Accelerated increase in plant species richness on mountain
summits linked to climate warming

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Globally accelerating trends in societal development and human environmental impacts since the mid-20th century are known as the Great Acceleration and discussed as a key indicator of the onset of the Anthropocene. While reports on ecological responses (e.g., species range shifts or local extinctions) to the Great Acceleration are multiplying, it is unknown whether such biotic responses are undergoing a similar acceleration over time. This knowledge gap stems from the limited availability of time series data on biodiversity changes across large temporal and geographical extents. Here, we use a unique dataset of repeated plant surveys from 302 mountain summits across Europe, spanning 145 years of observation, to assess the temporal trajectory of mountain biodiversity changes as a globally coherent imprint of the Anthropocene. We find a continent-wide acceleration in the rate of plant species richness increase, with five times higher species enrichment over the last decade compared to fifty years ago. This acceleration is strikingly synchronized with accelerated global warming, and not linked to alternative global change drivers. The accelerating increases in species richness on mountain summits across this broad spatial extent demonstrate that acceleration in climate-induced biotic changes is occurring even at remote places on Earth, with potentially far-ranging consequences not only for biodiversity, but also for ecosystem functioning and services.
Mountains are particularly sensitive to ecological change and are experiencing some of the highest rates of warming under anthropogenic climate change\cite{10,11}. Numerous reports of species re-distribution towards the summits\cite{8,12-14} and warming-induced changes in biodiversity on summits\cite{13,15,16} suggest that mountain biota are highly sensitive to increasing temperatures\cite{17}. The current accelerating trends in temperature increase\cite{1,6} should therefore also affect the velocity of changes observed for mountain biota. Appropriate empirical assessments of the rate of change in the velocity of ecological responses (biodiversity and ecosystem trajectories) to accelerated global warming require long-term resurveys (e.g. time series) of species communities, but these are scarce and localized. Mountain summits are especially suited for long-term studies of biotic responses to environmental changes because they represent natural permanent study sites that are easy to re-locate over time\cite{18,19}, thus allowing to record reliable time series. By repeatedly resurveying alpine plant communities on 302 European mountain summits dating back as far as 1871, we generated time series for century-scale and continent-wide biodiversity dynamics to assess potential acceleration trends in plant diversity dynamics (Fig. 1). Using these time series data, we tested whether the recent acceleration of climate change is driving a similarly accelerating change in species richness on mountain summits across the continent.

Here we show that plant species richness has strongly increased over the past 145 years on the vast majority (87%) of Europe’s summits (generalized linear mixed effects model: $p<0.001$; Fig. 2; Extended Data Table 1) and the increase has accelerated in the most recent years. This trend is consistent across all nine covered geographical regions, with no single region showing the opposite pattern. Across all summits, this increase in plant species richness has accelerated over time (linear mixed effects models: $p<0.001$; Fig. 3; Extended Data Table 2), and the acceleration has been particularly pronounced during the last 20-30 years (Figs 2 and 3). Fifty years ago (1957 to 1966), the rate of increase in species numbers averaged 1.1 species per decade (Fig. 3), while during the last decade (2007 to 2016) the summits gained 5.4 additional species on average (Fig. 3). There is a positive relationship
between the magnitude of increase in plant species richness and the rate of warming across all
302 time series (linear mixed effects models: p<0.001; Fig. 4a and Extended Data Figure 2a;
Extended Data Table 3). The temporal and spatial congruence between the velocity of climate
change and the species accumulation rates on mountain summits across Europe corroborates
the hypothesis that warming is the primary driver of locally observed upward shifts of species
ranges in mountains (Fig. 2)\textsuperscript{12,13,20} and their recent acceleration\textsuperscript{16,21}. Our findings thus align
with those of shorter-term studies demonstrating plant community thermophilization\textsuperscript{15,17} and
range shifts driven by warming\textsuperscript{7}.

The observed relationship between temperature change and species richness change
over the past 145 years is consistent across all nine regions. Changes in precipitation and
nitrogen deposition also correlate with species richness changes regionally, but the direction
and magnitude of these effects differ strongly between regions (Extended Data Figure 2b, c).
While precipitation change (∆P/year) has a moderate (positive) effect on species richness
trends across Europe (Extended Data Table 3; Fig. 4b, c), its effect is not consistent and
significant across all analysed regions (Extended Data Table 6; Extended Data Figure 2b) and
is minor compared to the effect of temperature change (∆T/year; Extended Data Table 4 and
6). Changes in grazing and tourism could also affect changes in plant species richness on
summits\textsuperscript{21}. Local studies suggest that grazing\textsuperscript{22} and frequent disturbance by tourists\textsuperscript{15} may
suppress the elevational advance of alpine plants in response to warming in mountains. While
quantification is challenging, locally declining levels in domestic livestock are often in
synchrony with recovery of wild ungulate populations. Hiking tourism increased on some
summits, but intensities vary strongly. Land-use changes may thus explain parts of the local
variation in species richness trends, however, they vary greatly within and between regions.
Without a consistent impact on species re-distribution, it is unlikely that changes in grazing
and tourism can account for the consistent, continent-wide increase in plant species richness
evident in our data.
Some previous observations suggest that upslope species migration in mountains occurs almost in synchrony with climate warming\textsuperscript{17}, while other studies indicate strong lags in dispersal, establishment, and extinction expected for many alpine plant species\textsuperscript{23,24}. We systematically tested for time-lags (up to 10 years) in species richness increase following climate changes, but found that time-lags did not significantly improve the explanatory power of our models (Extended Data Table 5). This finding suggests that increases in species richness on European summits are a direct and immediate response to climate warming (see also Fig. 2) and, thus, can be expected to further accelerate as climate warming continues to accelerate\textsuperscript{1}. Because we focus on the average trend, and by not accounting for non-colonizing lower-altitude species, we cannot, however, exclude the possibility that only a fraction of species responded quickly to climate change, thus creating the observed relationship, while an unknown number of species lags behind the change in climate. Our observations may, therefore, underestimate the expected long-term species turnover on summits.

