Julius-Maximilians-Universität Würzburg

Studiengang Biologie (6-semestrig, 180 ECTS)

Climbing the summit: Alpine butterfly communities in the light of climate change

A local study in the Swiss National Park

Bachelor-Thesis

von

Korbinian Schrauth

Datum der Abgabe: 16.12.2025

Prüfer: Prof. Dr. Jörg Müller

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Abstract

Climate change is known to cause communities to shift to higher altitudes in mountainous regions. Butterflies have been extensively studied and are sensitive to changes in environmental conditions, making them well-suited for examining this effect. Between 1998 and 2004, as well as in 2025, butterflies in the Swiss National Park (SNP) were surveyed using the semi-quantitative transect method. Although the study areas were not identical, a high degree of consistency was found in the butterfly communities. It was shown that in 2025, the same species were found at an altitude on average 135 m higher than 21 years earlier, the increase being more pronounced for cold-adapted species. In addition, the Community Temperature Index rose, indicating more thermophilic communities, especially at low and medium altitudes. For the data collected in 2025, it was shown that the existing habitats are responsible to a great extent for the composition of the butterfly communities, while altitude alone plays a comparatively minor role and tends to have an effect in combination with habitat availability. The pronounced reaction of butterfly communities to global warming is particularly threatening to high-alpine species that are adapted to cold conditions and have a narrow temperature niche. In this context, the habitat dependence of butterflies may have negative effects in the future due to a mismatch of the altitudinal distribution of butterflies and their host plants, as well as positive effects due to a buffering effect by rather constant habitat conditions.

Zusammenfassung

Es ist bekannt, dass es durch den Klimawandel in Gebirgsregionen zu Verschiebungen von Artgemeinschaften in höhere Lagen kommt. Tagfalter sind gut erforscht und reagieren empfindlich auf Veränderungen in den Umweltbedingungen, weshalb sie sich gut eignen, diesen Effekt genauer zu beleuchten. Im Zeitraum von 1998-2004 sowie im Jahr 2025 wurden im Schweizerischen Nationalpark (SNP) Tagfalter mittels der semiquantitativen Transekt-Methode erfasst. Obwohl die Untersuchungsflächen nicht identisch waren, konnte eine große Übereinstimmung in den Tagfalter-Gemeinschaften gefunden werden. Es wurde gezeigt, dass dieselben Arten 2025 um durchschnittlich 135 m höher gefunden wurden als noch 21 Jahre zuvor, wobei der Anstieg bei kälteadaptierten Arten umso größer war. Zudem stieg der Community Temperature Index an, was eine gestiegene Thermophilie bedeutet. Hier waren vor allem niedrige und mittlere Höhenlagen betroffen. Für die 2025 erhobenen Daten wurde gezeigt, dass die vorhandenen Habitate zu einem weit größeren Teil für die Zusammensetzung der Tagfaltergemeinschaften verantwortlich sind als die Höhe allein, die eine vergleichsweise geringe Rolle spielt und eher in Kombination mit der Habitat-Verfügbarkeit wirkt. Die ausgeprägte Reaktion der Tagfaltergemeinschaften auf die Klimaerwärmung bringt vor allem hochalpine, kälteangepasste Arten mit einer engen Temperaturnische in Bedrängnis, wobei die Habitat-Bindung der Tagfalter in diesem Zusammenhang zukünftig sowohl negative Effekte durch eine Entkopplung der Höhenverbreitung der Tagfalter und ihrer Wirtspflanzen als auch eine abfedernde Wirkung bei konstanten Habitat-Eigenschaften haben kann.

1. Introduction

Since greenhouse gas emissions have increased with industrialisation in the 19th century, a global warming of 1.24 °C has been observed (Forster et al., 2025). Meanwhile, Switzerland has warmed by 2.9 °C already (Steinemann et al., 2025). This has to do with the country's location, as in the Alps, temperatures are rising even faster than elsewhere (Pepin et al., 2022). Apart from rising temperatures, climate change in the Alps also alters precipitation regimes (Gobiet et al., 2014) and drives glacier retreat, permafrost degradation (Biskaborn et al., 2019; Rounce et al., 2023) and geomorphic processes such as increased slope movements and instability (Stoffel and Huggel, 2012; East and Sankey, 2020), resulting in a drastic change in environmental conditions.

At the same time, mountain regions as the Swiss Alps are generally known to be hotspots of biodiversity (Rahbek et al., 2019). Despite its comparatively small area, Switzerland is inhabited by 202 different butterfly species (Baudraz et al., 2020), accounting for 40% of the 496 species known in Europe (Wiemers et al., 2018). The Alps play a major role in this diversity of butterflies, 25 % of butterfly species in Switzerland are mountainous and alpine species, further 10 % are confined to the Alps in Switzerland (Baudraz et al., 2020). The topographic variety and the elevational gradient of mountain ranges resulting in a great diversity of environmental conditions and vegetation on a small spatial scale (Badgley et al., 2017) is one of the reasons for butterfly richness in Switzerland. The vast majority of butterfly species are associated with a limited set of host plants for their larval development (Schweizerischer Bund für Naturschutz, 1987; Klaiber et al., 2017). Thus, the distribution of butterflies is restricted by the range of their host plants. Apart from host plant availability, other factors as microclimate, soil chemistry, nutrient availability and vegetation structure limit suitable habitats (Schweizerischer Bund für Naturschutz, 1987; Weidemann, 1995; Hanspach et al., 2014). However, the factors limiting the distribution of butterflies are not always clearly distinguishable from one another. In high mountains, for example, altitude and habitat are often closely intertwined as drivers, since many species are specialised in specific montane and alpine habitats, which in turn are limited in their altitudinal distribution (Schweizerischer Bund für Naturschutz, 1987; Sonderegger, 2005). It is therefore often unclear to what extent temperature niches and available habitats including host plants and further parameters are responsible for the distribution of alpine butterflies.

However, understanding these drivers is becoming increasingly important. With current climate change, mountain ecosystems worldwide are in a state of upheaval: as temperatures are rising, communities formerly well adapted for their ecological niches in the cold and harsh conditions in alpine regions are becoming increasingly thermophilic (Gottfried et al., 2012; Roth et al., 2014; Khaliq et al., 2024). To maintain their physiological temperature niche, species shift to higher elevations (Parmesan and Yohe, 2003; Parolo and Rossi, 2008; Chen et al., 2009), whereby cold-adapted species decline as warm-adapted species increase in range (Engelhardt et al., 2022). The butterfly communities of the Alps are not exempt from these changes (Parmesan and Yohe, 2003; Parolo and Rossi, 2008; Chen et al., 2009).

Due to their complex ecology and as ectotherms, they are known to respond especially sensitive to environmental changes, making them particularly suitable for studying these processes (Schweizerischer Bund für Naturschutz, 1987; Reinhardt et al., 2021).

Equally well suited for studying long-term environmental changes is the Swiss National Park (SNP): As the oldest national park of the Alps, it can look back over more than a century of research, which was started with its foundation in 1914 (Haller et al., 2014). One of the first taxa to be studied in the SNP region was butterflies. From 1920 to 1941, A. Pictet surveyed butterflies in the SNP region and provided a detailed description of the distribution of species in the region (Pictet, 1942). 60 years later, A. Besson, M. Bouchard, M. Macherez and A. Pasche took an inventory of butterflies in the SNP that was designed to obtain as complete a record as possible with minimal effort on only 20 plots with surveys in 1998, 2001 and 2004. For the first time, they provided not only qualitative information but also quantitative data about the butterflies of the SNP (Pasche et al., 2007; Gonseth et al., 2013). As a result of the inventory, PASCHE et al. (2007) found upper as well as lower limits of altitudinal ranges shifted upward for several species in comparison to the descriptions given by PICTET (1942), reflecting their responses to climate change. However, it was not possible to make a general statement or quantification, as PICTET (1942) only provided qualitative data. Today, with a data basis enlarged by the inventory and climate change proceeding, the thorough butterfly studies in the SNP region are an excellent resource for examining developments in alpine butterfly communities over recent decades and situating them within a long-term climate change trend.

Against this background, another butterfly survey was performed in the SNP region in 2025. Two continuous transects over an altitudinal gradient of 880 m and 1125 m, respectively, were established for an accurate record of altitudinal ranges per species. On these transects, butterflies were counted weekly for three months of alpine spring and summer. Based on this data and a habitat map of the SNP, an attempt was made to disentangle the influences of altitude and habitats as determinants for the composition of alpine butterfly communities. Additionally, this study aims to quantitatively verify the shifts previously observed and to demonstrate the responses to climate warming generally known for butterflies in the Alps in the SNP, using the inventory data from 1998 to 2004. Therefore, the following hypotheses were tested:

H1: Drivers of alpine butterfly communities: Available habitats and altitude each influence the composition of butterfly communities in an alpine context.

H2: Community response to climate change: As a result of climate change, butterfly communities are more thermophilic today compared to 21 years ago.

H3: Species response to climate change: As temperatures have risen since the beginning of the millennium, butterfly species are distributed in higher elevations today compared to then.

2. Material & Methods

2.1. Study area

This study was conducted in the Swiss National Park (SNP) in the Central Alps. The SNP is located at the south-eastern edge of Switzerland. Established in 1914, the SNP is aiming for a strict preservation of natural processes. This wilderness area of Category 1a, according to the classification scheme of the International Union for Conservation of Nature (IUCN), has a surface area of 170.3 km^2, including various habitats in an altitudinal range from 1’380 m a.s.l. up to 3’173 m a.s.l. (Schlüchter et al., 2021). Adjacent areas to the SNP, which can be difficult to access due to their location in high alpine terrain, are used extensively for livestock farming and forestry.

Compared to other regions in the Alps, the climate in the region of the SNP is dry and continental with a pronounced annual cycle. In winter, there is a continuous blanket of snow for months. Due to the alpine terrain, temperatures are mainly determined by altitude and exposition (Gubler and Robinson, 2025; Haller et al., 2014). In Buffalora at the eastern edge of the SNP (1’971 m a.s.l.), mean annual temperature (MAT) is 1.1 °C with a mean annual precipitation of 936 mm (MeteoSwiss, 2025). Since 1917, MAT has increased by 2.1 °C with warming accelerating since the late 1980s, while mean annual precipitation has been decreasing since 2010 after a long period of stability (Gubler and Robinson, 2025).

The study sites are located inside or in the immediate surroundings of the SNP. Two transects were established, both following hiking trails: one of them (Transect 1) is in the valley Val dal Botsch (VdB) at the center of the national park (Figure 1). The lowest parts are on the north-facing southern bank of the Fuorn stream, whereas the majority of the transect follows the south-facing valley and climbs its south-exposed slopes on porous dolomite (Swisstopo, 2025) . Transect 1 covers an altitudinal range of 883 metres from 1’794 m a.s.l. to 2’677 m a.s.l. on 5.8 kilometres horizontal distance. In the lowest part of the transect, former pastures border the transect. The dominating tree species around this area is the mountain pine (*Pinus mugo* TURRA), other tree species occur occasionally in the lowest parts of the transect (Haller et al., 2014). The forest line is around 2’050m and is followed by a dynamic mosaic of isolated trees, shrubs, alpine meadows, scree, and the stream bed. From 2’250 m a.s.l. upwards, garland-shaped grass patterns shape the vegetation. From 2’500 m a.s.l. onwards, alpine grasslands interspersed with scree fields and exposed rock take over.

