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**Faculté de biologie
et de médecine**

Ecole de biologie

**TWENTY YEARS OF CLIMATE CHANGE IN SUBALPINE-ALPINE
OPEN LANDS IN THE WESTERN SWISS ALPS**

**Travail de Maîtrise universitaire ès Sciences en comportement, évolution et
conservation**

Master Thesis of Science in Behaviour, Evolution and Conservation

par

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Abstract

Mountain ecosystems are under the threat of global warming with an increase in temperatures and a decrease of snow precipitations. These changes impact the subalpine and alpine vegetation. However, there are contrasting responses between habitat types, whose evolution is not well understood. To assess this evolution, 71 plots were reinventoried 19 – 20 years after previous exhaustive historical plant inventories. These plots are distributed in four different habitat types (scree, snowbeds, high-mountain grasslands and nutrient-rich grasslands) in the Western Swiss Alps. The species richness, the Simpson reciprocal index, the Bray-Curtis dissimilarity index, ecological indicators values, species cover in respective inventories and PCA were used to compare historical and recent inventories. None of the four habitat types showed any changes in alpha-diversity or shift in species composition through time, but a between-plots homogenization of composition in high-mountain grasslands and a heterogenization in scree and snowbeds were observed. Moreover, the two latter became respectively more acidic or drier, and the species composition of both indicated an increase in average temperature. The few species that changed in mean cover were all in high-mountain and nutrient-rich grasslands. Overall, our results showed that climate change already impacted the vegetation in these habitat types in 20 years.

Résumé

Les écosystèmes de montagnes sont vulnérables face au changement climatique en raison d'une augmentation des températures et d'une diminution des précipitations sous forme de neige, ce qui impacte la végétation des étages subalpin et alpin. Cependant, les milieux réagissent différemment à ces modifications climatiques et leur évolution n'est pas bien comprise. Pour mieux appréhender cette évolution, 71 parcelles ont été réinventoriées 19 – 20 ans après les précédents inventaires floristiques exhaustifs. Ces parcelles sont réparties dans quatre milieux (éboulis, combes à neige, pelouses et pâturages maigres d'altitude et prairies grasses) dans les Alpes vaudoises. La richesse spécifique, l'indice de Simpson, l'indice de Bray-Curtis, les valeurs indicatrices des espèces, les recouvrements des espèces et des ACP ont été utilisés pour comparer les relevés historiques et récents. Aucun des quatre milieux ne montre de changements significatifs d'alpha-diversité ou de composition spécifique au cours du temps. En revanche, une homogénéisation entre parcelles de la composition des pelouses et pâturages maigres d'altitude ainsi qu'une hétérogénéisation des éboulis et combes à neiges ont été observées. De plus, ces deux derniers milieux sont devenus respectivement plus acide ou plus sec, et les espèces présentes montrent une augmentation des températures moyennes. Les quelques espèces ayant subi un changement de recouvrement moyen se trouvent toutes dans les pelouses et pâturages maigres d'altitude ainsi que dans les prairies grasses. Dans l'ensemble, nos résultats montrent que les effets du changement climatique sur ces milieux sont déjà observables après 20 ans.

Introduction

Global warming is known as one of the most important threats to biodiversity (Verrall & Pickering, 2020). Since 1961, the 0 °C isotherm already shifted 300 to 400 m upward in Switzerland (OFEV et al., 2020). Moreover, since 1970, the number of days with snow precipitations decreased by 20 % above 2'000 m (OFEV et al., 2020), particularly at the end of the autumn and at the beginning of the spring (Serquet et al., 2013). Mountains ecosystems are expected to undergo a significant rate of temperature increase with + 0.25 °C of warming per decade until 2050 (Gobiet et al., 2014). The associate effect of an increase in temperatures and decrease in snow precipitations induces a smaller layer of snow on the ground and a premature thawing. This extends the growing season for vegetation (Dye, 2002), which lasts two to four weeks longer than in 1961 (OFEV et al., 2020). For this reason, the vegetation is expected to change considerably, with the arrival of more competitive species at higher elevations that could threaten other plant species adapted to cold conditions (Alexander et al., 2015; Winkler et al., 2019).

The impact of climate change on mountain vegetation has recently received an increasing interest, principally by quantifying vegetation changes with revisited historical plant inventories. For instance, Rumpf et al. (2019) found with a meta-analysis that plant species, as well as invertebrates and vertebrates species, migrate upslope toward mountain summits. This upward migration increases plant species richness at higher elevations, as it has been shown by Wipf et al. (2013) on a 168 years survey on Piz Linard, in south-eastern Switzerland. Moreover, using data collected from 1871 to 2016 on 302 mountains summits across Europe, Steinbauer et al. (2018) concluded that the rate of increase in species richness was higher between 2007 and 2016 than between 1957 and 1966. However, it has also been shown that land use can have a stronger influence than climate warming on vegetation changes in subalpine grasslands in the northern Swiss Alps (Vittoz et al., 2009). Modification of land use, like a reduction of grazing or land abandonment, has been observed since the early 1900 in the Alps (Bätzing, 1992). More precisely, the area of summer pastures declined by 5.42 % in the canton of Vaud between 1979 - 1981 and 2012 – 2014 (OFS et al., 2015). The decrease of grazing, alongside climate warming, can promote the upward shift of the treeline in the subalpine belt (Gehrig-Fasel et al., 2007), therefore reducing non-forest habitats and causing

the loss of less competitive alpine species that colonized the subalpine belt thanks to grazing (Dirnböck *et al.*, 2003).

While general trends in plant responses to climate and land use changes have been observed, contrasting responses for different habitat types have also been reported. Mountain grasslands with a dense vegetation cover and root system have been shown to be more stable regarding species composition than snowbeds (Choler *et al.*, 2001; Matteodo *et al.*, 2016). A similar stability has also been observed for nutrient-rich grasslands (Pignatti & Pignatti, 2014). The reasons behind this observed stability are that these habitats have little available space between established species for newcomers and they undergo a regular grazing each year which prevents the growth of shrubs and trees (Gehrig-Fasel *et al.*, 2007; Matteodo *et al.*, 2016). The colonization of new species from lower elevations can take time because of the lack of available space and because the new species have to establish among species better adapted to the local conditions (Alexander *et al.*, 2018). Other habitats, such as screes, are unstable landforms undergoing a steady input of rocks through time, preventing the formation of a dense vegetation (Delarze *et al.*, 2015). Scree host very specialized plant species, which have roots and stalks adapted to a moving habitat and have a large ecological range regarding elevation (Delarze *et al.*, 2015). In contrast, snowbeds are high mountain habitats characterized by a longer snow cover and have been shown to be more sensitive to colonization by new species than other alpine habitats, because of the short stature of the vegetation and the low plant density (Matteodo *et al.*, 2016; Liberati *et al.*, 2019). Finally, the response of vegetation to climate change might also vary along the elevation gradient. In this sense, it has been previously postulated that grasslands located around the treeline (approximately between 1'800 and 2'200 m) might present a higher species turnover, as they are located in the transition zone between the alpine and subalpine belts (Descombes *et al.*, 2017). If the evolution of snowbeds under climate change was already studied (Matteodo *et al.*, 2016; Liberati *et al.*, 2019), the one of subalpine and alpine grasslands was much less (Vittoz *et al.*, 2009; Matteodo *et al.*, 2016), particularly considering their diversity and questions around the stability that was observed up to now. Moreover, as far as we know, the impact of climate change on scree communities was not yet investigated.

While changes in species composition and richness have been reported, ecological indicator values (EIVs, Ellenberg, 1993; Landolt *et al.*, 2010) can be used to interpret the ongoing plant community changes. EIVs are based on the idea that species grow and reproduce better within specific ecological conditions, determined by abiotic factors such as temperature, light availability, abundance of nutrients, soil humidity or pH (Landolt *et al.*, 2010). EIVs provide proper insight of environmental conditions where a species can grow (Scherrer & Körner, 2011; Ischer *et al.*, 2014). For instance, by using EIVs, it has been shown that the species composition in snowbeds is tending towards species better adapted to drier soil conditions (Matteodo *et al.*, 2016; Liberati *et al.*, 2019). Moreover, Gritsch *et al.* (2016) found that the vegetation in high-mountain grasslands is becoming more thermophilous and Rumpf *et al.* (2019) found that the lower distribution of species adapted to harsh environmental conditions was retreating toward higher elevation. EIVs are therefore useful to help identify average environmental changes between historical and recent plant inventories (Gottfried *et al.*, 2012; Matteodo *et al.*, 2016; Liberati *et al.*, 2019).

