

# Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps

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## Summary

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**Key words:** alpine–nival ecotone, climate change impact indicator, GLORIA, high mountain plants, long-term monitoring, species composition change, species richness, thermophilisation.

- High mountain ecosystems and their biota are governed by low-temperature conditions and thus can be used as indicators for climate warming impacts on natural ecosystems, provided that long-term data exist.
- We used data from the largest alpine to nival permanent plot site in the Alps, established in the frame of the *Global Observation Research Initiative in Alpine Environments* (GLORIA) on Schrankogel in the Tyrolean Alps, Austria, in 1994, and resurveyed in 2004 and 2014.
- Vascular plant species richness per plot increased over the entire period, albeit to a lesser extent in the second decade, because disappearance events increased markedly in the latter period. Although presence/absence data could only marginally explain range shift dynamics, changes in species cover and plant community composition indicate an accelerating transformation towards a more warmth-demanding and more drought-adapted vegetation, which is strongest at the lowest, least rugged subsite.
- Divergent responses of vertical distribution groups of species suggest that direct warming effects, rather than competitive displacement, are the primary causes of the observed patterns. The continued decrease in cryophilic species could imply that trailing edge dynamics proceed more rapidly than successful colonisation, which would favour a period of accelerated species declines.

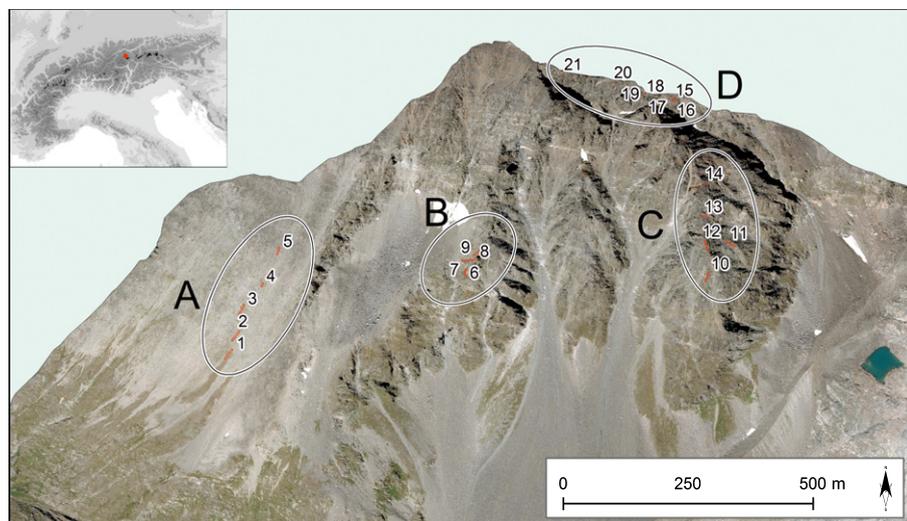
## Introduction

High mountain plants are adapted to low-temperature conditions (Körner & Larcher, 1988) and, apart from low latitudes, to a short growing season, which makes them sensitive to increasingly warmer climates. Alpine and subnival plants, however, may respond only little to short-term climatic oscillations, but rather to longer lasting climatic trends, because most species are persistent, slow growing and long lived; annual and short-lived species are rare above the treeline (Billings & Mooney, 1968; Körner, 2003; de Witte & Stöcklin, 2010). High mountain ecosystems, especially above the alpine grassland zone, are governed by climatic factors, whereas the importance of biotic factors, such as competition among species for light and nutrient resources and direct human impacts, for example through farming and livestock grazing, decreases with elevation. Therefore, changes in the occurrence of alpine and subnival plant species and in the composition of their assemblages are highly relevant as indicators of ecological impacts of climate change (Theurillat & Guisan, 2001; Grabherr *et al.*, 2010; Malanson *et al.*, 2011).

The last three decades were globally the warmest on record and, in the northern hemisphere, the period from 1983 to 2012

was probably the warmest of the last 1400 years (Hartmann *et al.*, 2013; Luterbacher *et al.*, 2013). Moreover, global climate warming tends to amplify in high-elevation areas, compared with lowland areas (Barry, 2008; Ohmura, 2012; Mountain Research Initiative EDW Working Group, 2015), with a *c.* 1.2 times faster rise in annual mean temperatures at high-elevation stations (> 500 m above sea level, asl) over the period 1961–2010 (Wang *et al.*, 2016). Across the European Alps, high-elevation stations show uniform warming trends of 0.8°C annual mean between 1981 and 2010, and 2.5°C mean from April to June, which is 3.5 times larger than the corresponding northern hemisphere temperature rise (Marty & Meister, 2012). Changes in precipitation show a larger regional and seasonal variability, especially in Europe (Kovats *et al.*, 2014). Nevertheless, increases in evaporation and atmospheric humidity, as well as reductions in snow amount and snowpack period, are corresponding consequences of climate warming (Jiménez Cisneros *et al.*, 2014). Although the spatial patterns of snow are determined by topography and the prevailing wind direction, the temporal patterns of snowmelt are directly linked to temperature change (Friedel, 1961; Kirkpatrick *et al.*, 2017), and snow cover duration in the Alps showed a declining trend during the last decades (Gottfried *et al.*, 2011; Cramer *et al.*, 2014). Future scenarios predict a continued shift from snow to rain in mountainous regions, which alone could

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**Fig. 1** Location of permanent plots on Mount Schrankogel. Plots are grouped in transects clustered into four topographic blocks: (A) uniformly shaped southwest slope, rich in scree; (B) rugged south-facing ridge; (C) rugged south-southeast-facing ridge; and (D) south-facing, high-elevation plots along the east ridge. Orthophotos (© Land Tirol) modified with ARC GIS 10.3. for Desktop, Esri Inc. Details of transects are shown in Supporting Information Fig. S1.

lead to a significant decrease in snow cover duration in central Europe (Steger *et al.*, 2013; Jiménez Cisneros *et al.*, 2014). This would result in an increase in the length of the growing seasons, and hence in a potential threat to high-elevation plant species through the opening of immigration pathways for competitors from lower elevations (Dullinger *et al.*, 2007; Steger *et al.*, 2013). Increased drought risk has already been detected in central Europe over the past century, with surface warming as the primary cause after the mid-1980s, and can be expected for the region of the Alps in the future (Dai *et al.*, 2004; Gobiet *et al.*, 2014). The climatically suitable area of alpine habitats is therefore successively shrinking. Depending on the climate change scenario, model projections suggest a loss of > 80% of habitats in some European mountains, including parts of the Alps, for up to 55% of the alpine species studied, until the end of the century (Engler *et al.*, 2011).