The Zeznina-Macun (ZM) transect (Transect 2) is located further west at the high alpine lake plateau of Macun, an exclave of the national park (Figure 1). The majority of this transect is outside the protected areas in the north facing valley Val Zeznina crossing the border into the national park when reaching the Macun plateau, which is passed in its upper part. This second transect covers an altitudinal range of 1’125 m from 1’730 m a.s.l. up to 2’855 m a.s.l. on 7.6 kilometres in north- and north-west facing slopes. At 1’730 m a.s.l., the transect starts in a cattle-grazed spruce forest, which leads into an equally grazed

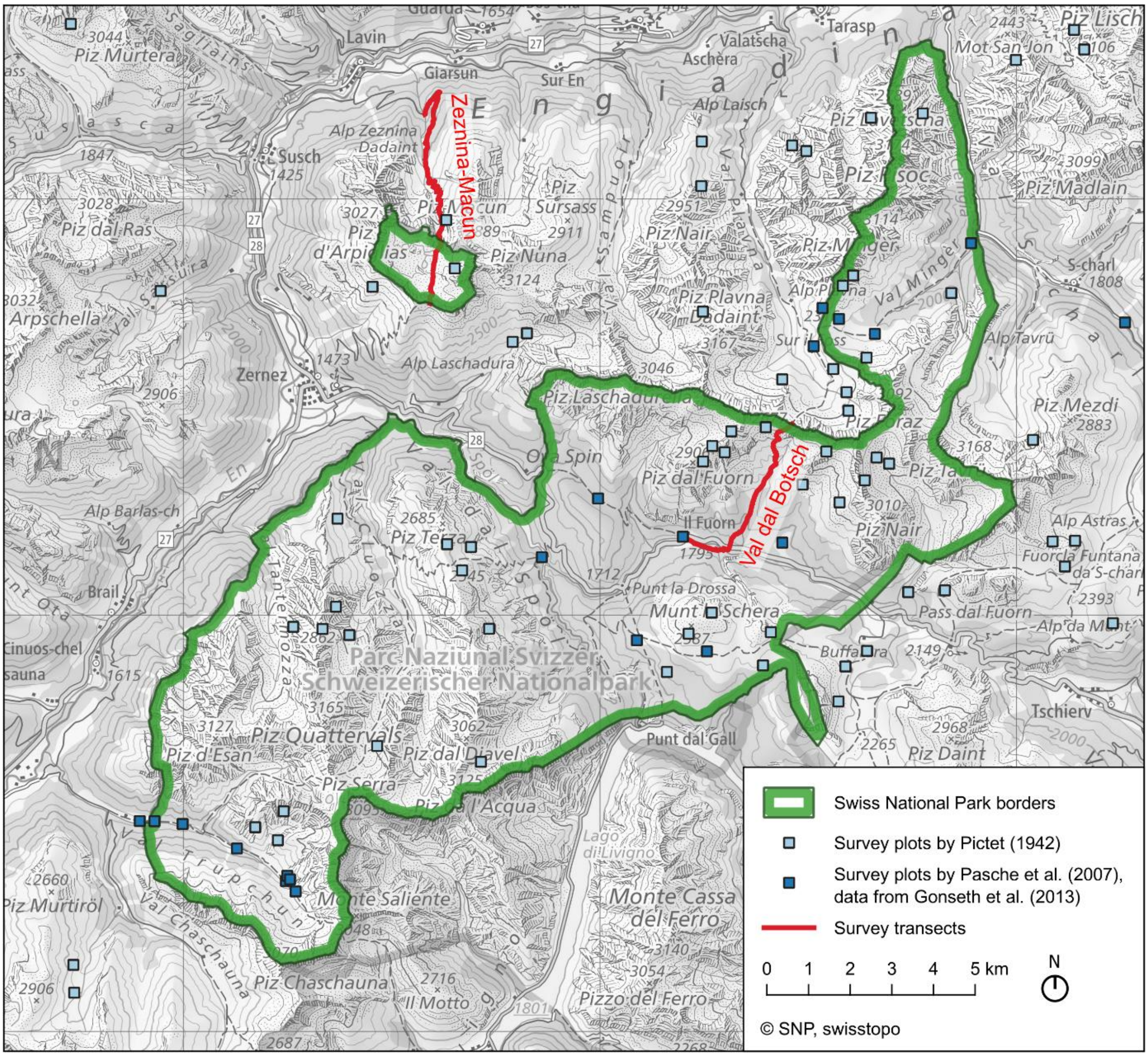

Figure 1: Butterfly research in and around the Swiss National Park: map of the study area. The transects surveyed in 2025 are displayed in red, transect 1 (VdB) in the east within the borders of the national park, transect 2 (ZM) crossing its border from Val Zeznina to the Macun high plateau. The dark blue plots resemble the study plots used by Pasche et al. (2007), whose data were used for analyses in this study. The six plots in the center of the national park (region Il Fuorn) were surveyed in 1998, eight plots in Val Trupchun in the south-west of the national park in 2001 and six plots in the north-east of the national park in 2004. The light blue plots are mentioned by A. Pictet for his findings in the period from 1922 to 1942 (Pictet 1942). The data structure does not allow for quantitative analyses, but due to the long observation period and the large spatial coverage, his observations and descriptions of frequencies can make a valuable contribution to contextualising data and results within a larger time frame.

forest of larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.), before the transect reaches the alpine pastures around the Alp Zeznina Dadaint at 1’920 m a.s.l.. Here it continues up to the Macun lake plateau entering the national park on 2’550 m a.s.l. after traversing several scree fields. On the plateau, the transect passes alpine grasslands interspersed with rocks, scree and very sparsely vegetated areas. From 2’750 m a.s.l. upwards nearly bare scree and a few isolated snowfields are crossed. Shortly before reaching the upper end at 2’855 m a.s.l., some sparse vegetation is found. In contrast to transect 1 in VdB, transect 2 in ZM is located on crystalline and thus silicate bedrock such as gneisses and amphibolites (Gubler and Robinson, 2025; Swisstopo, 2025).

The butterfly surveys conducted in 1998, 2001, and 2004 in the SNP region used 20 study plots of an area of a 0.25 ha which are scattered across the SNP on elevational gradients at three distinct sites (Gonseth et al., 2013; Pasche, 2005). The first six plots surveyed in 1998 are in the catchment area of the Pass dal Fuorn at the center, eight plots surveyed in 2001 are in Val Trupchun to the south, and the last six plots surveyed in 2004 are in Val Mingér to the north of the SNP (Figure 1). Most of the plots used in this study are located on dolomite bedrock, except in Val Trupchun, which is located on marl bedrock (Haller et al., 2014; Swisstopo, 2025). The covered habitats largely resemble those which are passed by the two transects, although forest areas and scree fields are underrepresented (Pasche, 2005; Haller et al., 2014).

2.2. Butterfly survey

The butterfly surveys were based on the methodology used in the Swiss Biodiversity Monitoring (BDM, Biodiversitäts-Monitoring Schweiz 2021) which was applied to the two transects established in the perimeter of the SNP. In the three months from June 10th to September 10th, each transect was surveyed twelve times in a weekly interval (3 to 11 days in between each transect walk, average 6.5 days, Table 1). The number of transect surveys and the length of the transects represent differences from the BDM method, since for the BDM, transects of 2.5 kilometres are surveyed back and forth seven, six or four times, respectively, during the vegetation period regarding to altitude. From the start of the sampling period to August 10th, the transects were walked in a time interval between 10 a.m. and 5 p.m.. After August 10th, this time interval was shortened by one hour in the morning to 11 a.m. to 5 p.m. due to the later sunrise and longer shade in the valley areas. All individuals of butterflies (Lepidoptera: Papilionoidea) and burnet moths (Lepidoptera: Zygaenidae) that were within a 5 m radius of the observer or flew through this area were counted while the transect was walked at a maximum speed of 3 km/h. For wide paths (e.g. forest roads), the recording area consisted of a hemisphere with a radius of 5 m at the position of the operator, half on the left and half on the right side of the path, including the path or road section in between. The observations were recorded using the Webfauna app (Gerber et al., 2025), which located all individuals precisely via GPS coordinates. Suitable weather conditions were a prerequisite for a transect survey. The maximum acceptable wind speed was 3 Bf or 19 km/h. Air temperatures one metre above the ground had to be at least 13 °C, and there had to be sunshine (meaning shadows are clearly visible) on at least 80 % of the length of the transect. At high elevations, lower temperatures and higher wind speeds were accepted if there was usual butterfly activity, but the transects were only walked in high altitudes when there was sunshine. In case of passing clouds and persistent strong winds, the walk was paused and only resumed 5 minutes after suitable weather conditions returned (Biodiversitäts-Monitoring Schweiz, 2021). On July 31st the transect walk had to be abandoned due to unstable and unsuitable weather conditions. To avoid biases by diurnal activity patterns, the start time of the transect walks was varied and the surveys were started in different sections: at the upper end, the lower end and the middle of the transect. Shading due to exposition was avoided as far as possible by choosing a favourable time of day. Due to its length, transect 2 was surveyed on two consecutive days. This practice was also once applied on transect 1 because weather conditions did not allow for surveying the whole transect on a single day. Whenever possible, butterflies were identified at the species level by visual inspection. If this was not possible due to distance or butterflies were only flying past, these individuals were caught with a net for identification. In cases of doubt, the identification key given by Baudraz et al. (2020) was consulted. Grizzled skippers (Hesperiidae: *Pyrgus sp*.) that could not be identified based on external characteristics, individuals out of the *Melitaea athalia* – complex and Forester moths (Zygaenidae: Procridinae) were collected and identified by genital dissection. The species complexes *Leptidea sinapis – juvernica* and *Colias alfacariensis – hyale* were not identified at the species level. Heavily worn individuals that could no longer be reliably identified were not included. The nomenclature was adopted from Wiemers et al. (2018).

Table 1: Dates of the transect walks for each round and transect.

round	Transect 1 (VdB)	Transect 2 (ZM)
1	11.06.2025	18./19.06.2025
2	17.06.2025	24./25.06.2025
3	28.06.2025	29.06.2025
4	04.07.2025	10./11.07.2025
5	12.07.2025	14./15.07.2025
6	18.07.2025	20./22.07.2025
7	29./30.07.2025	31.07.2025
8	08.08.2025	05./06.08.2025
9	13.08.2025	10./11.08.2025
10	18.08.2025	15./17.08.2025
11	26.08.2025	23./24.08.2025
12	07.09.2025	03./04.09.2025

For the old data, butterflies were surveyed on 20 plots at three different sites. Within each plot, a transect of 320 or 350 m was established, where butterflies were counted using the same method as was used in 2025. Burnet moths were not recorded. Each transect was surveyed five to six times from mid-June to early September at regular intervals (Pasche, 2005).

From 1920 to 1941, A. Pictet compiled an inventory of the butterflies in the SNP region. In 22 field seasons from May until September with about 30 field days each, butterflies and their abundances were recorded in the SNP and its surroundings (Figure 1), which was summarized in a thorough description for each species (Pictet, 1942). Although the data structure does not allow for quantitative analyses, his observations and descriptions of frequencies can make a valuable contribution to contextualising later observations, data and results within a larger time frame due to the long observation period and the large spatial coverage.

