

# Continent-wide response of mountain vegetation to climate change

Michael Gottfried<sup>1</sup>, Harald Pauli<sup>2\*</sup>, Andreas Futschik<sup>3</sup>, Maia Akhalkatsi<sup>4</sup>, Peter Barančok<sup>5</sup>, José Luis Benito Alonso<sup>6</sup>, Gheorghe Coldea<sup>7</sup>, Jan Dick<sup>8</sup>, Brigitta Erschbamer<sup>9</sup>, María Rosa Fernández Calzado<sup>10</sup>, George Kazakis<sup>11</sup>, Ján Krajčí<sup>5</sup>, Per Larsson<sup>12</sup>, Martin Mallaun<sup>13</sup>, Ottar Michelsen<sup>14</sup>, Dmitry Moiseev<sup>15</sup>, Pavel Moiseev<sup>15</sup>, Ulf Molau<sup>16</sup>, Abderrahmane Merzouki<sup>10</sup>, Laszlo Nagy<sup>17,18</sup>, George Nakhutsrishvili<sup>19</sup>, Bård Pedersen<sup>20</sup>, Giovanni Pelino<sup>21</sup>, Mihai Puscas<sup>22</sup>, Graziano Rossi<sup>23</sup>, Angela Stanisci<sup>21</sup>, Jean-Paul Theurillat<sup>24,25</sup>, Marcello Tomaselli<sup>26</sup>, Luis Villar<sup>6</sup>, Pascal Vittoz<sup>27</sup>, Ioannis Vogiatzakis<sup>28</sup> and Georg Grabherr<sup>2</sup>

**Climate impact studies have indicated ecological fingerprints of recent global warming across a wide range of habitats<sup>1,2</sup>. Although these studies have shown responses from various local case studies, a coherent large-scale account on temperature-driven changes of biotic communities has been lacking<sup>3,4</sup>. Here we use 867 vegetation samples above the treeline from 60 summit sites in all major European mountain systems to show that ongoing climate change gradually transforms mountain plant communities. We provide evidence that the more cold-adapted species decline and the more warm-adapted species increase, a process described here as thermophilization. At the scale of individual mountains this general trend may not be apparent, but at the larger, continental scale we observed a significantly higher abundance of thermophilic species in 2008, compared with 2001. Thermophilization of mountain plant communities mirrors the degree of recent warming and is more pronounced in areas where the temperature increase has been higher. In view of the projected climate change<sup>5,6</sup> the observed transformation suggests a progressive decline of cold mountain habitats and their biota.**

The decade 2000–2009 was the warmest since the beginning of global climate measurements<sup>7</sup>, surpassing the 1990s, which unveiled ecological responses of many animals and plants<sup>8</sup>. Several of these previous studies were made in mountain areas where an increase in plant species richness has been shown<sup>9–13</sup>, and which coincide with projections of distribution models suggesting warming-induced upward range shifts<sup>14–16</sup>. These field studies, however, have been based on incidental historical data from a limited number of sites.

Based on a standardized and multiple-scale dataset for European mountain systems (GLORIA; ref. 17), we test the hypothesis of a synchronous change of plant communities towards a composition and structure that indicates a warming effect. In 2001, at 60 summit sites of different elevations distributed over 17 major European mountain regions, 1 × 1 m permanent plots, arranged in clusters of four quadrats (plot clusters), were established in each cardinal direction (Fig. 1c; ref. 17). In 2001 and 2008, data on species occurrences and cover were collected in the same standardized way. Our dataset comprised 764 vascular plant species (see Supplementary Information).

