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1 Rapid upwards spread of non-native plants in mountains globally

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3 Evelin Iseli¹, Chelsea Chisholm¹, Jonathan Lenoir², Sylvia Haider^{3, 4}, Tim Seipel⁵, Agustina
4 Barros⁶, Anna L. Hargreaves⁷, Paul Kardol⁸, Jonas J. Lembrechts⁹, Keith McDougall¹⁰, Irfan
5 Rashid¹¹, Sabine B. Rumpf¹², José Ramón Arévalo¹³, Lohengrin Cavieres^{14, 15}, Curtis
6 Daehler¹⁶, Pervaiz A. Dar¹⁷, Bryan Endress¹⁸, Gabi Jakobs¹⁹, Alejandra Jiménez^{15, 20},
7 Christoph Küffer^{1, 21}, Maritza Mihoc^{14, 15}, Ann Milbau²², John W. Morgan²³, Bridgett J.
8 Naylor²⁴, Aníbal Pauchard^{15, 20}, Amanda Ratier Backes^{3, 4}, Zafar A. Reshi¹¹, Lisa Rew⁵,
9 Damiano Righetti^{25, 26}, James M. Shannon²³, Graciela Valencia^{14, 15}, Neville Walsh²⁷,
10 Genevieve T. Wright¹⁰, Jake M. Alexander¹

11
12 ¹Institute of Integrative Biology, ETH Zurich, 8092 Zurich, Switzerland; ²UMR CNRS 7058 «
13 Ecologie et Dynamique des Systèmes Anthropisés », Université de Picardie Jules Verne,
14 80000 Amiens, France; ³Institute of Biology / Geobotany and Botanical Garden, Martin
15 Luther University Halle-Wittenberg, 06108 Halle (Saale), Germany; ⁴German Centre for
16 Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany,
17 ⁵Department of Land Resources and Environmental Sciences, Montana State University,
18 Bozeman Montana, MT 59717, USA; ⁶Instituto Argentino de Nivología, Glaciología y
19 Ciencias Ambientales, CCT-Mendoza, CONICET, Argentina; ⁷Department of Biology, McGill
20 University, Montreal QC H3A 1B1, Canada; ⁸Department of Forest Ecology and
21 Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden;
22 ⁹Research group Plants and Ecosystems, University of Antwerp, 2610 Wilrijk, Belgium;
23 ¹⁰Department of Planning, Industry and Environment, Queanbeyan 2622, Australia;
24 ¹¹Department of Botany, University of Kashmir, Srinagar-190006, Jammu and Kashmir,
25 India; ¹²Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne,
26 Switzerland; ¹³Department of Botany, Ecology and Plant Physiology, Faculty of Sciences,
27 University of La Laguna, 38206 La Laguna, Spain; ¹⁴Departamento de Botánica, Facultad de
28 Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C,
29 Concepción, Chile; ¹⁵Instituto de Ecología y Biodiversidad, Santiago, Casilla 653, Chile;
30 ¹⁶School of Life Sciences, University of Hawaii at Manoa, Honolulu, HI 96822, USA;
31 ¹⁷Department of Botany, Amar Singh College, Srinagar-190008, India; ¹⁸Eastern Oregon
32 Agricultural Research Center, Oregon State University, La Grande, OR 97850, USA;
33 ¹⁹Atelierschule Zurich, 8032, Zurich, Switzerland; ²⁰Laboratorio de Invasiones Biológicas,
34 Facultad de Ciencias Forestales, Universidad de Concepción, Casilla 160-C, Concepción,
35 Chile; ²¹Eastern Switzerland University of Applied Sciences, 8640 Rapperswil, Switzerland;
36 ²²Department of Sustainable Environment and Nature Policy, Province of Antwerp, 2018
37 Antwerpen, Belgium; ²³Research Centre for Applied Alpine Ecology, Department of Ecology,
38 Environment and Evolution, La Trobe University, Bundoora 3086, Victoria, Australia; ²⁴USDA
39 Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Lab, La
40 Grande, OR 97850, USA; ²⁵Centre for Ocean Life, Technical University of Denmark, 2800
41 Kgs Lyngby, Denmark; ²⁶Swiss Federal Research Institute, 8903 Birmensdorf, Switzerland;
42 ²⁷Royal Botanic Gardens Victoria, South Yarra 3141, Australia

43 **Corresponding Author**

44 Evelin Iseli Institute of Integrative Biology, ETH Zurich, Universitätsstrasse 16, CH-8092
45 Zurich, Switzerland; evelin.iseli@usys.ethz.ch

46 **Introductory Paragraph (199 words)**

47

48 High-elevation ecosystems are among the few ecosystems worldwide that are not yet
49 heavily invaded by non-native plants. This is expected to change as species expand their
50 range limits upwards to fill their climatic niches and respond to ongoing anthropogenic
51 disturbances. Yet, whether and how quickly these changes are happening has only been
52 assessed in a few isolated cases. Starting in 2007, we conducted repeated surveys of non-
53 native plant distributions along mountain roads in 11 regions from five continents.
54 We show that over just a 5-10 year period, the number of non-native species increased on
55 average by approximately 16% per decade across regions. The direction and magnitude of
56 upper range limit shifts depended on elevation in all regions. Supported by a null-model
57 approach accounting for range changes expected by chance alone, we found greater than
58 expected upward shifts at lower/mid elevations in at least seven regions. After accounting for
59 elevation dependence, significant average upward shifts were detected in a further three
60 regions (revealing evidence for upward shifts in 10 of 11 regions). Together, our results
61 show that mountain environments are becoming increasingly exposed to biological
62 invasions, emphasizing the need to monitor and prevent potential biosecurity issues
63 emerging in high-elevation ecosystems.

64

65

66

67 **Keywords**

68 Invasive species, Biodiversity redistribution, Biological invasions, Climate change, Expansion
69 dynamics, Mountain ecosystems, Null model, Species range shifts

70

71

72

73 **Introduction**

74 Species' distributions are being reshuffled across the globe at unprecedented rates¹⁻⁵. These
75 redistributions are particularly visible in mountain ecosystems, where species can cross
76 large environmental gradients across relatively short distances^{6,7}. While many native species
77 are on the move in mountains in response to changing climate⁸⁻¹⁰, mountain ecosystems
78 have so far experienced comparatively few invasions by non-native species^{11,12}. Possible
79 reasons for this include less-intense human activity and disturbance at high elevation, or that
80 few non-native species can thrive in high-elevation conditions^{11,13-16}. However, this situation
81 is changing with climate warming and increasing human pressures at high elevation^{11,15,17}.
82 For instance, road verges in mountain ecosystems are already known to provide more
83 suitable conditions for non-native plants at higher elevations than would be expected without
84 disturbances^{14,18,19}, and within individual regions, non-native plants are expanding their
85 ranges upward faster than native species^{15,20}.

86
87 Understanding how quickly the richness and elevational distribution of non-native species is
88 changing in mountain regions is important if we are to react appropriately to the challenges
89 (e.g., conservation issues) and opportunities (e.g., ecosystem services) they may pose. The
90 few regional studies assessing temporal changes of non-native plant distributions in
91 mountains have revealed either no average expansion over a decade (in Europe²¹) or
92 upward range expansions over several decades to a century (in Europe¹⁵, Hawaii²² and
93 California²⁰). However, we have so far lacked the necessary time-series data to assess how
94 consistent range limit changes are worldwide or whether (and ultimately why) they differ
95 among regions with contrasting climates, land use histories and species introductions.

96
97 Studies have shown that most non-native plant species in mountains are initially introduced
98 at low elevation and from there spread upwards to fill their climatic niche¹³. As a result,
99 species that have been introduced for a longer period tend to reach progressively higher
100 elevations²³⁻²⁵. This leads to the prediction that, over time and under stable climatic
101 conditions, upward range shifts will be most pronounced for non-native species that are
102 found initially at low elevation and spread upwards to fill their climatic niche, and less evident
103 for species already found at high elevation, although climate warming could contribute to
104 accelerate upward shifts also at high elevation²⁰. Studies of climate-induced range shifts in
105 native plant species have repeatedly found a similar negative relationship between species'
106 initial upper range limits and the magnitude of their upper range limit expansion (Fig. 1).
107 Contrasting mechanisms have been proposed to explain this pattern, including: (i) stronger
108 responses of warm-adapted (i.e. low elevation) species to climate warming^{15,26}; (ii) changes
109 in climatic water balance or biotic interactions driving downward migrations at higher

110 elevation^{27,28}; (iii) longer growing seasons and correspondingly greater opportunities for
111 dispersal and spread at lower elevation²⁹; (iv) broader environmental tolerances of high-
112 elevation species, necessitating smaller absolute range shifts to track changing climate¹⁰;
113 and (v) greater microsite variation at high elevation, buffering the need for range shifts^{7,30}.

114

115 Here, we propose and examine an alternative hypothesis, that larger upward range limit
116 shifts among species previously found at lower elevations are in fact expected by chance
117 alone. This null expectation applies to any range observations made across a finite
118 elevational gradient, for two reasons. Firstly, the statistical phenomenon of regression
119 toward the mean describes the fact that unusually large or small values of a variable on
120 average tend to be followed by measurements closer to the mean, giving rise to a negative
121 correlation between the initial value of a variable and the change in paired measurements of
122 that variable over time (refs ^{31,32}, for further explanations see Supplementary Methods). In
123 the context of range limits, this means that under the assumption that range limit changes
124 occur at random, species with originally especially low or high initial upper range limits are
125 expected to have range limits closer to the mean elevation in the next time step. This leads
126 to a null expectation of a negative relationship between species' initial upper range limit and
127 its change over time.

