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Supplementary Materials for

Recent Plant Diversity Changes on Europe's Mountain Summits

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Materials and Methods

Study regions and field sites

We surveyed 66 summit sites of 17 mountain regions, distributed across Europe from the northern boreal to the temperate and to the Mediterranean zone (Fig. 1). Mediterranean mountain regions were defined as those lying within the Mediterranean biome according to Olson et al. (*28*). Sites were first recorded in the European Commission's FP5 project GLORIA-Europe in 2001 and surveys were repeated in 2008. In each mountain region, four sites (in two regions only three because of terrain constraints) on mountain summits of different altitude span an elevation gradient from the treeline ecotone to the uppermost zone where vascular plants occur. The study sites are part of the international long-term monitoring network GLORIA (Global Observation Research Initiative in Alpine Environments; http://www.gloria.ac.at), focusing on effects of climate change on high-mountain plant diversity.

Each summit site was divided into eight sampling areas (summit area sections), which covered the summit terrain from its top down to the 10-m contour line (see Fig. S1 and reference *13* in the main text). Each summit area section was surveyed separately for a complete list of vascular plant species.

Species lists and endemics

Field teams were trained in critically identifying all vascular taxa at the vegetative stage by leading experts of the regional flora before the actual start of the surveys, and in each of the teams at least one expert participated in the 2001 and the 2008 surveys. Doubtful cases usually were collected for subsequent identification (for species with rare occurrences, however, from outside the survey area). Synonym names were carefully checked across all regions before data were entered into the database. Species names refer to Flora Europaea (*29*).

Endemic taxa: As generally defined in biogeography, an endemic species is restricted to a particular geographical region of variable extension, sometimes of a very restricted range (narrow endemics). In this study we considered those species as endemics that are exclusive to a single mountain system: i.e., from north to south: the Scandes, Urals, Carpathians, Alps, Pyrenees, Greater Caucasus, Apennines, or the Baetic Cordillera of southern Spain. In the case of the Mediterranean island sites: Corsica and Sardinia or Crete and the Aegean region (compare Fig. 1). Most of the endemic species are, in fact, narrow endemics having a very limited distribution within the respective mountain system. In addition, their vertical range is restricted in many cases to the upper part of the mountains (*30*). Hence their distribution is highly fragmented and comparable to geographic islands. However, a narrow endemic may not be particularly rare within an observation site.

Pre-processing of data

Collecting species lists is prone to observation errors. In particular, rare and inconspicuous species might be overlooked and related species, e.g., those from the same genera, might be confounded in consecutive monitoring cycles hence causing a spurious species turnover (*31*). To reduce the noise from such errors in our data, we filtered species lists in two ways: first, all species which have been recorded in only one summit area section (*SAS*) of a particular summit in either 2001 or 2008 (or in both years) were eliminated from the species lists of this summit in both years. Put it another way, both the 2001 and 2008 lists of a particular summit only contained those species which were detected in at least two *SAS* in both years; or which were observed in at least two *SAS* in the respective year, but not detected at all in the other one. From this reduced list we, second, eliminated all pairs of congeners with a mutually exclusive record in just one year, i.e., all cases of apparent turnover between species of the same genus.

We have, however, repeated all analyses in the paper with the unfiltered raw data (compare Fig. S2 and Tables S1 to S4) and the results were qualitatively consistent throughout.

Change in species richness

To analyse changes in species richness at the summit level, we pooled the records of its *SAS*. First we calculated the difference in the number of species found per summit in both years of observation, i.e., we subtracted the species counts of 2001 from those of 2008. These differences were then tested for deviation from zero by means of a linear mixed effects model (function *lme* in R-package *nlme*) (*32*) with the summits grouped by the study region they belong to. At the region level, the same procedure was applied except for using a simple generalized linear model with an identity link function. Distributional assumptions were tested by means of qq-plots beforehand.

We moreover analysed how the change in species number on a particular summit between 2001 and 2008 depends on this summit's relative altitude. Relative altitude was defined as the elevational difference between a particular summit and the lowest summit in the respective region. We, again, used linear mixed effects model with the summits grouped by the study region they belong to in this analysis. The difference in species numbers was the response and the summit's relative altitude the fixed-effect predictor in these models.