Habitat loss, however, may not be immediately accompanied by a rapid species decline, which could lag behind for several decades, because of the long-lived nature of most alpine plants (Dullinger *et al.*, 2012b). A topographically diverse habitat situation may further buffer against the loss of climatically suitable habitats (Scherrer & Körner, 2011; Opedal *et al.*, 2015). Upwardly advancing treelines, however, have been repeatedly observed (Kullman, 2002; Harsch *et al.*, 2009; Hagedorn *et al.*, 2014), as well as increasing numbers of vascular plant species at alpine to nival sites (Grabherr *et al.*, 1994, 2001; Bahn & Körner, 2003; Klanderud & Birks, 2003; Holzinger *et al.*, 2008; Vittoz *et al.*, 2008; Stöckli *et al.*, 2011; Pauli *et al.*, 2012; Wipf *et al.*, 2013; Steinbauer *et al.*, 2018). Among the colonising species, an over-representation of more warm-demanding (i.e. thermophilic) species was found on summits distributed across the alpine life zone from the Mediterranean to boreal Europe (i.e. thermophilisation; Gottfried *et al.*, 2012), which was primarily caused by an upward shift of plant species ranges (Pauli *et al.*, 2012).

In order to determine climate-driven changes in species distribution, an extensive setting of permanent plot transects was established in 1994 across the alpine–nival ecotone of

Schrankogel in the central Tyrolean Alps as part of the *Global Observation Research Initiative in Alpine Environments* (GLORIA, www.gloria.ac.at; Pauli *et al.*, 2015). This ecotone is the transition zone between closed alpine grassland and open subnival plant assemblages (Gottfried *et al.*, 1998; Pauli *et al.*, 1999). The elevation of the ecotone on Schrankogel was found to strongly coincide with that of the median summer snow duration (i.e. where the probability of snow cover is 50% during the period June to August) derived from data across the Alps (Gottfried *et al.*, 2011). Changes in species composition can be expected to be discernible earlier at the alpine–nival ecotone, where the upper range limits of the more thermophilic alpine grassland species and the lower margins of cold-adapted (i.e. cryophilic) subnival–nival species coincide (Gottfried *et al.*, 1999, 2011). The GLORIA master site Schrankogel is the largest permanent plot site close to the elevation limits of vascular plant life in the Alps, with four spatially separated subsites (blocks), representing elevations and different topographic complexity of the mountain's southerly oriented slope system (Fig. 1). Resurveys were undertaken in 2004 and 2014, thus spanning the period of amplified anthropogenic climate warming (Böhm *et al.*, 2001; Marty & Meister, 2012; Hartmann *et al.*, 2013).

After the first decade, an increase in species richness, resulting from colonisations of species into the plots, but hardly any disappearances from the plots, was observed. The novel aspect, however, was the evidence of decreasing abundance of all subnival–nival, i.e. outstandingly cold-adapted, species (Pauli *et al.*, 2007). Through the third survey in 2014, we assess whether the observed changes in species distribution patterns constitute ongoing trends in relation to recent climate warming by addressing the following four topics and inherent hypotheses. (1) Changes in vascular plant species diversity: (1a) species richness continues to increase, but (1b) the ratio of colonisations vs disappearances shifts towards the latter. (2) Changes in vascular plant cover: (2a) the total cover of vascular plants is increasing because (2b) the continued expansion of more thermophilic alpine and alpine–subnival pioneer species exceeds the ongoing decline of cryophilic high-elevation species. (3) Changes in community-weighted ecological indicators: the

composition of species and their abundances change directionally in relation to climate trends, resulting in (3a) a thermophilisation of plant communities (Gottfried *et al.*, 2012) and (3b) a more drought-tolerant species composition. (4) Topography and elevation: plots in rugged habitats and in high elevations show lower rates of change, because habitat complexity in rocky terrain as well as low-temperature conditions buffer against colonisation events and the expansion of established species.

## Materials and Methods

### Study area and design

The GLORIA master site Schrankogel (3497 m) is located in the Stubai Alps, Tyrol, Austria. The bedrock mainly consists of gneiss (Hammer *et al.*, 1929; Purtscheller, 1978); typical soil types are leptosols and cambisols (Hofmann *et al.*, 2016). Characteristic plant communities of the upper alpine zone are grassland with *Carex curvula* and *Oreochloa disticha* (Caricion curvulae) and subnival to nival plant assemblages on siliceous screes (Androsacion alpinae; Grabherr, 1993; Abrate, 1998; Dullinger, 1998). Schrankogel is part of the protected area 'Ruhegebiet Stubai Alpen', ranked in the International Union for Conservation of Nature (IUCN) category IV (UNEP-WCMC & IUCN, 2018), and of the Long-Term Socio-economic and Ecosystem Research (LTSER) platform Tyrolean Alps (Mirtl *et al.*, 2015).

In 1994, c. 1000 plots of  $1 \times 1 \text{ m}^2$  were established as permanent plots across and above the alpine–nival ecotone (2911–3457 m), arranged in transects in order to cover the main habitat types of the alpine–nival ecotone of Schrankogel's southwest- to southeast-facing slope system (Gottfried *et al.*, 1998). Transects were grouped into four blocks (A, B, C and D), where (A) encompasses the uniformly shaped southwest slope which extends uninterruptedly from the alpine grassland belt to the alpine–nival ecotone, (B) encompasses the rugged south-facing middle, (C) encompasses the rugged south–southeast-facing eastern part within the ecotone and (D) encompasses the south-facing, high-elevation outposts in the nival zone along the east ridge (Fig. 1, Supporting Information Fig. S1; Table S1). The steep, mostly unvegetated, northern face and gullies and cliffs on the southern side had to be excluded, because of inaccessibility, unstable material and a high rockfall frequency.

In 2004, a representative subset of 362 plots was resurveyed in order to include all predominant plant communities (Pauli *et al.*, 2007) distinguished by Pauli *et al.* (1999) and, in 2014, a larger subset of 661 plots was reinvestigated.

In each of the three survey campaigns, all vascular plant species were recorded and the percentage cover of each vascular plant species was estimated visually in each plot. At both resurvey campaigns, only data recorded without the aid of previous survey data were used.