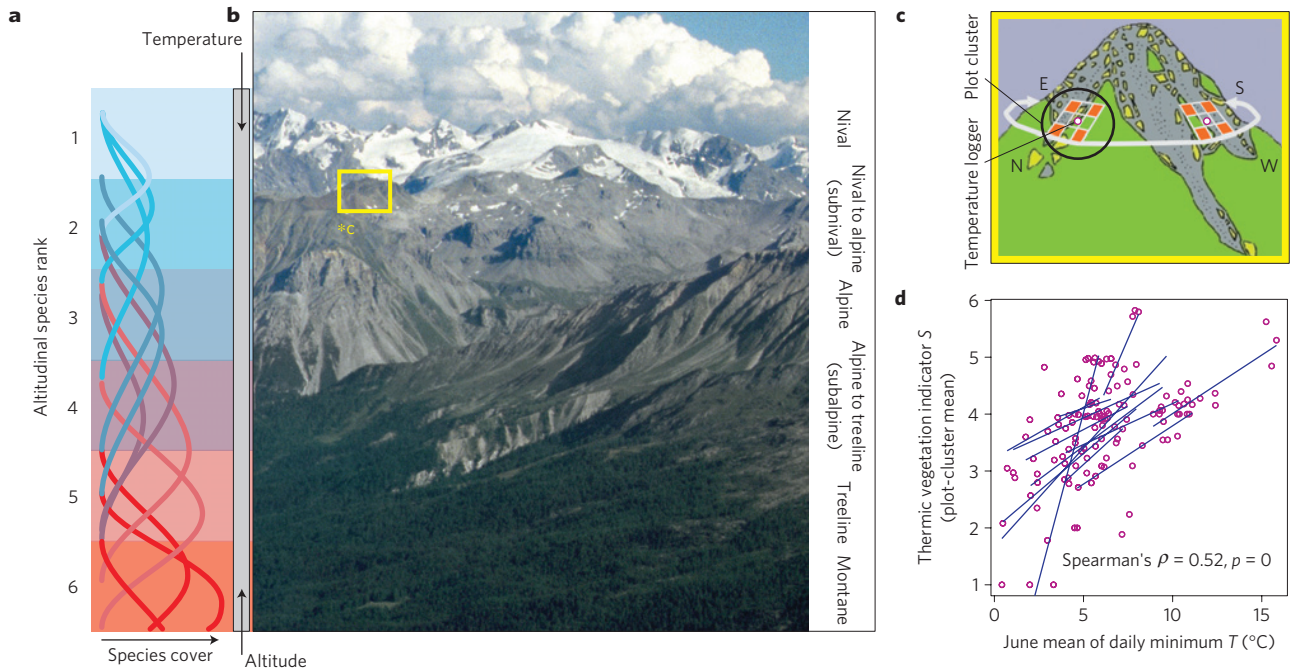
For detection of a warming effect, here termed thermophilization, we used the indicative value of the species found in a plot. The ecological indicator concept<sup>18</sup> relies on the realized position of a species along an environmental gradient, in our case altitude, which resembles a thermal gradient<sup>19</sup> (Fig. 1a). For some species their optimum performance is found in the treeline ecotone, whereas for others it is in the alpine zone, and in some cases close to the limits of plant life (nival zone; ref. 20; Fig. 1b). According to standard floras, an altitudinal rank was assigned to all recorded species (for details on ranking and effects of misclassifications see Supplementary Section S1 and Methods). For each plot, a composite score (that is, a weighted average<sup>21</sup>) in the following thermic vegetation indicator  $S$  was then calculated as

$$S = (\sum \text{rank}(\text{species}_i) \times \text{cover}(\text{species}_i)) / \sum \text{cover}(\text{species}_i) \quad (1)$$

