LETTER

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

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Globally accelerating trends in societal development and human environmental impacts since the mid-twentieth century[1–7] are known as the Great Acceleration and have been discussed as a key indicator of the onset of the Anthropocene epoch[6]. While reports on ecological responses (for example, changes in species range or local extinctions) to the Great Acceleration are multiplying[8,9], 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 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 increase in plant species richness, with five times as much species enrichment between 2007 and 2016 as fifty years ago, between 1957 and 1966. This acceleration is strikingly synchronized with accelerated global warming and is 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 change is occurring even in 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[10,11]. Numerous reports of species redistribution towards summits[8,12–14] and warming-induced changes in biodiversity on summits[13,15,16] suggest that mountain biota are highly sensitive to increasing temperatures[17]. The current accelerating trend in temperature increase[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 (for example, 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[18,19], thus making it possible 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.

We found that plant species richness has increased strongly 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 Fig. 1, Extended Data Table 1) and that 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, the 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 past 20–30 years (Figs. 2, 3). Fifty years ago (1957 to 1966) the rate of increase in species number averaged 1.1 species per decade (Fig. 3), whereas during the past 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

Fig. 1 | Geographical and temporal distribution of studied summits and surveys. The study is based on 698 surveys dating back to 1871 from 302 summits in nine mountain regions across Europe. Each sampled summit is indicated by one line (bottom right), with black crosses indicating survey dates. Many of the historical surveys were conducted by leading pioneers in vegetation ecology in Europe (for example, J. Braun-Blanquet, E. Du Rietz, E. Rübel and B. Pawlowski). Numbers in brackets beside the region names indicate the number of summits/surveys. Photographs reproduced with permission from ref. [31] (left, second left and second right; Botanic Garden Museum, Jagiellonian University, Kraków) and ref. [32] (middle photograph; Wiley). Right-hand figure reproduced from ref. [33]. Geospatial data for the map in all figures are from the WorldClim project (http://www.worldclim.org/).

the rate of warming across all 302 time series (linear mixed effects models, $P < 0.001$; Fig. 4a, Extended Data Fig. 2, 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
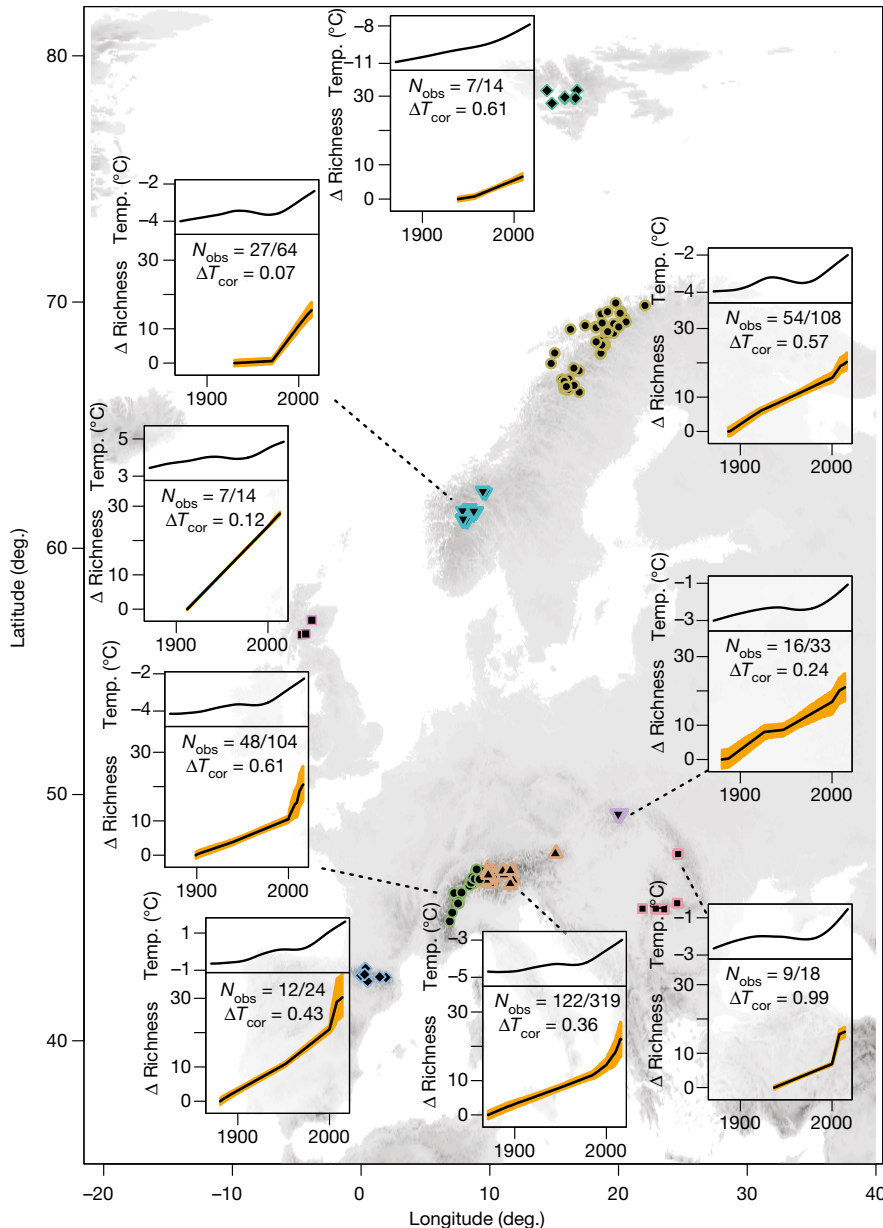
Fig. 2 | Average species richness change on mountain summits over time compared to mean annual temperature over time. Upper parts of inset panels, mean annual temperature; lower part, change in species richness (in species numbers). N_{obs}, number of summits/surveys within the mountain region providing data for the panel. Correlation between rate of change in species richness and rate of change in temperature (ΔT_{cor}) is positive for all mountain regions (Extended Data Fig. 2). 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 Fig. 1 for methodological details.
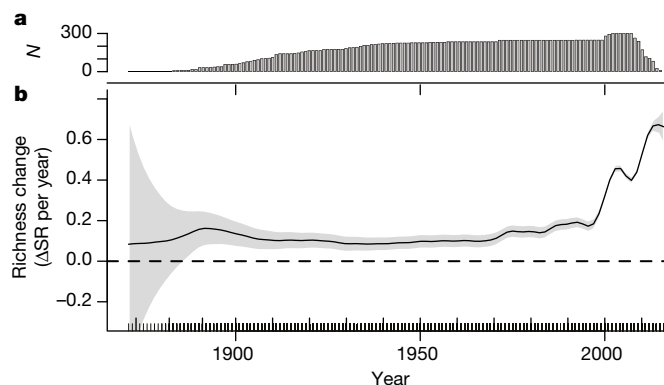
Fig. 3 | Rate of species richness change over time. a, Number of slope parameters per year (*N*; comparisons of earlier survey and later sampled resurvey). **b**, Rate of change in species richness (mean, black line). Positive values indicate an increase in species richness on summits and negative values indicate a decrease. Rates (ΔSR per year $=$ (SR$_{t2}$ $-$ SR$_{t1}$)/ ($t_2 - t_1$) where SR is species richness and *t* is 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 $\pm$ s.e.m.

