Dieback and expansions: species-specific responses during 20 years of amplified warming in the high Alps

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Abstract
The largest alpine–nival vegetation permanent plot site in the Alps, the GLORIA mastersite Schrankogel (Tirol, Austria), provided evidence of warming-driven vegetation changes already 10 years after its establishment in 1994. Another decade later, in 2014, substantial compositional changes with increasing ratios of warmth-demanding to cold-adapted species have been found. The current study deals with species-specific responses involved in an ongoing vegetation transformation across the alpine–nival ecotone on Schrankogel by using presence/absence as well as cover data from permanent plots, situated between 2900 and 3400 masl. The number of occupied plots per species remained constant or even increased during the first decade, whereas disappearance events became more frequent during the second one, especially for cold-adapted specialists (subnival–nival species). Remarkably, the latter was accompanied by continued strong losses in cover of all subnival–nival species. These losses were more frequent in plots with a more thermophilous species composition, suggesting an increasing maladaptation of subnival–nival species to warmer habitat conditions and a successive trailing-edge decline. Several species with a distribution centre at lower elevations (alpine–subnival) markedly increased in cover, comparatively more so in colder plots, indicating a leading-edge expansion. Moreover, our findings show an increase in occupied plots and cover of almost all snowbed species, suggesting that areas previously with a too long snowpack period are now becoming suitable snowbed habitats. Vegetation gaps arising from population dieback of cold-adapted species, however, could only be partly filled by advancing species, indicating that species declines have occurred already before the onset of strong competition pressure.

Keywords Alpine · Biodiversity · Climate change · Ecotone · Migration · Nival · Schrankogel · Species

Introduction
Cold-adapted mountain plant species are expected to suffer severe area losses because of warming-driven upward range shifts into high-elevation zones where space is limited (Engler et al. 2011; Freeman et al. 2018; Lenoir and Svenning 2015). However, revisitation studies of historical sites most commonly show increases in species numbers (Erschbamer et al. 2011; Grabherr et al. 1994; Grytnes et al. 2014; Walther et al. 2005; Wipf et al. 2013). A pan-European study found that the increase in species richness on summits was highly synchronous with warming trends and was related to climate-sensitive plant functional traits of alpine to subnival species in all European study regions. In contrast, changes in patterns of precipitation and nitrogen deposition did not or only regionally coincide with increasing plant diversity (Steinbauer et al. 2018). The congruency of the acceleration of warming with species accumulation rates thus reinforced the hypothesis that warming is the primary driver of upward
shifting leading range margins of species. This finding is remarkable, however, with respect to the known slow growth rates of most high mountain plants (Körner 2003). Although model projections forecast reductions of suitable alpine habitats (Engler et al. 2011), refined models suggested delayed responses to warming due to the capability of long-lived alpine species to persist even in unsuitable habitats until life spans of resident individuals are reached (Cotto et al. 2017; Dullinger et al. 2012). This might explain why evidence of increasing species numbers through colonisation events, so far, outweighs observations of species declines. Alternatively, however, this imbalance may also reflect the scarcity of data from old enough permanent plots with information on species’ abundances and/or their distribution across their entire vertical ranges.

A study comparing vegetation relevés dating back at least 45 years with recent surveys across the Eastern Alps showed that trailing edges are shifting at least as fast as leading edges and that both are ascending faster the lower they are situated (Rumpf et al. 2018). Given the conical shape of mountain summits, this could lead to a rapid narrowing of species ranges (Bertuzzo et al. 2016). Changes in the abundance of species even showed stronger signals compared to range shifts (Rumpf et al. 2018). Indeed, shifting abundances, such as in-filling or declines of resident populations, should be more immediate responses than actual shifts of their distribution ranges, given the high stochasticity involved in dispersal and recruitment of plant species (Giménez-Benavides et al. 2018) and the commonly rather long time until populations of perennial alpine species will have disappeared completely.

