where long-term adaptation to adverse or atypical conditions fosters distinct genetic signatures (Ducci, Donnelly 2018).

It has been hypothesised that these specific landforms induce a micro-site continentalisation of the climate, creating a 'continental-like microclimate' that effectively overrides the regional oceanic influence (Doutaz et al. 2006). Observations suggest that large boulders mimic these conditions by promoting early snowmelt on their summits and edges due to wind exposure and gravity. This reduction in snow cover duration extends the growing season and increases daily thermal fluctuations by exposing the substrate to direct solar radiation (Körner 2012; Vittoz et al. 2008). While the link between *P. cembra* and boulder micro-relief has been described through vegetation analysis and height-class distributions, empirical measurements of the thermal regime on these boulders remain scarce. Most hypotheses regarding the 'continental' nature of these blocks rely on indirect indicators, such as the presence of continental lichen species (*Cladonia-Cetraria*) or observations of snow retraction (Doutaz et al. 2006).

We seek to quantify the degree of thermal and hygric decoupling provided by these boulders to evaluate their function as climatic microrefugia. By employing high-resolution data loggers, this study empirically characterises the microclimate of the Forest of Le Lapé, a primary forest established on an ancient, massive rockfall. Specifically, we aim to determine whether these large limestone boulders provide a distinct environmental regime that deviates significantly from the surrounding conditions.

To this end, we aim to answer the following questions: (*i*) To what extent does the microclimate on the summits of large limestone boulders deviate from the conditions measured at their base?; (*ii*) Do these boulders exhibit 'continental' char-

acteristics – specifically higher daily thermal amplitudes and earlier snowmelt – compared to the surrounding oceanic environment?; and (*iii*) Can the presence of *P. cembra* at this oceanic margin be explained by a measurable microclimatic decoupling provided by the rockfall topography?

MATERIAL AND METHODS

Study area. The study was conducted in the Forest of Le Lapé, an ancient forest located in the Swiss Prealps within the Canton of Fribourg, Switzerland (46°33'22"N, 7°13'45"E). The site is situated at an elevation of approximately 1 750 m a.s.l. The local climate can be categorised as mountainous, yet it retains a strong oceanic influence. This is characterised by high humidity levels and frequent cloud cover throughout the year. Additionally, the region experiences significant snowfall during the winter months, leading to a substantial and persistent snowpack. This forest developed on an ancient rockfall from the Dent de Savigny, characterised by a chaotic topography with large limestone boulders, some of which reach the size of buildings. Due to this rugged terrain, the forest has never been commercially exploited and is currently a protected area. *P. cembra* is also a protected species in the Canton of Fribourg and is not subject to harvesting.

Data collection. To investigate the microclimatic conditions favouring *P. cembra* growth, 10 large boulders were randomly selected in the field (Figure 1). The selection criteria were: (*i*) accessibility, given the difficulty of movement within
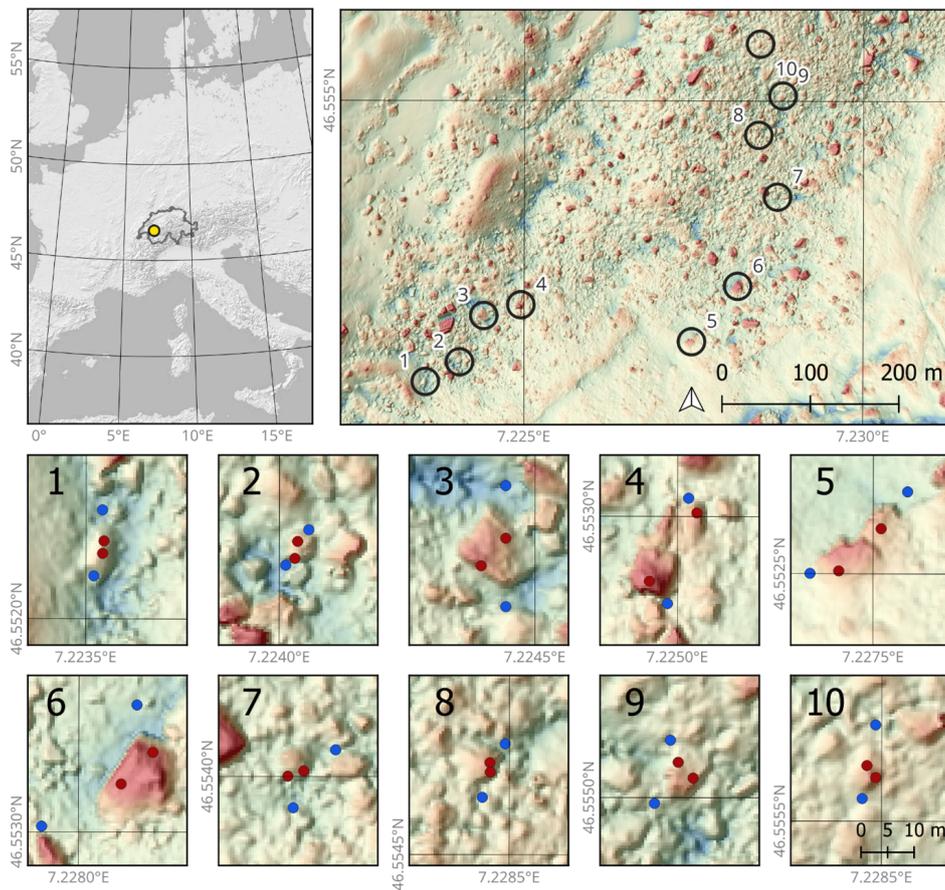

