

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

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82 **Globally accelerating trends in societal development and human environmental**
83 **impacts since the mid-20th century¹⁻⁷ are known as the Great Acceleration and**
84 **discussed as a key indicator of the onset of the Anthropocene⁶. While reports on**
85 **ecological responses (e.g. species range shifts or local extinctions) to the Great**
86 **Acceleration are multiplying^{8,9}, it is unknown whether such biotic responses are**
87 **undergoing a similar acceleration over time. This knowledge gap stems from the limited**
88 **availability of time series data on biodiversity changes across large temporal and**
89 **geographical extents. Here, we use a unique dataset of repeated plant surveys from 302**
90 **mountain summits across Europe, spanning 145 years of observation, to assess the**
91 **temporal trajectory of mountain biodiversity changes as a globally coherent imprint of**
92 **the Anthropocene. We find a continent-wide acceleration in the rate of plant species**
93 **richness increase, with five times higher species enrichment over the last decade**
94 **compared to fifty years ago. This acceleration is strikingly synchronized with**
95 **accelerated global warming, and not linked to alternative global change drivers. The**
96 **accelerating increases in species richness on mountain summits across this broad spatial**
97 **extent demonstrate that acceleration in climate-induced biotic changes is occurring even**
98 **at remote places on Earth, with potentially far-ranging consequences not only for**
99 **biodiversity, but also for ecosystem functioning and services.**

100 Mountains are particularly sensitive to ecological change and are experiencing some
101 of the highest rates of warming under anthropogenic climate change^{10,11}. Numerous reports of
102 species re-distribution towards the summits^{8,12-14} and warming-induced changes in
103 biodiversity on summits^{13,15,16} suggest that mountain biota are highly sensitive to increasing
104 temperatures¹⁷. The current accelerating trends in temperature increase^{1,6} should therefore also
105 affect the velocity of changes observed for mountain biota. Appropriate empirical
106 assessments of the rate of change in the velocity of ecological responses (biodiversity and
107 ecosystem trajectories) to accelerated global warming require long-term resurveys (e.g. time
108 series) of species communities, but these are scarce and localized. Mountain summits are
109 especially suited for long-term studies of biotic responses to environmental changes because
110 they represent natural permanent study sites that are easy to re-locate over time^{18,19}, thus
111 allowing to record reliable time series. By repeatedly resurveying alpine plant communities
112 on 302 European mountain summits dating back as far as 1871, we generated time series for
113 century-scale and continent-wide biodiversity dynamics to assess potential acceleration trends
114 in plant diversity dynamics (Fig. 1). Using these time series data, we tested whether the recent
115 acceleration of climate change is driving a similarly accelerating change in species richness
116 on mountain summits across the continent.

117 Here we show that plant species richness has strongly increased over the past 145
118 years on the vast majority (87%) of Europe's summits (generalized linear mixed effects
119 model: $p < 0.001$; Fig. 2; Extended Data Table 1) and the increase has accelerated in the most
120 recent years. This trend is consistent across all nine covered geographical regions, with no
121 single region showing the opposite pattern. Across all summits, this increase in plant species
122 richness has accelerated over time (linear mixed effects models: $p < 0.001$; Fig. 3; Extended
123 Data Table 2), and the acceleration has been particularly pronounced during the last 20-30
124 years (Figs 2 and 3). Fifty years ago (1957 to 1966), the rate of increase in species numbers
125 averaged 1.1 species per decade (Fig. 3), while during the last decade (2007 to 2016) the
126 summits gained 5.4 additional species on average (Fig. 3). There is a positive relationship

127 between the magnitude of increase in plant species richness and the rate of warming across all
128 302 time series (linear mixed effects models: $p < 0.001$; Fig. 4a and Extended Data Figure 2a;
129 Extended Data Table 3). The temporal and spatial congruence between the velocity of climate
130 change and the species accumulation rates on mountain summits across Europe corroborates
131 the hypothesis that warming is the primary driver of locally observed upward shifts of species
132 ranges in mountains (Fig. 2)^{12,13,20} and their recent acceleration^{16,21}. Our findings thus align
133 with those of shorter-term studies demonstrating plant community thermophilization^{15,17} and
134 range shifts driven by warming⁷.

135 The observed relationship between temperature change and species richness change
136 over the past 145 years is consistent across all nine regions. Changes in precipitation and
137 nitrogen deposition also correlate with species richness changes regionally, but the direction
138 and magnitude of these effects differ strongly between regions (Extended Data Figure 2b, c).
139 While precipitation change ($\Delta P/\text{year}$) has a moderate (positive) effect on species richness
140 trends across Europe (Extended Data Table 3; Fig. 4b, c), its effect is not consistent and
141 significant across all analysed regions (Extended Data Table 6; Extended Data Figure 2b) and
142 is minor compared to the effect of temperature change ($\Delta T/\text{year}$; Extended Data Table 4 and
143 6). Changes in grazing and tourism could also affect changes in plant species richness on
144 summits²¹. Local studies suggest that grazing²² and frequent disturbance by tourists¹⁵ may
145 suppress the elevational advance of alpine plants in response to warming in mountains. While
146 quantification is challenging, locally declining levels in domestic livestock are often in
147 synchrony with recovery of wild ungulate populations. Hiking tourism increased on some
148 summits, but intensities vary strongly. Land-use changes may thus explain parts of the local
149 variation in species richness trends, however, they vary greatly within and between regions.
150 Without a consistent impact on species re-distribution, it is unlikely that changes in grazing
151 and tourism can account for the consistent, continent-wide increase in plant species richness
152 evident in our data.

153 Some previous observations suggest that upslope species migration in mountains
154 occurs almost in synchrony with climate warming¹⁷, while other studies indicate strong lags in
155 dispersal, establishment, and extinction expected for many alpine plant species^{23,24}. We
156 systematically tested for time-lags (up to 10 years) in species richness increase following
157 climate changes, but found that time-lags did not significantly improve the explanatory power
158 of our models (Extended Data Table 5). This finding suggests that increases in species
159 richness on European summits are a direct and immediate response to climate warming (see
160 also Fig. 2) and, thus, can be expected to further accelerate as climate warming continues to
161 accelerate¹. Because we focus on the average trend, and by not accounting for non-colonizing
162 lower-altitude species, we cannot, however, exclude the possibility that only a fraction of
163 species responded quickly to climate change, thus creating the observed relationship, while an
164 unknown number of species lags behind the change in climate. Our observations may,
165 therefore, underestimate the expected long-term species turnover on summits.

166 The accelerated increase of species richness on mountain summits likely results from
167 an upward shift of the upper range limits of an increasing number of species. Trait analyses
168 indeed show that new colonizers exhibit growth strategies characterizing lower elevations,
169 having larger size ($p < 0.001$), higher specific leaf area ($p < 0.01$) and a general association with
170 warmer temperatures ($p < 0.001$; Extended Data Table 7). Ultimately, the lower range limits of
171 species will also shift upwards, but these limits are often determined and changed by biotic
172 interactions and are, therefore, only indirectly related to temperature²⁵. As more species
173 establish at high-elevation sites, local extinctions will likely occur due to competitive
174 replacement of slow-growing, stress-tolerant alpine species by more vigorous generalists that
175 benefit from warming, rather than by direct adverse effects of warming on the summit
176 species²⁶. However, competitive replacement of resident species requires that colonizers build
177 up sufficiently large populations. Local extinctions should hence follow colonization with a
178 time-lag. Consequently, accelerating plant species richness increases would be a transient
179 phenomenon which hides the accumulation of a so-called extinction debt^{23,27}. The relaxation

180 time until this debt is paid off is likely characterized by continuous shifts in abundance ratios
181 which may serve as sensitive early-warning signals of upcoming extinctions¹⁵. The length of
182 the relaxation time likely depends on factors such as the longevity of high-elevation species,
183 plant clonal abilities, and the local microhabitat diversity, supporting the persistence of cold-
184 climate microrefugia for high-alpine species^{28,29}. Although these processes, along with others
185 such as the species' intrinsic ability to tolerate changing climates, may buffer local
186 extinctions, rapid loss of alpine-nival species may occur under accelerated climate warming.
187 Additionally, if major changes and extinctions in alpine systems are not gradual, but initiated
188 by threshold-like dynamics (e.g. shrub and tree encroachment), critical tipping points may be
189 approached with increasing speed under accelerated climate warming.

