






RESEARCH ARTICLE

Cliff-edge forests: Xerothermic hotspots of local biodiversity and models for future climate change

Yann Fragnière¹  | Luca Champoud¹  | Nicolas Küffer¹ | Luc Brillard²  | Michael Jutzi³ | Thomas Wohlgemuth⁴  | Gregor Kozłowski^{1,5,6} 

¹Department of Biology and Botanic Garden, University of Fribourg, Fribourg, Switzerland

²Department of Geosciences, University of Fribourg, Fribourg, Switzerland

³Info Flora, the National Data and Information Center on the Swiss Flora, Bern, Switzerland

⁴Swiss Federal Institute of Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

⁵Eastern China Conservation Centre for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, Shanghai, China

⁶Natural History Museum Fribourg, Fribourg, Switzerland

Correspondence

Yann Fragnière, Department of Biology and Botanic Garden, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland.
Email: yann.fragniere@unifr.ch

Abstract

Cliffs are remarkable environments that enable the existence of microclimates. These small, isolated sites, decoupled from the regional macroclimate, play a significant role in maintaining species biodiversity, particularly in topographically homogeneous landscapes. Our study investigated the microclimate of south-exposed forests situated at the edge of sandstone cliffs in the western part of the North Alpine Foreland Basin in Switzerland and its role in local forest community composition. Using direct measurements from data loggers, as well as vegetation analyses, it was possible to quantify the microclimate of the cliff-edge forests and compare it with that of the surrounding forests. Our results highlighted the significant xerothermic and more variable nature of the cliff-edge forest microclimate, with a mean soil temperature up to 3.72°C warmer in the summer, higher annual (+28%) and daily (+250%) amplitudes of soil temperature, which frequently expose vegetation to extreme temperatures, and an 83% higher soil drying rate. These differences have a distinct influence on forest communities: cliff-edge forests are significantly different from surrounding forests. The site particularities of cliff edges support the presence of locally rare species and forest types, particularly of Scots pine. Cliff edges must therefore be considered microrefugia with a high conservation value for both xerothermic species and flora adapted to more continental climates. Moreover, the microclimate of cliff-edge forests could resemble the future climate in many ways. We argue that these small areas, which are already experiencing the future climate, can be seen as natural laboratories to better answer the following question: what will our forests look like in a few decades with accelerated climate change?

KEYWORDS

azonal forests, escarpments, microclimate, microrefugia, natural experiment, sandstone cliffs, Switzerland

1 | INTRODUCTION

Areas decoupled from the regionally dominant macroclimate allow species to persist locally outside their main distribution range (Lenoir et al., 2017; Millar et al., 2018). Such sites with atypical microclimates

that support isolated populations are defined as climatic microrefugia (Ashcroft, 2010; Rull, 2009). Microrefugia play a central role in species resilience, allowing survival during unfavorable episodes and subsequent range expansion (Hylander et al., 2015). The topic of climatic microrefugia and their associated microclimate is currently

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Authors. *Global Change Biology* published by John Wiley & Sons Ltd.

generating much interest and ongoing research, mainly in relation to the problem of global climate warming, where particularly humid/cold microclimates could allow species to persist in isolated areas in the future (Finocchiaro et al., 2023; Hannah et al., 2014; Millar et al., 2018; Morelli et al., 2016; Pastore et al., 2022). In contrast, dry/warm microrefugia are rarely studied (e.g., Ashcroft et al., 2012) but are of similar importance for the conservation of biodiversity. In the context of global warming, they represent the so-called “leading edge” of the distribution range of some species (Hampe & Petit, 2005) but potentially also refugia of former warmer periods (Larson et al., 2005). Some populations of warm-adapted species have persisted locally in these refugia far outside their main distribution range, even during episodes of drastically unfavorable climatic conditions (Hewitt, 1999; Parducci et al., 2012). Such marginal populations may contain unique genetic diversity arising from adaptation to adverse or unusual conditions (Ducci & Donnelly, 2018).

For microrefugia to exist, terrain influences must allow climatic conditions to deviate from regional averages (i.e., allow the formation of a local microclimate that is warmer, colder, wetter, or drier than regional averages, Dobrowski, 2011). The diversity in topography (sometimes called topodiversity) is the key factor increasing the climatic diversity of the landscape (Körner & Spehn, 2019). Microrefugia exist where the topography is heterogeneous (Ellenberg, 1988) and hence accentuated in mountainous areas (Körner & Spehn, 2019). Apart from the topography, the vegetation itself can also play a major role in the formation of microclimates at a local scale, with the canopy in particular playing a decisive role (Zellweger et al., 2019).

The North Alpine Foreland Basin, also referred to as the Molasse Basin, is a flexural foreland basin that developed in front of the Alpine mountain range (Sommaruga et al., 2012). In Switzerland, this basin is situated between the Jura Mountains and the Alps, creating a topographically relatively homogenous to hilly landscape known as the Swiss Plateau. It is a densely populated and urbanized region, where forests are widely considered human-shaped ecosystems (Bürgi & Schuler, 2003). By erosive action of rivers, sandstone cliffs and canyons evolved in certain areas. These geomorphological peculiarities act as rare “hotspots and islands of topodiversity” in the overall landscape (Härtel et al., 2007; Schmid, 1945).

Cliffs are thus remarkable exceptions: apart from a few other habitats, such as bogs, cliffs are the only “primary” habitats and support remnants of the original vegetation (Larson et al., 2005; Lüth, 1993; Schmid, 1941). Cliffs often support both boreal and Mediterranean species that are relicts from the Holocene (Larson et al., 2005). Dry south-facing cliffs support a mixture of xeric and mesic plants (i.e., adapted to low water resources and to moderate water resources, respectively) and provide unique microenvironments for plant establishment (Graham & Knight, 2004). Cliffs are also refugia from competition by more competitive level-ground vegetation for some species and from grazing (Larson et al., 2005). They contribute more to the biodiversity of a region than their surface coverage would indicate: cliffs all over the world are refugia for a large diversity of endemic plants and endangered species. Cliffs

hold 35–66% of the endemic plant taxa of most countries (March-Salas et al., 2023). They have been recognized as sites that harbor ancient forests (Kuntz & Larson, 2006). Moreover, small cliff fragments can support plant biodiversity similar to that of large continuous forests (Haig et al., 2011). Although cliffs are generally well preserved, some human infrastructures or activities can endanger these ecosystems, such as stone exploitation (e.g., quarries), stabilizations, constructions (e.g., bridges, electric lines, dams), trampling due to over frequentation (e.g., at the cliff edge), and climbing (Clark & Hessel, 2015; Müller et al., 2004).

Forests growing at the boundary between the flat or sloping land and the steep drop-off of a cliff (which we call cliff-edge forests here) are often considered “azonal”, meaning that local conditions overrule the effects of prevailing (so-called “zonal”) macroclimate (Ellenberg, 1963, 1988; Larson et al., 2005; Walter & Breckle, 1985). They form generally narrow forest strips at the top of the cliff, where the trees are still able to grow. These forests are poorly studied: cliffs in general have attracted little scientific interest (Lüth, 1993). Because they occupy only small areas on a map, cliffs are often ignored or only seen as limits to other habitats. Moreover, they are little explored due to difficult access. Few researchers have made quantitative measurements on cliffs, and even fewer have tried to show the quantitative links between the physical environment and the organization of the biota (Larson et al., 2005). However, studying surfaces with microclimatic particularities presents an interesting opportunity. These locations can be viewed as natural laboratories or experiments, offering valuable insights into how forests respond to specific climatic conditions. This is especially pertinent when considering conditions similar to those expected with current climate change.

Efforts to conserve biodiversity increasingly focus on identifying microrefugia at the local scale (Barrows et al., 2020; Greiser et al., 2020). By specifically studying cliff-edge forest characteristics, our approach aims to provide a better understanding of what makes such microrefugia unique in the landscape. We tested the following hypotheses: (1) the microclimate of south-exposed cliff-edge forests is significantly different from that of the surrounding (zonal) forests, and (2) the forest community responds to these local microclimatic conditions and differs from average. Moreover, we evaluated whether cliff-edge forests should be considered hotspots for local biodiversity, acting as habitats for rare plant species, and discuss their importance for conservation. Finally, we discussed the opportunity to consider cliff-edge forests as natural laboratories for climate change.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area comprises a portion of the North Alpine Foreland Basin over the Swiss cantons of Bern, Fribourg and Vaud (approximately 100kmW–E and 70kmS–N, Figure 1) and ranges from 430 to 850 m a.s.l. This part of the basin is relatively narrow, with cliffs