In this study, we asked the two following questions: (1) Can we observe changes in plant community composition in the Vaud Alps after 20 years of climate warming? and (2) How do changes differ between habitat types? To answer these questions, we resurveyed 71 exhaustive plant inventories after 19 to 20 years in the Western Swiss Alps, among which high-mountain grasslands, nutrient-rich grasslands, screes and snowbeds (Figure 1). The first surveys were made in 2002 – 2003 (historical inventories) and the resurveys in 2021 – 2022 (recent inventories). In this paper, “site” refers to a specific place where two inventories were done, one historical and one recent, to compare these paired inventories through time.

We hypothesize that most changes will be observed in snowbeds, which are supposed to be very sensitive to climate warming (Matteodo *et al.*, 2016; Liberati *et al.*, 2019). In screes, we hypothesize that the vegetation will be to a limited extent responsive to climate change, as plants specialized in screes have a large elevation range. We also hypothesize to find few changes in high-mountain and nutrient-rich grasslands, because the dense vegetation cover limits new species establishment (Choler *et al.*, 2001). Finally, because the sites are located between 1'512 and 2'617 m, we expect to see more replacement in vegetation composition

through time – also known as turnover – in the low elevations of the altitudinal range of each plant communities than in the high elevations.

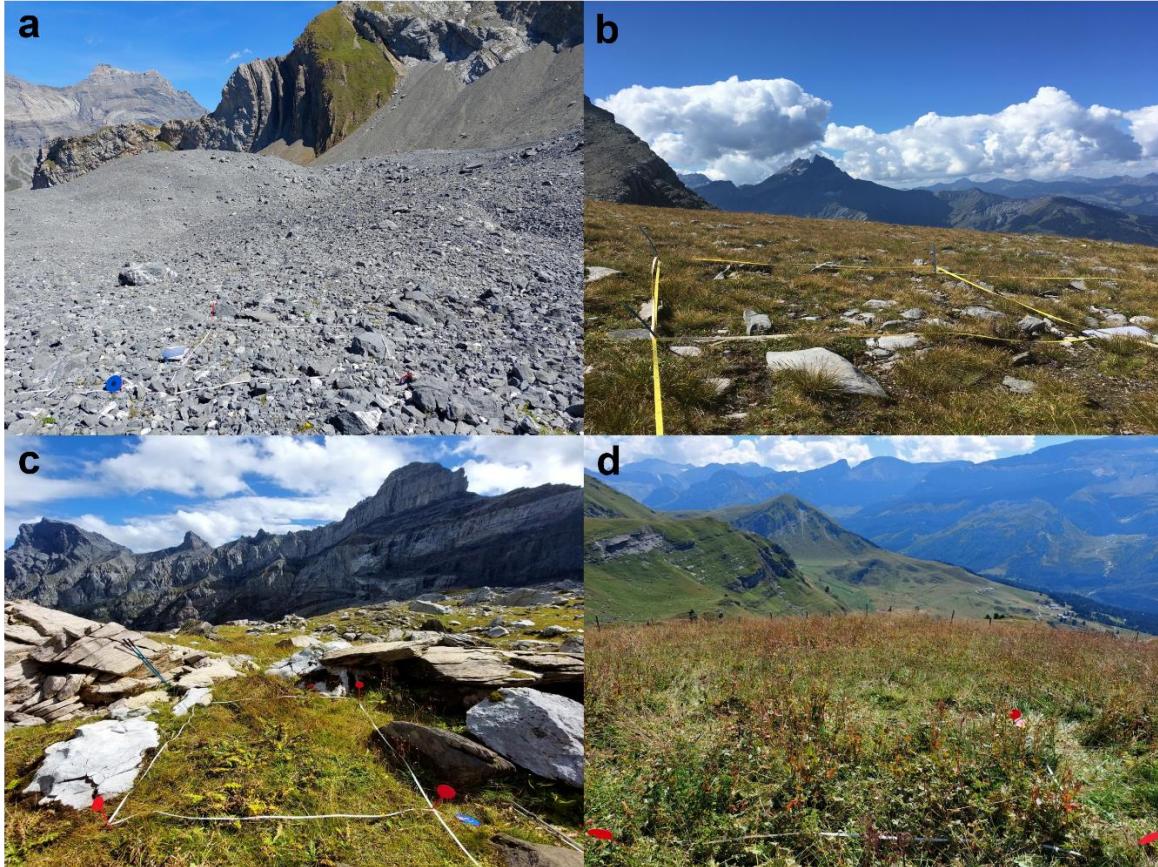


Figure 1. Floristic inventories made in the different mountain habitats like screes (a), high-mountain grasslands (b), snowbeds (c) and nutrient-rich grasslands (d). (© Pictures a, c and d: Mélanie Perret, © Pictures b: Loïc Liberati)

Materiel and methods

Study area

The study area is situated in the Western Swiss Alps ($46^{\circ}10' - 46^{\circ}30' \text{ N}$; $6^{\circ}50' - 7^{\circ}10' \text{ E}$), in the Canton of Vaud. The plots are located between 1'512 m to 2'617 m, in the subalpine and alpine belts (Figure 2). The geology of the region is principally dominated by limestone (www.swisstopo.admin.ch). The area has a temperate, semi-continental climate (Reynard, 2021) with a mean annual temperature of 3 °C at 2'000 m for the period 1981 – 2010 (Fallot, 2022). The mean annual sum of precipitation lies between 1'200 and 2'600 mm according to the elevation (Bouët, 1985). The grasslands below the treeline and in accessible areas above the treeline (i.e. 1'900 m; Gehrig-Fasel *et al.*, 2007) is mostly grazed by cattle in summer,

whereas the vegetation in non-accessible areas, such as steep slopes or screes, undergoes less human influence (Descombes *et al.*, 2017). Several plots are located in nature reserves, like in the Vallon de Nant, where the grazing by sheeps is forbidden (OFEV *et al.*, 2011).

Vegetation inventories

In 2002 and 2003, several hundred vegetation plots were selected in open habitats (grasslands, screes, rocks) of the study area, along the whole elevation gradient (375 to 3'210 m) according to a random stratified sampling. This sampling was performed regarding elevation, slope, aspect and geology (Randin *et al.*, 2009). In each 4 m² plot, an exhaustive floristic inventory was done by recording the species, completed by a visual estimation of their cover according to the Braun-Blanquet scale (Braun-Blanquet, 1964).

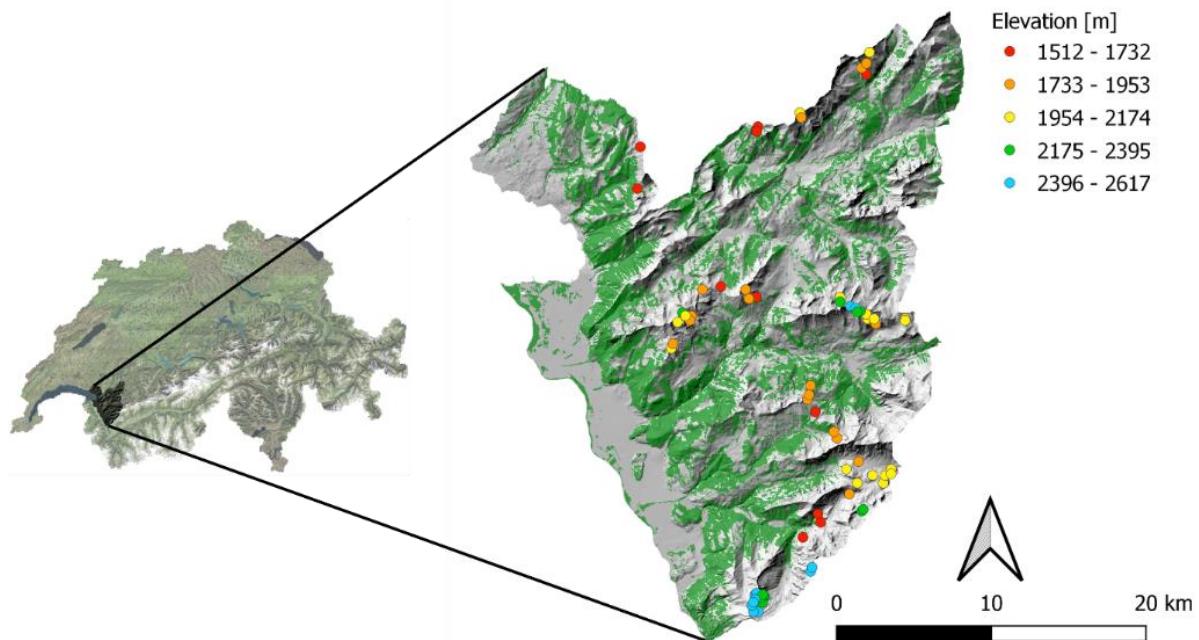


Figure 2. Location of the study area in the Western Swiss Alps in the Canton of Vaud, with the spatial distribution of the 71 sample sites. The colors represent the distribution of the sites along the elevation gradient. The forest is in green; the open habitats considered in this study are in the grey color scale.