High-elevation plant assemblages above the closed grassland of the alpine zone should be especially useful for elucidating species-specific climate change effects, because they are less affected by biotic interactions and human land use, and species are highly adapted to low-temperature conditions. Data from the largest high-alpine to nival permanent plot site in the Alps (Schrankogel in the central Tyrolean Alps), comprising several hundred 1 m² permanent plots, provided one of the first evidence of declining species covers already a decade after its setup in 1994 (Pauli et al. 2007). A repeated survey in 2014 showed thermophilisation effects of the same magnitude as the European average (Gottfried et al. 2015), which significantly accelerated in the recent decade (Lamprecht et al. 2018). Although this shift was accompanied by a net increase in species richness, the gain in species numbers slowed down due to species disappearances from the permanent plots, which were almost exclusively observed in the recent decade (Lamprecht et al. 2018).

In the light of the observed alteration of community composition and shifting balances of species gains and losses, we here focus on responses on the species level, i.e. we evaluate whether species adapted to high-elevation climates (subnival–nival species) respond consistently differently from species with lower distribution optima (alpine–subnival species). The focus on the level of individual species should enable to discern if species of similar vertical distribution show consistent response patterns and to contribute to a vulnerability assessment of high mountain plant species in the context of future conservation strategies.

Specifically, we ask:

(i) Do the dynamics of colonisation and disappearance events reflect homogenous tendencies within each species group (i.e. predominantly alpine–subnival species and subnival–nival species)?
(ii) Do cover increases of alpine–subnival species and cover decreases of subnival–nival species constitute to ongoing trends?
(iii) Do subnival–nival species decrease more pronouncedly in warmer plots and less in colder plots and vice versa for alpine–subnival species and therefore indicate gains at leading edges and losses at trailing edges?

Methods

The study site Schrankogel (3497 m; Stubaier Alpen, Tyrol, Austria) is located in the eastern central Alps within the protected area “Ruhegebiet Stubaier Alpen” (IUCN category IV). It is part of the Long-Term Socio-economic and Ecosystem Research (LTSER) platform Tyrolean Alps (Mirtl et al. 2015) and the Global Observation Research Initiative in Alpine Environments (GLORIA, http://www.gloria.ac.at). The bedrock is composed of siliceous material, mostly amphibolite and gneiss (Hammer et al. 1929). Annual precipitation sum at the closest nival observatory (Sonnbliek 3109 msl, 200 km east of Schrankogel) ranged between 1400 and 2300 mm in the period 1991–2014. Mean monthly air temperature of June, July and August at Brunnenkogel (3440 msl, located 30 km southwest of Schrankogel) varied roughly between −2.9 and 3.9 °C between 2004 and 2014 (Zentralanstalt für Meteorologie und Geodynamik, http://www.zamg.ac.at).

Vegetation sampling and dataset

With the intention of detecting climate-driven vegetation changes, around 1000 1 m² permanent plots were established along the southwest to east facing slope system of Schrankogel in 1994 (Lamprecht et al. 2018). Plots were arranged in transects which were grouped in four spatially divided blocks (Fig. S1). Field sampling comprised the visual estimation of the percentage cover of surface types (solid rock, scree, bare ground and vegetation) and of each
vascular plant species present in a permanent plot, where a cover of 1% refers to 1 dm². Resurveys of the permanent plots were conducted in 2004 (362) and 2014 (661 plots). Plots with high disturbance due to rockfall were excluded, leaving 355 plots in 2004 and 654 in 2014. Two datasets were compiled for further analysis: (1) A dataset comprising 654 permanent plots for changes across a time span of 20 years (1994 to 2014; dataset-2s), and (2) a smaller subset of 355 permanent plots, where data available from all three surveys (1994, 2004 and 2014; dataset-3s) allowed for the comparison among the two decades. Species names follow Fischer et al. (2008) except for Senecio incanus subsp. carniiolicus where we used Senecio carniiolicus agg. (Flatscher et al. 2015).

Statistical analyses
All statistical analyses were performed using the statistical software R version 3.5.0 (R Core Team 2018) and figures were created with ggplot2 (Wickham 2016). Generalised linear mixed effects models (GLMMs) were fitted to analyse changes in the number of occupied plots (presence/absence) and cover across the surveys in both datasets and colonisations and disappearances in dataset-3s in the two decades for each species. To reflect the spatial structure of the dataset, plot nested in transect nested in block was included as random intercept term in all models. Only species present in at least 30 plots and with at least ten colonisations or disappearances events were analysed individually. Hypothesis testing of all models was conducted by a simultaneous inference procedure implemented in function glht from the multcomp package (Hothorn et al. 2008). Model diagnostic graphs were checked visually for outliers, homogeneity of variance and independence of residuals. Outliers were subsequently removed. The annual Euphrasia minima was excluded from analysis, because it shows high inter-annual fluctuations both in occurrence and abundance (Table S1), which may reflect shorter-term weather conditions over one or two seasons rather than longer-term climatic changes (Lampecht et al. 2018).