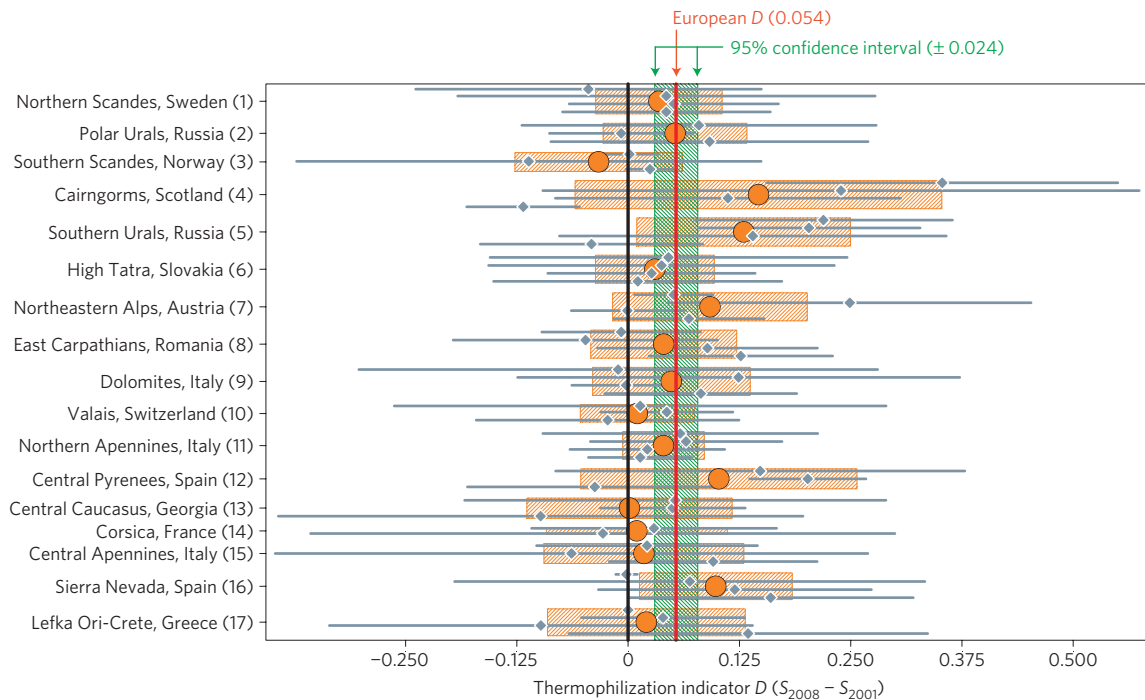
To justify the use of  $S$  as thermic indicator, we tested its correlation with habitat temperature, expressed by the average June daily minimum temperature ( $T_{\min}$ ), measured in the soil over the years 2001–2007 (Fig. 1d and Supplementary Section S2).

Differences of the thermic vegetation indicator  $S$  between 2001 and 2008 were used to quantify transformations of the plant communities, and termed thermophilization indicator  $D$  hereafter ( $D = S_{2008} - S_{2001}$ ).

