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Species and community dynamics on siliceous summits of the Texelgruppe – Gruppo di Tessa, South Tyrol, Northern Italy

Abstract

Climate change will fundamentally affect the vegetation in high elevations. Via long term monitoring programs, substantial information can be obtained about the ongoing dynamics. The aim of the present study was to analyze diversity changes at four summits of the GLORIA target region Texelgruppe – Gruppo di Tessa (South Tyrol, Northern Italy) from 2003 to 2017. Knowing that new colonization mainly occurs on the eastern and southern aspects of the Alpine summits, we compared the summit vegetation to the plant communities along the southern slopes of each summit from the treeline upward. We expected to gain information on potential migrators approaching the summits. We asked if cryophilic species disappear on the summits and if thermophilic species approach the summit area. With exception of the highest summit, an increase in species numbers throughout the years occurred. The newcomers at the lower summits were predominantly thermophilic species. Here, invasion of thermophilic species might limit cryophilic species in the near future. This process will be intensified due to increasing abundance of dwarf shrubs and trees. At the higher summits, where cryophilic species are still dominant, we assume that this species group will prevail on the long term.

Keywords: alpine, cryophilic species, GLORIA, nival, thermophilic species

Zusammenfassung

Der Klimawandel beeinflusst die Hochgebirgsvegetation ganz entscheidend. Die Dynamik der Veränderung in der Artenzusammensetzung kann mit Hilfe von Monitoring-Programmen untersucht werden. Das Ziel der vorliegenden Arbeit war es, die Änderungen der Diversität auf den vier Gipfeln der GLORIA-Region Texelgruppe von 2003 bis 2017 zu untersuchen und herauszufinden, welche potentiellen Einwanderer jeweils unterhalb der Gipfel vorkommen. Weiters sollte untersucht werden, ob kryophile Arten auf den Gipfeln verschwinden und ob die Neuankömmlinge als thermophil zu bezeichnen sind. Aus dem Alpenraum ist bekannt, dass die höchste Artenvielfalt und Zuwanderung in südlicher und östlicher Exposition zu finden sind, daher wurde in der vorliegenden Untersuchung die Gipfelvegetation mit den Pflanzengesellschaften am südlichen Höhengradienten von der Baumgrenze aufwärts verglichen. Die Ergebnisse zeigen mit Ausnahme des höchsten Gipfels einen deutlichen Anstieg der Artenzahl. Die Neuankömmlinge auf den niederen Gipfeln sind überwiegend thermophile Arten, vor allem Zwergsträucher und Bäume dehnen ihr Areal nach oben hin aus. In diesen Bereichen dürften die Zuwanderer die vorhandenen kryophilen Arten in nächster Zukunft verdrängen. Auf den höheren Gipfeln dominieren kryophile Arten und es ist anzunehmen, dass diese Artengruppe auch in Zukunft überwiegen wird.

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Introduction

Alpine biodiversity is governed by climate (Körner 2003, Nagy & Grabherr 2009); thus, climate change will essentially influence alpine species number and composition. Alpine species are expected to react more pronouncedly than species from the lowlands to the ongoing changes (Pauli et al. 2007, Steinbauer et al. 2018). Up to 50% of alpine species are threatened to go extinct by the end of the 21st century due to competitive displacement by newly invading species from lower elevations (Thuiller et al. 2005, Parolo & Rossi 2008, Engler et al. 2011, Dullinger et al. 2012, Rumpf et al. 2018). Experiments suggest that new plant communities may evolve in the future due to climate change (Alexander et al. 2015, 2018). At present, significant increases in plant diversity were recorded in temperate and boreal European mountains (GOTTFRIED et al. 2012, Pauli et al. 2012), with considerable acceleration during the last decades (Stein-BAUER et al. 2018), while in the dry alpine Mediterranean regions species richness is declining or highly fluctuating (Pauli et al. 2012, Fernández Calzado & Molero Mesa 2013, Jiménez-Alfaro et al. 2014), mainly due to the present precipitation and drought regimes (LAMPRECHT et al. 2021, KAZAKIS et al. 2021). Elevated species richness after 14 years was also found in the western Dolomites of Northern Italy (Unterluggauer et al. 2016), showing especially striking increases in species numbers at the highest summits. Several studies demonstrate that the new species arriving at the summits are mainly thermophilic ones, i.e. species from lower elevations or species with a broad distribution range (Pauli et al. 2012, Gottfried et al. 2012, Lamprecht et al. 2018). On the long term, the invasion of thermophilic species may lead to considerable problems for the persistence of cryophilic species, i.e. for those specialists that inhabit the summit areas. Most of the cryophilic species are weak competitors, which will hardly survive when vegetation cover increases. Moreover, their potential habitats shrink under climate warming (Engler et al. 2011, Lamprecht et al. 2018, Rumpf et al. 2018, 2019) and further upward migration might be impossible, especially on low mountain summits.

Climate change effects on species number and composition can only be assessed by long-term monitoring programs, surveying the vegetation in high elevations through time. The Global Observation Research Initiative in Alpine Environments (GLORIA, https://www.gloria.ac.at) has developed a worldwide research program in more than 130 mountain regions on all continents. The summit regions are monitored according to a standard protocol (Pauli et al. 2015). In Trentino-South Tyrol in Italy, two GLORIA target regions were established: one in the western Dolomites in 2001 (Erschbamer et al. 2003, 2011, Unterluggauer et al. 2016) and one in the Nature Park Texelgruppe – Gruppo di Tessa in 2003 (Erschbamer et al. 2010, Erschbamer et al. 2017). In both target regions, species number, abundance and composition were recorded every 5 to 7 years, using two scales, (1) the summit area scale, and (2) the 1 m² plot scale considering each aspect of the summit at the 5 m contour line. The first GLORIA results in the European Alps clearly showed that the highest diversity as well as the highest number of newly arriving species occur at the eastern and southern aspects (Pauli et al. 2012, Winkler et al. 2016). Based on these results, we expected to gain relevant information from analyses of the southern slopes below the summits. These investigations are not yet part of the GLORIA protocol and we expected to be able to propose a scenario for future changes at the local scale.

