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ABSTRACT

Climate warming causes dramatic glacier retreat and intense vegetation changes in alpine regions. High-elevation nunataks, that is bedrock islands protruding from glaciers with uppermost flowering plants, are no exception. Yet the consequences of climate change on nunatak vegetation remain relatively unexplored. Here, we report findings from a re-visit of historical plant surveys carried out on six nunataks situated between 2180 m a.s.l. and 3509 m a.s.l. amidst the glaciers of the Mont-Blanc range (France). We compared vegetation surveys conducted in 2020 to those made 150 years before, and performed remote sensing analyses to depict changes in vegetation productivity during recent decades. We report an increase in plant species richness for the lowest and least isolated nunataks, which contributed to a strong signal of vegetation greening over the last 35 years. This trend was due to the upward migration of competitive species, but also due to species colonization from neighboring high alpine areas into recently unglaciated microsites. We also highlight striking ecological trajectories that have been little discussed so far, such as stable vegetation composition in the highest and most isolated nunataks, an increase of plant species associated with non-permanent snow-cover and water run-off, an increase of graminoids at lower elevations, and of phanerophytes at higher elevations. We argue that high alpine vegetation changes are not driven by the sole upward migration of lowland competitive species, and that careful monitoring of ongoing ecological changes over broad elevation gradients is necessary to better understand the rapid transformation of high alpine landscapes.

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Introduction

The accelerating retreat of glaciers at the global scale is a spectacular illustration of Anthropocene impacts on mountain environments, with an estimated 50% decline in glacier extent in the French Alps since the end of the Little Ice Age in the mid-nineteenth century (Gardent et al. 2014). However, our understanding of the responses of high mountain vegetation to Anthropocene warming remains limited and much less documented than the effects on the cryosphere. High alpine vegetation changes can be investigated through the study of high elevation nunataks (e.g. Vittoz et al. 2008). These isolated bedrock islands protruding from glaciers constitute well delimited geomorphological features that are typical of polar and alpine regions. They harbor the most extreme environments where angiosperm plants can thrive (Marx et al. 2017; Dentant 2018; Pauli and Halloy 2019), particularly at the uppermost elevations of the European Alps (Körner 2011; Boucher et al. 2021). Unsurprisingly, global warming has been impacting the vegetation of temperate mountains with many reported consequences, including: (i) upward colonization of lower elevated thermophilous species

(Gottfried et al. 2012), (ii) increasing species richness on summits (Steinbauer et al. 2018), and (iii) increasing vegetation productivity and biomass (Carlson et al. 2017; Choler et al. 2021; Rumpf et al. 2022). These changes are expected to become particularly intense towards higher elevations where climate change is the most pronounced (Steinbauer et al. 2018), particularly in regions where warming is amplified towards greater elevations (Wang et al. 2014; Mountain Research Initiative EDW Working Group 2015).

Despite the complexity highlighted by numerous authors regarding the response of alpine vegetation to climatic changes (Kammer et al. 2007; Choler 2018; Mamantov et al. 2021), the hypothesis of a generalized upward migration of plants due to increasing temperatures has been broadly championed in both the scientific literature and by the press. This Anthropocene upward migration hypothesis has become widely accepted mostly due to its intuitiveness to a large audience, rendering other plausible hypotheses less audible, including: (i) the re-colonization of plants from neighboring summits following the Little Ice Age (Kammer et al. 2007) through dispersal of local species onto other nunataks or recently

deglaciated areas, and (ii) the influence of microclimatic refugia and available substrate on plant persistence through time due to dramatic hillside effects (Randin et al. 2009; Patsiou et al. 2014; Kulonen et al. 2018), which preserve suitable micro-habitats and mimic pre-Anthropocene climates across short distances. It is important to note that these two potential mechanisms are not mutually exclusive and imply dispersal between areas of equivalent or even higher elevations, and not only from lower elevations.

Determining which ecological mechanisms drive high alpine vegetation changes at local scale is not easy. These changes indeed depend on how local habitat heterogeneity is being transformed by geomorphological changes due to glacier retreat, soil formation, water runoff, and local snow dynamics (Campbell 2019; Rahbek et al. 2019; Khedim et al. 2020; Muhlfeld et al. 2020). The examination of species traits can help unravel these rather complex processes of vegetation changes (Choler 2005). In temperate high alpine areas, some studies have indeed documented an increased dominance of woody and graminoid plants, as well as species with strategies of rapid resource acquisition and with animal-dependent dispersal (Matteodo et al. 2013; Rumpf et al. 2018). Some of these patterns may be consistent with the expected upward migration of lowland adapted species, and with the increased productivity of high alpine vegetation (i.e. so-called greening) as captured by satellite imagery (Carlson et al. 2017; Choler et al. 2021; Rumpf et al. 2022; Bayle et al. 2023). However, we also hypothesize that the local diversification of micro-scale ecological niches may drive patterns of increased plant diversity at high elevations, for instance due to the emergence and persistence of moist or snow-beds habitats (Muhlfeld et al. 2020).

Enabled by the efforts of botanists during years past, re-surveying historical observations today provides a straightforward and informative approach for monitoring vegetation changes over time, and to investigate the processes underlying these changes, such as upward migration and/or re-colonization. In a seminal piece of work, Wipf et al. (2013) compiled available botanical records beginning in 1835, and carried out repeated surveys during recent years, in order to demonstrate an acceleration in the accumulation of plant species on a Swiss mountain top (Piz Linard) above 3000 m since the 1990s, a temporal pattern now demonstrated across European mountains (Steinbauer et al. 2018). In addition to elucidating the response of plant species to environmental changes, this “historical ecology” approach provides continuity between botanists and plant ecologists today and their predecessors, both in terms of fundamental questions and methodology (Stöckli et al. 2012). This continuity is also a powerful source of motivation for ecologists today to continue carrying

out challenging fieldwork in remote areas, even if sources of inspiration are seldom acknowledged in the scientific literature (Gabillet et al. 2020).

Here, we present the results of a historical botany study conducted in the Mont-Blanc massif near Chamonix, France. In order to compare present-day plant communities with botanical data published about 150 years ago (from 1854 to 1868) by the naturalist Venance Payot, we resurveyed the vegetation growing on six nunataks located among Mont-Blanc’s glaciers and distributed along an elevation gradient from 2160 m a.s.l. to 3509 m a.s.l. (Figure 1; Payot 1854, 1862, 1868). We applied a historical botany approach to quantify long-term trajectories of high mountain plant assemblages by comparing vegetation surveys on these nunataks between 1868 and 2020. We quantified changes in species occurrences and biological traits: (i) Raunkjaer’s life forms in order to seek a signal of upward migration of shrubs and/or trees, (ii) Grime’s ecological strategies to test whether “winners” were more likely to be competitors (C strategy) rather than stress tolerant species (S strategy), and (iii) dispersal traits to assess whether particular dispersal mechanisms were predominantly influencing vegetation changes.