Figure 1. Map of the study area

The upper panel shows an overview of the 10 selected boulders located in the Lapé forest where data loggers were installed; the lower panels provide a detailed view of each boulder with the specific locations of the sensors: 'Top' data loggers are indicated in red and 'bottom' data loggers in blue; the background consists of a high-resolution LiDAR-derived Digital Elevation Model (DEM), highlighting the micro-topography (Federal Office of Topography swisstopo 2022); the colour gradient represents elevation levels, with red shades indicating higher topographic positions

the forest and the inaccessibility of certain blocks; (*ii*) a minimum height of about 5 m; and (*iii*) a minimum distance of about 50 m between boulders. The boulders were selected directly in the field, as it was difficult to anticipate which ones would be accessible beforehand. Once a boulder meeting the selection criteria was identified, a North-South axis was established to orient the placement of the sensors. However, the final positioning was primarily determined by the terrain, for example where

the substrate was deep enough to install a data logger. Four were installed on each boulder: two were positioned at the base (approximately North and South aspects) and two at the summit (approximately North and South aspects). The summits of the boulders provided sufficient substrate for the installation of the data loggers (Figure 2).

A total of 40 TMS-4 data loggers (TOMST, Czech Republic) were installed to record environmental data at 15-minute intervals (Wild et al. 2019).
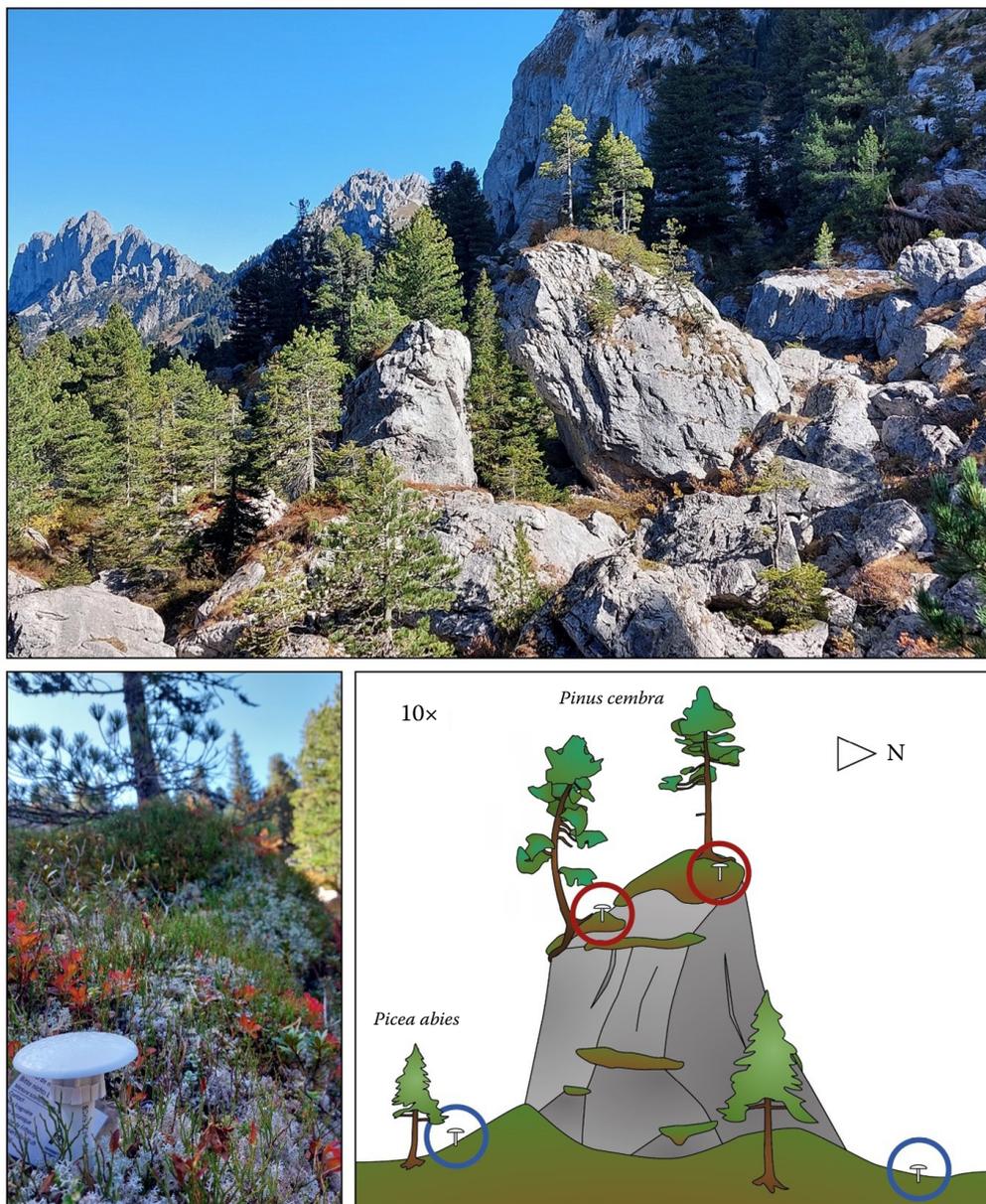

Figure 2. Representation of the study site and sensor deployment