The aim of the present study was to analyze species diversity changes at four summits of the GLORIA target region Texelgruppe – Gruppo di Tessa between 2003 and 2017. We expected information on disappearing cryophilic and appearing thermophilic species by analyzing species turnover on the summits. With the comparison of the summit vegetation to the plant communities along the slopes of the southern aspects from the summit to the treeline, we aimed to infer how summit vegetation might change in the future. Specifically, we asked the following questions:

(1) How does species diversity change over 14 years at summit areas and at 1 m² permanent plots per aspect? Do frequency changes of species occur within the 1 m² plots? Do cryophilic species disappear from the summits?

(2) Which plant communities prevail along the southern slopes of the summits? Can summit vegetation be discriminated from the slope communities? Do thermophilic species approach the summit area at the southern slopes?

Material and Methods

Study area

The study area GLORIA target region IT_TEX lies in the Nature Park Texelgruppe – Gruppo di Tessa in South Tyrol (Northern Italy). According to the GLORIA protocol (Pauli et al. 2015), four summits were chosen in 2003 and most of them were named by the investigators due to the lack of topographical names (Fig. 1): summit 1 = Faglmugl (FAG, 2180 m a.s.l.) at the treeline ecotone; summit 2 = Schafberg (SBG, 2619 m a.s.l.) in the upper alpine zone; summit 3 = Da Wöllane (DWO, 3074 m a.s.l.) in the subnival zone; summit 4 = Kasererwartl (KAS, 3287 m a.s.l.) in the nival zone. Geologically, FAG and SBG belong to the Texel Complex, located in a side valley of Passeiertal; DWO and KAS are part of the Ötztal Complex (Geobrowser Autonome Provinz Bozen 2019), both in side valleys of Schnalstal.

Field work

The surveys were made on three different scales: (1) on the summit area scale, i.e. the whole area from the highest summit point down to the 10 m contour line was sampled in the years 2003, 2011, 2017 (i.e. summing up species number and composition of all 8 summit area sections, Fig. 1); (2) on the 1 m² plot scale, i.e. 3×3 m summit clusters were established at the 5 m contour line below the highest summit point, considering 3-4 plots of 1 m² per aspect (Fig. 1, not all aspects could be recorded equally due to inaccessible ground) in the years 2003, 2011, 2017; (3) on transects along the southern aspect; every 50 m of elevation from the summit plot cluster down to the treeline (Fig. 2) relevés were performed in 2018 similarly to the clusters at the 5 m contour line. All plots were permanently marked. Within the summit area, all occurring vascular plant species were listed using a semi-quantitative abundance scale (PAULI et al. 2015). In the 1 m² plots, the cover of the vascular plant species was estimated in percent and the frequency of the species was recorded by means of a grid divided into 100 subplots, within which the presence of each species was recorded. Additionally, also the cover of surface types (vascular plants, litter, bare ground, scree and rock) was estimated in percent in each 1 m² plot. At the transect clusters, the percent cover of every vascular plant species was recorded in each of the four 1 m² plots and mean cover values were calculated for each species per cluster.

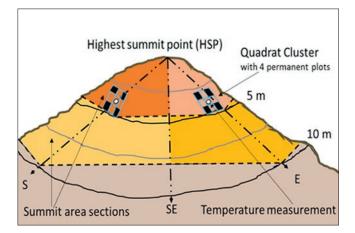
Nomenclature of species follows Fischer et al. (2008). Several species were grouped to aggregates when determination was problematic (*Alchemilla alpina* agg., *Anthoxanthum odoratum* agg., *Helianthemum nummularium* agg., *Ranunculus montanus* agg., *Vaccinium uliginosum* agg. (according to Silbernagl & Schönswetter 2019, subalpine *V. uliginosum* s. str. and *V. gaultherioides* can only be distinguished by genome and flower size, which was not checked) or only determined to the genus level (*Taraxacum* sp.). *Cerastium uniflorum* includes also *C. pedunculatum*, which was overlooked during the initial field work.

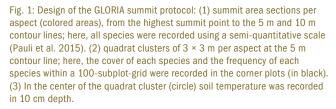
Data analysis

New species were defined as those not present at the first relevé in 2003 but present at the last one in 2017, lost species were defined as those present at the first but not at the last relevé.

Transect communities were classified by Trenkwalder (2019) using a Two Way INdicator SPecies ANalysis (TWINSPAN) and described according to Grabherr (1993). Transects and summit cluster plots were compared by a NMDS (Nonmetrical MultiDimensional Scaling) ordination. Bray-Curtis dissimilarity metric was used. Species scores were Wisconsin double standardized. The final stress was 0.12. The communities already described in Trenkwalder (2019) were highlighted in the ordination plot.

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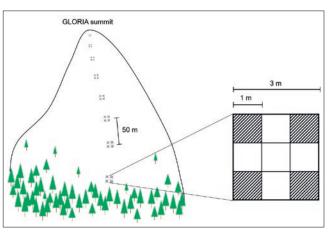


Fig. 2: Design of the field work at the southern aspect of each summit. The cover of each species in % was recorded within the four corner plots (1 m 2) of the 3 × 3 m plot cluster every 50 m of elevation.

Species were classified according to their distribution along the elevational gradient using the indicator value 'temperature' (Landolt et al. 2010). According to Evangelista et al. (2016), we then discriminated cryophilic and thermophilic species. Cryophilic species are exclusively distributed in the alpine and nival belts, while thermophilic species occur at lower elevations or across the whole elevation gradient. For the comparison between southern transects and southern summit clusters, only the uppermost 250 m of elevation of the transects were used. Considering a lapse rate of $-0.6~^{\circ}\text{C}$ per 100 m of elevation (Körner 2003), this shift migh be relevant for species migrations under a warming scenario of +1.5 $^{\circ}\text{C}$.

All statistical analyses were performed in the R statistical computing program R 3.4.3. (R Core Team 2017) using the Vegan package (Oksanen et al. 2013) and the twinspanR-package (Zeleny et al. 2016). Differences in mean species numbers and frequencies per 1 $\rm m^2$ plot between 2003 and 2017 were tested by paired, two-sided t-tests: 1) for the overall region and 2) for the summits separately.

