Title: Recent Plant Diversity Changes on Europe’s Mountain Summits

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Abstract: In mountainous regions, climate warming is expected to shift species' ranges to higher altitudes. Evidence for such shifts is still mostly from re-visitations of historical sites. We present recent (2001 – 2008) vascular plant species richness changes observed in a standardized monitoring network across Europe's major mountain ranges. Species have moved upslope on average. However, these shifts had opposite effects on the summit floras' species richness in boreal-temperate (+3.9 species on average) and Mediterranean (-1.4 species) mountain regions, probably because recent climatic trends have decreased water availability in the European south. As Mediterranean mountains are particularly rich in endemics, a continuation of these trends might shrink the European mountain flora despite an average increase in summit species richness across the region.

One sentence summary: An upward shift of species resulted in increasing species richness on northern summits, but in decreasing richness on southern summits.

Main text: Biodiversity scenarios for the 21st century consistently forecast reduction of alpine habitat and, ultimately, the regional loss of many European high mountain plants (*1, 2*). This process is supposedly driven by a general upward shift of plant species under a warming climate (*3*), resulting in a concurrent increase of species numbers at higher altitudes and local extinctions of those plants which already live near the upper margins of elevation gradients (*4, 5*). However, empirical evidence on recent plant diversity trends in mountain systems is still scarce and mostly based on resurveys of historical sites (*6-9*) (but see (*10, 11*)).

A worldwide observation network (*12, 13*) was initiated in the year 2000 as a standardized monitoring system of high mountain biodiversity changes. As part of this network, vascular plant species occurrence was recorded first in 2001 on 66 mountain summits distributed across 17 study regions which span all major mountain systems of Europe (Fig. 1). These summits were resurveyed in 2008. Here, we compare the data of all summits from both years of observations for changes in vascular plant species numbers.

Summits were grouped in a set of four within each region spanning an altitudinal range from the treeline to the alpine/nival ecotone (*13, 14*), or to the uppermost peaks on lower mountain ranges. The sampling areas covered the summits from their top down to the 10-m contour line and were divided into eight sections (fig. S1) (*13*). For each section, a complete list of vascular plants was collected in 2001 and again in 2008. To avoid drawing conclusions from spurious species turnover caused by observation errors, we filtered the data to remove singleton records and potentially misidentified species from the list beforehand (*12*). Differences in number of species, i.e., the pooled species richness per summit and per region, respectively, between the two sampling dates were then compared by means of linear mixed effects models (*12*).

Between 2001 and 2008 vascular plant species numbers have increased on 45 mountain summits, decreased on 10 summits, and remained unchanged on 11 summits (Fig. 2A, table S1). Across all 66 summits, average numbers of species per summit increased from 34.9 to

37.7, i.e., by *c.* 8 %, a change that was significantly different from the null hypothesis of constant species richness ($t = 2.9$, df = 49, $p = 0.006$). Changes were, however, strikingly divergent among biomes: most summits in boreal and temperate regions have gained additional species (43 out of 52; average increase from 38.0 to 41.9, $t = 4.0$, df = 39, $p = 0.0004$) and only two have lost one species each. By contrast, from the 14 summits in Mediterranean regions, the majority (eight) had lower species counts in 2008 than in 2001, and only two have gained additional species (average decrease from 23.6 to 22.2, $t = -2.9$, df = 10, $p = 0.018$; Fig. 2A).

At the regional scale, observed changes were congruent with summit-level trends: species richness increased in 12, decreased in three, and remained constant in two regions (Fig. 1 and 2A). On average, species numbers per region were rising from 75.4 to 80.6 ($t = 2.8$, df = 16, $p = 0.013$). All 12 regions with higher species richness in the second survey were located in the boreal or temperate zone (mean increase in species numbers from 83.2 to 90.8, $t = 3.82$, df = 12, $p = 0.001$), whereas species counts were decreasing in three out of four Mediterranean regions, although this was not statistically significant because of the low sample size (average decrease from 50.0 to 47.5 species, $t = -2.1$, df = 3, $p = 0.12$; Fig. 2A).

To evaluate whether these changes in summit species richness might be related to a possible upward, or downward, move of species ranges we calculated an altitudinal index for each species within each region in both 2001 and 2008. To compute this index we first defined the relative altitude of each summit as the altitude above the lowest summit within the region it belongs to. Next, we weighted these relative altitudes by the species' frequencies on the respective summits in either 2001 or 2008. Finally, we calculated the species' altitudinal index for a particular region and monitoring campaign as the weighted average altitude of its distribution observed in the respective region and year (*12*). For all species recorded in both years we then compared these altitudinal indices between 2001 and 2008 using linear mixed effects models. The results suggest that species were indeed shifting their distributions to higher altitudes, by 2.7 m, on average (Table 1). This is in line with a recent related study which found evidence that the more warm-adapted species increase and the cold-adapted ones decline in European alpine summit vegetation (*15*). Interestingly, a general upward-shift, as indicated in our study, is consistent across the continent's biomes (Table 1). An overall upward move of species hence seems to be compatible with both an average increase and a decrease of summit plant richness.