2.3. Statistical analyses

All statistical analyses were conducted with R version 4.3.2 (https://www.r-project.org). To assess the influence of habitat and altitude on the composition of butterfly communities only the recent data were used to take advantage of the continuous elevational gradient and to avoid distortion of the altitude effect due to possible differences in the altitudinal distribution of butterfly species between the two points of time. Both transects were split up in sections of 200 m distance. This choice was based on observations that during capture-recapture surveys, the majority of individuals of examined alpine butterfly species was recaptured within an area of 100m from their initial capture (Polic et al., 2014; Junker et al., 2010; Ehl et al., 2019). The proportions of the different habitat types and degrees of coverage within a 100 m radius around the centres of these 200 m sections were extracted from the HABITALP dataset (Lotz, 2006) using the *sf*-package (Pebesma et al., 2025). Afterwards, a variance partitioning was performed for the butterfly communities in the 200 m-sections with the habitat parameters and the altitude of the centres of the sections as predictors using the *vegan*-package (Oksanen et al., 2025). The effects were tested for robustness using redundancy analyses followed by ANOVA. As a dependency between habitat parameters and altitude could be assumed, habitat parameters were tested for a correlation to altitude in the same way using redundancy analysis.

The cold adaptation of butterflies was represented using the Species Temperature Index (STI). This index represents the average MAT across the geographic range per species (Schweiger et al., 2014). For both the old and the recent dataset, every recorded individual was assigned the STI value corresponding to its species. Because the old data only covered the altitudinal range from 1’672 m to 2’431 m a.s.l., the recent data were truncated at 2450 m a.s.l. and data from below were used for temporal comparison. Burnet moths were excluded from all following analyses as well as five species for which no STI values were provided (Schweiger et al., 2014). To preserve the advantages of the continuous elevational gradient of the recent data, the Community Temperature Index (CTI) was not used as a mean of STI values within predefined elevation bands. Instead, the totality of all STI values assigned to all surveyed individuals was used to represent the CTI. To analyse the relationship between CTI and elevation, and to test for differences between survey periods, a Generalized Additive Model (GAM) was fitted using the *mgcv*-package (Wood, 2025). For STI values of all specimens as dependent variable, a smooth term over elevation per year ($k = 3$) and the year of the survey were included as explanatory variables. k-value was selected to avoid oversmoothing due to too low values and overfitting due to too high values taking model diagnostics into account. A Gaussian family and an identity link function were used. To visualize the relationship between CTI and altitude for both survey periods, the GAM was plotted.

Because STI is drawn from a great geographical range and does neither differentiate between lowland and alpine subspecies nor account for local conditions in the Central Alps, a more specific Swiss Species

Temperature Index (SwSTI) was calculated in the same manner as the Europe-wide. Therefore, butterfly data from 2013 to 2024 for altitudes above 1’500 m a.s.l. of the BDM (Weber et al., 2004) was used. This restriction regarding altitude was imposed to select only areas in montane to alpine regions comparable to the SNP region. Each observation within this dataset was assigned the MAT value of the nearest datapoint in a raster of MAT values of Switzerland from 1981 to 2010 out of the SWECO dataset (Külling and Adde, 2024) using the *terra*-package (Hijmans et al., 2025). The fact that the periods when these two datasets were created do not overlap was disregarded, as SwSTI is a relative index. Because for several species the geographical range was only partially covered due to the restriction for data above 1’500 m a.s.l., SwSTI values were validated based on distribution, correspondence to STI, and habitat usage (Annex B). Seven species for which SwSTI was uncertain were excluded from the analysis (Annex A). The same analysis performed with the Europe-wide STI was repeated using the SwSTI instead. The model was built the same way with a smooth term over elevation per year ($k = 3$) and the year of the survey as predictors. Again, Gaussian family and an identity link function were used.

To compare species’ altitudinal distribution, species with at least ten observed individuals within the overlapping altitudinal range in both survey periods were selected. Afterwards, the mean altitude within the overlapping range was calculated per species and survey, and the two survey periods were compared by a t-test paired per species. The difference of the means between the survey periods was calculated per species and checked for a correlation with STI and SwSTI. Therefore, a linear model was built using STI and SwSTI as predictors for the differences in mean altitude.

3. Results

3.1. Butterfly assemblages

Overall, 6'030 individuals were counted during the transect survey in 2025. 58 of the 82 recorded species were found on transect 1 (VdB), 63 on transect 2 (ZM). An intersection of 39 species (47,6%) was found on both transects. In contrast, there are 14'071 individuals from 84 species counted in the old data by Pasche et al. (2007). Here, the intersection between the three sites is 30 species (35,7 %). Excluding burnet moths, which were not recorded by Pasche et al. (2007), species in both datasets match by 74,2%. Species missing in 2025 were mostly found in Val Trupchun (10 out of 15) and species newly discovered in 2025 are predominantly found on transect 2 (ZM, 7 out of 9). The five most abundant species in 2025 were *Erebia euryale* Esper 1805 (1008 individuals), *Erebia tyndarus* Esper 1781 (521 individuals), *Boloria pales* [Denis & Schiffermüller] 1775 (520 individuals), *Erebia pandrose* Borkhausen 1788 (416 individuals) and *Plebejus idas* Linnaeus 1761 (252 individuals). In the altitudinal range overlapping with that of the old data, *Lysandra coridon* Poda 1761 replaced *E. pandrose* among the five most abundant species. In the surveys performed from 1998 to 2004, *E. tyndarus*, *P. idas, E. euryale, L. coridon* and *Erebia melampus* Fuesslin 1775 were the species with highest recorded abundances, in descending order.

3.2. Drivers

Testing habitat and altitude for their influence on butterfly community composition, habitat was found to explain almost 30 % of the variance. The impact of altitude however appeared to be comparatively low with only 2 % of the variance explained suggesting habitat to be a better explanator for which species occurring where and how abundant. The shared effect of altitude and habitat, meaning the availability of specific habitats at a specific altitude, explained 9% of the variance in butterfly communities. Nevertheless, most of the variance with 62% remained unexplained (Table 2). Yet, habitat and altitude are not independent: more than a quarter of the variance in habitats is for explained by altitude (Table 3).

Table 2: Results of the variance partitioning for habitat and altitude as predictors for butterfly community composition. Habitat explains 28%, altitude 2% of the variance, both effects are highly significant. The shared effect of habitat and altitude explains utter 9% of the variance, while 61% remain unexplained.

Effects	**Adjusted R^2**	**F-value**	**p-value**
Habitat (independent)	0.277	2.103	< 0.01
Altitude (independent)	0.019	8.664	< 0.001
Shared effect Habitat + Altitude	0.085	-	-
Residuals	0.619	-	-

Table 3: Results of the redundancy analysis for the relation of habitat and altitude. Altitude clearly has an impact on habitat and explains 26% of its variance.

Component	Inertia	Proportion	Adjusted R^2	F-value	p-value
Constrained (Altitude)	809	0.271	0.260	24.171	< 0.001
Unconstrained	2176	0.729	-	-	-

3.3. Community response

The GAM built for STI revealed a clear connection between STI values and altitude with decreasing index values at increasing elevation. This correlation was found to be clearly nonlinear for both survey periods (Figure 2), whereby the relation between altitude and STI was well differentiated between the two survey periods. While the slope decreased with increasing elevation from 1998-2004, it increased with elevation in 2025. On average, the CTI in 2025 was about 0.5 higher than they had been within the old data (Table 4). The model explains 7.4% of the deviance (R^2 (adj) = 0.074). Projecting the model on the data, the difference of the CTI between sampling periods is particularly evident at medium altitudes (1'900-2'300 m a.s.l.), while towards the edges of the covered range, the index values are converging (Figure 4).

For the GAM built using the SwSTI instead of the STI, results look very similar. This model also contains a clear negative relation between Temperature Index and altitude (Table 5), again nonlinear for both sampling periods. Differences in the correlation between altitude and index are less clear for SwSTI compared to STI, but despite the nearly constant gradient, the slope is steeper in 2025 compared to the previous sampling period (Figure 3). Not only CTI values but also SwCTI values were about 0.37 higher in 2025 compared to the previous sampling period (Table 5). However, with 26.2% (R^2 (adj) = 0.262), the SwSTI model explains more of the deviance than the STI model. Projected on the data, the result is similar to that of the STI model, however, there is no convergence between survey periods in low altitudes (Figure 5).

Table 4: Results of the STI-model. Elevation and CTI were correlated in both sampling periods with a nonlinear function in the period from 1998 to 2004 and a nearly linear function in 2025. The correlation differed between both sampling periods. Also, CTI was higher in 2025 compared to 1998-2004.

Term	Estimate	t-value	Pr(>|t|)
Year 2025	0.504	17.27	< 0.001
	edf	**F-statistics**	**p-value**
s(elevation), years 1998-2004	1.991	524.4	< 0.001
s(elevation), year 2025	1.916	174.9	< 0.001

Table 5: Results of the SwSTI-model. Like for CTI, elevation and SwCTI were correlated in both sampling periods with nonlinear functions. Analogous to CTI, also SwCTI was higher in 2025 compared to 1998-2004.

Term	**Estimate**	**t-value**	**Pr(>|t|)**
Year 2025	0.371	28.76	< 0.001
	edf	**F-statistics**	**p-value**
s(elevation), years 1998-2004	1.984	1749	< 0.001
s(elevation), year 2025	1.985	1538	< 0.001

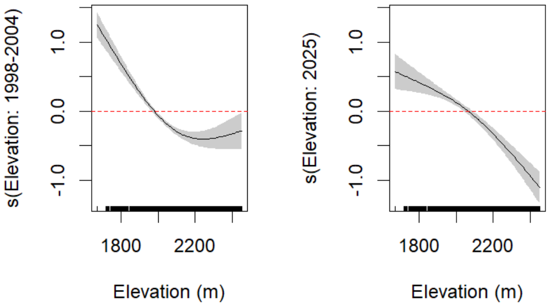

Figure 2: Visualisation of the correlation between elevation and CTI for both sampling periods, in the left 1998 to 2004, 2025 in the right. The dashed red line at y = 0 resembles where elevation does not influence the CTI. For both sampling periods, low altitudes result in a higher CTI and the other way around. The correlation was nonlinear for both survey periods with slope decreasing with increasing elevation from 1998 to 2004 and the other way around in 2025.

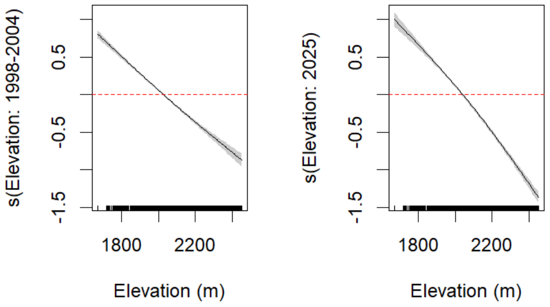

Figure 3: Visualisation of the correlation between elevation and SwCTI for both sampling periods, in the left 1998 to 2004, 2025 in the right. The dashed red line at y = 0 resembles where elevation does not influence the SwCTI. For both sampling periods, low altitudes result in a higher SwCTI and the other way around in a nonlinear correlation. Gradients appear to be nearly constant for both survey periods, but the slope appears to be steeper in 2025.

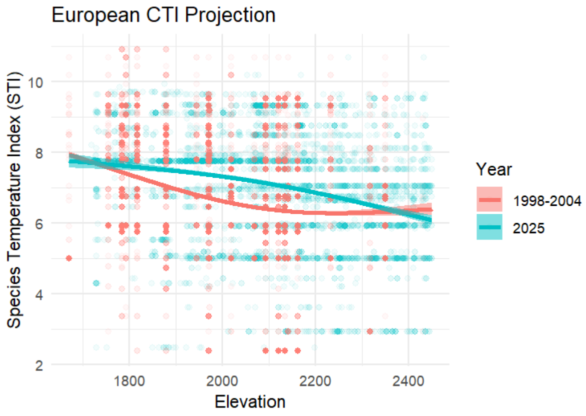

Figure 4: Projection of the STI-model on the data. In the overall trend, CTI decreases with increasing altitude for both sampling periods. In medium altitudes, CTI appears to be higher in 2025, whereas the curves resembling CTI of both survey periods converge towards the edges of the covered elevational range.