Results

Changes at the summit areas

From 2003 to 2017, species numbers at the summit areas increased with exception of the highest summit KAS (Fig. 3). The number of new species (period 2003–2017) exceeded the number of lost species (Table 1) at FAG, SBG, and DWO. Only at the highest summit KAS no new species occurred, while one species (*Leucanthemopsis alpina*) was lost during the period of 14 years. In 2003, only a few tree saplings were found at the summit areas of FAG and SBG: two *Larix decidua* individuals at FAG and one *Sorbus aucuparia* sapling at SBG. In 2017, at FAG the two *Larix decidua* individuals were still present together with five *Picea abies* and one *Sorbus aucuparia*. At SBG, one *Sorbus aucuparia* was still present. The complete species list for the summits in 2003, 2011 and 2017 can be found in the Appendix.

At FAG and SBG the newcomers were mainly thermophilic species, while at DWO the cryophilic ones prevailed. The lost species predominantly belonged to the cryophilic group on all summits.

Table 1: New and lost species between 2003 and 2017 at the uppermost 10 m of the summit areas in the GLORIA target region IT_TEX. T = classification of species according to their temperature value (Landolt et al. 2010): 1 = cryophilic, i.e. nival and alpine distribution only; 2 = thermophilic, i.e. distribution at the subalpine and/or the montane belt or from the montane to the alpine belt; n.a. = not available.

Summit	New	Т	Lost	Т
FAG	Carex atrata	1	Antennaria carpatica	1
	Erigeron alpinus	1	Cryptogramma crispa	1
	Festuca nigricans	1	Gentiana punctata	1
	Athyrium filix-femina	2	Luzula lutea	1
	Carex pallescens	2	Luzula spicata	1
	Carlina acaulis	2	Oreochloa disticha	1
	Dryopteris filix-mas	2	Agrostis capillaris	2
	Euphrasia picta	2	Rhinanthus glacialis	2
	Festuca laevigata	2		
	Galium anisophyllon	2		
	Galium mollugo	2		
	Picea abies	2		
	Poa nemoralis	2		
	Polygala chamaebuxus	2		
	Pseudorchis albida	2		
	Sorbus aucuparia	2		
SBG	Carex foetida	1	Erigeron uniflorus	1
	Festuca nigricans	1	Kobresia myosuroides	1
	Gentiana brachyphylla	1	Saxifraga exarata	1
	Luzula lutea	1	Pulsatilla vernalis	2
	Avenella flexuosa	2	Viola biflora	2
	Coeloglossum viride	2		
	Dactylorhiza maculata	2		
	Dryopteris expansa	2		
	Luzula multiflora	2		
	Ranunculus montanus agg.	2		
	Rhododendron ferrugineum	2		
	Taraxacum sp.	n.a.		
DWO	Achillea moschata	1	Cardamine alpina	1
	Juniperus communis ssp. nana	1		
	Pedicularis kerneri	1		
	Poa alpina	1		
	Sibbaldia procumbens	1		
	Veronica bellidioides	1		
	Sempervivum montanum	1		
	Agrostis agrostiflora	2		
	Coeloglossum viride	2		
	Dactylorhiza maculata	2		
KAS	-		Leucanthemopsis alpina	1

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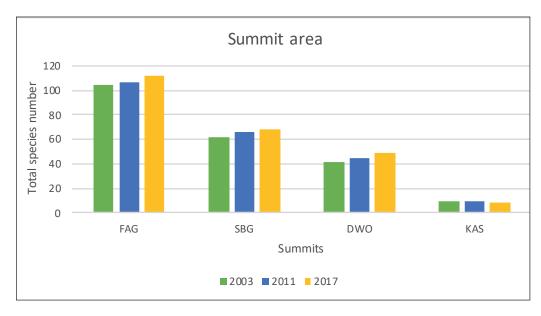


Fig. 3: Total species number at the summit areas (i.e. area from the highest summit point down to the 10 m contour line) per sampling year (2003, 2011, 2017).

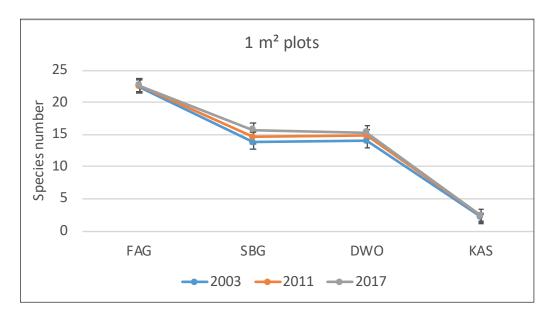


Fig. 4: Mean species number \pm standard error per 1 m² plot at the four GLORIA summits of the target region IT_TEX in 2003, 2011, and 2017.

Table 2: Total frequency per 1 m^2 plot for every summit (mean \pm standard error) from 2003, 2011, 2017, and difference between 2003 and 2017 in %, based on the frequency of 2003. n = number of plots per summit.

Summit	2003	2011	2017	2017-2003	n
FAG	641 ± 56	648 ± 55	664 ± 54	3.6%	15
SBG	486 ± 44	501 ± 39	533 ± 39	9.8%	13
DWO	301 ± 21	312 ± 25	335 ± 29	11.1%	11
KAS	32 ± 8	44 ± 11	56 ± 12	77.2%	11

Changes at the 1 m² plots

Increases in species numbers were also observed at the scale of 1 $\rm m^2$. Overall, species number increased significantly by 0.94 from 2003 to 2017 (p < 0.001). The highest diversity was found at the 1 $\rm m^2$ plots of the lowest summit FAG with more than 22 species per plot (Fig. 4), increases from 2003 to 2017 being rather small and not significant (Fig. 4). Higher increases occurred at SBG (2003: 13.77 species, 2017: 15.77; p < 0.001) and DWO (2003: 14 species, 2017: 15.36; p = 0.002). Very few species were found at KAS (2003: 2.18 species, 2017: 2.45; Fig. 4; n.s.).

Total species frequency increased at all summits from the first to the last monitoring (p < 0.001), being highest at KAS where the changes amounted to approximately +77% (Table 2). Also at SBG total frequency increased significantly (p = 0.003), whereas at DWO and FAG no significant increases occurred.

At FAG, species with increase in frequency by more than 45 subplots and new species as well as lost species predominantly belonged to the thermophilic species group (Table 3). At the remaining three summits species turnover occurred within the cryophilic group. Only at SBG one newcomer belonged to the thermophilic group (*Deschampsia cespitosa*, Table 3).