190 Our results underline the link between accelerating climate warming and species
191 richness change in mountains. We thus provide a particularly compelling example of the
192 human-driven impact on terrestrial biota that is highly consistent with the recently reported
193 Great Acceleration in Earth system trends in the Anthropocene and strikingly synchronous
194 with the recent accelerating trends observed in many socio-economic indicators⁶. The
195 observed acceleration of biodiversity change in mountain ecosystems highlights the rapid and
196 widespread consequences of human activities on the biosphere, with important consequences
197 for ecosystem functioning, human well-being, and the dynamics of climate change³⁰.

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199 **References:**

- 200 1. Smith, S. J., Edmonds, J., Hartin, C. A., Mundra, A. & Calvin, K. Near-term acceleration
201 in the rate of temperature change. *Nat. Clim. Change*. **5**, 333-336 (2015).
- 202 2. Comiso, J.C., Parkinson, C.L., Gersten, R. & Stock, L. Accelerated decline in the Arctic
203 sea ice cover. *Geophys. Res. Lett.* **35**, L01703 (2008).
- 204 3. Kintisch, E. Sea ice retreat said to accelerate Greenland melting. *Science* **352**, 1377
205 (2016).

- 206 4. Hughes, T.P. *et al.* Global warming and recurrent mass bleaching of corals. *Nature* **543**,
207 373-377 (2017).
- 208 5. Hollesen, J., Matthiesen, H., Møller, A.B. & Elberling, B. Permafrost thawing in organic
209 Arctic soils accelerated by ground heat production. *Nat. Clim. Change*. **5**, 574–578
210 (2015).
- 211 6. Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O. & Ludwig, C. The trajectory of the
212 Anthropocene: The Great Acceleration. *The Anthropocene Review* **2**, 81 – 98 (2015).
- 213 7. Alstad, A.O. *et al.*, The pace of plant community change is accelerating in remnant
214 prairies. *Science Advances* **2**, e1500975 (2016).
- 215 8. Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. Rapid range shifts of
216 species associated with high levels of climate warming. *Science* **333**, 1024-1026 (2011).
- 217 9. Wiens, J.J. Climate-related local extinctions are already widespread among plant and
218 animal species. *PLoS Biology* **14**, e2001104 (2016).
- 219 10. Gobiet, A. *et al.* 21st century climate change in the European Alps - A review. *Sci. Total*
220 *Environ.* **493**, 1138–1151 (2014).
- 221 11. Pepin, N. *et al.* Elevation-dependent warming in mountain regions of the world. *Nat.*
222 *Clim. Change*. **5**, 424–430 (2015).
- 223 12. Lenoir, J., Gégout, J.-C., Marquet, P.A., de Ruffray, P. & Brisse, H. A significant upward
224 shift in plant species optimum elevation during the 20th century. *Science* **320**, 1768–1771
225 (2008).
- 226 13. Pauli, H. *et al.* Recent plant diversity changes on Europe’s mountain summits. *Science*
227 **336**, 353–355 (2012).
- 228 14. Grytnes, J.-A. *et al.* Identifying driving factors behind observed species range shifts on
229 European mountains. *Global Ecol. Biogeogr.* **23**, 876–884 (2014).
- 230 15. Gottfried, M. *et al.* Continent-wide response of mountain vegetation to climate change.
231 *Nat. Clim. Change*. **2**, 111–115 (2012).

- 232 16. Wipf, S., Stöckli, V., Herz, K. & Rixen, C. The oldest monitoring site of the Alps
233 revisited: Accelerated increase in plant species richness on Piz Linard summit since 1835.
234 *Plant Ecol. Divers.* **6**, 447-455 (2013).
- 235 17. Bertrand, R. *et al.* Changes in plant community composition lag behind climate warming
236 in lowland forests. *Nature* **479**, 517-520 (2011).
- 237 18. Stöckli, V., Wipf, S., Nilsson, C. & Rixen, C. Using historical plant surveys to track
238 biodiversity on mountain summits. *Plant Ecol. Divers.* **4**, 415-425 (2012).
- 239 19. Verheyen, K. *et al.* Combining biodiversity resurveys across regions to advance global
240 change research. *BioScience* **67**, 73-83 (2017).
- 241 20. Odland, A., Høitomt, T. & Olsen, S.L. Increasing vascular plant richness on 13 high
242 mountain summits in Southern Norway since the early 1970s. *Arct. Antarct. Alp. Res.* **42**,
243 458–470 (2010).
- 244 21. Walther, G.-R., Beißner, S. & Burga C.A. Trends in the upward shift of alpine plants. *J.*
245 *Veg. Sci.* **16**, 541–548 (2005).
- 246 22. Speed, J.D.M., Austrheim, G., Hester, A.J. & Myrsterud A. Elevational advance of alpine
247 plant communities is buffered by herbivory. *J. Veg. Sci.* **23**, 617–625 (2012).
- 248 23. Dullinger, S. *et al.* Extinction debt of high-mountain plants under twenty-first-century
249 climate change. *Nat. Clim. Change.* **2**, 619–622 (2012).
- 250 24. Hülber, K. *et al.* Uncertainty in predicting range dynamics of endemic alpine plants under
251 climate warming. *Glob. Change Biol.* **22**, 2608–2619 (2016).
- 252 25. Vetaas, O.R. Realized and potential climate niches: a comparison of four *Rhododendron*
253 tree species. *J. Biogeogr.* **29**, 545–554 (2002).
- 254 26. Alexander, J.M., Diez, J.M. & Levine, J.M. Novel competitors shape species' responses
255 to climate change. *Nature* **525**, 515–518 (2015).
- 256 27. Cotto, O. *et al.* A dynamic eco-evolutionary model predicts slow response of alpine plants
257 to climate warming. *Nature Communications* **8**, 9 (2017).
- 258 28. Scherrer, D. & Körner, C. Topographically controlled thermal-habitat differentiation
259 buffers alpine plant diversity against climate warming. *J. Biogeogr.* **38**, 406-416 (2011).