In order to complement floristic surveys and connect long-term (1868–2020) plant trajectories with more recent changes in vegetation productivity, we also utilized the available Landsat satellite archive to test whether observed changes in vegetation structure (i.e. species richness, beta diversity, composition) are reflected by increases in the Normalized Difference Vegetation Index (NDVI), i.e. vegetation greening on study nunataks, measured between 1985 and 2020. We hypothesized that correlations between long-term floristic changes over the last 150 years and greening trends observed during the past 35 years could suggest a recent acceleration in vegetation changes occurring in association with accelerated climate warming. We also hypothesized that observed greening trends would be particularly strong in the context of snowbed habitats characterized by the presence of permanent summer snow fields in aerial photographs from the 1980s, when high elevation sites in the French Alps were characterized by both colder air temperatures and longer lasting snow cover duration (Dedieu et al. 2016).

Material and methods

Sites

The study nunataks are six islets of rock and vegetation protruding from glaciers (Figure 1), namely: Tacul (TC, 2190 m a.s.l.); Leschaux (LS, 2500 m a.s.l.); Couvercle (CV, 2600 m a.s.l.); Talèfre (TL, 2785 m a.s.l.); Grands Mulets (GM, 3040 m a.s.l.) and Rocher

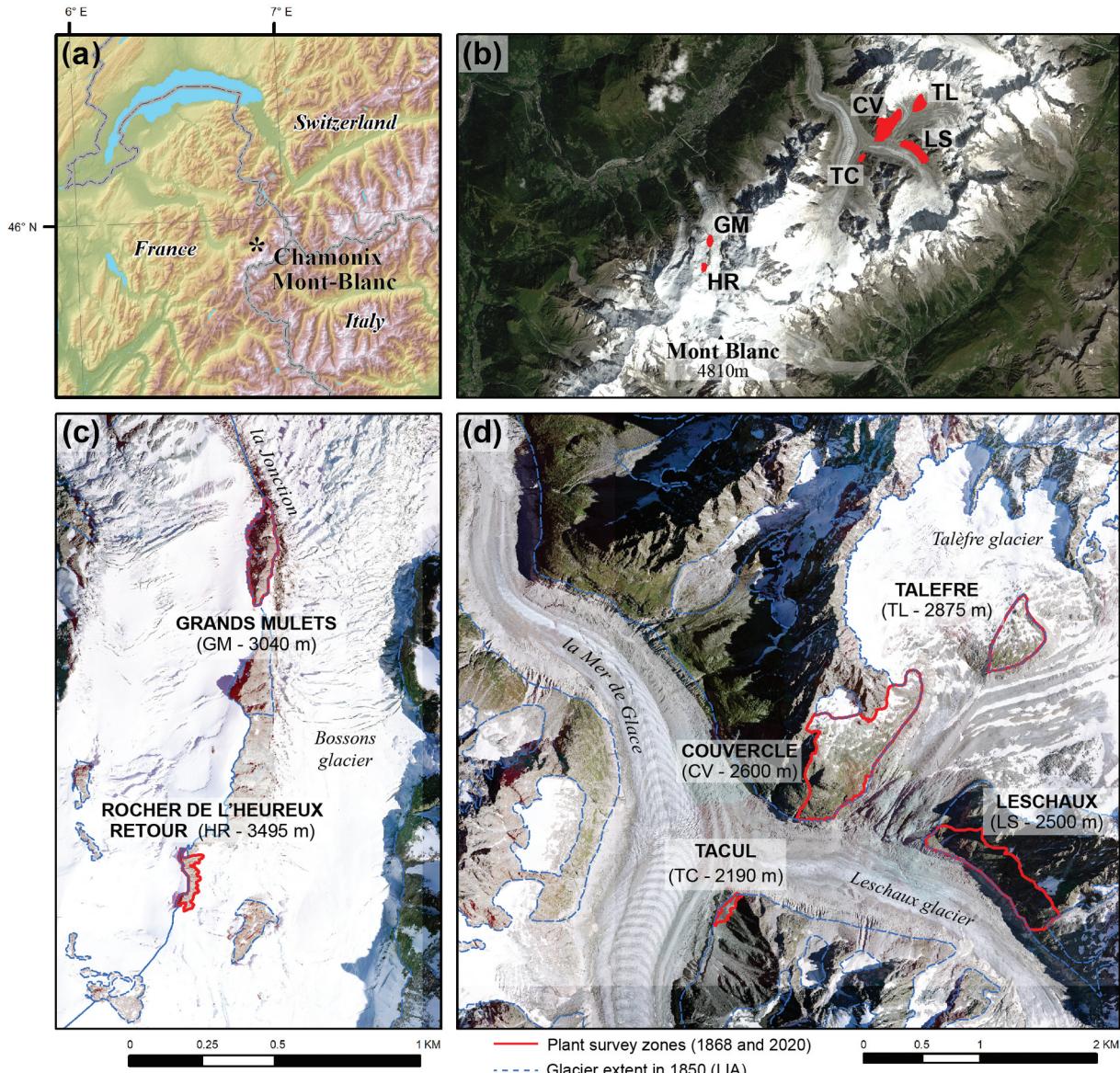


Figure 1. Map of study nunataks (red line contours) with Little Ice Age glacier extent (dashed blue line contours), within the Mont-Blanc range. Given elevation for each site is the median. We chose to focus on the locations visited in 1868 and excluded recent surfaces freed up by glacier retreat, to avoid biases in the comparison of vegetation composition between the study dates.



Figure 2. Geomorphological changes of the Tacul nunatak (TC) through the Anthropocene. View from the CV nunatak painted in 1820 by Jean Antoine Linck (left) and picture taken in 2020 during our expedition (photo C.Dentant). This nunatak has evolved from a glacial lake, with relatively easy access, to an alpine lawn and heath atop a high, unstable moraine.

de l'Heureux Retour (HR, 3495 m a.s.l.) (given elevations are the median values). In the following work, we will sometimes make a distinction between higher nunataks (TL, GM, HR) and lower ones (TC, LS, CV), as our field experience suggests that these two groups experience distinct vegetation dynamics ([Figure 1\(c,d\)](#)). All study nunataks are dominated by granite or gneiss bedrock, except TL, which is a former glacial lake ([Figure 2](#)), and is now made of moraine material (locally derived from the erosion of granite) and includes layers of kame. Overall slope aspect, in addition to micro-topographic heterogeneity, for the study nunataks is variable (south for CV, north for GM) but all sites are characterized by long-lasting seasonal snow cover and abrupt nearby topography limiting sun exposure.