Change in altitudinal distributions

For all species that have been found both in 2001 and 2008 we calculated an altitudinal index of their distribution within a particular mountain region for each of the two monitoring campaigns as:

$$Index_{i,r,M} = \frac{\sum_{s=1}^{n} \Delta m_{s,r} * SAS_{i,s,r,M}}{\sum_{s=1}^{n} SAS_{i,s,r,M}}$$

The value of the index for species *i* within region *r* at campaign *M* is hence calculated by first computing a weighted sum over the relative altitudes $\Delta m_{s,r}$ of all summits *s* belonging to this region (defined as above). The weighting factor $SAS_{i,s,r,M}$ is the frequency of the species *i* at the respective summit during campaign *M* (i.e., the number of summit area sections, *SAS*, within which the species was observed on summit *s*). To rescale this sum to unit altitude we divide by the species' total frequency within region *r* at campaign *M* (i.e., the total number of summit area sections, *SAS*, within which it was observed on all four summits of this region). Altogether, the index hence represents the weighted average of a species' altitudinal distribution within a particular region and monitoring campaign.

We then tested whether the altitudinal index values of the species have changed between 2001 and 2008, i.e., if there is any indication of an up- or downslope shift of their distributions. We therefore used linear mixed effects models with the index value as the response and the year of observation as the fixed-effects predictor variable as well as species nested in mountain region *r* as grouping factors with separate random intercept terms.

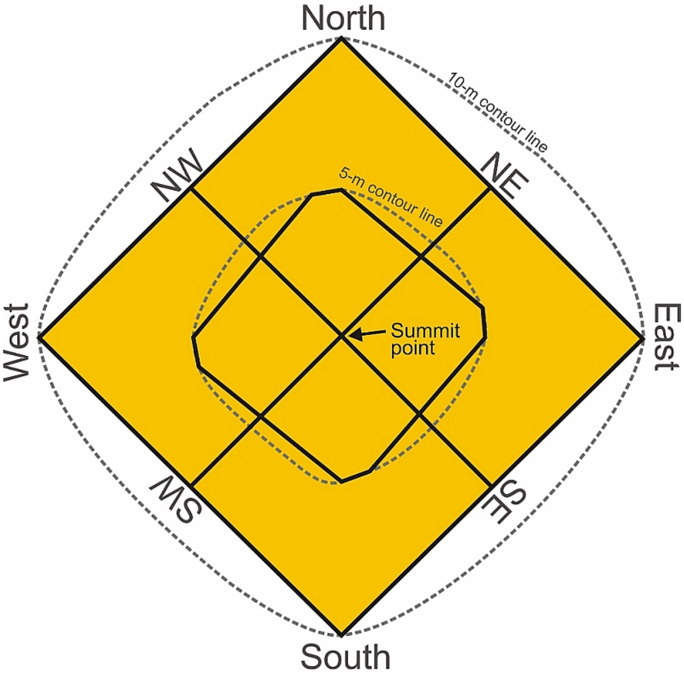

Fig. S1. Basic design of a study summit, divided into eight summit area sections (*SAS*) that were used as sampling areas; the upper four areas extend from the summit point down to the 5-m contour line, the four lower from the 5-m to the 10-m contour line.