### Data analyses

After removing plots in which disturbances (through rockfalls and substrate movements) had occurred, the dataset involving all

three surveys (1994–2004–2014; Table S1) included 355 plots. A second dataset was constructed, only involving the first and third surveys (1994–2014), with a total of 654 plots (results are shown only in Supporting Information). Two annual species (*Euphrasia minima* and *Gentianella tenella*; Table S2) were removed from the datasets because of high inter-annual fluctuation, which can strongly influence colonisation and disappearance rates.

Analyses were carried out using the entire dataset and also separately for each topographic block (A, B, C and D). As a result of the spatial arrangement of plots in transects, clustered in blocks, and the temporal dimension of the data (resurveys of the same plots at decadal intervals), all statistical models included a random intercept term with the structure: plot nested in transect (except for block D, where transects consisted of too few plots; Table S1), nested in block (the latter only for analyses over the entire study area).

All statistical analyses were performed in R v.3.1.3 (R Core Team, 2015). The significance of the effects of the predictor variables of all models was tested with the *lsmeans* function; for pairwise comparison, the *cld* function was used (package *LSMEANS*; Tukey's honestly significant difference (HSD); Lenth, 2016). Table 1 gives an overview of the statistical models employed and the hypotheses they address.

### Changes in vascular plant species diversity

For the response variables species richness, colonisation and disappearance, here treated as counts, the appropriate distribution for the models was determined by building two generalised mixed-effects models (GLMMs), one assuming a Poisson distribution and one assuming a negative binomial distribution, which better fits many zero values (zero inflation; *glmer* and *glmer.nb* from *LME4* package, respectively; Bates *et al.*, 2015). A likelihood ratio test between these two models was performed (ANOVA function from *STATS* package) to determine the appropriate model in each case ( $P < 0.05$ ). For both models, over-dispersion was tested with the *overdisp.glmer* function from the *RVAIDEMEMOIRE* package (Hervé, 2016). In cases of over-dispersion, the function *glmmPQL* from the *MASS* package (Venables & Ripley, 2002) was used, which employs penalised quasi-likelihood and takes an over-dispersion parameter into account.

Species richness was calculated as the number of species per plot and survey, and was analysed as Poisson distributed counts with year (i.e. survey) as predictor. Species richness data within the blocks were over-dispersed (over-dispersion parameter of the *glmer* model  $> 1.2$ ), and therefore the function *glmmPQL* was used.

Colonisations were defined as the number of species per plot present at the time of the resurvey, which were absent in the respective plot at the previous survey, and disappearances were defined as the number of species per plot absent at the time of the resurvey, which were present at the previous survey. These counts were analysed with GLMMs with a negative binomial distribution, with type (colonisation or disappearance) and decade as fixed effects.

**Table 1** Overview of the statistical models employed

| Hypotheses | Response  | Fixed effects                     | Random effects               | Model type (function) | Error distribution | Results shown in                                |
|------------|---|-----------------------------------|------------------------------|-----------------------|--------------------|---|
| 1, 4       | Species richness per plot                               | Year                              | Block/transect/plot          | GLMM (glmmPQL)        | Poisson            | Fig. 2(a); Supporting Information Tables S4, S5 |
| 1          | Species richness per plot and AR                        | Year × AR                         | Block/transect/plot          | GLMM (glmmPQL)        | Negative binomial  | Fig. S3(b); Tables S6, S7                       |
| 1, 4       | Number of colonisation or disappearance events per plot | Decade × Type (Colon. or Disapp.) | Block/transect/plot          | GLMM (glmer)          | Negative binomial  | Fig. 2(b); Tables S8, S9                        |
| 1          | Colonisation success per AR                             | Decade × AR                       | Block/transect/plot, Species | GLMM (glmmadmb)       | Binomial           | Fig. S4(a); Tables S10, S11                     |
| 1          | Disappearance success per AR                            | Decade × AR                       | Block/transect/plot, Species | GLMM (glmmadmb)       | Binomial           | Fig. S4(b); Tables S10, S11                     |
| 2, 4       | Cover sum per plot                                      | Year                              | Block/transect/plot          | LMM (lmer)            | Gaussian           | Fig. 3; Tables S12, S13                         |
| 2          | Cover sum per species and AR                            | Year × AR                         | Species                      | LMM (lmer)            | Gaussian           | Fig. S5(b); Tables S14, S15                     |
| 3, 4       | Thermic indicator per plot                              | Year                              | Block/transect/plot          | LMM (lmer)            | Gaussian           | Fig. 4(a); Tables S16–S18                       |
| 3, 4       | Soil moisture indicator per plot                        | Year                              | Block/transect/plot          | LMM (lmer)            | Gaussian           | Fig. 4(b); Tables S19–S21                       |
| 4          | Topographic differences among blocks                    | Block                             | Transect                     | LMM (lmer)            | Gaussian           | Figs S7, S8; Table S22                          |

Given are the hypotheses addressed, model type (GLMM, generalised linear mixed-effects model; LMM, linear mixed-effects model) and corresponding R function used, error distribution, response variables, fixed and random effects, and figures and tables in which the results are shown. AR, altitudinal rank.

As a proxy for the thermal preferences of species, species with different distributions along the elevation gradient were assigned to species groups of different altitudinal ranks (ARs) after Gottfried *et al.* (2012) (Table S3). To determine which AR species group drives the observed changes, species richness and relative colonisation and disappearance events (the proportion of the number of plots not yet occupied in the case of colonisation, and of previously occupied plots in the case of disappearance) were calculated for each AR separately, and the above analyses on species richness were repeated with AR included in the fixed effects. Colonisation and disappearance events were treated as Bernoulli trials (1, successful colonisation of an empty plot or disappearance from an occupied plot of a given species; 0, plot not colonised or species not disappeared from a plot) and modelled as binomial GLMMs (function `glmmadmb` in package `GLMMADMB`; Fournier *et al.*, 2012).

### Changes in vascular plant cover

Changes in cover sums (i.e. cumulative cover of all species present in a plot) were modelled using linear mixed-effect models (LMMs, function `lmer` of package `LME4`) with survey year as the only fixed effect, and, additionally, with AR as another fixed effect.

### Changes in community-weighted ecological indicators

To investigate directional changes in plant species composition, the following ecological indicator values of the species occurring in a plot were used: AR (Table S3) and the soil moisture indicator values in Landolt *et al.* (2010), which were available for all species.