128

129 Secondly, the geometric constraint imposed by the boundaries of a finite gradient, e.g. from
130 the valley bottom to the mountain summit, means that upward shifts cannot be observed for
131 species already present at the highest surveyed elevation, and vice versa for downward
132 shifts of species previously limited to the lowest elevation, leading to a mid-domain effect in
133 terms of degrees of freedom that is well recognized in the scientific literature³³. A common
134 approach to mitigate this problem has been to remove species already reaching either end
135 of the studied gradient (e.g. refs ^{10,29}). However, the geometric constraint on the magnitude
136 and direction of observable range shifts (cf. refs ^{33,34}) applies across the whole gradient, and
137 not only to species whose ranges already reach the top or bottom of the elevational survey.
138 As Fig. 1 demonstrates, large upward shifts can only be observed for species originally
139 restricted to the lower part of the gradient, while large downward shifts can only be observed
140 for species originally restricted to the upper part. Therefore, even if range shifts were
141 completely random within a set of species (i.e. no average upward or downward shifts), we
142 would expect a negative relationship between the initial elevational distribution of range
143 limits and range limit shifts, simply due to constraints on the observable magnitude and
144 direction of range shifts along elevational gradients (Fig. 1). Excluding species occurring at
145 the top and bottom of the gradient does not remove this effect (Fig. 1D). Consequently,
146 before seeking ecological explanations for observed patterns of range dynamics across

147 environmental gradients, these patterns should be evaluated against appropriate null
148 models^{27,33,35}. However, very few studies of climate-related range shifts use null models to
149 interpret patterns of range limit shifts or to fully account for geometric constraints^{10,35}.

150

151 Here, we analysed data from a standardized survey of non-native plant distributions
152 (developed by the Mountain Invasion Research Network MIREN;
153 www.mountaininvasions.org³⁶) to quantify and compare temporal patterns of invasions in
154 mountains across the globe. We surveyed elevational gradients along mountain roads and
155 adjacent semi-natural vegetation in eleven mountain ranges from five continents, ranging
156 from 68° N (Norway) to 37° S (Australia). Our data includes nearly 15000 observations of
157 616 non-native plant species from 651 sampling transects resurveyed every five years
158 across a 5-year (five regions) or 10-year (six regions) period. We analyzed temporal
159 changes in the richness and upper elevational limits of non-native plant species, introducing
160 a null model approach to interpret patterns of range shifts across elevational gradients after
161 accounting for geometric constraints, and compare these patterns across regions.

162 Specifically, we ask: (1) Has the richness of non-native plant species in mountains increased
163 during the last decade? (2) Are the upper elevation limits of non-native species moving
164 upslope, and if so, are upslope shifts occurring faster than expected at lower elevations?

165

166 **Results and Discussion**

167 After first excluding species occurring only once in a region to reduce possible bias caused
168 by very infrequent species (reducing the total number of non-native species from 616 to
169 480), the total non-native plant species richness increased in 7 out of 11 (64%) regions over
170 the whole study period. Increases ranged from 2 to 15 species depending on the region, but
171 changes were non-monotonic in three of the five regions that were sampled three times (Fig.
172 2A). Four regions (Oregon [USA], Central Chile, Victoria [Australia] and Kashmir [India])
173 experienced a small net loss of non-native species, and in Central Chile, the loss occurred
174 after initial gains in species richness during the first five-year interval. Overall, this resulted in
175 a close to significant increase in non-native species richness across all regions of $0.46 \pm$
176 0.23 (mean \pm SE) species per year ($\chi^2 = 3.190$, $p = 0.074$). Expressed as percentage
177 changes (Fig. 2B), this corresponded to a significant net increase of $1.56 \pm 0.57\%$ in non-
178 native species richness per year (model slope \pm SE, $\chi^2 = 6.822$, $p = 0.009$), or approximately
179 16% over a decade, due to proportionally larger increases in regions with fewer non-native
180 species.

181

182 Temporal trends in non-native plant species richness within individual regions may be
183 partially obscured by environmental conditions in the year of the survey. For example,

184 unusually dry conditions in 2017 may explain the decline in non-native species richness
185 detected during that year in Switzerland, while the increase in non-native species richness in
186 New South Wales (Australia) in 2012 was likely caused by much higher rainfall in 2011.
187 However, independent of whether regional changes in non-native species richness are
188 influenced by climate anomalies or survey artifacts (such as observer effects), by pooling
189 observations from multiple independent regions located across the globe, we could detect an
190 overall trend of non-native plant richness generally increasing in mountain regions over time,
191 even over a short 5- to 10-year period.

192

193 On average, non-native plant species shifted their upper elevational limits (defined as the
194 90th percentile of their observed elevations of occurrence) upslope in all regions except
195 Montana (USA) and Hawaii. Mean upslope shifts between the first and last survey were
196 significant in four regions (and close to significant [$p < 0.1$] in a further two regions; intercept-
197 only linear models on unstandardized elevation, with observations weighted according to
198 species' overall frequency of occurrence; Fig. 3A, Table S1). We found the same pattern for
199 mean annual upslope shifts (Fig. S1A, Table S2). These results were also robust to applying
200 stricter filters excluding less common species to examine the influence of low species
201 frequency in some of the regions: retaining only species with >5 (filter 1) and >10 (filter 2)
202 occurrences per region over all years resulted in identical trends with upslope shifts in all
203 regions except Hawaii and Montana (USA) and significant upslope changes in three regions.
204 As the overall occurrence of non-native plant species was very low in Norway, the upslope
205 shift was no longer significant for filter 1 and the region was excluded for analysis with filter
206 2, as fewer than five species remained in the data set (Table S3). When only retaining
207 species with >10 occurrences per region and year (filter 3), three regions (Norway,
208 Switzerland and Central Chile) had fewer than five species remaining and were therefore
209 excluded. The range shift direction did not change for the remaining eight regions (with the
210 same three regions showing significant upslope shifts), except for South Chile, where
211 changes were always non-significant (Table S3).

212

213 Overall changes in upper elevation limits across regions (standardized range limit shift =
214 0.07 ± 0.04 in an intercept-only linear mixed-effects model with region as a random effect: t
215 = 1.77, d.f. = 9.43, $p = 0.109$) were obscured by large variation in the magnitude and
216 direction of shifts along gradients and among regions. Regional variation in the magnitude of
217 range shifts was partly due to differences in the extent of the studied elevational gradients
218 and therefore in the average distances between surveyed transects (ranging from 17 m in
219 Norway and Victoria [Australia] to 76 m in Kashmir [India]) with Kashmir, Hawaii, Tenerife
220 and Central Chile all having relatively large average distances of > 50 m between transects;

221 Table S4). In regions with greater distances between surveyed plots we tend to both fail to
222 detect small shifts, and potentially to register small shifts as larger than they actually are.
223 This effect may be amplified if species are mostly found along a single road per region, as
224 average distances between transects along a single road will exceed the average distance
225 between transects within regions as a whole. For example, the mean distance between
226 adjacent transects in Hawaii along any given road is 156 m, and many species (32%) were
227 only recorded from a single road, which might explain the large downward average upper
228 limit shift in this region. Consequently, large mean range shifts must be interpreted with
229 caution for regions with large average distances between transects.

230

231 Across regions, and as predicted, the upper range limits of non-native plants shifted upslope
232 at low elevations with linearly decreasing magnitude across the elevational gradient, with
233 slight average downslope shifts at high elevations in some regions (linear mixed-effects
234 model of range shifts on initial elevation limit, weighted by species' frequencies of
235 occurrence: $F_{1,579.89} = 54.82$, $p < 0.001$; Fig. 4). This relationship was significant in six regions
236 when regressions were fitted within individual regions (Table S6). On average, upslope shifts
237 at low elevation tended to outweigh downslope shifts at high elevation. To account for these
238 effects of elevation on the average upper range limit shifts, we evaluated the range limit shift
239 at the median of each elevational gradient based on the fitted values of linear regressions in
240 each region. Retaining all species present at least twice per region, upper range limit shifts
241 between the first and last survey were significantly upslope in seven regions (Fig. 3B, for
242 annual shifts see Fig. S1B). Though still upslope, range limit shifts were no longer significant
243 for Norway (filter 1) and for Switzerland (filter 2), when excluding less common species.
244 Excluding species occurring fewer than 10 times per region and year resulted in non-
245 significant shifts at the midpoint for South Chile and Oregon (USA) (Table S5; regions with
246 fewer than five species remaining after filtering were excluded from the analysis). This might
247 be due to the low sample size in some regions (Switzerland and Norway), or also reflect the
248 expectation that more widespread species will tend to have been introduced for longer and
249 so more likely to be in equilibrium with their climatic limits²⁴. To conclude, accounting for the
250 elevation-dependence of species' shifts at the upper range limit strengthened our inference
251 that non-native plant species have rapidly expanded their ranges upslope in mountains
252 globally.

253

254 Previous studies of both non-native and native species have sought ecological explanations
255 for similar elevation-dependent range shifts to those that we describe here^{10,15,26,28,29,37}.
256 However, the bounded nature of survey gradients means that a negative relationship is in
257 fact the default expectation, and range shift patterns should therefore be compared against

258 an appropriate null model before they can be interpreted ecologically³⁵. Our null-model
259 approach (Methods; Fig. 1) revealed that the observed negative relationships between initial
260 upper elevation limits and range limit shifts fell outside of the 95% confidence intervals of null
261 expectations in seven regions (both Australian regions, South Chile, Tenerife, Hawaii,
262 Kashmir [India] and Montana [USA]; Fig. 4). In all seven cases, observed relationships fell
263 above the confidence intervals of expected relationships in the lower part of the elevational
264 gradients (or in the middle part of the gradient in Kashmir [India]), indicating that species
265 initially restricted to lower (or middle) elevations spread upwards significantly more than
266 expected by chance alone. Greater downward shifts than expected by chance were also
267 observed at high elevation in Tenerife and Montana (Fig. 4). Alternative null models (differing
268 in the vectors of initial elevation limits used to derive expected relationships; see Methods for
269 further details) supported an additional significantly greater upward range shift at low
270 elevation than expected by chance in Oregon (USA) (Fig. S2, S3). Support for greater
271 downward shifts than expected by chance also differed depending on the null model used
272 (zero to three regions; Fig. 4, S2, S3).