- 260 29. Winkler, M. *et al.* The rich sides of mountain summits – a pan-European view on aspect
261 preferences of alpine plants. *J. Biogeogr.* **43**, 2261–2273 (2016).
- 262 30. Pecl, G.T. *et al.* Biodiversity redistribution under climate change: Impacts on ecosystems
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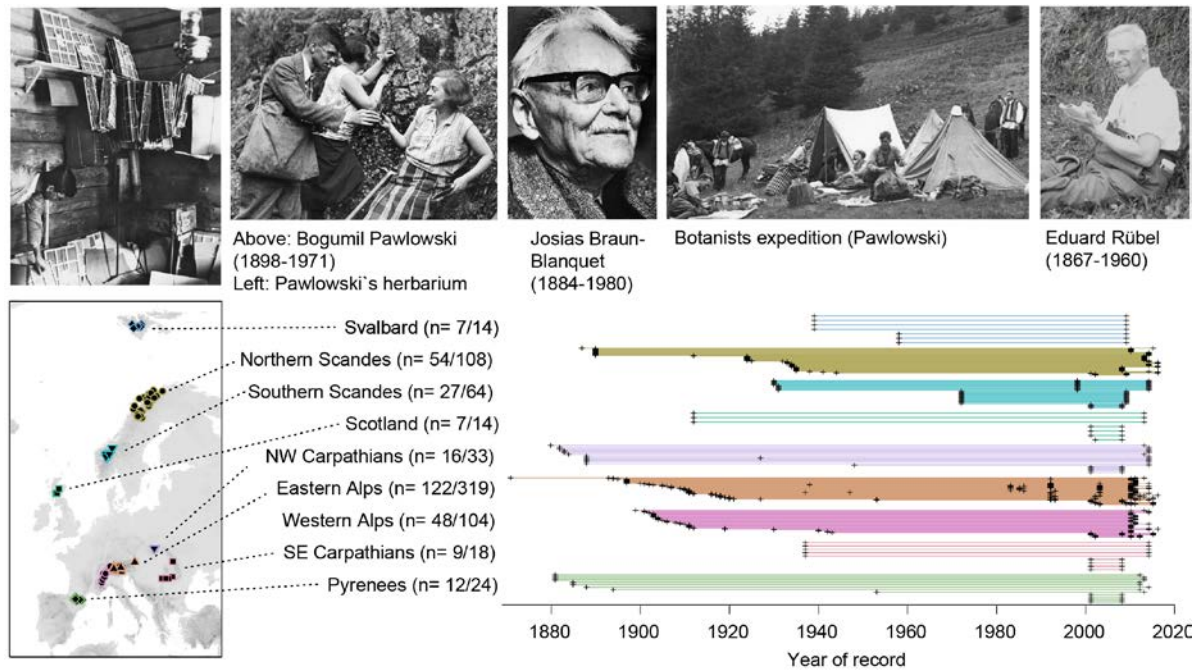
310 **Data and code availability** Data and R code is freely available via the corresponding authors
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312

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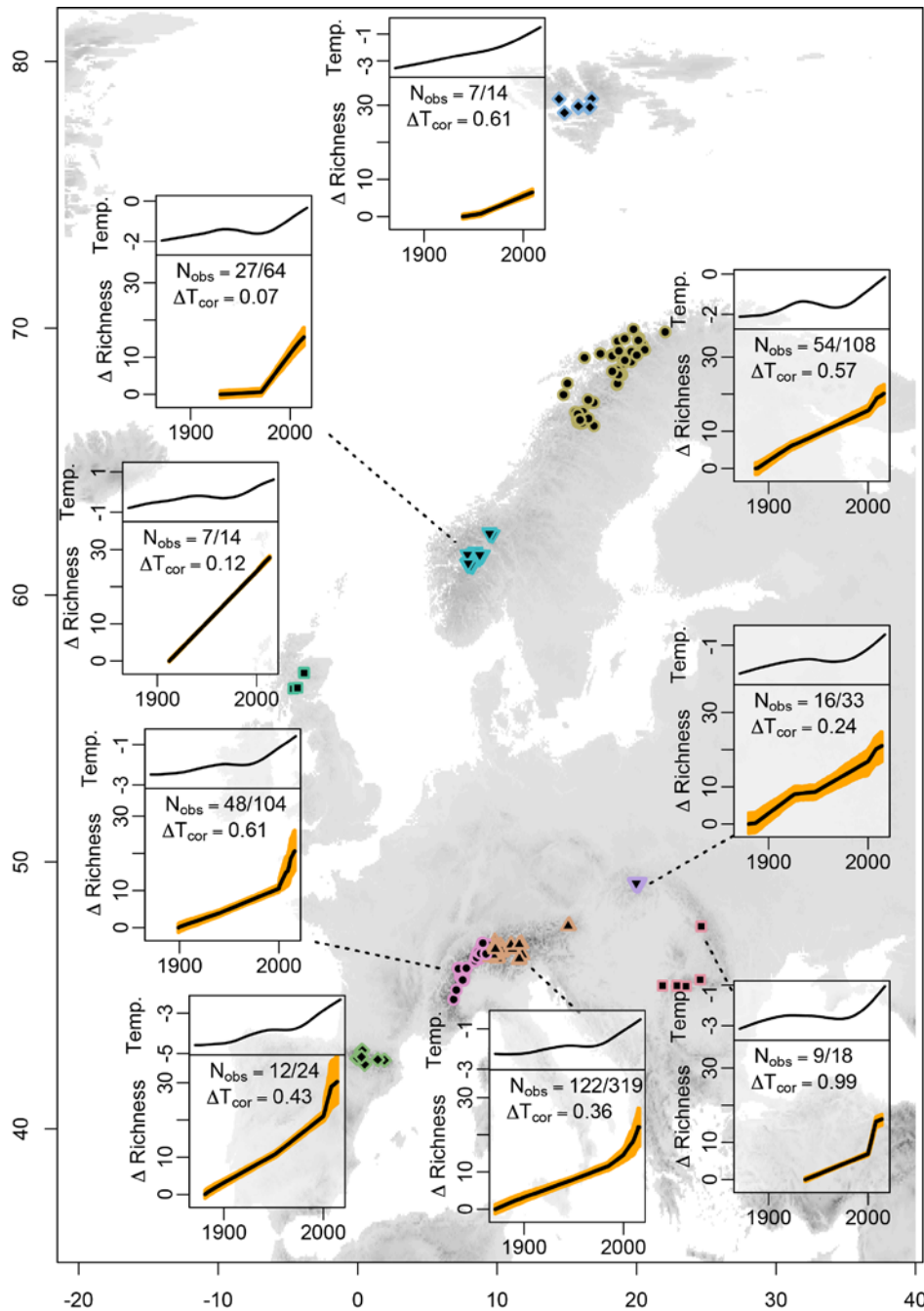
318 **Figures**
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322 **Figure 1 | The study is based on 698 surveys from 302 summits in nine mountain regions**
323 **across Europe dating back to 1871.** Each sampled summit is indicated by one line, with
324 black crosses indicating survey dates. The historical surveys were often conducted by leading
325 pioneers in vegetation ecology in Europe (B. Pawlowski, J. Braun-Blanquet, E. Rübel, E. Du
326 Rietz etc.). Numbers in brackets beside the region names indicate the number of
327 summits/surveys. Picture references for Pawlowski (Zemanek, 2012, Florist. Geobot. Polon.),
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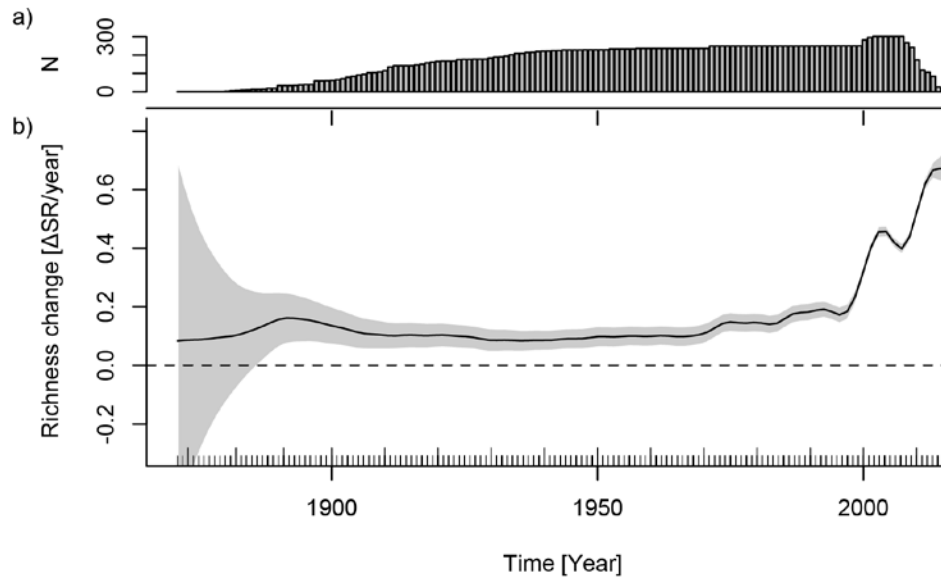
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 332 **Figure 2 | Average species richness change (in species numbers) on mountain summits**
 333 **over time (lower part of panels) compared to mean annual temperature over time (upper**
 334 **part of panels). “N_{obs}” indicates the number of summits/surveys within the mountain region**
 335 **providing data for the respective panel. Correlation between rate of change in species richness**
 336 **and rate of change in temperature (ΔT_{cor}) is positive for all mountain regions (see also**
 337 **Extended Data Figure 2a). Orange shading marks the 5th and 95th percentiles of the resulting**
 338 **richness change values from a bootstrapping approach across all summits in one region; see**
 339 **Extended Data Figure 1 for methodological details.**

