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Anthropocene trajectories of high alpine plant communities on Mont-Blanc nunataks

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Abstract

Climate warming currently causes dramatic glacier shrinkage and intense vegetation changes in alpine regions. High-elevation nunataks, that is bedrock islands protruding from glaciers and harboring the uppermost occurrences of flowering plants, are no exception to these trends. Yet the consequences of climate change on nunatak plant communities remains relatively unexplored. Here we report a study of historical botany on six nunataks occurring from 2180m a.s.l. to 3509m a.s.l. among the glaciers of the Mont-Blanc range (France). We compared modern vegetation surveys conducted in 2020 to those made by Venance Payot 150 years [ago](#) before, and performed remote sensing analyses to depict recent changes in vegetation productivity. We report an increasing plant species richness in the lowest and least isolated nunataks, driving an important signal of vegetation greening as also captured through satellite imagery. 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 in literature, such as stable plant communities in the highest and most isolated nunataks, an increase of plant communities associated with non-permanent snow-cover and water run-offs, an increase of graminoids at lower elevations, and an increase 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 a close monitoring of ecological changes is necessary to better understand the rapid transformation of high alpine landscapes.

Keywords : alpine biodiversity, high alpine summits, extreme environments, colonization-extinction dynamics, range shifts, Mont-Blanc range

Introduction

The concept of the Anthropocene remains disputed (Corlett 2015; Maris 2018), however, dating discrepancies aside, it adequately depicts the recent period of overwhelming human impacts on the biosphere. Several authors strongly support a beginning of this new era in the mid-1800s, when industrial signals became detectable in the atmosphere (Ruddiman 2013). 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-19th century (Gardent et al. 2014).

However, our understanding of the responses of high mountain plant communities to Anthropocene warming remains limited and much less documented than the effects on the cryosphere. Investigating high alpine plant species implies taking high elevation nunataks into account. These isolated bedrock islands protruding from glaciers constitute geomorphological features that are typical of polar and alpine regions. They harbor the most extreme environments where angiosperm plants can thrive (Pauli & Halloy 2019; (Marx et al. 2017; Dentant 2018), particularly at the uppermost elevations of the European Alps (Körner 2011), and very likely served as refugia for rock dwelling high elevation plant species during Pleistocene glaciations (Schneeweiss & Schönswetter 2011; Boucher et al. 2020). 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). These changes are expected to become particularly intense towards higher elevations where climate change is the most pronounced - a phenomenon known as the alpine amplification (Wang et al. 2014; Rottler et al. 2019).

Despite the complexity highlighted by numerous authors regarding the responses of plant communities 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 encountered tremendous success, not only among ecologists but also in the public audience. This Anthropocene upward migration hypothesis has ineluctably become widely accepted mostly due to its intuitiveness to a large audience, making less audible other equally plausible hypotheses: (i) the re-colonization from neighboring summits following the Little Ice Age (Kammer et al. 2007), that is to say the increased dispersal of local alpine species on other nunataks as well as on newly available surfaces resulting from

deglaciation; and (ii) the influence of microclimatic refugia on plant persistence through time due to dramatic hillside effects (Randin et al. 2009; Patsiou et al. 2014), leading to the persistence at high elevations of suitable micro-habitats that mimic pre-Anthropocene climates and to which plant can migrate to within short distances. It is important to note that these two potential mechanisms are mutually non-exclusive and imply dispersal between areas of equivalent or even higher elevations, not from lower elevations.

A large variety of ecological mechanisms may thus potentially drive plant community changes at local scale within high mountain environments, depending on how local habitat heterogeneity is being transformed by geomorphological changes due to glacier retreat, soil formation, and local snow dynamics (Campbell 2019; Khedim et al. 2020; Muhlfeld et al. 2020). The problem was well summarized by Rahbek et al. (2019), who highlighted the complexity of mechanisms involved in plant community changes in high mountains and stated that *‘the complex configuration of mountain climates means that current models, based on simple upslope shifts of species, are insufficient and potentially misleading’*. The examination of species traits can help unravel these rather complex processes of community changes. 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 (Rumpf et al. 2018; Matteodo et al. 2013; Venn et al. 2014). 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). However, we also hypothesize that a process of 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 to monitor plant community changes over time, and to investigate the processes underlying these changes, such as upward migration and/or re-colonization. In an inspiring 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. In addition to elucidating the responses of plant communities to climate and other external drivers, this approach often termed as « historical ecology » 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 motivational support, which is seldom acknowledged (Gabillet et al. 2020), to investigate these harsh areas.

