



Identifying the driving factors behind observed elevational range shifts on European mountains

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ABSTRACT

Aim In recent decades species ranges have shifted upwards in elevation and northwards in latitude. These shifts are commonly interpreted as a response to recent climate warming. However, several alternative hypotheses have been proposed to explain the elevational shifts, including increased deposition of atmospheric nitrogen, changes in precipitation and dispersal limitation. We evaluate these hypotheses and attempt to identify the dominant drivers for the observed shifts in the upper range limits of alpine plant species.

Location European mountains from Svalbard to the southern Alps.

Methods We assembled data on observed shifts in the upper range limit of alpine plants over 40 to 100 years on 114 mountains. We related the observed shifts to recent changes in temperature and precipitation and to recent deposition of atmospheric nitrogen. Changes in traits and habitat preferences of species in the summit assemblages were used to evaluate the potential role of different drivers.

Results Seventy per cent of the species that showed a detectable change in their upper range limits between surveys shifted their range limits upwards. The same species tend to move up on different mountains. There are, however, large differences between mountains in the proportion of species shifting upwards. This proportion is not found to be statistically related to local changes in temperature. Correspondingly, warmth-demanding species did not move upward more frequently than expected by chance. Snow-bed species have become more common on summits.

Main conclusions Our data do not support the idea that climate warming is the dominant factor causing the observed range shifts of alpine plant species on European mountains: first, the amount of change in species assemblages on the summits studied is not related statistically to the amount of climate warming; second, those species that have moved upwards are not particularly warmth demanding.

Keywords

Alpine vascular plants, climate change, dispersal traits, global warming, mountain summits, nitrogen deposition, precipitation, snow beds.

INTRODUCTION

We have known for a long time that climate, especially temperature, is one of the most important factors limiting species geographical ranges at broad scales (e.g. Grinnell, 1917; Iversen,

1944; Woodward, 1987; Dahl, 1998; Gaston, 2003). Global temperatures are increasing, and we therefore expect species to shift their ranges along elevational and/or latitudinal gradients by tracking their climatic niche (Thuiller *et al.*, 2005; Engler *et al.*, 2011). Observational studies along elevational gradients have

confirmed these expectations as there is increasing evidence for upward species range shifts in recent decades (e.g. Grabherr *et al.*, 1994; Klanderud & Birks, 2003; Parmesan, 2006; Lenoir *et al.*, 2008; Tingley *et al.*, 2009; Chen *et al.*, 2011; Gottfried *et al.*, 2012; Pauli *et al.*, 2012; Matteodo *et al.*, 2013). By combining observations about how temperature may limit broad-scale species distributions with observations about recent climate changes, most authors interpret these upward range shifts as responses to a warmer climate. However, several alternative hypotheses have been proposed to explain these range shifts, e.g. increased deposition of atmospheric nitrogen (Klanderud & Birks, 2003; Johnson *et al.*, 2011), dispersal limitation resulting in a lag in species colonization at high elevations after the 'Little Ice Age' (Kammer *et al.*, 2007; Vittoz *et al.*, 2009), changes in precipitation or moisture availability (Tingley *et al.*, 2009; Crimmins *et al.*, 2011; McCain & Colwell, 2011) or biotic interactions including changes in grazing pressures (Speed *et al.*, 2012). A better understanding of what causes shifts in species ranges is needed before reliable predictions can be made about future distributional shifts (Dawson *et al.*, 2011). To achieve this, we need in-depth analyses of comprehensive data sets that relate environmental changes to observed range shifts that have already occurred over recent decades to try to assess the causes of the range shifts.

Changes in the upper limits of alpine plants are the most popular topic for studies of species range shifts. There are several reasons for this. The most important is probably that the tolerance of alpine plants to the harsh environment at the upper elevational limits of species has fascinated ecologists for a long time (e.g. Körner, 2003; Nagy & Grabherr, 2009), and for ecologists studying alpine habitats the upper limits of species are particularly intriguing (e.g. Körner, 2011). This has resulted in a unique set of baseline data on the upper limits of species in different areas prior to the onset of human-induced global warming over the last century (Stöckli *et al.*, 2011). Another reason for the focus on the upper boundaries of alpine plant ranges is that they are thought to be primarily related to ambient temperature (MacArthur, 1972; Vetaas, 2002; Körner, 2003, 2011), and are therefore expected to be especially responsive to changes in temperature. Dispersal limitation is probably less important along elevational gradients than across latitudes, because distances between different thermal and vegetation zones on mountains are shorter compared with such zones along latitudinal gradients (Körner, 2007). Hence, any migrational responses of species to climate change should be more readily detectable along an elevational gradient than along a latitudinal gradient. Overall, all these features make shifts in the upper elevational range limits of high-alpine plants an ideal study system for evaluating the potential drivers for recently observed range shifts on mountains.