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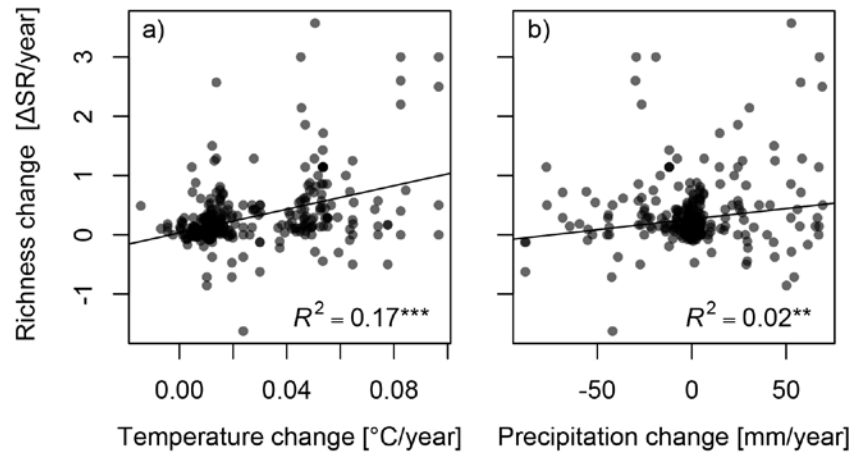


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345 **Figure 3 | Rate of species richness change over time** (black line, b). Positive values indicate
346 an increase in species richness on summits and negative values indicate a decrease. Rates
347 ($\Delta SR/year = (SR_{t_2} - SR_{t_1}) / (t_2 - t_1)$) [SR = species richness, t = time] were averaged across all
348 summits and inversely weighted by the number of years between observations ($t_2 - t_1$) to
349 account for temporal resolution as a longer period between surveys might mask short-term
350 fluctuations. The black line interpolates across all summits with a generalized additive
351 (spline) smooth model (R package mgcv version 1.8-17, the smooth term ($k = 50$) was chosen
352 to allow enough degrees of freedom to closely represent the underlying pattern). The shaded
353 grey area represents ± 1 standard error around the mean value (black solid line). a) The
354 histogram at the top of the figure indicates the number of slope parameters per year (N;
355 comparisons of earlier survey and later sampled resurvey) that support the line graph.

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Figure 4 | Rate of species richness change ($\Delta SR/year = (SR_{t2}-SR_{t1})/(t_2-t_1)$) 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.

371 **METHODS**

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

388

389 **Environmental data.** For each summit, mean monthly temperature and precipitation were
390 calculated following the established change factor methodology³³, which combines statistical
391 downscaling with temporal trend analyses. First, temporal data available from CRU TS 3.23
392 (0.5 degree resolution, 1901-2015)³⁴ and the European Gridded Monthly Temperature (0.5
393 degree resolution, 1765-2000)³⁴ were statistically related to the higher spatial resolution of
394 WorldClim monthly mean climatic grids (30 arc-second resolution) for the overlapping period
395 of 1950 to 2000 using the change factor method³³. We assumed that anomalies (cf. mean
396 value over the period 1950-2000 of the coarse-grained climatic conditions minus the climatic
397 conditions within each smaller pixel of WorldClim) computed for the overlapping period
398 (1950-2000) remain the same prior to 1950 and after 2000. Second, elevational differences

399 between summits and the mean elevation of the corresponding WorldClim digital elevation
400 model were included as an additional correction term ($-0.006^{\circ}\text{C} \times \Delta\text{elevation in m}$) for mean
401 temperature data. By combining the two corrections, temporal trends available from the 0.5
402 degree resolution temporal data were corrected for i) differences originating from scale and
403 climate model and ii) the precise elevation of the summit (temperature only). While we
404 consider the resulting temporal trends for the temperature data to be reliable due to the
405 generally higher spatial and temporal autocorrelation and a higher correlation with elevation,
406 the precipitation data do not show a systematic change with elevation and are less predictable
407 over small spatial distances³⁶ and, therefore, need to be interpreted more cautiously.
408 Environmental variables were included in the models after calculating temporal changes (see
409 end of the Methods section). Consequently, environmental variables are unbiased by
410 weaknesses in the spatial interpolations. For temperature and precipitation, time series from
411 CRU TS 3.23 (1901-2015) and the European Gridded Monthly Temperature (1765-2000)
412 were combined to match the study period (1880-2016) by taking the mean per grid cell for the
413 overlapping years (Spearman $r = 0.97$ for the overlapping period 1901-2000). As none of the
414 two data sources extends to 2016, climate values for 2015 were taken again for 2016 for the
415 19 affected summits. Further, historical nitrogen deposition data (NH_x and NO_x modeled
416 from 1850-2010) were extracted from the European Fluxes Database ([www.europe-
417 fluxdata.eu](http://www.europe-fluxdata.eu)) and interpolated for the missing five years (2011-2016). The data originate from
418 the global chemistry Transport Model version 5 (TM5, annual data with a 0.25° lat/long
419 resolution)³⁷. Data handling and all subsequent analyses were conducted in R version 3.3.1³⁸.

420

421 **Statistical analyses.**

422 *The velocity of species richness changes:* Species richness (SR) on mountain summits was
423 analyzed for its change with time (t: year of record) across all summits by implementing a
424 generalized linear mixed effects model (GLMM) with a Poisson family error distribution (SR
425 ~ t) and a random effect (intercept) of mountains to account for repeated samples (GLMM 1
426 in Extended Data Table 1, mixed effects models always built with R package *lme4* version

427 1.1-12)³⁹. Further, we ran the models including random effects (intercept) of region
428 (mountains nested in region; GLMM 2 in Extended Data Table 1) and observation ID (to
429 account for over dispersion; see reference 40; GLMM 3 in Extended Data Table 1). All
430 models provided qualitatively equivalent results (Extended Data Table 1).