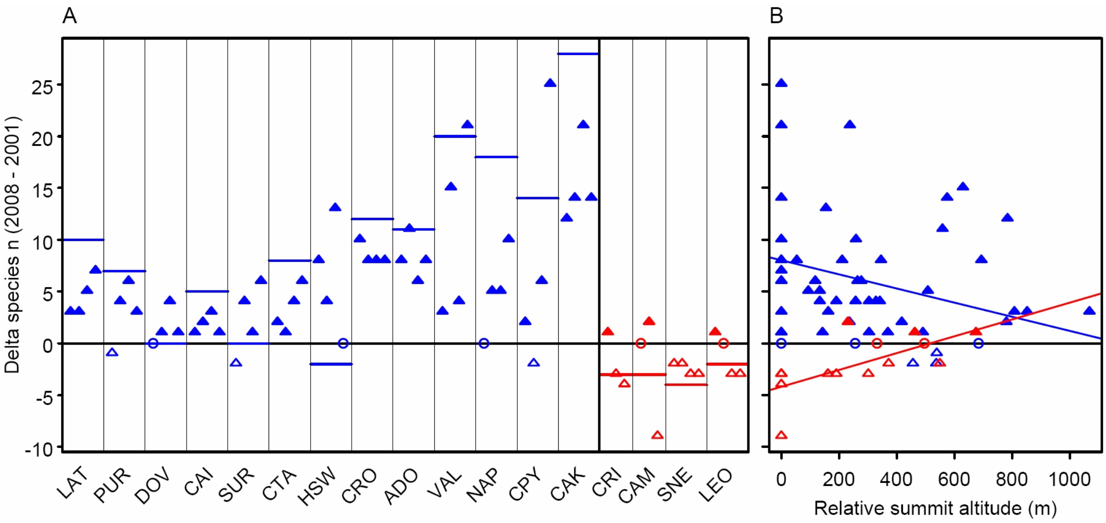

Fig. S2. Changes in vascular plant species numbers on 66 European summits between the years 2001 and 2008, based on unfiltered raw data. (**A**) Summits within 13 boreal-temperate (blue) and 4 Mediterranean (red) mountain regions are arranged from north to south, and from high to low altitude within 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: -0.007, $t = -2.7$, df = 38, $p = 0.01$; Mediterranean summits: 0.008, $t = 3.03$, df = 9, $p = 0.014$).

Table S1. The number of species (with the number of regionally endemic species in parenthesis) found on the 66 European summits (grouped into 17 mountain regions, sorted from north to south) during the first and second monitoring campaign in the years 2001 and 2008, respectively. Raw data columns refer to unprocessed data, filtered data columns to the data pre-processed as defined in Materials and Methods.

Region	Summit	Altitude (m)	Raw data		Filtered data	
			2001	2008	2001	2008
N-Scandes/Sweden (LAT)	KTJ	1560	4 (0)	7 (0)	3 (0)	4 (0)
N-Scandes/Sweden (LAT)	LCH	1300	54 (0)	57 (0)	37 (0)	39 (0)
N-Scandes/Sweden (LAT)	KVA	1000	91 (0)	96 (0)	69 (0)	74 (0)
N-Scandes/Sweden (LAT)	RVA	492	92 (0)	99 (0)	72 (0)	78 (0)
Polar Ural/Russia (PUR)	POU	839	4 (0)	3 (0)	0 (0)	0 (0)
Polar Ural/Russia (PUR)	MPO	641	50 (0)	54 (0)	39 (0)	41 (0)
Polar Ural/Russia (PUR)	SLA	417	38 (0)	44 (0)	32 (0)	33 (0)
Polar Ural/Russia (PUR)	SHL	300	35 (0)	38 (0)	23 (0)	24 (0)
S-Scandes/Norway (DOV)	SKI	1845	6 (0)	6 (0)	3 (0)	3 (0)
S-Scandes/Norway (DOV)	KOL	1651	21 (0)	22 (0)	14 (0)	14 (0)
S-Scandes/Norway (DOV)	VKO	1418	14 (0)	18 (0)	13 (0)	13 (0)
S-Scandes/Norway (DOV)	VAR	1161	56 (1)	57 (1)	41 (1)	43 (1)
Cairngorms/UK (CAI)	SGO	1111	7 (0)	8 (0)	6 (0)	7 (0)
Cairngorms/UK (CAI)	UNK	978	9 (0)	11 (0)	7 (0)	9 (0)
Cairngorms/UK (CAI)	CAM	904	9 (0)	12 (0)	6 (0)	8 (0)
Cairngorms/UK (CAI)	MIG	742	8 (0)	9 (0)	7 (0)	9 (0)
S-Ural/Russia (SUR)	BIR	1565	38 (10)	36 (8)	27 (7)	26 (5)
S-Ural/Russia (SUR)	MIR	1437	54 (7)	58 (6)	41 (6)	43 (6)
S-Ural/Russia (SUR)	NUR	1413	36 (9)	37 (7)	28 (6)	29 (6)
S-Ural/Russia (SUR)	TAG	1109	30 (2)	36 (3)	24 (2)	27 (3)
High Tatra/Slovakia (CTA)	KRA	2336	40 (4)	42 (5)	25 (4)	28 (4)
High Tatra/Slovakia (CTA)	SED	2061	38 (4)	39 (3)	31 (2)	32 (2)
High Tatra/Slovakia (CTA)	VEK	2052	28 (3)	32 (3)	23 (2)	23 (2)
High Tatra/Slovakia (CTA)	KRI	1919	42 (3)	48 (3)	37 (3)	41 (3)
NE-Alps/Austria (HSW)	ZAK	2255	78 (17)	86 (21)	57 (14)	61 (16)
NE-Alps/Austria (HSW)	GHK	2214	96 (24)	100 (23)	75 (21)	77 (21)
NE-Alps/Austria (HSW)	WEK	2065	91 (21)	104 (25)	69 (17)	70 (17)
NE-Alps/Austria (HSW)	ZIK	1910	146 (25)	146 (25)	108 (19)	109 (19)
E-Carpathians/Romania (CRO)	REB	2268	24 (4)	34 (6)	16 (2)	21 (3)
E-Carpathians/Romania (CRO)	BUH	2221	22 (2)	30 (4)	18 (2)	25 (4)
E-Carpathians/Romania (CRO)	GRO	2063	34 (2)	42 (4)	27 (1)	28 (2)
E-Carpathians/Romania (CRO)	GOL	2010	30 (1)	38 (2)	26 (1)	30 (1)
S-Alps/Italy (ADO)	MTS	2893	30 (8)	38 (13)	20 (3)	27 (6)
S-Alps/Italy (ADO)	RNK	2757	73 (11)	84 (14)	49 (10)	53 (12)
S-Alps/Italy (ADO)	PNL	2463	79 (12)	85 (15)	54 (9)	58 (11)
S-Alps/Italy (ADO)	GRM	2199	145 (8)	153 (8)	117 (7)	128 (7)
W-Alps/Switzerland (VAL)	BOV	3212	6 (1)	9 (1)	4 (1)	4 (0)
W-Alps/Switzerland (VAL)	PAR	2989	49 (7)	64 (9)	24 (2)	31 (4)
W-Alps/Switzerland (VAL)	BRU	2550	70 (7)	74 (7)	48 (3)	51 (3)