273

274 Non-native plant species distributions along elevational gradients tend to display a nested
275 pattern, with species with small ranges mainly restricted to lower elevation sites, where
276 human population density and corresponding opportunities for introduction and
277 establishment are greatest^{13,15}. Greater upward shifts in elevation limits for species previously
278 restricted to lower or middle elevations are therefore consistent with a scenario of ongoing
279 dispersal, in which many of these species have only recently been introduced to lower
280 elevation sites. On average, we would not expect recently introduced species to be in
281 equilibrium with their climatic limits, but rather to be in a phase of active range expansion
282 (i.e. climatic niche filling), in contrast to species that have already established at higher
283 elevations and are closer to their cold limit. Consistent with this hypothesis, recently-
284 introduced non-native species in Tenerife tend to have narrower elevation ranges than older
285 introductions²⁴, while time since introduction of non-native plant species in Central Europe is
286 positively related to their maximum elevation²³, elevation range²⁵ and to the magnitude of
287 upward range shifts¹⁵. Conditions at lower elevation might also be more conducive to
288 spread, with longer growing seasons, at least in temperate regions, and greater
289 anthropogenic disturbances and propagule pressure associated with settlements, agriculture
290 and industry. Similar reasons have been proposed to explain the more pronounced
291 elevational shifts and abundance increases of native plants in the European Alps at lower
292 elevation²⁹. We hypothesize that a combination of these mechanisms is responsible for the
293 rapid (within 5 to 10 years) expansion of species' upper elevation limits that we document in
294 most of our study regions. While climate warming might also have contributed to the upward

295 spread, we did not find a relationship between the average yearly temperature increase
296 between 2000 and 2016 within regions (Table S8) and the respective mean regional range
297 limit shifts (linear model of range shifts on average yearly temperature change, $F_{1,9} = 0.447$,
298 $p < 0.521$). Similarly, we did not see a tendency for regions with 10 years of survey data to
299 display greater range shifts over the whole sampling period than regions with only 5 years of
300 survey data, as might be expected if climate change was an important driver. Indeed,
301 significant deviations from null expectations of shifts were already detected over intervals of
302 5 years in four of five regions with a 10-year time series (Table S10). Over the longer term,
303 however, climate warming will extend the suitable elevational range of species to higher
304 elevations, presumably leading to enhanced upslope shifts also in the upper part of the
305 elevational gradients.

306

307 In contrast to upward shifts at low elevation, significant deviations from the downward shifts
308 at high elevation predicted by the null model were more scarce. Possible explanations for
309 the few cases of significant downslope shifts might be active removal of non-native species
310 at high elevation in some regions, pushing their upper limits to lower sites³⁸, or harsh
311 environmental conditions preceding the final survey (e.g. a greater probability of mortality or
312 failed reproduction due to cooler temperatures or severe frost events^{21,39}). Downward shifts
313 might also have arisen stochastically, especially if species reaching high elevation tended to
314 be rare and assuming that rarer species are more prone to large range contractions due to
315 stochastic local extinction events^{21,27}. Our models partly accounted for this by weighting
316 species based on their frequency of occurrence. In unweighted models, negative
317 relationships between initial elevation limits and range limit shifts were more pronounced in
318 eight regions (Table S7), suggesting that stochasticity in colonization and extinction events
319 contribute at least partly to the magnitude of upward and downward shifts.

320

321 In summary, the different lines of evidence we have presented collectively reveal that non-
322 native plant species are expanding their upper elevation limits in 10 out of the 11 surveyed
323 regions. Specifically, upward shifts were chiefly represented by average upper limit changes
324 within regions either before (four regions; Fig. 3A) or after (additional three regions; Fig. 3B)
325 accounting for elevation, or more than expected by chance for species at low/mid elevation
326 (additional three regions; Fig. 4). The only region showing no evidence of significant
327 changes in non-native species' upper range limits was Central Chile. That these upper range
328 limit changes were observed after just five years in five of the regions indicates how rapidly
329 non-native plant species are spreading upwards in mountains around the world, especially
330 along road corridors. By comparison, native plants in the European Alps are moving upslope
331 on average by 28.2 m per decade⁴⁰, which is substantially less than what we report for non-

332 native species (Fig. 3). Roads provide favourable habitat and anthropogenic dispersal routes
333 for many non-native plant species, and range expansion along roads are therefore expected
334 to be more rapid than in undisturbed habitats. Non-native plant species spreading away from
335 roads into the surrounding undisturbed vegetation has so far been limited at higher
336 elevation^{11,16}, but this might change with increasing anthropogenic disturbance and changing
337 climate. Roadside surveys like ours³⁶ might therefore be valuable for the early detection of
338 possible emerging threats to native species and ecosystems. To support such measures,
339 future work should continue to interrogate which species traits promote fastest rates of
340 spread^{15,16,29,41,42}, which species have the potential for greatest impacts, and which features
341 of high elevation ecosystems (e.g. native community structure, disturbance regimes, rates of
342 climatic or land use changes) are associated with greater levels of invasion^{16,43}. Additionally,
343 while negative relationships between historical range positions and range shifts are
344 pervasive, our simulations demonstrate that such patterns can also emerge in the absence
345 of biological changes. As time-series data of species' distribution changes become
346 increasingly available², null models can be powerful tools for evaluating the magnitude and
347 direction of range shifts within given observational constraints and will become crucial to
348 support robust interpretation of range shift dynamics across environmental gradients³⁵.
349 Finally, this study suggests that in an era of local and global anthropogenic changes, non-
350 native plant species in mountains will continue to expand upwards regardless of their
351 introduction point. Therefore, any threat posed by non-native species to higher elevation
352 ecosystems will likely increase, making it even more necessary to enact monitoring and
353 management plans in mountain regions around the world.

354

355 **Methods**

356 *Data collection*

357 Data were collected by the Mountain Invasion Research Network (MIREN) using a standard
358 protocol³⁶. Sampling started in 2007/ 2008, is repeated every five years and is still ongoing.
359 We used data from 11 mountainous regions around the world: the Australian Alps (two
360 regions, New South Wales and Victoria); the Swiss Alps; the Andes (two regions, Central
361 and South Chile); the Montana-Yellowstone National Park (USA); the Blue Mountains
362 (Oregon, USA); Hawaii (USA); Tenerife (Canary Islands, Spain); Kashmir (India); and the
363 Northern Scandes (Norway). For information about geolocation, climate, elevational range
364 and sampling period, see Table S4. In each region, three roads were selected (two in
365 Central Chile, four in Hawaii, five in Victoria), all of them open to vehicle traffic for at least
366 part of the year. The bottom of each road was defined as the point below which no major
367 elevational change occurred, while the top was set by the highest point of the road³⁶. Each
368 road was evenly stratified by elevation into 20 sampling transects (i.e. 60 per region, though

369 this varied due to local logistics; see Table S4), totaling 651 sampling transects. At each
370 location, three 2 × 50 m plots were placed in a T-shape, with one plot parallel to the road
371 and two plots placed adjacent and perpendicular to the first plot, to distinguish between
372 disturbed habitats directly next to the road and more semi-natural habitats away from the
373 road (i.e. up to 50 and 100 m away from road verges). The two perpendicular plots were only
374 surveyed when there were no impassable barriers such as cliffs and rivers, resulting in
375 unequal numbers of plots per sampling transect (respectively 651, 481 and 440 plots at 0, 50
376 and 100 m from the road). Sampling was repeated during the peak growing season at 5-year
377 intervals (Table S4). The identity of non-native vascular plant species according to the World
378 Flora Online⁴⁴ and their abundance (scale 1 = 1-10 individuals or ramets, 2 = 11-100
379 individuals and 3 > 100 individuals) was recorded in every plot. Data from the three plots at
380 each sample transect (elevation) were combined to presence-absence data for each
381 transect for the analyses presented here. The two semi-natural plots together accounted for
382 only 35% of the total observations of non-native plant species across years, and only 11% of
383 unique observations of non-native plant species within sample transects (i.e. observations of
384 species away from but not at the roadside). Further, analyses conducted with data separated
385 into road and semi-natural plots revealed no consistent differences in average upper limit
386 shifts (Table S9). Species not identified to species level were excluded, as were species that
387 were only recorded once in a given region.

388

389 *Data analysis*

390 All analyses were carried out in R, version 4.0.3, using the lme4 package⁴⁵. All models were
391 checked for compliance with model assumptions. To explore changes in non-native species
392 richness over time, the total number of non-native plant species was calculated for each
393 region and year ($N = 27$ observations of regions/years). Species richness was fitted with
394 linear mixed-effects models (LMMs; Gaussian error distribution). Year since first survey (0, 5
395 or 10 years) was used as a linear predictor and region included as a random intercept term
396 to account for the spatial nestedness of the data. Subsequently, these models were
397 compared to an intercept-only model, but still including the same random effect, with a
398 likelihood ratio test. We also fitted LMMs to the percentage change in richness, setting the
399 intercept to zero (i.e. percentage change in species richness is always zero in the first year
400 of the survey).

401

402 To investigate range expansion of individual non-native species, we calculated for each
403 species the change in upper elevational limit between the first and last time points (i.e. over
404 either a 5 or 10 year period). We therefore only retained species present at least once in
405 both the first/last sampling year. Additionally, to assess the influence of less common

406 species on average regional range shifts, we defined three data sets with stricter filters only
407 including species occurring >5 and >10 times per region over all years (filters 1 and 2) and
408 >10 times per region and year (filter 3). The upper elevation limit was defined as the 90th
409 percentile of all species' occurrences along the elevational gradient. While the 90th percentile
410 approximates the highest occurrence point when species are scarce, it reduces the influence
411 of extreme outlier occurrences when sufficient data points are available to be informative
412 and so provides more conservative estimates of range changes. Range limit changes were
413 quantified as the difference in 90th percentiles between the first (t1) and last time point (t2 or
414 t3) in each region (t2-t1 or t3-t1). To facilitate comparisons between regions with very
415 different elevation ranges, elevation was centered and scaled (mean = 0, standard deviation
416 = 1) within regions prior to calculating range limit changes . We first fitted an intercept-only
417 LMM of range limit changes across all species and regions, with region as a random
418 intercept term, to test for overall changes in upper elevation limits across all regions
419 combined. To investigate region-specific patterns, we then fitted intercept-only linear models
420 to unstandardized data from each region separately. In all models, observations were
421 weighted by species' total frequency of occurrence across the first and last surveys using the
422 "weights" argument within the model formula. We assumed that range-limit estimates for
423 frequently occurring species will be less affected by outlier occurrences than estimates for
424 rare species and therefore gave greater weight to estimates of range shifts for common
425 species.