Glacier retreat has dramatically changed the access to all nunataks since the end of the Little Ice Age (LIA). While the access to the GM and HR already required alpinism techniques in the 1860s to safely cross crevasses, reaching the four sites in the Mer de Glace glacier (TC, CV, LS, TL) have become substantially more challenging over recent years (Mourey and Ravanel [2017](#)): hundreds of meters of steep ladders or unstable moraine, and increasing rock debris on glacier surfaces. Also due to recent glacier retreat, study nunataks, especially below 3000 m a.s.l., have increased in land area. The comparison of historical surveys to contemporary ones is subject to many pitfalls and comparison biases, including potential mismatch between historical and contemporary survey locations (Stöckli et al. [2012](#); Moret et al. [2019](#)). To limit such bias, we used all available geographical information provided by Payot in his field reports and compiled his published sources to delineate the estimated surfaces of the nunataks in the 1860s (Payot [1854, 1862, 1868; Figure 1\(d\)](#)). We also included the spatial delimitation of glacier extent during the end of the LIA produced by Gardent ([2014](#)). We thoroughly re-surveyed these areas in 2020, with some adjacent, recently unglaciated areas which were surveyed in addition (blue dashed lines, [Figure 1\(d\)](#)). However, we did not include these additional data in the statistical analysis to maintain strict geographical comparison with Payot's explorations.

Floristic data and analysis (1868–2020)

Plant field surveys

Historical data consisted of plant species lists established by the naturalist and mountain guide Venance Payot between 1854 and 1868, when he published his last synthesis entitled “*îlots de la Mer de Glace*” (i.e. “Islets of the Mer de Glace”; Payot [1854, 1868](#)). For the GM nunatak, Payot published a single list in 1862, combining his 1861 survey performed during William Pitchner's expedition for the Prussian

emperor with another species list established by Charles Martins in 1846 (Payot [1862](#)). For the HR nunatak, we only had the observation made by Horace Bénédict de Saussure following his ascent of Mont Blanc in 1787 (Saussure (de) [1779–1796](#)). Given the lack of subsequent observations during Payot's period of activity, we decided to combine this 1787 observation with Payot's ([1868](#)) list, thereby assuming that the HR did not change in its botanical composition between 1787 and 1868. We consider this choice to be acceptable considering the period being included in the LIA, with persistently cold climatic conditions limiting plant colonization (Protin et al. [2019](#)).

Payot listed both vascular and non-vascular plants, but we decided to focus our study on tracheophytes, yielding a list of 144 taxa recorded in 1868. This list was harmonized in light of the numerous advances in plant taxonomy since the nineteenth century (see Table Sx1) for a complete species list). We returned to the GM and HR nunataks on 2nd and 3rd June 2020 and to the CV, LS, TL and TC nunataks from 20th to 24th July 2020. We – four observers – spent at least 6 hours of investigation on each nunatak, stopping our relevés after more than 1 hour without any new species to be listed, thereby ensuring near-exhaustivity. Plant specimens were collected for potential further taxonomic verifications as well as for herbarium records, i.e. field proofs (see Table Sx2 for herbarium samples). A total of 186 taxa were recorded during the 2020 campaign, giving an overall dataset of 201 taxa for both dates. We generated lists of observed species for each nunatak and also carried out 65 geolocalized vegetation surveys across the different sites in order to facilitate future resurveying efforts.

Our sampling strategy clearly differs from Payot's approach: each of our exhaustive surveys lasted up to 12 hours on each nunatak, while by contrast Payot synthesized over 20 years of botanical observations made during various excursions, mostly carried out alone. His observations certainly resulted from locally exhaustive surveys but also perhaps sometimes from punctual observations. It is important to note that given the objective risks resulting from rapid climate change, glacier retreat and meteorological uncertainty in our study area, some nunataks can only be visited during a very narrow time-window each year and cannot be visited several times. Also, safety constraints in high mountain environments do not allow different observers to perform separate vegetation surveys and to use these as distinct sets of observations, as suggested by some authors (e.g. Stöckli et al. [2012](#)). Nevertheless, as both our approach and the one of Payot enable an exhaustive picture of predominantly long-lived perennial high alpine vegetation (only a couple of plant species are annual), we consider that our modern surveys can be safely compared to Payot's observations.

Changes in vegetation composition

As Payot's data did not provide any indications of local species abundance, our reference dataset consisted of 201 distinct taxa, which were coded as present (1) or absent (0) for each nunatak (TC, LS, CV, TL, GM, HR) and for each date (Payot 1868, 2020). This coding allowed the definition of three types of trajectories between study dates: "winners", for species gaining at least one nunatak; "stable", for species occupying the same number of nunataks; and "losers", for species losing at least one nunatak. To highlight and analyze species showing particularly strong colonization trends, we defined and listed "grand winners" as species that have colonized at least three nunataks from 1868 to 2020. There is no equivalence for losers (i.e. "grand losers") because no species disappeared from more than two nunataks: 25 disappeared from one nunatak and only two species disappeared from two nunataks.

We tested whether plant species richness occurring on each nunatak increased between 1868 and 2020. As our data could not be assumed to be normally distributed, we performed a one-tailed Wilcoxon signed-rank test to assess whether species richness remained constant (H_0) over the study period or increased (H_1). It is important to note that recent literature on the evolution of summit flora (e.g. Steinbauer et al. 2018) strongly motivates the expectation that species richness should also increase in our study nunataks; hence, we applied a one-tailed test.

We also quantified turnover in vegetation composition for each nunatak by estimating the temporal beta diversity of species composition between 1868 and 2020. To do so, we used the approach of Baselga (2010, 2013), which enables partitioning beta diversity between its two components *nestedness* and *turnover*. The *nestedness* component corresponds to species loss or colonization within a nunatak, whereby vegetation composition for one date is nested within the composition of the other date. In contrast, the *turnover* component describes the process of species replacement within a single nunatak between the two study dates. This analysis was performed using the "beta-part" package in R (Baselga and Orme 2012).

Plant functional traits

We extracted functional trait values for listed taxa using the ANDROSACE database (<https://originalps.osug.fr/>), which is based on a combination of *in situ* trait measurements throughout the French Alps and trait values extracted from the literature. We selected the following traits: (i) Raunkiaer's life form (five categories: *therophyte*, *phanerophyte*, *hemicryptophyte*, *geophyte*, *chamaephyte*), (ii) Grime's ecological strategies (CRS split into four categories: CC, RR, SS, CRS); (iii) dispersal agent (five categories: *wind*, *water*, *vertebrates*, *mechanic*, *ants*). We subsequently

tested whether these traits drove species dynamics across study nunataks between 1868 and 2020. To do so, we performed Fisher exact tests on contingency tables, considering species temporal dynamics (winner, stable, loser) as columns and trait categories as rows. Since several trait values were sometimes possible for certain species, all analyses were bootstrapped 999 times by randomly drawing traits for the species having several possible trait values. We report the mean p-values in the results below.