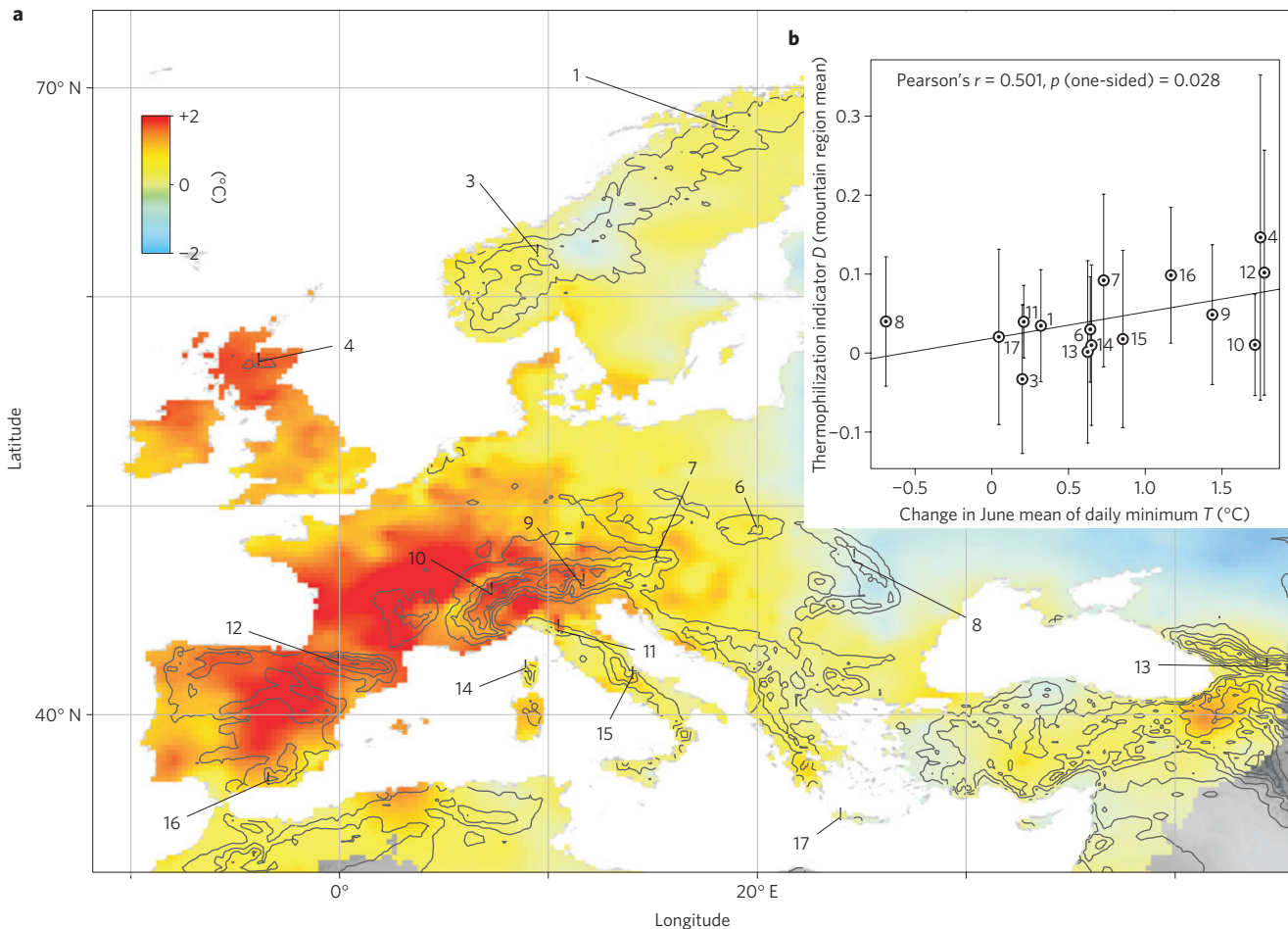
This transformation is driven by species cover changes within the plot and by immigration or disappearance of species. Positive differences (thermophilization) may result from increased cover and/or immigration of species with a higher rank (that is, of lower elevational ranges (thermophilic)) and/or the decline or loss of species of lower ranks (that is, higher elevational ranges (cryophilic)). Alpine plants are long-lived<sup>22</sup> and internal processes in alpine plant communities work at a slow rate<sup>23</sup>, thus it can be assumed that species cover does not vary much from year to year but shows a clear trend with increasing time intervals. Applying mixed-effects models, differences  $D$  were calculated at the continental scale as well as for each region and each summit. To interpret  $D$  in terms of climate change we used  $T_{\min}$  in June from gridded European temperature data at a resolution of 0.25° (E-OBS data<sup>24</sup>). As the climatic conditions during the preceding years of a survey (termed here as prior periods) are expected to



**Figure 1 | Plant species distribution and vegetation patterns in mountains.** **a**, Mountain plant species (symbolized as curves) are distributed along altitudinal gradients. The amplitudes of the curves reflect varying species abundances, which generally decrease towards higher elevations. To each studied species, an altitudinal indicator value was assigned using six ranks (1–6, blue to red). **b**, Species constitute vegetation patterns that form bioclimatic belts; example from the European Alps. In each of these belts, monitoring plots were installed in a hierarchical scheme: in 17 European mountain regions, four summits (one of them exemplified by the yellow rectangle in **b**) spanning the gradient from the region’s treeline to its altitudinal limit were selected. **c**, On each summit’s four cardinal directions (east, south, west and north), a cluster of four 1 × 1 m monitoring plots was installed. For each plot, a vegetation score *S* was calculated as the average of the altitudinal ranks of the contributing species, weighted by their respective cover (see equation (1)). Soil temperature was measured hourly in the centre of each plot-cluster over the years 2001–2007. **d**, The vegetation score *S*, calculated for 2008 and averaged for each cardinal direction’s plot cluster, is correlated with soil temperature. It is therefore coined as the thermic vegetation indicator *S*. Circles, pooled data of plot clusters from several mountain regions. Blue lines, linear regressions of *S* from particular mountain regions on June mean of daily minimum temperature.