Table 3: Species with frequency increase by more than 45 subplots (winners), species with decreasing frequency by more than 45 subplots (losers), new and lost species for the period 2003 until 2017 at the four GLORIA summits of the target region IT_TEX. T = classification of species according to the temperature value (Landolt et al. 2010): 1 = cryophilic, i.e. distribution exclusively at the alpine and nival belt; 2 = thermophilic, i.e. distribution at the subalpine and/or the montane belt or from the montane to the alpine belt; n.a. = not available.

Summit	Winners	Т	Losers	T	New	Т	Lost	Т
FAG	Avenula versicolor	1	Agrostis alpina	1	Poa alpina	1	Gentianella anisodonta	1
	Euphrasia minima	1	Carex curvula	1	Agrostis agrostiflora	2	Luzula lutea	1
	Avenella flexuosa	2	Phyteuma hemisphaericum	1	Ajuga pyramidalis	2	Myosotis alpestris	1
	Calamagrostis villosa	2	Festuca nigrescens	2	Polygala chamaebuxus	2	Arnica montana	2
	Crocus albiflorus	2	Leontodon hispidus	2	Pseudorchis albida	2	Coeloglossum viride	2
	Homogyne alpina	2	Rhododendron ferrugineum	2	Veronica officinalis	2	Deschampsia cespitosa	2
	Nardus stricta	2	Thymus praecox	2			Hieracium pilosella	2
			Vaccinium vitis-idaea	2			Laserpitium halleri	2
			Anthoxanthum odoratum agg.	n.a.			Leontodon hispidus	2
							Silene vulgaris	2
SBG	Avenula versicolor	1	Oreochloa disticha	1	Doronicum clusii	1	Campanula scheuchzeri	1
	Euphrasia minima	1	Pedicularis kerneri	1	Gnaphalium supinum	1	Luzula spicata	1
	Leucanthemopsis alpina	1	Primula glutinosa	1	Luzula lutea	1		
	Persicaria vivipara	1			Soldanella pusilla	1		
	Phyteuma hemisphaericum	1			Deschampsia cespitosa	2		
	Poa alpina	1						
	Salix herbacea	1						

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Summit	Winners	Т	Losers	Т	New	Т	Lost	Т
DWO	Euphrasia minima	1			Draba fladnizensis	1		
	Festuca halleri	1			Gentiana brachyphylla	1		
	Leucanthemopsis alpina	1						
	Luzula spicata	1						
KAS	Cerastium uniflorum	1			Draba fladnizensis	1	Leucanthemopsis alpina	1
	Poa laxa	1						

Transects at the southern aspects and summit plots

The plant communities of the two lower summits were rather similar (Fig. 5), being classified as dwarf shrub rich Caricetum sempervirentis. These are long-leaved grasslands ranging from 1950 m up to 2600 m a.s.l. with a mean cover of 65% and a mean species number of 20 per m². Alongside *Carex sempervirens*, the following species occurred: *Anthoxanthum odoratum* agg., *Festuca nigrescens*, *Nardus stricta*, *Campanula scheuchzeri*, *Thymus praecox*, *Potentilla aurea and Scorzoneroides helvetica*. The community was further enriched by dwarf shrubs such as *Vaccinium vitis-idaea*, *V. myrtillus*, *Calluna vulgaris* and *Rhododendron ferrugineum*.

On the lower transects of DWO and KAS the Caricetum sempervirentis was dominated by *Poa variegata* (Fig. 5). These plots showed a mean cover of 62% and a mean species number of 26. Further species are *Festuca halleri*, *Phyteuma hemisphaericum*, *Juncus trifidus*, and *Veronica bellidioides*.

The highest transect record of SBG, the higher elevated plots of DWO and most records on the KAS transect were assigned to the Caricetum curvulae (Fig. 5), the typical short-growing grasslands of the siliceous mountains in the Alps, with a specific dominance of *Festuca halleri* together with *Carex curvula*. These transects ranging from 2550 m to 3000 m a.s.l. had a mean vegetation cover of 44% and a mean species number of 18 per m². Typical species were *Leucanthemopsis alpina*, *Phyteuma hemisphaericum*, *Salix herbacea*, *Agrostis rupestris*, *Minuartia sedoides*, *Silene exscapa* and *Euphrasia minima*. The uppermost records on DWO and KAS at > 2950 m a.s.l. were sparsely vegetated scree slopes (Fig. 5) with 12.2% plant cover and 6 species per m². These plots can be classified as initial stage of the Androsacetum alpinae; the most common species were *Poa laxa*, *Ranunculus glacialis*, *Cerastium uniflorum*, *Saxifraga bryoides*. The typical representatives of the Androsacetum alpinae, i.e. *Androsace alpina* and *Saxifraga oppositifolia* were only rarely found.

The communities described along the southern transects were found to be present also at the summits with exception of the Caricetum sempervirentis with *Poa variegata* (Fig. 5). All summit plots changed from the first to the last survey with the exception of the northern summit plots of KAS (K-N). Summit FAG corresponds entirely to the transect community Caricetum sempervirentis with dwarf shrubs. The SBG summit plots can be attributed to the Caricetum curvulae (S-E, S-W, S-N), while the southern summit cluster (S-S, Fig. 5) showed a transition towards the Caricetum sempervirentis community. The eastern and southern summit plots of DWO can be assigned to the Caricetum curvulae, while the northern and western summit plots were more connected to the scree slope community. The summit plots of KAS and the uppermost transects of this summit form a heterogeneous scree slope community. The northern aspect of summit KAS is an outlier (K-N, Fig. 5), nearly without vegetation. The most important environmental parameters shaping the observed pattern were elevation and temperature.

Comparing the uppermost 250 m of elevation of the transects to the summit cluster plots, species numbers per 1 m² differed only slightly and they had a considerable

number of species in common (Table 4). However, the transects of the lower summits showed a substantial number of thermophilic species not present at the summit plots. At FAG, 16 thermophilic and 1 cryophilic species were present exclusively on the transect; at SBG 4 thermophilic and 9 cryophilic species were recorded exclusively on the transect, while the DWO transect showed one thermophilic and 14 cryophilic species, which did not occur at the summit plots. At KAS no thermophilic species and 9 cryophilic species were found across the 250 m transect below the summit plots.