Remote sensing analysis (1985–2020)

Landsat imagery and greening trend estimation

We downloaded images from the Landsat Collection 1 (<https://earthexplorer.usgs.gov>) for all available dates from 1985 to 2020 between 1st June and 31st August at surface reflectance level for the following satellites: Landsat 5 Thematic Mapper (TM), Landsat 7 Enhanced Thematic Mapper + (ETM+) and Landsat 8 Operational Land Imager (OLI). We utilized only images with less than 80% of cloud cover and high geolocation accuracy (geolocation error <12 m). To enable robust comparison across dates and sensors, we corrected for inter-sensor calibration issues and Bidirectional Reflectance Distribution Function (BRDF) effects using the methods described in Roy et al. (2016) and Roy et al. (2016), respectively. We corrected for slope and aspect effects on reflectance using the Sun-Canopy-Sensor + C model (Soenen et al. 2005) following parameter recommendations from Sola et al. (2016). Slope and aspect were derived from the 25 m EU-DEM resampled to the 30 m Landsat resolution. Clouds and cloud shadows were removed using the Mountainous Fmask (MFmask) version 4.0 (Qiu et al. 2019), which is essential in high elevation studies where soil temperature tends to be similar to cloud temperature thus limiting the performance of broadly used cloud masks. In addition, we manually masked a small portion of the GM site as it was exposed to shadows shown by a very high-resolution image captured at the same hour as Landsat scenes (around 9:45 a.m.).

For each scene, we computed the Normalized Difference Vegetation Index (NDVI) based on the red and near infra-red bands (Tucker 1979). We computed the annual maximum NDVI (NDVImax) for each year and pixel as a proxy of plant canopy productivity and quantified temporal trends in NDVImax for each site (Table Sx3). As shown by Berner et al. (2020), it is challenging to reliably estimate annual NDVImax using Landsat since these estimates are sensitive to the number of cloud- and snow-free observations acquired each summer. The annual number of usable summer observations increased from 1984 to 2020, with typically few usable summer observations during

the 1980s and 1990s (Zhang et al. 2022). This bias results in a systematic underestimation of NDVI_{max} when few observations are available (Figure Sx1), leading to spurious trends throughout the Landsat period. Nonetheless, estimates of NDVI_{max} increase asymptotically with little to no differences with more than three observations (Figure Sx2). To limit the bias impact, we first identified years with detected vegetation based on common threshold (Bayle et al. 2023). Then, we removed years with vegetation and less than three observations from the greening trends estimation as they tend to be unreliable (Figure Sx1).

We computed linear models based on Theil-Sen single median slope regression using the “mblm” R package (Komsta and Komsta 2013). The Theil-Sen estimator of the linear trend is much less sensitive to outliers than the least squares estimator. We used the non-parametric, rank based, Mann-Kendall (MK) monotonic test to assess the significance of NDVI_{max} time-series trends using the “trend” R package (Pohlert 2018).

Greening in snowbed habitats

We downloaded a scanned version of an aerial photograph covering the Mer de Glace portion of the study area from the French National Institute of Geographic and Forest Information data portal (<https://www.geoportail.gouv.fr/>), acquired on 3rd September 1980. After orthorectifying the photograph using spline transformation in ArcGIS version 10.3.1, the resulting image had a ground resolution of 50 cm. We proceeded to digitize snowfields present within nunatak boundaries based on visual photo interpretation. We restricted our analysis to isolated snowfields surrounded by rocky and vegetated areas in the 1980 photograph, and did not include large continuous snowfields or glaciers present at the summit of the Couvercle and Talèfre nunataks. The resulting dataset of 94 polygons allowed us to subsequently test for differences between overall greening trends for each

nunatak and greening trends within former snowfields, using a non-parametric Kruskal-Wallis test.

Results

Changes in vegetation composition

Overall we observed a significant increase in plant species richness occurring on study nunataks in 2020 compared to 1868 (Wilcoxon signed-rank test, $p < 0.01$; Figure 3). In terms of species-specific temporal dynamics, we found that the “grand winners” consisted of 20 species gaining three or more nunataks (Figure 4), among which five different groups emerge: (i) two *Vaccinium* species which showed a signal of massive colonization, increasing from zero (or one) to four nunataks (*V. myrtillus*, *V. uliginosum microphyllum*, respectively) during the study period; (ii) three fern species (*Dryopteris filix-mas*, *Athyrium distentifolium*, *Cryptogramma crispa*); (iii) three phanerophytes (*Salix helvetica*, *Salix appendiculata*, *Juniperus communis nana*) which were either absent in 1868 (*Salix* spp.) or present only in LS (*Juniperus*), and colonized the three surrounding nunataks over the study period (TC, CV and TL). *Juniperus communis nana* currently forms extensive heaths over large surfaces in CV; (iv) *Salix herbacea*, which shows a similar increase in frequency than *Juniperus communis nana* and aforementioned *Salix* spp., but in a completely different context, i.e. concave snowbed topography; (v) graminoid species typical of alpine grasslands, such as *Agrostis schradieriana*, *Carex sempervirens* or *Phleum alpinum*, which also drastically increased across study nunataks.

When focusing on the 32 initially frequent species in 1868 (i.e. initially occupying at least 3 nunataks, Table Sx1), we found that their occurrence frequencies generally increased, even slightly. While only three of these species decreased in frequency, 12 and 8 species now occur on four and five nunataks, respectively. *Silene acaulis bryoides* constitutes a very unique case in our data: it was the only species present in all nunataks during the entire study period.

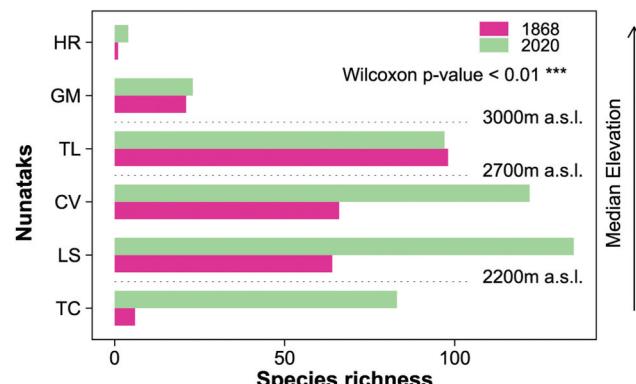


Figure 3. Observed changes in plant species richness in all study nunataks. Nunataks are ordered from the lowest elevation (TC, at the bottom) to the uppermost elevation (HR, at the top).

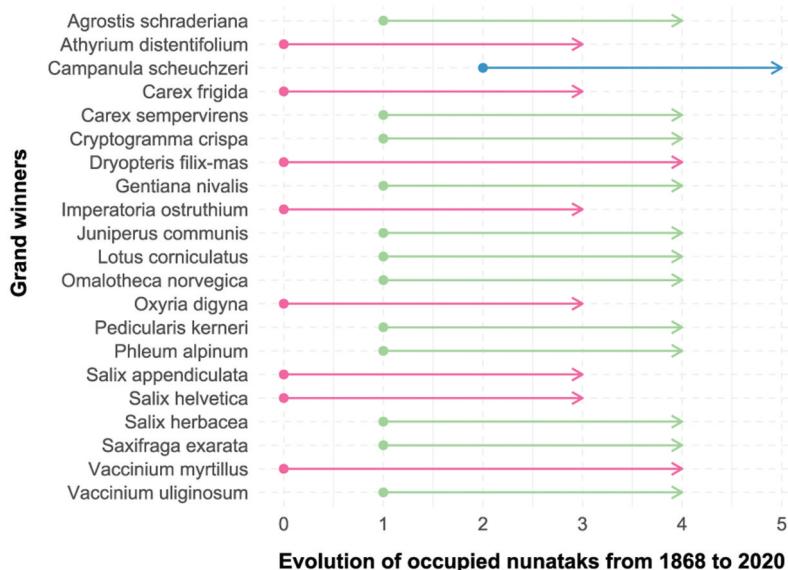


Figure 4. Species showing the most striking increasing trends among study nunataks (“grand winners”), that is species absent or rare in 1868 that have colonized more than three nunataks in 2020.