The accelerated increase of species richness on mountain summits likely results from an upward shift of the upper range limits of an increasing number of species. Trait analyses indeed show that new colonizers exhibit growth strategies characterizing lower elevations, having larger size (\(p<0.001\)), higher specific leaf area (\(p<0.01\)) and a general association with warmer temperatures (\(p<0.001\); Extended Data Table 7). Ultimately, the lower range limits of species will also shift upwards, but these limits are often determined and changed by biotic interactions and are, therefore, only indirectly related to temperature\textsuperscript{25}. As more species establish at high-elevation sites, local extinctions will likely occur due to competitive replacement of slow-growing, stress-tolerant alpine species by more vigorous generalists that benefit from warming, rather than by direct adverse effects of warming on the summit species\textsuperscript{26}. However, competitive replacement of resident species requires that colonizers build up sufficiently large populations. Local extinctions should hence follow colonization with a time-lag. Consequently, accelerating plant species richness increases would be a transient phenomenon which hides the accumulation of a so-called extinction debt\textsuperscript{23,27}. The relaxation
The time until this debt is paid off is likely characterized by continuous shifts in abundance ratios which may serve as sensitive early-warning signals of upcoming extinctions. The length of the relaxation time likely depends on factors such as the longevity of high-elevation species, plant clonal abilities, and the local microhabitat diversity, supporting the persistence of cold-climate microrefugia for high-alpine species. Although these processes, along with others such as the species’ intrinsic ability to tolerate changing climates, may buffer local extinctions, rapid loss of alpine-nival species may occur under accelerated climate warming. Additionally, if major changes and extinctions in alpine systems are not gradual, but initiated by threshold-like dynamics (e.g. shrub and tree encroachment), critical tipping points may be approached with increasing speed under accelerated climate warming.

Our results underline the link between accelerating climate warming and species richness change in mountains. We thus provide a particularly compelling example of the human-driven impact on terrestrial biota that is highly consistent with the recently reported Great Acceleration in Earth system trends in the Anthropocene and strikingly synchronous with the recent accelerating trends observed in many socio-economic indicators. The observed acceleration of biodiversity change in mountain ecosystems highlights the rapid and widespread consequences of human activities on the biosphere, with important consequences for ecosystem functioning, human well-being, and the dynamics of climate change.

References:


**Supplementary Information** is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions

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SP, HP, MP, VP, BS, KS, VS, CR, GT, J-PT, PV and SW contributed data. MJS led the
manuscript writing, with contributions from all authors.

Data and code availability

Data and R code is freely available via the corresponding authors
(MJS or SW).

Author Information

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www.nature.com/reprints. The authors declare no competing financial interests. Readers are
welcome to comment on the online version of the paper. Correspondence and requests for
materials should be addressed to MJS (steinbauer@bios.au.dk) or SW (sonja.wipf@slf.ch).
Figure 1 | The study is based on 698 surveys from 302 summits in nine mountain regions across Europe dating back to 1871. Each sampled summit is indicated by one line, with black crosses indicating survey dates. The historical surveys were often conducted by leading pioneers in vegetation ecology in Europe (B. Pawlowski, J. Braun-Blanquet, E. Rübel, E. Du Rietz etc.). Numbers in brackets beside the region names indicate the number of summits/surveys. Picture references for Pawlowski (Zemanek, 2012, Florist. Geobot. Polon.), Braun-Blanquet (Ellenberg 1982, doi 10.1111/j.1438-8677.1982.tb02874.x) and Rübel (ETH-Bibliothek Zürich, doi 10.3932/ethz-a-000073833).
Figure 2 | Average species richness change (in species numbers) on mountain summits over time (lower part of panels) compared to mean annual temperature over time (upper part of panels). “Nobs” indicates the number of summits/surveys within the mountain region providing data for the respective panel. Correlation between rate of change in species richness and rate of change in temperature ($\Delta T_{cor}$) is positive for all mountain regions (see also Extended Data Figure 2a). Orange shading marks the 5th and 95th percentiles of the resulting richness change values from a bootstrapping approach across all summits in one region; see Extended Data Figure 1 for methodological details.
Figure 3 | Rate of species richness change over time (black line, b). Positive values indicate an increase in species richness on summits and negative values indicate a decrease. Rates ($\Delta SR$/year = ($SR_{t2}$-$SR_{t1}$)/($t_2$-$t_1$)) [SR = species richness, t = time] were averaged across all summits and inversely weighted by the number of years between observations ($t_2$-$t_1$) to account for temporal resolution as a longer period between surveys might mask short-term fluctuations. The black line interpolates across all summits with a generalized additive (spline) smooth model (R package mgcv version 1.8-17, the smooth term (k = 50) was chosen to allow enough degrees of freedom to closely represent the underlying pattern). The shaded grey area represents $\pm$1 standard error around the mean value (black solid line). a) The histogram at the top of the figure indicates the number of slope parameters per year (N; comparisons of earlier survey and later sampled resurvey) that support the line graph.
Figure 4 | Rate of species richness change (ΔSR/year = (SR_{t2}-SR_{t1})/(t_{2}-t_{1})) related to the rate of: a) temperature change; and b) precipitation change across all sampled mountains in Europe. Note that this pattern differs considerably among regions (see Extended Data Figure 2 for more details at the regional level). Dots are semitransparent, with darker symbols indicating overlapping points. Trend lines and R^2 values are based on univariate linear regressions and significance, indicated by stars, is based on F-statistics (see text and Extended Data Table 3 for multivariate analysis). The relationship between change in species richness and accumulated nitrogen (not shown) is not significant, because nitrogen deposition varies strongly across Europe whereas the change of species richness shows the same trend across the continent. See text and methods section for more detailed analyses with generalized mixed effects offset models including regional differences.
METHODS