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

440

441 *Acceleration of species richness changes:* The potential acceleration in the average velocity
442 of species richness changes on mountain summits between 1871 and 2016 was tested by
443 means of a linear mixed effects model (LMM) with a Gaussian family error distribution
444 ($\Delta SR/\Delta t \sim t_{MP}$). With the model, we analyzed the rate of change in species richness over time
445 (midpoint year between two surveys $t_{MP} = (t_1+t_2)/2$). The dependent variable $\Delta SR/\Delta t$ was
446 calculated based on the difference in species richness and the difference between years of
447 observation of two consecutive surveys on the same summit ($(SR_{t_2}-SR_{t_1})/(t_2-t_1)$). A random
448 effect (intercept) of mountain was included to account for repeated samples. We also ran the
449 model including a random effect (intercept) of mountain nested within region but found
450 qualitatively similar results (Extended Data Table 2). Mathematically, $\Delta SR/\Delta t$ is independent
451 from richness on the summits as well as from time elapsed between sequential visits on the
452 summit. However, more species-rich systems seemed to be associated with higher rates of
453 changes, as indicated by a significant positive effect if baseline (cf. the first survey) species
454 richness of the summit was included as an explanatory variable in the fixed component of the

455 LMM (Extended Data Table 2). We also tested if there was an effect of the number of years
456 between two consecutive surveys on $\Delta SR/\Delta t$, as a longer period between surveys might mask
457 short-term fluctuations, but this effect was not significant (Extended Data Table 2).

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

462 In the raw data, the average rate of species richness increase per summit was found to
463 be much higher in the last decade (2007–2016; +2.9 species) compared to fifty years earlier
464 (1957–1966, +1.1 species). When the slopes are averaged across all summits with an
465 observation prior and after a respective year, inversely weighted by the number of years
466 between observations (to account for temporal resolution, as a longer period between surveys
467 might mask short-term fluctuations), the differences become even more apparent (+5.4
468 species in the last decade as opposed to +1.1 species per decade fifty years earlier).

469

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

477 The changes in species richness per year ($\Delta SR/\Delta t$) accumulated over time and result
478 in an absolute change in species richness (Extended Data Figure 1b). These absolute changes
479 in species richness are visualized for each region in Fig. 2 (black line). In order to also
480 visualize variability within regions, confidence intervals were calculated based on the
481 standard deviation of richness change among summits in a region (see Extended Data Figure
482 1c and 1d and related figure caption).

483

484 *Importance of environmental drivers:* The average velocity of species richness changes
485 ($\Delta SR/\Delta t$) was related to the change in mean annual temperature ($\Delta T/\Delta t$; T = temperature) and
486 precipitation ($\Delta P/\Delta t$; P = precipitation) for the same period (see below for further details), as
487 well as to the accumulated nitrogen deposition (N_{accum} ; N = nitrogen, details explained
488 below) across all summits, by implementing LMMs with a Gaussian family error distribution
489 that included each of the three potential explanatory variables (different rows in Extended
490 Data Table 3, model formula can be seen in table caption). Variable performance was
491 compared using the corrected version (for small sample size) of the Akaike Information
492 Criteria (AIC_c^{41}). All LMMs consistently detected a clear positive relationship between
493 species richness changes and temperature changes while a slightly weaker positive
494 relationship with precipitation changes was also detected. Particularly the relationship with
495 temperature changes is surprisingly strong considering that climate models are built on long-
496 term air temperature measurements at two meters above ground in climate stations that are
497 mainly located in valleys and can only approximate changes in growth conditions for summits
498 species. No relationship with the accumulated nitrogen deposition was detected across Europe
499 (Extended Data Table 3).

500 The explanatory variables $\Delta T/\Delta t$ and $\Delta P/\Delta t$ were calculated as the mean change per
501 year (e.g. $\Delta T/\Delta t = T_{t_2} - T_{t_1} / t_2 - t_1$). Climate variables like temperature and precipitation are
502 usually integrated over longer time periods to level out short-term fluctuations. As we were
503 interested in the effect of such shorter-term fluctuations, we systematically tested which
504 periods would provide the best fit within our LMM framework (1–30 years). Besides mean
505 annual temperature and precipitation, we further tested alternative measurements of the
506 climate variables. If species' ranges are limited primarily by growing season temperatures, we
507 would expect spring and summer warming to best explain temporal changes in species
508 richness. Alternatively, if many alpine species are limited not by growing season temperature,
509 but rather by climatic extremes, winter temperatures or precipitation might be more important
510 in determining which species can survive in a given location. We therefore systematically

511 pre-analyzed temperature and precipitation variables by testing for the effect of winter
512 precipitation (Dec–Feb) and of snow accumulation (precipitation in months with a mean
513 temperature below freezing).

514 Further, nitrogen from deposition may accumulate in the soil, particularly in high
515 elevation systems with limited resource cycling^{42,43}. In our data, nitrogen deposition has
516 declined sharply in recent decades³⁶, although its accumulated effect may still influence
517 community dynamics⁴³. We thus calculated accumulated deposition of both NH₄ and NO₃
518 since 1850 for each vegetation survey.

519 The systematic test of different variables and time periods (Extended Data Table 4)
520 identified annual summer temperature (15-year mean), annual precipitation (1-year mean) and
521 NO₃ (referred to as N_{accum}) as the most suitable predictors, and these variables were then used
522 in all subsequent analyses. As this type of variable selection biases analyses towards
523 significant relationships, all analyses were repeated with mean annual values (10-year mean),
524 resulting in qualitatively similar results. Model residuals were visually checked for temporal
525 autocorrelation signal without any sign of a temporal trend in the residuals.

526

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

536 An alternative approach to analyzing the average velocity of species richness changes
537 ($\Delta SR/\Delta t$) with rates of change in environmental predictors ($\Delta T/\Delta t$; $\Delta P/\Delta t$, see Extended Data
538 Table 3) is to directly relate species richness changes (ΔSR) to changes in environmental

539 variables over the same time period (ΔT ; ΔP). This approach is more intuitive (and closer to
540 the data) but ignores differences in time between sampling events. Analyses with this
541 approach yielded results qualitatively similar to the results of the main analysis (Extended
542 Data Table 3), with the exception that the effect of precipitation changes was not significant
543 (Extended Data Table 6).

544

545 **Trait based analyses.**

546 *Differing trait signal in colonizing species:* Changes in plant life strategies as well as
547 dispersal constraints would be indicated by a systematic difference in indicative traits. We thus
548 compared specific leaf area (SLA)⁴⁵, plant height⁴⁵ as well as seed mass⁴⁵ between colonizing
549 species as well as species in the resident community in a LMM framework setting *resurvey* as
550 a random effect. To test for the colonization and establishment, within the recipient
551 community, of warmth tolerating species from lower elevations, we used Landolt species
552 indicator values for temperature⁴⁵. Temperature indicator values⁴⁵ were available for 91% of
553 the observations. For 364 resurveys (altogether 20583 observations for 871 species) direct
554 comparisons of plant trait values of species in a resurvey that were newly established
555 colonizers with those species that had been present already in the previous survey (recipient
556 community) indicate significantly increased SLA ($p < 0.01$) and plant height ($p < 0.001$) of
557 successful colonizers but no significant difference in seed mass ($p = 0.053$). Colonizers are
558 more adapted to warmer climates than species of the resident communities ($p < 0.001$;
559 Extended Data Table 7).