The upper panel shows a general view of the Lapé forest, featuring the prominent boulders; the lower-left panel displays a data logger installed on the top of a boulder; the lower-right panel provides a schematic diagram of the experimental setup on a single boulder: 'Top' data loggers are indicated in red and 'bottom' data loggers in blue

Each logger measured temperature at three levels: 6 cm below the soil surface, at the surface interface (not used in the analyses), and 15 cm above the ground. Top radiation shields were used to shield the air temperature sensors from direct sunlight. Soil moisture was also recorded, with raw counts converted to volumetric water content using the manufacturer's standard calibration. The monitoring period lasted from August 22, 2023, to October 16, 2025. No physical protection against wildlife was necessary due to the low animal density and minimal human disturbance at the site.

By the end of the experiment, several data loggers were damaged, primarily at the base of the boulders due to snow movements. Four sensors were physically broken and were entirely excluded from all analyses. Additionally, seven sensors had missing or damaged radiation shields, and four had been partially pushed deeper into the soil. These eleven sensors were excluded from air temperature analyses but were retained for soil temperature and moisture measurements.

Data analysis. Data processing and statistical analyses were conducted in the R environment (R Core Team 2023). The 15-minute interval measurements were first aggregated to calculate daily means, extrema (minimum and maximum), and thermal amplitudes. To account for temporal autocorrelation, these daily metrics were further aggregated by season for each sensor prior to modelling (Zuur et al. 2009). Seasons were defined on a meteorological basis (e.g. spring: March–May).

