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Continent-wide response of mountain vegetation to climate change

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Climate impact studies have indicated ecological fingerprints of recent global warming across a wide range of habitats[1,2]. 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[3,4]. 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[5,6] 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[7], surpassing the 1990s, which unveiled ecological responses of many animals and plants[8]. Several of these previous studies were made in mountain areas where an increase in plant species richness has been shown[9–13], and which coincide with projections of distribution models suggesting warming-induced upward range shifts[14–16]. 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[18] relies on the realized position of a species along an environmental gradient, in our case altitude, which resembles a thermal gradient[19] (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[21]) in the following thermic vegetation indicator *S* was then calculated as

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

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[22] and internal processes in alpine plant communities work at a slow rate[23], 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[24]). As the climatic conditions during the preceding years of a survey (termed here as prior periods) are expected to

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