426

427 To test our hypothesis that range expansions are more pronounced at lower elevations, we
428 again fitted a LMM with shift in upper range limit as the response variable and species' upper
429 elevation limits during the first (t1) survey (standardized within region) as the only fixed
430 effect. Region was used as a random effect (random intercept only) and range shift
431 observations were weighted by species' total frequency of occurrence as above. We then
432 fitted weighted linear models to data from each region separately (with elevation
433 unstandardized) to test region-specific trends, and also fitted unweighted models for
434 comparison. We used the weighted models from each region to estimate mean range shifts
435 of species after accounting for elevation. Specifically, we used the models to predict the
436 mean upper range limit shift, and its confidence interval, at the median elevation of species'
437 upper range limits in the first survey (i.e. by setting the predictor variable to the median
438 elevation of the elevational gradient within a given region). If this value is significantly greater
439 than 0, it indicates that average range limit shifts are upslope across the majority of the
440 elevational gradient in a given region.

441

442 Finally, we constructed null models in each region to assess the expected relationship
443 between species' upper elevation limits in the first survey and shifts in upper elevation limits,
444 under the assumption that observed shifts are entirely stochastic with respect to elevation
445 (i.e. that observed shifts are placed at random across the elevational gradient). This analysis
446 was performed to account for the fact that the bounded nature of elevational gradients
447 constrains the magnitude and direction of range shifts that are possible to observe at low
448 and high elevation (Fig. 1). Within each region, the observed elevation shifts were
449 randomized across the elevation gradient by randomly drawing new initial elevations (with
450 replacement) from the vector of surveyed elevations (i.e. the approx. 60 plots per region;
451 Table S4). To account for the geometric constraint, the vectors of possible initial elevations
452 for a given iteration of randomized range shift were truncated to values \leq the maximum
453 elevation minus the range shift value in the case of upward range shift values, or values \geq
454 the minimum elevation plus the range shift value in the case of downward range shift values.
455 This procedure was repeated 10,000 times, each time fitting a weighted linear regression of
456 range shift at the upper elevation limit (the response variable) against the initial position of
457 the upper elevation limit (the only predictor variable). Since bootstrap regressions may differ
458 in intercept but not in slope, inference about whether upward shifts differ from the null
459 expectation cannot be based solely on a comparison of the observed and expected slope
460 estimates. For each bootstrap replicate, we therefore retained the fitted values of the
461 regression and used the 10,000 vectors of fitted values to compute 95% confidence intervals
462 around the regression expected under the assumption that range shifts occur at random
463 across the elevational gradient. We compared the observed and expected relationships
464 graphically, concluding that the observed relationship deviated significantly from the null
465 expectation if a non-zero fraction of the regression line fell outside of the 95% confidence
466 intervals. We also explored two alternative null models that differed in how the vectors of
467 new initial elevations were defined, and therefore in the variation among bootstrap
468 regressions: (1) a less conservative approach (yielding narrower confidence intervals around
469 the expected regression) that used a vector of 200 equally-spaced initial elevations, instead
470 of the approximately 60 elevations that were actually surveyed in each region (results in Fig.
471 S2); and (2) a somewhat more conservative approach (yielding wider confidence intervals
472 around the expected regression) that used only the observed initial elevations within each
473 region, i.e. with a vector length corresponding to the observed number of species (Fig. S3).

474
475

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493

494 **Data Availability Statement**

495 All datasets generated before 2016 (except two roads in Victoria, Australia) and analysed
496 during the current study are available through the Global Biodiversity Information Facility
497 (GBIF, <https://www.gbif.org/publisher/76388ab6-61ca-439a-ab09-e1fe73eb224a>) and the
498 complete data set is available on Zenodo (<https://doi.org/10.5281/zenodo.5529072>).

499 Environmental data and a summary file containing all species and range shifts are provided
500 as supplementary files.

501 **Code Availability Statement**

502 The code used to perform the analysis is available as a supplementary file.

503

504 **Author Contributions**

505

506 E.I., C.C., S.H., T.S., A.B., A.L.H., P.K., J.J.L., J.L., K.M., I.R., S.B.R., L.C., A.P. and J.M.A.
507 designed the study. S.H., T.S. and D.R. managed the data collected by S.H., T.S., J.J.L., K.M.,
508 J.A., L.C., C.D., P.A.D., B.E., G.J., A.J., C.K., M.M., A.M., J.W.M., B.J.N., A.P., A.R.B., Z.A.R.,
509 L.R., D.R., J.S., G.V., N.W., G.W. and J.M.A.. E.I. and J.M.A. analysed the data and drafted
510 the manuscript with feedback from J.L. on statistical analyses and the Regression Towards
511 the Mean (RTM). C.C., S.H., T.S., A.B., A.L.H., P.K., J.J.L., J.L., K.M., I.R., S.B.R., L.C., C.D.,
512 A.P., A.R.B., D.R. and N.W. edited and commented the paper.

513

514

515 **References**

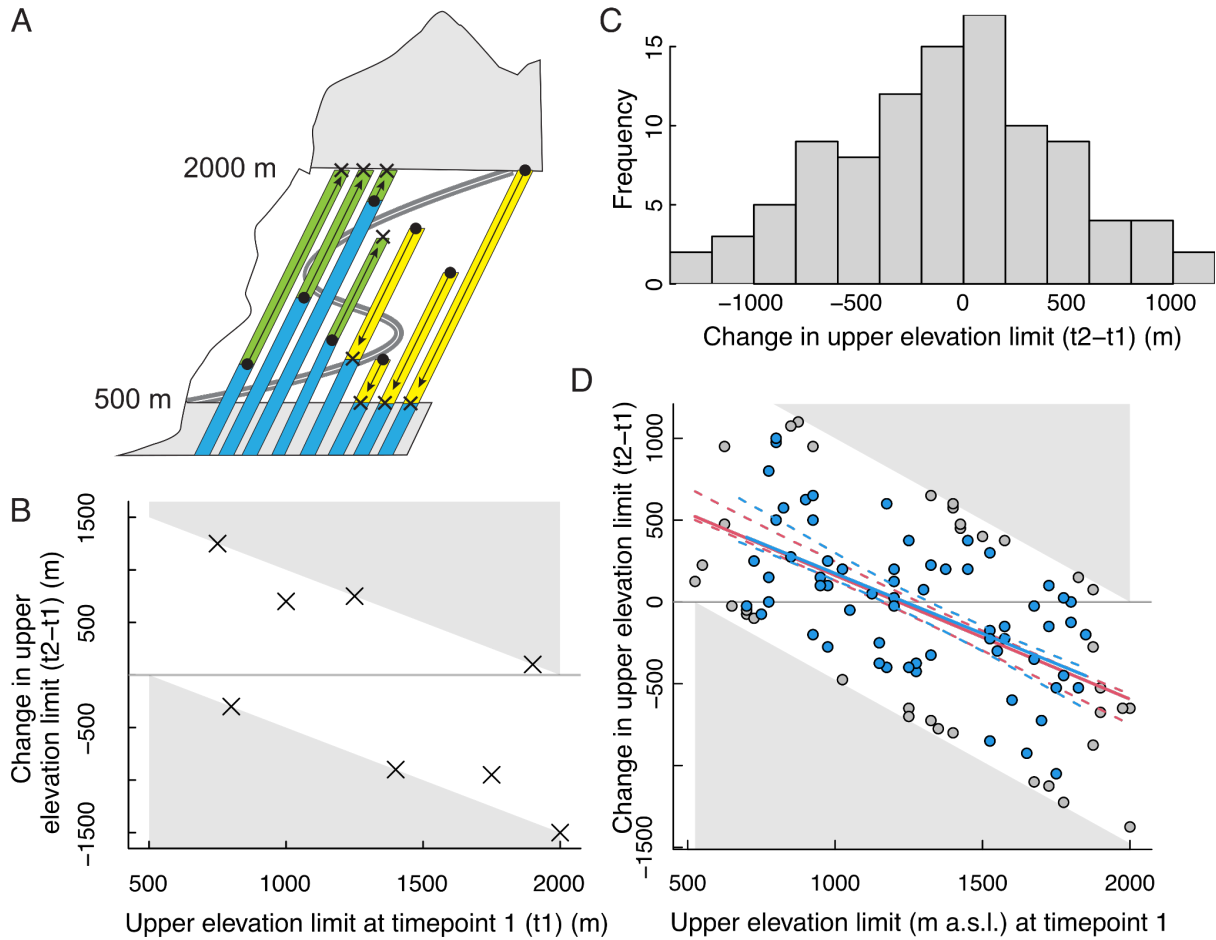
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653

Possible changes in upper elevation limits

Elevation-dependence of randomly generated upper limit shifts



655

656

657 **Figure 1. A null model approach to explaining species' range limit shifts across an**

658 **elevational gradient.** (A) Possible changes in observed upper elevation limit for eight

659 species (bars) shifting their upper limits upwards (green portions of bars: expansions) or

660 downwards (yellow portions of bars: contractions) along an elevational gradient from time

661 point 1 (t_1 ; points) to time point 2 (t_2 ; crosses). The species' distributions are surveyed at

662 sites along a hypothetical mountain road between 500-2000 m a.s.l. (i.e., within the

663 unshaded region), although all of them also occur at lower elevations below the surveyed

664 elevational window. (B) The observed range shifts of the upper elevation limit for the eight

665 example species (crosses) are plotted against their upper elevation limits at t_1 . The grey

666 triangles delimit the boundaries of the surveyed elevational gradient (cf. grey shaded regions