Fig. 4 | Rate of species richness change related to the rate of temperature change and precipitation change across all sampled mountains in Europe. a, Rate of species richness change (ΔSR per year $=$ (SR$_{t2}$ $-$ SR$_{t1}$)/ ($t_2 - t_1$)) related to the rate of temperature change. **b**, Rate of species richness change related to the rate of precipitation change. Note that this pattern differs considerably among regions (see Extended Data Fig. 2 for more details at the regional level). Dots are semi-transparent, 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 Methods and Extended Data Table 3). 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 in species richness shows the same trend across the continent. Figures and models are based on 396 observations (comparison of all 698 survey and resurveys for the 302 summits). See text and Methods for more detailed analyses with generalized mixed effects offset models, including regional differences.

of locally observed upward shifts of species ranges in mountains[12,13,20] (Fig. 2) and their recent acceleration[16,21]. Our findings thus align with those of shorter-term studies demonstrating plant community thermophilization[15,17] and range shifts driven by warming[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 regionally with changes in species richness, but the direction and magnitude of these effects differ strongly among regions (Extended Data Fig. 2). Although precipitation change (ΔP per year) has a moderate (positive) effect on species richness trends across Europe (Extended Data Table 3, Fig. 4b), its effect is not consistent and significant across all analysed regions (Extended Data Table 4, Extended Data Fig. 2) and is minor compared to the effect of temperature change (ΔT per year; Extended Data Tables 4, 5). Changes in grazing and tourism could also affect changes in plant species richness on summits[21]. Local studies have suggested that grazing[22] and frequent disturbance by tourists[15] may suppress the elevational advance of alpine plants in response to warming in mountains. Although quantification of these relationships is challenging, locally declining levels of domestic livestock have often coincided with recovery of wild ungulate populations. Hiking tourism has increased on some summits, but intensities of human impact vary strongly. Land-use changes may thus explain parts of the local variation in species richness trends, but they vary greatly within and among 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 have suggested that upslope species migration in mountains occurs almost in synchrony with climate warming[17], whereas findings from other studies indicate that long lags in dispersal, establishment and extinction can be expected for many alpine plant species[23,24]. We systematically tested for time-lags (up to 10 years) in increases in species richness following changes in climate, but found that the inclusion of time-lags did not significantly improve the explanatory power of our models (Extended Data Table 6). This finding suggests that increases in species richness on European summits are a direct and immediate response to climate warming (Fig. 2) and, thus, can be expected to accelerate further as climate warming continues
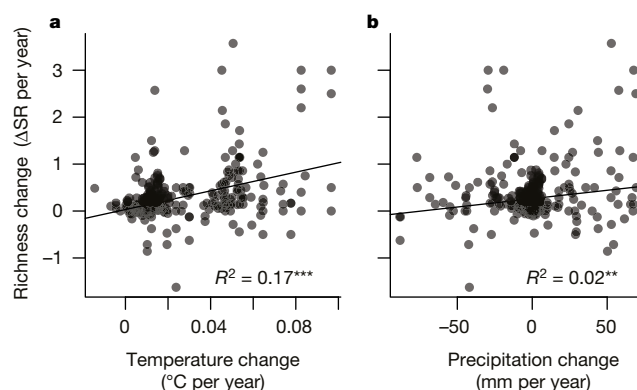
to accelerate[1]. However, because we focus on the average trend and do not account for non-colonizing lower-altitude species, we cannot exclude the possibility that only a fraction of species responded quickly to climate change, thus creating the observed relationship, while an unknown number of species lags behind the change in climate. Our observations may, therefore, underestimate the expected long-term species turnover on summits.

The accelerated increase in species richness on mountain summits is likely to result from an upward shift in the upper range limits of an increasing number of species. Trait analyses show that new colonizers exhibit growth strategies characteristic of species from lower elevations, such as larger size ($P < 0.001$), higher specific leaf area ($P < 0.001$) and a general association with warmer temperatures ($P < 0.001$; Extended Data Table 7) compared to established species. 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[25]. As more species become established at high-elevation sites, local extinctions will be likely to result from 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[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 are expected to be a transient phenomenon that hides the accumulation of a so-called extinction debt[23,27]. The relaxation time until this debt is paid off is likely to be characterized by continuous shifts in abundance ratios, which may serve as sensitive early warning signals of upcoming extinctions[15]. The length of this relaxation time will probably depend 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[28,29]. Although these processes, along with species' intrinsic ability to tolerate changing climates, may buffer local extinctions, a 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 are instead initiated by threshold-like dynamics (for example, 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[6]. 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 wellbeing, and the dynamics of climate change[30].

Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at https://doi.org/10.1038/s41586-018-0005-6.