560

561 **Data reliability**

562 *Sampling intensity:* Our analysis of the rate of change is relatively robust with respect to
563 different sampling periods. The increasing sampling intensity over time (Fig. 1) helped to
564 reliably quantify the rates of change in later time periods and thus to support our conclusion
565 on an acceleration in richness change. Consistent continent-wide and short-term fluctuations
566 in species richness that might have occurred in the early 20th century would likely go

567 undetected due to the lower data availability in the early 20th century of our time series data,
568 but long-term trends would be well visible. We thus have no evidence that the unbalanced
569 sampling effort over time and different sampling intervals hide unobserved fluctuations in
570 early periods. In line with this, the summits for which we have a high number of repeated
571 surveys show little short-term fluctuations but confirm the detected steady increase of
572 richness over time and an acceleration in recent years¹⁶.

573 *Observer errors:* Previous studies explicitly addressing observer errors of summit resurveys,
574 have demonstrated a reliable quantification for vegetation change over long time periods³².
575 Many of the early records have been collected by expert botanists with a scientific interest in
576 long-term changes and the explicit aim to allow a later resurvey. To further reduce potential
577 sampling and observer errors, recent records were done without knowledge of the past species
578 lists, because surveyors who know the historical species composition have a higher chance of
579 finding certain species again. Approximately 15 % of all summits of this dataset have species
580 records collected in the 1980s and 1990s (partly they were even done by the same people).
581 Even if these early re-surveyors also considered the above methodological issues, we cannot
582 rule out that the observer effort of the early re-surveyors was higher than the historical one.
583 However, we are sure that our recent observer effort did not exceed that of the early re-
584 surveyors during the 1980s and 1990s. Given this, the clear signal that most of the increase in
585 species richness occurred after 1980s/1990s is a strong indication that a possible increase in
586 observer effort, if present, is only responsible for a limited amount of the increase in species
587 richness. We are, thus, confident, that observer errors did not systematically influence our
588 analyses.

589

590 **Method references**

- 591 31. Braun, J. Die Vegetationsverhältnisse der Schneestufe in den Rätisch-Lepontischen
592 Alpen. Ein Bild des Pflanzenlebens an seinen äußersten Grenzen. Neue Denkschr. Schweiz.
593 Naturf. Ges. **48**, 1-347 (1913).

- 594 32. Burg, S., Rixen, C., Stöckli, V. & Wipf, S. Observation bias and its causes in botanical
595 surveys on high-alpine summits. *J. Veg. Sci.* **26**, 191–200 (2015).
- 596 33. Anandhi, A. *et al.* Examination of change factor methodologies or climate impact
597 assessment. *Water Resour. Res.* **47**, W03501 (2011).
- 598 34. Harris, I., Jones, P.D., Osborn, T.J. & Lister, D.H. Updated high-resolution grids of
599 monthly climatic observations - the CRU TS3.10 Dataset. *Int. J. Climatol.* **34**, 623-642
600 (2014).
- 601 35. Casty, C., Raible, C.C., Stocker, T.F., Wanner, H. & Luterbacher J. European Gridded
602 Monthly Temperature, Precipitation and 500hPa Reconstructions. IGBP PAGES/World
603 Data Center for Paleoclimatology Data Contribution Series # 2008-023. NOAA/NCDC
604 Paleoclimatology Program, Boulder CO, USA (2008).
- 605 36. Daly, C., Neilson, R.P. & Phillips, D.L. A statistical topographic model for mapping
606 climatological precipitation over mountainous terrain. *J. Appl. Meteor.* **33**, 140-158
607 (1994).
- 608 37. Huijnen, V. *et al.* The global chemistry transport model TM5: description and evaluation
609 of the tropospheric chemistry version 3.0. *Geosci. Model Dev.* **3**, 445-473 (2010).
- 610 38. R Core Team, R: A language and environment for statistical computing. R Foundation for
611 Statistical Computing, Vienna, Austria (2016).
- 612 39. Bates, D, Maechler, M., Bolker, B. & Walker S. Fitting linear mixed-effects models using
613 lme4. *J. Stat. Softw.* **67**, 1-48 (2015).
- 614 40. Harrison, X.A. Using observation-level random effects to model overdispersion in count
615 data in ecology and evolution. *PeerJ* **2**, e616 (2014).
- 616 41. Burnham, K.P. & Anderson, D.R. Model selection and multimodel inference: A practical
617 information-theoretic approach (2nd ed.). New York: Springer (2002).
- 618 42. Burns, D.A. The effects of atmospheric nitrogen deposition in the Rocky Mountains of
619 Colorado and southern Wyoming, USA—a critical review. *Environ. Pollut.* **127**, 257-269
620 (2004).
- 621 43. Körner, C. Mountain ecosystems in a changing environment. *Ecomont* **6**, 71-77 (2014).

- 622 44. Bobbink, R. *et al.* Global assessment of nitrogen deposition effects on terrestrial plant
623 diversity: a synthesis. *Ecol. Appl.* **20**, 30-59 (2010).
- 624 45. Kleyer, M. *et al.* The LEDA Traitbase: A database of life-history traits of Northwest
625 European flora. *Journal of Ecology* **96**, 1266-1274 (2008).
- 626 46. Landolt, E. *et al.* Flora indicativa. Haupt Verlag, Bern (2010).
- 627
- 628

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.

Model	Fixed effect (coefficients ±std. error)		Random effects (std. deviations)			
	Intercept	Year of record	Mountain	Region:Mountain	ID	AICc
GLMM 1	-5.78 ±0.35***	0.004 ±0.0002***	0.97	-	-	5785
GLMM 2	-5.78 ± 0.35***	0.004 ±0.0002***	0.86	0.41	-	5787
GLMM 3	-7.33 ± 0.58***	0.005 ±0.0003***	0.47	0.84	0.23	5596
GLM	-7.52±0.33***	0.006 ±0.0002***	-	-	-	18299

Model	Intercept	Time < BP	Time > BP	Mountain	Region:Mountain	ID	AICc
GLMBM	2.71 ±0.07***	0.001 ±0.001	0.013 ±0.001***	0.96	-	-	5709
GLMBM	2.71 ±0.07***	0.001 ±0.001	0.013 ±0.001***	0.87	0.41	-	5711
GLMBM	2.64 ±0.08***	0.001 ±0.001	0.014 ±0.001***	0.42	0.86	0.21	5560

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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 ($\Delta SR/\Delta t \sim t$), 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)			Random effect (std. deviations)			
Intercept	Time	Richness	Period	Mountain	Region: Mount.	AICc
-15.5±2.03***	0.008±0.001***	-	-	5.2×10 ⁻⁸	-	570.3
-15.5±2.06***	0.008±0.001***	-	-	9.6×10 ⁻⁸	4.8×10 ⁻⁸	572.4
-13.4±2.05***	0.007±0.001***	0.004±0.001***	-	1.8×10 ⁻⁸	-	562.6
-11.7±4.77*	0.006±0.002*	0.004±0.001***	n.s.	1.1×10 ⁻⁷	-	576.0
-13.4±2.05***	0.007±0.001***	0.004±0.001***	-	-	-	530.7

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	.	571.3
0.07±0.05	0.002±0.003	0.013±0.002***	-	-	0.0	0.0	573.3
0.02±0.05	0.0001±0.003	0.011±0.002***	0.004±0.001***	-	0.0	-	568.5
-0.09±0.14	0.0004±0.004	0.012±0.004***	0.004±0.001***	n.s.	1.1×10 ⁻⁸	-	581.5
0.02±0.05	0.0001±0.003	0.010±0.002***	0.004±0.001***	-	-	-	527.8