Here we present the results of a historical botany study conducted in the Mont-Blanc range, near Chamonix, France. In comparison to historical data published about 150 years ago (from 1854 to 1868) by the naturalist Venance Payot, we revisited and resurveyed plant communities over six nunataks located among the glaciers of the Mont-Blanc, distributed along an elevation gradient from 2180m a.s.l. to 3509m a.s.l. (Figure 1). We applied a historical botany approach to quantify long-term trajectories of high mountain plant assemblages in the Mont-Blanc massif by comparing surveys of plant communities on these nunataks between 1868 and 2020. We used species occurrences and biological traits : (i) Raunkiaer'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 community changes.

In order to complement floristic surveys and draw links with recent changes in vegetation productivity, we also utilized the available Landsat satellite archive to test whether observed long-term changes in plant communities (i.e. species richness, beta diversity, composition) are reflected by recent increases in the Normalized Difference Vegetation Index (NDVI), i.e. vegetation greening on study nunataks. 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 plant community changes occurring in association with accelerated climate warming. We also hypothesized that observed greening trends would be particularly strong in snowbed habitats characterized by the presence of 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.A, 1.B), namely : Tacul (TC, ca. 2180-2200m a.s.l.); Couvercle (CV, ca. 2250-2750m a.s.l.); Leschaux (LS, ca. 2500-2700m a.s.l.); Talèfre (TL, ca. 2700-3050m a.s.l.); Grands Mulets (GM, ca. 3020-3057m a.s.l.) and Rocher de l'Heureux Retour (HR, ca. 3480-3509m a.s.l.). 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 ~~seem to~~ experience distinct vegetation dynamics (Figure 1.C, 1.D. All study nunataks are dominated by granite or gneiss bedrocks, 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. 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) has become substantially more challenging over recent years (Mourey & Ravanel 2017): hundreds of meters of steep ladders or unstable moraine, and increasing rock debris on glacier surfaces. Also due to recent glacier retreat, studied nunataks, especially below 3000m 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 1860's (Payot 1854, 1862, 1868; [Figure 1.D](#)). We also included the spatial delimitation of glacier extent during the end of the Little Ice Age 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 keep a 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; Payot 1868). For the GM nunatak, Payot published a single list in 1862, combining his 1861 relevé performed during Pitchner's expedition for the Prussian emperor with another species list established by Charles Martins from 1846 (Payot 1862). For the HR nunatak, we only had the observation made by Horace-Bénédict de Saussure following his ascent of the Mont Blanc in 1787 (Saussure 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 Little Ice Age, with persistently cold climatic conditions limiting plant colonizations (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 June 2nd and 3rd, 2020, and to the CV, LS, [TL](#) and TC nunataks from July 20th to 24th, 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 ([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 plant community surveys across the different sites in order to facilitate future resurveying efforts.

Our sampling strategy clearly differs from the one of Payot: 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. His observations certainly resulted from locally exhaustive surveys but also perhaps sometimes from punctual observations. It is important to note that given the dramatic hazards 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 the ones of Payot.