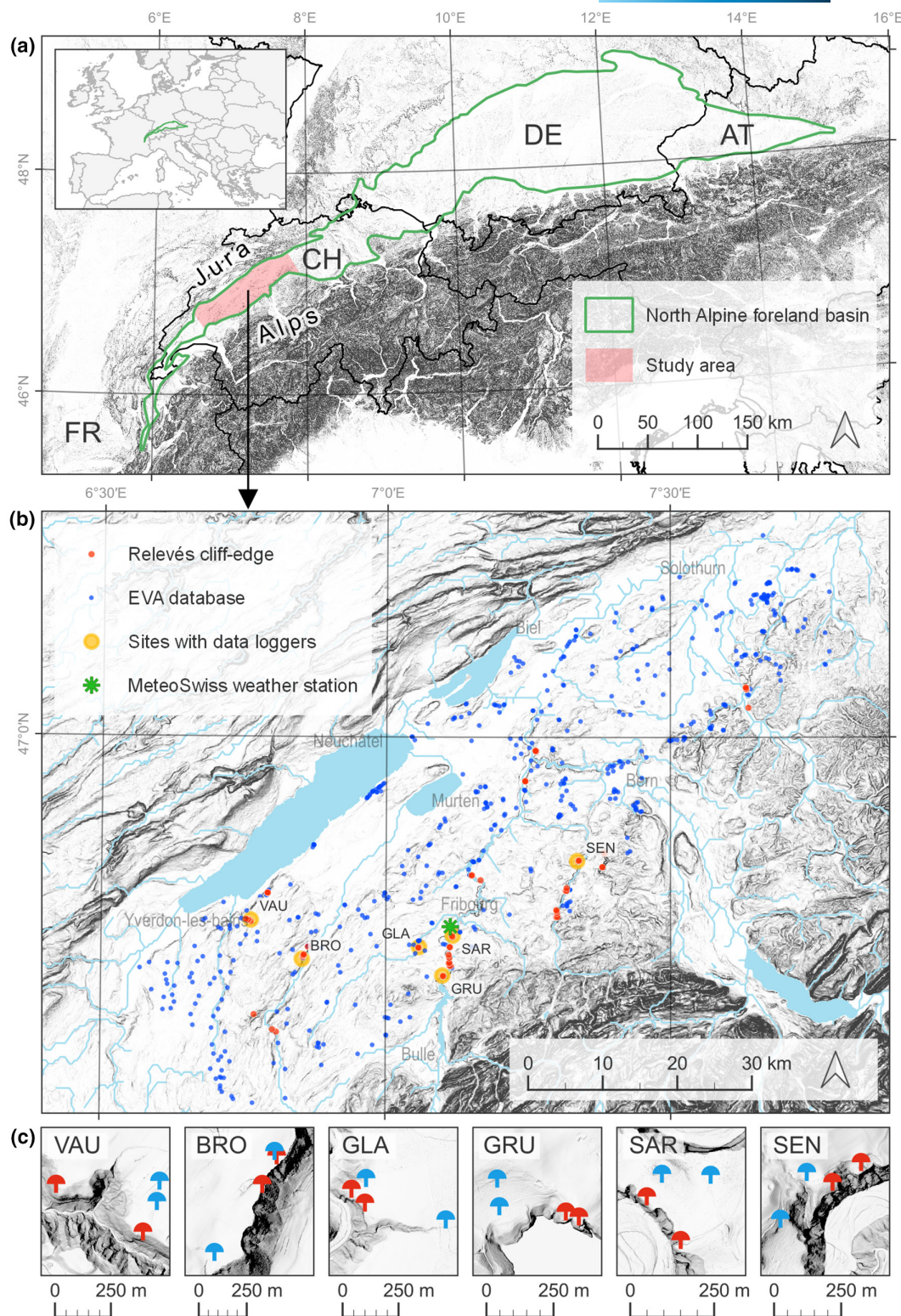


FIGURE 1 Map of the study area. (a) Location of the study area within the North Alpine Foreland Basin. (b) Detailed map of the study area. Red dots: Vegetation relevés in cliff-edge forests; blue dots: Relevés from the European Vegetation Archive (EVA) database; yellow circles: sites with data loggers; green asterisk: MeteoSwiss weather station of Grangeneuve. (c) Data logger distribution within each site (red symbols: cliff-edge forests, blue symbols: nearby beech forests). The grey scale indicates slopes on all maps. Explanations of the study site abbreviations are given in [Table S1](#).

and deep canyons in some areas. The bedrock is uniformly formed of sandstones, which are part of the Sense-Formation (Upper Marine Molasse, Burdigalien, ca. 18 million years ago; Weidmann, 2006).

Locally, beds of shelly sandstones that are hard and resistant to erosion form more prominent cliffs. The bedrock is relatively permeable and carbonated. At the cliff edge, the soils tend to be shallow and

sandy and sometimes superficially decarbonated (thus becoming more acidic) closer to the top.

Between 800 and 1200 millimeters of precipitation falls in an average year, predominantly as rain, and the mean annual temperature is between 8 and 10°C (MeteoSwiss, 2023a). The macroclimate can be considered temperate suboceanic to subcontinental (Beck et al., 2018). European beech (*Fagus sylvatica*) forests can be described as the zonal climax community (Delarze et al., 2015; Leuschner & Ellenberg, 2017).

A digital elevation model (Federal Office of Topography swiss-topo, 2022) was used to detect the main cliffs in the study area. Only south-west to south-east oriented cliffs were retained, with a minimum height of approximately 40m (from the river to the top plateau).

2.2 | Microclimate measurement

The microclimate was measured in the field during two consecutive years (March 2021–April 2023) using data loggers developed by TOMST, model TMS-4 (Wild et al., 2019). A total of 24 loggers were placed at six sites with cliffs (Figure 1; Figure S1 and Table S1 in the online supplementary material). At each site, two data loggers were placed at the cliff edge, above the vertical section of the cliff, and on the steep slope where the forest is still able to grow (Figure 2). The soil was sufficiently deep to fix the data loggers in the substrate. Damage by animals was unlikely, as the data loggers were hardly accessible, although chamois occasionally visit these places.

At each of the selected sites, two further data loggers were placed on the top plateau in a beech forest (alliance *Fagetalia sylvaticae*, sometimes mixed with spruce) farther away from the cliff edge but within a radius of maximum 400m from the data loggers situated at the cliff edge (Figures 1c, 2). These data loggers were placed in a cage to prevent damage by animals.

The TMS-4 data loggers each took temperature and soil moisture measurements every 15min at three different levels: (1) 8cm deep in the soil, (2) on the soil surface (0cm), and (3) 15cm above the soil surface (Wild et al., 2019). We used both shields (recommended by the manufacturer at the time), but recent studies showed that it is better not to use the lower shield (Maclean et al., 2021), which can influence the temperature at the ground surface (0cm), so a slight bias is possible for this data. We also used data from an official MeteoSwiss weather station (Grangeneuve, 46°46'17" N, 7°06'49" E, 651 m.a.s.l., MeteoSwiss, 2023b), located approximately in the center of the study area (Figure 2b), to compare our measurements with macroclimatic values (free air temperature at 2m elevation and precipitation).

2.3 | Vegetation analyses

Vegetation relevés, involving systematic field surveys of plant species and their relative abundance within specific plots, were conducted in selected cliff-edge forests of the study area (Table S2). Accessibility was often difficult, and climbing equipment was needed for security.

Areas of approximately 100m² were investigated, with a more or less elongated rectangular shape along the cliff edge depending on the field characteristics (Figure 2a). All vascular plant species were recorded using the FlorApp application developed by the National Data and Information Center on the Swiss Flora (Info Flora, 2023). Species abundance was evaluated using the Braun-Blanquet scale (Braun-Blanquet, 1932) and transformed into an ordinal scale for numerical analysis (van der Maarel, 1979). For each species, ecological indicator values were extracted (soil moisture, soil reaction, soil nutrients, continentality, temperature, and light). Indicator values are numerical assessments assigned to plant species based on their preferences for specific environmental conditions, developed from expert assessments. They are widely used in vegetation science to estimate difficult-to-measure edaphic and climatic variables from lists of plant species and their abundances. We used Landolt values (Landolt et al., 2010), which are an adaptation for Switzerland of the Ellenberg indicator values (Ellenberg, 1991) and range from 1 to 5. An arithmetic weighted mean of indicator values of all species was calculated for each relevé, where the cover code of each species was used as a weight.

We considered all existing forest vegetation relevés in the study area from the European Vegetation Archive (EVA) database (Chytrý et al., 2016). All relevés are part of the Swiss Forest Vegetation database: it includes relevés published in scientific publications, monographs or reports for regional mapping projects, recorded by different persons during the 20th century (Wohlgemuth, 2012). A total of 524 relevés were available in our study area and dated from 1924 to 1995; most of them dated from 1960 onwards. Their surface area varied from 20 to 1000m². The relevés of the EVA database were used as background to characterize the general pattern of forests in the study area and allow comparison with relevés from cliff-edge forests. The names of syntaxa used to describe forest communities were mainly based on Ellenberg and Klötzli (1972).

All plant species occurrences in the vicinity of cliffs were gathered from the National Data and Information Center on the Swiss Flora (Info Flora, 2023) and were used with expert elicitation to list species naturally occurring and predominantly restricted to exposed cliffs in the study area.

2.4 | Statistical analyses

The Wilcoxon rank sum test was used to test for significant differences in the means of the cliff-edge and beech forest microclimatic data. Only different sites were considered independent replicates for the tests, as the data loggers within the same site were spatially autocorrelated and the different seasons or periods measured were temporally autocorrelated. At each site, we computed the average data for a specific period using readings from two data loggers in the cliff-edge forest and two in the beech forest. Subsequently, we conducted the Wilcoxon rank sum test (with paired samples) to compare the data from the six sites in the cliff-edge forests with that from the six sites in the beech forests. While this approach resulted in small