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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 $\text{lmer}(\Delta SR/\Delta t \sim \Delta T/\Delta t + \Delta P/\Delta t + N_{\text{accum}} + \text{richness} + (1|\text{mountain}))$. 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 ($\Delta SR/\Delta t \sim 0.00 (\pm 0.04) + 0.39 (\pm 0.05) \times \Delta T/\Delta t^{***} + 0.21 (\pm 0.04) \times \Delta P/\Delta t^{***} + 0.21 (\pm 0.05) \times \text{Richness}^{***}$). 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 ($\Delta SR/\Delta t \sim -0.006 (\pm 0.05) + 9.5 (\pm 1.1) \times \Delta T/\Delta t^{***} + 0.005 (\pm 0.001) \times \Delta P/\Delta t^{***} - 0.13 (\pm 0.08) \times N_{accum} + 0.005 (\pm 0.05) \times \text{Richness}^{***}$).

<i>Intercept</i>	<i>ΔT/Δt</i>	<i>ΔP/Δt</i>	<i>N_{accum}</i>	<i>Richness</i>	<i>AICc</i>	<i>AICWt</i>
0.01 ±0.06	9.6 ±1.1***	0.005 ±0.001***	-0.15 ±0.09	0.004 ±0.001***	491.9	0.59
-0.06 ±0.04	9.4 ±1.1***	0.005 ±0.001***	-	0.005 ±0.001***	492.7	0.41
0.03 ±0.06	10.1 ±1.1***	-	-0.16 ±0.09	0.004 ±0.001***	512.6	0.00
0.14 ±0.06*	-	0.004 ±0.001***	-0.06 ±0.10	0.006 ±0.001***	560.4	0.00

633

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 $\text{lmer}(\Delta SR/\Delta t \sim \Delta T/\Delta t + \Delta P/\Delta t + N_{accum} + \text{richness} + (1|\text{mountain}))$. 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

Explanatory variable	Period	AICc	ΔAICc	AICc weights
Summer temperature	15	491.9	0.0	1.0
Annual temperature	15	501.1	9.2	0.0
Spring temperature	10	511.4	19.4	0.0
Annual temperature	7	513.4	21.5	0.0
Spring temperature	7	516.7	24.8	0.0
Summer temperature	7	518.7	26.8	0.0
Annual temperature	30	520.7	28.8	0.0
Annual temperature	10	521.2	29.3	0.0
Spring temperature	15	521.3	29.3	0.0
Annual temperature	3	530.5	38.6	0.0
Spring temperature	30	531.8	39.9	0.0
Summer temperature	5	532.0	40.1	0.0
Summer temperature	1	534.9	43.0	0.0
Summer temperature	30	536.0	44.1	0.0
Annual temperature	1	538.9	47.0	0.0
Annual temperature	5	539.2	47.2	0.0
Summer temperature	10	549.4	57.4	0.0
Spring temperature	5	550.4	58.5	0.0
Summer temperature	3	551.2	59.3	0.0
Spring temperature	1	552.4	60.5	0.0
Spring temperature	3	555.7	63.8	0.0

Precipitation

Explanatory variable	Period	AICc	ΔAICc	AICc weights
Annual precipitation	1	491.9	0.0	1.0
Winter precipitation	15	504.3	12.4	0.0
Annual precipitation	30	505.5	13.6	0.0

Winter precipitation	1	508.1	16.2	0.0
Snow precipitation	30	508.4	16.5	0.0
Winter precipitation	5	508.6	16.7	0.0
Summer precipitation	30	508.9	17.0	0.0
Snow precipitation	7	509.4	17.5	0.0
Summer precipitation	5	510.7	18.8	0.0
Winter precipitation	30	510.9	19.0	0.0
Snow precipitation	1	511.9	20.0	0.0
Snow precipitation	10	512.3	20.3	0.0
Annual precipitation	15	513.0	21.1	0.0
Snow precipitation	15	513.1	21.1	0.0
Annual precipitation	5	513.1	21.2	0.0
Winter precipitation	3	513.4	21.5	0.0
Annual precipitation	10	513.7	21.8	0.0
Summer precipitation	10	513.7	21.8	0.0
Summer precipitation	15	513.7	21.8	0.0
Summer precipitation	7	514.2	22.2	0.0
Winter precipitation	10	514.3	22.4	0.0
Summer precipitation	3	514.3	22.4	0.0
Snow precipitation	5	514.4	22.5	0.0
Snow precipitation	3	514.5	22.6	0.0
Annual precipitation	3	514.6	22.7	0.0
Summer precipitation	1	514.6	22.7	0.0
Annual precipitation	7	514.6	22.7	0.0
Winter precipitation	7	514.7	22.8	0.0

Nitrogen

Explanatory variable	Period	AICc	ΔAICc	AICc weights
NO accumulation	-	491.9	0.0	0.59
NH accumulation	-	492.6	0.7	0.41

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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 $\text{lmer}(\Delta\text{SR}/\Delta t \sim \Delta T/\Delta t + \Delta P/\Delta t + N_{\text{accum}} + \text{richness} + (1|\text{mountain}))$. 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)			
Time lag	AICc	ΔAICc	AICc weights
0	501.1	0.0	1.0
5	535.6	34.5	0.0
10	550.2	49.1	0.0
Annual precipitation (1-year mean)			
Time lag	AICc	ΔAICc	AICc weights
0	510.7	0.0	0.76
5	514.1	3.4	0.14
10	514.7	4.0	0.10
Nitrogen accumulation			
Time lag	AICc	ΔAICc	AICc weights
0	491.9	0.0	0.34
5	492.0	0.1	0.33
10	492.0	0.1	0.33

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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 $\text{lmer}(\Delta\text{SR} \sim \Delta T + \Delta P + N_{\text{accum}} + \text{richness} + (1|\text{mountain}))$. 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 ($\Delta\text{SR} \sim 0.05 (\pm 0.06) + 0.25 (\pm 0.05) \times \Delta T^{***} + 0.05 (\pm 0.04) \times \Delta P - 0.11 (\pm 0.05) \times N_{\text{accum}}^*$).

Intercept	$\Delta T/\Delta t$	$\Delta P/\Delta t$	N_{accum}	Richness	AICc	AICWt
7.6 \pm 1.6***	5.9 \pm 1.2***	-	-5.4 \pm 2.3*	-	3002.8	0.57
7.2 \pm 1.7***	6.3 \pm 1.3***	0.002 \pm 0.002	-5.1 \pm 2.3*	-	3003.8	0.34
2.23 \pm 1.15	8.25 \pm 1.92***	-0.011 \pm 0.010	-	-	3006.5	0.09
11.8 \pm 1.48***	-	-0.001 \pm 0.002	-3.7 \pm 2.4	-	3023.2	0.00