Changes in plant community 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 (1868, 2020). This coding allowed the definition of three types of trajectories between study dates: (i) "winners", for species gaining at least 1 nunatak; "stable", for species occupying the same number of nunataks; and "losers", for species losing at least 1 nunatak. To highlight and analyze species showing particularly strong colonization trends, we defined and listed "[biggrand](#) winners" as species that have colonized at least three nunataks from 1868 to 2020. There is no equivalence for losers (i.e. "[biggrand](#) 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 (H0) over the study period or increased (H1). It is important to note that recent literature on the evolution of summits flora (e.g. Steinbauer 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 temporal turnover in plant community 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 community 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 *betapart* 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 (5 categories: *therophyte*, *phanerophyte*, *hemicryptophyte*, *geophyte*, *chamaephyte*); (ii) Grime's ecological strategies (CRS split into 4 categories: CC, RR, SS, CRS); (iii) dispersal agent (5 categories: *wind*, *water*, *vertebrates*, *mechanic*, *ants*). We analyzed potential shifts in plant traits within each nunatak between 1868 and 2020 using Fisher exact tests for 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 01 June and 31 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 < 12m). 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. (2016a) and Roy et al. (2016b), 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 25m 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.

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. We computed linear models based on Theil-Sen single median slope regression using the ‘mblm’ R package (Komsta & 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 NDVImax time-series trends.

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 September 3, 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 plant community 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](#)). However, the overall trend of plant species enrichment was elevation dependent, as its magnitude declined at higher elevation sites. In fact, the three highest nunataks showed either a steady (TL, GM) or a nearly steady (HR) plant species richness from 1868 to 2020, while

species richness consistently increased in three lower study nunataks by 83% (CV), 111% (LS) and 1283% (TC) !

While looking at species-specific temporal dynamics, we found that the “[biggrand 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 0 (or 1) to 4 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* and *Juniperus communis nana*, which were either absent in 1868 (*Salix* spp.) or present only in LS (*Juniperus*), colonizing afterwards the 3 surrounding nunataks (TC, CV and TL). Currently, in CV, *Juniperus communis nana* forms strikingly extensive heaths over large surfaces; (iv) *Salix herbacea* shows a similar increase in frequency than *Juniperus communis nana* and aforementioned *Salix* sp., but in a completely different context: concave snowbed topography; (v) graminoid species typical of alpine grasslands, such as *Agrostis schraderiana*, *Carex sempervirens* or *Phleum alpinum*, which also drastically increased across study nunataks.

When focusing on the 32 initial [abundantfrequent](#) species in 1868 (i.e. initially occupying at least 3 nunataks – [Figure Sx1](#)), we found that their occurrence frequencies generally increased, even lightly: eight of these species colonized all the nunataks of the basin of the Mer de Glace (TC, LS, CV, TL), that is no more available nunataks to colonize in this part of the Mont Blanc range. *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.

[Table.1](#)

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

The different nunataks showed highly divergent, and very insightful temporal changes in plant communities, as captured by estimates of temporal beta diversity. 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 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 a very stable species richness between 1868 and 2020 (97 vs 98 species), though with temporal beta diversity driven by species turnover, due to massive species replacements between the two study dates : 23 species have disappeared since 1868 while 22 have colonized 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 analyses

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. Two opposite and significant trends were noticeable between upper nunataks (TL, GM and HR) and lower ones (TC, LS and CV): hemicryptophytes tended to be over-represented among winner species, i.e. that have colonized more nunataks over the study period (Figure 5.A1) but tended to be more stable or declining species in the upper nunataks (Figure 5.A2). Another significant trend concerned phanerophytes and geophytes that were over-represented among winners in the 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-value = 0.017, Figure Sx4.B). The community composition of higher nunataks regarding Grime strategies remained significantly unchanged from 1868 to 2020 (Figure 5.B2).

Dispersal mechanisms

Across all study sites, community composition was dominated by species with propagules showing adaptation for wind or mechanical dispersal, while vertebrate-, ant- and water-dispersed vectors were less common. We found that species which declined over study nunataks tended to be dispersed mechanically, a trend true for all nunataks (p-value = 0.037,

Figure Sx4.C) but particularly salient in lower nunataks (Figure 5.C1, C2). Winners 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; Figure Sx2, Sx3). 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 (Figure Sx2, Sx3). Landsat pixels covering the GM and HR sites did not detect plant cover either in 1985 or 2020, with NDVImax values close to 0 and no significant 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 $0.002 \text{ NDVI}_{\text{max}} \text{ year}^{-1}$, compared to 0.0028 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 = 30.65, $p\text{-value} < 0.0001$).