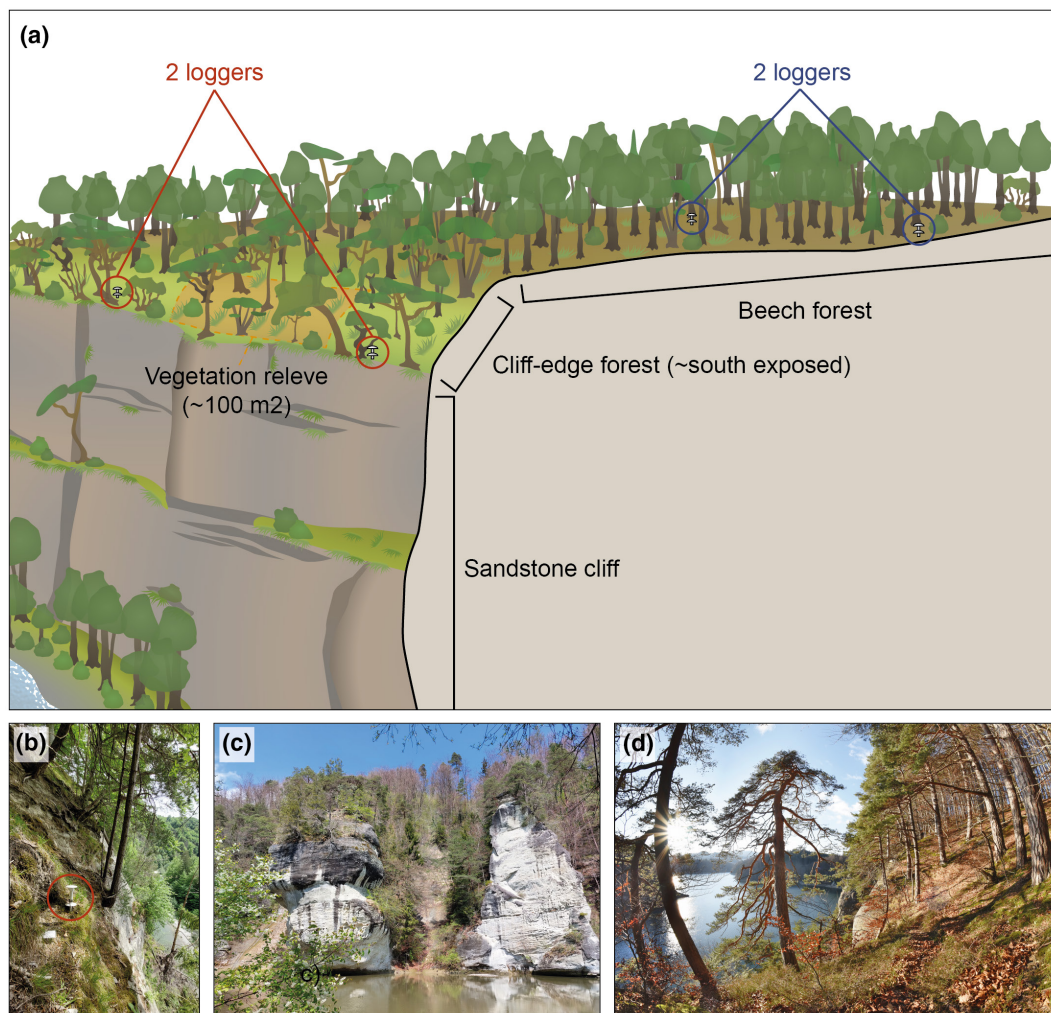


FIGURE 2 Schematic and examples of sandstone cliff-edge forests. (a) Illustration of the methodology: data logger placement and vegetation relevés. (b) Example of a data logger in a cliff-edge forest. (c) Example of sandstone cliffs, Sarine, canton of Fribourg. (d) Example of a Scots pine forest (*Pinus sylvestris*) at the cliff-edge, Lac de la Gruyère, canton of Fribourg.

sample sizes, it represents a more cautious strategy, addressing concerns related to the independence of the data.

Raw soil moisture data were transformed into volumetric soil moisture using the manufacturer 'TMS Calibr utility' (Wild et al., 2019). We calculated the rate of soil drying during periods without precipitation by fitting linear regressions. We excluded the cold period (November–March) when snow or frozen soil may prevail, rendering the sensor unable to measure reliable data. Although soil humidity exhibited non exact linear relationships over time, linear regression was employed to capture trends within specific periods, allowing for the comparison of slopes. For each precipitation-free period, we computed the mean of slopes of all data loggers in cliff-edge forests and beech forests. Subsequently, we averaged these values across different periods.

Nonmetric multidimensional scaling (NMDS, Kruskal, 1964), which is a good ordination method for ordinal scales (Podani, 2006), was performed for community analysis using the 'metaMDS' function in the vegan package (Oksanen et al., 2007). The Bray-Curtis

distance and two dimensions were used. The 'adonis2' function was applied to carry out Permutational multivariate analysis of variance (PerMANOVA), and the 'envfit' function to assess the relations between ecological indicator values and the ordination plot. This function fits multiple regressions of dependent variables with ordination scores, with significance determined by a permutation test. A Wilcoxon rank sum test was used to evaluate for differences in mean ecological indicator values between cliff-edge and EVA relevés.

Indicator Species Analysis (ISA) of the indicpecies package (Cáceres & Legendre, 2009), was used to determine lists of species that are associated to particular groups of sites (two groups: cliff-edge relevés vs. background). It calculates an index between the species occurrence/abundance and each site group and then looks for the group corresponding to the highest association value. Finally, the statistical significance of this relationship is tested using a permutation test. ISA was used to identify species that are strongly associated with cliff-edge forests. All analyses were performed in the R environment (R Core Team, 2022), R version 4.2.0.

3 | RESULTS

3.1 | Microclimate

Over the entire period, we calculated a mean soil temperature of 10.98°C (standard deviation, SD, across the different sites=0.94) in cliff-edge forests and 9.19°C (SD=0.45) in nearby beech forests (difference in means: 1.79°C, p value=.004). Differences greatly varied with the seasons (Figures 3, 4; Tables S3–S8): the soil of cliff-edge forests was up to 3.72°C warmer in the summer

(p value=.002), but the mean temperature was generally similar to that in beech forests in winter or even slightly colder (no significant difference). The mean daily soil temperature was more variable in cliff-edge forests: days with warmer mean temperatures occurred in every season compared to nearby beech forests, but colder mean temperatures also occurred during the winter, with, for example, days with mean soil temperatures below 0°C (minimum: -2.32°C) in cliff-edge forests, which never occurred in beech forests, with minimum temperatures of approximately 0°C (Figure 3; Table S3). The daily amplitude of temperature was also

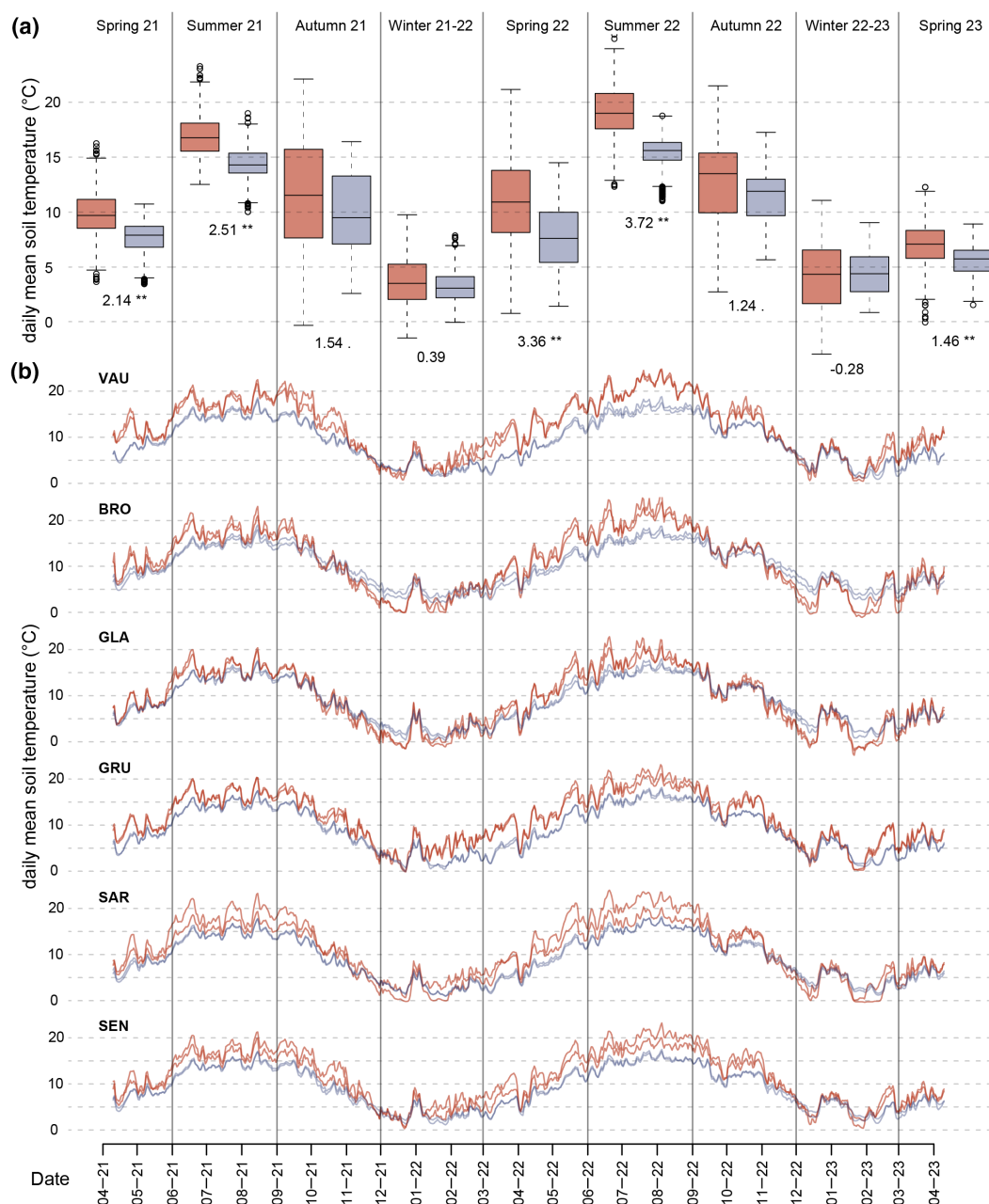


FIGURE 3 Mean daily soil temperature. (a) Boxplots illustrating seasonal variations in mean daily soil temperature (-8 cm), with all sites shown together, in cliff-edge forests (red) and nearby beech forests (blue). The numbers below the boxplots indicate the differences in means, with the level of significance (** p value $\leq .01$). (b) Evolution over time of the mean daily soil temperature in the different sites. Individual data loggers are represented by lines (red: cliff-edge forests, blue: beech forests). Explanations of the study site abbreviations are given in Table S1.