The influence of boulder position and seasonality on microclimatic variables was analysed using Linear Mixed-Effects Models (LME) via the 'nlme' package (Pinheiro et al. 2025). This approach is particularly suited for nested experimental designs (Bates et al. 2015). In these models, boulder position (top vs. bottom) and season were treated as fixed effects, while Boulder ID and Sensor ID were included as nested random effects to account for the spatial dependency of measurements taken on the same boulder unit. Finally, post-hoc pairwise comparisons were performed using the 'emmeans' package (Lenth, Piaskowski 2025) to identify significant differences between the summit and the base of the boulders within each season.

All raw sensor data, as well as summaries and outputs from the linear mixed-effects models (R console), are publicly available at Zenodo (https://doi.org/10.5281/zenodo.18281740).

RESULTS AND DISCUSSION

The analysis of the microclimatic data collected in the Forest of Le Lapé reveals a profound thermal and hygric divergence between the boulder summits and their bases.

Air temperature. Regarding air temperature close to the soil surface (15 cm), the boulder summits are characterised by significantly higher warmth throughout most of the year (Figures 3A, 4; Table 1). This contrast is particularly striking in spring, where the mean temperature at the summit reaches 2.95 °C compared to just 0.62 °C at the base due to persistent snow cover, a significant difference of 2.33 °C. This thermal gap persists through summer and autumn before undergoing a significant inversion in winter. During the cold season, the boulder tops become, on average, slightly but significantly colder than the bases (−1.00 °C vs. −0.37 °C, $P = 0.037$).

The daily air temperature range exhibits distinct seasonal patterns (Figures 3A, 4; Table 2). In summer, the daily range does not differ significantly between positions (approximately 13 °C), although higher maximum daily temperatures occur on the boulder tops, occasionally exceeding 40 °C. A sharp contrast exists between spring and autumn dynamics. While the daily range in autumn shows no significant difference between the top and the base, the discrepancy in spring is pronounced: 1.55 °C at the base versus 7.16 °C at the summit (a difference of 5.61 °C, $P < 0.001$).

In winter, the temperature amplitude remains substantially higher on the boulder summits. While temperatures at the base generally stay near 0 °C due to snow insulation, the summits frequently oscillate between positive and negative values, with 15 cm air temperatures occasionally dropping to −10 °C. Although the statistical models identified this winter amplitude difference as only marginally significant, the curves and box plots clearly illustrate the thermal extremes to which young *P. cembra* individuals are exposed on these elevated micro-sites.

Soil temperature. The decoupling observed in the air is mirrored in the soil temperature at a depth of 6 cm, although the fluctuations are significantly buffered compared to air temperatures (Figures 3B, 4; Table 1). In line with the atmospheric data, the soil at the boulder summits is significantly warmer than at the bases through-
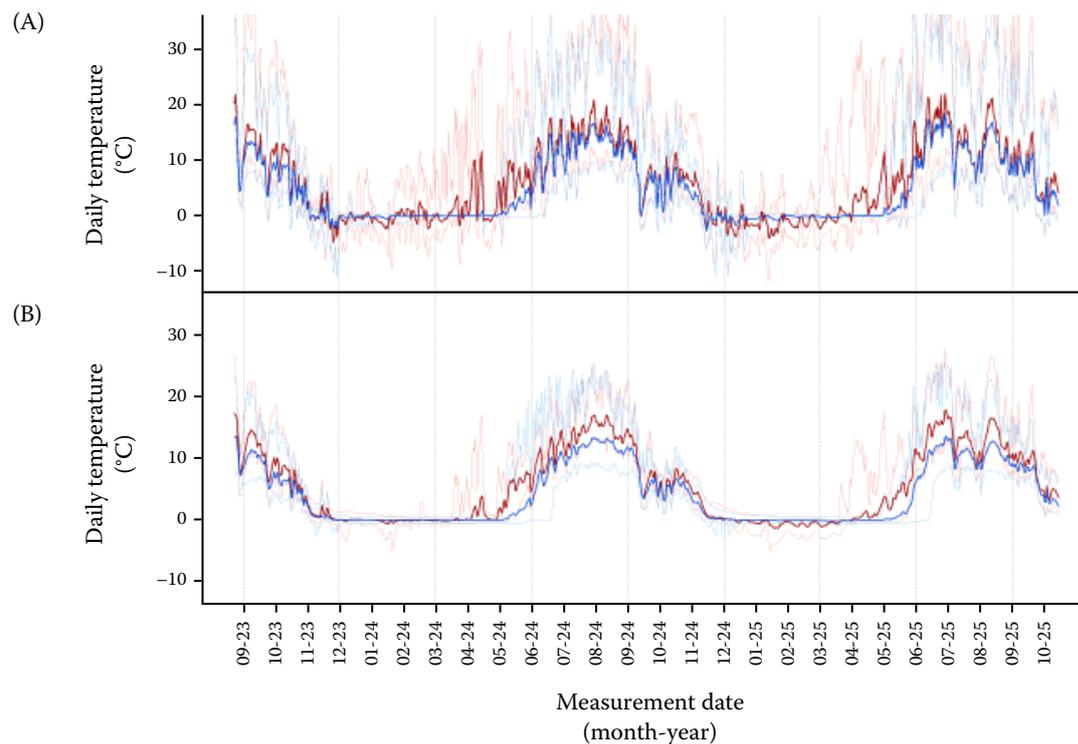
Figure 3. Temporal evolution of temperatures: (A) Air temperature recorded at 15 cm above the ground, (B) soil temperature recorded at −6 cm below the surface