When crossing floristic data with remote sensing observations, we unraveled an interesting pattern: the study nunataks where recent greening has ~~the~~ been the most intense were also the ones where plant communities have experienced the largest increases in species richness (Figure 7A) and composition turnover between 1868 and 2020 (Figure 7B). Overall

we found noticeable correlations between greening observed during the last 35 years and longer-term changes in plant community composition observed during the last 150 years.

Discussion

Studies of historical botany in high alpine environments have remained 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; [Morueta-Holme et al. 2015](#); Sklenář et al. 2021) did not use sophisticated statistical analyses because of the low number of study sites. With six nunataks to compare, we encountered similar constraints but despite what may appear to be a limitation, our study proposes a rather original combination of remote sensing and quantitative plant community 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 indeed depict compelling floristic changes occurring in some of the highest vegetated sites in Europe, and corroborate vegetation dynamics that have been highlighted in other mountain environments. In addition 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^{us} underlying contemporary vegetation changes at high elevation.

Species enrichment and greening of nunataks

A remarkable trajectory is the ~~overall dramatic~~significant increase in species richness and vegetation cover leading to alpine “greening” (Figure 9) 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 increase of both species richness over the past 150 years and vegetation NDVImax 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 (Figure Sx1), and also by (ii) species originally absent from the study area, which have colonized three or more nunataks since 1868 (Figure 4). This species enrichment matches other observations on other mountain tops of the European Alps (Wipf et al. 2013; Steinbauer et al. 2018). The spectacular increase in species richness is due to the combination of upward migration and re-colonization from surrounding high elevation habitats.

Observed vegetation dynamics can be clearly linked to particular species groups. In our study, several competitive species can be identified with confidence as driving greening dynamics, as these species typically have larger rates of biomass production. Some of these species are “biggrand winners”, that is are largely distributed across Mont-Blanc nunataks nowadays: *Salix helvetica*, *Salix appendiculata*, *Juniperus communis nana*, *Vaccinium myrtillus* and *Vaccinium uliginosum microphyllum*. The only tree species found in the whole study area (*Betula pendula*) occurs in one of these low nunataks (CV), and suggests an increasingly favorable habitat even for larger woody species - a potential trend that should be monitored over the next decades. Upward migration of competitive species is 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 competitive species as observed elsewhere (Carlson et al. 2017; Choler et al. 2021).

Interestingly, *Salix* and *Juniperus* species are thermophilous shrubs, and were observed with high abundance in lower nunataks in 2020. *Juniperus communis nana* is also a xerophilous species, able to encroach on cliffs and rocks up to 3000 m a.s.l. (Dentant & Lavergne 2013). Therefore its 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. The same dynamics of range expansion is underway with competitive ferns: *Dryopteris filix-mas* and *Athyrium distentifolium*. Both species are also amongst the “[biggrand](#) 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 [abundantfrequent](#) in some nunataks in 2020 (data not shown). In addition, it is interesting to note that, contrary to our expectations, no long distance dispersal agent seems to have favored species colonizations, 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 through two possible and non-mutually exclusive migration scenarios: (i) upward migration from lower elevation and (ii) re-colonization from surrounding areas.

On the other end of the gradient of species trajectories, many species identified as “losers” were typically classified as stress-tolerant. With increasing temperatures in mountains, stress-tolerant species may indeed undergo more competition (Choler et al. 2001). Some of these high alpine stress-tolerant species, especially the ones forming cushion life-forms, may 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*. In other words, some stress-tolerant nurse species may facilitate certain newly colonizing species that may later outcompete other stress tolerant species. This biotic stress may come in addition to an obvious physiological stress due to increasingly hot summer temperatures, which cause die-off events and decline of similar stress-tolerant species in sub-antarctic environments (Le Roux et al. 2005; Bergstrom et al. 2015). This overall 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.

