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### ► To cite this version:

Evelin Iseli, Chelsea Chisholm, Jonathan Lenoir, Sylvia Haider, Tim Seipel, et al.. Rapid upwards spread of non-native plants in mountains across continents. *Nature Ecology & Evolution*, 2023, 10.1038/s41559-022-01979-6 . hal-03969878

**HAL Id: hal-03969878**

**<https://u-picardie.hal.science/hal-03969878>**

Submitted on 26 Oct 2023

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

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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 rates<sup>1-5</sup>. These  
75 redistributions are particularly visible in mountain ecosystems, where species can cross  
76 large environmental gradients across relatively short distances<sup>6,7</sup>. While many native species  
77 are on the move in mountains in response to changing climate<sup>8-10</sup>, mountain ecosystems  
78 have so far experienced comparatively few invasions by non-native species<sup>11,12</sup>. 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<sup>11,13-16</sup>. However, this situation  
81 is changing with climate warming and increasing human pressures at high elevation<sup>11,15,17</sup>.  
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<sup>14,18,19</sup>, and within individual regions, non-native plants are expanding their  
85 ranges upward faster than native species<sup>15,20</sup>.

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 Europe<sup>21</sup>) or  
92 upward range expansions over several decades to a century (in Europe<sup>15</sup>, Hawaii<sup>22</sup> and  
93 California<sup>20</sup>). 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 niche<sup>13</sup>. As a result,  
99 species that have been introduced for a longer period tend to reach progressively higher  
100 elevations<sup>23-25</sup>. 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 elevation<sup>20</sup>. 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<sup>15,26</sup>; (ii) changes  
109 in climatic water balance or biotic interactions driving downward migrations at higher

110 elevation<sup>27,28</sup>; (iii) longer growing seasons and correspondingly greater opportunities for  
111 dispersal and spread at lower elevation<sup>29</sup>; (iv) broader environmental tolerances of high-  
112 elevation species, necessitating smaller absolute range shifts to track changing climate<sup>10</sup>;  
113 and (v) greater microsite variation at high elevation, buffering the need for range shifts<sup>7,30</sup>.

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 <sup>31,32</sup>, 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 literature<sup>33</sup>. 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 <sup>10,29</sup>). However, the geometric constraint on the magnitude  
136 and direction of observable range shifts (cf. refs <sup>33,34</sup>) 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<sup>27,33,35</sup>. 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<sup>10,35</sup>.

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.org](http://www.mountaininvasions.org)<sup>36</sup>) 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  $0.07 \pm 0.04$  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 limits<sup>24</sup>. 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<sup>10,15,26,28,29,37</sup>.  
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 ecologically<sup>35</sup>. 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<sup>13,15</sup>. 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 introductions<sup>24</sup>, while time since introduction of non-native plant species in Central Europe is  
286 positively related to their maximum elevation<sup>23</sup>, elevation range<sup>25</sup> and to the magnitude of  
287 upward range shifts<sup>15</sup>. 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 elevation<sup>29</sup>. 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 sites<sup>38</sup>, 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<sup>21,39</sup>). 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<sup>21,27</sup>. 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 decade<sup>40</sup>, 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<sup>11,16</sup>, but this might change with increasing anthropogenic disturbance and changing  
337 climate. Roadside surveys like ours<sup>36</sup> 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<sup>15,16,29,41,42</sup>, 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<sup>16,43</sup>. 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 available<sup>2</sup>, 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 gradients<sup>35</sup>.  
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 protocol<sup>36</sup>. 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 road<sup>36</sup>. 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 Online<sup>44</sup> 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 package<sup>45</sup>. 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 90<sup>th</sup>  
409 percentile of all species' occurrences along the elevational gradient. While the 90<sup>th</sup> 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 90<sup>th</sup> 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

## 476 **Acknowledgements**

477 This research was funded through the 2019-2020 BiodivERsA joint call for research proposals,  
478 under the BiodivClim ERA-Net COFUND programme (project "RangeX"), and with the funding

479 organisations Innovation Fund Denmark, Department of Science and Innovation Republic of  
480 South Africa, the Research Council of Norway, the Swiss National Science Foundation, the  
481 Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning and  
482 the German Research Foundation. SH and ARB acknowledge the support of iDiv funded by  
483 the German Research Foundation (DFG – FZT 118, 202548816). ALH was supported by a  
484 NSERC Discovery grant. PK acknowledges funding from the Swedish Research Council  
485 (Vetenskapsrådet) (Grant no. 2015-04214 ) and J.J.L. received funding from the Research  
486 Foundation Flanders (grant nr. 12P1819N). LC acknowledges funding from FONDECYT  
487 1171005 and 1211197, AP from FONDECYT 1180205 and ANID PIA AFB170008. DR  
488 acknowledges funding from the Swiss National Science Foundation, grant number  
489 P500PB\_203241. JMA received funding from the European Union’s Horizon 2020 research  
490 and innovation program (grant no. 678841) and from the Swiss National Science Foundation  
491 (grant no. 20BD21\_193809). We thank the plant ecology group from ETH Zurich for comments  
492 on the manuscript.