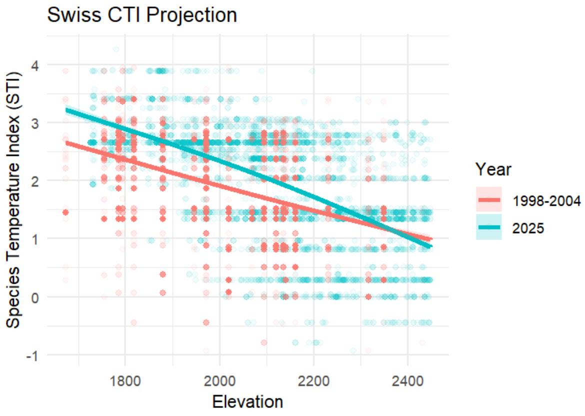

Figure 5: Projection of the SwSTI-model on the data. Same as for CTI, SwCTI decreases with increasing altitude for both sampling periods in the over-all trend. In low and medium altitudes, SwCTI was markedly higher in 2025, whereas both curves converge towards the upper edge of the covered elevational range.

3.4. Species response

Mean difference in altitudinal distribution between the two sampling periods ranged from -78 m (*Thymelicus lineola* Ochsenheimer 1808) to 345 m (*Erebia gorge* Hübner [1804]). *T. lineola* was the only species where a negative change meaning a downward shift was detected (Table 7). Overall, a clear upward shift was observed with a mean increase of 134 m in mean altitude (Table 6). Along with the mean values, also the observed altitudinal ranges, resembled by mean values +/- standard deviation did move upwards (Figure 6). While there was no correlation detected for the difference in altitude and STI values, it was found to be connected to SwSTI values: difference in altitude increased with decreasing SwSTI values, so species with low SwSTI values showed a more pronounced upwards shift (Table 8).

Table 6: Results of the paried t-test for mean altitudes per species between the sampling periods 1998 to 2004 and 2025. On average, species did shift 134.195 metres upwards in the meantime.

Effect	**Mean difference**	**t-statistic**	**df**	**p-value**
Year 2025	134.195 m	9.021	31	< 0.001

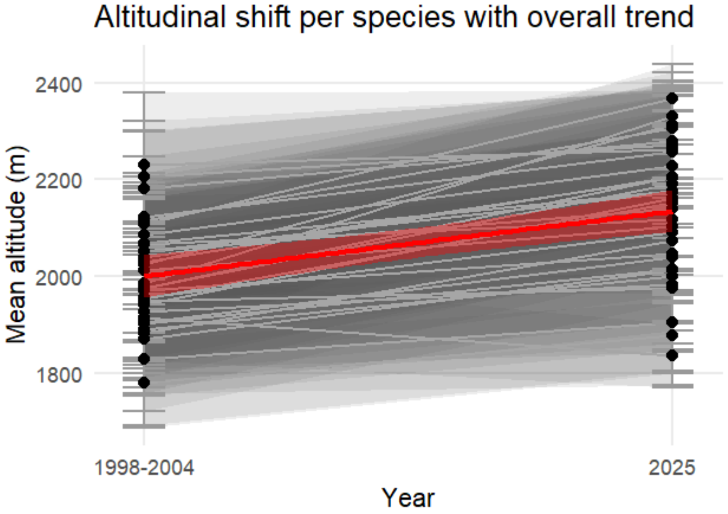

Figure 6: Illustration of the comparison of altitudinal distributions between the survey periods 1998-2004 and 2025. For each species, mean altitude and error bars are given per survey period. Mean values are connected by a light grey line, error bars by a light grey area displaying the overall trend for altitudinal niches. The red line with underlying red area represents the mean change with confidence interval. Detailed information per species is given in table 7.

Table 7: Underlying data used for species level analyses. For each species considered, this table provides abundance (n), mean and standard deviation (sd) in both sampling periods (1998-2004 and 2025). The difference in mean altitude (Diff) is given.

Species	**n 98-04**	**n 25**	**mean 98-04**	**sd 98-04**	**mean 25**	**sd 25**	**Diff**
Aglais urticae	69	78	2038.1	208.3	2204.2	190.6	166.0
Agriades glandon	174	29	2181.3	119.8	2277.8	109.9	96.4
Aricia artaxerxes	271	29	2051.0	110.9	2140.1	170.3	89.2

Boloria euphrosyne	58	81	1870.8	101.4	2013.0	125.6	142.3
Boloria pales	220	328	2229.7	149.5	2262.7	121.1	33.0
Callophrys rubi	12	16	1882.1	161.6	2073.6	130.4	191.5
Coenonympha gardetta	617	162	2050.3	109.9	2174.6	134.6	124.4
Colias phicomone	713	50	2115.1	183.3	2305.5	84.4	190.5
Cupido minimus	206	110	2028.1	145.4	2204.4	104.6	176.3
Cyaniris semiargus	141	98	1889.3	104.3	2000.2	141.0	110.9
Erebia epiphron	365	149	2122.5	63.6	2257.2	114.1	134.8
Erebia euryale	1550	1007	1948.8	140.1	1975.4	133.1	26.5
Erebia gorge	17	47	1984.7	122.2	2329.5	109.0	344.8
Erebia ligea	11	61	1779.5	87.6	1876.4	72.2	96.9
Erebia mnestra	32	14	1974.7	184.7	2190.7	152.0	216.1
Erebia pandrose	70	136	2205.0	115.5	2272.1	110.4	67.1
Erebia tyndarus	2441	449	2084.4	122.0	2226.5	148.5	142.1
Euphydryas aurinia	140	30	2108.3	103.7	2368.0	52.6	259.7
Fabriciana niobe	118	32	1904.7	105.8	2038.1	133.6	133.4
Hesperia comma	130	111	1942.3	126.7	2161.4	119.6	219.1
Leptidea sinapis/juvernica	13	80	1828.7	141.8	1904.1	105.6	75.4
Lysandra coridon	890	229	2012.9	150.3	2101.8	99.9	88.9
Oeneis glacialis	12	59	2066.0	106.2	2117.7	153.2	51.7
Pieris bryoniae	60	109	1956.1	133.2	2089.5	182.9	133.4
Pieris rapae	73	52	1902.3	150.0	2014.9	165.8	112.6
Plebejus idas	1591	224	2025.2	156.8	2312.3	91.6	287.1
Pyrgus alveus	24	26	2068.2	136.6	2176.0	75.9	107.8
Pyrgus serratulae	77	11	1971.4	142.3	2046.3	141.6	74.9
Speyeria aglaja	400	47	1952.7	137.4	2150.4	188.6	197.8
Thymelicus lineola	592	17	1913.9	88.5	1835.5	66.6	-78.5
Vanessa atalanta	11	48	1927.0	169.6	1983.8	208.1	56.8
Vanessa cardui	10	15	1976.5	217.9	2205.3	194.8	228.9

Table 8: Results of the Generalised linear model testing for the influence of STI and SwSTI on difference in mean altitude. While STI did not have an impact, differences in mean altitude decreased by 28.68 metres per unit increase in SwSTI.

Effects	**Estimate**	**se**	**t-value**	**Pr(>|t|)**
STI (EU)	2.281	9.354	0.244	0.809
SwSTI (CH)	-28.680	13.630	-2.104	< 0.05

4. Discussion

4.1. Butterfly assemblages

The butterfly communities observed in both surveys can be considered species-rich, with more than 80 species recorded in each case, representing around 40% of the butterflies present in Switzerland (Baudraz et al., 2020). Although different sites were examined, a high similarity was found between the butterfly communities recorded in the surveys from 1998-2004 and in 2025 with approximately 75 percent of the species recorded in both periods. This finding is particularly noteworthy given the considerable variation in community composition across sites within each survey. In addition to the overall similarity in species presence, it is striking that the five most abundant species were, with one exception, the same, further emphasising the consistency in butterfly communities. *E. melampus* which ranked among the five most abundant species in the old data by Pasche et al. (2007) was absent in 2025 because it exclusively occurs in the valley Val Trupchun, which was not included in the recent survey. Most species recorded in one survey only were confined to areas outside the region with dolomite bedrock, specifically in Val Trupchun surveyed in 2001 or on transect 2 (ZM) in 2025. For both areas, there were no geologically equivalent areas included in the respective other survey. Thus, reasons for differences in species composition between survey periods, but also across sites within both surveys, are most likely differences in bedrock resulting in different vegetation and habitat structures (Mota et al., 2002; Wohlgemuth, 2002). Differences in exposition may have contributed further. Apart from local environmental conditions, annual fluctuations in abundance and biannual life cycles as well as weather conditions during the life cycle may explain discrepancies in abundances (Schweizerischer Bund für Naturschutz, 1987; Roy et al., 2001; Reinhardt et al., 2021). The high correspondence of butterfly communities in both surveys suggests that the extensive livestock grazing along parts of transect 2 (ZM) does not compromise comparability with the old data recorded almost entirely within the SNP borders where livestock grazing is absent. Furthermore, a temporal comparison of butterfly distribution and inhabited altitudes is valid, despite only partially consistent methodologies and the fact that it was not the same areas surveyed in 2025 as from 1998 to 2004.

While geological and local conditions largely explain differences in species composition between survey periods, two of the species newly recorded in 2025, *Polygonia c-album* Linnaeus 1758 and *Pararge aegeria* Linnaeus 1758, had previously been considered not to reach these altitudes by Pasche et al. (2007). After Sgier (2015) reported single individuals of both species at 1'672 m a.s.l in the Fuorn region (Figure 1), they were regularly observed at altitudes up to 1'850 m a.s.l. with single individuals up to 2100 m a.s.l. in 2025 (Annex C). This upwards expansion represents a colonisation of formerly uninhabited elevations, most likely driven by rising temperatures in the SNP region in the context of global climate change (Haller et al., 2014; Gubler and Robinson, 2025). Observations of single individuals of *Maniola jurtina* Linnaeus 1758, and *Hipparchia semele* Linnaeus 1758 should also be interpreted from this perspective: Both species were previously considered restricted to substantially lower altitudes

(Pasche et al. 2007), but may now be next to colonise the SNP by expanding into higher altitudes. For the generalist *M. jurtina* this range expansion appears more likely than for *H. semele* which is specialised on xerothermophilous meadows and pastures and known for long distance dispersion flights. Yet it is known to inhabit subalpine habitats elsewhere (Schweizerischer Bund für Naturschutz, 1987). Similar upward range expansions resulting in colonisation of the SNP had been reported by Pasche et al. (2007) for other species already, although a general response of butterfly assemblages to global warming in recent decades had not yet been systematically investigated in the SNP region.

4.2. Species response

It is in fact not only single species but butterflies in general shifting their altitudinal ranges upward in the SNP region, as the present study demonstrates. Hypothesis 3 is therefore accepted. This conclusion is based on a broad set of 32 species. Although local changes in butterfly communities at the study sites from 1998-2004 remain unknown, the use of continuous transects covering a wide altitudinal range enables a robust assessment of species' elevational distributions and allows direct comparison with the old dataset.