In both panels, thick lines represent the daily mean temperature averaged across all sensors located at the bottom (blue) and top (red) of the boulders; upper thin lines indicate the daily maximum temperatures for the top (red) and bottom (blue) positions, while lower thin lines represent the daily minimum temperatures for the top (red) and bottom (blue) positions

out the growing season (spring, summer, and autumn), with mean differences of 1.48 °C, 2.59 °C, and 1.11 °C, respectively ($P < 0.001$). In winter, the soil temperature at the summits is slightly lower than at the base (−0.32 °C vs. −0.05 °C), but this difference is not statistically significant ($P = 0.37$).

A statistically significant difference in the daily soil temperature range was observed only during the spring (mean amplitude of 1.02 °C at the summit vs. 0.27 °C at the base, $P = 0.022$). However, the temporal evolution curves (Figure 3B) reveal that soil on boulder summits undergoes significantly more frequent freeze-thaw cycles. While the base positions exhibit a stable temperature, remaining remarkably constant near 0 °C throughout the winter and most of the spring, the soil on the summits frequently drops below freezing.

The linear mixed-effects models indicated that variance among boulders was low, suggesting that these microclimatic patterns are generalisable across the site. In contrast, variation among sensors was substantial, reflecting micro-scale heterogeneity. Although sensor aspect (North vs. South)

likely contributes to this variability, it could not be included in the models because damage to several data loggers left too few replicates per group, causing the models to fail to converge.

Soil humidity. Soil moisture content data (Figure 5) further distinguish the two micro-habitats, showing that boulder summits are consistently drier than the base of the blocks (37% drier). The linear mixed-effects model indicates a significant constant effect of position, with the summits being significantly drier across all seasons ($P = 0.0315$). Although the interaction between season and position was not significant ($P > 0.44$), summer and winter were generally the driest periods for both locations.