Table 1. Estimators of temporal beta diversity, i.e. plant diversity turnover between 1868 and 2020, for each study nunatak. Estimates of beta diversity were partitioned between species turnover (species replacement) and species nestedness (local colonization or local extinction).

Nunatak	Turnover	Nestedness	Total beta diversity
HR	0.00	0.75	0.75
GM	0.09	0.076	0.17
TC	0.38	0.00	0.38
CV	0.31	0.29	0.59
LS	0.32	0.33	0.65
TL	0.67	0.30	0.97

The different nunataks showed highly divergent temporal changes in vegetation composition, as captured by estimates of temporal beta diversity that are presented in [Table 1](#). The TC nunatak, which is the lowest study site and a former glacial lake ([Figure 2](#)), showed a massive shift in plant composition due to the strongest temporal species turnover among all study sites, while GM showed the most stable plant assemblage over time. The temporal beta diversity of the HR nunatak was mostly linked to nestedness dynamics, due to the mere colonization of three species in addition to the only one present in the 1868 survey (i.e. *Silene acaulis bryoides*). Contrary to HR, the TL nunatak showed very stable species richness between 1868 and 2020 (97 vs 98 species), though with temporal beta diversity driven by species turnover, due to many species replacements between the two study dates: 23 species disappeared since 1868 while 22 new species were recorded at this nunatak in 2020. Finally, the LS and CV nunataks had comparable and balanced turnover and nestedness components, yielding overall moderate temporal beta diversity estimates.

Plant trait analysis

Life form

The hemicryptophyte life form was by far the most dominant life form in all study sites, followed by chamaephytes, geophytes, phanerophytes and therophytes. We found that hemicryptophytes tended to be over-represented among winner species relative to other temporal dynamics categories in the lower nunataks TC, LS and CV ([Figure 5.A1](#)). However, hemicryptophytes tended to be more stable or declining species in the upper nunataks TL, GM and HR ([Figure 5.A2](#)). Another significant trend concerned phanerophytes and geophytes that were over-represented among winners in the three uppermost nunataks ([Figure 5.A2](#)).

Grime's strategies

As expected, most study species were classified as stress-tolerant (SS), followed by the ones with mixed or competitor strategies (CRS, CC, respectively), while ruderal species (RR) were very rare. We detected that stress-tolerant species (SS) were over-represented among declining species ([Figure 5.B1](#)), while competitive species (CC) tend to be colonizing, two trends that were particularly significant for lower nunataks ([Figure 5.B1](#)). Note that the decline of stress tolerant species was also found to be significant when all nunataks were analyzed together ($p\text{-value} = 0.017$, [Figure Sx3.B](#)). The vegetation composition of higher nunataks regarding Grime's strategies remained significantly unchanged from 1868 to 2020 ([Figure 5.B2](#)).

Dispersal mechanisms

Across all study sites, vegetation composition was dominated by species with propagules showing

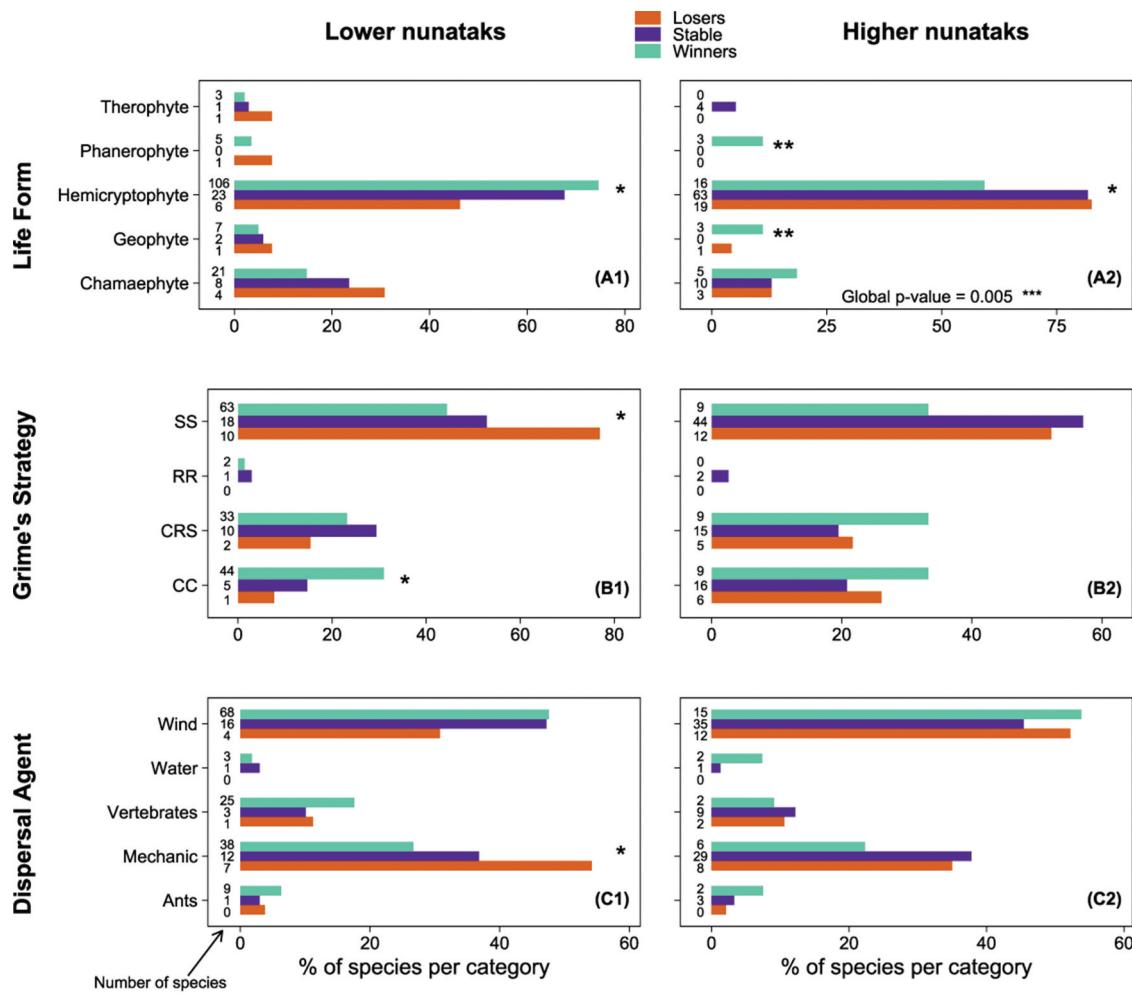


Figure 5. Contingency tables of species traits and classes of temporal dynamics, for lower nunataks (A1, B1, C1) and upper nunataks (A2, B2, C2). P-values from Fisher exact tests are reported when significant (p-value <0.1 *, p-value <0.05 **).