The general upward shift is underscored by the fact that all but one species exhibited an upward trend in elevation. However, the magnitude of this response to global warming is difficult to interpret because the abundance of species above 2'430 m a.s.l. in 1998-2004 remains unknown. The analysis was restricted to an altitudinal range of about 750 metres constraining the detectable upwards movement. In 2025, some species occurred primarily above the upper limit of the concerned altitudinal range (Annex C). Consequently, the average upwards shift of 135 metres in the last 25 years may represent an underestimate. Nevertheless, similar magnitudes of upward movement have been reported for butterflies in other parts of the Alps (Roth et al., 2014; Rödder et al., 2021; Kerner et al., 2023; Habel et al., 2023), supporting both the generality and plausibility of the identified alteration. This study therefore adds to the large body of evidence demonstrating range shifts across multiple organism groups in association with climate change, in the SNP region (Baur and Baur, 2013; Wipf et al., 2013; Gilgado et al., 2022), European mountain ranges in general, and globally (Parmesan and Yohe, 2003; Parolo and Rossi, 2008; Chen et al., 2009; Menéndez et al., 2014; Marshall et al., 2020).

The upwards shift observed in the present study is expressed not only in the expansion to higher elevations through the advance of upper range limits, but also through a consistent upward shift of entire altitudinal distributions, including the lower limit. In some cases, this retreat to higher altitudes is resulting in a significant reduction of the inhabited area. Historical data from the SNP region illustrate this long-term pattern. Pictet (1942) described the alpine species *Euphydryas cynthia* [Denis & Schiffermüller] 1775, *Euphydryas aurinia ssp. debilis* Oberthür 1909 and *Pontia callidice* Hübner [1800] as widespread and abundant at altitudes above 1'800 m a.s.l. During the surveys conducted from 1998-2004, Pasche et al. (2007) found only single individuals of *E. cynthia* and P. *callidice* below the upper range limit of the survey at 2'431 m a.s.l., while *E. aurinia* was rare below 2'000 m a.s.l.. In 2025, *E. aurinia* was no longer recorded below 2’250 m a.s.l., with most observations occurring above the altitudinal range of the old data (Annex C). Except for one single individual of *P. callidice* at about 2300 m a.s.l., both *P. callidice* and *E. cynthia* were absent below 2’500 m a.s.l. having completely vacated the altitudinal range covered by the earlier survey. Both species thus abandoned the altitudinal range of the old data. This ongoing retreat to ever higher elevations increases extinction risk for the species affected by reducing their habitat area and connectivity (Reinhardt et al., 2005), therefore posing a major threat to alpine butterfly diversity.

The magnitude of the upward shift was found to be negatively correlated to species’ SwSTI-values. As SwSTI values represent, by definition, the average MAT of the inhabited range per species, low SwSTI values indicate cold-adapted taxa, typically thriving in high altitudes. Thus, these high-altitude specialists appear to respond more strongly to climate change than less cryophilic species occurring in lower altitudes. This is of concern because they are also the most vulnerable to continued upward movement, as available area decreases towards mountain summits. Other studies have reported contrasting results: While Kerner et al. (2023) and Neff et al. (2022) also observed that mountain species with low temperature indices tend to move upwards more rapidly than lowland species, other studies found generalist and mobile species, which are usually associated with rather high temperature indices (Klaiber et al., 2017), expanding their altitudinal range upwards faster than cold-adapted alpine specialists shifted to higher elevations (Mamantov et al., 2021; Rödder et al., 2021). Since, in contrast to SwSTI, STI showed no correlation with the magnitude of upslope shift, the SwSTI-based result must be interpreted with some caution. Further investigations covering a larger geographical and a broader elevational range would help clarify this pattern.

Butterflies are known to be highly sensitive to environmental changes (van Swaay et al., 2006). Assuming an average temperature decline of 0.65 °C per 100 m elevation gain (Klose, 2008) and an average temperature increase of +0.9 °C at the Buffalora weather station (1’970 m a.s.l.) between 2001 and 2023 (Gubler and Robinson, 2025), an expected average upslope shift of approximately 140 metres since the last survey period can be derived. The observed mean upward displacement of 135 m is roughly in line with this value, suggesting that butterflies in the SNP region are largely keeping pace with local warming.

4.3. Community response

In contrast, a lag behind local warming was evident in the Community Temperature Indices. Both CTI and SwCTI increased by 0.53 and 0.36, respectively, in the average of preferred MAT of occurring species, but neither reached the observed +0.9 °C rise in regional MAT between 2001 and 2023. The actual composition of the species communities is largely disregarded here. The focus is primarily on the temperature adaptation of the butterfly communities as reflected by CTI and SwCTI. In line with theoretical expectations CTI values increased with warming confirming hypothesis 2 and decreased with altitude due to decreasing temperature. Warming-induced adaptations of species communities reflected by increased thermophily have been reported in other studies for various groups of organisms, including butterflies (Gottfried et al., 2012; Roth et al., 2014; Nieto-Sánchez et al., 2015; Cerrato et al., 2019; Bonelli et al., 2022; Khaliq et al., 2024; Ursul et al., 2025; Bruni et al., 2025). The results presented here thus fit well into the general picture of climate-induced community change in mountain ecosystems.

Although the results for both indices were generally consistent, a marked difference in absolute values and slopes is noticeable despite both indices being derived using the same methodological approach. These differences are most probably attributable to the underlying spatial resolutions of the temperature indices. The STI was calculated using MAT data from a 50 km × 50 km grid with data from across Europe (Schweiger et al., 2014). At this scale, climatic heterogeneity typical for mountainous regions is not fully captured, resulting in very similar MAT values for species occurring in topographically heterogeneous regions, even though they might inhabit different temperature niches. Thus, a limited sensitivity to local elevational gradients is the consequence. Conversely, SwSTI was derived from 25 m x 25 m raster data (Külling and Adde, 2024), which better reflects the fine-scale climatic variability of the Alps. Additionally, the exclusion of lower and thus warmer areas within and surrounding the Swiss Alps as well as the limited geographical range lead to lower overall values but greater variability within the SwSTI data (Annex A).

When taking a more differentiated look on the results of the CTI/SwCTI analyses, it is striking that, in contrast to low and medium elevations, both indices are nearly the same at high altitudes. Apart from the lower density of observations towards the upper edge of the altitudinal range in old data, this may reflect non-uniform upward-shifts among species: Consistent with the previous finding that cold-adapted species tend to move upslope more rapidly, lower elevations may have been abandoned by high alpine specialists as illustrated for *E. aurinia*, *E. cynthia*, and *P. callidice*, while less specialised species possibly can’t keep up their pace. Consequently, CTI/SwCTI values are higher today in low and medium altitudes, but not yet in high altitudes. Additionally, colonisation by thermophilic lowland-species extending their upper range limit increases temperature indices in low and even medium altitudes (Mamantov et al., 2021). Meanwhile, high elevations are still inhabited by cold adapted alpine species, whereas expansion of less cryophilic species is slower. Thereby habitat constraints are likely a main driver influencing the pace of range shifts.

4.4. Drivers of butterfly communities

The composition of alpine butterfly communities is determined not only by altitude, but also by the available habitats. According to the results of the Variance partitioning, habitats (28 % of variance explained) are more important in explaining alpine butterfly communities than altitude as an independent factor (2 % of variance explained). The influence of altitude is more apparent in combination with habitats, i.e. in the availability of specific habitats at a certain altitude (9 % of variance explained). Hypothesis 1 can therefore be accepted, although the influence between the two factors differs greatly. Mobile and migratory species found over a wide range may be partially responsible for the low explanatory power of altitude. However, most alpine species are rather sedentary (Polic et al., 2014; Klaiber et al., 2017). The reason for the major influence of habitats on alpine butterfly assemblages may be the close association of most butterflies with a limited set of host plants and, especially in the larval stage, a narrow microclimatic niche (Schweizerischer Bund für Naturschutz, 1987; Reinhardt et al., 2021). As a result, many of them only find suitable living conditions in a few specific habitats. However, the high proportion of 62% unexplained residual variance is striking. Characteristics of butterfly microhabitats including e.g. the presence of host plants, moisture, and high-resolution microclimate (Schweizerischer Bund für Naturschutz, 1987; Weidemann, 1995) are only superficially captured by the habitat dataset (Lotz, 2006). Additionally, only adult mobility and distribution is reflected by the results, while other life stages which are either sedentary or have limited mobility are neglected. Both these issues represent limitations to this study. To capture the complexity of ecosystems entirely is difficult in ecological research, which is why simplifications, as in this case the simplification of butterfly ecology, are common. These simplifications are the reason why the variance in ecological data sets can only be partially explained, as is the case here.

Since the occurrence of habitats also depends largely on altitude, it follows that climate change not only has a direct effect on butterfly communities by increasing average temperatures, but also an indirect effect through the resulting changes in habitats. This indirect effect however can be considered to act rather slow compared to the direct effect. Plants are of particular importance in terms of habitat changes as vegetation is one of the main characteristics of habitat types (Lotz, 2006) and the close association of many butterfly species to one or a few host plants (Schweizerischer Bund für Naturschutz, 1987; Reinhardt et al., 2021). However, plants, especially those inhabiting subalpine and alpine habitats, have been shown to lag considerably behind warming in their advance to higher altitudes (Roth et al., 2014; Alexander et al., 2018). This also applies to the tree line, whose advance brings about the most significant change in habitat characteristics (Körner and Hiltbrunner, 2024). For butterflies, shifting to higher altitudes faster than plants (Roth et al., 2014; Kerner et al., 2023), this poses a risk because especially towards their upper elevational range limit, host plant availability is limiting the distribution of butterfly species (Hanspach et al., 2014). Due to the different paces in shifting to higher elevations, the availability of host plants and suitable habitats may at some point limit the further upslope displacement of butterflies (Schweiger et al., 2008; Kerner et al., 2023). For example, *E. aurinia debilis* depends on *Gentiana clusii* [E. P. Perrier & Songeon] and *Gentiana acaulis* L. as larval host plants (Schweizerischer Bund für Naturschutz, 1987). Thus, the upslope shift of *E. aurinia debilis* cannot exceed the upper elevational margin of the distribution of these two gentian species, even if the species would need to move higher to follow its thermal niche, resulting in a narrowing altitudinal range. This kind of vertical butterfly-hostplant mismatch can be considered as another threat to alpine butterflies additional to range contractions and mountaintop extirpations.

On the other hand, the finding that butterfly assemblages are determined more by habitat than by altitude also means that habitats possibly can buffer the effects of climate change. Several alpine species are known to colonise areas well below their main altitudinal distribution, if suitable habitats are present. Such examples are for instance *Erebia gorge* and *Erebia pluto* De Prunner 1798 forming populations in fine scree slopes far below the tree line, *Erebia mnestra* Hübner [1804] and *Erebia tyndarus* Esper [1781] living in dry, patchy *Festuca*-grasslands in open mountain forests or *Polyommatus eros* Ochsenheimer 1808 colonising avalanche corridors and relict landslides below the otherwise populated alpine pastures (Schweizerischer Bund für Naturschutz, 1987; Sonderegger, 2005). For these species, habitats may have the ability to buffer for the upslope shift caused by climate warming and thus reduce vulnerability for range contractions and mountaintop extirpations. As butterflies have so far largely kept pace with warming, there is no evidence of buffering effects or butterfly-hostplant mismatches yet. However, the combined effect of habitat and altitude, thus the availability of specific habitats in certain altitudes, can be assumed to increase in importance for alpine butterfly assemblages with ongoing warming.

