ALPINE ECOLOGY

Rising plant extinction rates on European mountain summits

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Climate change increases plant species richness in alpine ecosystems. However, to what extent this diversity enrichment masks extinction dynamics of resident species remains elusive. In this study, we used floristic resurvey data from 896 permanent vegetation plots across 62 European mountain summits to show that local extinctions have increased over the past 21 years. Extinction rates rose with the magnitude of warming, and species were more likely to go extinct toward their low-elevation range margins and in communities undergoing stronger thermophilization. Moreover, local extinctions were significantly related to preceding abundance declines, which can serve as an early warning signal. These findings suggest that despite increasing plant species richness, plant assemblages above the treeline face an accelerating but so far neglected loss of their most characteristic species.

Vascular plant species richness on mountain summits has increased during recent decades (*1*, *2*). The likely driver of this species accumulation is the accelerating rate of climate warming at higher elevations (*3*), which has made previously inhospitable sites more amenable to vascular plant life and enabled less cold-tolerant species from lower-elevation habitats to shift or expand upslope and colonize mountain summits (*2*, *4*–*6*). However, this increase in species richness dominated by lower-elevation species may obscure a loss of resident specialists (*7*). Identifying and quantifying this possible loss is important because high-elevation floras tend to be rich in geographically restricted and often functionally exceptional or distinct species (*8*, *9*). Extinctions from this species pool can thus have disproportionate effects on functional and phylogenetic diversity, endemism, and rarity (*10*, *11*).

Local and regional studies suggest that species above the treeline do indeed sort into "winners" and "losers" in terms of abundance change with climate warming, and that specialists of highest elevations are disproportionately frequent among the losers (*12*–*14*). However, no continental-scale analysis has so far provided a systematic assessment of the magnitude of recent species losses in high-mountain plant communities or potential patterns of vulnerability among species and populations. Moreover, local- and regional-scale findings have often been based on a single resurvey of historical observations, in which directed abundance trends can most easily be confounded with stochastic population fluctuation or observation error (*15*, *16*). Whether the documented abundance declines are early warning signs of pending local- or larger-scale extinctions remains to be evaluated.

The Global Observation Research Initiative in Alpine Environments (GLORIA) (*17*) is the largest systematic monitoring scheme of climate effects on mountain summit floras (*18*). In Europe, its core sampling network consists of 62 summits distributed across 16 mountain regions (Fig. 1) that were surveyed four times, in 7-year intervals, between 2001 and 2022 [with a few minor deviations (*19*)]. During each survey, on each summit, the full list of vascular plants, together with their abundance (ground cover by means of visual estimation), was recorded on 16 permanent 1 m by 1 m plots. On the basis of these data, we analyzed temporal trends in local extinctions and their relationship with the magnitude of climate warming. We refer to local extinction as the disappearance of a species recorded in one survey but not rerecorded in the consecutive survey, although we do not know whether the species persisted on the same summit or in the same region outside of the surveyed plots. For the species that were present in the first survey, we further evaluated whether the likelihood of local extinction events was related to a preceding decrease in their cover and the position of the plot within the species' elevational range. Additionally, we evaluated whether extinctions were more likely in communities undergoing a more pronounced change toward predominance of warmth-demanding species: so-called thermophilization (*20*). To account for slight variation in observation methods between surveys, we used a resampling approach in the analyses and reported results as means and standard deviations of resamples (*19*). Temporal and geographical trends in local extinctions were assessed on the level of sampled plots, as well as on the aggregated levels of summits and mountain regions.

Rates and temporal trends of local extinctions and their relationship to climatic trends

Local extinction events were observed frequently in each resurvey. Across the three resurveys, the number of such extinction events varied as follows: 980 to 1451 ± 9 at the plot level, 118 to 185 ± 4 at the summit level, and 57 to 99 ± 2 at the mountain-region level. These numbers correspond to 11.1 to 15.7% ± 0.1%, 6.7 to 9.9% ± 0.2%, and 5.5 to 8.9% ± 0.2% of all species observations at the plot, summit, and mountain-region levels, respectively (table S1). However, a considerable percentage (34.2 ± 0.2%) of the plot-level extinctions documented in the second or third survey were followed by reobservation of the focal species during one of the subsequent surveys because of either real extinction and colonization dynamics, a lack of aboveground appearance of species in a certain year, or intermittent observer errors. In the most conservative accounting, which only considers species present in the first but missing from all three consecutive surveys, there were 578, 62, and 31 extinction events, corresponding to 6.5, 3.5, and 3% of the species observations at the plot, summit, and mountain-region levels, respectively.