adaptation for wind or mechanical dispersal, while vertebrate-, ant- and water-dispersed vectors were less common. We found that species which declined over the study period tended to be dispersed mechanically, a trend that was confirmed for all nunataks ($p\text{-value} = 0.037$, Figure Sx3.C) but particularly salient in the case of lower nunataks (Figure 5.C1, C2). Winner species displayed a wide range of dispersal strategies.

Greening trends on nunataks

Observed greening trends were strongly structured by the elevation gradient of studied nunataks, with the highest initial plant cover and fastest greening occurring at the low elevation site (TC; Figures Sx4, Sx5). Although the CV, LS and TL nunataks were already characterized by important plant cover in 1985 (with mean NDVImax values ranging from 0.15 to 0.25), we observed pronounced greening in these sites over the last 35 years with significant positive slope values with respect to the Mann-Kendall test (Figures Sx4, Sx5). Landsat pixels covering the GM and HR sites did not detect plant

cover either in 1985 or 2020, with NDVImax values close to zero and no significant observed greening trend.

We observed particularly strong greening dynamics in the context of summer snowfield habitats as compared to overall greening observed at the scale of nunataks (Figure 6). Median greening for pixels outside of snowfields for TC, LS, CV and TL nunataks was $0.0020 \text{ NDVImax year}^{-1}$, compared to $0.0028 \text{ for pixels covering summer snowfields identified in 1980}$. The difference in greening slope values between snowbed ($N = 77$) and non-snowbed pixels ($N = 1167$) was highly significant (Kruskal-Wallis chi-squared value = 18.04, $p\text{-value} <0.0001$).

When crossing floristic data with remote sensing observations, we unraveled an interesting pattern: the study nunataks where recent greening has been the most intense were also the ones where vegetation has experienced the largest increases in species richness (Figure 7(a)) and composition turnover between 1868 and 2020 (Figure 7(b)). Overall, we found noticeable correlations between greening observed during the last 35 years and longer-term changes in vegetation composition observed during the last 150 years.

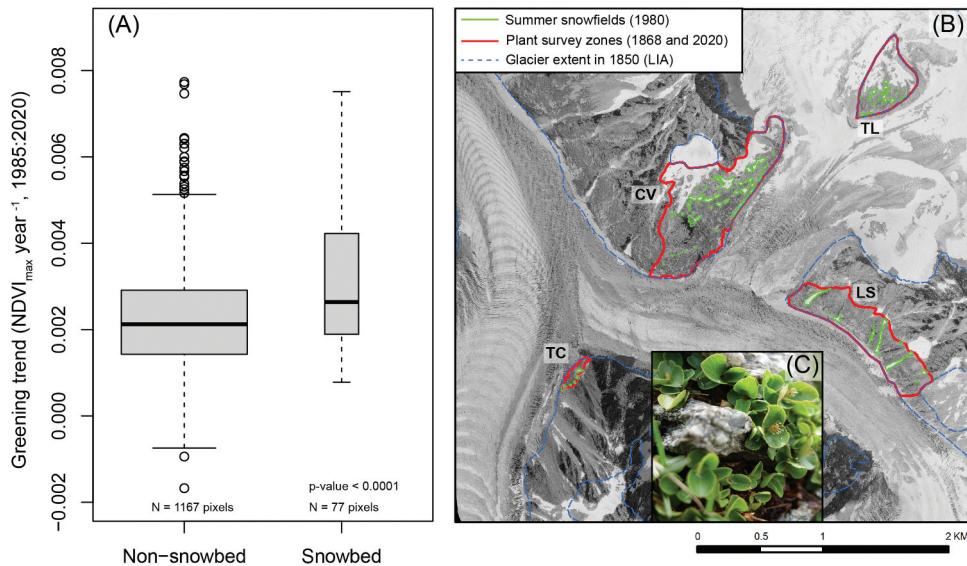


Figure 6. (a) Boxplots of greening trend values extracted for 30×30 m Landsat pixels within identified snowbed habitats (“Snowbed”) and for the pixels covering non-snowbed habitat within nunataks (“Non-snowbed”). The width of boxplots is proportional to the number of pixels available for each class. (b) An aerial photograph acquired on 3rd September 1980, which was used to identify the spatial distribution of summer snowfields (shown in green). The observed greening trend in these contexts suggests that some of these snowfields have receded and melted since the 1980s, and have since been colonized by snowbed vegetation. (c) A photograph of dwarf willow (*Salix herbacea*), which is a dominant snowbed species structuring these emerging plant communities (photo: C.Dentant).

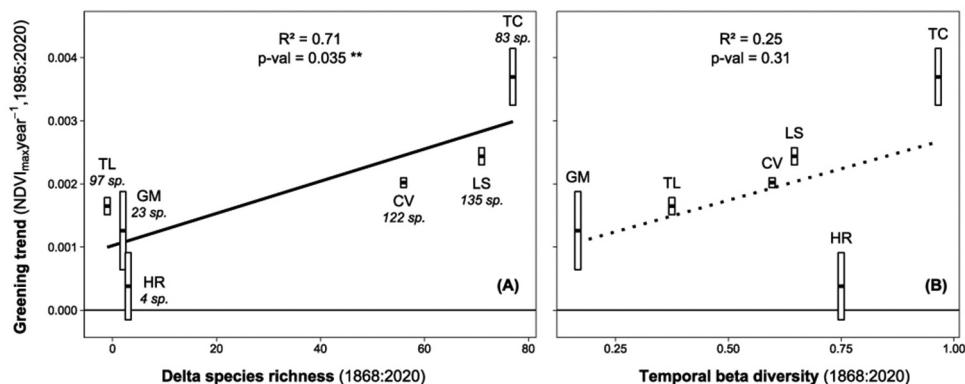


Figure 7. Greening trend ($\Delta NDVI > 0$) vs Δ species richness (a) and temporal beta diversity (b) ($p\text{-value} < 0.1$ *, $p\text{-value} < 0.05$ **). The species richness in 2020 is given for each nunatak.