Vegetation resurveys on European mountain summits. Precise relocation of vegetation records is possible on mountain summits. European botanists, fascinated by the limits of plant life, noted this potential more than a century ago (Fig. 1)\textsuperscript{18}: “On the basis of a comprehensive description of locations, it will not be difficult to verify my species lists, and an increase or decrease of species richness in the future will be possible to detect with high certainty” (Josias Braun-Blanquet in 1913, translated from 31, p. 329). The foresight and the data they gathered on mountain summits gives us the opportunity to study the effect of accelerated warming on plant species richness. Thus, summits are optimal for resurveys of species occurrences and for detecting change in plant species richness over time, even when the first surveys were carried out prior to the GPS era. In this study, 302 summits with historical vegetation records were resurveyed between one and five times, resulting in a total of \( n = 698 \) surveys. All vegetation surveys were conducted in summer. For each survey, all plant species occurring on the summit (generally delineated by the uppermost 10 meters of elevation)\textsuperscript{32} were noted. Vegetation surveys were compared for each summit. Species names were standardized to the nomenclature of Flora Europaea (or local floras for species absent in the Flora, see online Supplementary Information at www.nature.com/nature).

Environmental data. For each summit, mean monthly temperature and precipitation were calculated following the established change factor methodology\textsuperscript{33}, which combines statistical downscaling with temporal trend analyses. First, temporal data available from CRU TS 3.23 (0.5 degree resolution, 1901-2015)\textsuperscript{34} and the European Gridded Monthly Temperature (0.5 degree resolution, 1765-2000)\textsuperscript{34} were statistically related to the higher spatial resolution of WorldClim monthly mean climatic grids (30 arc-second resolution) for the overlapping period of 1950 to 2000 using the change factor method\textsuperscript{33}. We assumed that anomalies (cf. mean value over the period 1950-2000 of the coarse-grained climatic conditions minus the climatic conditions within each smaller pixel of WorldClim) computed for the overlapping period (1950-2000) remain the same prior to 1950 and after 2000. Second, elevational differences
between summits and the mean elevation of the corresponding WorldClim digital elevation model were included as an additional correction term (-0.006°C x Δelevation in m) for mean temperature data. By combining the two corrections, temporal trends available from the 0.5 degree resolution temporal data were corrected for i) differences originating from scale and climate model and ii) the precise elevation of the summit (temperature only). While we consider the resulting temporal trends for the temperature data to be reliable due to the generally higher spatial and temporal autocorrelation and a higher correlation with elevation, the precipitation data do not show a systematic change with elevation and are less predictable over small spatial distances and, therefore, need to be interpreted more cautiously. Environmental variables were included in the models after calculating temporal changes (see end of the Methods section). Consequently, environmental variables are unbiased by weaknesses in the spatial interpolations. For temperature and precipitation, time series from CRU TS 3.23 (1901-2015) and the European Gridded Monthly Temperature (1765-2000) were combined to match the study period (1880-2016) by taking the mean per grid cell for the overlapping years (Spearman r = 0.97 for the overlapping period 1901-2000). As none of the two data sources extends to 2016, climate values for 2015 were taken again for 2016 for the 19 affected summits. Further, historical nitrogen deposition data (NHx and NOx modeled from 1850-2010) were extracted from the European Fluxes Database (www.europe-fluxdata.eu) and interpolated for the missing five years (2011-2016). The data originate from the global chemistry Transport Model version 5 (TM5, annual data with a 0.25° lat/long resolution). Data handling and all subsequent analyses were conducted in R version 3.3.1.

**Statistical analyses.**

*The velocity of species richness changes:* Species richness (SR) on mountain summits was analyzed for its change with time (t: year of record) across all summits by implementing a generalized linear mixed effects model (GLMM) with a Poisson family error distribution (SR ~ t) and a random effect (intercept) of mountains to account for repeated samples (GLMM 1 in Extended Data Table 1, mixed effects models always built with R package lme4 version...
Further, we ran the models including random effects (intercept) of region (mountains nested in region; GLMM 2 in Extended Data Table 1) and observation ID (to account for over dispersion; see reference 40; GLMM 3 in Extended Data Table 1). All models provided qualitatively equivalent results (Extended Data Table 1).

We repeated all GLMMs allowing a breakpoint (bp) in the relationship between species richness and time by fitting independent slope coefficients for the time period prior and after the breakpoint (SR ~ ifelse(t < bp, bp - t, 0) + ifelse(t < bp, 0, t - bp) + random structure). The breakpoint was fitted independently by minimizing the model deviance (Extended Data Table 1). It is likely that the real breakpoint (cf. the onset) of the acceleration trend in the increase in plant species richness happened slightly later than the estimated breakpoint suggested by this particular analysis. Indeed, the estimated breakpoint approximates the timing of change as the year between two sequential surveys and thus mechanistically moves every change temporally towards the median of the time series.