During rainless periods, the curves reveal a steeper slope for the boulder summits (Figure 5), indicating more rapid water loss through evaporation and drainage compared to the bases. It should be noted, however, that some inconsistencies in moisture readings were observed. These are likely due to variations in sensor-to-soil contact and the physical effects of soil shrinking and swell-
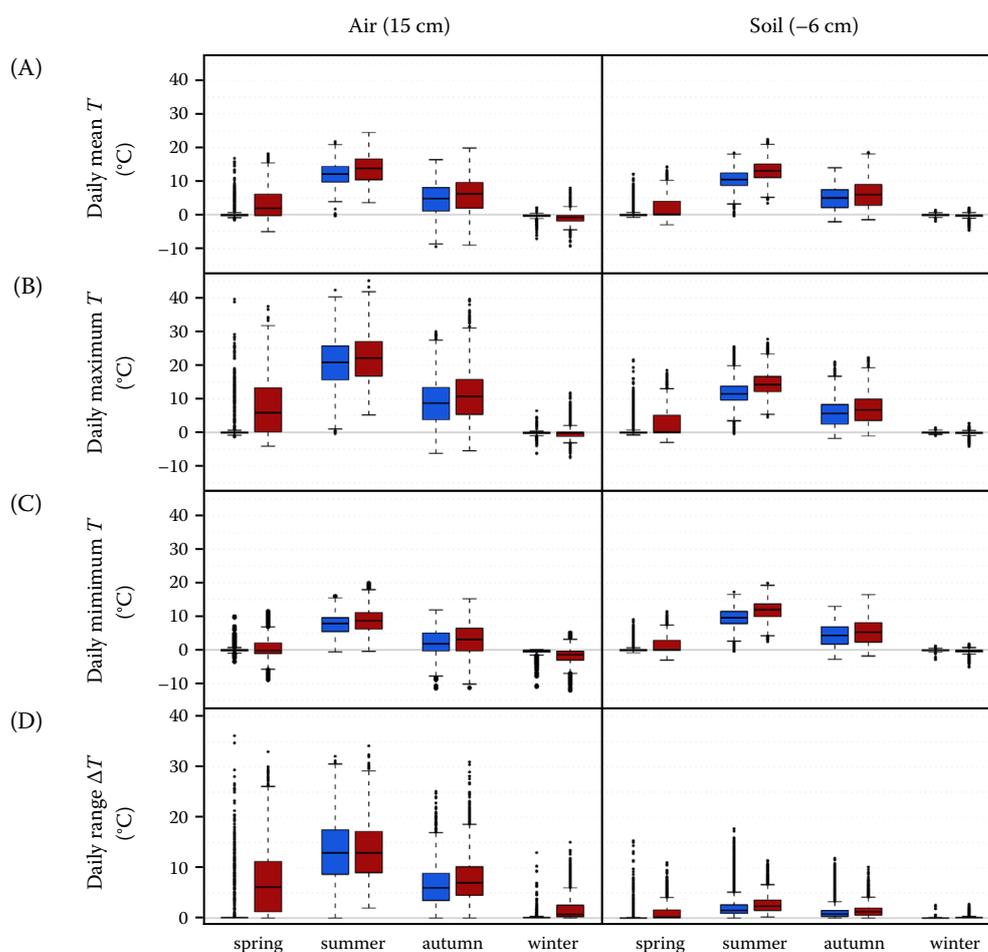
Figure 4. Seasonal temperature (*T*) variations at the top and bottom of the boulders: (A) daily mean temperature, (B) daily maximum temperature, (C) daily minimum temperature, and (D) daily thermal amplitude (range)

The left panels represent air temperature (15 cm above ground), and the right panels represent soil temperature (−6 cm depth); within each panel, blue boxplots represent the bottom positions and red boxplots represent the top positions across the four seasons

Table 1. Seasonal mean temperatures in air (15 cm above ground) and soil (−6 cm depth) at top and bottom boulder positions

Season	position bloc	Air (15 cm)			Soil (−6 cm)		
		mean (°C) (SE)	diff.	*P*-value	mean (°C) (SE)	diff.	*P*-value
Spring	bottom	0.62 (0.23)	–	–	0.32 (0.22)	–	–
	top	2.95 (0.16)	2.33	< 0.001	1.80 (0.20)	1.48	< 0.001
Summer	bottom	11.93 (0.23)	–	–	10.43 (0.22)	–	–
	top	13.57 (0.16)	1.64	< 0.001	13.02 (0.20)	2.59	< 0.001
Autumn	bottom	4.86 (0.23)	–	–	4.97 (0.22)	–	–
	top	5.95 (0.16)	1.09	0.001	6.08 (0.20)	1.11	< 0.001
Winter	bottom	−0.37 (0.23)	–	–	−0.05 (0.22)	–	–
	top	−1.00 (0.16)	−0.62	0.037	−0.32 (0.20)	−0.27	0.370

Values represent estimated marginal means (EMM) with standard errors (SE) in parentheses; differences (diff.) were calculated as 'top minus bottom' for each season; *P*-values indicate the significance of the difference between positions within each season, derived from linear mixed-effects models