To evaluate the potential effects of different drivers on changes in elevational range limits we first quantify the proportion of species on a mountain that have shifted their upper range limits upwards. Our primary hypothesis is that mountain areas that have experienced the strongest warming will have had most species shifting upwards. In addition to climate warming, we

also evaluate the relative importance of other driving factors that have been proposed to control the upper range limits of high-alpine plants, i.e. changes in precipitation, snow cover, atmospheric nitrogen deposition and dispersal. For our analysis we have assembled data from 114 European mountain tops and assessed the number and proportions of species shifting upwards. These observed shifts are then related to recorded changes in climate on the different mountains, as well as to changes in atmospheric deposition of nitrogen. We also compared the traits and habitat preferences of the species shifting upwards with the traits and habitat preferences of species that did not shift upwards to try to disentangle the likely importance of different driving factors.

METHODS

Data collation and collection

Information on how the observed upper limits of species have changed over recent decades was collated from published sources and from our own fieldwork. A summary of the features of the 114 mountains included is given in Appendix S1 in Supporting Information. Some of these mountains were sampled several times, but to avoid pseudo-replication we always used the first and the last sampling only. The time span between the two sampling periods varies from 36 years to more than 100 years. The 114 mountains were originally sampled in different ways. Some studies listed the summit flora above a certain elevation, other studies noted the highest elevation for all species above a certain elevation and some studies were based on resampling of vegetation plots with a detailed description of location (Table S1). The resampling on each mountain used the same methods as the original sampling.

Data analysis

Consistency between species and between mountains

For each species on a mountain we assessed if the uppermost observation of the species was higher, lower or at the same elevation in the re-survey compared with the initial survey. Due to the different sampling methods used between mountains we focus on the direction of change only rather than on the magnitude of change for each species. Observations of no change in a species' upper limit can have a different meaning from study to study depending on the sampling methods used. Therefore, we focus on species with observed changes, i.e. species that showed upward or downward shifts in their upper range margins. In some studies only a small change (found above or below an arbitrary elevation set as the cut-off for a summit) might result in a positive or negative change. The variability of sampling could make the final results more prone to random factors and, in turn, make it more difficult to find a robust pattern than if we were able to quantify the amount of change for each species.

If species-specific traits (e.g. dispersal) determine how species shift their ranges we expect the species to show consistent

patterns between mountains. We therefore tested if the range shift of a certain species is consistent and moves in the same direction across mountains. This was done by a chi-square test on the numbers of mountains on which each species had shifted upward or downward. Only species that had been observed to change (up or down) on more than 20 mountains were included.

To determine if the species shifts were related to environmental changes on the mountains, we performed a corresponding chi-square test of mountains with more than 20 species shifting their upper range margins. Setting a lower threshold than 20 species or mountains for inclusion in the chi-square test did not influence the results either for the species comparison or for the mountain comparison. In fact, the relationship between degrees of freedom and the chi-square value is approximately constant and is independent of which cut-off level is chosen (5, 10 or 20 observations were tried as thresholds).

Correlations with the proportion of species moving upwards

To test hypotheses about how different factors may have affected the proportion of species moving upwards on the different mountains, we used as a response variable the fraction of species showing upward shifts versus species showing any shifts (excluding species with no observed shifts) on each mountain. Changes in climate between the two time periods and atmospheric deposition of nitrogen in 1990 were used as predictor variables. Yearly climate data in the 10-year period prior to both sampling periods were provided by met.no (<http://www.met.no>) for Norway based on interpolation between the available meteorological stations, and we used information from HISTALP for the Alps (Auer *et al.*, 2007). The average temperatures for the 10-year period prior to sampling were regressed against the observed proportion of species moving upwards. The same was done for precipitation for the Norwegian mountains where total annual precipitation and summer precipitation (June–August) values are available. The available data on precipitation from the Alps are too coarse for our purpose. To estimate spatial differences in deposition of atmospheric nitrogen within Europe, we used information developed by EMEP (<http://www.emep.int>), and used data reported from 1990 on wet deposition of oxidized nitrogen. We assume that areas that received high nitrogen deposition in 1990 also received increased nitrogen in the whole period between the floristic sampling periods. The statistical relationships between the predictor variables (changes in temperature and precipitation, and atmospheric nitrogen) and the proportions of species moving upwards were assessed with generalized linear models (GLM), assuming a quasi-binomial distribution with a logistic link function. A quasi-binomial distribution and an *F*-test were used to avoid problems of overdispersion (Crawley, 2007). R version 2.15.1 was used for all statistical analyses (R Core Team, 2012). In addition a generalized linear mixed effect model (GLMM) (glmmPQL in the R package MASS) was used with region (Alps, Scandinavia, Arctic; Table S1) as a random factor, but the results are only