**Figure 2 | The thermophilization indicator *D* is significantly positive on the European level.** Diamonds and horizontal lines, *D* and 95% confidence intervals for the summits. Orange dots and horizontal bars, *D* and 95% confidence intervals for the mountain regions. The bar thickness refers to the number of summits in each mountain region (mostly four; three in Polar Urals, Southern Scandes, Valais, Central Pyrenees, Central Caucasus, Central Apennines; two in Corsica). Red line and green shading, European *D* and its 95% confidence interval. Black line, reference line at *D* = 0. Mountain regions are ordered from north to south (top to bottom), summits within regions from highest to lowest summit.



**Figure 3 | The thermophilization indicator  $D$  of mountain regions is correlated with temperature change.** **a**, Change in June mean of daily minimum temperature (map prepared from data provided by E-OBS; ref. 24, resolution  $0.25^\circ$ ), calculated as the difference of the averages of two time periods that precede plant data recording: prior 2008 (2003–2007)–prior 2001 (1996–2000). The numbers indicate the mountain regions and are referenced in Fig. 2. No temperature data are available for the Polar Urals and Southern Urals (2 and 5 in Fig. 2). **b**, Correlation of  $D$  with the change in June mean of daily minimum temperature (prior 2008–prior 2001) in the study regions (data derived from the map in **a**), using a one-sided test following the null hypothesis of no positive correlation. Vertical lines are 95% confidence intervals of  $D$  for the mountain regions and a linear regression line is shown.

have long-lasting effects, we applied average values for the period 1996–2000 (prior 2001) and the period 2003–2007 (prior 2008). The usefulness of  $T_{\min}$  in June and the choice of time spans of the prior periods were tested with our data and found acceptable (Supplementary Sections S2 and S5).

At the continental scale, the thermophilization indicator  $D$  was highly significantly positive ( $D = 0.054$ ,  $p < 0.0001$ ; Fig. 2). Sixteen of the 17 regions and 42 of the 60 summits had a positive  $D$ . The total variance in  $D$  resulted primarily from the among-plot differences (75%) and less so from nesting at larger spatial levels: 19% from cardinal directions, 6% from summits, and only 0.002% of the variance of  $D$  derived from differences between the mountain regions (for details see Methods and Supplementary Section S3).  $D$  was quite insensitive to possible misclassifications in the species' altitudinal ranks; the European  $D$  remained significantly positive up to a simulated misclassification rate of around 40% of the originally applied ranks. Neither the latitude of regions nor the elevation of summits had a significant effect on  $D$  (Supplementary Section S3).

The magnitude of  $D$  of the mountain regions reflects the pattern of the regional European climate development in the past decade and a half, that is, between prior 2001 and prior 2008. With an overall warming trend on the continental level<sup>7</sup> and

an average increase of  $0.76^\circ\text{C}$  in our study regions, June  $T_{\min}$  changed differently in different mountain regions (Fig. 3a). The thermophilization indicator  $D$  was significantly correlated with these regional climatic trends (Fig. 3b).

The transformation of plant communities on a continental scale within less than a decade can be considered a rapid ecosystem response to ongoing climate warming. Although the signal is not statistically significant for single mountain regions, it is clearly significant when data throughout Europe are pooled. This signal is expected to have a number of important implications. Biotic interactions were suggested to shift along abiotic stress gradients from mutualistic interactions under physically harsh conditions to more competitive interactions under less harsh conditions<sup>25</sup>. Thus, climate warming exposes short-stature, light-demanding and slow-growing cold-adapted alpine plant species to enhanced competition. A temperature-governed change of plant communities may lead to declines or even local disappearance of alpine plant species. In fact, declines of extreme high-altitude species at their lower range margins have recently been observed in the Alps<sup>12</sup>.