**Acceleration of species richness changes:** The potential acceleration in the average velocity of species richness changes on mountain summits between 1871 and 2016 was tested by means of a linear mixed effects model (LMM) with a Gaussian family error distribution ($\Delta$SR/Δt ~ tMP). With the model, we analyzed the rate of change in species richness over time (midpoint year between two surveys tMP = (t1+t2)/2). The dependent variable $\Delta$SR/Δt was calculated based on the difference in species richness and the difference between years of observation of two consecutive surveys on the same summit ((SRt2-SRt1)/(t2-t1)). A random effect (intercept) of mountain was included to account for repeated samples. We also ran the model including a random effect (intercept) of mountain nested within region but found qualitatively similar results (Extended Data Table 2). Mathematically, $\Delta$SR/Δt is independent from richness on the summits as well as from time elapsed between sequential visits on the summit. However, more species-rich systems seemed to be associated with higher rates of changes, as indicated by a significant positive effect if baseline (cf. the first survey) species richness of the summit was included as an explanatory variable in the fixed component of the
LMM (Extended Data Table 2). We also tested if there was an effect of the number of years between two consecutive surveys on $\Delta SR/\Delta t$, as a longer period between surveys might mask short-term fluctuations, but this effect was not significant (Extended Data Table 2).

A linear increase in the rate of change with time ($\Delta SR/\Delta t \sim t_{MP}$) corresponds to an accelerated richness increase. As Fig 2 and Fig 3 indicate a non-linearity in the relationship, we also run all models allowing a breakpoint in the relationship between the rate of change and the time between surveys (Extended Data Table 2).

In the raw data, the average rate of species richness increase per summit was found to be much higher in the last decade (2007–2016; +2.9 species) compared to fifty years earlier (1957–1966, +1.1 species). When the slopes are averaged across all summits with an observation prior and after a respective year, inversely weighted by the number of years between observations (to account for temporal resolution, as a longer period between surveys might mask short-term fluctuations), the differences become even more apparent (+5.4 species in the last decade as opposed to +1.1 species per decade fifty years earlier).

Visualization of temporal changes in richness: The average richness change per year ($\Delta SR/\Delta t = (SR_{t2}-SR_{t1}) / (t_2-t_1)$) across all summits was calculated (see Extended Data Figure 1a for method). Fig. 3 displays how the average in $\Delta SR/\Delta t$ across all summits changed over time. As values for $\Delta SR/\Delta t$ originating from summits with a higher temporal sampling density better represent the instant rate of change for that specific year (t), we inversely weighted the calculated values for $\Delta SR/\Delta t$ by the difference in years between observations ($t_2-t_1$) to account for temporal resolution.

The changes in species richness per year ($\Delta SR/\Delta t$) accumulated over time and result in an absolute change in species richness (Extended Data Figure 1b). These absolute changes in species richness are visualized for each region in Fig. 2 (black line). In order to also visualize variability within regions, confidence intervals were calculated based on the standard deviation of richness change among summits in a region (see Extended Data Figure 1c and 1d and related figure caption).
Importance of environmental drivers: The average velocity of species richness changes (ΔSR/Δt) was related to the change in mean annual temperature (ΔT/Δt; T = temperature) and precipitation (ΔP/Δt; P = precipitation) for the same period (see below for further details), as well as to the accumulated nitrogen deposition (Naccum; N = nitrogen, details explained below) across all summits, by implementing LMMs with a Gaussian family error distribution that included each of the three potential explanatory variables (different rows in Extended Data Table 3, model formula can be seen in table caption). Variable performance was compared using the corrected version (for small sample size) of the Akaike Information Criteria (AICc). All LMMs consistently detected a clear positive relationship between species richness changes and temperature changes while a slightly weaker positive relationship with precipitation changes was also detected. Particularly the relationship with temperature changes is surprisingly strong considering that climate models are built on long-term air temperature measurements at two meters above ground in climate stations that are mainly located in valleys and can only approximate changes in growth conditions for summits species. No relationship with the accumulated nitrogen deposition was detected across Europe (Extended Data Table 3).

The explanatory variables ΔT/Δt and ΔP/Δt were calculated as the mean change per year (e.g. ΔT/Δt = T_{t2} - T_{t1} / t_{2} - t_{1}). Climate variables like temperature and precipitation are usually integrated over longer time periods to level out short-term fluctuations. As we were interested in the effect of such shorter-term fluctuations, we systematically tested which periods would provide the best fit within our LMM framework (1–30 years). Besides mean annual temperature and precipitation, we further tested alternative measurements of the climate variables. If species’ ranges are limited primarily by growing season temperatures, we would expect spring and summer warming to best explain temporal changes in species richness. Alternatively, if many alpine species are limited not by growing season temperature, but rather by climatic extremes, winter temperatures or precipitation might be more important in determining which species can survive in a given location. We therefore systematically...
pre-analyzed temperature and precipitation variables by testing for the effect of winter
precipitation (Dec–Feb) and of snow accumulation (precipitation in months with a mean
temperature below freezing).

Further, nitrogen from deposition may accumulate in the soil, particularly in high
elevation systems with limited resource cycling\(^{42,43}\). In our data, nitrogen deposition has
deprecated sharply in recent decades\(^{36}\), although its accumulated effect may still influence
community dynamics\(^ {43}\). We thus calculated accumulated deposition of both NH\(_4\) and NO\(_3\)
since 1850 for each vegetation survey.