reported in the text when the GLM and GLMM gave different results. The relationships were also tested within the Alps and Scandinavia separately.

Comparison of traits between the two time periods

We explored the possible reasons for consistent shifts in the species by evaluating the traits and habitat preferences (both referred to as ‘traits’ hereafter) of all the species present. We assembled species traits from different sources (Appendix S2). Ecological indicator values characterize the preference of plant species for certain environmental conditions (nutrient availability, temperature, moisture, etc.) and have been developed independently by Ellenberg & Leuschner (2010) and Landolt *et al.* (2010) for the flora of central Europe and the European Alps, respectively. Generally, indicator values reflect measured environmental conditions well (e.g. Wamelink *et al.*, 2002; Diekmann, 2003; Scherrer & Körner, 2011; Lenoir *et al.*, 2013). Dispersal-mode data were assembled from Landolt *et al.* (2010). Since some species have more than one dispersal mode, we tested each dispersal mode separately.

When doing a preliminary test for changes in average temperature indicator values for the species assemblages at the summit across all mountains, we found that temperature indicator scores of the mountain assemblages have increased both for the Ellenberg (0.131 units) and Landolt (0.065 units) indicator values. Although these shifts are statistically significant when tested with a paired *t*-test, one should be cautious of taking this as support for the hypothesis that temperature is the main driver of the observed range shifts because the species from the lower part will most likely have a higher temperature indicator value than those present from the upper part. Any upward movements of species, independent of causal factor, will therefore result in higher average temperature indicator values. We therefore took an alternative approach using a randomization procedure to evaluate if the species assemblages found on the higher parts of the mountains today had a different mean trait value (or fraction of species with the trait in the case of dispersal modes or preference for snow-bed habitat) than the species assemblage found in the initial survey.

Before the randomizations we first established a new observational value to compare with the randomized values. To do so, the studied elevational range along each mountain was divided into two equal parts. The upper half, hereafter termed the ‘summit’, is the part on which we focus. For traits with a numeric value (i.e. temperature, moisture and nitrogen indicator values), the average trait score for species assemblages on the separate summits was estimated for both time periods. For the dispersal traits and snow-bed habitat, the proportion of species having the trait was estimated for both time periods. Observed change was estimated by the current mean (or proportion) trait value minus the previous mean trait value (i.e. a positive value indicates that the species assemblages on the summits have an increased average value for that trait). An average value of these change values was then compared with randomized values.

The randomizations were done by first identifying the species that had their upper limit in either the lower or the upper half for the initial sampling (t_0). The second step was to identify the species and the number of species (n_{new}) shifting from the lower part to the summit from the initial time to the resampling (t_1). Likewise, the identity and number of species lost (n_{lost}) from the summits by the time of resampling were determined. In the third step we randomly selected n_{new} from the species found in the lower half at t_0 and 'moved' these species upwards, and randomly selected n_{lost} species from the species found on the summit and 'moved' them downwards. This results in a new randomized species assemblage on the summits with a new average trait value for each summit, and was treated in the same way as the observed value described above. This gives the expected change value for the case that species shift at random in the same number as is observed. Then the average trait value or proportion on the summit that was actually observed on the summit was compared between t_0 and t_1 . In addition to the average change values we also compared the average values or proportions for the species lost and new to the summit. These observed values were compared with the values found from the randomizations, and Monte Carlo P -values were derived from 999 permutations. One-sided P -values are reported, and we therefore use 0.025 as the critical P -value.