Community stability and slow greening at high elevations

Our observation of rapid greening dynamics on nunataks situated below 3000m 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 for Landsat satellites at 30m resolution, are typically quite weak above 3000m 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 nunataks situated above 3000m (GM and HR, Fig. Sx3). Both sites are isolated (surrounded by ice) 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. Weak greening signals were correlated with relatively stable plant communities over the 150 year study period (Fig. 7), with only one new arrival at the GM site and three new species at the HR site. High mountain plant habitats 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 3000m will express pronounced greening trends in the years ahead as glaciers and permafrost continue to decay throughout the uppermost elevations of the Alps.

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, 6263m a.s.l) is congruent with one of the uppermost and isolated Mont-Blanc nunatak: the GM nunatak harbors a strikingly stable plant community over the study period, both in terms of species richness and species composition. Almost all observed species are longlived, stress-tolerant species, with the striking exception of the main newcomer: *Arabis alpina*. The location and harsh conditions of this site explain mainly this strong stability : surrounded by huge glaciers, this nunatak is isolated in the Mont Blanc North face, at 3000 m a.s.l.. This community stability is perfectly illustrated by the cushion species *Silene acaulis bryoides*, which is the only species occupying all nunataks in both 1868 and 2020. It 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 1779-1796).

Singular and undocumented ecological trajectories

Despite its remarkable stability in species richness, the plant community occurring on the TL nunatak experienced a very high 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 drivers of this change seem to largely mirror the ones highlighted above. The majority 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.

Stress-tolerant plants, defined as species able to cope with limited resources and harsh climate, showed heterogeneous responses in the Mont-Blanc range through the Anthropocene: despite a general declining tendency across all nunataks (discussed above), some stress-tolerant species are paradoxically "[biggrand](#) winners", such as *Salix herbacea*, *Oxyria digyna*, *Carex frigida* and *Gentiana nivalis*. The increase of such species may seem counterintuitive at first sight, but these ecological changes may be linked to different ecological strategies. First, the melting of permanent glaciers and snowfields (such as the Moine Glacier on the CV nunatak) 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 highlights particularly rapid greening dynamics in areas covered by permanent snowfields in the 1980s that have since become seasonally snow-free snowbed habitats. Second, the same melting of permanent snow cover, when more consequent and combined with greater spring and fall temperatures, generates water runoff, even of low intensity, which in turn favor wet-habitat specialists such as *Carex frigida*, but also *Molinia caerulea* or *Betula pendula* in lower and warmer location such as in the CV nunatak. For this “winning” trajectory of cold-[adapted](#) species and snowbed communities, a profound question arises as to the possible ecological threshold: up to what temperature can such winning dynamics be sustained? A third type of ecological trajectory concerns plant species, on the opposite side of the gradient of snow cover tolerance. We observed a well structured community dominated by *Carex myosuroides* in the LS nunatak. Although this species is not among the ones that have increased the most in the study area, it is clearly linked to very cold and early snow removal sites such as alpine ridges. Its presence highlights

the importance of topography in the maintenance of alpine plant diversity: species with opposite micro-climatic requirements can both be winners under global warming thanks to the presence of microrefugia (Patsiou et al. 2014).

Species classified as competitors are amongst the main winner species in lower nunataks, but another biological trait suggests interesting and rather unexpected ecological changes. A striking change concerns hemicryptophyte species, in particular graminoid species such as *Agrostis schraderiana*, *Carex sempervirens* or *Phleum alpinum*, which are among the “biggrand winners”, especially in lower nunataks. As these species play a key role in alpine grassland structure, their increased frequency across study nunataks indicate a spread of grasslands and therefore constitute another driver to the greening effect demonstrated by remote sensing analyses. Other increasing species classified as competitors are phanerophytes, noticeably at elevation as high as 3000 m a.s.l.! In such a case, *Salix helvetica* and *Salix appendiculata* play a key role in colonization, partially thanks to their long distance dispersal capacity. This case constitutes another relevant example of “upward migration”.