For Europe, approximately 2,500 vascular plant species (or approximately 20% of the continent's native vascular flora) were estimated to be centred in the alpine zone from the treeline



ecotone to the highest mountain summits<sup>26</sup>. This zone comprises only 3% of the terrestrial area of Europe and, hence, limited space would be available for future alpine habitats in warmer climates. A thermophilization of  $D = 1$  would relate to a shift in the magnitude of one vegetation belt (see Supplementary Section S1) according to our altitudinal rank definitions. This would theoretically imply that, for example, habitats of open and scattered subnival plant communities would be colonized by species of alpine grasslands. On the European level, we observed a transformation in the magnitude of about 5% of one vegetation belt after only seven years. Although a strong heterogeneity in microclimatic patterns<sup>27</sup> and a large vertical extension of mountains may provide local refugia<sup>14,28</sup>, our results indicate a progressive shrinking of the low-temperature, high-elevation habitats, including parts of the Alps and Mediterranean mountains, where many locally restricted species live<sup>29,30</sup>.

## Methods

**Field recording.** Species percentage cover was visually estimated as a percentage of the permanent plot with the aid of transparent templates. In each plot cluster, a temperature logger (Onset Stowaway Tidbit) was buried at 10 cm substrate depth. A total of 131 loggers yielded complete temperature series (2001–2007) and was entered for the analysis shown in Fig. 1d.

**Mixed-effects models.** To calculate  $D$  at the European level we applied a mixed-effects model with an intercept as fixed effect and plots, grouped in clusters arranged in the cardinal directions (further grouped into summits and mountain regions), as random effects using restricted maximum likelihood estimation.  $D$  on lower nesting levels was calculated by fitting separate models with a similar but lower nesting structure. As fitting routine we used `lme()` from S-PLUS (TIBCO Spotfire S+ 8.1 for Windows). The function `intervals()` was applied to calculate confidence intervals for  $D$  (Supplementary Section S3).

**Sensitivities to errors in species rank classification and cover estimation.** To assess the sensitivity of  $D$  to the applied altitudinal classification scheme of the species, we randomly perturbed the originally assigned ranks with normally distributed errors with increasing standard deviation and rounded the perturbed ranks to the nearest integer on our scale. For each standard deviation, we simulated 1,000 sets of perturbed ranks and computed the effect on  $D$  as well as the misclassification rate, averaged over the sets (Supplementary Section S1).

Visual cover estimation includes two error components: a systematic error that varies between different observers; and a random error that an observer makes from one estimate to the next. The random component is dealt with appropriately by our model. Using a pilot study we estimated the influence of the systematic error to account for only approximately 4% of the total error in cover estimation and therefore decided not to model this negligible variance component (Supplementary Section S4).

Received 7 March 2011; accepted 15 November 2011;  
published online 10 January 2012

## References

- Walther, G. R. *et al.* Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).
- Root, T. L. *et al.* Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60 (2003).
- Tingley, M. W. & Beissinger, S. R. Detecting range shifts from historical species occurrences: New perspectives on old data. *Trends Ecol. Evol.* **24**, 625–633 (2009).
- Pereira, H. M. *et al.* Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501 (2010).
- Christensen, J. H. *et al.* in *IPCC Climate Change 2007: The Physical Science Basis* (eds Solomon, S. *et al.*) 847–940 (Cambridge Univ. Press, 2007).
- Kjellström, E. *et al.* 21st century changes in the European climate: Uncertainties derived from an ensemble of regional climate model simulations. *Tellus* **63**, 24–40 (2011).
- Arndt, D. S., Baringer, M. O. & Johnson, M. R. State of the climate in 2009. *Bull. Am. Meteorol. Soc.* **91**, S1–S224 (2010).
- Parmesan, C. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. S.* **37**, 637–669 (2006).
- Grabherr, G., Gottfried, M. & Pauli, H. Climate effects on mountain plants. *Nature* **369**, 448–448 (1994).
- Klanderud, K. & Birks, H. J. B. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene* **13**, 1–6 (2003).