1. Smith, S. J., Edmonds, J., Hartin, C. A., Mundra, A. & Calvin, K. Near-term acceleration in the rate of temperature change. *Nat. Clim. Chang* **5**, 333–336 (2015).
2. Comiso, J. C., Parkinson, C. L., Gersten, R. & Stock, L. Accelerated decline in the Arctic sea ice cover. *Geophys. Res. Lett* **35**, L01703 (2008).
3. Kintisch, E. Sea ice retreat said to accelerate Greenland melting. *Science* **352**, 1377 (2016).
4. Hughes, T. P. et al. Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373–377 (2017).
5. Hollesen, J., Matthiesen, H., Møller, A. B. & Elberling, B. Permafrost thawing in organic Arctic soils accelerated by ground heat production. *Nat. Clim. Chang* **5**, 574–578 (2015).
6. Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O. & Ludwig, C. The trajectory of the Anthropocene: The Great Acceleration. *Anthropocene Rev* **2**, 81–98 (2015).
7. Alstad, A. O. et al. The pace of plant community change is accelerating in remnant prairies. *Sci. Adv* **2**, e1500975 (2016).
8. Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026 (2011).
9. Wiens, J. J. Climate-related local extinctions are already widespread among plant and animal species. *PLoS Biol* **14**, e2001104 (2016).
10. Gobiet, A. et al. 21st century climate change in the European Alps—a review. *Sci. Total Environ* **493**, 1138–1151 (2014).
11. Mountain Research Initiative EDW Working Group Elevation-dependent warming in mountain regions of the world. *Nat. Clim. Chang.* **5**, 424–430 (2015).
12. Lenoir, J., Gégout, J.-C., Marquet, P. A., de Ruffray, P. & Brisse, H. A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320**, 1768–1771 (2008).
13. Pauli, H. et al. Recent plant diversity changes on Europe's mountain summits. *Science* **336**, 353–355 (2012).
14. Grytnes, J.-A. et al. Identifying driving factors behind observed species range shifts on European mountains. *Glob. Ecol. Biogeogr* **23**, 876–884 (2014).
15. Gottfried, M. et al. Continent-wide response of mountain vegetation to climate change. *Nat. Clim. Chang* **2**, 111–115 (2012).
16. Wipf, S., Stöckli, V., Herz, K. & Rixen, C. The oldest monitoring site of the Alps revisited: Accelerated increase in plant species richness on Piz Linard summit since 1835. *Plant Ecol. Divers* **6**, 447–455 (2013).
17. Bertrand, R. et al. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* **479**, 517–520 (2011).
18. Stöckli, V., Wipf, S., Nilsson, C. & Rixen, C. Using historical plant surveys to track biodiversity on mountain summits. *Plant Ecol. Divers* **4**, 415–425 (2012).
19. Verheyen, K. et al. Combining biodiversity resurveys across regions to advance global change research. *Bioscience* **67**, 73–83 (2017).
20. Odland, A., Høitomt, T. & Olsen, S. L. Increasing vascular plant richness on 13 high mountain summits in Southern Norway since the early 1970s. *Arct. Antarct. Alp. Res* **42**, 458–470 (2010).
21. Walther, G.-R., Beißner, S. & Burga, C. A. Trends in the upward shift of alpine plants. *J. Veg. Sci* **16**, 541–548 (2005).
22. Speed, J. D. M., Austrheim, G., Hester, A. J. & Mysterud, A. Elevational advance of alpine plant communities is buffered by herbivory. *J. Veg. Sci* **23**, 617–625 (2012).
23. Dullinger, S. et al. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat. Clim. Chang* **2**, 619–622 (2012).
24. Hülber, K. et al. Uncertainty in predicting range dynamics of endemic alpine plants under climate warming. *Glob. Change Biol* **22**, 2608–2619 (2016).
25. Vetaas, O. R. Realized and potential climate niches: a comparison of four *Rhododendron* tree species. *J. Biogeogr* **29**, 545–554 (2002).
26. Alexander, J. M., Diez, J. M. & Levine, J. M. Novel competitors shape species' responses to climate change. *Nature* **525**, 515–518 (2015).
27. Cotto, O. et al. A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nat. Commun* **8**, 15399 (2017).
28. Kulonen, A., Imboden, R. A., Rixen, C., Maier, S. B. & Wipf, S. Enough space in a warmer world? Microhabitat diversity and small-scale distribution of alpine plants on mountain summits. *Divers. Distrib* **24**, 252–261 (2018).
29. Winkler, M. et al. The rich sides of mountain summits — a pan-European view on aspect preferences of alpine plants. *J. Biogeogr* **43**, 2261–2273 (2016).
30. Pecl, G. T. et al. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355**, eaai9214 (2017).
31. Zemanek, A. Bogumił Pawłowski (1898–1971) — życie i dzieło. *Fragm. Florist. Geobot. Polon* **19**, 205–244 (2012).
32. Ellenberg, H. J. Braun-Blanquet 3.8.1884–22.9.1980 R. Tüxen 21.5.1899–16.5.1980–Jahre Pflanzensoziologie. *Ber. Deutsch. Bot. Ges* **95**, 387–391 (1982).
33. Unknown. Tschechoslowakei 1928. Mohelno. Prof. Rübel im Jihlavka-Tale. ETH-Bibliothek Zürich, Bildarchiv (1928).

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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)[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[34], p. 329). This foresight and the data these botanists gathered on mountain summits give 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 changes in plant species richness over time, even when the first surveys were carried out before the GPS era. In this study, 302 summits with historical vegetation records were resurveyed between one and six 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 m of elevation)[35] were noted. Vegetation surveys were compared for each summit. Species names were standardized to the nomenclature of Flora Europaea (or local flora for species absent in the Flora; see Supplementary Information).

Environmental data. For each summit, mean monthly temperature and precipitation were calculated following the established change factor methodology[36], which combines statistical downscaling with temporal trend analyses. First, temporal data available from CRU TS 3.23 (0.5° resolution, 1901–2015)[37] and the European Gridded Monthly Temperature (0.5° resolution, 1765–2000)[38] were statistically related to the higher spatial resolution of WorldClim monthly mean climatic grids (30 arcsec resolution) for the overlapping period of 1950 to 2000 using the change factor method[36]. We assumed that anomalies (compared with 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) remained the same before 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 ($-0.006\,°C \times \Delta$elevation (m)) for mean temperature data. By combining the two corrections, temporal trends available from the 0.5° degree resolution temporal data were corrected for differences originating from scale and climate model, and the precise elevation of the summit (temperature only). While we consider the resulting temporal trends for the temperature data to be reliable owing 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[39] and, therefore, need to be interpreted more cautiously. Environmental variables were included in the models after calculating temporal changes (see 'Importance of environmental drivers'). 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 neither of the two data sources extends to 2016, climate values for 2015 were taken again for 2016 for the 19 affected summits. Furthermore, historical nitrogen deposition data (NH_x and NO_x modelled from 1850 to 2010) were extracted from the European Fluxes Database (http://www.europe-fluxdata.eu/) and extrapolated 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° latitude/longitude resolution)[40]. Data handling and all subsequent analyses were conducted in R version 3.3.1[41].

The velocity of species richness changes. Species richness (SR) on mountain summits was analysed 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 mountain to account for repeated samples (GLMM 1 in Extended Data Table 1; all mixed effects models were built with R package *lme4* version 1.1-12)[42]. Further, we ran the models including random effects (intercept) of region (mountain nested in region; GLMM 2 in Extended Data Table 1) and observation ID (to account for overdispersion[43]; 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 before 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).

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 (ΔSR/Δt ~ t_{MP}). With the model, we analysed the rate of change

in species richness over time (midpoint year between two surveys $t_{MP} = (t_1 + t_2)/2$). The dependent variable ΔSR/Δt was calculated from the difference in species richness and the difference between years of observation of two consecutive surveys on the same summit (($SR_{t2} - SR_{t1})/(t_2 - t_1$)). 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, ΔSR/Δt is independent of richness on the summits as well as of time elapsed between sequential visits on the summit. However, more species-rich summits seemed to be associated with higher rates of change, as indicated by a significant positive effect if the species richness of the first survey was included as an explanatory variable in the fixed component of the LMM (Extended Data Table 2). We also tested whether there was an effect of the number of years between two consecutive surveys on ΔSR/Δt, 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 (ΔSR/Δt ~ t_{MP}) corresponds to an accelerated richness increase. As Figs. 2 and 3 indicate a nonlinearity in the relationship, we also ran all models allowing a breakpoint in the relationship between the rate of change and the time between surveys (Extended Data Table 2). It is likely that the real breakpoint (compared with the onset) of the acceleration trend in the increase in plant species richness happened slightly later than the 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.