Note that the absolute values in both the observed and expected change may seem small. The reason for this is that in the estimates of change include the constant species. This stabilizes the average values observed between the two time periods and decreases the amount of change observed. However, the effect is the same for the observed and for the randomized values and is thus accounted for in the permutation test performed. Prior to the analyses of change in mean trait values for the species assemblages, all mountains with a studied elevational range of less than 20 m were excluded, leaving 71 mountains for analysis. If the studied range was larger than 200 m, only the upper 200 m of the range was considered in this analysis to make the random draw of species from the lower part to the summits more realistic. Other threshold values for mountain ranges were tested and are reported in Appendix S4.

RESULTS

A total of 565 species was recorded on the 114 mountains. On these mountains, 3678 upward shifts and 1533 downward shifts of the local upper range margin of vascular plant species were observed. Hence, 70.6% of the species that changed their upper range margins between surveys shifted upwards. No change was observed 1272 times. A chi-square test of species that were found on more than 20 mountains shows that the upward or downward shifts are not randomly distributed across species ($\chi^2 = 141.4$, d.f. = 74, $P < 0.0001$). This means that there is a tendency for certain species to move in the same direction on all mountains. Thus, an approach that examines species-specific traits and habitat preferences is appropriate for exploring why certain species have expanded their ranges upwards whilst others have retreated downwards. A corresponding chi-square

test of mountains with more than 20 species shifting their upper range margins reveals that there are large differences between mountains regarding the proportions of species showing upward or downward shifts ($\chi^2 = 612.9$, d.f. = 84, $P < 0.0001$). This indicates that an environment-centred approach, in which differences between environmental conditions on different mountains are examined, should also be informative when investigating why species have shifted. In the following we use both the trait-centred/habitat preference-centred and the environment-centred approaches to evaluate the driving factors of observed changes in range margins. We first consider climate variables as potential drivers of change. We then compare species traits, habitat type and nitrogen deposition to help identify and disentangle possible drivers of change.

Climate change

When relating change in seasonal temperature to the proportion of species shifting upwards, only the change in average spring temperature (March–May) is statistically significant ($F = 4.77$, $P = 0.031$, $n = 97$; Table 1). This relationship is, however, negative (Fig. 1a). Average temperature for the other three seasons and the average annual temperatures were not statistically significantly related to the proportion of species shifting upwards (Table 1). We therefore find no indication with this approach that temperature change is the dominant driver explaining the observed recent upward movement of species on European mountains. Looking at the temperature indicator values and comparing the observed changes with the expected changes shows that the changes in the temperature indicator scores are significantly lower than random expectation for Landolt indicator values ($P < 0.01$; Table 2). There is a non-significant trend but in the same direction for Ellenberg indicator values ($P = 0.083$). This lower than expected change in temperature indicator values on the summits may be caused by the extinction of warmth-demanding species from the summits or by species new to the summits being more cold-tolerant than expected at random. Further analyses show that average temperature indicator values of species lost from the summits are significantly higher than expected ($P < 0.01$ for both Landolt and Ellenberg indicator values; Table 2) whereas the average temperature indicator values of species new to the summits do not deviate from random expectation.

We find no significant statistical relationship between the proportion of species that change their ranges upwards and changes in annual precipitation ($F = 0.22$, $P = 0.64$, $n = 48$; Table 1). However, there is a statistically significant negative relationship with summer precipitation ($F = 5.81$, $P = 0.020$, $n = 48$). Summer precipitation has increased on all mountains where data are available, and a lower proportion of species migrated upwards on mountains that experienced the largest increase in summer precipitation (Fig. 1b). A comparison of the average ecological indicator values for moisture shows that 'moisture values' have changed no more than expected by chance on the summits (Table 2). The species lost from the summits are more moisture demanding than expected by

Table 1 Summary of the statistical relationships between the proportions of species moving upwards (of the species changing) and the explanatory variables considered. The first column gives the explanatory variable (and the number of summits for which these data are available). The logistic regressions (GLM) assume a quasi-binomial distribution, and the two last columns summarize the mixed-effect model with the same assumptions (GLMM), using geographical region (Alps, Scandinavia, Arctic) as random effects. Precipitation data are only available for Scandinavia and no GLMMs were performed. The same analyses performed for the regions separately are given in Appendix S3.