W-Alps/Switzerland (VAL)	LAL	2360	98 (9)	119 (9)	73 (7)	84 (7)
N-Apennines/Italy (NAP)	CAS	1978	108 (9)	108 (9)	79 (7)	81 (7)
N-Apennines/Italy (NAP)	MOM	1855	97 (5)	102 (5)	71 (5)	75 (4)
N-Apennines/Italy (NAP)	PCA	1815	92 (6)	97 (5)	75 (4)	77 (4)
N-Apennines/Italy (NAP)	FOG	1722	77 (6)	87 (5)	56 (4)	61 (4)
Central Pyrenees/Spain (CPY)	OLA	3022	11 (3)	13 (3)	8 (3)	8 (3)
Central Pyrenees/Spain (CPY)	TOB	2779	25 (3)	23 (3)	17 (2)	16 (2)
Central Pyrenees/Spain (CPY)	CUS	2519	63 (5)	69 (3)	46 (3)	49 (3)
Central Pyrenees/Spain (CPY)	ACU	2242	75 (10)	100 (10)	53 (7)	73 (7)
Central Caucasus/Georgia (CAK)	CP4	3024	28 (8)	40 (12)	26 (8)	36 (11)
Central Caucasus/Georgia (CAK)	CP3	2815	21 (3)	35 (7)	20 (2)	34 (6)
Central Caucasus/Georgia (CAK)	CP2	2477	73 (16)	94 (21)	70 (16)	90 (21)
Central Caucasus/Georgia (CAK)	CP1	2240	62 (20)	76 (23)	60 (19)	72 (22)
Corsica/France (CRI)	EBO	2607	7 (3)	8 (3)	2 (1)	3 (1)
Corsica/France (CRI)	BOR	2305	14 (4)	11 (5)	11 (4)	9 (4)
Corsica/France (CRI)	COR	2144	17 (5)	13 (5)	11 (4)	11 (4)
Central Apennines/Italy (CAM)	MAM	2737	20 (11)	20 (9)	15 (7)	15 (6)
Central Apennines/Italy (CAM)	MAC	2635	41 (11)	43 (12)	34 (10)	35 (10)
Central Apennines/Italy (CAM)	FEM	2405	68 (15)	59 (11)	47 (10)	43 (8)
Sierra Nevada/Spain (SNE)	MAC	3327	18 (15)	16 (14)	11 (9)	10 (8)
Sierra Nevada/Spain (SNE)	TCA	3150	40 (29)	38 (29)	24 (19)	24 (19)
Sierra Nevada/Spain (SNE)	CUP	2968	52 (31)	49 (28)	40 (22)	36 (20)
Sierra Nevada/Spain (SNE)	PUL	2778	47 (22)	44 (20)	38 (18)	36 (16)
Lefka Ori-Crete/Greece (LEO)	STR	2339	14 (5)	15 (6)	12 (3)	12 (3)
Lefka Ori-Crete/Greece (LEO)	SEK	2160	18 (5)	18 (6)	15 (4)	13 (4)
Lefka Ori-Crete/Greece (LEO)	CHO	1965	30 (12)	27 (11)	21 (8)	19 (8)
Lefka Ori-Crete/Greece (LEO)	LOW	1664	57 (23)	54 (19)	49 (21)	45 (17)