In the raw data, the average rate of species richness increase per summit was found to be much higher in the past 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 before and after a given 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 past decade as opposed to +1.1 species per decade fifty years earlier).

We analysed changes in absolute species numbers, as relative changes are sensitive to the richness values to which they are normalized. Still, repeating the linear mixed effects model with the changes in relative species richness (calculated by taking the difference between survey and resurvey normalized by resurvey richness and years between observations) revealed equivalent results and the same conclusions as using changes in absolute species numbers over time.

Visualization of temporal changes in richness. The average richness change per year (ΔSR/$\Delta t = (SR_{t2} - SR_{t1})/(t_2 - t_1$)) across all summits was calculated (Extended Data Fig. 1a). Figure 3 displays how the average in ΔSR/Δt across all summits changed over time. As values for ΔSR/Δt 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 ΔSR/Δt by the difference in years between observations ($t_2 - t_1$) to account for temporal resolution.

The changes in species richness per year (ΔSR/Δt) accumulate over time and result in an absolute change in species richness (Extended Data Fig. 1b). These absolute changes in species richness are visualized for each region in Fig. 2 (black line). In order also to visualize variability within regions, confidence intervals were calculated on the basis of the standard deviation of richness change among summits in a region (Extended Data Fig. 1c, d).

Importance of environmental drivers. The average velocity of species richness changes (ΔSR/Δt) was related to the change in mean annual temperature ($\Delta T/\Delta t$; T is temperature) and precipitation ($\Delta P/\Delta t$; P is precipitation) for the same period (see below for further details), as well as to the accumulated nitrogen deposition (N_{accum}, 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)[44]. 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 detected. In particular, the relationship with temperature change is surprisingly strong considering that climate models are built on long-term air temperature measurements at two metres 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 $\Delta T/\Delta t$ and $\Delta P/\Delta t$ were calculated as the mean change per year (for example, $\Delta T/\Delta t = (T_{t2} - T_{t1})/(t_2 - t_1$)). Climate variables such as 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 were 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 were 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-analysed temperature and precipitation variables by testing for the effect of winter precipitation (December–February) 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[45,46]. In our data, nitrogen deposition has declined sharply in recent decades[39], although its accumulated effect may still influence community dynamics[47]. 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 5) identified annual summer temperature (15-year mean), annual precipitation (1-year mean) and NO_3 (referred to as N_{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, and there was no 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], as species may need considerable time to spread and establish (compare migration and establishment lags). Therefore, observed species richness on a mountain summit at a given point in time could reflect climatic conditions from several years earlier. A systematic time-lag was therefore implemented between our species observations and the climate period used to relate the average velocity of species richness changes to changes in climatic conditions, and an increase in explanatory power by including a time-lag (5 or 10 years) was tested (Extended Data Table 6). 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 analysing 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 (ΔSR) to changes in environmental variables over the same period (ΔT, ΔP). This approach is more intuitive (and closer to the data) but ignores differences in time between sampling events. Analyses using 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 4).

Trait-based analyses. *Differing trait signal in colonizing species.* Changes in plant life strategies and dispersal constraints would be represented by a systematic difference in indicative traits. We thus compared specific leaf area (SLA)[48], plant height[48] and seed mass[48] among colonizing species and species in the resident community, using a LMM framework with '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[49]. For 364 resurveys (12,738 observations for 873 species), direct comparisons of plant trait values of newly established colonizers (that is, additional species recorded in a resurvey) with those of species that had been present in the previous survey (recipient community) indicate significantly increased SLA ($P < 0.001$) and plant height ($P < 0.001$) of successful colonizers, but no significant difference in seed mass ($P = 0.85$). Colonizers were also more adapted to warmer climates (showing higher Landolt temperature values) than species of the resident community ($P < 0.001$; 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 frequency over time (Fig. 1) helped to reliably quantify the rates of change in later time periods and thus to support our conclusion of 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 be likely to go undetected owing to the low data availability in the early 20th century of our time series data, but long-term trends would be clearly visible. There is, however, 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 large number of repeated surveys show small short-term fluctuations but confirm the detected steady increase of richness over time and an acceleration in recent years[16].

Observer errors. Previous studies explicitly addressing observer errors in summit resurveys have demonstrated reliable quantification of vegetation change over long time periods[35]. Many of the early records were collected by expert botanists with a scientific interest in long-term changes and the explicit aim of enabling accurate later resurveys. To further reduce potential sampling and observer errors, recent resurveys were conducted 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 (they were even carried out by the same people in some cases). 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 greater than that of the historical surveyors. However, our carefully implemented re-survey methodology made 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 the 1980s and 1990s is a strong indication that a possible increase in observer effort, if present, is responsible for only a limited amount of the increase in species richness. We are, thus, confident that observer errors did not systematically influence our analyses.

Summit area. Summit area may affect the observed changes in species richness, probably through its effect on species richness (compare with species–area relationship). We cover this potential effect of area on the change in species richness by including absolute species richness as a co-variate in our analyses. A potential direct effect of area could be tested only for the summits within Switzerland, as data of sufficient spatial resolution to calculate the surface of the uppermost 10 m of a summit was available to us only from this country (swissALTI3D model, a digital elevation model with 2-m resolution). The summit area for Swiss summits varied by as much as 40 times (392–16,720 m^2). Surprisingly, regression analyses indicated that there was no significant effect of summit area on the historical or recent species number, or on the change in species number (area was log-transformed to reach normal distribution). Further evidence of a limited effect of summit area is indicated by the fact that in recent resurveys the species numbers of historic surveys were reached within the uppermost 4–5 m of each summit, which on a summit with conical shape corresponds to a much smaller area than the originally sampled uppermost 10 m (Extended Data Fig. 3). We conclude that, on mountain summits, factors independent of area, for example, environmental conditions and micro-topographic variability[28], seem much more important for species richness or changes thereof than area per se.

Data and code availability. Data and R code are available from the corresponding authors.