	Logistic regression (GLM)				GLMM	
	Total deviance	Explained deviance	<i>F</i> -value	<i>P</i> -value	<i>t</i> -value	<i>P</i> -value
Spring temperature (<i>n</i> = 97)	591.7	25.0	4.7	0.03	−2.1	0.04
Summer temperature (<i>n</i> = 97)	591.7	1.9	0.4	0.55	−1.6	0.12
Autumn temperature (<i>n</i> = 97)	591.7	17.7	3.3	0.07	−2.2	0.03
Winter temperature (<i>n</i> = 97)	591.7	0.5	0.1	0.75	0.1	0.94
Annual temperature (<i>n</i> = 97)	591.7	13.4	2.5	0.11	−2.1	0.04
Annual precipitation (<i>n</i> = 48)	238.8	1.1	0.2	0.64		
Summer precipitation (<i>n</i> = 48)	238.8	26.0	5.8	0.02		
Nitrogen deposition (<i>n</i> = 114)	785.9	63.5	10.5	0.002	1.8	0.08

GLM, generalized linear model; GLMM, generalized linear mixed effect model.

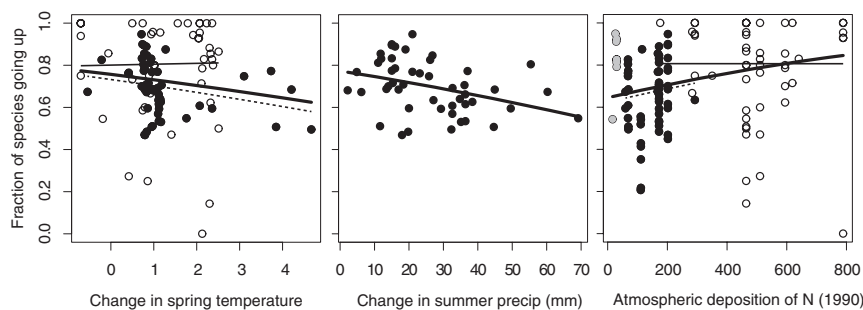


Figure 1 Relationships between the fraction of species moving upwards and – from left to right – changes in spring temperature (March to May), changes in summer precipitation (precip) (June to August) and atmospheric deposition of nitrogen (N) in 1990. The fitted lines are based on logistic regressions (see Table 1 and Appendix S3 for the regional models). Different symbols represent different regions: open circles and unbroken thin lines represent the Alps; closed black circles and dashed lines, Scandinavia; grey circles, the Arctic. Thick lines are for all data combined.

chance using the Ellenberg indicator values ($P = 0.011$, Table 2), and there is a trend in the same direction when using Landolt's indicator values ($P = 0.079$, Table 2). The average moisture indicator values for the new species on summits do not deviate from random expectations.

Species traits, habitat type and atmospheric nitrogen

The proportion of snow-bed plants (commonly associated with deep and long-lying snow cover) on summits has increased slightly, but is not significantly different from random expectation (Table 2). However, there is a statistically significant higher proportion of snow-bed species new to the summits (Table 2). There is no significant deviation from random expectation for the proportion of snow-bed species lost from summits (Table 2).

We find a statistically significant relationship between nitrogen deposition and the proportion of species new to summits

($F = 10.51$, $P = 0.002$, $n = 114$: Table 1). However, this cannot be separated from the multitude of other factors that differ between the two main regions included in this study, as this relationship is not significant when summits within the Alps and Scandinavia are tested separately or when a GLMM with region as a random factor is used (Table 2, Appendix S3). Correspondingly, average Ellenberg or Landolt nitrogen indicator values increase slightly less than expected by chance, but this is not statistically significant (Table 2).

If poor dispersal ability prevented some species from reaching the summits until now, a non-random subset of species in terms of dispersal mode should be new to the summits. Only one dispersal trait shows a statistically significant deviation from random expectation when investigating species new to the summits, namely endochory (dispersal within animals). The observed fraction of species new to the summits with endochory is 0.13, which is 0.07 lower than expected by chance ($P = 0.018$; Table 2).

Table 2 Comparison of means of indicator values, species traits and habitat preferences on the upper part of the studied mountains. Only mountains that have a studied range of more than 20 m are included ($n = 71$ mountains), and the maximum range included is 200 m. Other threshold values gave similar results (Appendix S4).