During the summers 2021 and 2022, we resampled 71 plots from the pool of historical inventories regarding elevation and aspect. Among these inventories, 40 were made by a single botanist in 2021 and 2022 (always the same person), and 31 were made by two students in 2022 with the help of three different experienced botanists. To decrease the complexity and dangerousness of the field work, only sites displaying a slope below 45° were revisited.

An approximate sampling relocation of the historical plots according to the coordinates recorded during the first survey was done with a GPS antenna Trimble R2. The sketch of the historical plot location and the list of the species recorded in the historical inventories were used to refine the relocation of the plot. The historical list of species was used to select the site with the closest species composition and corresponding elevation and aspect (Matteodo *et al.*, 2016). The plots can be considered as quasi-permanent (Kapfer *et al.*, 2017).

The majority of the 71 plots displayed a homogenous surface, within an area of 2 x 2 m². In each plot, an exhaustive record of plant species was performed, completed with a cover estimation according to the Braun-Blanquet scale (Braun-Blanquet, 1964), as in historical inventories (Table 1). As in 2002 – 2003, the cover class 2 was divided in 2a (6 to 15 % of species cover) and 2b (16 to 25 %) as recommended by Gillet (1998). For future surveys, two aluminum plates were put underground at two opposite corners to facilitate a very precise, future relocation of the plot.

*Table 1. Scale used to estimate the species cover in the plots. The median of the cover percentage was used to compare species covers between historical and recent inventories. The ordinal scale was used to look at changes in Simpson reciprocal index, Bray-Curtis dissimilarity index, PCA and environmental factors with the EIVs (Landolt *et al.*, 2010)*

| Braun-Blanquet scale | Cover percentage [%] | Median of the cover percentage [%] | Ordinal scale (Yıldırım <i>et al.</i> , 2022) |
|----------------------|----------------------|------------------------------------|---|
| r | 1 to 2 individuals | 0.05 | 1 |
| + | < 1 | 0.5 | 2 |
| 1 | 1 – 5 | 3 | 3 |
| 2a | 6 – 15 | 10.5 | 4 |
| 2b | 16 – 25 | 20.5 | 5 |
| 3 | 26 – 50 | 38 | 6 |
| 4 | 51 – 75 | 63 | 7 |
| 5 | 76 - 100 | 88 | 8 |

Between 2002 – 2003 and 2021 – 2022, nomenclature and aggregation levels may have changed for some species. Moreover, some errors in species identification may have occurred because different botanists performed the plant inventories and non-flowering species are always common in such surveys. Therefore, a conscientious control was made to bring out synonymies and combine frequently confused species.

In 2003, a classification of the inventories has been conducted to characterize the habitat types of the plots according to Delarze *et al.* (1998) (Martinoni, 2003). The classification done in 2003 is still valid (Delarze *et al.*, 2015) and was maintained in the present study to classify the plots. Among the 71 sites revisited for this study, only sites belonging to screes (*Thlaspium rotundifolii*, *Petasition paradoxi* according to Delarze *et al.*, 2015), high mountain grasslands (*Seslerion*, *Caricion ferruginea*, *Elynnion*, *Nardion*), snowbeds (*Arabidion caeruleae*, *Salicion herbaceae*), and nutrient-rich grasslands (*Polygono-Trisetion*, *Cynosurion*, *Poion alpinae*) were retained, which excluded five sites belonging to other habitats. The latter contained too few plant inventories to be considered. Moreover, two other sites were removed from the analyses: the first one was discarded because of a total absence of plants in historical and recent inventories, the second because of an impossibility to estimate the species cover, the plants in the plot being almost completely grazed. Overall, 64 pairs of plant inventories were used for the analyses.

Ecological indicator values

Among the 64 pairs of plant inventories, 448 species were recorded. For the 448 species, the EIVs were collected from *Flora Indicativa* (Landolt *et al.*, 2010). The most relevant EIVs were retained: temperature (T), light (L), soil humidity (F), soil pH (R) and soil nutrient content (N). For each species, an ordinal value ranging between 1 to 5 was attributed for all these factors by experienced botanists and ecologists. A value of 1 means that plants can support low temperatures, shaded areas, dry soils or acidic soils and low nutrient contents, while a value of 5 means that plant needs the opposite environmental factor. To improve the accuracy of the analyses, all the species that lacked at least one value out of the five EIVs were not retained in the analyses using EIVs. This is justified by the fact that the absence of an EIV for one species in Landolt *et al.* (2010) indicates a large ecological amplitude and keeping these species would

have not brought much information on the mean value of the plot. At the end, 433 species were kept for the analyses.

Data analyses

Changes in species alpha- and beta-diversity

We investigated differences in species richness between recent and historical inventories by comparing the number of species per plot and for each habitat type separately. As historical and recent inventories were done by different botanists, some species with low cover may have been overlooked (Vittoz & Guisan, 2007). For this reason, the alpha-diversity was also calculated with the Simpson reciprocal index (Equation 1) for each plot, as this index is less sensitive with species having a low cover (Matteodo *et al.*, 2016), following this formula:

$$\text{Simpson reciprocal index} = \frac{N(N - 1)}{\sum n_i(n_i - 1)} \quad (\text{Equation 1})$$

with N the total number of species per plot and n the cover of the species i . The difference in each site of the Simpson reciprocal index between historical and recent inventories was calculated within each plant community with the package R vegan (function *diversity*, Jari *et al.*, 2020). To calculate the Simpson reciprocal index, the Braun-Blanquet scale was previously converted to an ordinal scale (Table 1) according to Yıldırım *et al.* (2022), with the package R labdsv (function *vegtrans*, Roberts, 2016). The distribution of the differences of species richness and of the Simpson reciprocal index between paired plot was checked. Depending on the normality or non-normality of this distribution, a Student's paired t-test or a Wilcoxon signed-rank paired test was done, respectively.

A possible homogenization of the floristic composition between historical and recent inventories was investigated by using the Bray-Curtis dissimilarity index for each habitat types, with the package R vegan (function *vegdist*, Jari *et al.*, 2020). Before the analysis, the Braun-Blanquet scale was converted to the same ordinal scale as for the Simpson reciprocal index (Table 1). Within each habitat type, the dissimilarity matrix was computed between each historical inventory with all the other historical inventories, and between each recent

inventory with all the other recent inventories (Matteodo *et al.*, 2016; Liberati *et al.*, 2019). Then, the mean dissimilarity was calculated for each historical and recent inventories. Finally, the differences of the mean dissimilarity index between historical and recent inventories were calculated, and the distribution of these differences was checked to determine which statistical test to perform. As the distributions were normal, a Student's paired test was performed for each habitat type. This index varies between zero and one, the latter indicating that two sites have no species in common and are totally dissimilar.

We investigated the relationship between the turnover of species and the elevation of the sites. For this, the Braun-Blanquet scale was converted to the ordinal scale (Table 1) and the Bray-Curtis dissimilarity index between pairs of historical and recent inventories was calculated with the package R vegan (function *vegdist*, Jari *et al.*, 2020). The relationship was estimated with a Pearson's correlation test (normal distribution) or a Spearman's rank correlation test (non-normal distribution).