All other available indicators by Landolt *et al.* (2010) were not present in a sufficient dispersion along their gradients to enable a reasonable statistical analysis (e.g. temperature T), did not indicate any significant effects (e.g. continentality K, nutrients N) or were not meaningful in the context of this study (e.g. soil reaction R). Each rank was given a number which represents the position along an environmental gradient; for AR: 1 = subnival–nival, 2 = alpine–subnival, 3 = alpine, 4 = (montane–)treeline–alpine species; for soil moisture: 1 = very dry to 4 = very moist. The thermic and soil moisture indicators were calculated after Gottfried *et al.* (2012) for each plot, and survey as an averaged composite score of the AR and the soil moisture indicator values, respectively, weighted by the cover of the occurring species:

$$\text{Indicator} = \frac{\left(\sum \text{rank}(\text{species}_i) \times \text{cover}(\text{species}_i)\right)}{\sum \text{cover}(\text{species}_i)}$$

The thermic indicator was significantly positively correlated with temperature sums derived from *in situ* soil temperature measurements (Fig. S2). Each indicator was analysed after tests for normal distribution with survey year as fixed effect with LMMs. To indicate any direction of changes in community-weighted ecological indicators between surveys, the effect size of the predictor year and its associated confidence interval were used as  $\Delta$  indicator:

$$\Delta \text{ indicator} = \text{Indicator}_{t+1} - \text{Indicator}_t$$

The correlation between  $\Delta$  thermic indicator and  $\Delta$  soil moisture indicator per plot was modelled using LMMs with plot

(nested in transect nested in block) and decades as random intercept terms.

## Topography and elevation

To assess the topographic similarity among the four blocks, non-metric multidimensional scaling (NMDS) was used (function METAMDS, R package VEGAN; Oksanen *et al.*, 2018). A matrix was built with rescaled parameters for each plot, that is, estimated top cover of surface types (rock, scree, bare soil and vegetation) and topographic parameters (altitude, aspect, slope and ruggedness) derived from a digital elevation model (© Land Tirol). Ruggedness was calculated as the standard deviation of elevation with a  $100 \times 100 \text{ m}^2$  raster per plot using ARCGIS 10.3. for Desktop, Esri Inc. Plotting was performed using the package GGPLOT (Wickham, 2009). To analyse differences among blocks, an LMM with the first NMDS axis as response, block as fixed effect and transect as random effect was fitted.

## Results

Changes in species richness, colonisation, disappearances and community-weighted ecological indicators showed equal trends in dataset 1994–2004–2014 (involving three surveys with 355 plots, see below) and 1994–2014 (involving only the first and third surveys with 654 plots). Therefore, only the former is reported here (Figs 2–4, S3–S8; Tables S4–S22) and the latter is provided in Supporting Information (Tables S23–S30).

### (1) Changes in vascular plant species diversity

**Species richness** The total number of species increased from 51 species in 1994 to 54 in 2004 and 61 in 2014.

The mean species number per plot increased from 10.84 species in 1994 to 12.61 in 2004 and 13.08 in 2014 (Fig. 2a; Table S4), and was significantly higher at the later surveys than at the preceding ones (GLMMs,  $P < 0.001$  in all cases; Table S5).

Within ARs, the total number of species was stable with six and 20 species in each survey at AR1 and AR2, respectively, whereas species numbers increased slightly in AR3 (18, 19 and 20 species in 1994, 2004 and 2014, respectively), and more than doubled in AR4 between 1994 and 2014 (six, eight and 13 species; Table S3). Species richness summed over all plots (Fig. S3a) and mean species numbers per plot (Fig. S3b) were highest in AR2, followed by AR1, and increased significantly only between 1994 and 2004 within AR2 and AR3 (GLMMs,  $P < 0.0001$ ; Tables S6, S7).

**Colonisations and disappearances** The mean number of colonisations decreased significantly from 2.08 species per plot between 1994 and 2004 to 1.76 between 2004 and 2014. The mean number of disappearances increased significantly from 0.31 species per plot in the first decade to 1.29 in the second decade (means calculated from raw data; effect sizes from GLMMs,  $P < 0.05$ ; Fig. 2b; Tables S8, S9). No species, however, disappeared

completely from the whole area. By contrast, four and seven species were recorded for the first time in 2004 and 2014, respectively (Fig. S3). These new species belonged exclusively to AR3 (one and two new species in 2004 and 2014, respectively) and AR4 (three and five species). Colonisation in relation to previously unoccupied plots was highest among AR1 species (Fig. S4a; Table S10), but decreased significantly from the first to the second decade (GLMMs,  $P = 0.01$ ; Table S11), whereas there was no change among AR2–4 species. Relative disappearance was fairly low (2–3%) in AR1–3 in the first decade, whereas AR4 species disappeared from almost a quarter of their formerly occupied plots (Fig. S4b; Table S10). In the second decade, however, relative disappearance increased sharply and significantly by factors of 3.23, 2.65 and 6.9 in species of AR1–3, respectively, whereas AR4 remained stable (GLMMs; Table S11).

Exotic species and woody plants did not occur in or colonise the permanent plots during the study period.

### (2) Changes in vascular plant cover

(2a) The mean cover sum of all vascular plant species per plot decreased significantly from  $24.33 \text{ dm}^2$  in 1994 to  $21.9 \text{ dm}^2$  and  $20.83 \text{ dm}^2$  in 2004 and 2014, respectively (LMMs,  $P < 0.05$ ; Fig. 3; Tables S12, S13).

(2b) Cover sums over all plots for each AR were initially highest in AR1 and AR2, followed by AR3 and AR4 (Fig. S5a). Over time, cover sums of AR1 showed a pronounced linear decrease, whereas those of AR2 increased. The mean cover sums per species were highest in AR1 in all 3 years, but decreased significantly over time, whereas there was no change in the other ARs (GLMMs; Fig. S5b; Tables S14, S15).