To analyse differences in the number of occupied plots (presence/absence) between the surveys and differences in colonisations and disappearances, the binary response variable in year and presence in year+10 of a given species was used as fixed effect. A colonisation event is defined as when a species was present in a given permanent plot in year, and absent in year+10. Only plots which could potentially be colonised (i.e. where a species was not present in year), or from which a species could potentially disappear (i.e. where a species was present in year), respectively, were used. For Gnaphalium supinum and Sagina saginoides with no disappearance events in one decade, a negative binomial distribution was assumed, as the binomial GLMM did not converge due to a singular fit.

To analyse differences in species cover, all plots with a species present in at least one survey year were considered. Absent species were assigned a cover value of zero. As both datasets were heteroscedastic and asymmetric, we used GLMMs (function glmmTMB; Brooks et al. 2017) with a standard beta distribution (Cribari-Neto and Zeileis 2010) and year as fixed effect. Percentage cover of each species ($y$) within an interval of zero and one, where one represented the maximal possible value of 100%, was subsequently compressed to bound data away from zeros and ones. This was conducted according to Smithson and Verkuilen (2006) by

$$y' = \frac{(y(N-1) + 0.5)}{N},$$

where $N$ is the sample size. In dataset-2s, the assumption of independence in the residuals was violated in the case of Arenaria ciliata, Minuartia sedoides and Poa alpina and a negative binomial distribution was chosen instead.

Altitudinal ranks (ARs) are classifications of species according to their distributions along an altitudinal gradient ranging from subnival–nival (AR = 1) to subalpine–alpine (AR = 4). A community-weighted thermic indicator (TI) for each plot and survey year was calculated based on each species’ AR classification and weighted by its relative cover:

$$TI = \left(\frac{\sum AR(\text{species}_i) \times \text{cover}(\text{species}_i)}{\sum \text{cover}(\text{species}_i)}\right).$$

The TI of the permanent plots on Schrankogel was shown to be highly correlated with soil temperature (Lampecht et al. 2018) and was previously used as an indicator of temperature conditions (e.g. Gottfried et al. 2012).

To show changes in cover sum of AR species groups and of individual species across a temperature gradient between 1994 and 2014, the TI of the baseline year 1994 (TI$$_{94}$$) of each permanent plot in dataset-2s was used as a proxy for thermal conditions where TI$$_{94}$$ = 1 refers to subnival–nival and TI$$_{94}$$ = 3 to alpine conditions. Differences in cover between 1994 and 2014 across the TI$$_{94}$$ gradient for each AR were analysed using GLMMs assuming a beta distribution. Cover was used as response, the interaction of TI$$_{94}$$ and year as fixed effect and species as second random effect. Function ggpredict was used to plot model predictions (Lüdecke 2018).
Results

In dataset-2s (654 plots) and dataset-3s (355 plots), 72 and 63 vascular plant species were present, respectively, during the study period (Table S1). Eighteen species were recorded only in 2014 and two species only in 1994.

Changes in the number of occupied plots

The number of occupied plots increased for most of the species between 1994 and 2014 (dataset-2s). Thirty out of 40 modelled species increased significantly, including 1 AR1 ($P < 0.0001$), 15 AR2 ($P < 0.02$), 11 AR3 ($P < 0.01$) and 3 AR4 species ($P < 0.0001$; GLMMs, Table 1, Tables S1, S2). The number of occupied plots decreased only in the AR1 species Poa laxa ($P < 0.001$). Five out of nine snowbed species, associated with AR2 and AR3, showed an increasing tendency ($P < 0.0001$). Six AR3 and 12 AR4 species, respectively, were found for the first time in the plots in 2014. Significant changes in the number of occupied plots were increases in both decades for almost all AR2 and AR3 species, whereas AR1 species showed increases only in the first and decreases in the second decade (dataset-3s; Table S3).