Using generalized linear mixed-effects models for proportion data (*19*), we found that local extinction rates significantly increased over time (with each consecutive resurvey) on each level of aggregation: on the plot, summit, and mountain-region levels (Figs. 2 and 3A and table S2). Extinction rates rose in parallel with the total vascular plant cover per plot and species richness per plot and summit (Fig. 3B and tables S3 and S4). However, when fitting these extinction-rate models, we included local extinctions of all species, even if they were reobserved in consecutive surveys. This was necessary because the chance for an apparently extinct species to reappear decreases with the number of subsequent surveys. Hence, omitting local extinctions followed by reobservations would result in rising extinction rates per se. To assess whether the detected temporal trend is attributable to increased rates of natural fluctuation and observer error or rather indicates a rise in local extinction rates, we fitted two additional mixed-effects models for proportion data (*19*). In these additional models, we separately tested whether the likelihood of a transition of type presence-absence-presence

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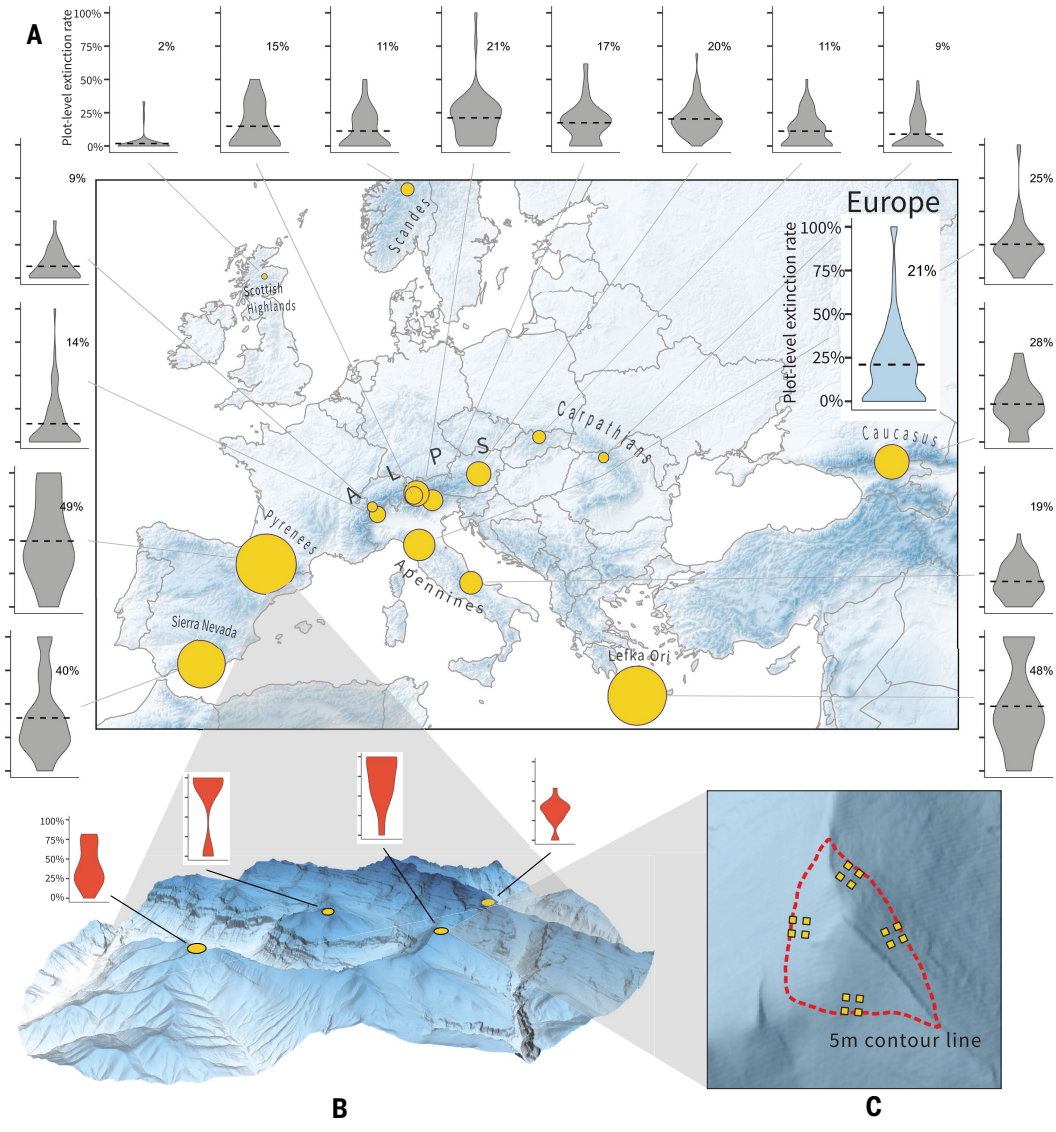