Changes in species composition and cover

To visualize vegetation shifts between historical and recent inventories within each habitat, a principal component analysis (PCA) of the plots was performed on the basis of their species composition and cover (ordinal scale, package R vegan, function *rda*, Jari *et al.*, 2020). As recommended by Borcard *et al.*, 2011, the data were submitted to a Hellinger transformation with the package R vegan (function *decostand*, Jari *et al.*, 2020). Then, the differences of the principal component (PC) scores between historical and recent inventories were calculated for the two first PC. A multivariate analysis of variance (MANOVA, package R stats, R Core Team, 2021) was performed on the differences against the intercept (Vittoz *et al.*, 2009; Matteodo *et al.*, 2016; Liberati *et al.*, 2019). This intercept-only model was done by using a constant (1 in our case) as a response variable, to test the variation of the differences through time. A Wilk's Lambda test was done to test if the means of the differences between groups were significant.

Potential changes in individual species cover were analyzed within each habitat type and the significance of the changes was calculated with a restricted permutation test (Matteodo *et al.*,

2016; Liberati *et al.*, 2019), as suggested by Kapfer *et al.* (2011). For this comparison of species cover, the Braun-Blanquet scale cover was previously converted with the median of the Braun-Blanquet cover scale (package R labdsv, function *vegtrans*, Roberts, 2016) following Matteodo *et al.* (2016). Within each habitat type, only the most frequent species present in 25 % of the historical plots and 25 % of the recent plots were retained. The mean cover of each species was calculated by taking into account only the plots where the species has been observed (i.e., when the cover was not equal to zero). The restriction permutation test was performed with a random permutation of species cover within historical and within recent plots. The test was done 999 times and at each step the mean species cover was calculated for the randomized plots. Finally, the significance level was assessed by counting the number of times the absolute difference of the mean cover for the randomized values was equal to or higher than the absolute difference of the mean cover for the observed values.

Changes in site-averaged ecological indicator values

We investigated changes in environmental conditions by averaging EIVs (Landolt *et al.*, 2010) for each historical and recent inventories, weighted by the species cover, which was previously converted from the Braun-Blanquet scale to an ordinate scale (Table 1). The differences between the plot averaged EIVs in 2002 – 2003 and 2021 - 2022 was tested for the different habitat types, with either a Student's paired test or a Wilcoxon signed-rank test according to the distribution of the differences. Finally, a PCA was performed to visualize the shifts of plot averaged EIVs with the package R vegan (function *rda*, Jari *et al.*, 2020). As for the vegetation shifts, the differences of the PC scores between historical and recent inventories were calculated for the two first PC and a MANOVA (package R stats, R Core Team, 2021) was performed on the differences against the intercept (Vittoz *et al.*, 2009; Matteodo *et al.*, 2016; Liberati *et al.*, 2019), with a constant-only model. A Wilk's Lambda test was done to test if the means of the differences between groups were significant.

All data analyses were performed the R statistical software, version 4.1.1 (R Core Team, 2021).

Results

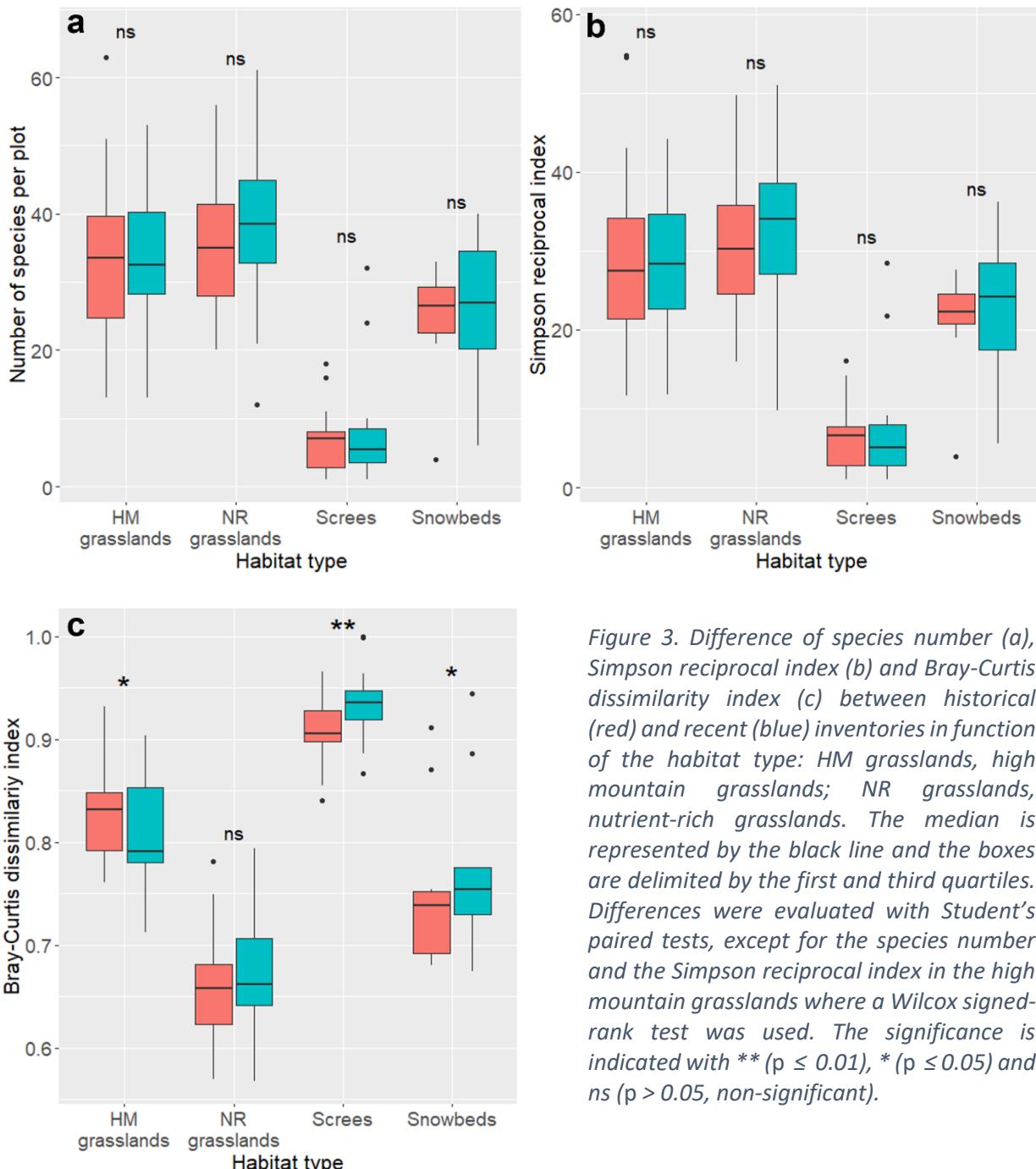
Changes in species alpha- and beta-diversity

We found no significant differences ($p > 0.05$) in species richness between historical and recent inventories for the four habitat types (Figure 3a). The average number of species in plots increased by 1.25 in screes (historical richness: $6.75 \text{ species} \pm 4.97$, recent richness: 8.00 ± 8.44), by 2.2 in nutrient-rich grasslands (historical: 36.0 ± 10.1 , recent: 38.2 ± 10.8) and by 2.4 in snowbeds (historical: $24.5 \text{ species} \pm 8.15$, recent: 26.9 ± 10.5) and decreased by 0.5 in high-mountain grasslands (historical: 34.2 ± 14.2 , recent: 33.8 ± 10.1). Likewise, the Simpson reciprocal index showed no significant differences in all habitat types between historical and recent inventories (Figure 3b). The index increased in average by 1.00 in screes (historical index: 6.16 ± 4.43 , recent index: 7.16 ± 7.57), by 1.4 in nutrient-rich grasslands (historical: 31.2 ± 8.89 , recent: 32.6 ± 9.56) and by 1.72 in snowbeds (historical: 21.3 ± 6.64 , recent: 22.9 ± 8.79) and decreased by 0.49 in high-mountain grasslands (historical: 28.9 ± 12.5 , recent: 28.5 ± 8.71).

The Bray-Curtis dissimilarity index (Figure 3c) showed a significant decrease between historical and recent inventories by 0.02 in average in high-mountain grasslands (historical index: 0.83 ± 0.05 , recent index: 0.81 ± 0.05 , Student's paired t-test: $p = 0.019$, $n = 18$) and significant increases by 0.02 in screes (historical: 0.91 ± 0.03 , recent: 0.93 ± 0.04 , Student's paired t-test: $p = 0.006$, $n = 16$) and by 0.02 in snowbeds (historical: 0.75 ± 0.08 , recent: 0.77 ± 0.08 , Student's paired t-test: $p = 0.013$, $n = 10$). There is no significant change between historical and recent inventories in nutrient-rich grasslands, even though the Bray-Curtis dissimilarity index increased by 0.01 (historical: 0.66 ± 0.06 , recent: 0.67 ± 0.06).