Table 4: Overview on mean species numbers per m² ± standard error at the southern summit cluster in 2017 and the transects 250 m below the summit cluster; total number of species occurring in common at the summits and transects, total number of species occurring only at the summit cluster and total number of species only at the transects, differentiated in cryophilic and thermophilic ones.

Species number	FAG	SBG	DWO	KAS
Species number	IAG	350	Divo	NAO
Summit	19.0 ± 1.1	18.3 ± 0.3	17.3 ± 0.3	2.7 ± 0.3
Transects	20.2 ± 0.9	15.2 ± 1.0	17.8 ± 2.2	4.6 ± 1.4
In common	22	18	19	3
cryophilic	8	16	19	3
thermophilic	14	2	0	0
Only summit	8	6	1	0
cryophilic	5	6	1	0
thermophilic	3	0	0	0
Only transects	17	13	15	9
cryophilic	1	9	14	9
thermophilic	16	4	1	0

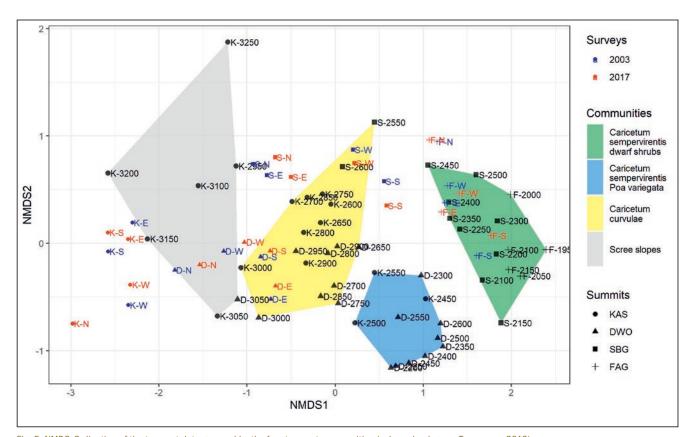


Fig. 5: NMDS-Ordination of the transect data grouped by the four transect communities (coloured polygons, Trenkwalder 2019) displayed together with the summit cluster plots per aspect (e.g. K-E = KAS east, K-S = KAS south, K-W = KAS west, K-N = KAS north) from the first survey 2003 (in blue) and the resurvey 2017 (in red). Dissimilarity metric for NMDS: Bray-Curtis; final stress: 0.12.

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Discussion

Changes over 14 years

On the summit area scale, species enrichment over time was detected at three summits of the study area, while at the highest summit KAS one species disappeared between the first and the last monitoring. The increases in species numbers were lower than in the GLORIA target region IT ADO in the western Dolomites (Unterluggauer et al. 2016) but similar to changes in other siliceous target regions of the European Alps (Nicklas et al. 2021) and the Apennines (Porro et al. 2019). Increasing species richness, with exception of the nival summit KAS, is in line with recent studies from the Central Alps (Lamprecht et al. 2018, Steinbauer et al. 2019), the European mountain ranges (Steinbauer et al. 2018), the Australian Alps (Verrall et al. 2021) and the Andes (Carilla et al. 2018). We did not recognize a stagnation of species enrichment on the lowest summit as it was found in the GLORIA site of the Altai mountains (ARTEMOV 2018). However, we recorded the lowest increase in diversity on the lowest summit (FAG, 8% increase from 2003 to 2017). The disappearance of one species (Leucanthemopsis alpina) at KAS during the 14 years period was surprising, however, the species can still be found along the southern transect. Seed production at this site may be suboptimal or even missing due to the short growing season and dispersal limitations along the elevation gradient might be a substantial problem on this summit. Topographical barriers (Dullinger et al. 2012, HÜLBER et al. 2016) at KAS, mainly large boulder zones and the glacier tongue, may limit range expansions. Although most high-alpine species are dispersed by wind (MATTEODO et al. 2013), it seems that nunatak-like summits such as KAS are too far away from seed sources, thus clonal propagation by the resident species is the method of choice. Moreover, seed limitation seems to be generally one of the essential factors of colonization in proglacial sites (Erschbamer & Caccianiga 2017).

On the 1 m² plot level, only small increases in species richness occurred throughout time. At the highest summit KAS – albeit the loss of one species at the summit area – a clear process of "in-filling" (Cannone & Pignatti 2014, Rumpf et al. 2018) is going on at the 1 m² plots, with around 77% of frequency increase by resident species such as *Cerastium uniflorum, Ranunculus glacialis, Saxifraga bryoides, Poa laxa*, and *Saxifraga exarata*. The relatively low increase in species frequency at the lower summit may partly be explained by the abundant presence of litter, limiting the growth of the resident species and preventing colonization of new species. This seems to be a special feature of our study site (Nicklas et al. 2021). In addition, the low frequency increase might also be the consequence of highly persistent resident species. They prevent invasions of new species as well as the spread of subordinate species (Olsen 2016).

Southern transects and summit vegetation

The plant communities along the southern transects are those typical for siliceous mountains on the southern slope of the main chain of the Alps (Grabherr 1993), and as expected, the community pattern reflects the elevation gradient (Nagy & Grabherr 2009) from thermophilic to cryophilic communities. The Caricetum sempervirentis with *Poa variegata* seems to be a specific community of the southern transects of DWO and KAS. This might be explained by the geological substrate (Ötztal complex). Similar communities can also be found on the north-facing slopes of the Ötztaler Alpen in the treeline ecotone of Obergurgl (Erschbamer unpubl. data). Peer (1980) did not mention such a community in his vegetation mapping of South Tyrol, however, the Aveno-Nardetum and the Festucetum halleri nardetosum – both typical for pasture communities on the south-facing main chain of the Alps – have several species in common with the Caricetum sempervirentis of our study area.

The summit cluster plots can be attributed to the community types described along the transects, although the highest summits showed considerable variation with aspect. This is in line with other temperate mountains, where remarkable differences in species numbers and composition occurred depending on aspect (WINKLER et al. 2016, NICKLAS et al. 2021), eastern and southern being the species richest sides, having also

the highest numbers of newcomers (Pauli et al. 2012). The similarity of summit cluster plots and transect communities contrasts the situation at the GLORIA site IT_ADO in the Dolomites. There, on two summits, specific communities were discriminated which did not occur along the transects (Bertol 2021).