Fig. 1. Local extinction rates on European mountain summits. (**A**) Geographical distribution of the 16 mountain regions surveyed. The sizes of the circles indicate the mean proportion of local extinctions from 2001 to 2022—of species observed in 2001 but not reobserved in 2022—across all plots of a given mountain region. The violin plots show the distribution of the plotwise extinction rates (percent per plot) across Europe (blue), in each mountain region (gray) [as well as in each summit in the Pyrenees in (B) (red)]. Dashed lines indicate the mean extinction rate across all plots in the respective region or across Europe. (**B**) Each mountain region comprises three to four summits as exemplified for the Pyrenees. (**C**) On each summit, up to 16 plots (yellow squares) are permanently installed, arranged in four plot clusters in each cardinal direction 5 m below the peak (the respective contour line is depicted as a dashed red line).

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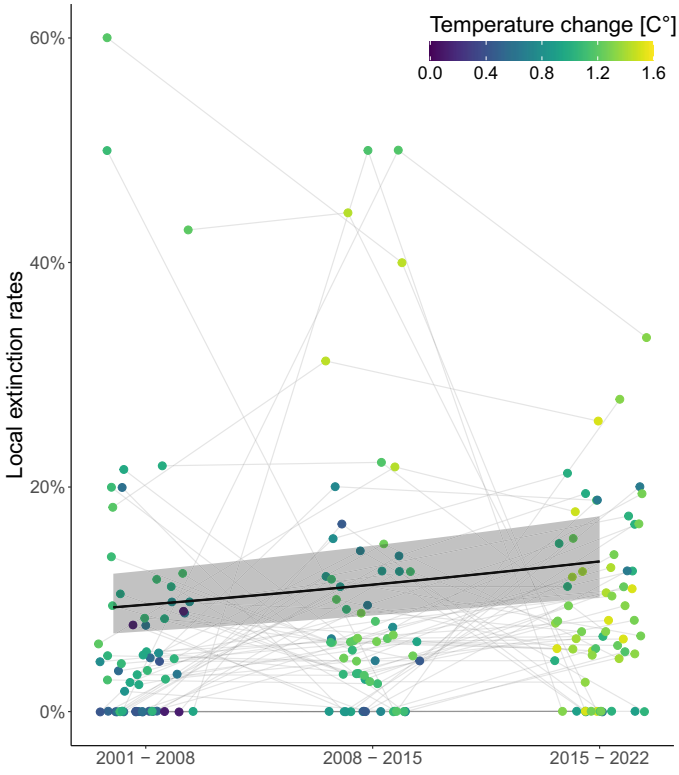