We found that nutrient-rich grasslands was the only habitat type displaying a significant negative correlation between species turnover and elevation (Pearson's correlation: $r = -0.446$, $p = 0.049$, $n = 20$, Figure S1 in the appendix). While relationships between species turnover and elevation were not significant for the other habitat types, snowbeds showed a positive trend (Spearman's rank correlation: $\rho = 0.539$, $p = 0.113$, $n = 10$), screes a negative

trend (Pearson's correlation: rho = -0.231, p = 0.389, n = 16) and high-mountain grasslands a negative trend (Pearson's correlation: -0.446, p = 0.063, n = 18).



*Figure 3. Difference of species number (a), Simpson reciprocal index (b) and Bray-Curtis dissimilarity index (c) between historical (red) and recent (blue) inventories in function of the habitat type: HM grasslands, high mountain grasslands; NR grasslands, nutrient-rich grasslands. The median is represented by the black line and the boxes are delimited by the first and third quartiles. Differences were evaluated with Student's paired tests, except for the species number and the Simpson reciprocal index in the high mountain grasslands where a Wilcoxon signed-rank test was used. The significance is indicated with ** (p ≤ 0.01), * (p ≤ 0.05) and ns (p > 0.05, non-significant).*

Changes in species composition and cover

The two first axes of the PCA based on species composition explained 18.77 % of the total variance (11.58 % for PC1 and 7.19 % for PC2; Figure 4). None of the four habitat types

displayed a significant composition shift between 2002 – 2003 and 2021 – 2022 (MANOVA *p*-values: snowbeds = 0.898, high-mountain grasslands = 0.104, screes = 0.324, nutrient-rich grasslands = 0.476).

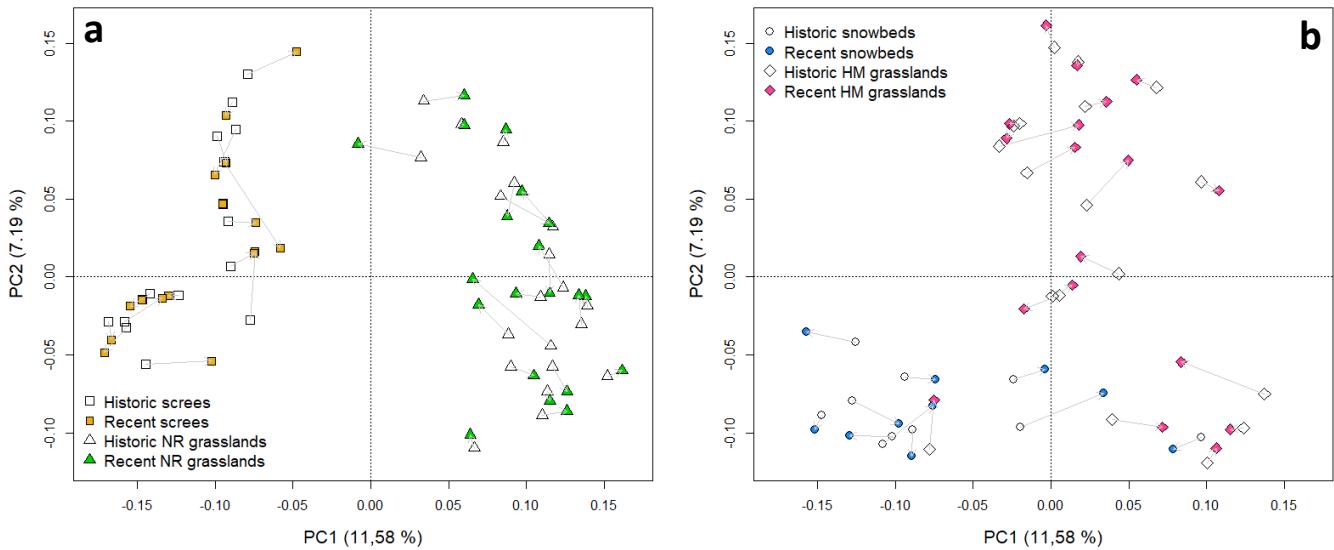


Figure 4. Principal component analysis (PCA) on species composition and cover of the four habitat types. Paired of historical (white) and recent (colored) plant inventories are linked with an arrow. No significant (MANOVA test) shift of species composition was observed in the four habitat types, represented by the shape of the points: screes and nutrient-rich grasslands (NR grasslands, a) and snowbeds and high-mountain grasslands (HM grasslands, b). The visual representation of the PCA was split to keep two habitat types per graph to facilitate the readability.

The restricted permutation tests showed that five species underwent a significant difference of mean cover between 2002 – 2003 and 2021 – 2022. In high-mountain grasslands, *Nardus Stricta* showed a decrease in relative mean cover (-63.42 %, *p* = 0.04), while the same species showed an increase in mean cover in nutrient-rich grasslands (+86.37 %, *p* = 0.026). Also in nutrient-rich grasslands, *Avellana flexuosa*, *Agrostis rupestris* and *Festuca rubra aggr.* showed a decrease in mean cover between historical and recent inventories, with a difference of relative mean cover of -97.84 % (*p* = 0.002), -84.38 % (*p* = 0.007) and -46.93 % (*p* = 0.02), respectively. No change in species cover was observed in snowbeds and screes.

Changes in site averaged EIVs

Significant increase in plot averaged EIVs was found for the temperature (T) in snowbeds by 0.08 (historical T: 1.42 ± 0.17 , recent T: 1.51 ± 0.15 , Student's paired-test: *p* = 0.021, *n* = 10) and by 0.14 in screes (historical T: 1.82 ± 0.55 , recent T: 1.96 ± 0.62 , Wilcoxon signed-rank

paired test: $p = 0.020$, $n = 16$, Figure 5e). Also, a significant decrease by 0.13 in soil humidity (F) was observed in snowbeds (historical F: 3.26 ± 0.14 , recent F: 3.13 ± 0.17 , Student's paired test: $p = 0.002$, $n = 10$, Figure 5a), showing that soil is getting drier in this habitat type. In screes, we found a significant difference of soil pH, with a decrease in site average EIVs for the soil pH (R) by 0.20 (historical R: 4.33 ± 0.57 , recent R: 4.13 ± 0.56 , Wilcoxon signed-rank paired test: $p = 0.004$, $n = 16$, Figure 5d). High-mountain pastures and nutrient-rich grasslands showed no significant differences between historical and recent inventories for all EIVs (Figure 5a to e). Moreover, none of the four habitat types showed a significant change of mean value of light (Figure 5b) and nutrient content (Figure 5c).

The first two axis of the PCA on site averaged EIVs explained 79.07 % of the total variance (53.66 % for PC1 and 26.04 % for PC2; Figure S2 in the appendix). There was no significant shift of the site averaged EIVs for the nutrient-rich grasslands and the high-mountain grasslands between historical and recent inventories. However, significant shifts were observed in snowbeds toward a lower soil humidity (MANOVA: $F(3,7) = 13.66$, $p = 0.003$) and in screes toward a lower pH and a higher temperature (MANOVA: $F(3,13) = 4.09$, $p = 0.03$).

Discussion

Our study provides a first overview of the impact of climate change on four different habitat types in 20 years in the Swiss Alps. Overall, no significant change in alpha-diversity was found, but changes in species composition and cover or ecological conditions could be observed for some habitat types. Species composition in screes and snowbeds became more heterogenous and more thermophilous through time. In addition, snowbeds became drier and screes became more acidic. In contrast, the high-mountain grasslands tended to become more homogenous through time. The nutrient-rich grasslands remained relatively stable in term of beta-diversity and regarding the ecological indicators, even though this habitat showed more changes of some species cover than the other habitat types. While our results show that changes under climate change in plant communities in 20 years are not obvious, it is already surprising to sense some of them over this short period.