34. Braun, J. Die Vegetationsverhältnisse der Schneestufe in den Rätisch-Lepontischen Alpen. Ein Bild des Pflanzenlebens an seinen äußersten Grenzen. *Neue Denkschr. Schweiz. Naturf. Ges* **48**, 1–347 (1913).
35. Burg, S., Rixen, C., Stöckli, V. & Wipf, S. Observation bias and its causes in botanical surveys on high-alpine summits. *J. Veg. Sci* **26**, 191–200 (2015).
36. Anandhi, A. et al. Examination of change factor methodologies or climate impact assessment. *Wat. Resour. Res* **47**, W03501 (2011).
37. Harris, I., Jones, P. D., Osborn, T. J. & Lister, D. H. Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *Int. J. Climatol* **34**, 623–642 (2014).
38. Casty, C., Raible, C. C., Stocker, T. F., Wanner, H. & Luterbacher, J. *European Gridded Monthly Temperature, Precipitation and 500hPa Reconstructions*; IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series # 2008-023 (NOAA/NCDC Paleoclimatology Program, Boulder, 2008).
39. Daly, C., Neilson, R. P. & Phillips, D. L. A statistical topographic model for mapping climatological precipitation over mountainous terrain. *J. Appl. Meteorol.* **33**, 140–158 (1994).
40. Huijnen, V. et al. The global chemistry transport model TM5: description and evaluation of the tropospheric chemistry version 3.0. *Geosci. Model Dev* **3**, 445–473 (2010).
41. R Core Team R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, 2016).
42. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw* **67**, 1–48 (2015).
43. Harrison, X. A. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* **2**, e616 (2014).
44. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* 2nd edn (Springer, New York, 2002).
45. Burns, D. A. The effects of atmospheric nitrogen deposition in the Rocky Mountains of Colorado and southern Wyoming, USA—a critical review. *Environ. Pollut.* **127**, 257–269 (2004).
46. Körner, C. Mountain ecosystems in a changing environment. *Ecomont* **6**, 71–77 (2014).
47. Bobbink, R. et al. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* **20**, 30–59 (2010).
48. Kleyer, M. et al. The LEDA Traitbase: A database of life-history traits of Northwest European flora. *J. Ecol* **96**, 1266–1274 (2008).
49. Landolt, E. et al. *Flora Indicativa* (Haupt, Bern, 2010).
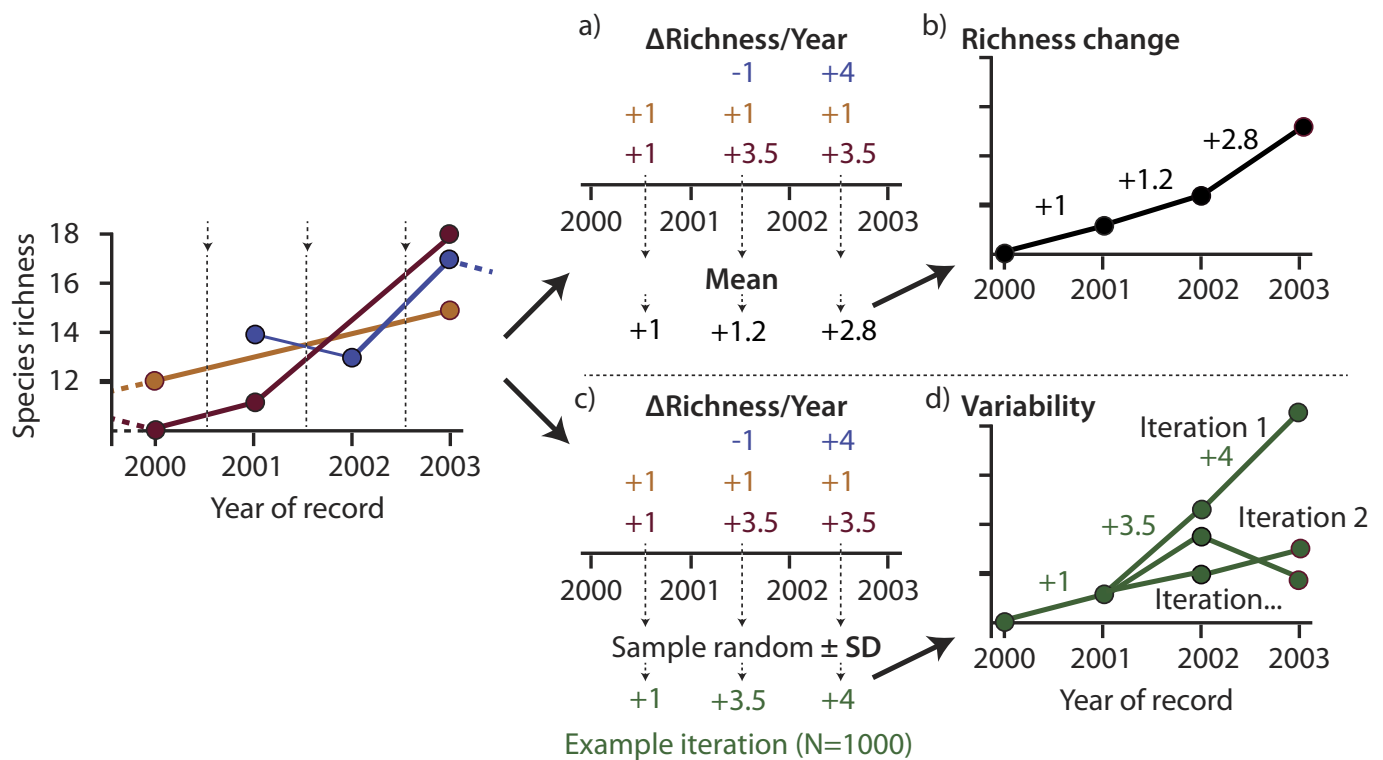
Extended Data Fig. 1 | Visualizing richness change. This conceptual figure shows the approach implemented in the main text to visualize richness change over time based on the raw data (Figs. 2, 3). **a**, The mean richness change per year ($\Delta SR/\Delta t = (SR_{t2} - SR_{t1})/(t_2 - t_1)$) across all summits was calculated (Fig. 3). **b**, The mean richness change per year accumulates with time to yield absolute changes in species richness (black line in Fig. 2). **c, d**, Variability in the absolute change in species richness was visualized by randomly sampling ΔSR from all mountains available each year, but adding the s.d. within a region and year. The displayed range in Fig. 2 illustrates the 5th and 95th percentiles of the resulting richness change values from 1,000 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).
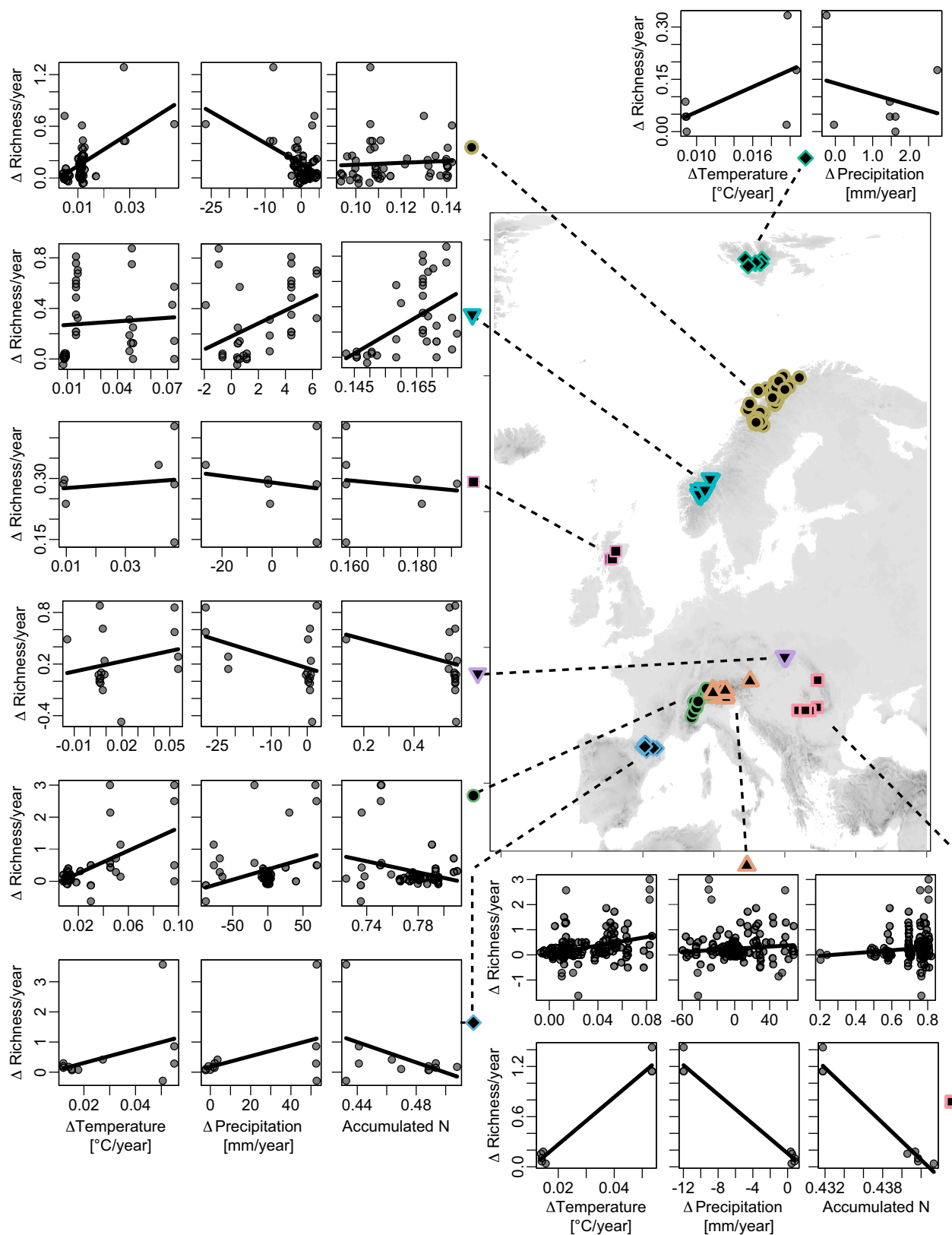
Extended Data Fig. 2 | Relationship between rates of changes in species richness across Europe and rates of increase in temperature (left column), rates of change in precipitation (middle column) and accumulated nitrogen deposition (right column). Trend lines are interpolated from a simple linear model and are in many cases not significant. Species richness was quantified as the difference between vegetation surveys from the same summit at different times (Extended Data Fig. 1). No nitrogen data were available for Svalbard. The number of observations (comparison of survey and resurveys) are: Svalbard, 7; Northern Scandes, 54; Southern Scandes, 27; Scotland, 7; NW Carpathians, 16; Eastern Alps, 122; Western Alps, 48; SE Carpathians, 9; Pyrenees, 12 (see Fig. 1 for more details).
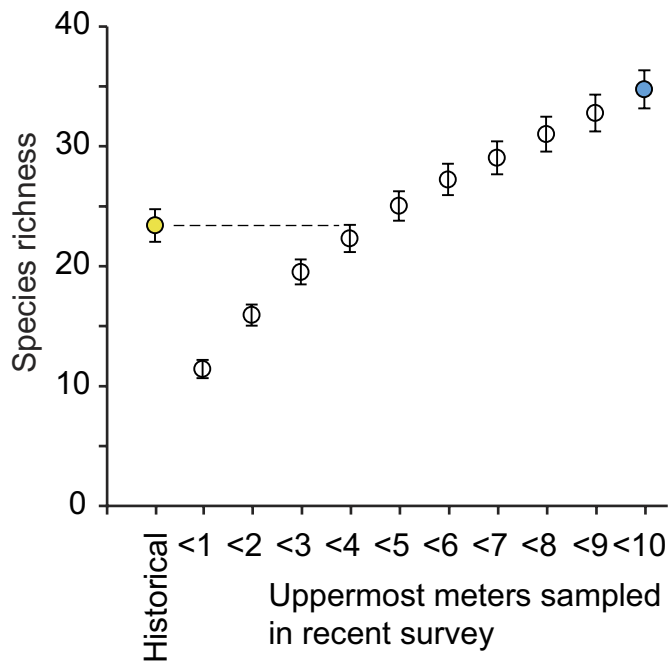
Extended Data Fig. 3 | Historical and recent species richness versus sampling area. Historical species richness was exceeded within a small sampling area during recent resurveys. Species richness of the historical survey (yellow) contrasted with a species richness accumulation curve of the recent surveys on summits where the highest occurrence of each recent species was estimated to the nearest 1-m elevation. The number of species found historically within the uppermost 10 m of a summit was exceeded within the uppermost 5 m in the most recent resurveys. This analysis includes all 157 European summits for which such data are available, regardless of whether the historical species number was reached in recent times. The blue circle visualizes average species richness of the recent surveys within the uppermost 10 m.