Fig. 2. Local extinctions increased across surveys. Values on the *y* axis are the percentage of species observed in one survey but not reobserved in the consecutive survey on the same summit (each dot indicates one of the 62 summits analyzed). Dot color indicates the temperature change during the 14 years before the respective time interval, compared with a summit-specific baseline climate of the years 1900 to 1950. The regression line is the fixed effect of a generalized linear mixed-effects model for the proportion of local extinctions against time ($P < 0.001 \pm 0.000$, $R^2m = 0.09 \pm 0.008$, $R^2c = 0.73 \pm 0.011$). The gray band indicates the 95% confidence interval (CI). All values—the percentage of local extinctions and the regression line—are the mean of 1000 resamples. The gray lines link the dots indicating one particular summit.

and of type presence-absence-absence has increased between the earlier (2001–2008–2015) and later (2008–2015–2022) three surveys. We thereby interpreted the latter type of transition as an indication of real local extinction events. We found that on all three levels of aggregation, only transitions of type presence-absence-absence became more frequent (estimate = 0.26 ± 0.009, $P < 0.001$; estimate = 0.37 ± 0.03, $P = 0.016 \pm 0.010$; and estimate = 0.45 ± 0.030, $P = 0.04 \pm 0.015$, respectively). These results suggest that natural fluctuation and observer error have not increased over time, but that the increase in extinctions drives the observed trend.

To evaluate whether climate warming could be the driver behind rising local extinction rates, we quantified the magnitude of macroclimatic warming for each survey on each summit. Therefore, we derived the difference between the mean temperature during the 14 years before each survey and the mean temperature during a baseline period between 1900 and 1950, using data from the Climate Research Unit (version 4.06) (*21*). We selected a 14-year time window for this analysis because it corresponds to two survey intervals and is consistent with the subsequent analyses presented below. Using the same type of generalized linear mixed-effects model as above, but exchanging time with the magnitude of warming as a fixed-effects predictor, we found that local extinction rates were positively related to climate warming (estimate = 0.38 ± 0.01, 0.37 ± 0.02, and 0.39 ± 0.02 on the plot, summit, and mountain-region levels, respectively; $P < 0.001$ in all cases) (table S5): With each additional 0.1°C of warming, the proportion of local extinctions has increased by 1.6, 1.1, and 1.0% at the three levels of aggregation. This model explained a considerably higher proportion of the observed variance in local extinction rates (as measured by marginal coefficient of determination (R^2) values, $R^2m = 0.14 \pm 0.004$, 0.27 ± 0.014, and 0.36 ± 0.018 on the plot, summit, and mountain-region levels, respectively) compared with the model that used time as a fixed-effects predictor ($R^2m = 0.03 \pm 0.001$, 0.09 ± 0.008, and 0.17 ± 0.018, respectively) (Fig. 3), which underpins the role of climate change in driving the increasing local extinction rates. Last, to assess whether local extinction rates show geographical trends, we also included latitude and longitude as additional fixed-effects predictors into the climate-warming model. We found that at the plot, but not at the summit or region levels, local extinction rates were greater at southern latitudes, whereas there was no east-west gradient at any of the three aggregation levels (Fig. 3A and table S6).

Declining cover predicts local extinctions

To assess whether a species' decrease in local abundance can be considered an indicator of its local extinction risk, we computed the change in the observed cover between the first and the third survey for each species on each plot. A logistic mixed-effects model revealed that the likelihood that a species was reported as locally extinct at a plot during the fourth survey in 2022 increased with a stronger decline in the cover of the focal species at this plot during the preceding 14 years (between 2001 and 2015) (Figs. 3C and 4B and table S7). The effect was independent of the species' cover value in the first survey. The latter variable was itself a significant predictor of local extinction (Fig. 3C and table S7), most likely because low cover in the first survey increases the probability of both subsequent local extinctions and observation errors. Prior cover decline predicted local extinctions in the fourth survey also when computed over a shorter observation window of 7 years, between the second and the third survey. However, the strength of the effect was weaker, probably because of stronger noise from random fluctuations (Figs. 3C and 4B and table S7).