Thermophilization trends

Thermophilization trends were described globally and across several organism groups (Chen et al. 2011) and particularly also for the alpine summit vegetation in Europe (Gottfried et al. 2012). In the Central Alps, cryophilic species decreased in cover mainly at the lower distribution ranges (Lamprecht et al. 2018, Steinbauer et al. 2020). Furthermore, our results suggest a thermophilization trend mainly at the lower summits. At FAG and SBG, the newcomers were predominantly thermophilic species, while at DWO only three out of ten newcomers were thermophilic. We have to mention that the number of thermophilic species might be even higher if we classify species ranges according to our field experience. Several species such as *Carex sempervirens*, *Gentiana acaulis*, *Gentiana punctata*, *Geum montanum*, *Juniperus communis* ssp. *nana*, *Luzula lutea*, *Mutellina adonidifolia*, *Persicaria vivipara*, *Poa alpina*, *Potentilla aurea*, had to be classified as alpine species (T = 1) according to Flora Indicativa (Landolt et al. 2010), while their distribution in the study area and in the Central Eastern Alps ranges from the upper montane-subalpine to the alpine belt. However, as databases such as Flora Indicativa are state of the art, we did not want to adjust the temperature values.

Thermophilization was already outlined by Erschbamer et al. (2011) and Gottfried et al. (2012) and confirmed by several following studies (Rumpf et al. 2018, Steinbauer et al. 2018). Several authors highlighted an increasing trend of thermophilic graminoids (Erschbamer et al. 2009, 2011, Stanisci et al. 2016, Gigauri et al. 2016, Lamprecht et al. 2018), called "grassification" by Verrall et al. (2021). In the long term, on the lowest summits a "shrubification" may be predicted due to an increasing abundance of dwarf shrubs and the growth of trees (*Picea abies, Larix decidua, Sorbus aucuparia*). Increase in dwarf shrubs was also found at the GLORIA summits in the Apennines and the southwestern Alps (Stanisci et al. 2014), in Norway (Vanneste et al. 2017), in Spain (Jiménez-Alfaro et al. 2014, Lamprecht et al. 2021), and in Australia (Verrall et al. 2021). Among the lost species in our study area, the cryophilic species group prevailed. Similarly, a dieback of cryophilic species was found at Mt Schrankogel in the Stubaier Alps (Steinbauer et al. 2019). Also from the Ukrainian Carpathians, losses of coldadapted species were confirmed (Kobiv 2017).

Considering the southern transect at FAG, 16 thermophilic species not present at the summit are "waiting" already 250 m below the summit cluster. The higher the summit, the lower the number of thermophilic species approaching the top: on SBG only four thermophilic species and on DWO only one was present as potential immigrators. The relatively high number of thermophilic species in common between the summit cluster and the 250 m transect of the lower summits can be seen as a signal of decrease or even disappearance of cryophilic species at lower summits. This process might even be enhanced when the invading young trees and dwarf shrubs grow taller and larger. Range expansion of trees and shrubs depend on growth rates as well as on dispersal and recruitment strategies of the particular species (Dullinger et al. 2003, 2004). The degree of invasibility of the alpine grassland is still an unknown topic and will be highly relevant for future studies.

Conclusion

Invasion of thermophilic species at the lower summits will limit the occurrence of cryophilic species on these sites. The grasslands will be transformed to dwarf shrub rich communities with single trees in the near future. For a limited period of time, the northern sides of the lower summits might offer surrogate habitats for cryophilic species. At the highest summits, the cryophilic species group was found to be dominant

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and we assume that this group will prevail also in the near future. Here, the filling processes will mainly be continued by cryophilic species. Similar to glacier forelands, the highest summit of the study site seems to experience dispersal limitations, i.e. cryophilic as well as thermophilic species might have considerable difficulties to invade the nival summit.

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Appendix

Presence/absence list of the species occurring at the summit areas from the highest summit point down to the 10 m contour line at the four GLORIA summits of the Nature Park Texelgruppe – Gruppo di Tessa in 2003, 2011 and 2017.

Species	FAG 2003	FAG 2011	FAG 2017	SBG 2003	SBG 2011	SBG 2017	DW0 2003	DW0 2011	DW0 2017	KAS 2003	KAS 2011	KAS 2017
Achillea moschata	0	0	0	1	1	1	0	0	1	0	0	0
Achillea millefolium	1	1	1	0	0	0	0	0	0	0	0	0
Agrostis agrostiflora	1	1	1	1	1	1	0	0	1	0	0	0
Agrostis alpina	1	1	1	1	1	1	1	1	1	0	0	0
Agrostis capillaris	1	0	0	0	0	0	0	0	0	0	0	0
Agrostis rupestris	1	1	1	1	1	1	1	1	1	0	0	0
Ajuga pyramidalis	1	1	1	0	0	0	0	0	0	0	0	0
Alchemilla alpina agg.	1	1	1	0	0	0	0	0	0	0	0	0
Androsace alpina	0	0	0	0	0	0	1	1	1	0	0	0
Antennaria carpatica	1	0	0	1	1	1	0	0	0	0	0	0
Antennaria dioica	1	1	1	0	0	0	0	0	0	0	0	0
Anthoxanthum odoratum agg.	1	1	1	1	1	1	0	0	0	0	0	0
Arenaria biflora	0	0	0	1	1	1	0	0	0	0	0	0
Arenaria marschlinsii	0	0	0	0	0	0	1	1	1	0	0	0
Arnica montana	1	1	1	0	0	0	0	0	0	0	0	0
Athyrium filix-femina	0	0	1	0	0	0	0	0	0	0	0	0
Atocion rupestre	1	1	1	0	0	0	0	0	0	0	0	0
Avenella flexuosa	1	1	1	0	1	1	0	0	0	0	0	0
Avenula versicolor	1	1	1	1	1	1	0	0	0	0	0	0
Poa variegata	1	1	1	0	0	0	0	0	0	0	0	0
Calamagrostis villosa	1	1	1	0	0	0	0	0	0	0	0	0
Calluna vulgaris	1	1	1	0	0	0	0	0	0	0	0	0
Campanula barbata	1	1	1	0	0	0	0	0	0	0	0	0
Campanula scheuchzeri	1	1	1	1	0	1	0	0	0	0	0	0
Cardamine alpina	0	0	0	0	0	0	1	1	0	0	0	0
Cardamine resedifolia	1	1	1	1	1	1	1	1	1	0	0	0