Changes in colonisations and disappearances (dataset-3s)

Colonisation rates increased significantly for Festuca intercedens ($P = 0.001$; AR2) and Sibbaldia procumbens ($P = 0.001$; AR3) between 1994–2004 and 2004–2014 (Table S4). In contrast, Androsace alpina and Ranunculus glacialis ($P < 0.03$; AR1), as well as Gla&lumum supinum, Sagina saginoides and Sedum alpestre ($P < 0.03$; AR3) showed significantly fewer colonisation events in the period 2004–2014. In the second decade, significantly more disappearances were recorded in four AR1 ($P < 0.01$), five AR2 ($P < 0.01$) and six AR3 species ($P < 0.03$; Table S5).

Changes in species cover

The cumulative cover of 13 species, including all 6 AR1 species ($P < 0.0001$), 3 AR2 ($P < 0.01$) and 4 AR3 species ($P < 0.02$) decreased significantly between 1994 and 2014 (dataset-2s; GLMMs; Table 1, Table S6). In contrast, none of the AR4 species decreased significantly. A significant increase in cover was observed in 16 species including 10 AR2 ($P < 0.03$), 4 AR3 ($P < 0.0001$) and 2 AR4 species ($P < 0.0001$). Six snowbed species increased their cover significantly, only Sedum alpestre declined ($P < 0.0001$). Overall, Cerastium uniflorum, Poa laxa, Saxifraga bryoides (AR1) and Carex curvula (AR3) showed the strongest decrease and Pedicularis aspleniifolia, Silene exscapa and Veronica alpina (AR2) the strongest increase in total cover during the study period ($P < 0.0001$).

All AR1 species declined in both decades ($P < 0.0001$), except Saxifraga oppositifolia with a significant decrease only in the period 2004–2014 ($P = 0.001$; dataset-3s, GLMMs, Fig. 1a, d; Table S7). Two AR2 species (Pedicularis aspleniifolia and Silene exscapa) increased in both decades ($P < 0.03$), and three (Festuca intercedens, Saxifraga exarata and Trisetum spicatum) in only one decade ($P < 0.04$; Fig. 1b, e; Table S7). In contrast, Gentiana bavarica decreased in both decades and Primula glutinosa only in the second decade ($P < 0.04$). The graminoid AR3 species Carex curvula and Poa alpina declined in one of the decades ($P < 0.0001$; Fig. 1c, f, Table S7). The snowbed species Veronica alpina and Sibbaldia procumbens increased in both decades ($P < 0.04$), while Sedum alpestre decreased in both decades ($P < 0.01$), and Sagina saginoides increased in cover between 1994 and 2004 and decreased between 2004 and 2014 ($P < 0.0001$; Fig. 1b, c, e, f; Table S7).

Species cover changes across a community-weighted thermic indicator gradient

Cover sums of individual species (Fig. S2) and of AR species groups (Fig. 2) revealed considerable differences when comparing the patterns of 1994 and 2014 along the TI gradient of the baseline year (TI94; Fig. 2; Fig. S2; Table S8). AR1 species had decreased considerably in cover over the entire TI94 gradient, which was slightly stronger in the warmer (alpine) plots ($P = 0.001$; Fig. 2e, Fig. S2; Table S8). AR1 species had decreased considerably in cover over the entire TI94 gradient, which was slightly stronger in the warmer (alpine) plots ($P = 0.001$; Fig. 2e, Fig. S2; Table S8). AR1 species had decreased considerably in cover over the entire TI94 gradient, which was slightly stronger in the warmer (alpine) plots ($P = 0.001$; Fig. 2e, Fig. S2; Table S8). AR1 species had decreased considerably in cover over the entire TI94 gradient, which was slightly stronger in the warmer (alpine) plots ($P = 0.001$; Fig. 2e, Fig. S2; Table S8). AR1 species had decreased considerably in cover over the entire TI94 gradient, which was slightly stronger in the warmer (alpine) plots ($P = 0.001$; Fig. 2e, Fig. S2; Table S8).