Parallel relationships between the magnitude of the observed changes and the relative altitude of the summits within one region (i.e., its altitudinal difference to the region's lowest summit site) offer a clue for interpreting this unexpected finding: both gains (in the boreal-temperate) and losses (in the Mediterranean regions) were more pronounced on the lower summits (Fig. 2B). This suggests that upward shifts of plants are mostly driven by leading edge expansions on boreal to temperate mountains with the higher number of new arrivals on the lower peaks likely resulting from larger nearby pools of potential invaders. By contrast, rear-edge retractions seem to make an important contribution to altitudinal species shifts in the Mediterranean.

We hypothesize that the range expansion in the boreal to temperate mountains is a result of warmer conditions, such as previously observed (e.g. *7, 9, 16*), whereas range retractions in the Mediterranean mountain ranges result from a combination of rising summer temperatures and stable to decreasing precipitation sums, such as was recently documented for southern Europe for the past decades (*17-19*). As a corollary, a possible attenuation of low temperature constraints on Europe's Mediterranean mountains is likely foiled by rising water stress, and particularly so at the lowest summits, because aridity generally decreases with altitude in the Mediterranean basin (*20*). In line with this interpretation, Crimmins et al. (*21*) have recently suggested rapid responses of Californian Mediterranean-type mountain plants to changing climatic water balance, though in the opposite direction; i.e., a downward shift of species' optimum elevations through increasing water availability. Yet, McCain and Colwell (*22*) suggested in a global study, albeit on vertebrates, that population extirpation risks in mountain areas due to climate warming would increase 10-fold, on average, when decreases in precipitation were also considered.

Species losses on Mediterranean summits are worrying because southern European mountain floras have high proportions of endemic plants (*12, 23*) (Fig. 1). Indeed, there were 31% endemics among the species not re-detected on those summits where they were recorded in 2001 (17 out of 55 species), but only 13% among the species first detected on a particular summit in 2008 (32 out of 239; test on proportional equality: $X^2 = 8.7$, df = 1, $p = 0.003$). This does not imply that mountain endemics are intrinsically more threatened by a warming climate but follows from simultaneous species loss in areas rich in endemics (Mediterranean) and species gains where endemics are rarer (boreal and temperate mountains). In total, the number of species recorded across all 66 summits increased from 821 to 869 species (i.e., by *c.* 6%), whereas the number of endemics increased at a much lower rate, from 201 to 203 species (i.e., *c.* 1%). Overall, the proportion of endemics within our sample of Europe's summit flora hence decreased from 24.5% to 23.4%. Although this decrease is not significant yet (test on proportional equality: $X^2 = 0.24$, df = 1, $p = 0.63$), it would become so after 25 years if average annual rates of species gains remain constant for both endemic, ~ 0.25 species / year, and non-endemic plants, ~ 5.75 species / year. In the long run, such a decrease in the share of endemics will tend to homogenize the species composition of mountain top communities across regions.

In summary, our observations match the general expectation of a climate warming driven upward shift of species distributions (*2, 3, 14, 15, 24*). However, they show that these upward shifts do not necessarily result in higher species richness on mountaintops. If rising aridity is actually the driver of observed species loss on many Mediterranean summits, this trend is likely to continue during the coming decades because climate models predict increasing temperatures, decreasing annual precipitation, and an extension of the dry summer season in southern Europe (*25-27*). Owing to the high degree of endemism in these regions, the species pool of the continent's mountain flora might shrink even if local diversity on the majority of boreal and temperate mountaintops increases.

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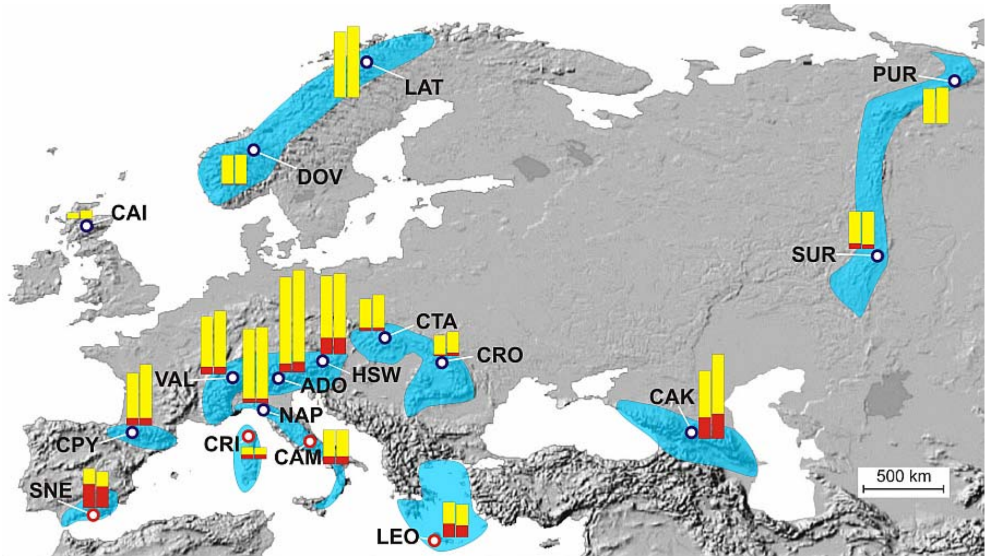