The relationship between declining cover and local extinction rate was significant, even though changes in cover before local extinction varied considerably in magnitude and direction, suggesting considerable background fluctuation. Of all local extinctions reported during the fourth survey, 57.6 ± 0.2% were preceded by a cover decline, 32.2 ± 0.2% were preceded by a cover increase, and 10.2 ± 0.1% were preceded by constant cover between the first and the third survey. To further support the conclusion that a declining cover leads to local extinction more often than expected by chance under this background fluctuation, we counted all trajectories of monotonic cover decrease toward extinction across the four surveys of type $\text{cover}_{\text{survey1}} > \text{cover}_{\text{survey2}} > \text{cover}_{\text{survey3}} > 0$. We then compared the number of such trajectories in the entire dataset with their number after randomly reshuffling the cover values (including 0) of each species at each plot across the four surveys. We found that these monotonic decline-to-extinction trajectories occurred 2.5 times more often than expected by chance (44.5 ± 6.5 and 112.8 ± 2.7 trajectories for reshuffled and observed data, respectively) (Fig. 4A), a highly significant difference (Student's *t* test, df = 1,333,209, $P < 0.001$).

Species are more prone to local extinctions toward their lower range margin and in communities undergoing stronger thermophilization

If local extinctions of plant species on mountain summits are—at least partly—driven by the changing climate, we would expect that extinction risk is greater the closer a summit is located toward a species' warmer, lower range margin. This is in line with scattered recent observations in various mountain plant and animal species (*12*, *22*). We tested this assumption on the basis of a six-level classification of

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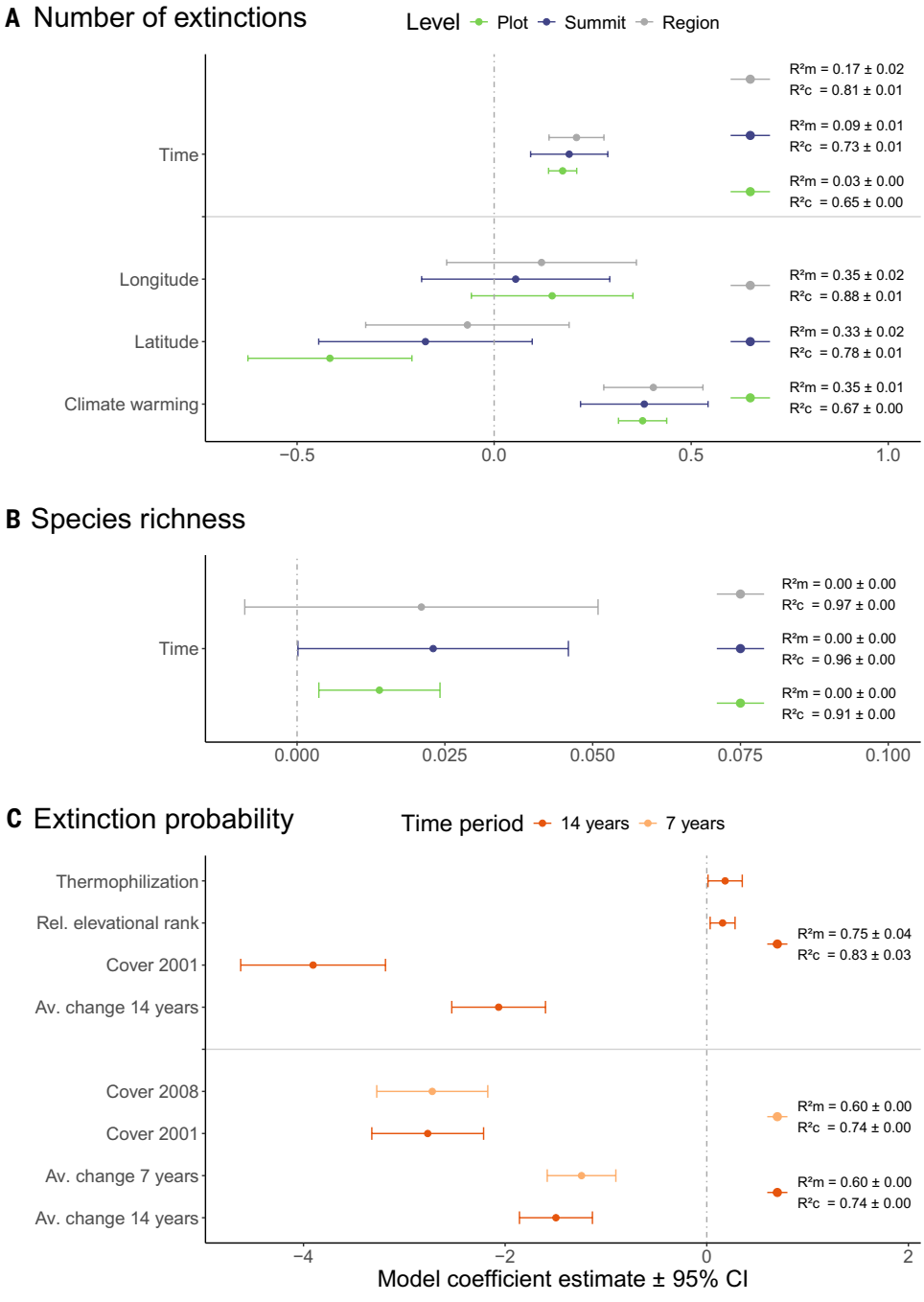