In the future, the high habitat influence will presumably have varying effects on alpine butterfly assemblages, depending on species. Species with a mostly temperature driven altitudinal distribution are more likely to be affected by butterfly-hostplant mismatches, range contractions and mountaintop extirpation. The more of altitudinal distributions is explained by habitat and host-plant distribution, the more likely are buffering effects of habitats to reduce vulnerability by climate change. To achieve a buffering effect, suitable habitats must be available over a broad altitudinal range. Land use changes as another driver in global change and threat to insect diversity, are known to interact with climate change (Forister et al., 2010; Guo et al., 2018) which most severely affects specialized species (Neff et al., 2022). A main implication for conservation is thus to ensure that high-quality and diverse habitats are preserved and, where possible, restored. Grazing by livestock and wild ungulates can mediate the upward shift of the tree line and contributes to the preservation of original alpine vegetation while at the same time enhancing plant diversity (Speed et al., 2010; Kaufmann et al., 2021). Together with landscape dynamics such as landslides and avalanches with following pioneer communities, grazing ungulates and traditional livestock farming may thus contribute to the preservation and diversification of alpine habitats by counteracting the slow, but evident upwards shift of vegetation altitudinal belts.

4.5. Prospects and research priorities

In multiple ways, this study has shown that high-alpine species with a narrow temperature niche, particularly those adapted to cold and harsh climates, are most vulnerable to climate change in the SNP region. Assuming a linear continuation of the recently observed upward shift, first local extinctions in the SNP region may occur by the end of the century, as the mean elevation of occurrences exceeds 3000 m a.s.l., the altitude of most mountain summits in the region. However, with regional warming accelerating (Gubler and Robinson, 2025) and mountaintop habitats being small and isolated, extinction events might occur even earlier (Reinhardt et al., 2005). These findings underscore the importance of climate refugia and high diversity in microclimates because of their ability to buffer against warming (Turlure et al., 2010; Suggitt et al., 2018), offering at least temporary preservation of alpine butterfly assemblages on a larger scale, even if local extinctions may not be averted (Wilkes et al., 2023; Biella et al., 2024). Today, some alpine butterflies already persist in deeply incised valleys below their usual altitudinal range (Schweizerischer Bund für Naturschutz, 1987; Sonderegger, 2005). Such locations along with north-facing glacier cirques and rock glaciers as those on the Macun plateau (Brighenti et al., 2021; Gubler and Robinson, 2025) are likely to be of key importance for the preservation of today's alpine butterfly assemblages. As glaciers melt and permafrost thaws, newly colonised habitats may emerge (Parolo and Rossi, 2008; Biskaborn et al., 2019; Rounce et al., 2023), providing potential refugia for some alpine species, especially since similar habitats are already colonised up to well above 3000 m a.s.l. (Sonderegger, 2005; Trusch et al., 2023). However, this type of refuge in Europe is largely confined the Alps and other mountain ranges covering an equivalent altitudinal range, where sufficient elevation and area remain. In smaller and lower mountain ranges where there is less space for upward shifts, risks for mountaintop extirpation are even higher (Bonifacino et al., 2022; Biella et al., 2024).

Apart from direct thermal effects and altered precipitation regimes (Gobiet et al., 2014), climate change also drives glacier retreat, permafrost degradation (Biskaborn et al., 2019; Rounce et al., 2023), and geomorphic processes such as increased slope movements and instability (Stoffel and Huggel, 2012; East and Sankey, 2020). Together with increased plant growth and an advancing treeline, these processes have the potential to transform alpine habitats up to landscape level (Eichel et al., 2023). Keeping the striking importance of habitats for alpine butterfly communities in mind, additional uncertainty is thus posed for future butterfly assemblages, especially as it remains speculation at this point what exactly future alpine landscape will look like (Eichel et al., 2023) and effects on mountain biodiversity remain poorly studied.

To keep track of future changes in alpine butterfly communities, previous and recent butterfly surveys in the SNP region should be repeated at regular intervals, e.g. every ten years. This regularity would also allow to detect a potential acceleration in butterfly responses to climate change, that may be expected due to acceleration in warming (Gubler and Robinson, 2025). Also, recent studies on the responses of alpine butterflies to climate change have exclusively surveyed Imagoes with high mobility, while the preimaginal development actually has the greatest influence on species distributions and community composition due to its high complexity (Reinhardt et al., 2021). Thus, in future studies it might be helpful to include recordings of sex ratio, oviposition observations and caterpillar surveys to get more thorough insights to how alpine butterflies respond to climate change.

5. Conclusion

This study has shown that, over recent decades, butterflies in the SNP region have responded to climate change through a pronounced upward shift and a transition towards more thermophilic communities. With temperatures rising further, these changes threaten high-altitude communities and species adapted to cold and harsh conditions. In line with findings from other alpine regions, such communities in their current form appear to be viable in the long term only within isolated climate refugia. Despite the evident influence of temperature and altitude, available habitats emerged as an even more important driver of alpine butterfly community composition. Although this correlation has not yet been reflected in current patterns, it is likely to shape future climate change response of alpine butterflies both positively and negatively. Given that alpine environments are not only affected by rising temperatures but also reshaped by resulting geomorphic and biotic processes altering landscapes and butterfly habitats, predictions about biodiversity trends remain uncertain, although large-scale trends are evident. The preservation of high-quality, diverse habitats will be of central importance for the conservation of alpine butterfly communities as flagships for mountain biodiversity.

Acknowledgements

Various people were involved in the success of this thesis project, and I would like to express my sincere thanks to them: First and foremost, Jérôme Pellet, who supported, supervised and advised me throughout the conception, planning and realisation of the project, the data analysis and the writing of the thesis. In addition, Jörg Müller provided me with valuable advice during the conceptual phase and the data analysis and agreed to supervise this external thesis. I would also like to express my special thanks to Thomas Rempfler, who supported me with planning and logistics and was always available to help with various issues during the field work. For their help with logistics and for providing material and valuable information, I am grateful to Ruedi Haller, Christian Rossi, Jan Schweizer, Hans Lozza and Not Armon Willy. Also, my thanks go to Stefanie Gubler, Julia Paterno and Angelika Abderhalden for their support in planning and the project application to the FOK-SNP. I would like to express my sincere thanks to all members of the SNP staff for the warm welcome in Zernez and their friendly and interested support for the project. I would like to thank Matthias Plattner for initiating the data export from the BDM, for his interest and advice during the conceptual phase, and for his helpful comments on the manuscript. For his help with identification and for providing valuable contacts, I would like to express my thanks to Julian Bittermann. Finally, I would like to thank the Federal Office for the Environment (FOEN) for providing data from the BDM. Also, I would like to thank the BDM field team for collecting the data.

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Appendix

Annex A: Overview over temperature indices (SwSTI for Switzerland and STI for Europe). Relative indices (CH_rel for SwSTI and EU_rel for STI) are calculated as deviation from the mean value divided by the mean deviation from the mean value of the respective index. The absolute difference between the relative indices (diff) is a measure of similarity between the two relative indices. From the Fauna Indicativa dataset, the sum of the assigned values within the categories “alpine” and “subalpine” (>1500 m a.s.l.) of the altitudinal distribution is given (Sum alt.). Values greater than or equal to four correspond to at least 60 % of occurrences of the respective species in Switzerland are in these altitudes, for values greater than zero, an considerable amount of occurrences in these altitudes can be assumed. The habitat criterion (hab. crit.) means that the respective species inhabits at least three different habitat types in subalpine and alpine altitudes or at least half of the inhabited habitat types are in these elevations. It is also drawn from the Fauna Indicativa dataset (Klaiber et al. 2017). Based on the criteria given in annex B, the SwSTI values per species are evaluated and categorized as either valid, uncertain or invalid (eval.). Species occurring in the datasets used for the quantitative analyses are marked (SNP).

Species	**SwSTI**	**STI (EU)**	**CH_rel**	**EU_rel**	**diff**	**Sum alt.**	**hab. crit.**	**eval.**	**SNP**
Aglais io	3.41	NA	0.83	NA	NA	0	FALSE	invalid	X
Aglais urticae	2.03	8.12	-0.59	-0.20	0.39	2	TRUE	valid	X
Agriades glandon	0.85	6.68	-1.80	-1.08	0.72	4	TRUE	valid	X
Agriades optilete	1.67	4.19	-0.96	-2.60	1.64	6	TRUE	valid	X
Agriades orbitulus	1.10	3.36	-1.55	-3.11	1.56	5	TRUE	valid	X
Anthocharis cardamines	3.56	NA	0.99	NA	NA	1	FALSE	uncertain	X
Apatura iris	4.57	8.51	2.03	0.04	1.99	0	FALSE	invalid	
Aphantopus hyperantus	4.32	7.9	1.77	-0.34	2.11	0	FALSE	invalid	
Aporia crataegi	3.46	9.14	0.88	0.42	0.46	1	FALSE	valid	X
Araschnia levana	3.88	8.62	1.31	0.10	1.21	0	FALSE	invalid	
Argynnis paphia	3.92	9.02	1.35	0.35	1.01	0	FALSE	uncertain	
Aricia agestis-Komplex	2.50	10.16	-0.10	1.04	1.14	4	TRUE	valid	
Aricia artaxerxes	2.82	6.45	0.22	-1.22	1.44	4	TRUE	valid	X
Aricia nicias	0.06	4.14	-2.62	-2.63	0.01	6	TRUE	valid	X
Boloria dia	3.70	9.28	1.13	0.51	0.62	0	FALSE	invalid	
Boloria euphrosyne	3.05	6.95	0.46	-0.92	1.38	2	TRUE	valid	X
Boloria napaea	0.88	2.37	-1.78	-3.72	1.94	6	TRUE	valid	X
Boloria pales	0.28	7.04	-2.39	-0.86	1.53	6	TRUE	valid	X
Boloria selene	2.43	6.93	-0.18	-0.93	0.75	2	FALSE	valid	X
Boloria thore	3.88	2.47	1.32	-3.66	4.97	4	TRUE	valid	X
Boloria titania	3.40	6.75	0.82	-1.04	1.87	3	TRUE	valid	X
Brenthis ino	2.55	6.86	-0.05	-0.97	0.92	1	FALSE	valid	X
Brintesia circe	4.58	11.07	2.04	1.60	0.44	0	FALSE	invalid	
Callophrys rubi	2.42	8.57	-0.19	0.07	0.26	1	FALSE	valid	X
Carterocephalus palaemon	3.26	6.9	0.67	-0.95	1.62	1	TRUE	valid	X
Celastrina argiolus	3.50	9.14	0.93	0.42	0.51	0	FALSE	valid	
Chazara briseis	3.98	10.29	1.41	1.12	0.29	0	FALSE	invalid	
Coenonympha arcania	3.38	9.04	0.80	0.36	0.44	0	FALSE	valid	
Coenonympha darwinia	1.84	NA	-0.79	NA	NA	5	TRUE	invalid	
Coenonympha gardetta	1.34	5.91	-1.30	-1.55	0.25	6	TRUE	valid	X
Coenonympha pamphilus	4.01	8.96	1.45	0.31	1.14	0	TRUE	uncertain	X