667 in A), and hence represent "non-observable" shifts in elevation limits. (C) Histogram of upper

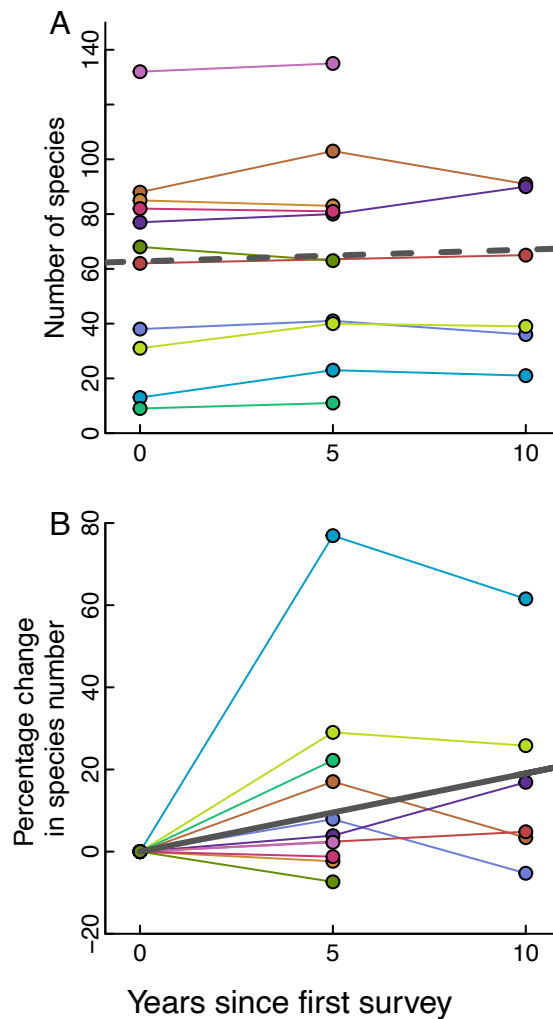
668 limit shifts for 100 species, generated randomly within the constraints imposed by the

669 boundaries of the observed elevational gradient (cf. panel B). (D) The boundaries of the

670 observed elevational gradient give rise to the null expectation of a negative relationship

671 between species' upper limits during t1 and their shift at the upper elevation limit due to
672 chance alone. The red line indicates the fitted relationship, and dotted red lines indicate 95%
673 confidence intervals for the expected relationship based on 1000 resamples (with
674 replacement) of the 100 species' elevational limits at t1, accounting for the geometric
675 constraint. Excluding species occurring in the top and bottom 10% of the gradient either at
676 time point 1 or time point 2 (remaining species colored in blue) results in the fitted
677 relationship depicted by the blue line. The dotted blue lines indicate 95% confidence

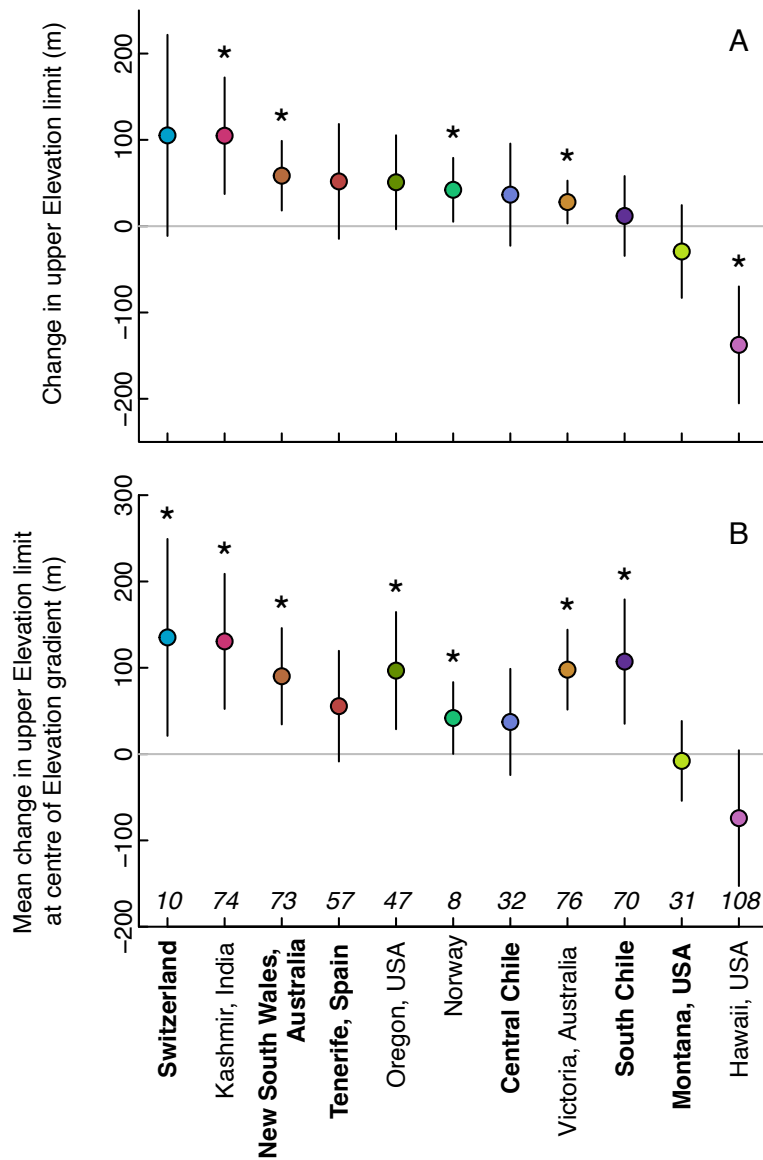
678 intervals calculated as described above, but excluding species falling in the top and bottom



679 10% of the gradient.

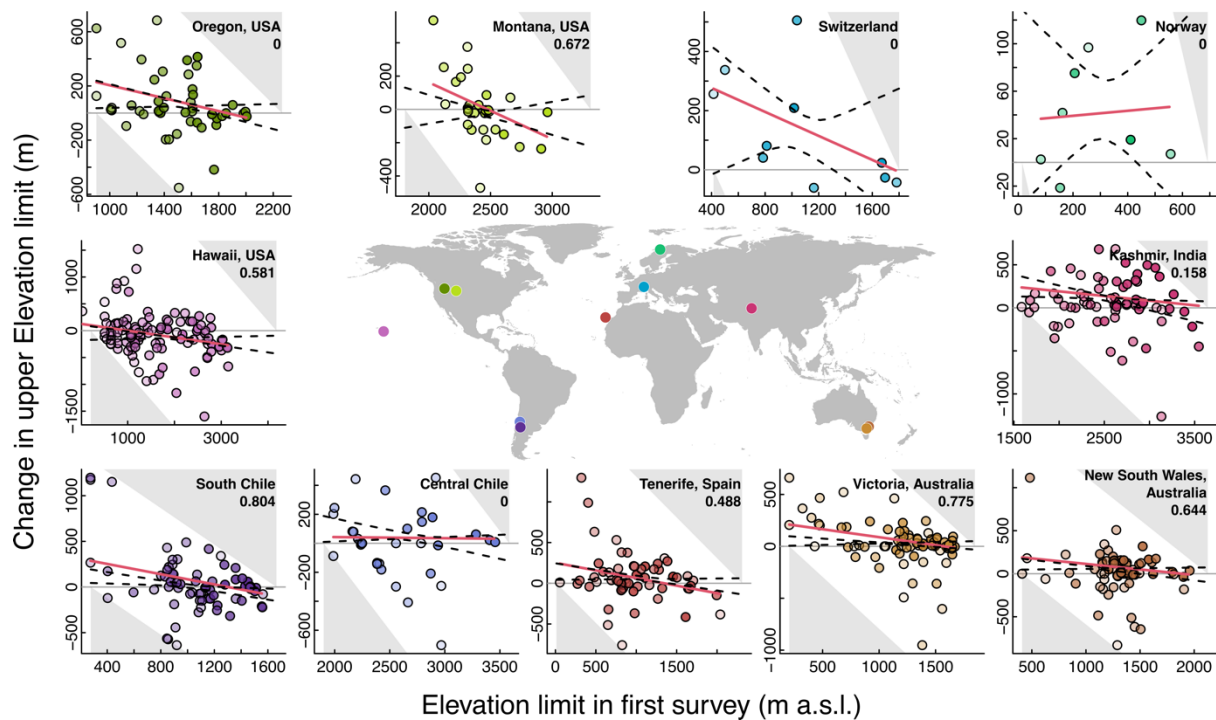
680 **Figure 2. Temporal changes of non-native plant species in 11 mountain regions.** Total
 681 species richness (A) and percentage change in species richness (B) over the 10-year
 682 sampling period. Solid and dashed heavy grey lines indicate significant and non-significant
 683 fits, respectively, from mixed-effects models including all non-native species (see text). Not

684 all regions were sampled in all years.



685
686 **Figure 3. Observed changes in species' upper elevational limits** ($\pm 95\%$ confidence
687 intervals). Both panels show mean shifts between the first and last survey in each region,
688 estimated from linear models that weight species by their total frequency of occurrence in
689 both years and are fitted to data from each region separately (for mean annual shifts see
690 Fig. S1). Panel A shows results of intercept-only models (i.e. grand mean shifts per region),
691 while panel B shows results of models that correct for elevation by including species' initial
692 elevation limit during the first survey as a linear predictor. Specifically, estimates in B
693 correspond to the predicted mean shift in elevation limits when evaluated at the median
694 elevation within a given region; values >0 therefore indicate that average shifts are upslope
695 across most of the elevational gradient (cf. Fig. 4). Regions are ordered by effect size in
696 panel A, with labels in regular and bold typeface indicating regions with 5- or 10-year survey

697 intervals, respectively. Estimates that differ significantly from zero are indicated by *.
 698 Numbers in italics describe the sample size.