Species	03	11	17	2003	11	2017	203	011	2017	03	11	17
	FAG 2003	FAG 2011	FAG 2017	SBG 20	SBG 2011	SBG 20	DW0 2003	DW0 2011	DW0 20	KAS 2003	KAS 2011	KAS 2017
Carex atrata	0	1	1	0	0	0	0	0	0	0	0	0
Carex curvula	1	1	1	1	1	1	1	1	1	0	0	0
Carex foetida	0	0	0	0	1	1	0	0	0	0	0	0
Carex pallescens	0	0	1	0	0	0	0	0	0	0	0	0
Carex sempervirens	1	1	1	1	1	1	0	0	0	0	0	0
Carlina acaulis	0	1	1	0	0	0	0	0	0	0	0	0
Cerastium cerastoides	0	0	0	1	1	1	0	0	0	0	0	0
Cerastium fontanum	1	1	1	1	1	1	0	0	0	0	0	0
Cerastium uniflorum	0	0	0	1	1	1	1	1	1	1	1	1
Cirsium spinosissimum	1	1	1	0	0	0	0	0	0	0	0	0
Coeloglossum viride	1	0	1	0	0	1	0	0	1	0	0	0
Crocus albiflorus	1	1	1	0	0	0	0	0	0	0	0	0
Cryptogramma crispa	1	1	0	0	0	0	0	0	0	0	0	0
Deschampsia cespitosa	1	1	1	1	1	1	0	0	0	0	0	0
Diphasiastrum alpinum	1	1	1	0	0	0	0	0	0	0	0	0
Doronicum clusii	0	0	0	1	1	1	1	1	1	0	0	0
Draba dubia	0	0	0	0	0	0	1	1	1	0	0	0
Draba fladnizensis	0	0	0	0	0	0	1	1	1	1	1	1
Dryopteris expansa	1	1	1	0	1	1	0	0	0	0	0	0
Dryopteris filix-mas	0	0	1	0	0	0	0	0	0	0	0	0
Empetrum hermaphroditum	1	1	1	0	0	0	0	0	0	0	0	0
Erigeron alpinus	0	1	1	0	0	0	0	0	0	0	0	0
Erigeron uniflorus	0	0	0	1	0	0	1	1	1	0	0	0
Euphrasia minima	1	1	1	1	1	1	1	1	1	0	0	0
Euphrasia officinalis ssp. picta	0	1	1	0	0	0	0	0	0	0	0	0
Euphrasia officinalis ssp. rostkoviana	1	0	1	0	0	0	0	0	0	0	0	0
Festuca halleri	1	1	1	1	1	1	1	1	1	0	0	0
Festuca nigricans	0	1	1	0	1	1	0	0	0	0	0	0
Festuca nigrescens	1	1	1	0	0	0	0	0	0	0	0	0
Festuca laevigata	0	0	1	0	0	0	0	0	0	0	0	0
Galium anisophyllon	0	1	1	0	0	0	0	0	0	0	0	0
Galium mollugo	0	0	1	0	0	0	0	0	0	0	0	0
Gentiana acaulis	1	1	1	1	1	1	0	0	0	0	0	0
Gentiana anisodonta	1	0	1	0	0	0	0	0	0	0	0	0
Gentiana bavarica	0	0	0	1	1	1	1	1	1	0	0	0
Gentiana brachyphylla	0	0	0	0	0	1	1	1	1	0	0	0
Gentiana punctata	1	1	0	0	0	0	0	0	0	0	0	0
Geranium sylvaticum	1	1	1	0	0	0	0	0	0	0	0	0
Geum montanum	1	1	1	1	1	1	0	0	0	0	0	0
Gnaphalium supinum	0	0	0	1	1	1	1	1	1	0	0	0
Gymnocarpium dryopteris	1	1	1	0	0	0	0	0	0	0	0	0
Hieracium alpinum	1	1	1	1	1	1	0	0	0	0	0	0
Hieracium angustifolium	1	1	1	0	0	0	0	0	0	0	0	0
Hieracium intybaceum	1	1	1	0	0	0	0	0	0	0	0	0
Hieracium murorum	1	1	1	0	0	0	0	0	0	0	0	0
Hieracium pilosella	1	1	1	0	0	0	0	0	0	0	0	0