Discussion

Studies of historical botany in high alpine environments remain relatively rare and absent from most mountain ranges of the world. With the notable exception of Steinbauer et al. (2018), most published studies (Kammer et al. 2007; Wipf et al. 2013; Sklenář et al. 2021) did not use sophisticated statistical analyses because of the low number of available study sites. With six nunataks to compare, we encountered similar constraints, but despite this limitation, our study proposes a novel combination of remote sensing and quantitative vegetation ecology. Well aware that inferring changes in species abundance from comparing diachronic surveys can be biased by uneven sampling effort between study dates (Lavergne et al. 2006), we consider that our data allows us to draw firm conclusions regarding the temporal dynamics of particular species by

comparing their prevalence across study nunataks between 1868 and 2020. Our results provide compelling evidence of vegetation changes occurring in some of the highest vegetated sites in Europe, and corroborate vegetation dynamics that have been highlighted in other mountain environments. Furthermore, our findings show that local sites may have experienced very heterogeneous ecological dynamics since the beginning of the Anthropocene (mid-1800s) and that upward plant migration is not the only process underlying contemporary vegetation changes at high elevation.

Species enrichment and greening of nunataks

A remarkable trajectory is the significant increase in species richness and vegetation cover contributing to alpine “greening” (Figure 7(a)) with plant communities

experiencing both species turnover and colonization. It is important to note that this trend was mostly driven by the lower nunataks (TC, LS and CV), which showed the largest increases of both species richness over the past 150 years and vegetation NDVI_{Max} over the past 35 years. This trend of increasing vegetation diversity and productivity was driven by (i) species already occupying at least two nunataks in 1868, which have spread to new nunataks in 2020 (Table Sx1), and also by (ii) species originally absent from the study area, which have colonized three or more nunataks since 1868 (Figure 4). The strong trend of increased species enrichment that we observed here aligns with observations carried out on other mountain tops throughout the European Alps (Wipf et al. 2013; Steinbauer et al. 2018). We attribute the spectacular increase in species richness to a combination of upward migration and colonization from surrounding high elevation habitats.

Our results show that observed vegetation dynamics may be linked to particular species groups. The statistically significant increase of many species characterized as competitive species appears as a primary driver of vegetation greening, as these species typically have larger rates of biomass production. Some of these species are “grand winners”, that is are largely distributed across high-alpine nunataks nowadays, in our study sites but also elsewhere (Vittoz et al. 2008): *Salix helvetica*, *Salix appendiculata*, *Juniperus communis nana*, *Vaccinium myrtillus* and *Vaccinium uliginosum microphyllum*. Among the many increasing competitive shrubs and trees, we found only one deciduous tree species in the whole study area (*Betula pendula*). This species occurs in one of the lower nunataks (CV), and suggests an increasingly favorable habitat even for larger woody species. Although anecdotal, this observation could indicate a potential trend that should be monitored over the next decades. Upward migration of many competitive species is thus congruent with the overall climate warming trend documented since the end of the Little Ice Age (Rubel et al. 2017). Study sites that were previously dominated by mineral surfaces (snow, ice or rocks) have turned “green” since then, due to encroachment of several species as observed elsewhere (Carlson et al. 2017; Choler et al. 2021).

It is noteworthy that among competitive species, *Salix* and *Juniperus* species are thermophilous shrubs, and were observed with high abundance in lower nunataks in 2020. Some of these species are already known to be present on cliffs up to 3000 m a.s.l. in the French Alps (Dentant and Lavergne 2013). Therefore, their dynamics of range expansion across study nunataks may be understood as a spread due to increasingly favorable conditions as discussed by Kammer et al. (2007) and Carlson et al. (2017), but not necessarily due to migration from lower elevations. Similar

range expansion dynamics appear to be underway for competitive fern species: *Dryopteris filix-mas* and *Athyrium distentifolium*. Both species are also amongst the “grand winners”: they were never observed on Mont-Blanc nunataks between 1854 and 1868, but have colonized more than three nunataks since then and were locally frequent in some nunataks in 2020 (data not shown). In addition, it is interesting to note that contrary to our expectations and previous studies (Vittoz et al. 2009), no long distance dispersal agent appears to have favored species colonization, suggesting that many of the winner species may have colonized study sites from nearby locations. Species classified as competitive thus appear to have a strong effect on species enrichment and related greening trends, and may have spread through two possible and non-mutually exclusive migration scenarios: (i) upward migration from lower elevation and (ii) re-colonization from surrounding areas.

Finally, species classified as stress-tolerant are disproportionately represented among species identified as “losers” by our analyses. In the context of warming, stress-tolerant species may indeed face increased competition from species that are less adapted to cold environments (Choler et al. 2021). Some of these high alpine stress-tolerant species, especially the ones forming cushion life-forms, may in addition facilitate some newly colonizing species, essentially ruderal or competitive species (Losapio et al. 2018). For example, we repeatedly observed that *Gentiana nivalis*, an annual species typically growing at lower elevations, was constantly growing in cushions of *Silene acaulis bryoides*. This illustrates that some stress-tolerant nurse species may facilitate certain newly colonizing species that may later outcompete other stress tolerant species. The biotic stress due to new coming species may be cumulative with the obvious physiological stress caused by increasingly hot summer temperatures, which are known to cause die-off events and decline of similar stress-tolerant species in sub-antarctic environments (Le Roux et al. 2005; Bonanomi et al. 2023). The overall significant trend of declining stress-tolerant species across our study nunataks suggests that many of these species may run the high risk of local extinction in the coming decades.

Vegetation stability and slow greening at high elevations

Our observation of rapid greening dynamics on nunataks situated below 3000 m a.s.l. is in accordance with analysis of greening trends at the scale of the European Alps, reporting widespread increases in

remotely sensed plant productivity in above treeline habitats since 2000 (Choler et al. 2021). Vegetation index signals, even from Landsat satellites at 30 m resolution, are typically quite weak above 3000 m a.s.l. in association with sparse plant cover in otherwise rocky and snowy high mountain habitats. Our results reflect these methodological limitations, as we detected little to no greening for the two highest nunataks (GM and HR, Figure Sx4). Both sites are spatially isolated and characterized by extremely harsh climate conditions, thus allowing the local long-term persistence of only nival and high alpine plant species despite recent climate warming. The weak greening signals observed for sites above 3000 m a.s.l. were correlated with relatively stable vegetation composition over the 150 year study period, a result which converged strongly with the findings of Vittoz et al. (2009). High mountain plant habitats thus clearly show spatially variable responses and sensitivity to overall changes in climate, and as warming continues it will be important to quantify the upward shift in this “greening line” where climate amelioration can be utilized by plants. Given the magnitude of predicted warming in the coming decades, we expect that even high mountain “sanctuary” nunataks above 3000 m a.s.l. will experience pronounced greening trends in the years ahead as glaciers and permafrost continue to decay throughout the uppermost elevations of the Alps (Huss et al. 2017).