### (3) Changes in community-weighted ecological indicators

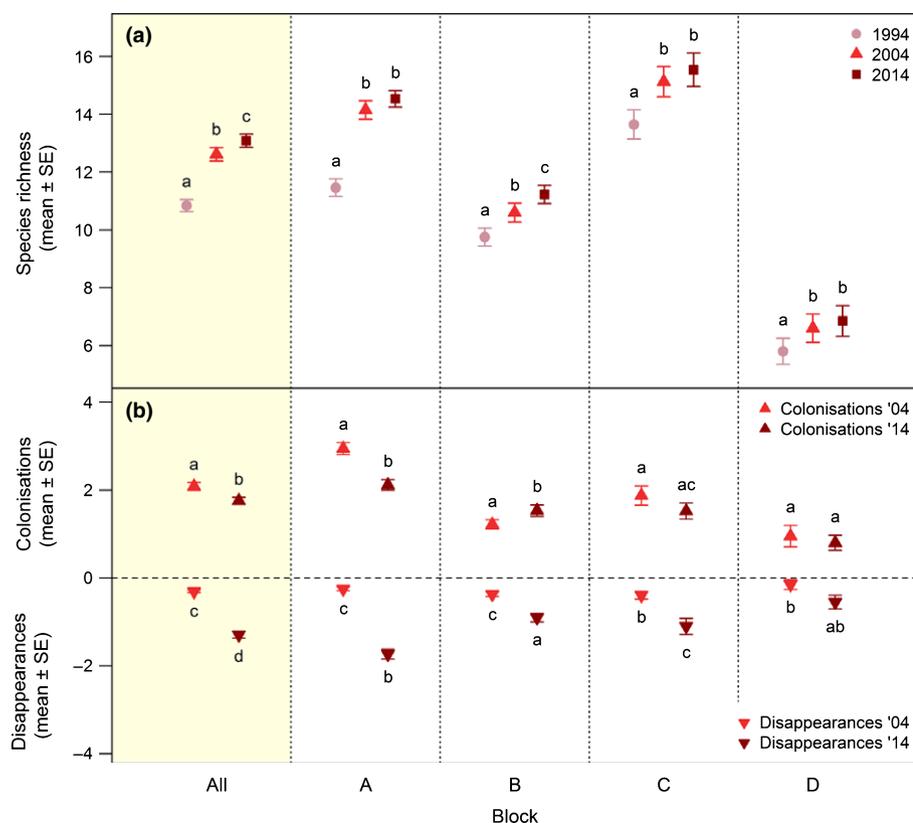
**Thermic indicator of plant communities** The thermic indicator increased significantly over successive surveys from 1.61 in 1994 to 1.67 in 2004 and 1.76 in 2014, with a  $\Delta$  thermic indicator of 0.06 in the first decade and 0.09 in the second decade (GLMMs,  $P < 0.001$ ; Fig. 4a; Tables S16–S18).

**Soil moisture indicator of plant communities** The soil moisture indicator decreased significantly over successive surveys from 2.95 in 1994 to 2.89 in 2004 and 2.79 in 2014, with a  $\Delta$  soil moisture indicator of  $-0.05$  for the first decade and  $-0.11$  for the second decade (GLMMs,  $P < 0.001$ ; Fig. 4b; Tables S19–S21).

ARs and the Landolt soil moisture indicator were not correlated at the species level (Spearman rank correlation,  $\rho = -0.196$ ,  $P = 0.134$ ). At the plot level, however,  $\Delta$  soil moisture indicator decreased significantly with increasing  $\Delta$  thermic indicator (LMM,  $P < 0.0001$ ; Fig. S6).

### (4) Topography and elevation

Plots in the lowest block A had, on average, the largest proportion of scree and vegetation cover, and the lowest proportion of



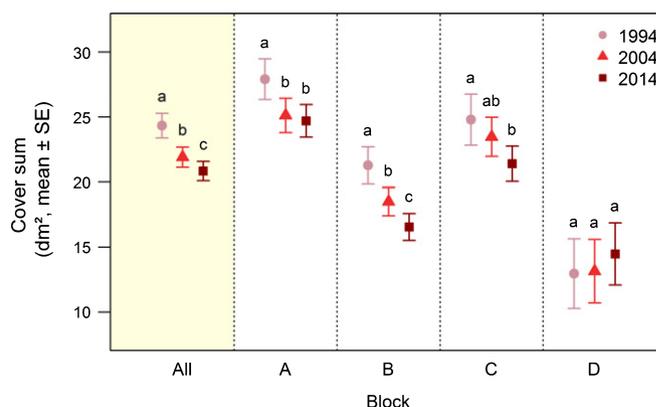
**Fig. 2** Changes in vascular plant species diversity on Mount Schrankogel. Mean  $\pm$  SE of raw data of (a) species richness (Supporting Information Table S4) and (b) numbers of colonising and disappearing species (Table S8) per plot on Mount Schrankogel in the survey years 1994, 2004 and 2014. Mean values over the entire study area (All, shaded) and for each block (A, B, C, D) are shown. For plot numbers per block, see Table S1. Different lowercase letters denote significant differences: (a) between the survey years within each block based on generalised mixed-effects models using penalised quasi-likelihood with a negative binomial distribution (Table S5); and (b) between the survey years and types (colonisations, disappearances) within each block based on generalised mixed-effects models with a negative binomial distribution (Table S9).

solid rock (Fig. S7). Further, they showed the lowest degree of ruggedness and steepness. The nival, that is, highest, block D was the most rugged and steepest block. The topographic parameters (first axis of NMDS; Fig. S8) of block A differed significantly from those of blocks B and D; block D differed significantly from all other blocks, whereas blocks B and C were not significantly different (Table S22).

Changes in species richness in individual blocks showed the same tendencies as in the entire dataset (Fig. 2a; Table S4), even though the increase in richness stagnated in all blocks, except in block B in the second decade (Table S5). The number of colonisations decreased significantly in block A as over the whole study area, whereas there was no significant change in blocks C and D, and, in block B, colonisations even increased in the second decade. The number of disappearances increased significantly in all blocks as in the entire dataset, except in block D, where no significant change was observed (Fig. 2b; Tables S8, S9).

Vascular plant cover decreased significantly over time in all blocks, except D, where no significant change in cover sums was observed. In block A, however, the decrease stopped in the second decade (Fig. 3; Tables S12, S13).

Changes in community-weighted ecological indicators per block did not fundamentally deviate from the results over all plots. A significant overall increase in the thermic indicator, however, was only reached in block B (Fig. 4a; Tables S16–S18), whereas a significant overall decrease in the soil moisture indicator was also found in blocks A and B (Fig. 4b; Tables S19–S21).