Fig. 3. Extinction probability increases with stronger warming, for higher-elevation species, and after longer phases of decline. (**A** to **C**) Mean model coefficients (of 1000 resamples) of linear mixed-effects models and their 95% CIs. CIs not overlapping with 0 indicate significant fixed effects. Mean marginal (m) and conditional (c) R^2 values and their standard deviation were also derived from the 1000 resamples. (A) Generalized linear mixed-effects models for proportion data with the proportion of extinctions as (top) the response and time or (bottom) climate warming, latitude, and longitude as fixed effects at the plot (green), summit (blue), and mountain-region (gray) levels. (B) Generalized linear mixed-effects models for count data with the total species number as response and time as fixed effects at the plot (green), summit (blue), and mountain-region (gray) levels. (C) Logistic mixed-effects models with local extinction (yes/no) as response and average cover change per year between the first or second and the third survey (representing a period of ~7 or 14 years; orange and dark red, respectively), and the cover at the beginning of the respective period as fixed effects. Negative estimates imply increased extinction risk for lower cover values as well as for stronger cover decreases. In the model represented at top, relative elevational rank and thermophilization are used as additional fixed effects. All predictors were scaled to zero mean and unit variance.

species according to the elevational belt where they most frequently occur [1 = nival; 2 = subnival or alpine-nival ecotone; 3 = alpine; 4 = alpine to the treeline; 5 = treeline ecotone; and 6 = montane (*20*)]. We calculated the relative rank of each species in each plot as the average elevational rank of all species co-occurring in the plot (the community-mean value) in 2001 minus the species' elevational rank. Hence, this species-by-plot-specific value of relative elevational rank is an indicator of the position of the plot within the elevational range of a species. Positive values indicate that the "average species" of a plot prefers lower elevations than the focal species, suggesting that the plot is located toward the lower range margin of the focal species. Conversely, negative values indicate that the plot is located toward the upper elevational range margin of the focal species. We added this relative elevational rank as a further predictor to the model used to analyze the relationship between local extinction probability in the fourth survey and cover change in the preceding 14 years. We found that the relative elevational rank was positively related to local extinction likelihood (Fig. 3C and table S7). Therefore, species had a higher risk of local extinction between 2015 and 2022 toward their lower elevational range margin. Moreover, we repeated the comparison of the "decline-to-extinction trajectories" against random expectations, as described above, separately for local extinction events of species with positive and negative relative elevational ranks. We found that such trajectories occur more often than expected by chance in both groups, in line with a general impact of prior cover decline on local extinction likelihood. However, the overrepresentation was stronger for the group with positive elevational ranks, underlining that populations at lower range margins faced a higher risk of local extinction over time (Fig. 4A). Last, we tested whether local extinctions in the fourth survey were more likely in communities undergoing a stronger general change toward warmth-demanding species (thermophilization) (*20*). Therefore, we calculated the change in the cover-weighted average elevational rank of plots between 2001 and 2022 [after removing the focal species (*19*)]. We added this change as a predictor variable to the model and found that local extinctions between 2015 and 2022 were more likely in communities that experienced a stronger thermophilization (Fig. 3C and table S7). This finding underlines that local extinctions are, at least partly, embedded into a climate-driven restructuring of the entire community.