The systematic test of different variables and time periods (Extended Data Table 4)
identified annual summer temperature (15-year mean), annual precipitation (1-year mean) and
NO\(_3\) (referred to as N\(_{\text{accum}}\)) as the most suitable predictors, and these variables were then used
in all subsequent analyses. As this type of variable selection biases analyses towards
significant relationships, all analyses were repeated with mean annual values (10-year mean),
resulting in qualitatively similar results. Model residuals were visually checked for temporal
autocorrelation signal without any sign of a temporal trend in the residuals.

**Time-lags in richness change:** Biotic responses may show a delayed response to climate
change\(^ {17,24}\). Therefore, observed species richness on a mountain summit at given point in time
could reflect climatic conditions from several years earlier, as species may need considerable
time to spread and establish (cf. migration and establishment lags). A systematic time-lag was
therefore implemented between our observation and the climate period used to relate the
average velocity of species richness changes with changes in climatic conditions and tested
for a potential increase in explanatory power (tested lags 5 and 10 years; Extended Data Table
5). Final results are presented without time-lags, because including them did not increase the
power in our analyses to explain the average velocity of species richness changes.

An alternative approach to analyzing the average velocity of species richness changes
\((\Delta SR/\Delta t)\) with rates of change in environmental predictors (\(\Delta T/\Delta t\); \(\Delta P/\Delta t\), see Extended Data
Table 3) is to directly relate species richness changes (\(\Delta SR\)) to changes in environmental
variables over the same time period ($\Delta T; \Delta P$). This approach is more intuitive (and closer to the data) but ignores differences in time between sampling events. Analyses with this approach yielded results qualitatively similar to the results of the main analysis (Extended Data Table 3), with the exception that the effect of precipitation changes was not significant (Extended Data Table 6).

**Trait based analyses.**

*Differing trait signal in colonizing species:* Changes in plant life strategies as well as dispersal constrains would be indicated by a systematic difference in indicative traits. We thus compared specific leaf area (SLA)$^{45}$, plant height$^{45}$ as well as seed mass$^{45}$ between colonizing species as well as species in the resident community in a LMM framework setting *resurvey* as a random effect. To test for the colonization and establishment, within the recipient community, of warmth tolerating species from lower elevations, we used Landolt species indicator values for temperature$^{45}$. Temperature indicator values$^{45}$ were available for 91% of the observations. For 364 resurveys (altogether 20583 observations for 871 species) direct comparisons of plant trait values of species in a resurvey that were newly established colonizers with those species that had been present already in the previous survey (recipient community) indicate significantly increased SLA ($p<0.01$) and plant height ($p<0.001$) of successful colonizers but no significant difference in seed mass ($p=0.053$). Colonizers are more adapted to warmer climates than species of the resident communities ($p<0.001$; Extended Data Table 7).

**Data reliability**

*Sampling intensity:* Our analysis of the rate of change is relatively robust with respect to different sampling periods. The increasing sampling intensity over time (Fig. 1) helped to reliably quantify the rates of change in later time periods and thus to support our conclusion on an acceleration in richness change. Consistent continent-wide and short-term fluctuations in species richness that might have occurred in the early 20th century would likely go
undetected due to the lower data availability in the early 20th century of our time series data, but long-term trends would be well visible. We thus have no evidence that the unbalanced sampling effort over time and different sampling intervals hide unobserved fluctuations in early periods. In line with this, the summits for which we have a high number of repeated surveys show little short-term fluctuations but confirm the detected steady increase of richness over time and an acceleration in recent years\textsuperscript{16}.

Observer errors: Previous studies explicitly addressing observer errors of summit resurveys, have demonstrated a reliable quantification for vegetation change over long time periods\textsuperscript{32}. Many of the early records have been collected by expert botanists with a scientific interest in long-term changes and the explicit aim to allow a later resurvey. To further reduce potential sampling and observer errors, recent records were done without knowledge of the past species lists, because surveyors who know the historical species composition have a higher chance of finding certain species again. Approximately 15\% of all summits of this dataset have species records collected in the 1980s and 1990s (partly they were even done by the same people). Even if these early re-surveyors also considered the above methodological issues, we cannot rule out that the observer effort of the early re-surveyors was higher than the historical one. However, we are sure that our recent observer effort did not exceed that of the early re-surveyors during the 1980s and 1990s. Given this, the clear signal that most of the increase in species richness occurred after 1980s/1990s is a strong indication that a possible increase in observer effort, if present, is only responsible for a limited amount of the increase in species richness. We are, thus, confident, that observer errors did not systematically influence our analyses.

Method references


### Extended Data Table 1 | Results of generalized linear mixed effect models (Poisson family error distribution), showing an increase in species richness with time (richness ~ year of record) when different random error structures are applied. The lower panel included a breakpoint in the relationship between rate of richness change and time. The breakpoint was fitted independently by minimizing model deviance and was estimated around the year 1970. All models are based on 698 observations. Significant effects are indicated by asterisks (*p<0.05, **p<0.01, ***p<0.001). “GLMM” = Generalized linear mixed-effects model, “GLM” = Generalized linear model, “BPGLMM” = Generalized linear mixed-effects breakpoint model; “ID” = Observation ID.