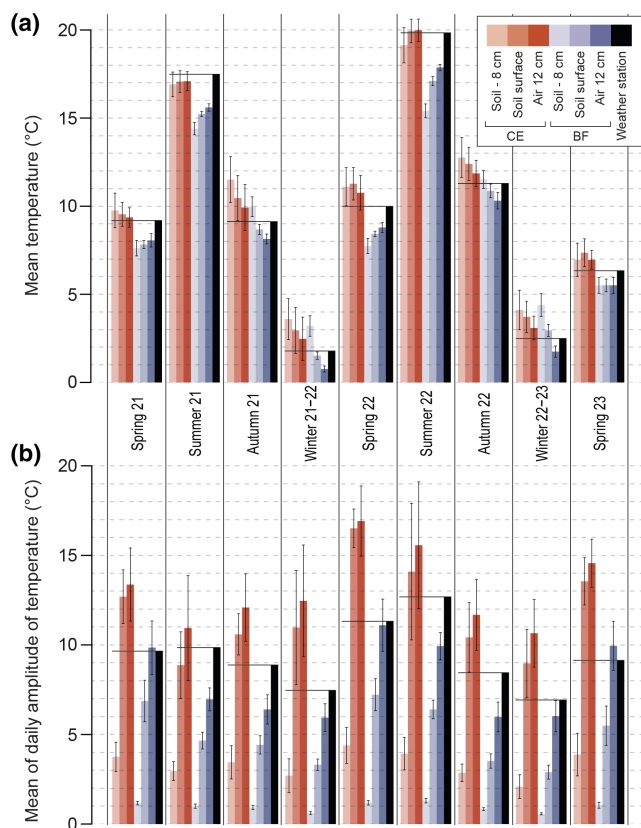


FIGURE 4 Bar plot of temperatures: (a) seasonal mean temperature and (b) seasonal mean daily amplitude of temperature. Colors' significance is indicated in the upper right legend. Red: cliff-edge forests; blue: nearby beech forests, light colors: soil (–8 cm); intermediate colors: soil surface (0 cm); dark colors: air (12 cm). The black bars and horizontal lines show the free air values (2 m above the soil surface, weather station, Grangeneuve). The error bars indicate the standard deviation across the six study sites.

significantly higher in cliff-edge forests (Figure S2). Over the entire period, we calculated a mean daily amplitude of soil temperature of 3.28°C (SD=0.63), but it was only 0.95°C (SD=0.07) in beech forests (difference: 2.33°C, p value=.002). This difference of approximately +250% in daily temperature amplitude was rather constant during all seasons. The daily amplitude of temperature in the soil could reach up to 17.88°C in the most extreme cases in cliff-edge forests (maximum of 6.62°C for nearby beech forests). The yearly amplitude of temperature (mean summer–mean winter) was 11.11°C in beech forests and 14.17°C in cliff-edge forests, a difference of approximately +28%.

At the soil surface (0 cm), the temperature was on average 10.37°C (SD=0.84) in cliff-edge forests and 8.86°C (SD=0.13) in beech forests (difference: 1.51°C, p value=.002) over the entire period. The daily amplitude of temperature was on average 11.59°C (SD=1.36) in cliff edge forests and 4.66°C (SD=0.54) in beech forests (difference: 6.93, p value=.002). The seasonal statistics are shown in Figure 4 and Table S4. Note that we encountered a configuration problem with the sensor at surface height for three sites during the first year (spring 2021 to spring 2022). Averages are

based on the remaining three sites during this period (GLA, GRU, SAR).

The air temperature at 12 cm above the soil surface was on average 10.96°C (SD=0.85) in cliff-edge forests and 9.29°C (SD=0.70) in beech forests (difference: 1.67°C, p value=.008). The daily amplitude of temperature was on average 13.05°C (SD=1.52) in cliff-edge forests and 7.79°C (SD=0.77) in beech forests (difference: 5.26, p value=.002) over the entire period. In cliff-edge forests, the air temperature above the soil surface was on average similar to the free air temperature (data from the official weather station in Grangeneuve) during the summer or moderately higher during the other seasons, by up to approximately 1°C (Figure 4). In contrast, it was approximately 1–2°C colder in the beech forests in every season. The daily air temperature amplitude 12 cm above the soil surface was on average higher in cliff edge forests than in beech forests or than free air temperature. Daily amplitudes of more than 30°C occurred every season. The maximal daily amplitude in beech forests and of free air temperature was between 14 and 24°C (Table S8).

Regarding soil humidity, we selected 17 intervals from 6 to 14 days without significant precipitation (Figure S3). The drying rate of the soil (slope) was on average 1.83 times higher (SD within the different intervals: 0.63) in cliff-edge forests than in nearby beech forests (i.e., the soil dried 83% faster).

3.2 | Vegetation

A total of 60 relevés were examined in the cliff-edge forests (Figure 1; Table S2). Overall, 180 different taxa (mainly species) were recorded. The mean number of species per relevé was 17.5 (SD=5.88). A total of 524 relevés from the EVA database were included (Figure 1). Overall, 426 taxa (mainly species) were included in the data. The mean number of species per relevé was 24.16 (SD=9.74), although this value cannot be directly compared to that of the cliff-edge forest surveys because the areas were not always equivalent.

Most of the relevés included in the EVA database can be classified as beech forests (*Fagion sylvaticae* alliance) in different associations (e.g., the most common: *Luzulo-Fagetum*, *Galio odorati-Fagetum*, *Milino-Fagetum*). A small proportion of the relevés were from more humid forests (e.g., from the *Alno-Fraxinion* alliance), and a few relevés represented different types of rarer dry or humid forest types.

On the basis of the FlorApp assessment and expert evaluation, the relevés included in the cliff-edge forests can be classified in the following alliances: different calcareous and acidic Scots pine forests (*Molinio-Pinion*, *Erico-Pinion*, *Dicrano-Pinion*), xero-thermophile oak forests (*Quercion pubescenti-petraeae*), calcareous xero-thermophile beech forests (*Cephalanthero-Fagion*) and acidic beech forests, especially dryer associations such as *Luzulo-Fagetum leucobryetosum*.

The NMDS ordination (Figure 5) showed a strong difference in community composition between the main forest types of the studied area (background, EVA database) and the cliff-edge forests. This was confirmed by the PerMANOVA test, which revealed a significant difference (F value: 43.34, p value <.001).

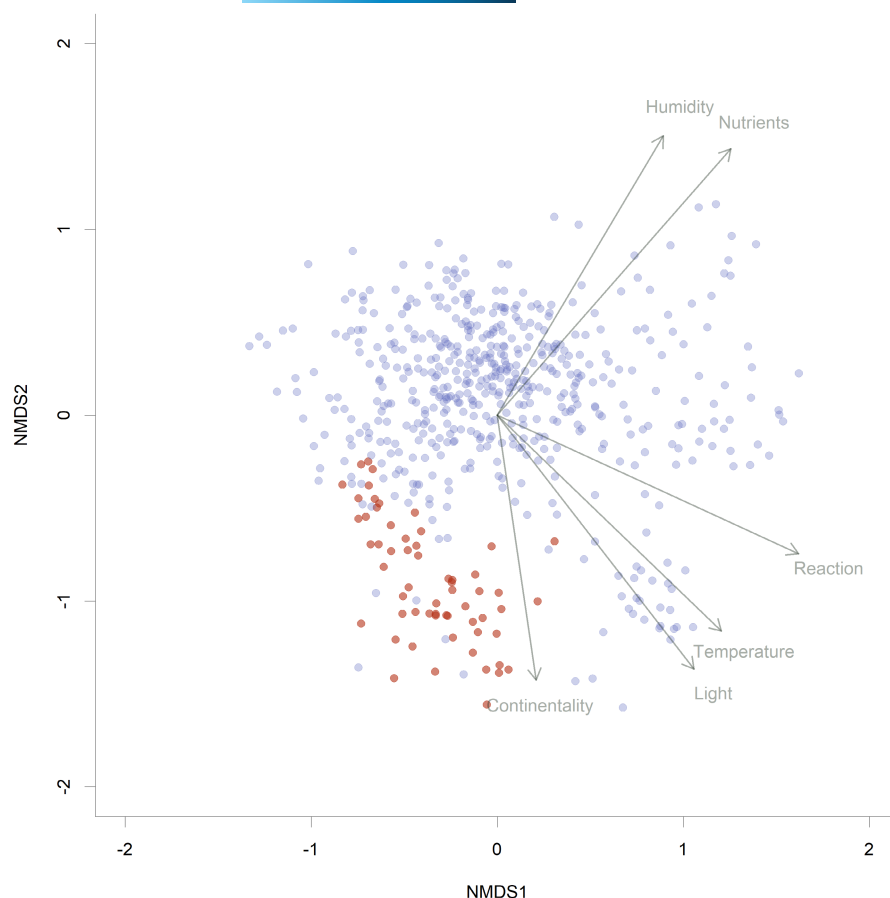


FIGURE 5 Ordination plot of an NMDS analysis based on the community composition of the vegetation relevés. Cliff-edge forest relevés are indicated by red dots, and relevés of the European Vegetation Archive (EVA) database are indicated by blue dots. The stress value was 0.2. Arrows show the relations between ecological indicator values and community composition (envfit results). The length of the arrows is proportional to significance. All relations were significant (p value $< .001$).

The analysis of the community mean ecological indicator values also revealed differences between the relevés of the EVA database (background) and cliff-edge forest relevés (Figure 6). Cliff-edge forest communities comprised more dry- and warm-adapted, lower nutrient- and higher light-demanding species, as well as species with a higher degree of affinity for continental climatic conditions. Concerning soil reactions, more calciphilous species were recorded on average, albeit with a higher degree of variability, as some communities on cliff edges were clearly acidophilic. For each ecological indicator, the pairwise difference was significant (Wilcoxon ranked test, p value $< .001$).

By analyzing all vegetation relevés, ISA revealed that 47 species were significantly (p value $< .01$) associated with cliff-edge forests (Table S9). This does not mean that these species were found only in cliff-edge forests but that on average, they were more frequent and abundant there than in other forests in the study area. For example, the four most significant were *Pinus sylvestris*, *Sorbus aria*, *Hippocrepis emerus*, and *Carex montana*. Based on the National Data and Information Center on the Swiss Flora and literature, we also compiled a list of forest types and species mainly restricted to cliff-edge forests and sandstone escarpments in the western Swiss Plateau, including rare species (Table S10). According to the regional Red List for the Swiss Plateau (Info Flora, 2023), 23 were near threatened (NT), and 12 were threatened (VU, EN or CR), for example, *Alyssum montanum*, *Dianthus gratianopolitanus*, and *Festuca filiformis*.