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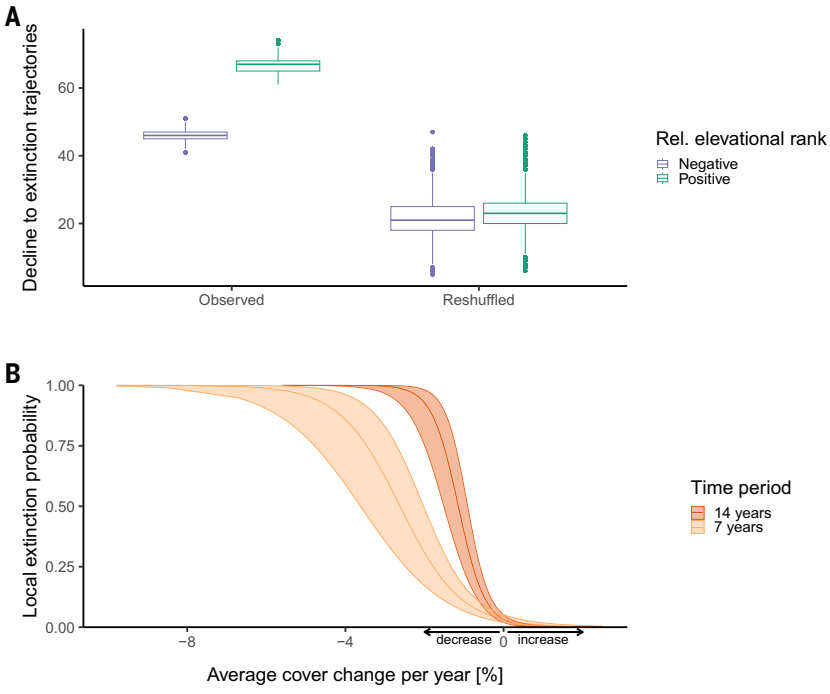

Fig. 4. Preceding change in cover is related to the probability of species' extinction. (**A**) Number of trajectories of monotonic cover decrease during the first three surveys, followed by extinction in the fourth one ($cover_{survey1} > cover_{survey2} > cover_{survey3} > 0$) in the observed data and after randomly reshuffling species cover values on each plot across the four surveys 100 times. The comparison was done separately for species with negative and positive relative elevational ranks, indicating a position of the monitoring plot toward the upper or lower range margin of the species, respectively. Boxplots indicate the variation across 100 reshuffles of 1000 resamples from the data. For both groups, the difference between the observed and reshuffled data was highly significant (Student's *t* test, df = 1,266,957/1,390,299, $P < 0.001$). Rel., relative. (**B**) The relationship between preceding cover change per year and the probability of a species going extinct in a plot—not being redetected in the fourth survey. Results of two logistic mixed-effects models with local extinction (yes/no) as a response variable and a random intercept for summit nested in the mountain region, as well as a random intercept for species. Fixed effects were the average cover change per year between the first or second and the third survey, covering a period of ~7 and 14 years, respectively, and the cover at the beginning of the respective period. Shaded areas indicate 95% CIs, averaged across 1000 resamples from the data. All predictors were scaled to zero mean and unit variance.

Discussion

Monitoring plant occurrence and cover on permanent plots is prone to observer error (*23*). Although relocation errors are minimized by the permanent-plot design of GLORIA and identification errors were reduced as much as possible by prior data cleaning (*19*), part of the local extinctions reported certainly result from species that were overlooked or from natural fluctuation. However, if all local extinctions were attributable to observer errors or random fluctuation, significant relationships with time, level of warming, or relative elevational rank should not emerge. The explanatory power of our models (marginal R^2 values reached up to 0.75) (Fig. 3 and tables S6 and S7) demonstrates that these variables explain a high proportion of the observed variation in local extinction rates. Moreover, transitions suggesting real local extinctions increased over time, and monotonic decline-to-extinction trajectories were far more frequent than expected by chance. Last, a complementary analysis of colonization dynamics, mirroring our analyses of extinction dynamics, further suggests that the data do not exclusively reflect natural fluctuation and observer error (*19*). In particular, this complementary analysis demonstrated that in correspondence with the patterns found for local extinctions, a monotonic increase in a species' cover after local colonization (a transition of type $0 < cover_{survey2} < cover_{survey3} < cover_{survey4}$) was much more likely than expected under random fluctuations and that local colonizations were significantly more frequent toward the species' upper elevational range limits. However, in contrast to extinctions, colonizations did not become more frequent over time. Last, the number of colonization events was also unrelated to the level of warming, most likely because of their strong dependence on the availability of potential colonizers in the plots' immediate surroundings (*24*, *25*).