Table 2. Seasonal daily temperature range in air (15 cm above ground) and soil (–6 cm depth) at top and bottom boulder positions

Season	position bloc	Air (15 cm)			Soil (–6 cm)		
		mean (°C) (SE)	diff.	*P*-value	mean (°C) (SE)	diff.	*P*-value
Spring	bottom	1.55 (0.65)	–	–	0.27 (0.23)	–	–
	top	7.16 (0.45)	5.61	< 0.001	1.02 (0.20)	0.75	0.022
Summer	bottom	13.12 (0.65)	–	–	2.20 (0.23)	–	–
	top	13.28 (0.45)	0.16	0.845	2.79 (0.20)	0.60	0.062
Autumn	bottom	6.53 (0.65)	–	–	1.13 (0.23)	–	–
	top	7.66 (0.45)	1.14	0.173	1.44 (0.20)	0.31	0.314
Winter	bottom	0.24 (0.65)	–	–	0.03 (0.23)	–	–
	top	1.74 (0.45)	1.49	0.079	0.11 (0.20)	0.08	0.792

Values represent estimated marginal means (EMM) with standard errors (SE) in parentheses; daily range was calculated as the difference between daily maximum and minimum temperatures; differences (diff.) were calculated as 'top minus bottom' for each season; *P*-values indicate the significance of the difference between positions within each season, derived from linear mixed-effects models
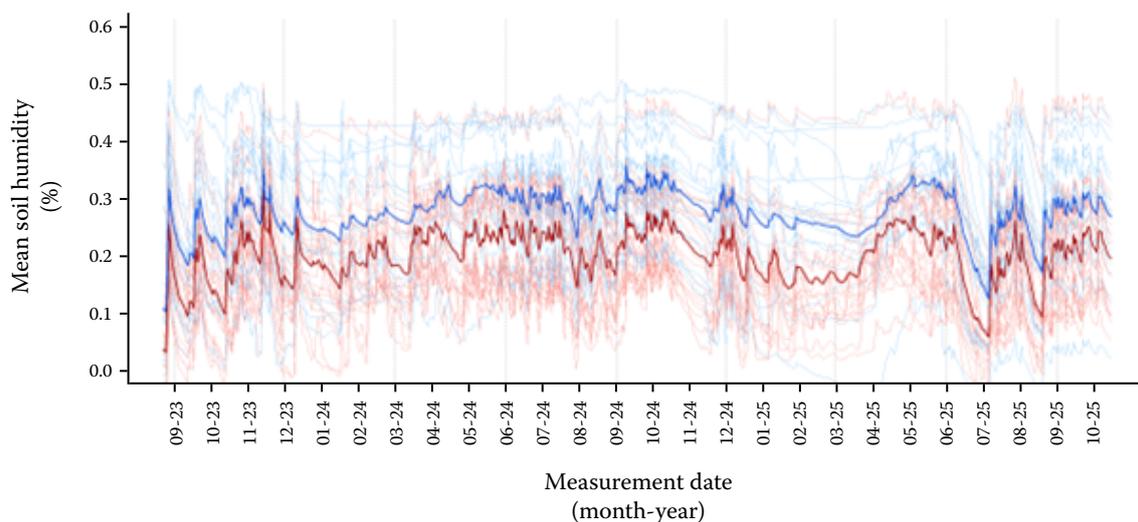

Figure 5. Temporal evolution of soil moisture content

The thick red line represents the mean value for sensors located at the top of the boulders, while the thick blue line represents the mean for sensors at the bottom; the thin lines show the individual trends for each sensor at the top (red) and bottom (blue) positions

ing (Wild et al. 2019). Furthermore, moisture data recorded during frozen periods are subject to bias and inconsistencies.