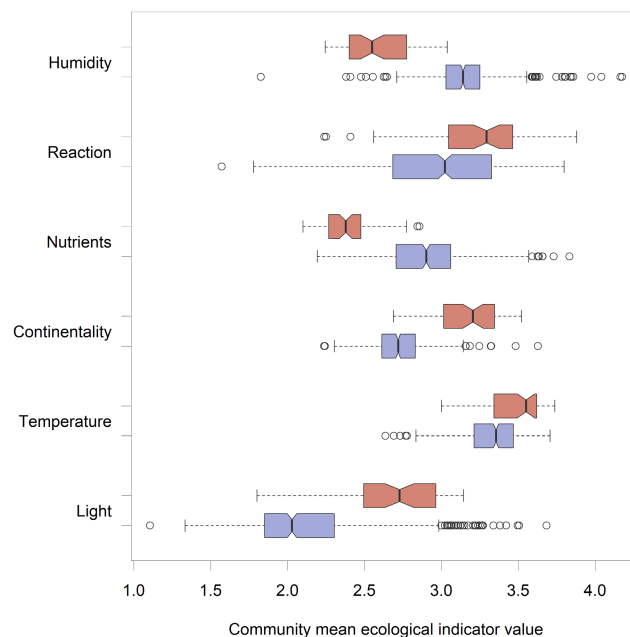


FIGURE 6 Boxplot comparing community mean ecological indicator values between cliff-edge forest relevés (red) and European Vegetation Archive (EVA) database relevés (blue). Six indicators are shown: soil moisture, soil reaction, soil nutrients, continentality, temperature, and light.

4 | DISCUSSION

Our study provides the first comprehensive microclimatic characterization of forest habitats on south-facing cliff edges. Direct analysis of microclimate and indirect analysis via vegetation and ecological indicator values highlight that the microclimate is distinctively different from that of surrounding forests and allowed, for the first time to our knowledge, quantification of this microclimate. The community composition was significantly influenced by these environmental conditions, and many species (47 according to our calculations) were significantly more common and abundant than in zonal surrounding forests. Moreover, several locally threatened species were present. Cliff-edge forests therefore meet the criteria to be qualified as microrefugia (Rull, 2009) and thus deserve special attention for their conservation (Barrows et al., 2020; Greiser et al., 2020). The cliff edge microclimate also offers another useful and overlooked opportunity highlighted by our results: it can be a model for studying future forests faced with climate change.

4.1 | Cliff-edge forest microclimate

Microclimatic conditions are still often overlooked or ignored. Our results support the importance of collecting field data rather than relying on inferences from databases and weather stations when studying vegetation (Körner & Hiltbrunner, 2018). Macroclimate information gives only general trends for a region, and thus, the need of studying climatic factors of small particular areas and their link to vegetation has long been recognized (Rytz, 1913).

4.1.1 | Temperature

It was shown that conditions measured by official weather stations, which are located on open land at a 2 m height, are not comparable to the microclimatic conditions inside a forest (Boehnke et al., 2017). Our results also showed a clear difference between free air temperatures and those found inside the beech forests, where the buffering effect of the canopy provides on average cooler and less fluctuating conditions. Compared to sites with no tree canopy, environments under forest canopies experience smaller variations between maximum and minimum temperatures due to reduced direct insolation and longwave emission (Wolf et al., 2021), as well as the cooling effect of evapotranspiration. The denser the vegetation cover is, the better the forest can buffer regional warming and mitigate extreme heat and extreme frost during the winter (De Frenne et al., 2021; Finocchiaro et al., 2023).

On the other hand, cliff-edge forests are less buffered and experience hotter and more fluctuating conditions. Results show that understory plants and juvenile trees are less decoupled from air temperature: on average, the air temperature above the soil surface is similar to the air temperature in summer and even up to 1°C warmer

during the other seasons. Forests that are hotter than the surrounding free air temperature are rare in temperate regions but occur in other areas, such as the Mediterranean (Haesen, Lembrechts, et al., 2023), where the sparser canopy is a key factor (Zellweger et al., 2019).

However, the air temperature above the soil surface can be a misleading measure, which can vary considerably and rapidly depending on the direct radiation. It does not always reflect what small plants and young trees are actually confronted with. The topsoil is more buffered and yields the best proxy for plant temperature (Scherrer & Körner, 2010).

The soil mean summer temperature was up to 3.72°C higher in summer (year 2022) and almost identical in winter (Figure 3; Table S3) compared to that in the nearby beech forests. The vegetation, evaluated through ecological indicator values, also indicated warmer conditions in cliff-edge forests. The edge effect undoubtedly played an important role. The edge effect of forest microclimate has already been studied in detail. Typically, mean and maximum air temperatures decrease from the forest edge into the interior, whereas minimum air temperatures and air humidity values tend to increase from edge to interior (De Frenne et al., 2021; De Pauw et al., 2023). In the study of Meeussen et al. (2021), conducted in different forests across Europe, forest soil was on average 2.3°C warmer during the summer months at the edge than in the forest interior and 1°C cooler in winter. The trend is similar in our results. However, it also indicates that the soil temperature of cliff-edge forests is higher in summer but also in winter than that of a “common” forest edge.

One obvious explanation is topography. First, the south-exposed slopes are more protected from cold north winds. Then, the fact that these forests are very steep and unproductive implies that very little litter accumulates on the ground, decreasing soil insulation from air and direct radiation. In summer, the soil heats more rapidly, and in winter, the low angle of the sun, almost perpendicular to the slope, helps to heat the soil by direct insolation. The canopy in cliff-edge forests is also sparser, allowing more radiation to reach the ground throughout the year and heating up the soil more quickly. The canopy density can have a significance influence on microclimate (Zellweger et al., 2019). The soil depth likely plays a significant role as well. The thinner soil in cliff-edge forests holds less water (see next chapter). It was shown that moister soils supported cooler understory microclimates, compared to drier soils (Greiser et al., 2024). Finally, snow cannot accumulate and melts rapidly in cliff-edge forests, again reducing the insulation effect. This absence of litter and snow also increases the diurnal variability of temperature, which can sometimes reach extreme values. On average, diurnal variations were slightly lower in summer, possibly because of the higher sun angle and the canopy reducing direct insolation of the soil (Figure S2).

4.1.2 | Humidity

The vegetation indicated a significant difference in soil moisture, with obviously drier conditions in cliff-edge forests (Figure 5). Our

direct soil humidity measurements made with data loggers yielded inconsistent results, which we could not use directly. The problem probably lies in the contact between the soil and the sensor, which was probably not consistent for the different data loggers, leading to incorrect values. This can occur during installation or because of shrinking and swelling soil (Wild et al., 2019). We therefore did not use absolute values. However, the fluctuations seemed consistent, and we decided to calculate the drying rate of the soil during periods of drought (see methods). This rate was 83% higher in cliff-edge forests than in nearby beech forests. To illustrate, we can assume that a 5-day dry period is sufficient in cliff-edge forests for the soil to dry out, whereas the period is 9 days in nearby forests.

Evaporation through increased direct radiation and higher temperatures, the absence of litter and topography favoring runoff are probably important factors explaining this result. Moreover, sandstones are porous rocks that can reduce water availability in the sub-soil (Novák et al., 2019).

The microclimate of cliff-edge forests can be described as drier and hotter but also more continental, as indicated by vegetation indicator values and the larger amplitude of temperatures (daily, annually). Vegetation experiences varying and opposing environmental conditions, often shifting between extremes.

4.2 | Vegetation

Our results show that the plant community of cliff forests is significantly different from that of the surrounding forests. The uniform geology and bedrock of our study area enable us to highlight differences due to other environmental factors. The diversity of vascular plants in forests is best explained by local-scale factors (Wohlgemuth et al., 2008), in our case, by the xerothermic microclimate close to the soil, exposing understory plants and juvenile trees to microclimatic extremes. Other factors, highlighted by ecological indicator values, also play a role in community composition. Higher light levels promote more heliophilous species. Cliff-edge forests are also influenced by soils with reduced nutrient levels. This characteristic probably has several causes: increased leaching, drier conditions that can, for example, reduce nitrification (Rennenberg et al., 2009), and less accumulation of litter on the ground.

Some sites can be classified as hosting alliances that are very rare in the North Alpine Foreland Basin and in Switzerland in general, especially different Scots pine forests (Ellenberg & Klötzli, 1972; Wohlgemuth et al., 2008). Scots pine forests that can be found on cliff edges undoubtedly have a fascinating biogeographical history. It was demonstrated in the Stołowe Mountains (Sudetes, Poland) that the pines growing at the top of the Jurassic sandstone rocks are most likely relicts from the boreal period of the Holocene (Schmid, 1941; Sobierajska et al., 2020). Similarly, in sandstone landscapes of the Czech Republic, it was shown via pollen analyses carried out in peat accumulations that pine forests were colonizing large areas in the early Holocene. However, in the middle Holocene,

with the extension of spruce and oak, pine has maintained its dominance only on rocky edges (Novák et al., 2019). A similar context on the Swiss Plateau (sandstone landscape, similar elevation) indicates that cliff-edge forests, investigated in this study, could have an analogous history.

Dense mixed *Pinus sylvestris* and *Betula* boreal forests already occurred across the entire Swiss Plateau in the Bølling (c. 14,500 BP) and Allerød (c. 13,500 BP) periods (Burga, 1988; Gobet et al., 2010; Rey et al., 2017). Protocratic trees (following deglaciation), such as *Pinus sylvestris*, have high reproduction rates, high rates of population increase, and high ecological tolerances but low competitive tolerances (Birks & Tinner, 2016). The glacial refugia of *Pinus sylvestris* were not necessarily located only in the Mediterranean borderlands. They probably also survived outside the Mediterranean region in areas farther north in Europe (Cheddadi et al., 2006), where warm microrefugia probably played an important role. Cliff-edge habitats today allow natural pine forests to persist by escaping competition, and *Pinus sylvestris* is able to tolerate harsh microclimates due to its wide tolerance to temperature, soil and drought (Landolt et al., 2010). It is therefore very likely that cliff-edge pine forests of the Swiss Plateau can be considered continental relicts from the postglacial period (Schmid, 1944). The oceanic–continental axis is a biogeographic dimension that is often ignored in discussions on species' responses to glacial/interglacial periods (Stewart et al., 2010).