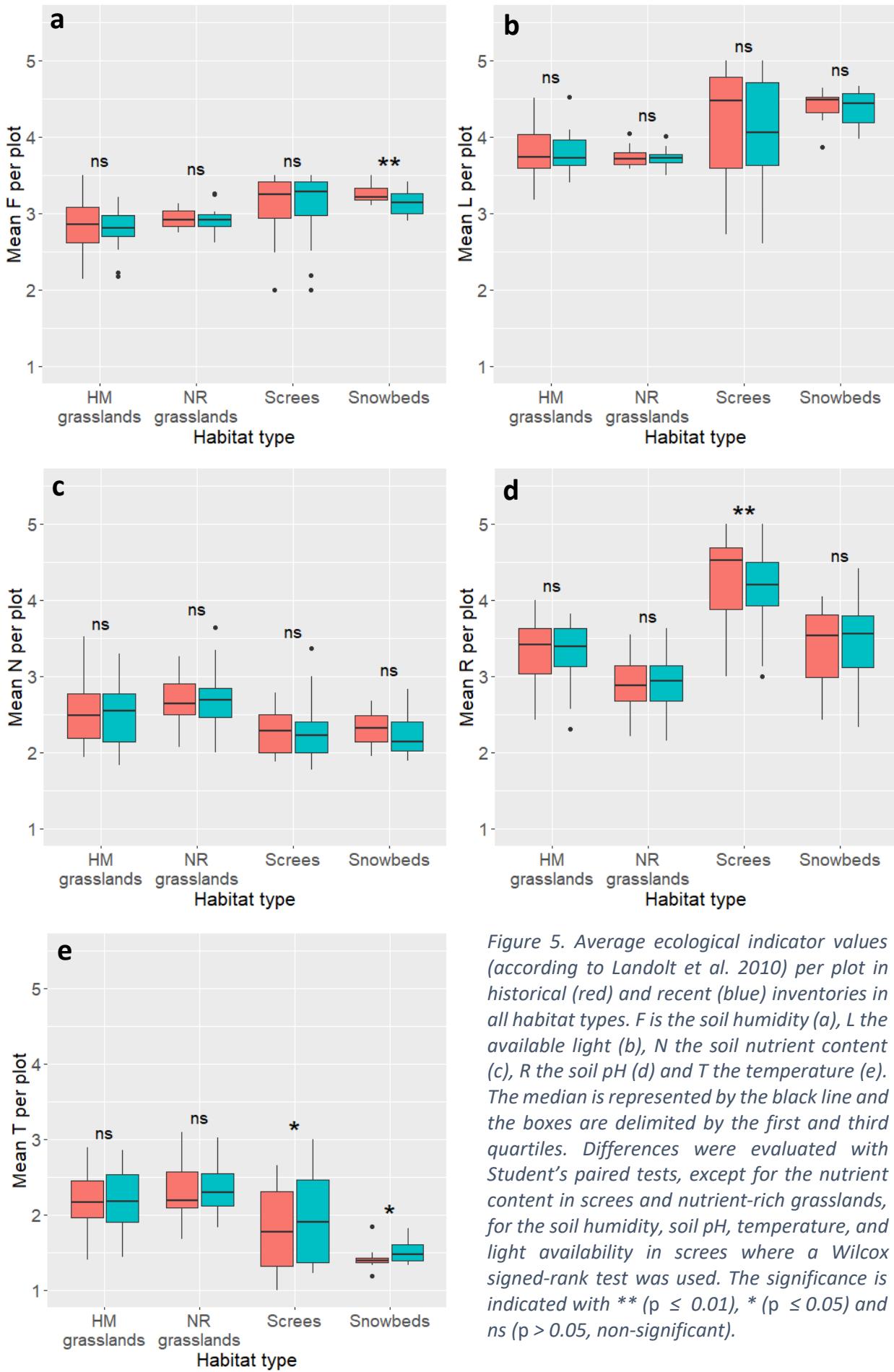


Figure 5. Average ecological indicator values (according to Landolt et al. 2010) per plot in historical (red) and recent (blue) inventories in all habitat types. F is the soil humidity (a), L the available light (b), N the soil nutrient content (c), R the soil pH (d) and T the temperature (e). The median is represented by the black line and the boxes are delimited by the first and third quartiles. Differences were evaluated with Student's paired tests, except for the nutrient content in screes and nutrient-rich grasslands, for the soil humidity, soil pH, temperature, and light availability in screes where a Wilcoxon signed-rank test was used. The significance is indicated with ** ($p \leq 0.01$), * ($p \leq 0.05$) and ns ($p > 0.05$, non-significant).

Changes in snowbeds

The snowbeds remained relatively stable in terms of alpha-diversity. There was no difference between historical and recent inventories in species richness per plot. This result confirms the finding of Gritsch *et al.* (2016), on a 14 years survey in the upper subalpine and alpine Alps in Northeastern Austria. The consistency of species number through time can be explained by the fact that the arrival of new species can compensate the loss of species historically present in the plots. No change of the Simpson reciprocal index means that even if new species from neighboring grasslands colonized the snowbeds and old species went extinct, the relative abundance of each species remained stable and none of the newcomers became dominant on the species adapted to snowbeds. Also in the Swiss Alps, but for a longer period, Matteodo *et al.* (2016) found a stable Simpson reciprocal index in typical snowbeds, which is a habitat on acidic soils, but an increase in wet snowbeds, localized under firs or close to running water (Matteodo *et al.*, 2016), whereas Liberati *et al.* (2019) observed a significant increase in the Simspon reciprocal index in typical and wet snowbeds. In our study, most of the snowbeds plots belonged to *Arabidion caeruleae*, which are calcareous snowbeds and which were not considered in previous studies. Because the rock cover is more important in calcareous snowbeds than in other types of snowbeds (Delarze *et al.*, 2015), the new species may need more time to establish.

The beta-diversity showed that the historical inventories were more similar to each other than recent ones, in accordance with Gritsch *et al.* (2016). Snowbeds form small patches between other habitats and are isolated from each other (Delarze *et al.*, 2015). Therefore, new plants that colonize the snowbeds may be distinct species in the different sites, which results in a higher heterogeneity between sites through time. Even if different species colonized the different plots, the mean indicator values (EIVs) of inventoried plant species in snowbeds suggest that globally they have a more thermophilous and less hygrophilous species composition in recent inventories than in historical ones. Those results are in accordance with observations made by Matteodo *et al.* (2016) and Liberati *et al.* (2019), who similarly found a significant increase in mean indicator values for temperatures in typical snowbeds in response to the colonization of grasslands species. Also, Liberati *et al.* (2019) found a significant decrease in soil humidity in typical and wet snowbeds. Under climate warming, the 0 °C

isotherm is moving upward, what decreases the snow precipitations (OFEV et al., 2020), reduces the snow depth and accelerates spring melting, therefore decreasing the period with snow cover, increasing the growing season (Dye, 2002) and reducing the available water. Therefore, our results are not surprising, showing that calcareous snowbeds are changing similarly to acidic snowbeds.

These changes in Bray-Curtis dissimilarity among historical and among recent inventories, and the change in ecological indicator values for temperature and soil humidity contrast with the absence of significant changes in species cover or vegetation shifts through time. We could have expected that the cover of the most thermophilous species would increase and the cover of specialized snowbeds species would decrease significantly. Moreover, the arrival of new species from neighboring grasslands would have induce a vegetation shift toward a more thermophilous habitat type. For example, Matteodo *et al.* (2016) found a shift for typical snowbeds toward siliceous alpine grasslands, and a shift toward typical snowbeds for the wet snowbeds. Similarly, other studies (Carbognani *et al.*, 2014; Pickering *et al.*, 2014) found an expansion of grasslands species in snowbeds because of modifications of environmental local conditions. Maybe our data did not reveal a so important shift because our study covers a shorter time span than the previous ones (20 years instead of 40 years in Matteodo *et al.* 2016). Moreover, the Bray-Curtis dissimilarity and the EIV may be more sensitive to changes than the analyses used to test the vegetation shifts. With the Bray-Curtis dissimilarity index, each inventory is compared with all the other inventories of the same year. The PCA shows spatial changes on a graph, which may be not yet noticeable with our data. Indeed, the colonization of snowbeds by different species in each site is reflected by individual shifts of each plot in all directions. To better understand these results, further investigations need to be done at species level, to see for example which species were not present in historical inventories but were observed in recent ones and vice versa.