	Change on summit			Lost from summit			New to summit		
	Observed mean	Expected mean	Sig.	Observed mean	Expected mean	Sig.	Observed mean	Expected mean	Sig.
Temperature (Landolt)	-0.011	0.024	**	1.607	1.411	**	1.445	1.523	n.s.
Temperature (Ellenberg)	-0.015	0.020	n.s.	1.999	1.745	**	1.977	1.985	n.s.
Moisture (Landolt)	-0.011	-0.025	n.s.	3.156	3.063	n.s.	3.122	3.110	n.s.
Moisture (Ellenberg)	-0.027	-0.027	n.s.	5.836	5.555	*	5.492	5.485	n.s.
Nitrogen (Landolt)	0.003	-0.003	n.s.	2.017	1.952	n.s.	1.969	2.002	n.s.
Nitrogen (Ellenberg)	0.089	0.064	n.s.	2.468	2.491	n.s.	2.836	2.719	n.s.
Snow-bed plants	0.004	-0.021	n.s.	0.567	0.614	n.s.	0.691	0.592	**
Boleochory							0.377	0.390	n.s.
Endochory							0.134	0.201	*
Meteorochory							0.592	0.559	n.s.
Dysochory							0.033	0.041	n.s.

The observed mean is the mean trait value for species observed in the different categories. The expected mean is the value found by 999 randomizations. 'Change on summit' is the observed new value minus the observed value from the original sampling. 'Lost from summit' is the average value for the species that were found on the summit in the original sampling but not in the resurvey. 'New to summit' is the average value for the species found in the resurvey but not in the original sampling. Only species 'new to summit' are tested for dispersal modes because we do not expect any relationship between species lost from the summits and dispersal mode.

Statistical significance (Sig.) is indicated with ** for $P < 0.01$, * for $P < 0.025$ and n.s. (not significant) for $P > 0.025$ from a one-sided permutation test.

DISCUSSION

The majority (*c.* 70%) of the species that have been observed to shift their ranges on the 114 mountains studied here have shifted upwards. This is in accordance with the large number of studies showing that species ranges have shifted upwards (e.g. Klanderud & Birks, 2003; Lenoir *et al.*, 2008; Chen *et al.*, 2011; Felde *et al.*, 2012; Lenoir & Svenning, 2013) or that species richness has increased on mountain summits during the last decades (e.g. Grabherr *et al.*, 1994; Klanderud & Birks, 2003; Odland *et al.*, 2010). It is also in line with the expectation that most species will shift upwards as a consequence of overall climatic warming (Engler *et al.*, 2011). Indeed the climate has become warmer between the two surveys on most mountains in our study (see the horizontal axis on Fig. 1a). It is therefore surprising that stronger regional warming is not associated with higher rates of upward shifts in our study. Our finding contrasts with observations by Chen *et al.* (2011) who find a positive correlation between the amount of warming and the rate of range shifts. However, they find that elevational range shifts have a much weaker correlation to climatic warming than latitudinal range shifts. Barbeito *et al.* (2012) and Elliott (2012) show that recent changes in tree composition at high elevations in the Swiss Alps and the Rocky Mountains, respectively, may reflect snow and temperature–precipitation interactions rather than temperature changes alone.

One problem associated with using interpolated air temperatures from meteorological stations for predicting species distributions is that the air temperatures will always differ from the actual temperatures that low-stature alpine plants experience

(Dahl, 1963; Scherrer & Körner, 2011; Scherrer *et al.*, 2011). Thus, changes in interpolated mean spring or summer air temperature may not be directly related to what is driving species upwards. A comparison of the average temperature indicator values shows that they have indeed increased on the summits. This increase is a common observation for summit floras (Gottfried *et al.*, 2012; Matteodo *et al.*, 2013). However, if a random subset of species shift upwards, and the shift is independent of warming and is a response to other drivers (e.g. changes in other climatic factors, dispersal lag after the 'Little Ice Age' or increased nitrogen deposition), the average temperature indicator value is lower than expected by chance on the summits. This pattern is only statistically significant for the Landolt temperature indicator value, but Ellenberg values show the same general tendency ($P = 0.083$). The decrease in warmth-demanding species on the upper parts of the mountains is caused by the extinction of such species on the summits and not by colonization of 'colder' species in the same area (Table 2). So when accounting for a random subset of species shifting upwards we find that the results from relating changes in temperature data to range shifts are consistent with the observations of change in temperature indicator values for the species. It also shows that comparing only changes in average values might lead to erroneous conclusions because any random upward range shift will result in a 'warmer' flora.