Discussion

Data from permanent plots distributed across the alpine–nival ecotone on Schrankogel provided an early signal of climate change-driven plant species declines, already 10 years after the baseline was set in 1994 (Pauli et al. 2007). After adding the data from 2014, another decade later, the previously observed cover declines could be confirmed, along with a continued increase in species richness, although
Table 1 Vascular plant species per altitudinal rank (AR) and their occurrences in 654 permanent plots across the alpine–nival ecotone on Schrankogel in 1994 and 2014 (dataset-2 s)

| Altitudinal rank | Species                     | Occupied plots | Colonisation/disappearance | Cover |
|------------------|-----------------------------|----------------|---------------------------|-------|
|                  |                             | 1994/2014      | 1994–2014                 |       |
|                  |                             | N              | P value                   | N     |
|                  |                             | 1994/2014      | 1994–2014                 |       |
|                  | Androsace alpina           | 247/228        | ↘                          | 51/70 |
|                  | Cerastium uniflorum        | 440/444        | ns                        | 51/47 |
|                  | Poa laxa                   | 614/581        | ↓↓↓                       | 15/48 |
|                  | Ranunculus glacialis       | 478/479        | ns                        | 54/53 |
|                  | Saxifraga bryoidea         | 540/590        | ↑↑↑                       | 61/11 |
|                  | Saxifraga oppositifolia    | 66/68          | ns                        | 12/10 |
|                  | Arenaria ciliata           | 32/37          | /                         | 7/2   |
|                  | Cardamine resedifolia      | 17/63          | ↑↑↑                       | 50/4  |
|                  | Draba fladnizensis         | 41/37          | ns                        | 13/17 |
|                  | Erigeron uniflorus         | 192/317        | ↑↑↑                       | 133/8 |
|                  | Festuca intercedens        | 12/218         | ↑↑↑                       | 107/13|
|                  | Gentiana bavarica var.     | 298/335        | ↑↑↑                       | 56/19 |
|                  | Leucanthemopsis alpina     | 504/577        | ↑↑↑                       | 81/8  |
|                  | Luzula spicata             | 445/523        | ↑↑↑                       | 101/23|
|                  | Oreochloa disticha         | 210/277        | ↑↑↑                       | 81/14 |
|                  | Pedicularis asplenifolia   | 32/92          | ↑↑↑                       | 63/3  |
|                  | Primula glutinosa          | 281/306        | ↑↑↑                       | 50/25 |
|                  | Saxifraga androsacea       | 17/4           | ↑↑↑                       | 34/10 |
|                  | Saxifraga exarata s.str.   | 122/193        | ↑↑↑                       | 93/22 |
|                  | Saxifraga seguieri         | 16/26          | ↑↑↑                       | 19/9  |
|                  | Silene exscapa             | 382/478        | ↑↑↑                       | 108/12|
|                  | Trisetum spicatum          | 27/79          | ↑↑↑                       | 57/5  |
|                  | Veronica alpina            | 113/235        | ↑↑↑                       | 122/0 |
|                  | Carex curvula              | 109/122        | ↑                          | 15/2  |
|                  | Cerastium cerastoides      | 18/21          | ns                        | 16/13 |
|                  | Gnaphalium supinum         | 69/227         | ↑↑↑                       | 161/3 |
|                  | Minuartia gerardii         | 75/99          | ↑↑                        | 41/17 |
|                  | Minuartia sedoides         | 368/456        | ↑↑↑                       | 104/16|
|                  | Phyteuma hemisphaericum    | 47/59          | ↑                          | 15/3  |
|                  | Poa alpina                 | 176/244        | ↑↑↑                       | 90/22 |
|                  | Sagina saginoides          | 40/117         | ↑↑↑                       | 93/10 |
|                  | Sedum alpestrum            | 191/241        | ↑↑↑                       | 71/21 |
|                  | Senecio carnolicus agg.    | 20/34          | ↑↑↑                       | 16/2  |
|                  | Sibbaldia procumbens       | 12/52          | ↑↑↑                       | 40/0  |
|                  | Veronica bellidioidea      | 25/55          | ↑↑                        | 34/4  |
|                  | Avenula versicolor         | 18/45          | ↑↑↑                       | 29/2  |
|                  | Potentilla aurea           | 0/31           | ↑↑↑                       | 31/0  |

AR denotes a species’ distribution range along the elevation gradient (after Gottfried et al. 2012). Shown are vascular plant species with significant differences either in the number of occupied plots or cover. P values were derived from generalised linear mixed effects model with the number of occupied plots or cover as response, year or decade as fixed effect and plot nested in transect nested in block as random effect. For further details and all study species see Tab S1-S2, S6.