Changes in screes

To the best of our knowledge, this is the first time that vegetation changes through time have been studied in screes. No change of alpha-diversity was observed in this habitat and this result was expected. Indeed, a recent study found the presence of permafrost in the Grand

Muveran mountain range and in the upper part of the Vallon de Nant, where we performed the plant inventories (Lambiel *et al.*, 2009). Under climate change, the permafrost is susceptible to thaw, which could destabilize the cliffs, thus increasing the rate of rockfalls (Gruber & Haeberli, 2007). Therefore, screes might be particularly unstable and hard to colonize because of regular disturbances (Delarze *et al.*, 2015). Once the rate of rockfalls decreases, screes become more stable. Then, specialized species, like *Salix serpyllifolia*, *Salix retusa* or *Dryas octopetala* on limestone can steady the rocks by blocking them. Once the rocks are immobilized, fine sediments are trapped which allows pedogenesis (Leuschner *et al.*, 2018). This scree stabilization can last hundreds of years (Giupponi *et al.*, 2022). Therefore, 20 years may be a too short period to find changes in alpha diversity and our data can be useful for further studies considering time series data in this habitat type, which changes more slowly than snowbeds for example.

An heterogenization of plant composition between historical and recent inventories was observed in screes. Plots in screes can be hard to localize and recent inventories may be not at the exact coordinates as the historical ones. Several species can inhabit a scree, but only a few of them are found in an area of 4 m². Moving the plot by a few meters could increase the risk of having other species in the plot, which changes the Bray-Curtis index between the historical and recent inventories and can explain why the Simpson reciprocal index did not change through years.

The new species composition of the screes resulted to mean ecological indicator values indicating an increase in average temperatures and a decrease of pH. Our plots were mainly located in calcareous habitats, with a high soil pH (Vonlanthen *et al.*, 2006). Hence, these changes could be explained by the increase in cover or the colonization of more thermophilous species in the community in response to the stabilization of the screes and an increasing proportion of organic matter. This phenomenon can be observed on glacial moraines, one part of the plots classified as screes because of their similar composition, where the withdrawal of a glacier allows the vegetation to colonize the habitat, which become a grassland after several decades and a slow enrichment of the soil with organic matter (Raffl & Erschbamer, 2004). However, the explanation suggesting that the changes in mean ecological indicator values come from a stabilization of the scree is paradoxical with respect to the explanation suggesting

that the consistency of the alpha-diversity through time comes from the fact that the screes are not yet stabilized. At the time of writing, we do not see what could lead to the resolution of this paradox.

Like in snowbeds, the heterogenization of scree communities and the change of ecological indicators is inconsistent with the fact that no significant change in species cover nor vegetation shift were observed through time. The vegetation shifts may need more than 20 years to be observable, as screes evolve only slowly (Giupponi *et al.*, 2022). As mentioned in changes in snowbeds, the Bray-Curtis dissimilarity index and the EIVs may be more sensitive to detect small changes. Therefore, our data will be useful for further surveys.

Changes in high-mountain grasslands

In high-mountain grasslands, we found no change of alpha-diversity, but the results are contrasting between the different studies. For example, Gritsch *et al.* (2016) found no significant change in mean species number in *Seslerio-Caricetum sempervirentis* but an increase in *Caricetum firmae*. The first habitat is found on south oriented slopes and generally displays a dense plant cover due to favorable climatic conditions, which increases competition between individuals, whereas the second habitat is found at higher elevation or in very windy conditions (weak snow accumulation) and displays a lower and more open plant cover. Thus, an increase in temperature under climate change could favor competitive species adapted to warmer environments and cold-adapted species are in risk to disappear from this habitat (Gritsch *et al.*, 2016). Vittoz *et al.* (2009) found an increase in mean species number in *Seslerion albicans* and *Caricion ferruginea*. However, this difference was partly explained by the fact that more botanists (one in 1970 and two to three in 2006) performed the plant inventories during the resurvey, which may have increased the quality of the sampling by reducing the number of overlooked species. In our case, the stability in species number can be related to the relatively low elevation, because changes in species number were more important at upper alpine and nival belts than at the elevation range where our plots were placed in this habitat (1'585 to 2'525 m; Stöckli *et al.*, 2011). Moreover, no change in the Simpson diversity index were observed, which confirms the results of Matteodo *et al.* (2016) on calcareous

grasslands (*Seslerion*). This habitat displays a high plant cover, thus it can take time to be colonized by species from lower elevation (Alexander 2018).

An increase of homogenization through time reflected with the decrease of the Bray-Curtis dissimilarity index between historical and recent inventories was observed for high-mountain grasslands. This means that plots became more similar to each other through time, and it is the only habitat type of our study where it occurred. According to Britton *et al.* (2009), Ross *et al.* (2012) and Carbognani *et al.* (2014), homogenization comes from the colonization in all plots belonging to an habitat type by species adapted to a high range of environmental conditions, namely generalists species, and the withdrawal from these plots of rare species. Unfortunately, as the restriction permutation test used to detect changes in species cover considered only the most frequent species, it was not possible to know if the cover of rare species decreased through time. But small changes in species cover affecting a high number of species may influence the Bray-Curtis dissimilarity index, even though these changes were not statistically significant. In our study, the only significant change of species cover is the decrease of *Nardus stricta* through time. This species benefits from grazing (Pakeman *et al.*, 2019), thus the decrease of grazing since 1979 (OFS *et al.*, 2015) in this habitat type due the decline of summer pasture in the canton of Vaud could explain the changes observed for *Nardus stricta*. Unfortunately, we lack precise data about summer pastures in the study area to better explain this difference. Another hypothesis to explain the decrease cover of this species could be that some *Nardion*, a habitat type included in high-mountain grasslands in this study and where the *Nardus stricta* is dominant (Delarze *et al.*, 2015), may have been regularly fertilized in the subalpine belt (Dubuis *et al.*, 2013). In this case, the *Nardion* is colonized by species from nutrient-rich grasslands (Delarze *et al.*, 2015).

No change in the mean ecological indicators nor significant species composition shift through time were found in high-mountain grasslands. Matteodo *et al.* (2016) found a significant increase in temperature in the calcareous grasslands (*Seslerion*) and no vegetation shift regarding species composition. They explained the observed increase in temperature by the arrival of species from lower elevation, such as *Cirsium acaule* or *Globularia cordifolia*. Moreover, they found that the siliceous subalpine grasslands (*Nardion*) were stable regarding the mean ecological indicators and species composition shifts. Therefore, the relative stability

of the grasslands in our study confirms the stability previously observed by Matteodo *et al.* (2016), even though we considered the *Seslerion* and the *Nardion* together. The difference of results regarding the increase in temperature in the calcareous grasslands may come from the fact that our study was conducted on 20 years span between plant inventories, which can explain why the ecological indicators did not change in our case.

Changes in nutrient-rich grasslands

Nutrient-rich grasslands were the most stable of our four habitat types. No change of alpha nor beta diversity, no change of EIVs and no vegetation shift were observed. The very dense vegetation cover leaves little space for new species to colonize this habitat type (Choler *et al.*, 2001). Although the changes of mean cover through time for a few species can not impact the whole habitat, there was an increase in mean cover for *Nardus stricta* and a decrease for *Avellana flexuosa*, *Agrostis rupestris* and *Festuca rubra aggr*. As *Nardus stricta* is a species that benefits from grazing (Pakeman *et al.*, 2019), this could indicate that plots of nutrient-rich grasslands are not located in areas where there was a decrease in grazing since 1979 (OFS *et al.*, 2015). Therefore, this species may have been recently favored by cattle grazing. *Avellana flexuosa* and *Agrostis rupestris* are species found in high-mountain grasslands, adapted to nutrient-poor conditions (Landolt *et al.*, 2010). *Festuca rubra aggr.* is a mesotrophic species, but is favored in absence of fertilization (Vaida *et al.*, 2021). Thus, the fertilization of grasslands could explain the decline of these species through time. However, this is inconsistent with the increase in mean cover for *Nardus stricta*, which should decrease if there are more nutrients in its habitat. The fact that different alliances according to (Delarze *et al.*, 2015) were merged into the group of nutrient-rich grasslands could be the cause of these contradictory results. Therefore, data from a larger number of sites and more precise analyses of the plant communities are needed in the future to confirm these changes in species cover.