Microclimatic niche. The empirical data from the Forest of Le Lapé confirm that the microclimate on the summits of large limestone boulders deviates significantly from the conditions at their base. These elevated micro-sites function as independent climatic units, allowing the vegetation to remain largely decoupled from the regional sub-oceanic influence. The earlier snowmelt on the boulders ex-

tends the growing season, a phenomenon typically reserved for inner-alpine continental valleys but here replicated at a micro-scale (Doutaz et al. 2006). This extended season is crucial for slow-growing species like *P. cembra*, as it compensates for the shorter duration of optimal physiological temperatures in alpine environments (Körner 2012; Vittoz et al. 2008). Li and Yang (2004) demonstrated that microsite conditions significantly influence *P. cembra* growth during early life stages, arguing that identifying suitable micro-environments is essen-

tial for successful forest restoration. On the summits of boulders, *P. cembra* is probably frequently exposed to drought stress in summer; however, studies suggest that the species tolerates shallow, permeable soils with limited water storage capacity, even on south-facing slopes (Oberhuber 2004).

Lower competitiveness of *Picea abies*. The absence of the regionally dominant *P. abies* from boulder summits suggests that these 'continental' extremes exceed its physiological tolerance. This exclusion is driven by an inability to survive the combined stress of frozen substrates and intense solar radiation. Winter desiccation, or frost drought, is triggered by needle overheating rather than wind speed (Baig, Tranquillini 1980). High radiation creates a steep vapour pressure gradient that leads to lethal water loss in *P. abies*, whereas *P. cembra* possesses the cuticular resistance necessary to limit transpiration when roots cannot access water (Baig, Tranquillini 1980, Tranquillini 2012).

Furthermore, the extreme thermal amplitudes measured on summits pose a severe phenological risk. Our data show that thermal divergence between summits and the base of the boulders peaks in spring, aligning with the vulnerability of *P. abies* to 'temperature backlashes'. Norway spruce, particularly seedlings and young trees with low energy reserves, is highly susceptible to sudden frost following warm periods that trigger early dehardening (Jönsson et al. 2004). Frequent spring fluctuations on summits likely cause repeated, lethal frost damage in young spruce, whereas the more resilient *P. cembra* maintains sufficient cold hardiness.

Escape from pathogens. Conversely, *P. cembra* is restricted to these summits because the stable snowpack, at the base of the boulders, favours snow blight (*Phacidium infestans*), a pathogen requiring six months of snow cover to proliferate (Vittoz et al. 2008). Historical data from Davos underscore this lethality, with infection rates reaching 47.6% (Schönenberger 1975; Li, Yang 2004) and survival rates as low as 5% (Barbeito et al. 2012, 2013). By occupying wind-swept, early-thawing summits, *P. cembra* achieves a 'pathogenic escape' from this subnivean environment.

This environmental divergence creates a strategic trade-off: while early snowmelt ensures the survival of *P. cembra* via pathogenic escape, it simultaneously exposes *P. abies* to lethal spring fluctuations. Boulder summits thus function as a high-stress refuge where survival is prioritised over rapid growth.

CONCLUSION

This study provides empirical evidence that the chaotic topography of the Forest of Le Lapé generates essential microclimatic heterogeneity. To our knowledge, this is the first study to empirically quantify the thermal and hygric regime of boulder microrefugia supporting *P. cembra* at its oceanic range margin.

Our findings address our initial research questions as follows: (*i*) We quantified a significant thermal and hygric decoupling, where boulders summits are warmer during the growing season, drier, and subject to much stronger thermal amplitudes than the surrounding. (*ii*) These results confirm that these boulders induce a 'continental-like' microclimate within a sub-oceanic matrix, characterised by earlier snowmelt and higher daily and yearly fluctuations. (*iii*) These specific conditions allow *P. cembra* to persist far from its primary range by providing a spatial escape from fungal diseases and the competitive pressure of *P. abies*.

While this study focuses on a single forest within the Western Prealps over a limited period, the results align with previous observations and can likely be extrapolated to other temperate mountain sites worldwide. Tree species occurring in rare habitats shaped by distinct regional conditions and microclimates that deviate from the norm should be prioritised for conservation. Such areas should, in principle, be shielded from exploitation, which is often already complicated by their complex topography. Research suggests that climate change may reduce the habitat suitability and distribution of *P. cembra* in the Alpine and Carpathian regions in the future (Casalegno et al. 2010). In this context of global warming, these topographically buffered sites will remain critical for the conservation of marginal populations and their unique genetic diversity. Topodiversity is an essential element of forest biodiversity and the long-term survival of relict species.

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