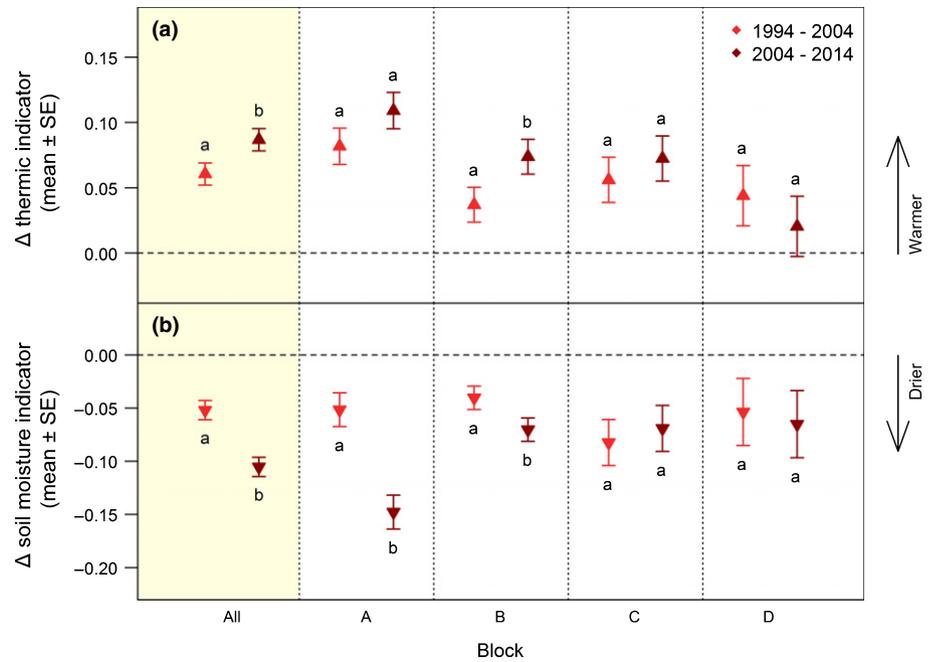


**Fig. 3** Changes in vegetation cover of vascular plants on Mount Schrankogel. Mean  $\pm$  SE of raw data of cover sum (Supporting Information Table S12) per plot on Mount Schrankogel in the survey years 1994, 2004 and 2014. Mean values over the entire study area (All, shaded) and for each block (A, B, C, D) are shown. For plot numbers per block, see Table S1. Different lowercase letters denote significant differences between the survey years within each block based on linear mixed-effects models (Table S13).

## Discussion

Over a decade ago, the first repeated survey of the 10-yr-old permanent plots in the alpine–nival ecotone of Schrankogel showed an increase in species numbers similar to other studies, but, most noteworthy, also a divergent change in species abundance, providing the first consistent evidence of population declines of cryophilic species (Pauli *et al.*, 2007). After 20 yr of progressing

**Fig. 4** Changes in community-weighted ecological indicators. Changes in (a) thermic indicator (Gottfried *et al.*, 2012) and (b) soil moisture indicator in the periods 1994–2004 and 2004–2014 (Supporting Information Tables S16, S19). Modelled effect sizes and  $\pm$  SE over the entire study area (All, shaded) and for each block (A, B, C, D) are shown (Tables S17, S20). For plot numbers per block, see Table S1. Different lowercase letters denote significant differences between the changes in indicators from the first to the second decade within each block based on linear mixed-effects models (Tables S18, S21).



climate warming, we find that (1) species turnover involves the disappearances of species almost exclusively in the second decade, (2) the decrease in vegetation cover constitutes an ongoing trend over both decades, (3) the plant community transformation towards more thermophilous species assemblages, which are increasingly adapted to drier soil conditions, has accelerated, and (4) differences among the blocks reflect the temperature gradient, topography and connectivity to lower elevation species pools.

### Changes in vascular plant species diversity

The prevailing net gain in vascular plant species richness found on Schrankogel (Fig. 2a) confirms the ample evidence from other parts of the Alps (Grabherr *et al.*, 1994; Stöckli *et al.*, 2011; Matteodo *et al.*, 2013), temperate to boreal mountains across Europe (Britton *et al.*, 2009; Pauli *et al.*, 2012; Grytnes *et al.*, 2014; Steinbauer *et al.*, 2018) and in parts of temperate–continental North America (Lesica, 2014). There is little doubt that the increase in species numbers has been caused by an upward shift of species previously occurring at lower elevations (Odland *et al.*, 2010; Pauli *et al.*, 2012). Range shifts towards higher elevation are commonly driven by climate warming (Chen *et al.*, 2011), which has been pronounced in the Alps during recent decades (Marty & Meister, 2012), whereas stagnating species numbers over a 14-yr period of rather stable temperature conditions have been found in southern Norway (Vanneste *et al.*, 2017). In the Alps, increases in species numbers have even been observed to accelerate at century-old study sites on high-alpine to nival summits during recent decades (Walther *et al.*, 2005; Wipf *et al.*, 2013; Steinbauer *et al.*, 2018).

The increase in species richness in our plots was smaller in the second decade (Fig. 2a), suggesting a slowing down of species upward shifts. The separate consideration of colonisation and disappearance of species, however, showed that the number of

colonisations decreased only slightly, whereas the number of disappearances increased markedly (Fig. 2b). Species disappearances at the alpine–nival ecotone can indicate retracting lower range margins, as expected through warming-driven competitive displacements (Engler *et al.*, 2011; Lenoir & Svenning, 2013). In particular, cold-adapted species have been found recently to have experienced range contractions in the Alps (Rumpf *et al.*, 2018) and alpine Mediterranean species have been shown to decline, possibly as a result of the combined effects of warming and a reduction in precipitation (Pauli *et al.*, 2012). Species disappearances on Schrankogel, however, did not only concern subnival–nival species (AR1), but also alpine–subnival pioneer species (AR2) and alpine species (AR3) in similar proportions (Fig. S4b). Species colonisation numbers remained stable in all altitudinal species groups, except for AR1, where they dropped significantly (Fig. S4a). We therefore cannot unequivocally attribute the observed species turnover to warming-driven range dynamics. The detection of leading edge shifts driven by climate warming is hampered by the stochastic nature of processes, such as the propagation of diaspores, germination and establishment of seedlings. Similarly, the disappearance of species may either be the final stage of a population decline or the result of an unsuccessful species establishment, which are difficult to disentangle (Grytnes *et al.*, 2014). Further, projected directional range shifts and associated local species extinctions in temperate and boreal mountains (Engler *et al.*, 2011) may still require longer periods for the usually long-lived perennial alpine plants. Species dwelling in cold environments may persist even in climatically unsuitable habitats, and thereby accumulate an extinction debt (Dullinger *et al.*, 2012a). Yet, the increase in richness in our plots was mainly driven by alpine–subnival pioneer species (AR2), whereas the number of subnival–nival species (AR1) decreased slightly (Fig. S3), which could already be an indication of warming-driven range shift dynamics. This also accounts for the fact that

newly appearing species all belong to the lower elevation groups (AR3 and AR4; Table S3), which is in line with increasingly rising species numbers on mountain summits in Europe (Steinbauer *et al.*, 2018).