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Species	003	111	2017	2003	2011	2017	003	011	2017	2003	011	2017
	FAG 2003	FAG 2011	FAG 20	SBG 20	SBG 20	SBG 20	DW0 2003	DW0 2011	DW0 2	KAS 20	KAS 2011	KAS 20
Homogyne alpina	1	1	1	1	1	1	0	0	0	0	0	0
Huperzia selago	1	1	1	1	1	1	1	1	1	0	0	0
Hypochaeris uniflora	1	1	1	0	0	0	0	0	0	0	0	0
Juncus trifidus	1	1	1	1	1	1	0	0	0	0	0	0
Juniperus communis ssp. nana	1	1	1	0	0	0	0	1	1	0	0	0
Kobresia myosuroides	0	0	0	1	1	0	1	1	1	0	0	0
Koeleria hirsuta	0	0	0	0	0	0	1	1	1	0	0	0
Larix decidua	1	0	1	0	0	0	0	0	0	0	0	0
Laserpitium halleri	1	1	1	0	0	0	0	0	0	0	0	0
Leontodon hispidus	1	1	1	0	0	0	0	0	0	0	0	0
Leucanthemopis alpina	1	1	1	1	1	1	1	1	1	1	1	0
Linaria alpina	0	0	0	0	0	0	1	1	1	0	0	0
Lloydia serotina	0	0	0	0	0	0	1	1	1	0	0	0
Loiseleuria procumbens	1	1	1	1	1	1	0	0	0	0	0	0
Lotus corniculatus	1	1	1	0	0	0	0	0	0	0	0	0
Luzula alpinopilosa	1	1	1	1	1	1	0	0	0	0	0	0
Luzula lutea	1	0	0	0	1	1	0	0	0	0	0	0
Luzula luzuloides	1	1	1	0	0	0	0	0	0	0	0	0
Luzula multiflora	1	1	1	0	1	1	0	0	0	0	0	0
Luzula spicata	1	0	0	1	1	1	1	1	1	1	1	1
Lycopodium clavatum	1	1	1	0	0	0	0	0	0	0	0	0
Minuartia recurva	0	0	0	1	1	1	1	1	1	0	0	0
Minuartia sedoides	0	0	0	1	1	1	1	1	1	0	0	0
Molinia caerulea	1	1	1	0	0	0	0	0	0	0	0	0
Mutellina adonidifolia	1	1	1	1	1	1	0	0	0	0	0	0
Myosotis alpestris	1	1	1	0	0	0	0	0	0	0	0	0
Nardus stricta	1	1	1	0	0	0	0	0	0	0	0	0
Oreochloa disticha	1	0	0	1	1	1	1	1	1	0	0	0
Pedicularis kerneri	0	0	0	1	1	1	0	0	1	0	0	0
Pedicularis tuberosa	1	1	1	0	0	0	0	0	0	0	0	0
Phegopteris connectilis	1	1	1	0	0	0	0	0	0	0	0	0
Phleum rhaeticum	1	1	1	0	0	0	0	0	0	0	0	0
Phyteuma betonicifolium	1	1	1	0	0	0	0	0	0	0	0	0
Phyteuma hemisphaericum	1	1	1	1	1	1	1	1	1	0	0	0
Picea abies	0	1	1	0	0	0	0	0	0	0	0	0
Pinguicula vulgaris	1	1	1	0	0	0	0	0	0	0	0	0
Poa alpina	1	1	1	1	1	1	0	1	1	0	0	0
Poa laxa	0	0	0	1	1	1	1	1	1	1	1	1
Poa nemoralis	0	0	1	0	0	0	0	0	0	0	0	0
Polygala chamaebuxus	0	1	1	0	0	0	0	0	0	0	0	0
Persicaria vivipara	0	0	0	1	1	1	0	0	0	0	0	0
Potentilla aurea	1	1	1	1	1	1	0	0	0	0	0	0
Potentilla erecta	1	1	1	0	0	0	0	0	0	0	0	0
Potentilla frigida	0	0	0	0	0	0	1	1	1	0	0	0
Primula glutinosa	0	0	0	1	1	1	1	1	1	0	0	0
Primula hirsuta	1	1	1	1	1	1	1	1	1	0	0	0

Species	FAG 2003	FAG 2011	2017	2003	SBG 2011	2017	DW0 2003	DW0 2011	2017	KAS 2003	KAS 2011	KAS 2017
	FAG	FAG	FAG	SBG	SBG	SBG	DWG	DMC	DWO	KAS	KAS	KAS
Pseudorchis albida	0	1	1	0	0	0	0	0	0	0	0	0
Pulsatilla alpina ssp. apiifolia	1	1	1	0	0	0	0	0	0	0	0	0
Pulsatilla vernalis	1	1	1	1	0	0	0	0	0	0	0	0
Ranunculus acris	0	1	0	0	0	0	0	0	0	0	0	0
Ranunculus glacialis	0	0	0	1	1	1	1	1	1	1	1	1
Ranunculus montanus agg.	0	0	0	0	0	1	0	0	0	0	0	0
Ranunculus nemorosus	0	1	0	0	0	0	0	0	0	0	0	0
Rhinanthus glacialis	1	0	0	0	0	0	0	0	0	0	0	0
Rhododendron ferrugineum	1	1	1	0	1	1	1	1	1	0	0	0
Rosa pendulina	1	1	1	0	0	0	0	0	0	0	0	0
Salix herbacea	0	0	0	1	1	1	1	1	1	0	0	0
Saxifraga aspera	1	1	1	0	0	0	0	0	0	0	0	0
Saxifraga bryoides	0	0	0	1	1	1	1	1	1	1	1	1
Saxifraga exarata	0	0	0	1	0	0	1	1	1	1	1	1
Saxifraga oppositifolia	0	0	0	0	0	0	0	0	0	1	1	1
Saxifraga stellaris	0	0	0	0	1	0	0	0	0	0	0	0
Scorzoneroides helvetica	1	1	1	1	1	1	0	0	0	0	0	0
Sedum alpestre	1	0	1	1	1	1	1	1	1	0	0	0
Sedum annuum	0	1	0	0	0	0	0	0	0	0	0	0
Selaginella selaginoides	1	1	1	0	0	0	0	0	0	0	0	0
Sempervivum montanum	1	1	1	0	0	0	0	1	1	0	0	0
Senecio incanus ssp. carniolicus	0	0	0	1	1	1	1	1	1	0	0	0
Sibbaldia procumbens	0	0	0	1	1	1	0	0	1	0	0	0
Silene exscapa	0	0	0	1	1	1	1	1	1	0	0	0
Silene nutans	0	1	0	0	0	0	0	0	0	0	0	0
Silene vulgaris	1	1	1	0	0	0	0	0	0	0	0	0
Soldanella pusilla	1	1	1	1	1	1	0	0	0	0	0	0
Solidago virgaurea	1	1	1	1	1	1	0	0	0	0	0	0
Sorbus aucuparia	0	1	1	1	1	1	0	0	0	0	0	0
Taraxacum sp.	0	0	0	0	1	1	0	0	0	0	0	0
Thesium alpinum	1	1	1	0	0	0	0	0	0	0	0	0
Thymus praecox	1	1	1	0	0	0	0	0	0	0	0	0
Trifolium alpinum	1	1	1	0	0	0	0	0	0	0	0	0
Urtica dioica	1	1	1	0	0	0	0	0	0	0	0	0
Vaccinium myrtillus	1	1	1	0	0	0	0	0	0	0	0	0
Vaccinium uliginosum agg.	1	1	1	1	1	1	0	0	0	0	0	0
Vaccinium vitis-idaea	1	1	1	0	0	0	0	0	0	0	0	0
Veronica alpina	0	0	0	1	1	1	1	1	1	0	0	0
Veronica bellidioides	1	1	1	1	1	1	0	1	1	0	0	0
Veronica chamaedrys	1	1	1	0	0	0	0	0	0	0	0	0
Veronica fruticans	1	1	1	0	0	0	0	0	0	0	0	0
Veronica officinalis	1	1	1	0	0	0	0	0	0	0	0	0
Viola biflora	1	1	1	1	0	0	0	0	0	0	0	0
Viola thomasiana	1	1	1	0	0	0	0	0	0	0	0	0

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