The observed pattern of warmth-demanding species going extinct combined with the increase in the number of snow-bed species on the summits may have an explanation that is consistent with general expectations about how alpine species may respond to global warming: Many of the summits studied have

small-sized glaciers or a large extent of snow cover that only rarely melts away. Under a warming climate, larger areas melt out during the summer and glaciers shrink. Shrinking glaciers are observed in both the Alps (Zemp *et al.*, 2006; Imhof *et al.*, 2011) and in the Scandes (Nesje *et al.*, 2008; Laumann & Nesje, 2009; Imhof *et al.*, 2011). The increasing melting of snow and ice will reveal more areas available for colonization, mostly snow-bed areas, which may result in a higher rate of colonization by snow-bed species on the summits (e.g. Matthews, 1992). We realize that this is a tentative working hypothesis, but in addition to explaining the patterns observed in this study it may help to explain why elevational shifts in range limits are not as clearly related to climatic warming as latitudinal shifts (Chen *et al.*, 2011). If our hypothesis is correct, the observed decrease in warmth-demanding species will be a temporary effect in most cases: once the extent of snow and ice has greatly diminished or even totally disappeared, warmth-demanding species might rapidly expand upwards. This effect might therefore contribute to a lag in species response to climate warming and be another potential contribution to the extinction debt seen in high-mountain plants (Dullinger *et al.*, 2012). However, more direct studies are needed to test this hypothesis.

Many studies have linked different species traits to observed colonization or range shifts (e.g. Holzinger *et al.*, 2008; Angert *et al.*, 2011; Felde *et al.*, 2012; Matteodo *et al.*, 2013). No clear consensus emerges from these studies. Our finding that the same species are consequently shifting upwards on different mountains more than is expected by chance indicates that traits or habitat preferences of individual species may potentially explain some of the variation in range shifts. However, comparing the chi-square values of the between-mountain comparison and the between-species comparison reveals that there is much more variation captured between mountains than between species ($\chi^2 = 612.9$ with 84 degrees of freedom versus $\chi^2 = 141.4$ with 74 degrees of freedom for mountains and species, respectively). This might suggest that environmental variations between mountains have a higher potential for explaining the variation in range shifts than species traits or habitat preferences.

For the traits and habitat preferences evaluated in this study, species from the snow-bed habitat are clearly over-represented among the species colonizing the summits. Comparable results were found in the Jotunheimen range in southern Norway where shifts in species elevational optima over 80 years showed that snow-bed species tended to have larger shifts in their observed optima (Felde *et al.*, 2012). Of the dispersal traits tested, only endochory (seeds dispersed by passing through the guts of animals) showed a statistically significant trend. However, there was a lower fraction of species found on the summits today than would be expected by a random draw of the lowland species. This means that a disproportionately low proportion of the lowland species with endochory have shifted to the summits. Yet it is mostly (around 80%) species with dispersal modes other than endochory that are actually showing range shifts causing these results, so we are reluctant to put too much emphasis on dispersal mode to explain these patterns. Although there are several reasons to expect that dispersal mode should be

an important predictor for range shifts we find little support for this, in accordance with other studies (Angert *et al.*, 2011; Felde *et al.*, 2012; Matteodo *et al.*, 2013).

Change in land use is a potential confounding factor in studies like this. Detailed knowledge about land-use change for each mountain is not available but would be needed to evaluate this further. Both increased tourism and changes in grazing regimes might have an effect on the expansion or contraction of species distributions. We cannot quantify these effects with the data we have available, so we cannot rule out that these factors may play a role in causing some of the observed range shifts. However, according to the original studies from which these data are assembled, land-use change does not seem to be a major factor in many of these areas (see references in Appendix S1).

In conclusion, our results suggest that the observed temperature increase alone has low statistical explanatory power for the range shifts experienced by the high-alpine plants on European mountains. Attributing the observed changes in species ranges to climatic variables that integrate the complex interaction of variables influencing organisms in their natural habitat (Walther, 2007) may better reflect and explain the observed shifts (see also Barbeito *et al.*, 2012; Elliott, 2012). When only a single variable such as temperature is considered, our results may suggest anomalous and contradictory responses by plants to climate change.

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Additional references may be found at the end of Appendix S4 in the online version of this article.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1 Description of the 114 mountain summits used in the study.

Table S2 Description of the species traits used in the trait analyses.

Table S3 Details of the statistical analyses explaining the fraction of species moving upwards.

Table S4 Comparison of the averages for different species traits on the upper half of the studied mountains.

BIOSKETCH

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