Another feature that has long fascinated botanists is the presence of sporadic populations of xerothermic species in the vicinity of sandstone cliffs of the Swiss Plateau, for example, *Sorbus torminalis*, *Amelanchier ovalis*, and *Arabis turrita*. Two hypotheses have been put forward, although this has rarely been studied in detail: (1) These species, recently arrived, have managed to migrate and form small populations in these suitable microhabitats. They form the "leading edge" of their distribution. (2) They are xerothermic relicts from a previously more widespread flora, originating from the Holocene climatic optimum (approximately 9500–5500 years BP), when the climate was warmer and drier (Rytz, 1913).

4.3 | Biodiversity hotspots needing protection

Although cliff-edge forests are not very diverse in terms of plant species richness, they are very important habitats for regionally rare species and communities. Cliff edges must be seen as xerothermic and continental microrefugia in temperate landscapes. Species requiring climatic conditions other than the predominant regional macroclimate can benefit from such sites (Hylander et al., 2015). More attention should be given to the protection of areas that connect current and future suitable climates (Carroll & Noss, 2020). The value of humid and cold areas is increasingly recognized, but dry and warm refugia are also of primary importance for conservation. Incorporating microrefugia into conservation planning requires that managers understand their different types, how they are spatially distributed, and their relative importance (Michalak et al., 2020). Then, these areas can be considered priorities for conservation,

and management can be adapted accordingly (Greiser et al., 2020; Morelli et al., 2020). Fortunately, many of cliff areas are naturally protected and have been little impacted by human activities.

Many other arguments can be put forward concerning the conservation value of cliff environments. They are small-scale “islands” in a uniform landscape, with their own characteristics, as was, for example, described for sandstone cliffs in the Czech Republic (Härtel et al., 2007). They are refugia for light-demanding species that can escape the concurrence of forest development only in such sites (Larson et al., 2005). They are hotspots of topodiversity, which is associated with higher biodiversity in general (Carroll et al., 2017): not only of flora but also of many other species linked to these areas on the Swiss Plateau, such as the chamois or the Eurasian eagle-owl. They are a rich source of information for biologists and geologists. Finally, they are among the last wild and more or less “untouched” places on the Swiss Plateau. For all these reasons, we strongly advocate the strict protection of cliff environments and cliff edges, with the same respect given to peat bogs, for example.

4.4 | A model for studying the impact of climate change on future forests

Knowing what forests will look like in a few decades as a result of climate change is a main goal of modern research, and scientists and practitioners in forestry are most interested in this topic. “Hotter drought” is an emerging characteristic of the Anthropocene (Allen et al., 2015). Uncertainties related to tree mortality in response to hotter drought pose a key challenge for Earth system modelers to predict future vegetation change and feedbacks to global climate with confidence. Increases in the frequency, duration, and/or severity of drought and heat stress associated with climate change could fundamentally alter the composition, structure, and biogeography of forests in many regions (Allen et al., 2010; Brodribb et al., 2020; Rigling et al., 2013).

Small areas in the landscape that already experience forecasted climatic conditions are naturally existing models that can help answer such questions. We argue, therefore, that south-exposed cliff-edge forests are a very interesting model system, notably for the following reasons:

- Cliff-edge forests are warmer on average, compared with surrounding forests, up to 3.72°C in summer according to our measurements (climate warmer from 2.5 to 4.5°C by the middle of this century according to climate scenarios for Switzerland, Fischer et al., 2022). Moreover, less snow accumulates and melts earlier on cliff edges, which will also be a general trend in the future.
- They experience significantly more intense periods of drought compared to nearby forests (climatic scenario by the middle of this century, less precipitation in summer and longer dry period, up to +9 days, Fischer et al., 2022).
- Climatic conditions are more variable in cliff-edge forests. Very high temperatures can arise frequently, but intense cold occurs in

winter, which will also be an important characteristic of the future climate (Fischer et al., 2022).

- More light penetrates the cliff-edge forests, and they are sparser than surrounding forests. With increasing tree mortality due to climate change, it is expected that future forests will be brighter with sparser canopies (Allen, 2007), mainly for soils with limited water holding capacity (Frei et al., 2022).

The microclimate of the cliff-edge forest therefore resembles the future climate at many points. This is an interesting opportunity to observe how the community is responding, on a small scale, in particular concerning the species composition and tree vigor, in forests that have generally formed without any human intervention. Cliff-edge forests have been and will be affected by hotter drought. This is one precondition for why cliffs are generally more open and hence host plant species that are poor in competitive ability. In the future, these sites will be of the same importance as they have been thus far: species of cliff vegetation mirror the long-term persistence of climate variability.

Predictive models based on relatively coarse-grained approaches that ignore microrefugia will lead to overestimates of extinction risk (Haesen, Lenoir, et al., 2023; Mosblech et al., 2011). For example, it has been modeled that, depending on the scenario, European beech (*Fagus sylvatica*) will virtually disappear from the Swiss Plateau (Meier et al., 2011). Our results revealed the species in 98% of our cliff-edge relevés, indicating that the ecological amplitude should not be underestimated.

Furthermore, tree populations contain substantial genetic variability in relation to tolerance to drought and heat stress (Allen et al., 2015). This is another important argument for the value of cliff-edge forests, which can be seen as a source of genes for the future.

5 | CONCLUSIONS

Our findings confirm that cliff-edge forests are unique ecosystems that exhibit a significant divergence in microclimatic conditions compared to the surrounding zonal forests. Furthermore, we have demonstrated that the forest community not only responds to these distinct microclimatic factors but also differs significantly from the average local forest community. Importantly, our study sheds light on the ecological significance of cliff-edge forests, identifying them as hotspots for local biodiversity. The presence of locally rare plant species within these ecosystems underscores their importance for conservation efforts. Beyond their intrinsic ecological value, we have explored the potential of cliff-edge forests to function as natural laboratories for understanding the dynamics and composition of future forests under the influence of climate change. Although this work was carried out on sandstone cliffs in a specific geographical context, it is expected that comparable results, with a degree of variation depending on local characteristics, can be extrapolated to numerous other types of lowland cliffs worldwide.

AUTHOR CONTRIBUTIONS

Yann Fragnière: Conceptualization; formal analysis; investigation; methodology; visualization; writing – original draft. **Luca Champoud:** Investigation; writing – review and editing. **Nicolas Küffer:** Validation; writing – review and editing. **Luc Braillard:** Investigation; writing – review and editing. **Michael Jutzi:** Investigation. **Thomas Wohlgemuth:** Validation; writing – review and editing. **Gregor Kozłowski:** Conceptualization; methodology; supervision; validation; writing – review and editing.

ACKNOWLEDGMENTS

We are greatly thankful to all experts and naturalists who provided species data to the Info Flora database and performed vegetation relevés in our study area during past decades, making this study possible. We also thank the European Vegetation Survey Working Group, particularly Dr. Ilona Knollová of the Department of Botany and Zoology of Masaryk University (Czech Republic), for providing the vegetation data. Finally, we thank the anonymous reviewers for their constructive comments that improved the quality of the manuscript. Open access funding provided by Université de Fribourg.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Microclimatic and vegetation data can be accessed at <https://doi.org/10.5281/zenodo.10516720>. Data from the EVA database are to be requested to the EVA database administrator (<http://euroveg.org/eva-database-obtaining-data>).