Extended Data Table 1 | Increase in species richness with time

	Fixed effect (coefficients ±std. error)			**Random effects** (std. deviations)			
Model	*Intercept*	*Year of record*		*Mountain*	*Region:Mount.*	*ID*	*AICc*
GLMM 1	-5.84 ± 0.35***	0.004 ±0.0002***		0.97	-	-	5758
GLMM 2	-5.84 ± 0.35***	0.004 ±0.0002***		0.88	0.41	-	5760
GLMM 3	-7.31 ± 0.57***	0.005 ±0.0003***		0.75	0.60	0.22	5585
GLM	-7.60 ± 0.33***	0.006 ±0.0002***		-	-	-	18256
Model	*Intercept*	*Time < BP*	*Time > BP*	*Mountain*	*Region:Mount.*	*ID*	*AICc*
GLMBM	2.73 ±0.07***	0.001 ±0.001	0.013 ±0.001***	0.96	-	-	5684
GLMBM	2.73 ±0.07***	0.001 ±0.001	0.013 ±0.001***	0.87	0.41	-	5686
GLMBM	2.64 ±0.07***	0.001 ±0.003	0.006 ±0.0004***	0.83	0.49	0.22	5583

Generalized linear mixed effects models (Poisson family error distribution) show an increase in species richness with time (richness ~ year of record). Different random effect structures were applied. The lower panel includes 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 (***$P < 0.001$). GLMM, generalized linear mixed effects model; GLM, generalized linear model; GLMBM, generalized linear mixed effects breakpoint model; ID, observation ID.