Colias crocea	2.34	10.69	-0.27	1.37	1.63	1	TRUE	valid	X
Colias hyale-Komplex	2.76	8.37	0.16	-0.05	0.21	1	FALSE	valid	X
Colias palaeno	1.68	3.62	-0.95	-2.95	2.01	4	FALSE	valid	X
Colias phicomone	1.52	6.76	-1.12	-1.03	0.08	5	TRUE	valid	X
Cupido minimus	2.05	8.76	-0.57	0.19	0.76	2	TRUE	valid	X
Cupido osiris	3.69	10.62	1.12	1.32	0.20	3	FALSE	invalid	
Cyaniris semiargus	2.53	7.91	-0.08	-0.33	0.25	2	TRUE	valid	X
Erebia aethiops	3.33	8.1	0.75	-0.22	0.97	1	TRUE	valid	
Erebia albergana	2.62	6.96	0.02	-0.91	0.93	4	TRUE	valid	X
Erebia arvernensis	2.50	8.01	-0.11	-0.27	0.16	6	TRUE	valid	
Erebia epiphron	0.81	7.52	-1.85	-0.57	1.28	6	TRUE	valid	X
Erebia eriphyle	2.32	10.93	-0.29	1.51	1.81	6	TRUE	valid	
Erebia euryale	2.66	7.74	0.06	-0.44	0.49	5	TRUE	valid	X
Erebia flavofasciata	1.18	3.93	-1.47	-2.76	1.29	6	TRUE	valid	
Erebia gorge	-0.44	6.89	-3.14	-0.95	2.19	1	TRUE	valid	X
Erebia ligea	3.88	5.51	1.32	-1.80	3.11	1	TRUE	valid	X
Erebia manto	2.70	6.57	0.10	-1.15	1.25	5	TRUE	valid	
Erebia medusa	2.99	8.4	0.40	-0.03	0.43	1	FALSE	valid	
Erebia melampus	2.36	5.74	-0.25	-1.66	1.40	5	TRUE	valid	X
Erebia meolans	3.69	8.94	1.12	0.30	0.82	2	TRUE	valid	
Erebia mnestra	0.38	4.73	-2.29	-2.27	0.02	5	TRUE	valid	X
Erebia montana	2.63	5.89	0.03	-1.57	1.60	4	TRUE	valid	X
Erebia nivalis	0.13	3.49	-2.55	-3.03	0.48	5	TRUE	invalid	
Erebia oeme	3.72	7.61	1.15	-0.51	1.67	4	TRUE	valid	
Erebia pandrose	-0.01	2.92	-2.69	-3.38	0.69	6	TRUE	valid	X
Erebia pharte	2.01	5.44	-0.61	-1.84	1.23	6	TRUE	valid	X
Erebia pluto	-0.79	5.92	-3.50	-1.55	1.95	6	TRUE	valid	X
Erebia pronoe s.l.	2.76	6.86	0.16	-0.97	1.14	4	TRUE	valid	
Erebia styx	NA	6.64	NA	-1.11	NA	5	TRUE	NA	X
Erebia sudetica	2.45	5.61	-0.15	-1.74	1.58	5	TRUE	valid	
Erebia triarius	2.54	9.28	-0.07	0.51	0.57	2	TRUE	valid	
Erebia tyndarus	1.45	4.99	-1.18	-2.12	0.93	6	TRUE	valid	X
Erynnis tages	2.63	9.12	0.03	0.41	0.38	1	FALSE	valid	X
Euchloe simplonia	2.41	6.98	-0.20	-0.90	0.70	3	FALSE	valid	X
Eumedonia eumedon	2.59	5.98	-0.01	-1.51	1.50	4	TRUE	valid	X
Euphydryas aurinia	0.51	9.53	-2.16	0.66	2.82	6	TRUE	valid	X
Euphydryas cynthia	-0.48	5.81	-3.18	-1.61	1.57	6	TRUE	valid	X
Euphydryas intermedia	1.93	4.3	-0.69	-2.54	1.85	5	TRUE	valid	X
Fabriciana adippe	3.42	8.37	0.85	-0.05	0.90	1	FALSE	valid	
Fabriciana niobe	2.21	8.5	-0.40	0.03	0.43	3	TRUE	valid	X
Glaucopsyche alexis	3.27	9.59	0.68	0.69	0.01	1	FALSE	invalid	
Gonepteryx rhamni	3.35	8.81	0.77	0.22	0.55	0	FALSE	valid	X
Hamearis lucina	4.94	9.11	2.41	0.40	2.01	0	FALSE	invalid	
Hesperia comma	2.78	8.47	0.18	0.01	0.17	2	TRUE	valid	X
Hipparchia fagi	5.8	10.53	3.29	1.27	2.03	0	FALSE	invalid	
Hipparchia genava	3.49	9.18	0.91	0.44	0.47	1	FALSE	valid	
Hipparchia semele	3.90	11.83	1.33	2.06	0.73	2	FALSE	valid	X

Hyponephele lycaon	3.84	9.14	1.28	0.42	0.86	2	FALSE	valid	
Iphiclides podalirius	3.47	10.87	0.89	1.48	0.59	0	FALSE	invalid	
Issoria lathonia	2.71	9.33	0.11	0.54	0.43	2	FALSE	valid	X
Lasiommata maera	3.66	8.56	1.09	0.07	1.03	1	FALSE	uncertain	X
Lasiommata megera	3.79	10.39	1.22	1.18	0.04	0	FALSE	valid	
Lasiommata petropolitana	2.93	5.07	0.33	-2.07	2.40	4	TRUE	valid	X
Leptidea sinapis aggr.	3.41	9.11	0.83	0.40	0.43	1	FALSE	valid	X
Lycaena alciphron	3.30	9.53	0.72	0.66	0.06	1	TRUE	invalid	
Lycaena helle	4.16	4.89	1.61	-2.18	3.78	1	TRUE	invalid	
Lycaena hippothoe	2.56	6.45	-0.04	-1.22	1.18	3	TRUE	valid	X
Lycaena phlaeas	3.90	9.29	1.34	0.51	0.83	0	FALSE	valid	X
Lycaena tityrus	2.59	9.35	-0.02	0.55	0.56	1	TRUE	valid	X
Lycaena virgaureae	2.90	7.27	0.30	-0.72	1.03	4	TRUE	valid	X
Lysandra bellargus	2.69	10.19	0.09	1.06	0.97	1	FALSE	valid	X
Lysandra coridon	2.37	9.31	-0.24	0.52	0.76	2	TRUE	valid	X
Maniola jurtina	4.26	9.85	1.71	0.85	0.85	0	FALSE	valid	X
Melanargia galathea	3.93	9.71	1.37	0.77	0.60	0	FALSE	valid	
Melitaea asteria	-0.73	3.74	-3.44	-2.88	0.56	5	TRUE	valid	
Melitaea athalia-Kplx	3.05	8.27	0.46	-0.11	0.57	1	FALSE	valid	X
Melitaea aurelia	2.13	8.68	-0.49	0.14	0.63	2	TRUE	valid	
Melitaea cinxia	3.28	9.6	0.70	0.70	0.00	1	FALSE	valid	
Melitaea diamina	2.99	8.03	0.40	-0.26	0.66	1	TRUE	valid	X
Melitaea didyma	3.31	10.42	0.73	1.20	0.48	1	FALSE	valid	
Melitaea phoebe	2.41	10.61	-0.20	1.32	1.52	1	FALSE	uncertain	X
Melitaea varia	0.07	6.83	-2.61	-0.99	1.62	6	TRUE	valid	X
Minois dryas	4.99	9.52	2.46	0.65	1.81	0	FALSE	invalid	
Nymphalis antiopa	2.84	7.61	0.25	-0.51	0.76	1	FALSE	valid	X
Nymphalis polychloros	2.81	9.68	0.21	0.75	0.54	0	FALSE	invalid	
Ochlodes sylvanus	3.57	NA	1.00	NA	NA	1	TRUE	valid	X
Oeneis glacialis	0.97	5.17	-1.69	-2.01	0.32	5	TRUE	valid	X
Papilio machaon	2.99	9.28	0.40	0.51	0.11	2	FALSE	valid	X
Pararge aegeria	3.41	9.71	0.83	0.77	0.06	0	FALSE	valid	X
Parnassius apollo	3.07	8.14	0.48	-0.19	0.67	3	TRUE	valid	
Parnassius mnemosyne	3.45	8.79	0.87	0.21	0.66	3	TRUE	invalid	
Parnassius phoebus	0.37	4.76	-2.31	-2.26	0.05	5	TRUE	valid	X
Phengaris alcon rebeli	0.64	NA	-2.02	NA	NA	2	TRUE	valid	
Phengaris arion	2.88	NA	0.29	NA	NA	3	TRUE	valid	X
Phengaris teleius	3.78	NA	1.21	NA	NA	0	FALSE	invalid	
Pieris brassicae	3.11	9.29	0.52	0.51	0.01	0	FALSE	valid	X
Pieris bryoniae	2.77	6.75	0.17	-1.04	1.21	3	TRUE	valid	X
Pieris napi	3.03	8.21	0.44	-0.15	0.59	0	FALSE	valid	X
Pieris rapae	2.35	9.63	-0.26	0.72	0.98	1	FALSE	valid	X
Plebejus argus	4.83	8.61	2.29	0.10	2.20	2	TRUE	invalid	
Plebejus idas	1.34	5.92	-1.30	-1.55	0.25	6	TRUE	valid	X
Polygonia c-album	3.72	8.6	1.15	0.09	1.06	0	FALSE	uncertain	X

Polyommatus amandus	2.65	7.66	0.05	-0.48	0.53	3	TRUE	valid	X
Polyommatus damon	2.77	8.66	0.17	0.13	0.05	4	FALSE	valid	X
Polyommatus dorylas	2.54	9.32	-0.07	0.53	0.60	1	FALSE	valid	
Polyommatus eros	1.46	8.22	-1.18	-0.14	1.04	6	TRUE	valid	X
Polyommatus icarus	3.36	9.07	0.78	0.38	0.40	0	FALSE	valid	X
Polyommatus thersites	3.28	10.59	0.70	1.31	0.61	1	FALSE	valid	
Pontia callidice	-0.94	6.09	-3.65	-1.44	2.21	6	TRUE	valid	X
Pseudophilotes baton	2.52	NA	-0.09	NA	NA	2	FALSE	uncertain	
Pyrgus alveus	2.19	7.98	-0.43	-0.29	0.14	5	TRUE	valid	X
Pyrgus andromedae	3.01	4.42	0.42	-2.46	2.88	6	TRUE	valid	X
Pyrgus cacaliae	0.04	5.84	-2.64	-1.60	1.05	6	TRUE	valid	X
Pyrgus carlinae	2.65	7.43	0.05	-0.62	0.67	5	TRUE	valid	
Pyrgus malvae	3.44	8.74	0.86	0.18	0.69	0	TRUE	valid	
Pyrgus malvoides	2.06	NA	-0.56	NA	NA	3	TRUE	valid	X
Pyrgus serratulae	1.99	9.19	-0.63	0.45	1.08	4	TRUE	valid	X
Pyrgus warrenensis	2.07	4.68	-0.55	-2.30	1.76	5	TRUE	invalid	
Satyrium spini	3.94	NA	1.38	NA	NA	1	FALSE	invalid	
Satyrus ferula	4.65	10.54	2.11	1.28	0.83	1	FALSE	valid	
Speyeria aglaja	2.71	7.79	0.11	-0.40	0.51	3	TRUE	valid	X
Spialia sertorius	3.94	10.44	1.38	1.21	0.16	1	FALSE	valid	X
Thymelicus lineola	2.78	8.69	0.18	0.15	0.04	1	TRUE	valid	X
Thymelicus sylvestris	3.86	9.87	1.30	0.87	0.43	1	TRUE	valid	
Vanessa atalanta	2.46	9.07	-0.15	0.38	0.53	2	FALSE	valid	X
Vanessa cardui	2.28	9.04	-0.33	0.36	0.69	2	TRUE	valid	X