699
 700 **Figure 4. Null-model tests of elevation-dependent shifts in upper elevation limit of**
 701 **non-native plant species in 11 mountain regions.** Each point shows the change in upper
 702 elevation limit (90th quantile of elevational distribution) of a single species, as a function of its
 703 limit in the first survey (darker shading of points corresponds to greater total log[frequency of
 704 occurrence] of a species in both surveys, ranging from n=2 [40 species in 10 regions] to
 705 n=187 [*Hypochaeris radicata* in Victoria, Australia]). Red regression lines are fitted
 706 relationships for observed range limit shifts, weighted by species' frequency of occurrence.
 707 Grey triangles indicate shifts that could not have been observed based on the elevational
 708 extent of the field survey (cf. Fig. 1); dashed lines are 95% confidence intervals for the
 709 expected null relationship between initial upper elevation limit and change in upper elevation
 710 limit after accounting for this constraint (see Methods and Fig. 1). The proportion of fitted
 711 values that fall above or below the confidence intervals in each region are indicated in the
 712 top-right of each panel, with non-zero values indicating a significant deviation from the null
 713 expectation.

714 **Supplemental Information**

715

716 **Table S1.** Average shifts in upper elevation limits in each region between the first and last
 717 survey. Estimates (expressed as m of elevation across the sampling period) are taken from
 718 intercept-only linear models fitted to observed shifts in unstandardized upper elevation limits
 719 of species in each region separately and weighted by species' frequency of occurrence.
 720 Regions are ordered according to effect size. Significant p-values are marked in bold.

721

	Estimate ± standard error	t-value	p	N	Sampling period (years)
Switzerland	105.2 ± 51.49	2.04	0.071	10	10
Kashmir, India	104.77 ± 33.86	3.09	0.003	74	5
New South Wales, Australia	58.48 ± 20.24	2.89	0.005	73	10
Tenerife, Spain	51.86 ± 33.2	1.56	0.124	57	10
Oregon, USA	50.88 ± 27.04	1.88	0.066	47	5
Norway	42.15 ± 15.63	2.7	0.031	8	5
Central Chile	36.52 ± 29.01	1.26	0.217	32	10
Victoria, Australia	27.94 ± 12.45	2.25	0.028	76	5
South Chile	11.83 ± 23.18	0.51	0.611	70	10
Montana, USA	-29.35 ± 26.32	-1.12	0.274	31	10
Hawaii, USA	-137.52 ± 34.15	-4.03	< 0.001	108	5

722

723 **Table S2.** Average annual shifts in upper elevation limits in each region. Estimates
 724 (expressed as m of elevation per year) are taken from intercept-only linear models fitted to
 725 observed shifts in unstandardized upper elevation limits of species in each region separately
 726 and weighted by species' frequency of occurrence. Regions are ordered according to effect
 727 size. Significant p-values are marked in bold.
 728

	Estimate ± standard error	t-value	<i>p</i>	N	Sampling period (years)
Kashmir, India	20.96 ± 6.77	3.09	0.003	74	5
Switzerland	10.52 ± 5.15	2.04	0.071	10	10
Oregon, USA	10.18 ± 5.41	1.88	0.066	47	5
Norway	8.43 ± 3.13	2.7	0.031	8	5
New South Wales, Australia	5.85 ± 2.02	2.89	0.005	73	10
Victoria, Australia	5.59 ± 2.49	2.25	0.028	76	5
Tenerife, Spain	5.19 ± 3.32	1.56	0.124	57	10
Central Chile	3.65 ± 2.9	1.26	0.217	32	10
South Chile	1.18 ± 2.32	0.51	0.611	70	10
Montana, USA	-2.94 ± 2.63	-1.12	0.274	31	10
Hawaii, USA	-27.5 ± 6.83	-4.03	< 0.001	108	5

729

730 **Table S3.** Average shifts in upper elevation limits between the first and last survey in each region based on three additional filters for excluding
731 less common species (standard filter >1 occurrence per species and region over all years). Filters used are >5 and >10 occurrences per
732 species and region over all years and >10 occurrences per species, region and year. Estimates (expressed as m of elevation across the
733 sampling period) are taken from intercept-only linear models fitted to observed shifts in unstandardized upper elevation limits of species in each
734 region separately and weighted by species' frequency of occurrence. P-values of significant range shifts are marked in bold. Models were not
735 fitted for regions with fewer than 5 species after filtering.
736

	>5 occurrences/ region over all years			>10 occurrences/ region over all years			>10 occurrences/ region and year		
	Estimate ± standard error	<i>p</i>	N	Estimate ± standard error	<i>p</i>	N	Estimate ± standard error	<i>p</i>	N
New South Wales, Australia	60.24 ± 21	0.006	66	59.7 ± 23.56	0.014	52	74.96 ± 19.33	0.001	24
Victoria, Australia	29.32 ± 11.75	0.016	55	28.29 ± 11.57	0.018	48	31.73 ± 12.02	0.013	33
Switzerland	103.24 ± 54.62	0.095	9	109.16 ± 58.48	0.104	8			2
Central Chile	40.64 ± 28.65	0.167	28	56.96 ± 34.14	0.116	16			4
South Chile	7.51 ± 22.74	0.742	58	7.72 ± 23.21	0.741	50	-3.85 ± 21.92	0.862	24
Tenerife, Spain	49.64 ± 38.64	0.206	40	15.86 ± 39.24	0.69	23	104.25 ± 49.53	0.089	6
Hawaii, USA	-150.63 ± 41.21	0.001	66	-175.72 ± 53.29	0.002	40	-172.75 ± 60.11	0.018	10
Kashmir, India	111.05 ± 43.48	0.014	47	149.29 ± 49.35	0.005	29	184.44 ± 60.44	0.009	15
Montana, USA	-27.64 ± 27.33	0.321	28	-29.93 ± 30.17	0.332	23	-59.28 ± 38.48	0.174	7
Norway	44.37 ± 20.68	0.098	5			3			1
Oregon, USA	48.94 ± 28.22	0.091	40	48.38 ± 28.9	0.103	36	40.91 ± 37.89	0.292	22

737

738 **Table S4.** Characteristics of the eleven regions of the survey, including: coordinates (latitude
739 and longitude in decimal degrees), the climatic context (Med, Mediterranean; Temp,
740 Temperate; Subtrop, Subtropical), number of roads included in the analysis (and total
741 number of sampling locations [“transects”] per region), the elevational range (and the
742 average distance \pm standard deviation between all transects of a region combined), the total
743 number of non-native species in the complete data set over all sampling years (after
744 discarding species not determined to the species level and species occurring less than twice
745 per region over all years), and the years in which regions were surveyed. All regions were
746 surveyed at 5-year intervals, except Tenerife (10 year interval).

747

	Geolocation (units)	Climate	Roads (transects)	Elevational range (m) (\bar{x} distance between transects)	Species richness	Sampling years
New South Wales, Australia	-35.984, 148.402	Med	3(60)	410–2125 (32.36 \pm 20.01)	141	2007, 2012, 2017
Victoria, Australia	-37.142, 147.105	Med	5(99)	205–1848 (17.29 \pm 15.7)	114	2012, 2017
Switzerland	46.262, 7.54	Temp	3(63)	415–1800 (26.15 \pm 18.76)	33	2007, 2012, 2017
Central Chile	-33.349, -70.299	Med	2(31)	1900–3585 (67.4 \pm 48.37)	50	2007, 2012, 2017
South Chile	-37.516, -71.61	Temp	3(60)	277–1664 (23.43 \pm 17.62)	113	2007, 2012, 2017
Tenerife, Spain	28.241, -16.563	Semiarid	3(56)	13–2310 (50.79 \pm 35.84)	89	2008, 2018
Hawaii, USA	20.046, -155.699	Tropical	4(74)	212–4180 (53.68 \pm 57.41)	235	2007, 2012
Kashmir, India	33.68, 74.888	Subtrop	3(28)	1590–3644 (75.9 \pm 56.74)	114	2012, 2017
Montana, USA	44.795, -110.188	Temp	3(60)	1807–3311 (25.43 \pm 27.61)	46	2007, 2012, 2017
Norway	68.263, 17.633	Subarctic	3(60)	14–692 (17.19 \pm 19.22)	14	2012, 2017
Oregon, USA	45.273, -117.625	Temp	3(60)	902–2264 (23.9 \pm 17.76)	103	2007, 2012

748

749 **Table S5.** Estimated mean shifts in upper elevation limits between the first and last survey when evaluated at the median elevation within a
750 given region. These estimates of shifts correct for elevation by including species' initial elevation during the first survey time point as a predictor
751 in a linear model (see Methods). Results show three additional filters as exclusion criteria for less common species (in comparison to the
752 standard filter of >1 occurrence per species and region over all years; Fig. 3). Filters used are >5 and >10 occurrences per species and region
753 over all years and >10 occurrences per species, region and year. Mean range shifts >0 indicate that average shifts are upslope across most of
754 the elevational gradient, and mean range shifts at the median of the elevational gradient are considered significant when 0 lies outside of the
755 95% confidence interval (marked in bold). Models were not fitted in regions with fewer than 5 species after filtering.
756

	>5 occurrences/ region over all years			>10 occurrences/ region over all years			>10 occurrences/ region and year		
	Predicted Range Shift	CI(95%)	N	Predicted Range Shift	CI(95%)	N	Predicted Range Shift	CI(95%)	N
New South Wales, Australia	91.4	(36.12; 146.67)	66	90.91	(27.1; 154.72)	52	70.62	(29.98; 111.25)	24
Victoria, Australia	77.59	(38.06; 117.13)	55	55.3	(23.18; 87.42)	48	74.54	(40.4; 108.68)	33
Switzerland	126.91	(3.83; 250)	9	136.44	(-6.17; 279.06)	8			2
Central Chile	40.5	(-20.99; 101.99)	28	58.52	(-19.69; 136.74)	16			4
South Chile	93.85	(16.79; 170.9)	58	99.41	(19.21; 179.61)	50	-2.61	(-66.32; 61.11)	24
Tenerife, Spain	38.52	(-37.57; 114.61)	40	11.51	(-71.2; 94.21)	23	110.67	(-29.61; 250.95)	6
Hawaii, USA	-113.29	(-200.81; -25.77)	66	-145	(-259.92; -30.08)	40	-131.76	(-276.41; 12.88)	10
Kashmir, India	143.8	(50.79; 236.81)	47	216.9	(105.09; 328.7)	29	170.53	(50.04; 291.01)	15
Montana, USA	-5.16	(-52.7; 42.38)	28	-4.18	(-57.9; 49.53)	23	-67.49	(-167.58; 32.6)	7
Norway	43.13	(-36.09; 122.36)	5			3			1
Oregon, USA	98.33	(23.84; 172.83)	40	69.59	(8.03; 131.15)	36	50.97	(-27.45; 129.39)	22

757

758 **Table S6.** Relationships between species' upper elevational limit in the first survey and the
759 change in upper elevation limit in the second survey, fitted for each region separately.
760 Regressions were weighted by species' frequency of occurrence. Significant p-values are
761 marked in bold.