Table S2. Results of linear mixed effects models comparing the number of species on the 66 European summits monitored in both 2001 and 2008. "Filtered data" are models based on a dataset where species had to be recorded with a minimum frequency, i.e., we restricted the 2001 and 2008 species lists of a summit to those species that have been recorded within at least two summit area sections in both years of observation, or in within at least two summit area sections in one year, and in none in the other one; and where pairs of congeners with complementary records on the same summit in the two monitoring periods have been removed. "Raw data" are models based on the data that have not been pre-processed. The coefficients (Coef) give the average increase or decrease in species numbers (NSp.) per decade across all summits, i.e., the fixed effects of the models. SE, df, t, and p are the standard errors of the coefficients, the degrees of freedom, the t-values and the associated p-values, respectively. p-values are for a two-sided test of the hypothesis of constant species richness. For more details see Materials and Methods.

	Coef (NSp.)	**SE**	**df**	t	p
All regions					
Filtered data	2.7	1.93	49	2.90	0.006
Raw data	4.2	1.19	49	3.47	0.001
Boreal & temperate					
Filtered data	3.9	0.10	39	3.95	0.0004
Raw data	6.0	1.23	39	5.37	< 0.0001
Mediterranean					
Filtered data	-1.4	0.48	10	-2.9	0.018
Raw data	-2.0	0.74	10	-2.7	0.022

Table S3. Change in the species' altitudinal distribution between 2001 and 2008, calculated from the raw data. 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	4.2	1.41	1506	2.94	0.004
Boreal & temperate	4.0	1.58	1282	2.52	0.012
Mediterranean	5.0	2.87	223	1.74	0.082

Table S4. Example of data pre-processing filters. Species records at the CPY-CUS summit (Central Pyrenees, Spain) in the years 2001 and 2008. The numbers refer to the number of summit area sections (*SAS*) a species was observed in. In blue are species filtered according to the doubleton criterion (only one *SAS* in one or both years), in red species filtered due to complementary congener criterion (two congeners with complementary records in both years).

Species	2001	2008
Agrostis alpina Scop.	4	4
Alchemilla alpina L.	6	0
Alchemilla lapeyrousii Buser	0	6
Antennaria dioica (L.) Gaertn.	3	2
Anthyllis vulneraria L. subsp. alpestris (Hegetschw.) Asch. & Graebn.	5	3
Arabis scabra All.	0	1
Arenaria ciliata L. subsp. moehringioides (Murr) Braun-Blanq.	8	7
Arenaria purpurascens Ramond ex DC.	8	8
Arenaria serpyllifolia L.	1	0
Asplenium trichomanes-ramosum L.	3	2
Botrychium lunaria (L.) Sw.	7	6
Campanula cochlearifolia Lam.	4	4
Campanula scheuchzeri Vill.	2	2
Carduus carlinoides Gouan subsp. carlinoides	1	0
Carex curvula All. subsp. rosae Gilomen	1	3
Carex ornithopoda Willd. subsp. ornithopoda	6	5
Carex rupestris All.	5	8
Cerastium arvense L.	0	2
Cirsium acaule Scop. subsp. acaule	0	1
Crepis pygmaea L. subsp. pygmaea	0	1
Cystopteris fragilis (L.) Bernh.	3	4
Erigeron uniflorus L.	7	8
Euphrasia salisburgensis Funck	6	7
Festuca gautieri (Hack.) K.Richt.	8	8
Festuca glacialis (Miégeville ex Hack.) K.Richt.	6	7
Festuca ovina agg.	0	1
Festuca pyrenaica Reut.	8	8
Festuca rubra agg.	4	1
Galium marchandii Roem. & Schult.	1	3
Galium pyrenaicum Gouan	6	7
Gentianella campestris (L.) Börner subsp. campestris	3	1
Gentiana nivalis L.	5	5
Gentiana verna L. subsp. verna	4	5
Geranium cinereum Cav. subsp. cinereum	8	8
Helictotrichon sedenense (DC.) Holub	8	8
Hieracium lactucella Wallr.	6	7
Leontodon hispidus L.	2	2
Leontodon pyrenaicus Gouan subsp. pyrenaicus	3	5
Leucanthemopsis alpina (L.) Heywood subsp. alpina	7	6