Annex B: Description of the criteria used for the evaluation of the SwSTI values. The evaluation is based on the sample size used for the calculation (n). From the Fauna Indicativa dataset, the sum of the assigned values within the categories “alpine” and “subalpine” (>1500 m a.s.l.) of the altitudinal distribution is drawn. Values greater than or equal to four correspond to at least 60 % of occurrences of the respective species in Switzerland are in these altitudes, for values greater than zero, a considerable amount of occurrences in these altitudes can be assumed. The habitat criterion means that the respective species inhabits at least three different habitat types in subalpine and alpine altitudes or at least half of the inhabited habitat types are in these elevations. It is also drawn from the Fauna Indicativa dataset (Klaiber et al. 2017). The absolute difference between the relative indices (diff) is a measure of similarity between the two relative indices and is given in Annex A. Based on the criteria given here, the SwSTI values per species are evaluated and categorized as either valid, uncertain or invalid.

n > 30 **?** → **no:** invalid

↓

yes: sum for alpine and subalpine > 3 (>60% of occurrences in these altitudes)? → **yes:** valid

↓

no: difference between relative indices < 1? → **no:** sum for alpine and subalpine > 0 (considerable amount of occurrences in these altitudes)? → **no:** uncertain

↓ ↓

yes: valid | **yes:** habitat criterion met (species inhabits 3 different habitats in subalpine and alpine elevations OR at least half of the inhabited habitat types in these altitudes)? → **no:** uncertain

↓

yes: valid

Annex C: Overview of the butterfly datasets used for quantitative analyses. For both survey periods (1998-2004 = 98-04 and 2025 = 25), the number of counted individuals (n), the mean elevation of the records per species in metres above sea level (mean) and the standard deviation of the mean elevation (sd) are given per species. Please note that the covered altitudinal ranges are not identical. From 1998-2004, altitudes an altitudinal range from 1670 m a.s.l. to 2440 m a.s.l., in 2025 from 1730 to 2850 m a.s.l. were studied. Complete datasets are available at the data center of the SNP: https://www.parcs.ch/snp/data.php (Accessed 18 Nov 2025).

Species	**n (98-04)**	**n (25)**	**mean (98-04)**	**mean (25)**	**sd (98-04)**	**sd (25)**
Aglais io	2	0	1733.00	NA	86.27	NA
Aglais urticae	70	215	2038.14	2463.67	208.26	234.85
Agriades glandon	166	165	2181.33	2523.28	119.78	135.27
Agriades optilete	6	9	1907.67	2119.33	119.71	124.86
Agriades orbitulus	66	0	2021.08	NA	131.08	NA
Anthocharis cardamines	2	0	1956.00	NA	195.16	NA
Aporia crataegi	1	10	1818.00	1776.40	NA	70.54
Aricia artaxerxes	264	29	2050.97	2140.14	110.92	170.33
Aricia nicias	24	0	1897.58	NA	87.40	NA
Boloria euphrosyne	58	81	1870.79	2013.05	101.38	125.55
Boloria napaea	489	0	2110.91	NA	53.13	NA
Boloria pales	222	521	2229.69	2381.48	149.51	191.78
Boloria selene	0	27	NA	1971.04	NA	61.23
Boloria thore	0	19	NA	1902.68	NA	102.24
Boloria titania	91	7	1830.74	1922.14	41.17	92.05
Brenthis ino	29	1	1794.72	1810.00	29.13	NA
Callophrys rubi	14	16	1882.07	2073.56	161.57	130.42
Carterocephalus palaemon	2	16	1832.00	1843.94	66.47	99.81
Celastrina argiolus	1	0	1755.00	NA	NA	NA
Coenonympha gardetta	617	175	2050.28	2196.68	109.95	151.21
Coenonympha pamphilus	2	1	2201.50	1924.00	324.56	NA
Colias crocea	24	6	1911.17	2523.17	175.62	168.57
Colias hyale/alfacariensis aggr.	3	1	2030.00	1877.00	287.36	NA
Colias palaeno	3	22	1912.67	2151.91	102.77	93.33
Colias phicomone	714	70	2115.05	2362.19	183.32	117.52
Cupido minimus	209	226	2028.13	2365.66	145.44	177.60
Cyaniris semiargus	144	98	1889.27	2000.19	104.28	140.95
Erebia alberganus	664	0	1813.02	NA	45.98	NA
Erebia epiphron	366	203	2122.46	2329.91	63.56	158.15
Erebia euryale	1550	1008	1948.85	1975.92	140.14	134.10
Erebia gorge	19	109	1984.68	2473.41	122.25	156.54
Erebia ligea	12	61	1779.50	1876.36	87.60	72.24
Erebia medusa	1	0	1785.00	NA	NA	NA
Erebia melampus	817	0	1961.20	NA	134.63	NA
Erebia mnestra	32	14	1974.66	2190.71	184.73	151.98
Erebia montana	176	1	1891.37	1940.00	52.43	NA
Erebia pandrose	73	416	2205.04	2480.51	115.55	166.63
Erebia pharte	71	0	2031.80	NA	129.29	NA
Erebia pluto	6	55	2150.17	2572.85	137.58	174.75
Erebia styx	8	98	1825.00	2261.78	93.91	71.43

Erebia tyndarus	2242	521	2084.42	2265.49	121.99	169.77
Erynnis tages	9	20	1995.78	2038.85	146.30	118.69
Eumedonia eumedon	4	13	1924.50	2182.08	93.00	165.71
Euphydryas aurinia	140	77	2108.34	2498.74	103.92	84.03
Euphydryas cynthia	1	2	2135.00	2586.50	NA	55.86
Euphydryas intermedia	0	30	NA	1882.07	NA	139.51
Fabriciana niobe	118	32	1904.69	2038.09	105.79	133.61
Gonepteryx rhamni	1	1	1755.00	2077.00	NA	NA
Hesperia comma	130	119	1942.27	2188.78	126.75	155.34
Hipparchia semele	0	1	NA	1772.00	NA	NA
Issoria lathonia	7	1	1956.14	2031.00	272.40	NA
Lasiommata maera	1	8	1794.00	1842.25	NA	89.89
Lasiommata petropolitana	5	103	1834.40	1994.35	106.18	107.89
Leptidea sinapis	15	0	1828.73	NA	141.76	NA
Leptidea sinapis/juvernica aggr.	0	80	NA	1904.14	NA	105.63
Lycaena hippothoe eurydame	6	19	2008.33	1923.89	172.99	70.79
Lycaena phlaeas	0	1	NA	1774.00	NA	NA
Lycaena tityrus subalpina	2	23	1878.50	1935.65	123.23	49.26
Lycaena virgaureae	7	1	1789.71	1770.00	12.47	NA
Lysandra bellargus	35	4	1913.51	2092.50	149.37	51.90
Lysandra coridon	890	229	2012.93	2101.81	150.31	99.90
Maniola jurtina	0	1	NA	1780.00	NA	NA
Melitaea athalia aggr.	174	4	1876.97	1782.50	79.36	20.04
Melitaea diamina	62	1	1874.53	1911.00	52.12	NA
Melitaea phoebe	22	0	1817.27	NA	37.14	NA
Melitaea varia	87	1	2020.56	2284.00	5.25	NA
Nymphalis antiopa	0	1	NA	1734.00	NA	NA
Ochlodes sylvanus	5	2	1828.80	1809.50	80.77	106.77
Oeneis glacialis	14	85	2066.00	2246.49	106.22	235.48
Papilio machaon	3	2	1914.00	2482.50	275.40	161.93
Pararge aegeria	0	21	NA	1836.62	NA	44.38
Parnassius sacerdos	12	0	2014.75	NA	191.16	NA
Phengaris arion	49	10	1886.98	2156.00	130.52	48.16
Pieris brassicae	1	0	1794.00	NA	NA	NA
Pieris bryoniae	64	110	1956.14	2093.69	133.19	189.22
Pieris napi	51	3	1925.55	1825.67	168.78	115.30
Pieris rapae	75	65	1902.32	2137.46	150.03	292.74
Plebejus idas	1591	252	2025.19	2330.47	156.85	101.48
Polygonia c-album	0	6	NA	1814.00	NA	144.04
Polyommatus amandus	54	1	1827.28	1810.00	65.52	NA
Polyommatus damon	60	0	1798.17	NA	30.76	NA
Polyommatus eros	92	9	1940.52	2255.22	77.27	111.04
Polyommatus icarus	45	9	1844.82	2004.67	141.69	75.47
Pontia callidice	2	30	2144.50	2653.20	243.95	114.06
Pyrgus alveus	26	26	2068.23	2176.00	136.55	75.94
Pyrgus andromedae	2	81	2128.00	2375.52	48.08	213.17
Pyrgus cacaliae	6	64	2146.17	2437.02	27.74	209.63

Pyrgus malvoides	80	1	1980.74	1927.00	150.71	NA
Pyrgus serratulae	57	11	1971.39	2046.27	142.29	141.56
Speyeria aglaja	400	48	1952.69	2157.40	137.35	192.66
Spialia sertorius	5	0	1865.80	NA	91.76	NA
Thymelicus lineola	592	17	1913.95	1835.47	88.46	66.58
Vanessa atalanta	16	56	1927.00	2080.27	169.57	308.41
Vanessa cardui	13	26	1976.46	2357.15	217.87	234.81
Zygaena exulans	NA	93	NA	2436.45	NA	169.09
Zygaena filipendulae	NA	12	NA	1963.42	NA	122.84
Zygaena lonicerae	NA	1	NA	1799.00	NA	NA
Zygaena transalpina	NA	16	NA	1923.69	NA	78.71

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Versicherung zur selbständigen Leistungserbringung

Titel der Bachelorarbeit:

Climbing the summit: Alpine butterfly communities in the light of climate change. A local study in the Swiss National Park.

Thema bereitgestellt von (Titel, Vorname, Nachname, Lehrstuhl):

Prof. Dr. Jörg Müller, Chair of conservation biology and forest ecology

Eingereicht durch (Vorname, Nachname, Matrikel):

Korbinian Schrauth, 2875628

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☐ Mit dem Prüfungsleiter bzw. der Prüfungsleiterin wurde abgestimmt, dass für die Erstellung der vorgelegten schriftlichen Arbeit Chatbots (insbesondere ChatGPT) bzw. allgemein solche Programme, die anstelle meiner Person die Aufgabenstellung der Prüfung bzw. Teile derselben bearbeiten könnten, entsprechend den Vorgaben der Prüfungsleiterin bzw. des Prüfungsleiters eingesetzt wurden. Die mittels Chatbots erstellten Passagen sind als solche gekennzeichnet.

Der Durchführung einer elektronischen Plagiatsprüfung stimme ich hiermit zu. Die eingereichte elektronische Fassung der Arbeit ist vollständig. Mir ist bewusst, dass nachträgliche Ergänzungen ausgeschlossen sind.

Die Arbeit wurde bisher keiner anderen Prüfungsbehörde vorgelegt und auch nicht veröffentlicht. Ich bin mir bewusst, dass eine unwahre Erklärung zur Versicherung der selbstständigen Leistungserbringung rechtliche Folgen haben kann.

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Ort, Datum, Unterschrift