762

	Intercept ± standard error	Slope ± standard error	F	df	p
New South Wales, Australia	241.87 ± 114.76	-0.128 ± 0.079	2.63	71	0.109
Victoria, Australia	241.21 ± 62.48	-0.153 ± 0.044	12.07	74	0.001
Switzerland	358.04 ± 151.34	-0.203 ± 0.116	3.08	8	0.117
Central Chile	58.29 ± 189.23	-0.008 ± 0.066	0.01	30	0.908
South Chile	364.5 ± 108.94	-0.28 ± 0.085	10.91	68	0.002
Tenerife, Spain	251.19 ± 91.08	-0.187 ± 0.08	5.46	55	0.023
Hawaii, USA	127.36 ± 97.49	-0.127 ± 0.044	8.34	106	0.005
Kashmir, India	408.51 ± 238.95	-0.108 ± 0.084	1.65	72	0.203
Montana, USA	842.42 ± 230.87	-0.34 ± 0.09	14.39	29	0.001
Norway	35.03 ± 47.63	0.021 ± 0.133	0.03	6	0.878
Oregon, USA	443.25 ± 184.89	-0.238 ± 0.111	4.6	45	0.038

763

764

765 **Table S7.** Relationships between species' upper elevational limit in the first survey and the
766 change in upper elevation limit in the second survey, fitted for each region separately. In
767 contrast to Table S7, regressions were not weighted by species' frequency of occurrence.
768 Significant p-values are marked in bold.

769

	Intercept ± standard error	Slope ± standard error	F	df	p
New South Wales, Australia	250.13 ± 124.66	-0.177 ± 0.094	3.53	71	0.064
Victoria, Australia	337.65 ± 75.49	-0.257 ± 0.06	18.6	74	< 0.001
Switzerland	374.03 ± 130.58	-0.222 ± 0.11	4.06	8	0.079
Central Chile	259.89 ± 273.92	-0.101 ± 0.105	0.92	30	0.345
South Chile	495.12 ± 121.97	-0.432 ± 0.111	15.2	68	< 0.001
Tenerife, Spain	268.27 ± 98.01	-0.206 ± 0.091	5.08	55	0.028
Hawaii, USA	145.79 ± 87.75	-0.143 ± 0.05	8.27	106	0.005
Kashmir, India	198.72 ± 191.53	-0.06 ± 0.074	0.66	72	0.419
Montana, USA	1256.23 ± 351.27	-0.516 ± 0.144	12.76	29	0.001
Norway	24.36 ± 38.52	0.064 ± 0.119	0.29	6	0.608
Oregon, USA	416.23 ± 173	-0.234 ± 0.115	4.18	45	0.047

770

771 **Table S8.** Average yearly temperature change for all regions. Using CHELSA cruts monthly
 772 minimum and maximum temperature data between 2000 and 2016^{1,2} downloaded for all
 773 sampling points included in the study, we fitted linear models of average annual temperature
 774 over time separately for all regions, resulting in an estimated yearly temperature change.
 775 Based on the average yearly temperature change, a total change between 2000 and 2016
 776 was calculated. Significant temperature changes are marked in bold.

777

	Estimate ± standard error	Temperature increase over 17 years	<i>p</i>	<i>N</i>
New South Wales, Australia	0.03 ± 0.02	0.45	0.146	17
Victoria, Australia	0.03 ± 0.01	0.54	0.05	17
Switzerland	0.03 ± 0.02	0.44	0.31	17
Central Chile	0.04 ± 0.02	0.63	0.061	17
South Chile	0.04 ± 0.02	0.62	0.05	17
Tenerife, Spain	0.02 ± 0.01	0.3	0.224	17
Hawaii, USA	0.02 ± 0.02	0.41	0.183	17
Kashmir, India	-0.01 ± 0.02	-0.09	0.765	17
Montana, USA	0.03 ± 0.03	0.54	0.367	17
Norway	0.03 ± 0.03	0.44	0.447	17
Oregon, USA	0.05 ± 0.03	0.89	0.077	17

778

779 **Table S9.** Linear model results of the effect of plot type (disturbed plots alongside the road
780 vs. semi-natural plots away from the road) on range shifts (elevation \pm standard error), fitted
781 separately for all regions with enough occurrence points (>1 per region over all years for
782 both plot types) in both road and semi-natural plots and weighted by species' frequency of
783 occurrence. Significant differences between plot types are marked in bold (only South Chile).
784 Across all regions combined, fitting a LMM of range limit changes on plot type (region
785 included as a random factor, regression weighted by species' frequency of occurrence) and
786 comparing it to an intercept only model with a likelihood ratio test revealed no significant
787 effect of plot type ($\chi^2= 1.989$, $p < 0.159$).
788

	Semi-natural plot \pm standard error	Effect roadplot \pm standard error	F	df	p
New South Wales, Australia	90.76 \pm 53.83	-25.15 \pm 57.87	0.19	93	0.665
Switzerland	-54.36 \pm 91.14	162.19 \pm 105.82	2.35	14	0.148
Central Chile	29.07 \pm 34.93	6.86 \pm 49.95	0.02	46	0.891
South Chile	-31.28 \pm 26.38	85.34 \pm 36.19	5.56	116	0.02
Tenerife, Spain	-17.9 \pm 43.36	89.59 \pm 54.38	2.71	84	0.103
Kashmir, India	106.55 \pm 40.19	-8.64 \pm 58.52	0.02	122	0.883
Montana, USA	-21.95 \pm 42.64	-0.43 \pm 51.85	0	48	0.993
Oregon, USA	57.19 \pm 34.82	-6.03 \pm 44.52	0.02	81	0.893

789

790 **Table S10.** Proportions of fitted values that fall above or below the 95% confidence interval
791 for the expected null relationship between initial upper elevation limit and change in upper
792 elevation limit after accounting for the geometric constraint (see Fig. 1; the calculations are
793 based on the original null model used for Fig. 4, see Methods). The deviations from null
794 expectations of shifts were determined for both five-year intervals for all regions surveyed for
795 a total of 10 years. Non-zero values suggest a significant deviation from the null expectation.
796 Trends for New South Wales and Montana in years 0 to 5 are identical to Figure 4, whereas
797 values deviating from the 95% confidence interval of the null relationship in South Chile were
798 mainly falling above the confidence interval in the middle of the gradient and not in the lower
799 part of the gradient as in Figure 4. Trends in New South Wales, Central Chile, South Chile and
800 Montana in years 5 to 10 are identical to Figure 4.

801

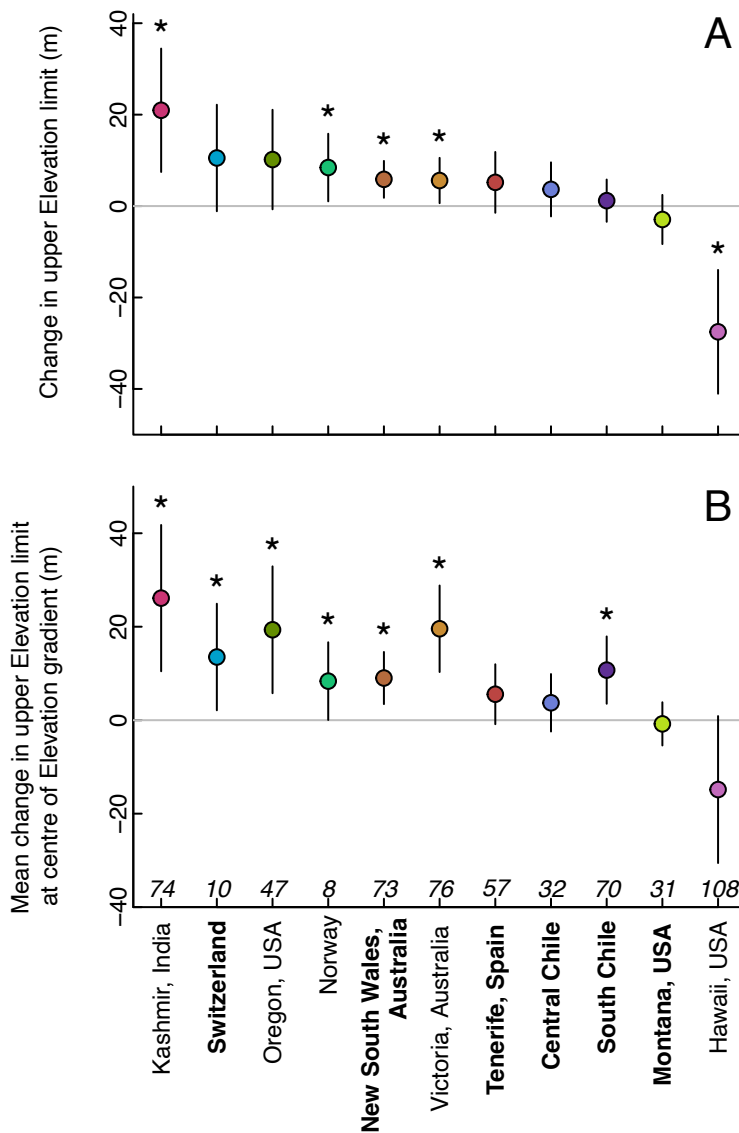
	Proportion of fitted values falling outside of 95% confidence interval	
	Years 0 to 5	Years 5 to 10
New South Wales, Australia	0.633	0.54
Switzerland	0	0
Central Chile	0	0.789
South Chile	0.174	0.73
Montana, USA	0.59	0.649