#### Fixed effect (coefficients ±std. error) vs. Random effects (std. deviations)

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept</th>
<th>Year of record</th>
<th>Mountain</th>
<th>Region:Mountain</th>
<th>ID</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLMM 1</td>
<td>-5.78 ±0.35***</td>
<td>0.004 ±0.0002***</td>
<td>0.97</td>
<td>-</td>
<td>-</td>
<td>5785</td>
</tr>
<tr>
<td>GLMM 2</td>
<td>-5.78 ±0.35***</td>
<td>0.004 ±0.0002***</td>
<td>0.86</td>
<td>0.41</td>
<td>-</td>
<td>5787</td>
</tr>
<tr>
<td>GLMM 3</td>
<td>-7.33 ±0.58***</td>
<td>0.005 ±0.0003***</td>
<td>0.47</td>
<td>0.84</td>
<td>0.23</td>
<td>5596</td>
</tr>
<tr>
<td>GLM</td>
<td>-7.52 ±0.33***</td>
<td>0.006 ±0.0002***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>18299</td>
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</table>

#### Random effects

<table>
<thead>
<tr>
<th>Intercept</th>
<th>Time &lt; BP</th>
<th>Time &gt; BP</th>
<th>Mountain</th>
<th>Region:Mountain</th>
<th>ID</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>GLMM</td>
<td>2.71 ±0.07***</td>
<td>0.001 ±0.001</td>
<td>0.013 ±0.001***</td>
<td>0.96</td>
<td>-</td>
<td>5709</td>
</tr>
<tr>
<td>GLMM</td>
<td>2.71 ±0.07***</td>
<td>0.001 ±0.001</td>
<td>0.013 ±0.001***</td>
<td>0.87</td>
<td>0.41</td>
<td>5711</td>
</tr>
<tr>
<td>GLMM</td>
<td>2.64 ±0.08***</td>
<td>0.001 ±0.001</td>
<td>0.014 ±0.001***</td>
<td>0.42</td>
<td>0.86</td>
<td>0.21</td>
</tr>
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</table>

### Extended Data Table 2 | Results of linear mixed effects models (Gaussian family error distribution) showing an acceleration of the increase in species richness over time (ΔSR/Δt~t), where different random-effects structures are implemented (see Random effects below). Baseline richness of the summit and the number of years between two consecutive observations (Period) were included as additional explanatory variables. The lower panel further included a breakpoint in the relationship between rate of richness change and time. The breakpoint was fitted independently by minimizing model deviance and was estimated for the year 1971. All models were based on 396 observations (comparison of survey and resurveys). Significant effects are indicated by asterisks (*p<0.05, **p<0.01, ***p<0.001). Note that models without random structure performed best.

#### Fixed effect (coefficients ±std. error) vs. Random effect (std. deviations)

<table>
<thead>
<tr>
<th>Intercept</th>
<th>Time &lt; BP</th>
<th>Time &gt; BP</th>
<th>Richness</th>
<th>Period</th>
<th>Mountain</th>
<th>Region: Mount.</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>-15.5 ±2.03***</td>
<td>-0.008 ±0.001***</td>
<td>-</td>
<td>-</td>
<td>5.2 × 10^8</td>
<td>-</td>
<td>570.3</td>
<td></td>
</tr>
<tr>
<td>-15.5 ±2.06***</td>
<td>-0.008 ±0.001***</td>
<td>-</td>
<td>-</td>
<td>9.6 × 10^8</td>
<td>4.8 × 10^8</td>
<td>572.4</td>
<td></td>
</tr>
<tr>
<td>-13.4 ±2.05***</td>
<td>0.007 ±0.001***</td>
<td>0.004 ±0.001***</td>
<td>0.96</td>
<td>1.8 × 10^8</td>
<td>-</td>
<td>562.6</td>
<td></td>
</tr>
<tr>
<td>-11.7 ±4.77*</td>
<td>0.006 ±0.002*</td>
<td>0.004 ±0.001***</td>
<td>n.s.</td>
<td>1.1 × 10^-7</td>
<td>-</td>
<td>576.0</td>
<td></td>
</tr>
<tr>
<td>-13.4 ±2.05***</td>
<td>0.007 ±0.001***</td>
<td>0.004 ±0.001***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>530.7</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Intercept</th>
<th>Time &lt; BP</th>
<th>Time &gt; BP</th>
<th>Richness</th>
<th>Period</th>
<th>Mountain</th>
<th>Region: Mount.</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.07 ±0.05</td>
<td>0.002 ±0.003</td>
<td>0.013 ±0.002***</td>
<td>-</td>
<td>0.0</td>
<td>-</td>
<td>-</td>
<td>571.3</td>
</tr>
<tr>
<td>0.02 ±0.05</td>
<td>0.0001 ±0.003</td>
<td>0.011 ±0.002***</td>
<td>0.004 ±0.001***</td>
<td>-</td>
<td>0.0</td>
<td>-</td>
<td>568.5</td>
</tr>
<tr>
<td>-0.09 ±0.14</td>
<td>0.0004 ±0.004</td>
<td>0.012 ±0.004***</td>
<td>0.004 ±0.001***</td>
<td>n.s.</td>
<td>1.1 × 10^-8</td>
<td>-</td>
<td>581.5</td>
</tr>
<tr>
<td>0.02 ±0.14</td>
<td>0.0001 ±0.003</td>
<td>0.010 ±0.002***</td>
<td>0.004 ±0.001***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>527.8</td>
</tr>
</tbody>
</table>