Extended Data Table 2 | Acceleration of the increase in species richness over time

Fixed effect (coefficients ±std. error)				**Random effect** (std. deviations)		
Intercept	*Time*	*Richness*	*Period*	*Mountain*	*Region: Mount.*	*AICc*
-15.5±2.06***	0.008±0.001***	-	-	5.8×10⁻⁸	-	570.1
-15.5±2.06***	0.008±0.001***	-	-	0.0	0.0	572.1
-13.4±2.05***	0.007±0.001***	0.004±0.001***	-	0.0	-	561.7
-11.7±4.76* (p=0.014)	0.006±0.002* (p=0.012)	0.004±0.001***	n.s.	0.0	-	575.1
-13.4±2.05***	0.007±0.001***	0.004±0.001***	-	-	-	529.9

Intercept	*Time < BP*	*Time > BP*	*Richness*	*Period*	*Mountain*	*Region: Mount.*	*AICc*
0.07±0.05	0.002±0.003	0.013±0.002***	-	-	0.0	-	571.0
0.07±0.05	0.002±0.003	0.013±0.002***			0.0	0.0	573.1
0.02±0.05	0.0001±0.003	0.011±0.002***	0.004±0.001***	-	0.0	-	567.8
-0.09±0.14	0.0004±0.004	0.012±0.004***	0.004±0.001***	n.s.	0.0	-	580.7
0.02±0.05	0.0001±0.003	0.011±0.002***	0.004±0.001***	-	-	-	527.0

Linear mixed effects models (Gaussian family error distribution) showed an acceleration of the increase in species richness over time ($\Delta SR / \Delta t \sim t$). Different random effect structures were implemented. The species richness from the summit's first survey and the number of years between two consecutive observations (period) were included as additional explanatory variables. The lower panel further includes 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 (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; P values > 0.001 are additionally reported in brackets). Note that models without random structure performed best.

Extended Data Table 3 | Explanatory variables for velocity in species richness changes

Intercept	$\Delta T/\Delta t$	$\Delta P/\Delta t$	N_{accum}	Richness	AICc	AICWt
0.01 ±0.06	9.8 ±1.1***	0.005 ±0.001***	-0.16 ±0.09	0.004 ±0.001***	488.1	0.64
-0.06 ±0.04	9.5 ±1.1***	0.005 ±0.001***	-	0.004 ±0.001***	489.3	0.36
0.03 ±0.06	9.1 ±1.1***	-	-0.17 ±0.09	0.004 ±0.001***	509.2	0.00
0.14 ±0.06*	-	0.004 ±0.001***	-0.07 ±0.10	0.006 ±0.001***	556.2	0.00

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 summits was added as a further independent variable and indicated that species-rich systems showed a larger net change. The implemented model formula was lmer($\Delta SR/\Delta t \sim \Delta T/\Delta t + \Delta P/\Delta t + N_{accum} + $ richness $+ (1|$mountain$)$). Model performance was compared using AICc, which also defines the order of models, with the best one on top. In addition, significant results from tests using F statistics are indicated by asterisks (***$P < 0.001$). All values indicate model coefficients ± s.e. Rerunning the analyses after centring (subtracting the means) and scaling (dividing by s.d.) the explanatory variables indicated a larger coefficient and thus stronger effect of temperature than that of precipitation ($\Delta SR/\Delta t = 0.00 (\pm 0.04) + 0.39 (\pm 0.05) \times \Delta T/\Delta t$*** $+ 0.22 (\pm 0.04) \times \Delta P/\Delta t$*** $+ 0.21 (\pm 0.05) \times$ richness***; asterisks indicate significant effects with ***$P < 0.001$). As no nitrogen data were available for the seven summits on Svalbard, the analyses presented in the table were performed on a subset of 389 temporal comparisons (comparing surveys and resurveys resulting from 684 observations). To account for spatial autocorrelation, we further repeated the full model averaging over all summits sampled over the same time period and falling in the same grid cell of the original climate data. The results of this model were qualitatively similar ($\Delta SR/\Delta t = -0.004 (\pm 0.05) + 9.7 (\pm 1.1) \times \Delta T/\Delta t$*** $+ 0.005 (\pm 0.001) \times \Delta P/\Delta t$*** $- 0.14 (\pm 0.09) \times N_{accum} + 0.005 (\pm 0.001) \times$ richness***).

Extended Data Table 4 | Explanatory variables for species richness changes

Intercept	$\Delta T/\Delta t$	$\Delta P/\Delta t$	N_{accum}	Richness	AICc	AICWt
7.7 ±1.6***	5.8 ±1.2***	-	-5.4 ±2.3* (p= 0.02)	-	2950.2	0.56
7.3 ±1.7***	6.2 ±1.3***	0.002 ±0.002	-5.1 ±2.4* (p= 0.03)	-	2951.1	0.34
4.7 ±1.2***	5.9 ±1.3***	0.003 ±0.002	-	-	2953.6	0.10
12.0 ±1.5***	-	-0.001 ±0.002	-3.8 ±2.4	-	2969.9	0.00

Linear mixed effects models (Gaussian family error distribution) showing the direct relationship between species richness changes and changes 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 ~ $\Delta T + \Delta P + N_{accum} +$ 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 (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; P values > 0.001 are additionally reported in brackets). All values indicate model coefficients ± s.e. Rerunning the analyses after centring (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) × ΔT*** + 0.05 (±0.05) × ΔP − 0.11 (±0.05) × N_{accum}*). The analyses were performed with the same data as specified in Extended Data Table 3.

Extended Data Table 5 | Model evaluation for different explanatory variables and time periods

Temperature

Explanatory variable	Period	AICc	ΔAICc	AICc weights
Summer temperature	15	488.1	0.0	1.0
Annual temperature	15	496.5	8.4	0.0
Spring temperature	10	507.6	19.5	0.0
Annual temperature	7	509.1	20.9	0.0
Spring temperature	7	513.2	25.1	0.0
Summer temperature	7	514.7	26.6	0.0
Annual temperature	10	516.0	27.9	0.0
Annual temperature	30	517.4	29.3	0.0
Spring temperature	15	517.6	29.4	0.0
Summer temperature	5	526.7	38.5	0.0
Annual temperature	3	526.9	38.7	0.0
Spring temperature	30	528.3	40.2	0.0
Summer temperature	1	530.6	42.5	0.0
Summer temperature	30	532.5	44.4	0.0
Annual temperature	1	534.9	46.8	0.0
Annual temperature	5	535.5	47.3	0.0
Summer temperature	10	545.6	57.5	0.0
Spring temperature	5	546.2	58.1	0.0
Summer temperature	3	547.1	58.9	0.0
Spring temperature	1	548.2	60.1	0.0
Spring temperature	3	551.4	63.3	0.0