802

803 **Supplementary Methods: Regression Toward the Mean**

804

805 Regression toward the mean (RTM) occurs whenever there is a non-perfect correlation
 806 between measurements of observational units over time and was first described by Sir
 807 Francis Galton³. Galton observed that unusually large or small values on average tend to be
 808 followed by measurements closer to the mean. This results in a negative correlation between
 809 the change in measurements over time and their initial state. While RTM is widely discussed
 810 in other fields, such as medicine and psychology^{4,5}, there has been reported to be less
 811 awareness of this phenomenon in ecology⁶ (but see ref. ⁷). In order to correct for RTM,
 812 Mazalla⁶ proposes to always include initial measurements in analyses on temporal change.
 813 In our study, the geometric constraint of a finite environmental gradient adds another layer of

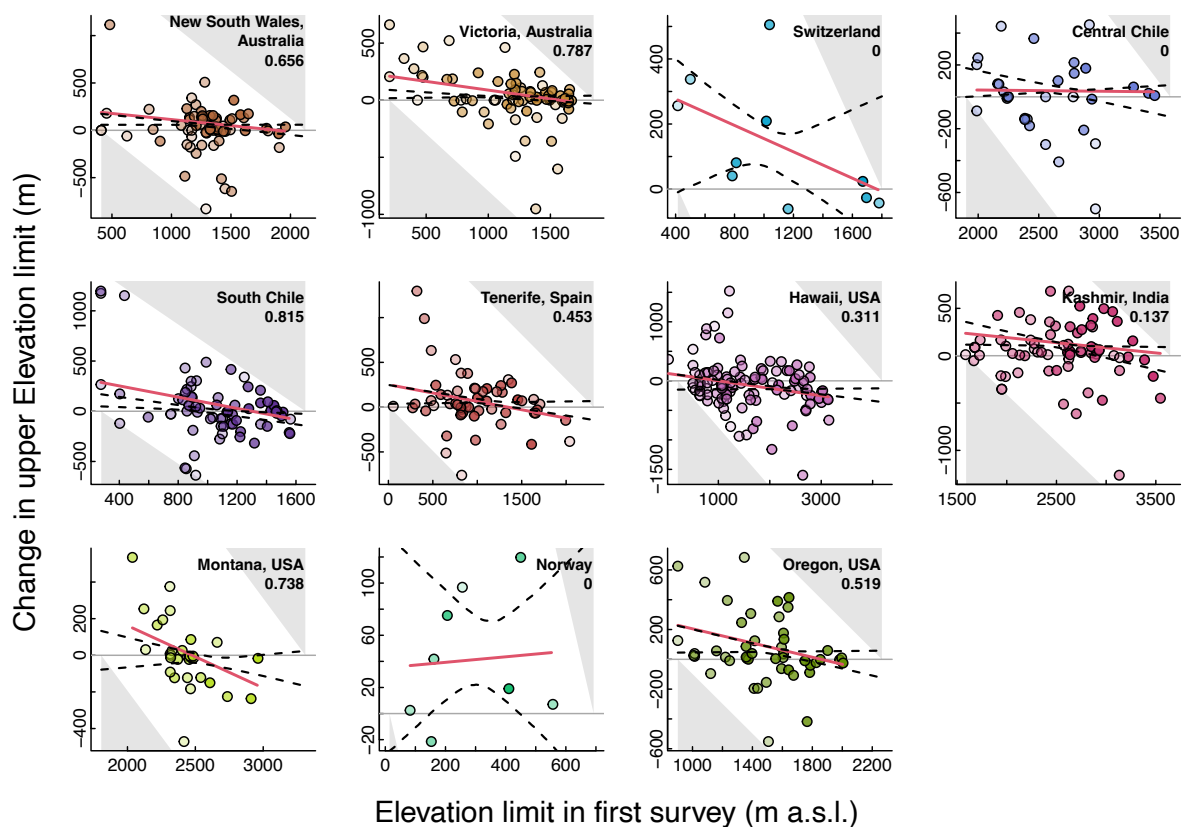


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815

816 **Fig. S1. Observed annual changes in species' upper elevational limits ($\pm 95\%$**
 817 **confidence intervals).** Both panels show mean annual shifts, estimated from linear models

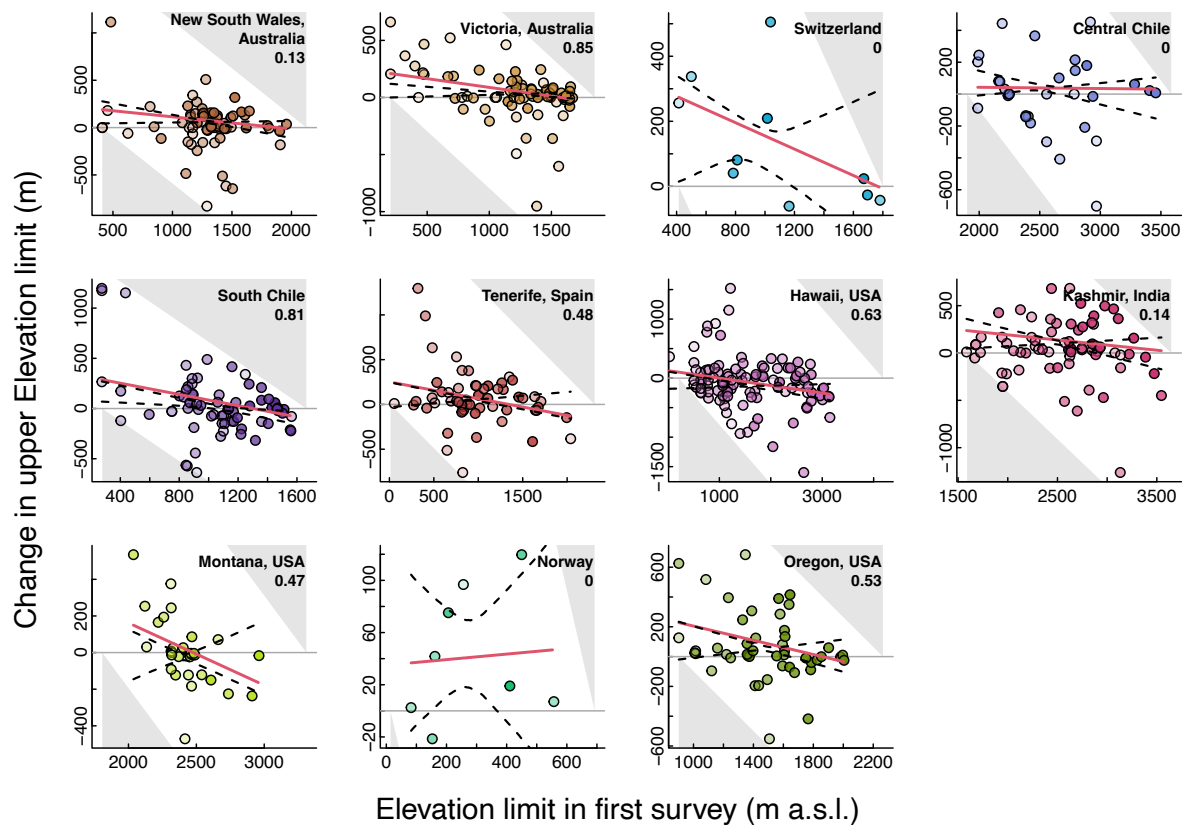
818 that weight species by their total frequency of occurrence in both years and are fitted to data
 819 from each region separately. Panel A shows results of intercept-only models (i.e. grand
 820 mean shifts per region), while panel B shows results of models that correct for elevation by
 821 including species' initial elevation limit during the first survey as a linear predictor.
 822 Specifically, estimates in B correspond to the predicted mean shift in elevation limits when
 823 evaluated at the median elevation within a given region; values >0 therefore indicate that
 824 average shifts are upslope across most of the elevational gradient (cf. Fig. 4). Regions are
 825 ordered by effect size in panel A, with labels in regular and bold typeface indicating regions
 826 with 5- or 10-year survey intervals, respectively. Estimates that differ significantly from zero
 827 are indicated by *. Numbers in italics describe the sample size.



829
 830

831 **Fig. S2. Null-model tests of elevation-dependent shifts in upper elevation limit of non-**
 832 **native plants in 11 mountain regions.** Each point shows the change in upper elevation
 833 limit (90th quantile of elevational distribution) of a single species, as a function of its limit in
 834 the first survey (darker shading corresponds to greater total log[frequency of occurrence] of
 835 a species in both surveys). Dashed lines are 95% confidence intervals for the expected null
 836 relationship between initial upper elevation limit and change in upper elevation limit after
 837 accounting for geometric constraints. This plot differs from Fig. 4 in the vector of new initial

838 elevations used for bootstrapping, which in this case split the surveyed elevational gradient
839 into 200 equidistant elevational bins (see Methods). For further explanation about the plot,
840 see Fig. 4.



841
842

843 **Fig. S3. Null-model tests of elevation-dependent shifts in upper elevation limit of non-**
 844 **native plants in 11 mountain regions.** Each point shows the change in upper elevation
 845 limit (90th quantile of elevational distribution) of a single species, as a function of its limit in
 846 the first survey (darker shading corresponds to greater total log[frequency of occurrence] of
 847 a species in both surveys). Dashed lines are 95% confidence intervals for the expected null
 848 relationship between initial upper elevation limit and change in upper elevation limit after
 849 accounting for geometric constraints. This plot differs from Fig. 4 in the vector of new initial
 850 elevations used for bootstrapping, which in this case only sampled from within the vector of
 851 observed initial elevation limits (i.e. with length equal to the number of recorded species; see
 852 Methods). For further explanation about the plot, see Fig. 4.
 853

854 **Supplementary References**

855

856

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