- Walther, G.-R., Beißner, S. & Burga, C. A. Trends in upward shift of alpine plants. *J. Veg. Sci.* **16**, 541–548 (2005).
- Pauli, H. *et al.* 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**, 147–156 (2007).
- Britton, A. J., Beale, C. M., Towers, W. & Hewison, R. L. Biodiversity gains and losses: Evidence for homogenisation of Scottish alpine vegetation. *Biol. Conserv.* **142**, 1728–1739 (2009).
- Gottfried, M., Pauli, H., Reiter, K. & Grabherr, G. A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Divers. Distrib.* **5**, 241–251 (1999).
- Thuiller, W. *et al.* Climate change threats to plant diversity in Europe. *Proc. Natl Acad. Sci. USA* **102**, 8245–8250 (2005).
- Engler, R. *et al.* 21st century climate change threatens mountain flora unequally across Europe. *Glob. Change Biol.* **17**, 2330–2341 (2011).
- Pauli, H. *et al.* *The GLORIA Field Manual—Multi-Summit Approach* (European Commission DG Research, EUR 21213, Office for Official Publications of the European Communities, European Commission, 2004).
- Ellenberg, H. *Vegetation Ecology of Central Europe* (Cambridge Univ. Press, 1988).
- Körner, C. The use of ‘altitude’ in ecological research. *Trends Ecol. Evol.* **22**, 569–574 (2007).
- Nagy, L. & Grabherr, G. *The Biology of Alpine Habitats* (Oxford Univ. Press, 2009).
- Ter Braak, C. J. F. & Barendregt, L. G. Weighted averaging of species indicator values: Its efficiency in environmental calibration. *Math. Biosci.* **78**, 57–72 (1986).
- de Witte, L. C. & Stoeklin, J. Longevity of clonal plants: Why it matters and how to measure it. *Ann. Bot.* **106**, 859–870 (2010).
- Körner, C. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems* 2nd edn (Springer, 2003).
- Haylock, M. R. *et al.* A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *J. Geophys. Res.* **113**, D20119 (2008).
- Callaway, R. M. *et al.* Positive interactions among alpine plants increase with stress. *Nature* **417**, 844–848 (2002).
- Väre, H., Lampinen, R., Humphries, C. & Williams, P. in *Alpine Biodiversity in Europe—A Europe-Wide Assessment of Biological Richness and Change* (eds Nagy, L., Grabherr, G., Körner, C. & Thompson, D. B. A.) 133–148 (Springer, 2003).
- Scherrer, D. & Körner, C. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob. Change Biol.* **16**, 2602–2613 (2010).
- Randin, C. F. *et al.* Climate change and plant distribution: Local models predict high-elevation persistence. *Glob. Change Biol.* **15**, 1557–1569 (2009).
- Dirnböck, T., Essl, F. & Rabitsch, W. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob. Change Biol.* **17**, 990–996 (2010).
- Blanca, G., Cuento, M., Martínez Lirola, M. J. & Molero Mesa, J. Threatend vascular flora of Sierra Nevada (Southern Spain). *Biol. Conserv.* **85**, 269–285 (1998).

## Acknowledgements

We acknowledge the E-OBS dataset from the EU-FP6 project ENSEMBLES (<http://ensembles-eu.metoffice.com>) and the data providers in the ECA&D project (<http://eca.knmi.nl>). We thank the European Topic Centre on Biological Diversity for stimulating discussions, G.-R. Walther, S. Dullinger, K. Green and T. Stuessy for internal reviewing, C. Klettner for data compilation, S. Laimer for project administration, R. Töchterle for help with Fig. 3 and approximately 80 co-workers for performing field recording. The study was financed by the European Commission, the Austrian Academy of Sciences, the University of Vienna, the MAVA foundation (Switzerland) and many other national authorities of the partner groups.

## Author contributions

G.G., H.P. and M.G. coordinated the monitoring program, performed field work and wrote the text. M.G. and H.P. conceived the study and compiled data, and M.G. and A.F. performed the statistical analyses. All other authors organized and performed field work as well as data compilation, and edited the manuscript.

## Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on [www.nature.com/natureclimatechange](http://www.nature.com/natureclimatechange). Reprints and permissions information is available online at <http://www.nature.com/reprints>. Correspondence and requests for materials should be addressed to H.P.

<sup>1</sup>Faculty Centre of Biodiversity, University of Vienna, Rennweg 14, 1030 Wien, Austria, <sup>2</sup>Institute of Mountain Research (IGF), Austrian Academy of Sciences, c/o University of Vienna, Rennweg 14, 1030 Wien, Austria, <sup>3</sup>Department of Statistics and Operations Research, University of Vienna, Universitätsstraße 5, 1010 Wien, Austria, <sup>4</sup>Institute of Ecology, Ilia State University, K. Cholokashvili Avenue 3/5, 0162 Tbilisi, Georgia, <sup>5</sup>Institute of Landscape Ecology of the Slovak Academy of Sciences, Stefanikova 3, 81499 Bratislava, Slovakia, <sup>6</sup>Instituto Pirenaico de Ecología, Consejo Superior de Investigaciones Científicas, Avenida Regimiento Galicia, 6. 22700 Jaca, Spain, <sup>7</sup>Department of Taxonomy and Plant Ecology, Institute of Biological Research, 48 Republicii Str., 400015 Cluj-Napoca, Romania, <sup>8</sup>Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, Scotland, UK, <sup>9</sup>University of Innsbruck, Sternwartestr. 15, 6020 Innsbruck, Austria, <sup>10</sup>Department of Botany, Faculty of Pharmacy, University of Granada, Campus Universitario de Cartuja, 18071 Granada, Spain, <sup>11</sup>Mediterranean Agronomic Institute of Chania, Department of Environmental Management, PO Box 85, 73100 Chania, Greece, <sup>12</sup>University of Göteborg, c/o Fallaengsvaegen 39 A, 671 51 Arvika, Sweden, <sup>13</sup>University of Innsbruck, c/o Hirzingerweg 23, 6380 St Johann i. T., Austria, <sup>14</sup>The Industrial Ecology Programme, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway, <sup>15</sup>Institute of Plant and Animal Ecology, Russian Academy of Sciences, 8 Marta, 202, 620144 Ekaterinburg, Russia, <sup>16</sup>Department of Plant and Environmental Sciences, University of Göteborg, SE 405 30 Göteborg, Sweden, <sup>17</sup>EcoScience Scotland, 2/1 27 Glencairn Drive, Glasgow G41 4QP, Scotland, UK, <sup>18</sup>Instituto Nacional de Pesquisa da Amazonia, Av. André Araújo, 2936, Aleixo, Manaus, Brazil, <sup>19</sup>Institute of Botany, Georgian Academy of Sciences, Kojori Road 1, 380007 Tbilisi, Georgia, <sup>20</sup>Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway, <sup>21</sup>Lab. Environmetrics, University of Molise, C. da Fonte Lappone, 86090 Pesche (Isernia), Italy, <sup>22</sup>Al. Borza Botanical Garden, Babes-Bolyai University, 42 Republicii Str., 400015 Cluj-Napoca, Romania, <sup>23</sup>Department of Earth and Environmental Sciences, University of Pavia, Via S. Epifanio 14, I-27100 Pavia, Italy, <sup>24</sup>Centre alpin de Phytogéographie, Fondation J.-M. Aubert, Case postale 71, CH-1938 Champex-Lac, Switzerland, <sup>25</sup>Section of Biology, University of Geneva, Case postale 60, CH-1292 Chambésy, Switzerland, <sup>26</sup>Department of Evolutionary and Functional Biology, University of Parma, Via G.P. Usberti 11/A, I-43100 Parma, Italy, <sup>27</sup>Department of Ecology and Evolution, University of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland, <sup>28</sup>School of Pure & Applied Sciences, Open University of Cyprus, PO Box 12794, 2252 Latsia, Nicosia, Cyprus. \*e-mail: Harald.Pauli@univie.ac.at.