### Changes in vascular plant cover

In contrast with increasing species numbers, cover sums of vascular plant species showed a decreasing trend (Fig. 3). This was mainly driven by a strong continued population decline of all subnival–nival species (AR1), which could not be compensated by the ongoing increase in alpine–subnival species (AR2; Fig. S5).

The strongly divergent cover change of altitudinal species groups clearly depicts a shift in habitat suitability at the range margins of species, and is consistent with Cotto *et al.* (2017) and Rumpf *et al.* (2018), suggesting that population declines are occurring more rapidly than range shifts. This could lead, at least transitionally, to a disruption of distribution patterns, rather than to a rapid greening of the alpine–nival ecotone. The importance of directional changes in species cover was also shown in alpine permanent plots in the Montana Rocky Mountains by Lesica (2014), who noted that changes in species abundance can reveal far more sensitive responses to climate change effects than presence/absence data.

The most relevant potential mechanisms underlying the observed patterns are, first, a successive competitive displacement of the high-elevation species (AR1) through expansion of lower elevation species (AR2, AR3) and, second, direct climatic effects which may deteriorate the performance of cryophilic species. Competition effects, as were verified experimentally (Elmendorf *et al.*, 2012; Alexander *et al.*, 2015), are potentially relevant; however, conspicuous signs of competition pressure, such as for light through taller growing species, are not common at the alpine–nival ecotone, as all species are dwarf-stature plants. Further, the typical habitats at the alpine–nival ecotone do not have a closed vegetation cover (*c.* 10–25% of the plot surface; Fig. S7). Although species of different elevational distribution preferences can grow in the direct neighbourhood, habitats at the alpine–nival ecotone are governed by abiotic, mostly climatic, factors, where the stress gradient hypothesis (Bertness & Callaway, 1994; Callaway *et al.*, 2002) would posit that facilitative interspecific interactions outweigh competitive effects.

Overall, however, vascular plant cover is decreasing, which suggests that advancing alpine–subnival species (AR2) cannot fill the space released by AR1 species. We therefore assume that direct climatic effects may be of superior relevance for an increasing maladaptation and population decline of cryophilic species. Ecophysiological studies of cryophilic species have not been conducted often, but some species, including several of our AR1 group, have been found to show high heat sensitivity and low ability to acclimate respiration rates to higher temperatures, causing detrimentally high respiration rates, and thus the plants rapidly attain a negative carbon balance (Larigauderie & Körner, 1995; Larcher *et al.*, 1997; Cooper, 2004). Such metabolic disadvantages may explain the continued population decline even in

the absence of competition through higher temperatures alone. Drier conditions, through earlier snowmelt and stronger evapotranspiration, can further deteriorate the situation by leading to lower soil moisture levels, and thus to warmer soils, which could cause detrimentally high root respiration rates (Cooper, 2004; Lesica, 2014).

### Changes in community-weighted ecological indicators

Changes in plant community composition in our plots show a transformation towards a more thermophilic vegetation in both decades (Fig. 4a), in congruence with Gottfried *et al.* (2012). Most noteworthy, the thermophilisation signal, already significant in the first decade of observation 1994–2004 (Table S17), was significantly stronger during the second decade 2004–2014 (Table S18).

Thermophilisation effects have substantial consequences for subnival plant communities in the alpine–nival ecotone, where AR1 species have the centre of their distribution close to their rear edge (Gottfried *et al.*, 1999). This ecotone was found to strongly coincide with the altitude of the summer snow line (Gottfried *et al.*, 2011). Plant assemblages at the ecotone should therefore respond sensitively to warming and associated shifts in temporal patterns of snow duration. High-altitude weather stations distributed over the central and northern Alps show a uniform temperature increase in annual mean temperatures of 0.8°C during the last three decades (Marty & Meister, 2012), which would correspond to 0.53°C in the period 1994–2014. Using the environmental lapse rate of  $-0.65^{\circ}\text{C}$  per 100 m elevation, a temperature increase of 0.53°C corresponds to a difference of *c.* 80 m in elevation. As an approximation, one unit of the thermic indicator translates roughly to the elevation range of an entire vegetation belt, for example, the alpine belt on Schrankogel ranges from *c.* 2300 to 2800 m (Dullinger, 1998). The observed thermophilisation values of 0.06, 0.09 and 0.15 units during the first and second decade, and the 20-yr period, respectively, thus approximate to 6%, 9% and 15% of a vegetation belt. This is within the same magnitude of change as observed by Gottfried *et al.* (2012) on the European level (*i.e.* 5% of one vegetation belt after 7 yr). Given a vegetation belt of a vertical extent of 500 m, the observed change of 0.15 units in the thermic vegetation indicator corresponds to 75 m in elevation. Thus, the vegetation at the alpine–nival ecotone seems to be largely tracking recent climate warming.

An even stronger amplification effect was detected for the soil moisture indicator (Table S21). Our results show a shift of the species composition towards more drought-tolerant plant compositions, that is, an aridisation (Fig. 4b). Delta values of the community-level soil moisture and thermic indicators were highly negatively correlated (Fig. S6), and hence mainly reflect changes in the same species. Yet, this does not necessarily mean that all species experiencing a disadvantage through warmer conditions effectively suffer from drought stress.

Higher temperatures, however, cause greater evapotranspiration, leading to reduced water availability, which alone can increase the probability of drought stress (Beniston, 2003).

Regional scenarios on precipitation change are inconsistent; however, projections for central Europe show that mean precipitation tends to decrease in summer and increase in winter (Schmidli *et al.*, 2007), with increasingly more rain instead of snow in mountainous regions (Steger *et al.*, 2013). Snow cover is generally declining in the Alps, although patterns of changes in the amount of snowfall are also rather patchy (Gobiet *et al.*, 2014). Moreover, the significant trend towards a longer annual snow-free period has been shown to be consistent with reported trends of longer growing seasons (Dye, 2002; Giménez-Benavides *et al.*, 2007). Combined effects of higher temperatures and concomitant drier conditions can result in strong transforming forces on cold-adapted plant communities (Lesica, 2014), which was also experimentally confirmed (De Boeck *et al.*, 2016).

### Topography and elevation

Despite the deviating habitat situations among the four spatially separated blocks (Figs S7, S8), which may lead to different response patterns (Scherrer & Körner, 2011), changes in species occurrence, cover and composition were generally consistent, especially across the blocks in the ecotone (Figs 2–4). The observed deviations from the common trends, however, can contribute to a better understanding of possible causes and mechanisms behind the observed changes.