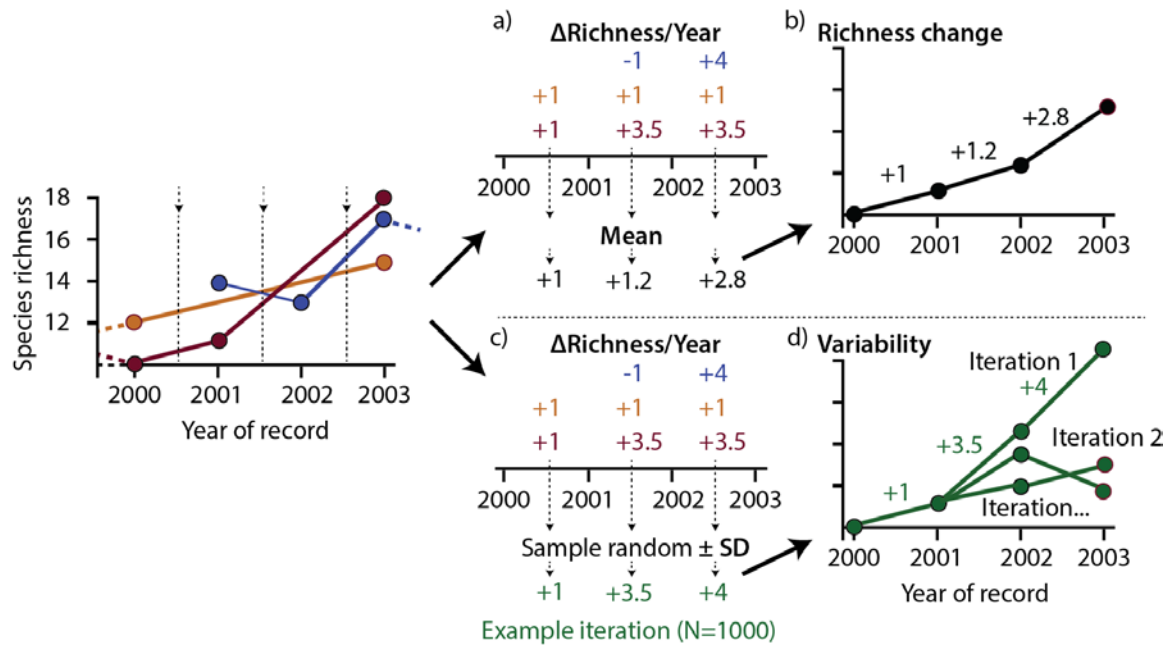
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Extended Data Table 7 | Results of linear mixed effects models (Gaussian family error distribution) analyzing systematic trait differences between colonizing species and the resident community. Analyses are implemented for 258 mountains (750 species) 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.

Trait	Fixed effect (coefficients \pm std. error)		Random effect (std. deviations)
Trait	Intercept	Difference of colonizer relative to established species	Mountain
Plant height	-1.92 \pm 0.02***	+ 0.20 \pm 0.02***	0.20
SLA	2.870 \pm 0.006***	+ 0.021 \pm 0.008**	0.04

Seed mass	-1.50 ±0.03**	non sign.	0.08
Temperature indicator	2.60 ±0.05***	+ 0.37 ±0.05***	0.53

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640 **Extended Data Figure 1 | Conceptual figure showing the approach implemented in the**

641 **main text to visualize richness change over time based on the raw data (Fig. 2 and 3). a)**

642 The mean richness change per year ($\Delta\text{SR}/\Delta t = (\text{SR}_{t_2} - \text{SR}_{t_1}) / (t_2 - t_1)$) across all summits was

643 taken (see Fig. 3 for result). b) The mean richness change per year accumulates with time to

644 yield absolute changes in species richness (see black line in Fig. 2 for results). c) and d)

645 variability in the absolute change in species richness was visualized by randomly sampling

646 ΔSR from all mountains available each year, but adding the standard deviation within a

647 region and year. The displayed range in Fig. 2 illustrates the 5th and 95th percentiles of the

648 resulting richness change values from 1000 runs (orange shading in Fig. 2). This approach

649 reveals changes in variability among mountains over time while also showing overall

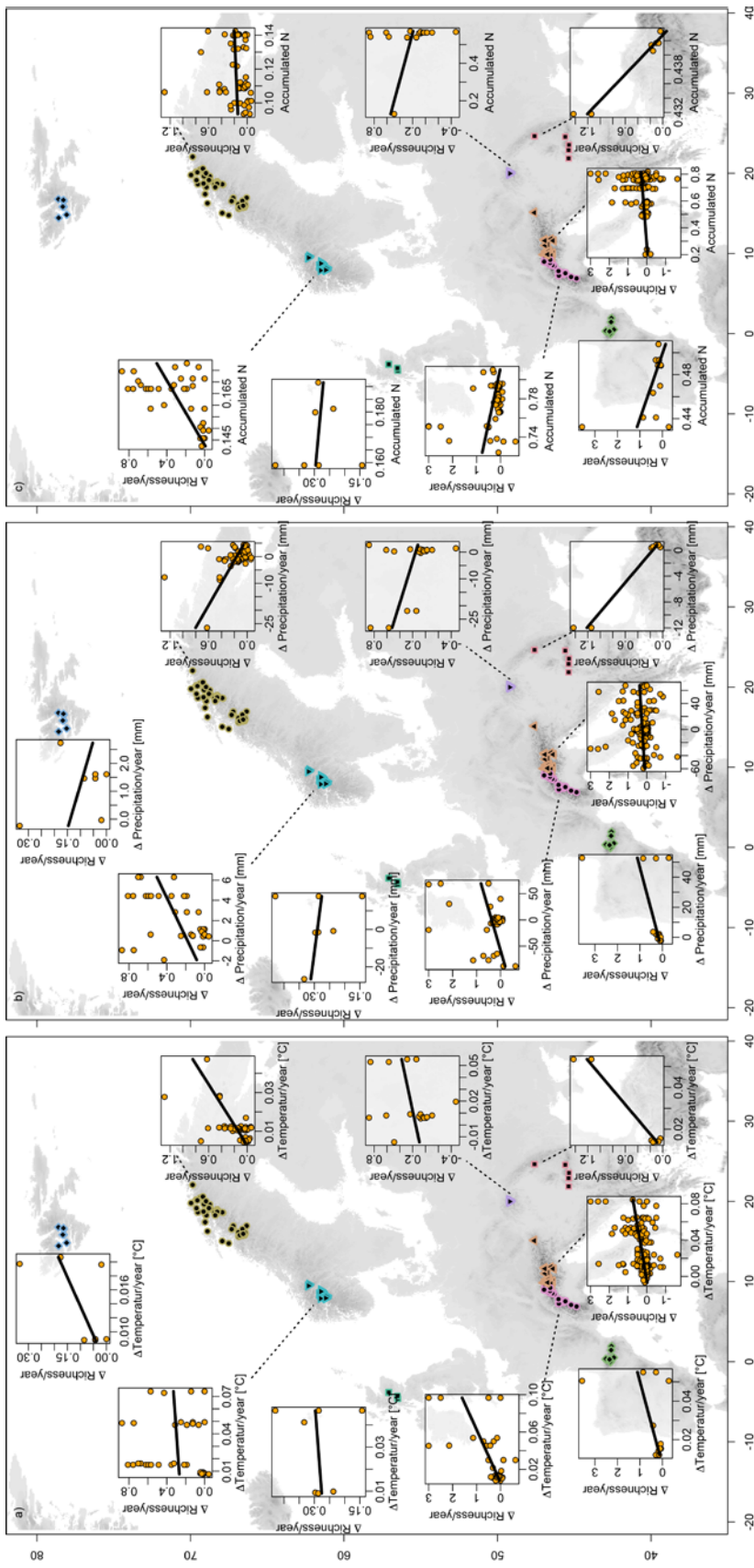
650 variability for time steps where only a few summits were sampled (particularly in early time

651 periods).

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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.

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