Particular plant occurrences require further investigation as they bring to light subtle but relevant ecological dynamics. This seems to be the case for *Kernera saxatilis*, a hemicryptophyte mainly dispersed by water and wind, and *Arctostaphylos uva-ursi*, a chamaephyte mainly dispersed via endochory. Both are very thermophilous species only present in two locations: *Kernera* was observed on a cliff in CV, far away from its usual habitat (i.e. limestone cliffs heated by the sun, at lower elevations); *Arctostaphylos* occupied a mound at the most south-exposed side of the lowest nunatak (TC). These singular presences imply local dry and hot conditions on nunataks, and may be indicative of increasing moisture limitation even at high elevation sites on the slopes of Mont Blanc (Figure 2). The arrival of plants that are tolerant of warm and dry conditions in high alpine sites echos the results of a recent dendroecological study demonstrating that moisture availability has become the main

factor limiting the annual radial growth of rhododendron stems rather than snow cover duration and temperature (Francon et al. 2021). Soil moisture limitation may indeed curb greening trends in the coming decades and influence future shifts in alpine plant community composition, and in our view represents a key parameter for the future monitoring of vegetation shifts on Mont-Blanc nunataks.

Conclusion

We observed highly varied responses of high-elevation plant communities to ongoing climate changes since the mid-1800s in one of Europe's largest glacier basins. Our study confirms plant dynamics already documented elsewhere: (i) species enrichment in the lowest and least isolated nunataks (TC, LS, CV); “winning” trajectory of competitive species, supporting (ii) 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 dynamics of species turnovers at lower elevations; (ii) increase of plant communities associated with non-permanent snow-cover (snow-beds, wet habitats), both showed by plant community data and remote sensing analyses; (iii) increase of hemicryptophyte species, mainly graminoids, at lower elevations, and increase of phanerophytes at higher elevations. This complex set of plant community responses underscores the need to not only focus on global vegetation trends but also to promote field ecology at a fine geographical scale. Ongoing monitoring of ecological shifts in high mountain environments in the years ahead will be of the utmost importance in order to understand future trajectories of both plant communities and the alpine landscapes they compose in the context of accelerating climate change.

In 1810, 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 encouraged 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

C.D. had the original idea of the study ; C.D., B.Z.C., and S.L. designed the study ; N.B., S.L. and C.D. performed the statistical analyses, B.Z.C. and A.B. performed the remote sensing analyses ; C.D., B.Z.C., and S.L. wrote the first draft of the manuscript. C.D., B.Z.C, N.B. and S.L. contributed to the sample collection. C.D. coordinated and mounted the reference herbarium collection. The project as a whole was coordinated by C.D. and S.L.

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Appendices

Table Sx1. List of plant species observed in the study nunataks.

Table Sx2. List of herbarium samples.

Figure Sx1. Temporal trends of nunatak occupancy for the species occupying at least half of the nunataks in 1868.

Figure Sx2. Temporal changes of greening signal (expressed in $\text{NDVI}_{\text{max}} \cdot \text{year}^{-1}$) for all study nunataks between 1985 and 2020.

Figure Sx3. Violin plots depicting the dispersion of greening trend values ($\Delta\text{NDVI} > 0$) for all study nunataks. The legend indicates each nunatak's altitude.

Figure Sx4. Contingency tables of species traits and classes of temporal dynamics, across all study nunataks : Life forms (A), Grime's Strategies (B), Dispersal Agents (C). (p-value < 0.1 *, p-value < 0.05 **).

Figure captions

Figure 1. Map of study nunataks (red line contours) with Little Ice Age glacier extent (dashed blue line contours), within the Mont Blanc range. 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 plant communities 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.

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 (“[Biggrand](#) winners”), that is species absent or rare in 1868 that have colonized more than three nunataks in 2020.

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 **).

Figure 6. (A) Boxplots of greening trend values extracted for 30x30 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 September 3, 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 ($\Delta\text{NDVI}>0$) vs Δ species richness (A) and temporal beta diversity (B) (p-value<0.1 *, p-value<0.05 **)

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).