NA, model not available; ns, not significant; ↑, increase; ↓, decrease; /\, P = 0.05–0.1; ↑↓, P = 0.01–0.05; ↑↑/↓↓, P = 0.01–0.001; ↑↑↑/↓↓↓, P < 0.001; AR1, subnival–nival; AR2, alpine–subnival; AR3, alpine; AR4, subalpine–alpine; sn, refers to snowbed species.

Psuedo-R²: 0.67
less pronounced in the second decade, and a progressing transformation of the community composition towards more warmth-demanding and drought-tolerant species (Lamprecht et al. 2018). Here, we show that these changes were strongly driven by a continued decrease in cover of all cryophilic AR1 species. The resulting gaps were only partly filled by species from lower elevations (mainly AR2 species). In addition, AR1 species showed declining numbers of successful colonisations and growing numbers of disappearances from the plots.

**Trailing-edge contraction of cryophilic species and leading-edge expansion of lower-elevation species**

The majority of species have expanded their distribution over the alpine–nival permanent plots on Schrankogel during the 20 years of observation (Table 1, Tables S1–S5), corroborating recently found increases in species richness in other parts of the Alps (Erschbamer et al. 2011; Wipf et al. 2013) and on more than 300 mountain summits distributed across Europe (Grytnes et al. 2014; Pauli et al. 2012; Steinbauer et al. 2018).

Even though the high-elevation species group (AR1) showed both colonisations and disappearances (Table 1, Tables S1, S4, S5), colonisations became rarer and disappearances more frequent in the second decade. Such a decrease in the gain/loss ratio signals a trailing-edge contraction (i.e. trailing edge moving closer to the leading edge; Lamprecht et al. 2018). Propagation capabilities of at least some AR1 species, however, should be sufficient for reaching new habitats. Tackenberg and Stöcklin (2008) reported that seeds of *Saxifraga bryoides* can be transported more than 1000 m by wind. At the same time, observations of
colonisation events are fairly unlikely, as most AR1 species already occupy a large number of plots, rendering the interpretation of decreasing colonisation events difficult (e.g. *Cerastium uniflorum*, *Poa laxa*, *Ranunculus glacialis* and *Saxifraga bryoides* are present in more than two-thirds of all plots; Table 1, Table S1).

Most of the AR2 species show a clear prevalence of colonisations over disappearances (Table 1, Tables S1, S4, S5), suggesting a leading-edge expansion of this species group, similar to previous observations of elevational and latitudinal range shifts (Carilla et al. 2018; Parmesan and Yohe 2003; Rumpf et al. 2018). Among the common AR2 species, *Silene exscapa* exhibited a moderate but steady increase and hardly any losses, whereas others like *Festuca intercedens* showed contrasting changes with both numbers of colonisations and disappearances significantly increasing from the first to the second decade (Tables S1, S4, S5). Such varied fluctuations presumably reflect different ratios of successful/failed establishments, rather than trends in range expansion or contraction. Despite overall warming, late frost...
events or cold spells during summer continue to occur and can affect temperature-sensitive seedlings and young plants (Ladinig et al. 2013), which may have contributed to the observed variation in species occurrences.

Furthermore, 18 of the colonising species were new, i.e. not observed previously in any of the plots, whereas only 2 disappeared from the single plot they had previously occupied (Table S1). All newcomers were alpine or species from lower elevations (AR3, AR4), having shifted their upper ranges to the alpine–nival ecotone during two decades (1994–2014), most likely driven by strongly rising temperatures within this period (Chen et al. 2011; Marty and Meister 2012).

Generally, all common AR3 species show more colonisation than disappearance events, however, with some fluctuations among decades, e.g. for the short-lived Sagina saginoides, which exhibits annual behaviour and plentiful seed production (Tables S1, S5, S6; Cannone et al. 2008). The same was true within the AR4 group, which showed a strong increase in the number of occupied plots, although this group is so far rather negligible concerning the total number of plots.

Regarding research question i, we cannot confirm a consistent response pattern within ARs. While an overall increase of alpine–subnival (AR2) and lower elevational species could be detected, some species reacted in other ways. In contrast, although a decline of subnival–nival (AR1) species is visible most notably in the second decade, the overall signal obtained by presence/absence data is weak.