Fig. 1. Vascular plant species numbers in the 17 study regions. Blue circles indicate boreal and temperate, red circles Mediterranean regions. Bars show the number of species found in 2001 (left) and 2008 (right bar); the proportion of endemic species is shown in red. Species number (endemic number) per region in 2001/in 2008: LAT (N-Scandes/Sweden, 109(0)/118(0); PUR (Polar Urals/Russia), 58(0)/60(0); DOV (S-Scandes/Norway), 49(1)/50(1); CAI (Cairngorms/UK), 10(0)/14(0); SUR (S-Urals/Russia), 62(9)/62(7); CTA (High Tatra/Slovakia), 53(5)/60(5); HSW (NE-Alps/Austria), 130(27)/134(27); CRO E-Carpathians/Romania), 33(2)/40(5); ADO (S-Alps/Italy), 158(14)/170(17); VAL (W-Alps/Switzerland), 96(12)/105(12); NAP (N-Apennines/Italy), 123(7)/126(7); CPY (Central Pyrenees/Spain), 87(12)/101(12); CAK (Central Caucasus/Georgia), 113(35)/140(41); CRI (Corsica/France), 20(7)/19(7); CAM (Central Apennines/Italy), 57(13)/57(13); SNE (Sierra Nevada/Spain), 65(39)/60(35); LEO (Lefka Ori-Crete/Greece), 58(22)/54(19). Blue shaded areas indicate the respective maximum distribution of species defined as endemic (*12*); note that most endemics have a by far more narrow distribution area.

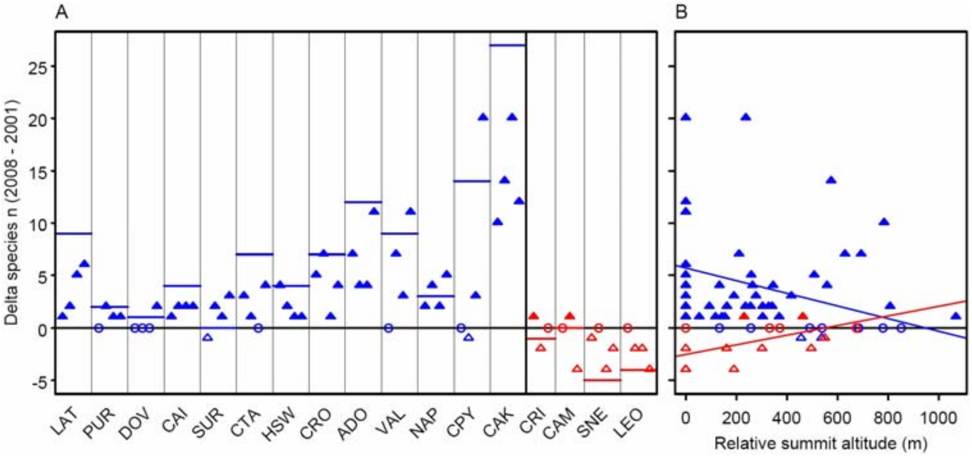

Fig. 2. Changes in vascular plant species numbers on 66 European summits between the years 2001 and 2008. (**A**) Summits within 13 boreal-temperate (blue) and 4 Mediterranean (red) mountain regions are arranged from north to south, and from high to low altitude within regions. Triangles represent the increase (filled) or decrease (empty) of observed species numbers per summit, horizontal lines the changes in species numbers per region. Summits where species numbers did not change are symbolized by empty circles. Region-scale changes were calculated after pooling species lists of all the summits surveyed within the respective region, i.e., each species was only counted once per region and observation year. For full region names see Fig. 1. (**B**) Summits are arranged along the x-axis according to their relative altitudes within regions, with a value of zero for the lowest summit in the respective region. Lines are drawn based on the fixed effect coefficients of linear mixed effects models regressing the change in species number per summit on this summit's relative altitude. The slope coefficients are significantly different from zero in both cases (boreal-temperate summits: -0.006, t = -3.3, df = 38, p = 0.002; Mediterranean summits: 0.005, t = 2.5, df = 9, p = 0.034).

Table 1. Change in the species' altitudinal distribution between 2001 and 2008. Coefficients measure the average shift of the species' altitudinal index between 2001 and 2008 (in meters). SE, df, *t*, and *p* are the standard errors of the coefficients, the degrees of freedom, the *t*-values of the coefficient given the specified degrees of freedom, and the associated two-sided *p*-values.

	Coef (m)	**SE**	**df**	***t***	***p***
All summits	2.7	1.10	1246	2.5	**0.012**
Boreal and temperate	2.7	1.23	1060	2.2	**0.028**
Mediterranean	2.5	1.1	185	2.3	**0.024**

Supplementary Materials:

Materials and Methods

Figs. S1, S2

Tables S1-S4

References (*28-32*)