A recent study based on historical botany in the tropical Andes (Sklenář et al. 2021) reported shifts in the elevation ranges of species without any significant increase in species richness. This observation on one of the highest mountains in South America (Chimborazo, 6263 m a.s.l.) is congruent with one of the uppermost and isolated Mont-Blanc nunataks: the GM nunatak harbors a strikingly stable plant composition over the study period, both in terms of species richness and species composition. The location and harsh conditions of this site explain this strong stability: surrounded by massive glaciers below Mont Blanc’s north face, this nunatak (and HR) is much more isolated than sites located around the Mer de Glace basin. This stability of vegetation composition at high elevation is perfectly illustrated by the cushion species *Silene acaulis bryoides*, which is also the first plant ever observed on the rooftop of the European Alps (on the HR nunatak), during Saussure’s expedition on Mont Blanc in 1787 (Saussure (de) 1779–1796).

Singular and undocumented ecological trajectories

One study site showed a remarkable trajectory: vegetation occurring on the TL nunatak remained particularly stable in terms of species richness, while

undergoing pronounced species turnover due to a massive species replacement between 1868 and 2020. Indeed, about 25% of species have changed over the 150-year study period, and the underlying ecological processes of this change seem to largely mirror the ones highlighted above. A large portion of the 22 newcomer species were classified as competitors (ca. 41%) while most of the 23 species that disappeared were stress-tolerant (ca. 57%). In addition, some species that are now commonly found on TL indicate other ecological changes and even a pattern of local scale niche disparity.

Despite an overall decline in the occurrence of stress-tolerant species across all nunataks, certain stress-tolerant species were paradoxically “grand winners”, such as *Salix herbacea*, *Oxyria digyna*, *Carex frigida* and *Gentiana nivalis*. The striking spread of certain of these species, sometimes over extensive areas, is symptomatic of profound changes in snow and water dynamics that occurred in our study nunataks during the study period. First, the melting of permanent glaciers and snowfields on some study nunataks converted former permanently ice-covered areas into seasonally snow covered zones, thus allowing the development of snowbed plant communities, typically dominated by *Salix herbacea*. Remote-sensing analyses of satellite images through the last 35 years highlight particularly rapid greening dynamics in areas covered by permanent snowfields in the 1980s that have since become seasonally snow-free snowbed habitats (Figure 6). Second, the same melting of permanent snow cover, enhanced by warmer spring and fall temperatures, generates water runoff, even of low intensity, which in turn favors wet-habitat specialists such as *Carex frigida*, but also *Molinia caerulea* or *Betula pendula* in lower and warmer locations. A third type of ecological trajectory concerns plant species occurring on the opposite side of the gradient of snow cover tolerance. We observed well-structured communities dominated by *Carex myosuroides* in the LS nunatak, which is a clear indicator of sites characterized by very cold and early snow melt-out such as alpine ridges. These extensive ecological changes highlight the importance of local topography for maintaining alpine plant diversity: species with opposite micro-climatic requirements can both be winners under global warming thanks to local scale environmental heterogeneity (Patsiou et al. 2014). In the context of recent observed expansion of cold-adapted and snowbed specialist species, an important question arises: up to what temperature and snow cover duration thresholds can such dynamics be sustained?

The increased vegetation productivity demonstrated by remote sensing analyses was also clearly driven by an extensive spread of two particular plant life forms. First, we found a statistically significant increase of

hemicryptophyte species, in particular graminoid species such as *Agrostis schraderiana*, *Carex sempervirens* or *Phleum alpinum*, which were among the “grand winners” in lower nunataks. Given the key structuring role of these species in alpine grasslands, their increased frequency across study nunataks indicates an extensive spread of grasslands driving increased vegetation NDVI. Second, phanerophyte occurrence also increased significantly, which was particularly noticeable at elevations as high as 3000 m a.s.l. This case constitutes another relevant example of “upward migration”, which was certainly facilitated by the long distance dispersal potential of some of these increasing phanerophytes, such as *Salix helvetica* and *Salix appendiculata*.

In addition to the statistically significant and spatially extensive ecological changes discussed above, some particular species occurrences deserve to be highlighted because they shed light on subtle but relevant ecological dynamics which may require further investigation. This is the case of two thermophilous species found in the lower nunataks: the hemicryptophyte *Kernera saxatilis*, which was observed on a cliff, quite far away from its usual habitat (i.e. low-elevation, sun-exposed limestone cliffs), and the chamaephyte *Arctostaphylos uva-ursi*, which was found on a south-facing mound on the TC nunatak at 2200 m a.s.l. These singular presences may imply local dry and hot conditions on nunataks, and thus be indicative of increasing moisture limitation even at high elevation sites on the slopes of Mont Blanc (Figure 2). Our observation that some new coming species in high alpine sites are tolerant of warm and dry conditions clearly echoes the observation made on the Isla Persa nunatak, where *A. uva-ursi* was also found to strongly increase over the last 100 years (Vittoz et al. 2008). Soil moisture limitation may indeed curb greening trends in the coming decades and influence future shifts in alpine vegetation composition, and in our view represents a key parameter for future monitoring of vegetation shifts on Mont-Blanc nunataks.

Conclusion

We observed highly varied responses of high-elevation vegetation to ongoing climate changes since the mid-1800s in one of Europe’s largest glacier basins. Our study confirms plant dynamics already documented elsewhere, including: (i) species enrichment in the lowest and least isolated nunataks (TC, LS, CV), (ii) “winning” trajectory of competitive species, supporting upward migration and (iii) local re-colonization, which we linked to a significant greening effect for the past 35 years. However, our results also highlight trajectories that, to our knowledge, have been little discussed in literature: (i) stability in terms of species richness and species compositions in higher and isolated sites but important species turnover dynamics at low and mid-elevation sites (up to

2800 m a.s.l.), (ii) increase of plant species associated with shifts from annual to seasonal snow-cover (snow-beds, wet habitats), a trend that was confirmed by both vegetation surveys and remote sensing analysis, (iii) increase of hemicryptophyte species, mainly graminoids, at lower elevations, and increase of phanerophytes at higher elevations. This complex set of vegetation responses underscores the need to not only focus on general vegetation trends such as upward migration, but also to promote field ecology at a fine spatial scale. Ongoing monitoring of ecological shifts in high mountain environments in the years ahead will be of the utmost importance in order to understand and anticipate future trajectories of both plant diversity and alpine landscapes in the context of accelerating climate change.

In 1810, Alexander von Humboldt, the inventor of biogeography, declared the following about high mountain expeditions: “*These painful excursions, whose stories generally excite the interest of the public, offer only a very small number of results useful to the progress of science*”. Rather, our study of high elevation biodiversity during the Anthropocene led us to agree with Edward Whymper’s response to Humboldt: “*High-mountain explorations, although perhaps of little interest to the general public, are of great value to Science*” (Whymper 1892).

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Author contributions

CD had the original idea of the study; CD, BZC, and SL designed the study; NB, SL and CD performed the statistical analyses; BZC and AB performed the remote sensing analyses; CD, BZC, and SL wrote the first draft of the manuscript. CD, BZC, NB and SL contributed to the sample collection. CD coordinated and mounted the reference herbarium collection. The project as a whole was coordinated by CD and SL.

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