Contrary to the others, species patterns in the nival block D were rather stable over the 20-yr period, which could be explained by the larger distance to the alpine species pool. Obviously, low-temperature conditions suitable for cryophilic species still prevailed, that is, these populations occurred well above their lower range margin and above the upper margins of alpine species. Block D, however, consisted of fewer plots with fewer species, compared with the others. The results should therefore be treated with some caution.

The higher numbers of both colonising and disappearing species (Fig. 2b) and the stronger thermophilisation and aridisation signals (Fig. 4) at the uniform slope in the ecotone (block A) conform with the lowest elevation and closest connection to the alpine grassland zone. The different magnitudes of change among the four blocks reflect a gradient of increasing low-temperature conditions and a thinning of species pools, and thus the importance of the particular position along the thermal gradient for the velocity of warming-driven vegetation dynamics. This corresponds to recently observed effects over larger elevation ranges, where both species ranges and abundances changed more rapidly the lower a species was situated historically (Rumpf *et al.*, 2018). In the alpine–nival ecotone on Schrankogel, vascular plant species cover decreased in general (Fig. 3). Interestingly, however, the cover remained stable in block A in the second decade, which could signal an early stage of infilling processes. Combined with the strong thermophilisation signal, this is likely to indicate an enhanced expansion of the more thermophilous species. By contrast, cover continued to decrease in the rugged blocks B and C, together with a significant thermophilisation (Table S17), and thus was mainly driven by the dieback of subnival–nival species. Rugged terrain did not restrain the decline of cryophilic species,

but may have provided a barrier to the expansion of potential competitors. We therefore suggest that factors other than competition, such as direct temperature effects on plant metabolism, have strongly contributed to the decrease in cover of the cold-adapted, high-elevation species.

In conclusion, we argue that a combination of continued temperature rise and decreased snow cover duration has a major impact on the composition, performance and persistence of plant species in subnival communities. This is manifested by an accelerating loss of subnival plant communities in the central Alps. The longevity and persistence abilities of high-elevation plants may have delayed the disappearance of species from habitats which have become climatically unsuitable (Dullinger *et al.*, 2012a). Increasing maladaptation of cryophilic high-elevation species to warmer and longer growing seasons, however, has led to their continued retraction, even in the absence of competitive displacement. An incomplete infilling through succeeding species from lower elevation further suggests that trailing edge dynamics proceed faster than leading edge advances in environments above the alpine grassland zone. If this holds true in further progress, it could imply that the pay-off of a rising extinction debt (Kuussaari *et al.*, 2009; Cotto *et al.*, 2017) enters into force before colder habitats, if available, can be reached.

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### Author contributions

H.P., M.W., A.L. and K.S. designed the study and were part of the recording team. P.R.S., A.L., K.S. and M.W. analysed the output data. H.P. managed the study. A.L., P.R.S. and H.P. wrote the manuscript. All authors discussed the results and implications, and commented on the manuscript at all stages. A.L. and K.S. contributed equally to this work.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

**Fig. S1** Location of permanent plots on Mount Schrankogel with transect details.

**Fig. S2** Correlation between thermic indicator and temperature sum on Mount Schrankogel.

**Fig. S3** Vascular plant species richness per altitudinal rank in the survey years 1994, 2004 and 2014.

**Fig. S4** Relative colonisation and disappearance per altitudinal rank in the periods 1994–2004 and 2004–2014.

**Fig. S5** Cover sum of vascular plant species per altitudinal rank in the survey years 1994, 2004 and 2014.

**Fig. S6** Correlation between the changes in thermic indicator and changes in soil moisture indicator per plot in the periods 1994–2004 and 2004–2014.

**Fig. S7** Topographic parameters per block on Mount Schrankogel.

**Fig. S8** Non-metric multidimensional scaling (NMDS) of topographic parameters of plots.

**Table S1** Setup of permanent plots for the monitoring of vascular plant species on Mount Schrankogel

**Table S2** Frequency of annual plant species

**Table S3** Vascular plant species per altitudinal rank in the survey years 1994, 2004 and 2014

**Table S4** Vascular plant species richness in the survey years 1994, 2004 and 2014

**Table S5** Changes in vascular plant species richness in the periods 1994–2004, 1994–2014 and 2004–2014

**Table S6** Vascular plant species richness per altitudinal rank in the survey years 1994, 2004 and 2014

**Table S7** Changes in vascular plant species richness per altitudinal rank in the periods 1994–2004, 1994–2014 and 2004–2014

**Table S8** Number of colonising and disappearing species at the end of periods 1994–2004 and 2004–2014

**Table S9** Differences between numbers of colonising and disappearing species within and among the periods 1994–2004 and 2004–2014

**Table S10** Relative colonisation and disappearance per altitudinal rank in the periods 1994–2004 and 2004–2014

**Table S11** Changes in relative colonisation and disappearance per altitudinal rank in the periods 1994–2004 and 2004–2014

**Table S12** Cover sum of species in the survey years 1994, 2004 and 2014

**Table S13** Changes in cover sum of species in the periods 1994–2004, 1994–2014 and 2004–2014

**Table S14** Cover sum of vascular plant species per altitudinal rank in the survey years 1994, 2004 and 2014

**Table S15** Changes in mean cover sum of vascular plant species per altitudinal rank in the periods 1994–2004, 1994–2014 and 2004–2014

**Table S16** Thermic indicator in the survey years 1994, 2004 and 2014

**Table S17** Thermophilisation in the periods 1994–2004, 1994–2014 and 2004–2014

**Table S18** Changes in thermophilisation between the periods 1994–2004 and 2004–2014

**Table S19** Soil moisture indicator in the survey years 1994, 2004 and 2014

**Table S20** Change in soil moisture indicator in the periods 1994–2004, 1994–2014 and 2004–2014

**Table S21** Changes in  $\Delta$  soil moisture indicator between the periods 1994–2004 and 2004–2014

**Table S22** Differences in abiotic factors between blocks on Mount Schrankogel

**Table S23** Vascular plant species richness in the survey years 1994 and 2014

**Table S24** Changes in vascular plant species richness in the period 1994–2014

**Table S25** Number of colonising and disappearing species in the period 1994–2014

**Table S26** Differences between numbers of colonising and disappearing species in the period 1994–2014

**Table S27** Thermic indicator in the survey years 1994 and 2014

**Table S28** Thermophilisation in the period 1994–2014

**Table S29** Soil moisture indicator in the survey years 1994 and 2014

**Table S30** Changes in soil moisture in the period 1994–2014

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