ORCID

Yann Fragnière  <https://orcid.org/0000-0003-4167-379X>

Luca Champoud  <https://orcid.org/0009-0003-9517-1768>

Luc Braillard  <https://orcid.org/0000-0003-4380-4300>

Thomas Wohlgemuth  <https://orcid.org/0000-0002-4623-0894>

Gregor Kozłowski  <https://orcid.org/0000-0003-4856-2005>

REFERENCES

- Allen, C. D. (2007). Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. *Ecosystems*, 10(5), 797–808. <https://doi.org/10.1007/s10021-007-9057-4>
- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8) art129, 55. <https://doi.org/10.1890/ES15-00203.1>
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., & Hogg, E. T. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4), 660–684.
- Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, 37(8), 1407–1413. <https://doi.org/10.1111/j.1365-2699.2010.02300.x>
- Ashcroft, M. B., Gollan, J. R., Warton, D. I., & Ramp, D. (2012). A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, 18(6), 1866–1879. <https://doi.org/10.1111/j.1365-2486.2012.02661.x>
- Barrows, C. W., Ramirez, A. R., Sweet, L. C., Morelli, T. L., Millar, C. I., Frakes, N., Rodgers, J., & Mahalovich, M. F. (2020). Validating climate-change refugia: Empirical bottom-up approaches to support management actions. *Frontiers in Ecology and the Environment*, 18(5), 298–306.
- Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A., & Wood, E. F. (2018). Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data*, 5, 180214.
- Birks, H. J. B., & Tinner, W. (2016). *OK Past forests of Europe*.
- Boehnke, D., Gebhardt, R., Petney, T., & Norra, S. (2017). On the complexity of measuring forests microclimate and interpreting its relevance in habitat ecology: The example of Ixodes ricinus ticks. *Parasites & Vectors*, 10(1), 549.
- Braun-Blanquet, J. (1932). *Plant sociology. The study of plant communities*. McGraw-Hill.
- Brodribb, T. J., Powers, J., Cochard, H., & Choat, B. (2020). Hanging by a thread? Forests and drought. *Science*, 368(6488), 261–266. <https://doi.org/10.1126/science.aat7631>
- Burga, C. A. (1988). Swiss vegetation history during the last 18 000 years. *New Phytologist*, 110(4), 581–662. <https://doi.org/10.1111/j.1469-8137.1988.tb00298.x>
- Bürgi, M., & Schuler, A. (2003). Driving forces of forest management—An analysis of regeneration practices in the forests of the Swiss central plateau during the 19th and 20th century. *Forest Ecology and Management*, 176(1), 173–183. [https://doi.org/10.1016/S0378-1127\(02\)00270-0](https://doi.org/10.1016/S0378-1127(02)00270-0)
- Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90(12), 3566–3574. <https://doi.org/10.1890/08-1823.1>
- Carroll, C., & Noss, R. F. (2020). Rewilding in the face of climate change. *Conservation Biology*, 35(1), 155–167.
- Carroll, C., Roberts, D. R., Michalak, J. L., Lawler, J. J., Nielsen, S. E., Stralberg, D., Hamann, A., Mcrae, B. H., & Wang, T. (2017). Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. *Global Change Biology*, 23(11), 4508–4520.
- Cheddadi, R., Vendramin, G. G., Litt, T., François, L., Kageyama, M., Lorentz, S., Laurent, J.-M., Beaulieu, J.-L. D., Sadori, L., Jost, A., & Lunt, D. (2006). Imprints of glacial refugia in the modern genetic diversity of *Pinus sylvestris*. *Global Ecology and Biogeography*, 15(3), 271–282. <https://doi.org/10.1111/j.1466-8238.2006.00226.x>
- Chytrý, M., Hennekens, S. M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F., Landucci, F., Schaminée, J. H. J., Ačić, S., Agrillo, E., Ambarlı, D., Angelini, P., Apostolova, I., Attorre, F., Berg, C., Bergmeier, E., Biurrun, I., Botta-Dukát, Z., Brisse, H., ... Yamalov, S. (2016). European Vegetation Archive (EVA): An integrated database of European vegetation plots. *Applied Vegetation Science*, 19(1), 173–180. <https://doi.org/10.1111/avsc.12191>
- Clark, P., & Hessel, A. (2015). The effects of rock climbing on cliff-face vegetation. *Applied Vegetation Science*, 18, 705–715. <https://doi.org/10.1111/avsc.12172>
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., ... Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, 27(11), 2279–2297. <https://doi.org/10.1111/gcb.15569>
- De Pauw, K., Depauw, L., Calders, K., Caluwaerts, S., Cousins, S. A. O., De Lombaerde, E., Diekmann, M., Frey, D., Lenoir, J., Meeussen, C., Orczewska, A., Plue, J., Spicher, F., Zellweger, F., Vangansbeke, P., Verheyen, K., & De Frenne, P. (2023). Urban forest microclimates across temperate Europe are shaped by deep edge effects and

- forest structure. *Agricultural and Forest Meteorology*, 341, 109632. <https://doi.org/10.1016/j.agrformet.2023.109632>
- Delarze, R., Gonseth, Y., Eggenberg, S., & Vust, M. (2015). *Guide des milieux naturels de Suisse: Écologie, menaces, espèces caractéristiques*. Rossolis.
- Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, 17(2), 1022–1035. <https://doi.org/10.1111/j.1365-2486.2010.02263.x>
- Ducci, F., & Donnelly, K. (2018). Forest tree marginal populations in Europe—Report on the state of knowledge on forest tree marginal and peripheral populations in Europe. *Annals of Silvicultural Research*, 41(3), 1–12. <https://doi.org/10.12899/asr-1586>
- Ellenberg, H. (1963). *Vegetation Mitteleuropas mit den Alpen: In kausaler, dynamischer und historischer Sicht*. Ulmer.
- Ellenberg, H. (1988). *Vegetation ecology of central Europe*. Cambridge University Press.
- Ellenberg, H. (1991). Zeigerwerte von pflanzen in Mitteleuropa. *Scr Geobot*, 18, 1–248.
- Ellenberg, H., & Klötzli, F. A. (1972). Waldgesellschaften und waldstandorte der Schweiz. Eidgenössische Anstalt für das Forstliche Versuchswesen.
- Federal Office of Topography swisstopo. (2022). *swissALTI3D, The high precision digital elevation model of Switzerland*. <https://www.swiss topo.admin.ch/en/geodata/height/alti3d.html>
- Finocchiario, M., Médail, F., Saatkamp, A., Diadema, K., Pavon, D., & Meineri, E. (2023). Bridging the gap between microclimate and microrefugia: A bottom-up approach reveals strong climatic and biological offsets. *Global Change Biology*, 29(4), 1024–1036. <https://doi.org/10.1111/gcb.16526>
- Fischer, A. M., Strassmann, K. M., Croci-Maspoli, M., Hama, A. M., Knutti, R., Kotlarski, S., Schär, C., Schnadt Poberaj, C., Ban, N., Bavay, M., Beyerle, U., Bresch, D. N., Brönnimann, S., Burlando, P., Casanueva, A., Fatichi, S., Feigenwinter, I., Fischer, E. M., Hirschi, M., ... Zubler, E. M. (2022). Climate scenarios for Switzerland CH2018—Approach and implications. *Climate Services*, 26, 100288. <https://doi.org/10.1016/j.cliser.2022.100288>
- Frei, E. R., Gossner, M. M., Vitasse, Y., Queloz, V., Dubach, V., Gessler, A., Ginzler, C., Hagedorn, F., Meusburger, K., Moor, M., Samblás Vives, E., Rigling, A., Uitentuis, I., von Arx, G., & Wohlgemuth, T. (2022). European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland. *Plant Biology (Stuttgart, Germany)*, 24(7), 1132–1145. <https://doi.org/10.1111/plb.13467>
- Gobet, E., Vescovi, E., & Tinner, W. (2010). Ein paläoökologischer Beitrag zum besseren Verständnis der natürlichen Vegetation der Schweiz. *Botanica Helvetica*, 120(2), 105–115. <https://doi.org/10.1007/s00035-010-0080-2>
- Graham, L., & Knight, R. L. (2004). Multi-scale comparisons of cliff vegetation in Colorado. *Plant Ecology*, 170(2), 223–234. <https://doi.org/10.1023/B:VEGE.0000021675.32902.7f>
- Greiser, C., Ehrlén, J., Meineri, E., & Hylander, K. (2020). Hiding from the climate: Characterizing microrefugia for boreal forest understory species. *Global Change Biology*, 26(2), 471–483. <https://doi.org/10.1111/gcb.14874>
- Greiser, C., Hederová, L., Vico, G., Wild, J., Macek, M., & Kopecký, M. (2024). Higher soil moisture increases microclimate temperature buffering in temperate broadleaf forests. *Agricultural and Forest Meteorology*, 345, 109828. <https://doi.org/10.1016/j.agrformet.2023.109828>
- Haesen, S., Lembrechts, J. J., De Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M. B., Kopecký, M., Luoto, M., Maclean, I., Nijs, I., Niittynen, P., van den Hoogen, J., Arriga, N., Bruna, J., Buchmann, N., Čiliak, M., Collalti, A., De Lombaerde, E., Descombes, P., ... Van Meerbeek, K. (2023). ForestClim—Bioclimatic variables for microclimate temperatures of European forests. *Global Change Biology*, 29(11), 2886–2892. <https://doi.org/10.1111/gcb.16678>
- Haesen, S., Lenoir, J., Gril, E., De Frenne, P., Lembrechts, J. J., Kopecký, M., Macek, M., Man, M., Wild, J., & Van Meerbeek, K. (2023). Microclimate reveals the true thermal niche of forest plant species. *Ecology Letters*, 26, 2043–2055. <https://doi.org/10.1111/ele.14312>
- Haig, A. R., Matthes, U., & Larson, D. (2011). Effects of natural habitat fragmentation on the species richness, diversity, and composition of cliff vegetation. *Canadian Journal of Botany*, 78, 786–797. <https://doi.org/10.1139/b00-047>
- Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, 8(5), 461–467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>
- Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, 29(7), 390–397. <https://doi.org/10.1016/j.tree.2014.04.006>
- Härtel, H., Cílek, V., Herben, T., Jackson, A., & Williams, R. (2007). *Sandstone landscapes*. Academia Praha.
- Hewitt, G. M. (1999). Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, 68(1–2), 87–112. <https://doi.org/10.1111/j.1095-8312.1999.tb01160.x>
- Hylander, K., Ehrlén, J., Luoto, M., & Meineri, E. (2015). Microrefugia: Not for everyone. *Ambio*, 44(1), 60–68. <https://doi.org/10.1007/s13280-014-0599-3>
- Info Flora. (2023). The National Data and Information Center on the Swiss Flora. <https://www.infoflora.ch/en/>
- Körner, C., & Hiltbrunner, E. (2018). The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics*, 30, 16–21. <https://doi.org/10.1016/j.ppees.2017.04.004>
- Körner, C., & Spehn, E. M. (2019). *Mountain biodiversity: A global assessment* (Vol. 7). CRC Press.
- Kruskal, J. B. (1964). Nonmetric multidimensional scaling: A numerical method. *Psychometrika*, 29(2), 115–129.
- Kuntz, K. L., & Larson, D. W. (2006). Microtopographic control of vascular plant, bryophyte and lichen communities on cliff faces. *Plant Ecology*, 185(2), 239–253.
- Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmli, W., Nobis, M., Rudmann, K., Schweingruber, F. H., Theurillat, J.-P., Urmi, E., Vust, M., & Wohlgemuth, T. (2010). *Flora indicativa: Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Haupt Verlag.
- Larson, D. W., Matthes, U., & Kelly, P. E. (2005). *Cliff ecology: Pattern and process in cliff ecosystems*. Cambridge University Press.
- Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, 40(2), 253–266. <https://doi.org/10.1111/ecog.02788>
- Leuschner, C., & Ellenberg, H. (2017). *Ecology of central European forests: Vegetation ecology of Central Europe, volume I*. Springer International Publishing. <https://doi.org/10.1007/978-3-319-43042-3>
- Lüth, M. (1993). *Felsen und Blockhalden*. Landesanstalt für Umweltschutz Baden-Württemberg.
- Maclean, I. M. D., Duffy, J. P., Haesen, S., Govaert, S., De Frenne, P., Vanneste, T., Lenoir, J., Lembrechts, J. J., Rhodes, M. W., & Van Meerbeek, K. (2021). On the measurement of microclimate. *Methods in Ecology and Evolution*, 12(8), 1397–1410. <https://doi.org/10.1111/2041-210X.13627>
- March-Salas, M., Lorite, J., Bossdorf, O., & Scheepens, J. F. (2023). Cliffs as priority ecosystems. *Conservation Biology*, 37(5), e14166. <https://doi.org/10.1111/cobi.14166>
- Meeussen, C., Govaert, S., Vanneste, T., Bollmann, K., Brunet, J., Calders, K., Cousins, S. A. O., De Pauw, K., Diekmann, M., Gasperini, C., Hedwall, P.-O., Hylander, K., Iacopetti, G., Lenoir, J., Lindmo, S., Orczewska, A., Ponette, Q., Plue, J., Sanczuk, P., ... De Frenne, P. (2021). Microclimatic edge-to-interior gradients of European deciduous forests. *Agricultural and Forest Meteorology*, 311, 108699. <https://doi.org/10.1016/j.agrformet.2021.108699>