Precipitation

Explanatory variable	Period	AICc	ΔAICc	AICc weights
Annual precipitation	1	488.1	0.0	1.0
Snow precipitation	1	495.2	7.1	0.0
Winter precipitation	15	501.3	13.2	0.0
Annual precipitation	30	502.7	14.5	0.0
Snow precipitation	3	502.9	14.8	0.0
Winter precipitation	1	504.4	16.2	0.0
Snow precipitation	30	504.7	16.5	0.0
Winter precipitation	5	505.6	17.5	0.0
Summer precipitation	30	506.0	17.9	0.0
Winter precipitation	30	507.7	19.6	0.0
Summer precipitation	5	507.7	19.6	0.0
Snow precipitation	10	508.2	20.1	0.0
Snow precipitation	15	509.2	21.1	0.0
Snow precipitation	5	509.5	21.3	0.0
Annual precipitation	5	509.7	21.6	0.0
Annual precipitation	15	509.7	21.6	0.0
Winter precipitation	3	509.8	21.6	0.0
Annual precipitation	10	510.3	22.1	0.0
Summer precipitation	15	510.4	22.2	0.0
Summer precipitation	10	510.4	22.3	0.0
Summer precipitation	3	510.6	22.5	0.0
Summer precipitation	7	510.9	22.8	0.0
Winter precipitation	10	511.0	22.9	0.0
Annual precipitation	3	511.2	23.1	0.0
Annual precipitation	7	511.2	23.1	0.0
Snow precipitation	7	511.2	23.1	0.0
Summer precipitation	1	511.3	23.1	0.0
Winter precipitation	7	511.3	23.1	0.0

Nitrogen

Explanatory variable	Period	AICc	ΔAICc	AICc weights
NO accumulation	-	488.1	0.0	0.6
NH accumulation	-	489.0	0.9	0.4

Linear mixed effects models (Gaussian family error distribution) analysing the relationship between average velocity of species richness changes and the change in potential explanatory variables (temperature, precipitation and nitrogen deposition). The implemented model formula was lmer($\Delta SR/\Delta t \sim \Delta T/\Delta t + \Delta P/\Delta t + N_{accum}$ + richness + (1 | mountain)). Within each new model, the focal variable (left column) was exchanged, while the remaining variables were held constant. Variables were calculated as the mean value across a period before the survey (Period). The analyses were performed with the same data as in Extended Data Table 3.

Extended Data Table 6 | Model evaluation for different time lags

Summer Temperature (15-year mean)

Time lag	AICc	ΔAICc	AICc weights
0	496.5	0.0	1.0
5	531.3	34.8	0.0
10	546.5	50.0	0.0

Annual precipitation (1-year mean)

Time lag	AICc	ΔAICc	AICc weights
0	507.7	0.0	0.72
5	510.7	3.3	0.16
10	511.3	3.6	0.12

Nitrogen accumulation

Time lag	AICc	ΔAICc	AICc weights
0	488.1	0.0	0.34
5	488.2	0.1	0.33
10	488.2	0.1	0.33

Linear mixed effects models (Gaussian family error distribution) analysing the relationship between average velocity of species richness changes and the change in potential explanatory variables (temperature, precipitation and nitrogen deposition). The implemented model formula was lmer(ΔSR/Δt ~ $\Delta T/\Delta t + \Delta P/\Delta t + N_{accum}$ + richness + (1 | mountain)). Explanatory variables were calculated as the mean value across a period before the survey. Within each new model, the focal explanatory variable implemented with a differing time lag (time between the period and survey; left column) was exchanged while the remaining variables were held constant. The analyses were performed with the same data as in Extended Data Table 3.

Extended Data Table 7 | Trait differences between colonizing and old-established species

Trait	Fixed effect (coefficients ±std. error)		Random effect (std. deviations)
	Intercept	Difference of colonizer relative to established species	Resurvey
Plant height	-0.234 ±0.022***	+ 0.292 ±0.022***	0.31
SLA	-0.077 ±0.017***	+ 0.158 ±0.024***	0.13
Seed mass	-0.014 ±0.017	+ 0.003 ±0.025	0.09
Temperature indicator	-0.188 ±0.023***	+ 0.221 ±0.020***	0.35

Linear mixed effects models (Gaussian family error distribution) revealed systematic trait differences between colonizing and old-established species. Analyses were implemented for 364 resurveys (12,738 observations with 815 species) with a random effect of resurvey. Temperature indicator values[49] were available for 90%, specific leaf area (SLA)[48] for 61%, plant height[48] for 76%, and seed mass[48] for 53% of the observations. Significant effects are indicated by asterisks (***$P < 0.001$). Trait raw data were first log-transformed, then centred to zero mean and scaled to s.d. = 1 before analysis.

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☐ Initial submission ☐ Revised version ☒ Final submission

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▶ Experimental design

1. Sample size

Describe how sample size was determined.

> All mountain summits in Europe with repeated vegetation surveys known to the authors were integrated in the analyses.

2. Data exclusions

Describe any data exclusions.

> Historic records were excluded if data description did not allow an evaluation of data quality and completeness of sampling (see Burg et al. 2015 JVS for detailed discussion). Only one record fulfilling this criteria was excluded (Monte Perdido, Pyrenees), because it was sampled in 1802 (70 years before the next sample in the data, no coverage with climate data).

3. Replication

Describe whether the experimental findings were reliably reproduced.

> No experimental treatments were applied. Reproducability of field surveys (i.e. observer bias) was studied and described for a subset of field sites (see Burg et al 2015 JVC for details) and discussed in supplementary materials.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

> Mountain regions were used as random factors in analyses. Mountain regions were defined according to their geographical distinctness within the European continent.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

> Blinding was applied in data collection with respect to results of the previous survey (no knowledge of historical species lists during summit resurveys). As group allocation was based on geography, blinding to group allocation is not relevant nor possible in this study.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. **Statistical parameters**

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed	
☐	☒	The <u>exact sample size</u> (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☐	☒	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	A statement indicating how many times each experiment was replicated
☐	☒	The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☐	☒	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒	The test results (e.g. *P* values) given as exact values whenever possible and with confidence intervals noted
☐	☒	A clear description of statistics including <u>central tendency</u> (e.g. median, mean) and <u>variation</u> (e.g. standard deviation, interquartile range)
☐	☒	Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

▶ **Software**

Policy information about availability of computer code

7. **Software**

Describe the software used to analyze the data in this study.	All analyses are implemented in R (R Core Team 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.)

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

▶ **Materials and reagents**

Policy information about availability of materials

8. **Materials availability**

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.	No unique materials were used in this study.

9. **Antibodies**

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	No antibodies were used in this study.

10. **Eukaryotic cell lines**

a. State the source of each eukaryotic cell line used.	No cell lines were used in this study.
b. Describe the method of cell line authentication used.	No cell lines were used in this study.
c. Report whether the cell lines were tested for mycoplasma contamination.	No cell lines were used in this study.
d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	No cell lines were used in this study.

▶ **Animals and human research participants**

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. **Description of research animals**

Provide details on animals and/or animal-derived materials used in the study.	No animals were used in this study.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population
characteristics of the human research participants.

No humans were used in this study.