Although our results indicate a substantial impact of climate change on rising local extinction rates, we cannot exclude additional effects resulting from other anthropogenic drivers. In the case of GLORIA, strong impacts of land-use changes are unlikely because summits were selected with the explicit purpose of minimizing them (*17*). A possible effect of atmospheric nitrogen deposition (*12*) remains to be tested, even if an earlier study, based in part on GLORIA data, did not detect any consistent impact of nitrogen deposition on local plant species richness of European mountain summits (*2*). Besides these nonclimatic factors, climate-related changes other than warming temperatures could foster extinction rates, especially decreasing water availability and a shortened snow cover period (*13*, *26*). Robust data on how these factors have developed across GLORIA summits are not available; hence, their impact cannot yet be disentangled from that of warming. However, changes in these factors are likely correlated with higher temperatures because the latter increase evaporative demand (*27*), shift the ratio of rain and snow (*28*), and advance spring snowmelt (*29*, *30*). Hence, we emphasize that the demonstrated link between exposure to climate warming and local extinction rates does not necessarily indicate an impact of temperature per se, but rather reflects a response to a set of conditions altered by rising temperatures. These changes may also include alterations of the biotic environment. The combination of rising species numbers, increasing total vegetation cover (Fig. 3B and tables S3 and S4), and community thermophilization may indicate that increasing competitive pressure has already contributed to the rise in local extinction events (*31*, *32*). Such competitive effects would be in line with the widely accepted hypothesis that the climatically more favorable range margins, where we found extinctions to be more frequent, are primarily set by competitive interactions (*33*–*36*). However, a conclusive distinction between direct and indirect effects of climate change on local extinctions can only be confirmed through experiments (*31*).

Our results show that climate change does not only add additional species to European summit floras (*2*, *4*) but also causes loss of former residents, with local extinctions being more frequent toward the species' lower range margin. As a consequence, the species characteristic of the highest elevations will also face the highest extinction risk because they have the least opportunities to offset lower-margin losses through upper-margin expansion. The focus on the salient biodiversity increase has to a certain extent masked simultaneous extinctions, and the latter have received more attention only over the most recent years (*13*, *14*, *24*, *37*). This may reflect that local extinctions are intrinsically more difficult to demonstrate than local colonizations. However, the recent rise in attention to extinctions may also suggest that climate-driven local extinctions occur more slowly than colonizations, which is likely the case for long-lived and stress-tolerant alpine plants (*25*, *38*, *39*). This is consistent with the rising number of local extinction events detected in this study and might imply that an extinction

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debt, accumulated since at least the most recent amplification of climate change during the 1980s (*40*), is starting to be paid off.

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SUPPLEMENTARY MATERIALS

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Materials and Methods; Tables S1 to S12; References (*42–49*); MDAR Reproducibility Checklist

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Rising plant extinction rates on European mountain summits

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Editor's summary

Mountain-dwelling plant species are shifting upward with climate change, leading to concerns that species already at the highest elevations will go extinct due to warming or competition with species that encroach from below. Wessely *et al*. identified local extinctions across 16 European mountain regions using vegetation plots that were resampled multiple times across two decades. Species losses occurred more often at the lower-elevation portions of their ranges and were more frequent in years preceded by faster warming. Upward range shifts increased species richness but at the expense of higher-elevation species, with potential for extinction debts stretching into the future. Abundance declines predicted species losses, indicating that declines in species cover could be a useful indicator for future extinction. —Bianca Lopez

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