Linaria alpina (L.) Mill.	2	4
Lotus alpinus (DC.) Schleich. ex Ramond	5	5
Luzula spicata (L.) DC.	5	5
Minuartia verna (L.) Hiern subsp. verna	1	2
Nardus stricta L.	0	1
Oxytropis pyrenaica Godr. & Gren.	0	3
Paronychia kapela (Hacq.) A.Kern. subsp. serpyllifolia (Chaix) Graebn.	0	1
Phyteuma hemisphaericum L.	3	5
Phyteuma orbiculare L.	0	1
Plantago alpina L.	0	2
Poa alpina L.	8	8
Poa glauca Vahl	1	0
Polygala alpestris Rchb. subsp. alpestris	1	0
Polygonum viviparum L.	6	7
Potentilla brauniana Hoppe	1	3
Potentilla nivalis Lapeyr.	6	5
Potentilla tabernaemontani Asch.	3	6
Ranunculus parnassiifolius L. subsp. heterocarpus P.Küpfer	8	8
Salix pyrenaica Gouan	1	0
Saxifraga aizoides L.	2	3
Saxifraga exarata Vill. subsp. moschata (Wulfen) Cavill.	8	8
Saxifraga oppositifolia L.	8	8
Saxifraga paniculata Mill.	6	8
Sedum atratum L. subsp. atratum	1	2
Sedum brevifolium DC.	1	0
Sempervivum montanum L. subsp. montanum	4	4
Silene acaulis (L.) Jacq.	8	8
Taraxacum apenninum agg.	8	8
Thalictrum alpinum L.	2	3
Thymus nervosus J.Gay ex Willk.	8	8
Trifolium alpinum	0	1
Trifolium pratense L.	5	3
Trifolium thalii Vill.	8	6
Veronica aphylla L.	1	3
Veronica nummularia Gouan	1	2
Vitaliana primuliflora Bertol. subsp. canescens O.Schwarz	1	1

References and Notes

1. W. Thuiller, S. Lavorel, M. B. Araújo, M. T. Sykes, I. C. Prentice, Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 8245 (2005). doi:10.1073/pnas.0409902102 Medline

2. R. Engler *et al.*, 21st century climate change threatens mountain flora unequally across Europe. *Glob. Change Biol.* **17**, 2330 (2011). doi:10.1111/j.1365-2486.2010.02393.x

3. I. C. Chen, J. K. Hill, R. Ohlemüller, D. B. Roy, C. D. Thomas, Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024 (2011). doi:10.1126/science.1206432 Medline

4. J.-P. Theurillat, A. Guisan, *Clim. Change* **50**, 77 (2001). doi:10.1023/A:1010632015572

5. R. K. Colwell, G. Brehm, C. L. Cardelús, A. C. Gilman, J. T. Longino, Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* **322**, 258 (2008). doi:10.1126/science.1162547 Medline

6. G. Grabherr, M. Gottfried, H. Pauli, Climate effects on mountain plants. *Nature* **369**, 448 (1994). doi:10.1038/369448a0

7. K. Klanderud, H. J. B. Birks, Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene* **13**, 1 (2003). doi:10.1191/0959683603hl589ft

8. A. E. Kelly, M. L. Goulden, Rapid shifts in plant distribution with recent climate change. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 11823 (2008). doi:10.1073/pnas.0802891105 Medline

9. P. Vittoz, J. Bodin, S. Ungricht, C. Burga, G. R. Walther, One century of vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps. *J. Veg. Sci.* **19**, 671 (2008). doi:10.3170/2008-8-18434

10. H. Pauli, M. Gottfried, K. Reiter, C. Klettner, G. Grabherr, Signals of range expansions and contractions of vascular plants in the high Alps: Observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Glob. Change Biol.* **13**, 147 (2007). doi:10.1111/j.1365-2486.2006.01282.x

11. K. J. Feeley *et al.*, Upslope migration of Andean trees. *J. Biogeogr.* **38**, 783 (2011). doi:10.1111/j.1365-2699.2010.02444.x

12. Materials and methods are available as supplementary materials on *Science* Online.

13. H. Pauli *et al.*, *The GLORIA Field Manual—Multi-Summit Approach* (Office for Official Publications of the European Communities, Luxembourg, 2004).