- Meier, E. S., Edwards, T. C., Jr., Kienast, F., Dobberty, M., & Zimmermann, N. E. (2011). Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography*, 38(2), 371–382. <https://doi.org/10.1111/j.1365-2699.2010.02405.x>
- MeteoSwiss. (2023a). *Climate normals, Federal Office for Meteorology and Climatology*. <https://www.meteoswiss.admin.ch/climate/the-climate-of-switzerland/climate-normals.html>
- MeteoSwiss. (2023b). *Data portal for teaching and research (IDAweb), Federal Office for Meteorology and Climatology*. <https://gate.meteoswiss.ch/idaweb/>
- Michalak, J. L., Stralberg, D., Cartwright, J. M., & Lawler, J. J. (2020). Combining physical and species-based approaches improves refugia identification. *Frontiers in Ecology and the Environment*, 18(5), 254–260. <https://doi.org/10.1002/fee.2207>
- Millar, C. I., Charlet, D. A., Westfall, R. D., King, J. C., Delany, D. L., Flint, A. L., & Flint, L. E. (2018). Do low-elevation ravines provide climate refugia for subalpine limber pine (*Pinus flexilis*) in the Great Basin, USA? *Canadian Journal of Forest Research*, 48(6), 663–671.
- Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020). Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, 18(5), 228–234. <https://doi.org/10.1002/fee.2189>
- Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing climate change refugia for climate adaptation. *PLoS One*, 11(8), e0159909. <https://doi.org/10.1371/journal.pone.0159909>
- Mosblech, N. A. S., Bush, M. B., & van Woesik, R. (2011). On metapopulations and microrefugia: Palaeoecological insights. *Journal of Biogeography*, 38(3), 419–429.
- Müller, S. W., Rusterholz, H.-P., & Baur, B. (2004). Rock climbing alters the vegetation of limestone cliffs in the northern Swiss Jura Mountains. *Canadian Journal of Botany*, 82(6), 862–870. <https://doi.org/10.1139/b04-058>
- Novák, J., Abraham, V., Šída, P., & Pokorný, P. (2019). Holocene forest transformations in sandstone landscapes of The Czech Republic: Stand-scale comparison of charcoal and pollen records. *The Holocene*, 29(9), 1468–1479. <https://doi.org/10.1177/0959683619854510>
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. (2007). The vegan package. *Community Ecology Package*, 10(631–637), 719.
- Parducci, L., Jørgensen, T., Tollefsrud, M. M., Elverland, E., Alm, T., Fontana, S. L., Bennett, K. D., Haile, J., Matetovici, I., Suyama, Y., Edwards, M. E., Andersen, K., Rasmussen, M., Boessenkool, S., Coissac, E., Brochmann, C., Taberlet, P., Houmark-Nielsen, M., Larsen, N. K., ... Willerslev, E. (2012). Glacial survival of boreal trees in northern Scandinavia. *Science*, 335(6072), 1083–1086. <https://doi.org/10.1126/science.1216043>
- Pastore, M. A., Classen, A. T., D'Amato, A. W., Foster, J. R., & Adair, E. C. (2022). Cold-air pools as microrefugia for ecosystem functions in the face of climate change. *Ecology*, 103(8), e3717. <https://doi.org/10.1002/ecy.3717>
- Podani, J. (2006). Braun-Blanquet's legacy and data analysis in vegetation science. *Journal of Vegetation Science*, 17(1), 113–117. <https://doi.org/10.1111/j.1654-1103.2006.tb02429.x>
- R Core Team. (2022). *R: A Language and Environment for Statistical Computing, version 4.1.3*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rennenberg, H., Dannenmann, M., Gessler, A., Kreuzwieser, J., Simon, J., & Papen, H. (2009). Nitrogen balance in forest soils: Nutritional limitation of plants under climate change stresses. *Plant Biology*, 11(s1), 4–23. <https://doi.org/10.1111/j.1438-8677.2009.00241.x>
- Rey, F., Gobet, E., van Leeuwen, J. F., Gilli, A., van Raden, U. J., Hafner, A., Wey, O., Rhiner, J., Schmocker, D., & Zünd, J. (2017). Vegetational and agricultural dynamics at Burgäschisee (Swiss plateau) recorded for 18,700 years by multi-proxy evidence from partly varved sediments. *Vegetation History and Archaeobotany*, 26(6), 571–586.
- Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf, U., Mayer, P., Vacchiano, G., Weber, P., Wohlgemuth, T., Zweifel, R., & Dobberty, M. (2013). Driving factors of a vegetation shift from scots pine to pubescent oak in dry alpine forests. *Global Change Biology*, 19(1), 229–240. <https://doi.org/10.1111/gcb.12038>
- Rull, V. (2009). Microrefugia. *Journal of Biogeography*, 36(3), 481–484. <https://doi.org/10.1111/j.1365-2699.2008.02023.x>
- Rytz, W. (1913). Geschichte der Flora des Bernischen Hügellandes zwischen Alpen und Jura. *Mitteilungen der Naturforschenden Gesellschaft in Bern aus dem Jahre, 1912*, 49–221.
- Scherrer, D., & Körner, C. (2010). Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology*, 16(9), 2602–2613. <https://doi.org/10.1111/j.1365-2486.2009.02122.x>
- Schmid, E. (1941). Vegetationsgürtel und Biocoenose. *Bericht der Schweizerischen Botanischen Gesellschaft*, 51, 461–474.
- Schmid, E. (1944). Kausale Vegetationsforschung. *Berichte Des Geobotanisches Institut ETH, Stiftung Rübel*, 35, 44–68.
- Schmid, E. (1945). *Vegetationskarte der Schweiz, 1: 20000, in 4 Blättern*. Pflanzengeogr. Kommission der Schweiz. Naturf. Gesellschaft.
- Sobierajska, K., Wachowiak, W., Zaborowska, J., Łabiszak, B., Wójcikiewicz, B., Sękiewicz, M., Jasińska, A. K., Sękiewicz, K., Boratyńska, K., & Marcysiak, K. (2020). Genetic consequences of hybridization in relict isolated trees *Pinus sylvestris* and the *Pinus mugo* Complex. *Forests*, 11(10), 1086.
- Sommaruga, A., Eichenberger, U., & Marillier, F. (2012). *Seismic atlas of the Swiss Molasse Basin (Federal Office of Topography swisstopo, Swiss Geophysical Commission)*.
- Stewart, J. R., Lister, A. M., Barnes, I., & Dalén, L. (2010). Refugia revisited: Individualistic responses of species in space and time. *Proceedings of the Royal Society B: Biological Sciences*, 277(1682), 661–671. <https://doi.org/10.1098/rspb.2009.1272>
- van der Maarel, E. (1979). Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio*, 39(2), 97–114. <https://doi.org/10.1007/BF00052021>
- Walter, H., & Breckle, S.-W. (1985). *Ecological systems of the geo-biosphere*. Springer.
- Weidmann, M. (2006). Feuille 1184 Payerne, Notice explicative. In *Geologischer Atlas des Schweiz—Atlas géologique de la Suisse 1:25 000*. Bundesamt für Topographie—Office fédéral de la topographie.
- Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J., & Haase, T. (2019). Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. *Agricultural and Forest Meteorology*, 268, 40–47. <https://doi.org/10.1016/j.agrformet.2018.12.018>
- Wohlgemuth, T. (2012). Swiss forest vegetation database. *Biodiversity and Ecology*, 4, 340–340. <https://doi.org/10.7809/b-e-00131>
- Wohlgemuth, T., Moser, B., Brändli, U.-B., Kull, P., & Schütz, M. (2008). Diversity of forest plant species at the community and landscape scales in Switzerland. *Plant Biosystems—An International Journal Dealing with all Aspects of Plant Biology*, 142(3), 604–613. <https://doi.org/10.1080/11263500802410975>
- Wolf, K. D., Higuera, P. E., Davis, K. T., & Dobrowski, S. Z. (2021). Wildfire impacts on forest microclimate vary with biophysical context. *Ecosphere*, 12(5), e03467. <https://doi.org/10.1002/ecs2.3467>
- Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., Kirby, K. J., Brunet, J., Kopecký, M., Máliš, F., Schmidt, W., Heinrichs,

S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K., & De Frenne, P. (2019). Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, 28(12), 1774–1786. <https://doi.org/10.1111/geb.12991>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Fragnière, Y., Champoud, L., Küffer, N., Braillard, L., Jutzi, M., Wohlgemuth, T., & Kozłowski, G. (2024). Cliff-edge forests: Xerothermic hotspots of local biodiversity and models for future climate change. *Global Change Biology*, 30, e17196. <https://doi.org/10.1111/gcb.17196>