### Extended Data Table 3 | Results of linear mixed effects models (Gaussian family error) showing the relationship of the average velocity in species richness changes with the change in potential explanatory variables (temperature, precipitation, nitrogen deposition). Initial species richness on the summit was added as a further independent variable and indicated that species-rich systems showed a larger net change. The implemented model formula was lmer(ΔSR/Δt ~ ΔT/Δt + ΔP/Δt + N_acum + richness + (1|mountain)). Variable performance was compared using AICc, which also sets the order of models, with the best one on top. In addition, significant results from tests using F statistics are indicated by asterisks (*p<0.05, **p<0.01, ***p<0.001). Rerunning the analyses after centering (subtracting the means) and scaling (dividing by standard deviations) the explanatory variables
indicated a larger coefficient and thus stronger effect of temperature than that of precipitation ($\Delta SR/\Delta t \sim 0.00 \pm 0.04 + 0.39 \pm 0.05 \times \Delta T/\Delta t$) + 0.21 (±0.04) $\times \Delta P/\Delta t$ + 0.21 (±0.05) $\times$ Richness***). The analyses presented in the table were performed on a subset of the data, as no nitrogen data were available for the 7 summits of Svalbard. This subsetting resulted in 389 temporal comparisons (summits and revisits that resulted from 684 observations). We further repeated the full model combining all summits sampled over the same time period and falling in the same grid cell of climate data that were not downscaled (by taking the mean) to account for spatial autocorrelation. Results of this model were qualitatively similar ($\Delta SR/\Delta t \sim -0.006 \pm 0.05 + 9.5 \pm 1.1 \times \Delta T/\Delta t$ + 0.005 (±0.001) $\times \Delta P/\Delta t$ - 0.13 (±0.08) $\times$ Naccum + 0.005 (±0.05) $\times$ Richness***).

### Extended Data Table 4 | Model evaluation for linear mixed effects models (Gaussian family error distribution) showing the relationship between average velocity of species richness changes and the change in potential explanatory variables (temperature, precipitation, nitrogen deposition).

The implemented model formula was lmer($\Delta SR/\Delta t \sim \Delta T/\Delta t + \Delta P/\Delta t + N_{\text{accum}} + \text{richness} + (1|\text{mountain})$). During each model run, the focal variable (left column) was exchanged while the remaining model was held constant. Variables were calculated as the mean value across a period prior to the survey (Period).

#### Temperature

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>Period</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summer temperature</td>
<td>15</td>
<td>491.9</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Annual temperature</td>
<td>15</td>
<td>501.1</td>
<td>9.2</td>
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<tr>
<td>Spring temperature</td>
<td>10</td>
<td>511.4</td>
<td>19.4</td>
<td>0.0</td>
</tr>
<tr>
<td>Annual temperature</td>
<td>7</td>
<td>513.4</td>
<td>21.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Spring temperature</td>
<td>7</td>
<td>516.7</td>
<td>24.8</td>
<td>0.0</td>
</tr>
<tr>
<td>Summer temperature</td>
<td>7</td>
<td>518.7</td>
<td>26.8</td>
<td>0.0</td>
</tr>
<tr>
<td>Annual temperature</td>
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<td>520.7</td>
<td>28.8</td>
<td>0.0</td>
</tr>
<tr>
<td>Annual temperature</td>
<td>10</td>
<td>521.2</td>
<td>29.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Spring temperature</td>
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<td>521.3</td>
<td>29.3</td>
<td>0.0</td>
</tr>
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<td>Annual temperature</td>
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<td>38.6</td>
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</tr>
<tr>
<td>Spring temperature</td>
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<td>531.8</td>
<td>39.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Summer temperature</td>
<td>5</td>
<td>532.0</td>
<td>40.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Summer temperature</td>
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<td>534.9</td>
<td>43.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Summer temperature</td>
<td>30</td>
<td>536.0</td>
<td>44.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Annual temperature</td>
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<td>538.9</td>
<td>47.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Annual temperature</td>
<td>5</td>
<td>539.2</td>
<td>47.2</td>
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</tr>
<tr>
<td>Summer temperature</td>
<td>10</td>
<td>549.4</td>
<td>57.4</td>
<td>0.0</td>
</tr>
<tr>
<td>Spring temperature</td>
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<td>550.4</td>
<td>58.5</td>
<td>0.0</td>
</tr>
<tr>
<td>Summer temperature</td>
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<td>551.2</td>
<td>59.3</td>
<td>0.0</td>
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<tr>
<td>Spring temperature</td>
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<td>552.4</td>
<td>60.5</td>
<td>0.0</td>
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<td>Spring temperature</td>
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<td>555.7</td>
<td>63.8</td>
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</table>

#### Precipitation

<table>
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<tr>
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<th>ΔAICc</th>
<th>AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual precipitation</td>
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<td>491.9</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Winter precipitation</td>
<td>15</td>
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<td>12.4</td>
<td>0.0</td>
</tr>
<tr>
<td>Annual precipitation</td>
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<td>505.5</td>
<td>13.6</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Period</td>
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<td>ΔAICc</td>
<td>AICc weights</td>
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<td>------------------------------</td>
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<td>-------</td>
<td>-------</td>
<td>--------------</td>
</tr>
<tr>
<td>NO accumulation</td>
<td>-</td>
<td>491.9</td>
<td>0.0</td>
<td>0.59</td>
</tr>
<tr>
<td>NH accumulation</td>
<td>-</td>
<td>492.6</td>
<td>0.7</td>
<td>0.41</td>
</tr>
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</table>
Extended Data Table 5 | Model evaluation for linear mixed effects models (Gaussian family error distribution) showing the relationship between average velocity of species richness changes and the change in potential explanatory variables (temperature, precipitation, nitrogen deposition). The implemented model formula was lmer(ΔSR/Δt ~ ΔT/Δt + ΔP/Δt + Naccum + richness + (1|mountain)). Variables were calculated as the mean value across a period prior to the survey. During each model run, the focal variable implemented with a differing time-lag (time between the period and first survey; left column) was exchanged while the rest of the model was held constant.