14. M. Gottfried *et al.*, Coincidence of the alpine-nival ecotone with the summer snowline. *Environ. Res. Lett.* **6**, 014013 (2011). doi:10.1088/1748-9326/6/1/014013

15. M. Gottfried *et al.*, Continent-wide response of mountain vegetation to climate change. *Nat. Clim. Change* **2**, 111 (2012). doi:10.1038/nclimate1329

16. G.-R. Walther, S. Beißner, C. A. Burga, Trends in the upward shift of alpine plants. *J. Veg. Sci.* **16**, 541 (2005). doi:10.1111/j.1654-1103.2005.tb02394.x

17. A. Mariotti *et al*., Mediterranean water cycle changes: Transition to drier 21st century conditions in observations and CMIP3 simulations. *Environ. Res. Lett.* **3**, 044001 (2008). doi:10.1088/1748-9326/3/4/044001

18. S. del Río, L. Herrero, R. Fraile, A. Penas, Spatial distribution of recent rainfall trends in Spain (1961-2006). *Int. J. Climatol.* **31**, 656 (2011). doi:10.1002/joc.2111

19. A. Toreti, G. Fioravanti, W. Perconti, F. Desiato, Annual and seasonal precipitation over Italy from 1961 to 2006. *Int. J. Climatol.* **29**, 1976 (2009). doi:10.1002/joc.1840

20. H. Walter, S. W. Breckle, *Spezielle Ökologie der Gemäßigten und Arktischen Zonen Ausserhalb Euro-Nordasiens* (Gustav Fischer Verlag, Stuttgart, Germany, 1991).

21. S. M. Crimmins, S. Z. Dobrowski, J. A. Greenberg, J. T. Abatzoglou, A. R. Mynsberge, Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* **331**, 324 (2011). doi:10.1126/science.1199040 Medline

22. C. M. McCain, R. K. Colwell, Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecol. Lett.* **14**, 1236 (2011). doi:10.1111/j.1461-0248.2011.01695.x Medline

23. L. Nagy, G. Grabherr, C. Körner, D. B. A. Thompson, *Alpine Biodiversity in Europe* (Springer, Berlin, 2003), vol. 167.

24. C. M. Van de Ven, S. B. Weiss, W. G. Ernst, Plant species distributions under present conditions and forecasted for warmer climates in an arid mountain range. *Earth Interact.* **11**, 1 (2007). doi:10.1175/EI205.1

25. J. H. Christensen *et al*., in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, S. Solomon *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 2007), pp. 847–940.

26. D. Nogués Bravo, M. B. Araújo, T. Lasanta, J. I. López Moreno, Climate change in Mediterranean mountains during the 21st century. *Ambio* **37**, 280 (2008). doi:10.1579/0044-7447(2008)37[280:CCIMMD]2.0.CO;2 Medline

27. B. Benito, J. Lorite, J. Penas, Simulating potential effects of climatic warming on altitudinal patterns of key species in Mediterranean-alpine ecosystems. *Clim. Change* **108**, 471 (2011). doi:10.1007/s10584-010-0015-3

28. D. M. Olson *et al*., Terrestrial ecoregions of the world: A new map of life on Earth. *Bioscience* **51**, 933 (2001). doi:10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

29. T. G. Tutin *et al*., *Flora Europaea*, vols. 1 to 5 and CD (Cambridge Univ. Press, Cambridge, 2001).

30. H. Pauli, M. Gottfried, T. Dirnböck, S. Dullinger, G. Grabherr, in *Alpine Biodiversity in Europe—A Europe-Wide Assessment of Biological Richness and Change*, L. Nagy, G. Grabherr, C. Körner, D. B. A. Thompson, Eds. (Springer, Berlin, 2003), pp. 195–207.

31. P. Vittoz *et al*., Reproducibility of species lists, visual cover estimates and frequency methods for recording high-mountain vegetation. *J. Veg. Sci.* **21**, 1035 (2010). doi:10.1111/j.1654-1103.2010.01216.x

32. J. C. Pinheiro, D. M. Bates, S. DebRoy, D. Sarkar, R-Core-team, nlme: Linear and nonlinear mixed effects models. R package version 3.1-89 (2008).