### The dieback of the cryophiles

In contrast to presence/absence data, almost all high-elevation specialist species (AR1) showed a clear signal of cover reduction. This decrease in abundance was already found 10 years after the baseline survey (Pauli et al. 2007) and remained unbroken during the second decade across all AR1 species (Fig. 1a, Table 1, Tables S1, S6, S7). This negative abundance change of resident species was to be expected as a first response to climate warming, as it reflects changes in growth performance. Range shifts, in contrast, do not only depend on climatic factors but also involve uncertainties of successful establishment. Evidence of abundance declines in alpine plants is scarce in the literature compared to the ample evidence of changing species numbers, as suitable long-term data series are lacking.

The few studies involving abundance records, indeed, found significant decreases of cold-adapted species: Lesica (2014) reported that species restricted to high elevations declined more than species with broader elevation amplitudes in the Montana Rocky Mountains between 1988 and 2011. In the alpine zone of the central Appenines, a reversion study found decreasing abundances of cryophilic species after 42 years (Evangelista et al. 2016). A comparison of old plots (before 1970) with resurveys at nearby locations with similar habitat conditions showed that changes in abundance were stronger than shifts of lower and upper range margins, with above-average declines found for the high-elevation species (Rumpf et al. 2018).

Given that all AR1 species are perennial plants, the compelling evidence of their cover decrease suggests a response to increasingly unsuitable climate at their present habitats, rather than responses to short-term weather events. While several studies proposed an extinction debt associated with the persistence of high-elevation species, which delays species-specific responses to climate warming (Alexander et al. 2018; Dullinger et al. 2012) until their life spans are reached (Cotto et al. 2017), our findings indicate the onset of debt repayment through a progressing dieback at their lower range margins. Considering the second research question ii, a consistent decrease in cover of each AR1 species reflects a continued trend also in the second decade, whereas such a pattern is less homogenous for species advancing from lower elevations.

The continued cover declines of the high-elevation specialists may have been caused either by direct climatic factors or by competitive displacement through advancing species from lower down. The overall decrease of vegetation cover, however, suggests that the shrinkage of AR1 species was faster than the expansion of other species (Fig. 2; Lamprecht et al. 2018). The majority of permanent plots on Schrankogel are located on raw soils, rock and scree, where species were found to be less exposed to competitive pressure, compared to habitats with developed soils rich on organic material (Kulonen et al. 2018). In turn, direct negative effects of warmer temperatures on cryophilic species through respiratory losses of carbohydrates are probable, if their limited capability to adapt respiration rates to higher temperatures, as reported for Cerastium uniflorum and Ranunculus glacialis (Cooper 2004; Körner 2003; Larigauderie and Körner 1995), holds true for the majority of AR1 species. Another more recent study found that higher temperatures cause increasing drought stress with negative effects on annual growth for Saxifraga oppositifolia in Spitsbergen (Opala-Owczarek et al. 2018). On Schrankogel, an increasing transformation towards a community composition adapted to drier soil conditions was indicated for the 20-year study period (Lamprecht et al. 2018).

High topographic variation of adjacent microhabitats was suggested to buffer effects of rising temperatures on local species survival (Scherrer and Körner 2011). The observed continued decrease in cover of all AR1 species in a large number of permanent plots, however, does not confirm this hypothesis. Thus, referring to research question iii, cold-adapted AR1 species tend to decrease slightly more in warmer plots, while species of AR2 and AR3
showed higher cover increases in colder plots (Fig. 2). Although the latter increase could not keep pace with an overall decrease of AR1 species, some common advancing species, such as Silene exscapa (AR2), may have exerted competitive pressure on AR1 species. In the baseline year 1994, its total cover was well below that of the then most dominant species Saxifraga bryoides (AR1), but only 20 years later Silene exscapa was undisputedly the number one in terms of total cover (Fig. 1; Table 1, Tables S1, S6, S7). Several other AR2 species showed gains in cover, such as Festuca intercedens, Trisetum spicatum, P偶像us aspleniifolia, and Erigeron uniflorus, but they are far less abundant than Silene exscapa.