In nutrient-rich grasslands, a significant decrease in species turnover with elevation was observed. This means that the rate of species replacement is more important in lower than in higher elevation. This could be the consequence of a varying land use along elevation. Indeed, grazing, as well as fertilization, decreases with elevation (Strebel & Bühler, 2015). Thus, a change in land use management will have a higher impact at the elevations where the land

use is more intensive. On one hand, longer growing season under climate change could induce an intensification of land use at lower elevations, which could favor competitive species that grow well with more nutrients and reduce stress-tolerant species (Niedrist *et al.*, 2009). On the other hand, land abandonment in the form of an interruption of grazing promotes the establishment of taller species like bushes or trees which can reduce the number of species specialized to open areas (Gehrig-Fasel *et al.*, 2007; Boch *et al.*, 2021). Both modification of land-use management may impact the species composition, and these vegetation changes are reflected with a higher turnover at low elevation in nutrient-rich grasslands. But additional data are needed to confirm the decrease in species turnover with elevation, especially below 1'500 m where the land use is more pronounced.

Limitations

The summer 2022 was one of the driest and warmest in Switzerland since 1864 (www.meteosuisse.ch). This did not facilitate the identification of plants in the field, because a relatively high proportion of the plant species were at the vegetative stage, even at the beginning of the field work. *Crocus albiflorus* was not much observed in 2022 because after the flowering the leaves were quickly burned by the drought. However, we expect that the inventories performed in 2022 are of good quality, given that experts were present and because we considered only subalpine and alpine grasslands (> 1'500 m) that were less impacted by the drought. Also, some of the methods of this study may have influenced the differences in species composition observed through time. First, we used the list of species of the historical inventories to relocate more precisely the sampling sites. This could have led to detect fewer changes in species composition than were actually present. However, while it would be better to not refer to the historical list of species, we needed to proceed this way because no aluminum plates were placed underground in 2002 – 2003. Second, the area of the plots can also influence the changes in species composition. Indeed, the differences in species composition could be more important by comparing inventories performed in smaller plots than in larger plots. This point must be considered when comparing our results with other studies. Finally, our samples were also relatively small in each habitat type (16 sites in screes, 10 in snowbeds, 18 in high-mountain grasslands and 20 in nutrient-rich grasslands) and this decreases the power of the statistical tests.

Conclusion

Overall, our results suggest that 20 years of climate change already impacted the species composition of subalpine and alpine habitat types. They help to better understand the evolution of different plant communities under climate warming in the Western Swiss Alps. From the discussion, it clearly appears that the results obtained throughout this work are hard to interpret and that further research are required to complement our comprehension. For example, additional investigation must be done in each habitat type to see which species entered the community and which species disappeared from it through time to understand the community dynamics, given that no significant shift in species composition could explain the changes in homogenization or ecological indicators through time. Moreover, different alliances regarding Delarze *et al.* (2015) were merged into either snowbeds, screes, high-mountain grasslands or nutrient-rich grasslands in this study. Further studies considering more precise level of each habitat type could enlighten some of the changes that were observed. For example, modification in mean cover for species sensitive to land use changes, such as an increase or decrease of grazing or fertilization, could be better understood if analyses consider the alliance level of the habitat types. Hence, in the next years, more vegetation data need to be collected to increase the sample size in each habitat type to better assess the effect of climate warming and land-use change on subalpine and alpine vegetation.

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Appendix

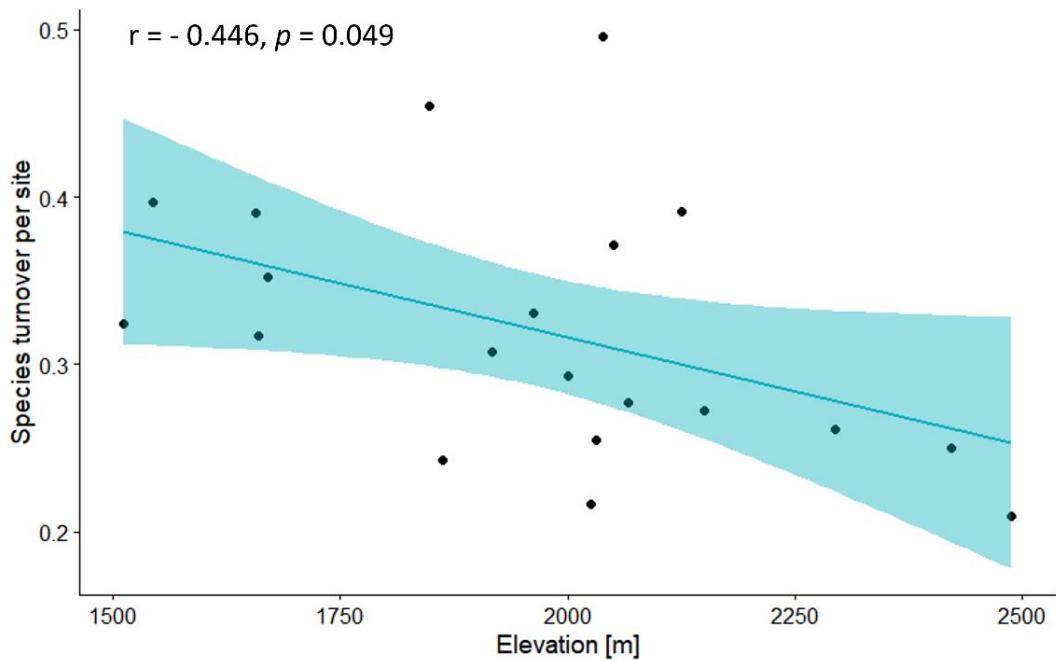


Figure S1. Correlation between the elevation and the species turnover through time in nutrient-rich grasslands. r indicates the Pearson's correlation coefficient. Each dot represents a site, the blue line represents the regression line between elevation and species turnover and the blue area around the line represents the 95% confidence interval of the correlation.

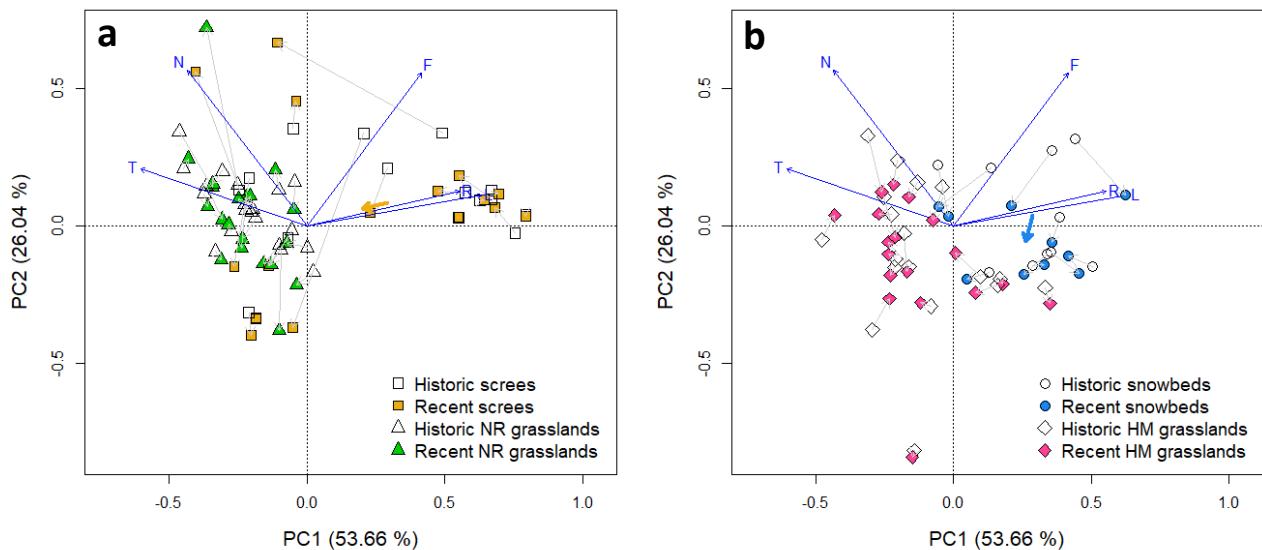


Figure S2. Principal component analysis (PCA) on plot averaged EIVs. Paired of historical (white) and recent (colored) plant inventories are linked with an arrow. The four habitat types are represented by the shape of the points: screes and nutrient-rich grasslands (NR grasslands, a) and snowbeds and high-mountain grasslands (HM grasslands, b). Significant shifts are represented by a yellow arrow in screes (MANOVA: $p = 0.03$) and a blue arrow in snowbeds (MANOVA: $p = 0.003$).