### Summer Temperature (15-year mean)

<table>
<thead>
<tr>
<th>Time lag</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>501.1</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>5</td>
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<td>34.5</td>
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<td>10</td>
<td>550.2</td>
<td>49.1</td>
<td>0.0</td>
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</tbody>
</table>

### Annual precipitation (1-year mean)

<table>
<thead>
<tr>
<th>Time lag</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weights</th>
</tr>
</thead>
<tbody>
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<td>510.7</td>
<td>0.0</td>
<td>0.76</td>
</tr>
<tr>
<td>5</td>
<td>514.1</td>
<td>3.4</td>
<td>0.14</td>
</tr>
<tr>
<td>10</td>
<td>514.7</td>
<td>4.0</td>
<td>0.10</td>
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</tbody>
</table>

### Nitrogen accumulation

<table>
<thead>
<tr>
<th>Time lag</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICc weights</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>491.9</td>
<td>0.0</td>
<td>0.34</td>
</tr>
<tr>
<td>5</td>
<td>492.0</td>
<td>0.1</td>
<td>0.33</td>
</tr>
<tr>
<td>10</td>
<td>492.0</td>
<td>0.1</td>
<td>0.33</td>
</tr>
</tbody>
</table>

Extended Data Table 6 | Linear mixed effects models (Gaussian family error distribution) showing the direct relationship between species richness changes and change in potential explanatory variables (temperature, precipitation, nitrogen deposition). Initial species richness on the summit was not added as a further independent variable, as it did not show significant effects in any of the models. The implemented model formula was lmer(ΔSR ~ ΔT + ΔP + Naccum + richness + (1|mountain)). Variable performance was compared using AICc, which also sets the order of models, with the best one on top. Additional significance tests using F statistics are indicated by asterisks (*p<0.05, **p<0.01, ***p<0.001). Rerunning the analyses after centering (subtracting the means) and scaling (dividing by standard deviations) indicated a larger coefficient and thus stronger effect of temperature compared to that of precipitation (ΔSR ~ 0.05 (±0.06) + 0.25 (±0.05) x ΔT*** + 0.05 (±0.04) x ΔP - 0.11 (±0.05) x Naccum*).

<table>
<thead>
<tr>
<th>Intercept</th>
<th>ΔT/Δt</th>
<th>ΔP/Δt</th>
<th>Naccum</th>
<th>Richness</th>
<th>AICc</th>
<th>AICWt</th>
</tr>
</thead>
<tbody>
<tr>
<td>7.6 ±1.6***</td>
<td>5.9 ±1.2***</td>
<td>-</td>
<td>-5.4 ±2.3*</td>
<td>-</td>
<td>3002.8</td>
<td>0.57</td>
</tr>
<tr>
<td>7.2 ±1.7***</td>
<td>6.3 ±1.3***</td>
<td>0.002 ±0.002</td>
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<td>-</td>
<td>3003.8</td>
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</tr>
<tr>
<td>2.23 ±1.15</td>
<td>8.25 ±1.92***</td>
<td>-0.011 ±0.010</td>
<td>-3.7 ±2.4</td>
<td>-</td>
<td>3006.5</td>
<td>0.09</td>
</tr>
<tr>
<td>11.8 ±1.48***</td>
<td>-</td>
<td>-0.001 ±0.002</td>
<td>-3.7 ±2.4</td>
<td>-</td>
<td>3023.2</td>
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</tbody>
</table>

Extended Data Table 7 | Results of linear mixed effects models (Gaussian family error distribution) analyzing systematic trait differences between colonizing species and the resident community. Analyses are implemented for 258 mountains (750 species) with a random effect on mountain. Significant effects are indicated by asterisks (*p<0.05, **p<0.01, ***p<0.001). Trait data were log transformed before analysis.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Fixed effect (coefficients ±std. error)</th>
<th>Random effect (std. deviations)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height</td>
<td>-1.92 ±0.02*** + 0.20 ±0.02***</td>
<td>0.20</td>
</tr>
<tr>
<td>SLA</td>
<td>2.870 ±0.006*** + 0.021 ±0.008**</td>
<td>0.04</td>
</tr>
</tbody>
</table>
Seed mass: $-1.50 \pm 0.03^{**}$ non sign. $0.08$
Temperature indicator: $2.60 \pm 0.05^{***} + 0.37 \pm 0.05^{***} 0.53$

Extended Data Figure 1 | Conceptual figure showing the approach implemented in the main text to visualize richness change over time based on the raw data (Fig. 2 and 3). a) The mean richness change per year ($\Delta SR/\Delta t = (SR_{t2}-SR_{t1}) / (t_2-t_1)$) across all summits was taken (see Fig. 3 for result). b) The mean richness change per year accumulates with time to yield absolute changes in species richness (see black line in Fig. 2 for results). c) and d) variability in the absolute change in species richness was visualized by randomly sampling $\Delta SR$ from all mountains available each year, but adding the standard deviation within a region and year. The displayed range in Fig. 2 illustrates the 5th and 95th percentiles of the resulting richness change values from 1000 runs (orange shading in Fig. 2). This approach reveals changes in variability among mountains over time while also showing overall variability for time steps where only a few summits were sampled (particularly in early time periods).
Extended Data Figure 2 | Relationship between rates of changes in species richness across Europe and a) rates of increase in temperature, b) rates of change in precipitation and c) and accumulated nitrogen deposition. Trend lines are interpolated from a simple linear model. Species richness was quantified as the difference between vegetation surveys from the same summit at different time steps (Extended Data Figure 1). No nitrogen data was available for Svalbard.