The pronounced expansion and/or filling of six out of nine species associated with snowbed habitats was surprising, since higher temperatures should lead to earlier snow melt and, thus, to a shrinkage of snowbed habitats (Fig. 1; Table 1, Tables S1, S6, S7). Alpine snowbed species and communities are thought to be highly vulnerable to climate change effects (Björk and Molau 2007). They have been found to be affected by competition through encroaching taller-growing species from neighbouring communities in the subalpine to lower alpine zone in the Swiss Alps (Matteodo et al. 2016) and showed rapid reduction in growth performance when transplanted to alpine ridge habitats in New Zealand (Lord et al. 2018). In turn, increases of snowbed species’ abundances were found in southern Norway in combination with increasing snow cover (Felde et al. 2012). A pan-European study, comparing historical and new alpine–subnival summit flora inventories, found an above-average increase in the number of snowbed species on the summits (Grytnes et al. 2014), where an enforced melting of ice and snow patches, which liberates new habitats for colonisation, was suggested as explanation for the advance of snowbed species. Given that many of their summits were situated at the alpine–nival ecotone, our observations on Schrankogel could likely be additional evidence supporting their hypothesis. Subnival and nival environments, formerly mostly providing habitats for AR1 species only, which are capable of dealing with both low-temperature conditions and short growing seasons (Gottfried et al. 2002), are increasingly suitable for the less cold-adapted snowbed species.

An ongoing decline in cover of two AR3 graminoids, Carex curvula and Poa alpina was unexpected as well (Fig. 1, Fig. S2, Table 1, Tables S1, S6, S7), as both are common elements of alpine grassland vegetation, which should have shifted their distributions higher up. A similar decline of Carex curvula was observed by Cannone et al. (2007) and Cannone and Pignatti (2014) in the Italian Alps, who suggested negative effects of increased disturbance through permafrost degradation. We cannot test this hypothesis, although we observed an increasing surface destabilisation on Schrankogel.

**Limitations of the study**

While we are confident that our results are representative for ongoing vegetation changes across the alpine–nival ecotone, a number of limitations might have biased the observed species-specific changes. Such are a non-random study design, with permanent plots organised in transects. These were not homogenously distributed, which might have caused over- or underrepresentation of certain habitat types and species, but we accounted for the spatial structure inherent in the dataset by using permanent plots as random term in the GLMMs. Influences of ungulate herbivory by Capra ibex and additionally by sheep and goats in the lowermost plots cannot be excluded, but grazing signs were minor and impacts would not cause a directional change of plant species. Interference with concurrently changing patterns of soil microorganisms, micro- and mesofauna might have an influence on plant performance, but requires further studies. Another source of error might arise from inter-annual species fluctuation in phenology, which we attempted to minimise by resurveys in the same month in the peak growing season. Finally, observer errors unavoidably occur when using visual cover estimations. A recent study on observer variability, which included data from the Schrankogel permanent plots, indicated that observer errors did not exceed changes over time in cover, species turnover and the TI for observation periods ≥ 10 years (Futschik et al. 2019).

**Conclusions**

The current study provides evidence of severe species-specific vegetation changes in permanent plots across the alpine–nival ecotone during the period 1994–2014 on Schrankogel. An overall increase in colonisations and a more pronounced increase in cover of most AR2 and lower elevational species in colder plots suggest a continued leading-edge expansion. The surprisingly prolific performance of most of the snowbed species may indicate the liberation of new microhabitats through an elongated snow-free period.

All subnival–nival AR1 species provide evidence of a rear-edge decline by showing the highest rates of disappearances combined with a consistent and strong decrease in cover, which was more pronounced in warmer plots. AR2 to AR4 species could not compensate these decreases, which points towards low levels of competition, but a continued maladaptation of high-elevation specialists to the current climate. Notably, this study revealed substantial differences between presence/absence and cover data. While, for example, only Poa laxa decreased in the number of occupied plots, all AR1 species declined consistently in cover. This underpins the importance of including species abundance data in studies analysing climate-driven vegetation changes.
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Author contributions HP, MW, AL and KS designed the study and were part of the recording team. KS, AL, PS and MW analysed the output data. HP managed the study. KS, AL and HP wrote the manuscript. All authors discussed the results and implications and commented on the manuscript at all stages.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This study does not involve research on human participants or animals.

Informed consent Informed consent was obtained from all individual participants included in the study.

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