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

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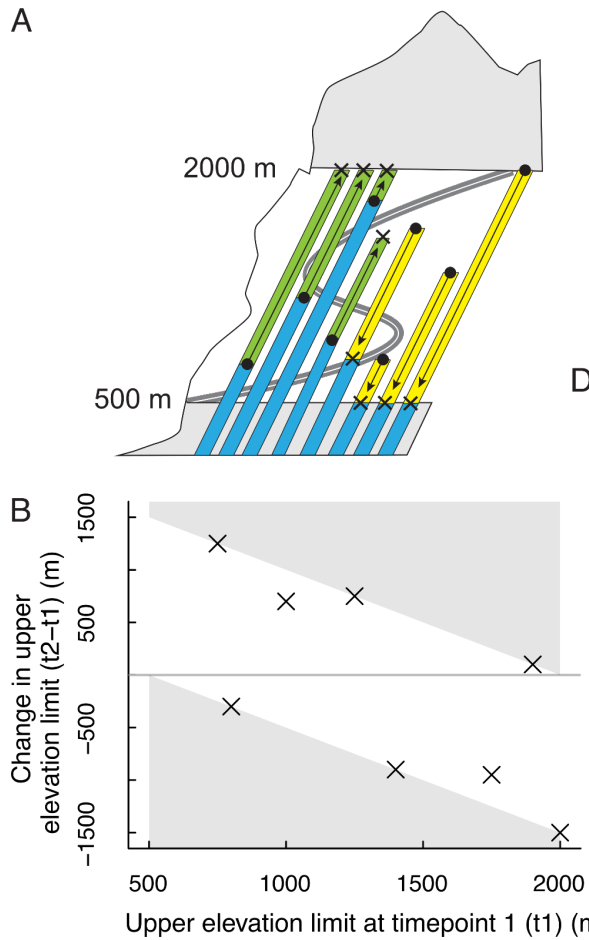
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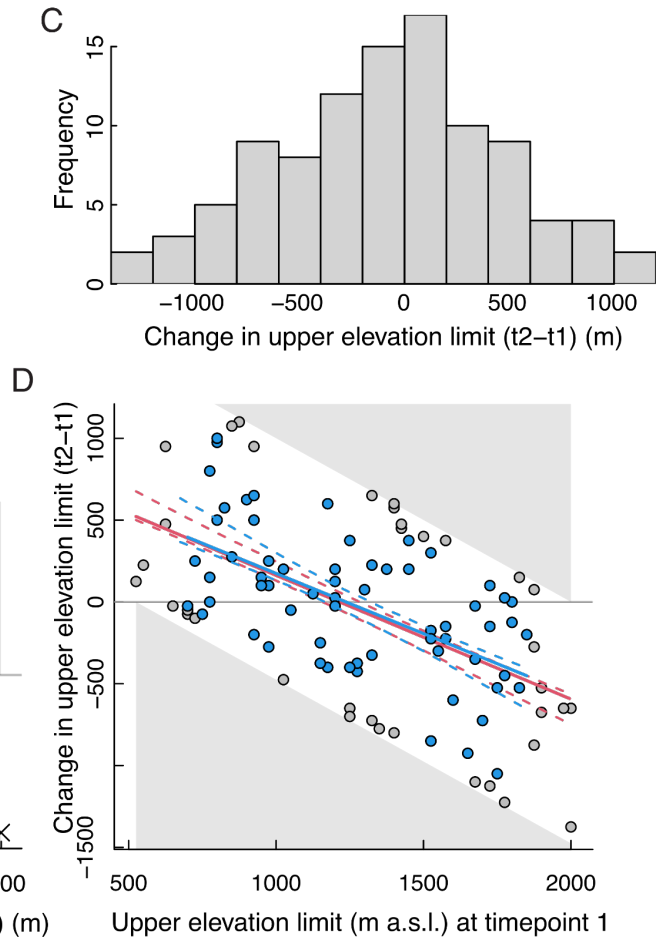
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653

**Possible changes in upper elevation limits**



**Elevation-dependence of randomly generated upper limit shifts**

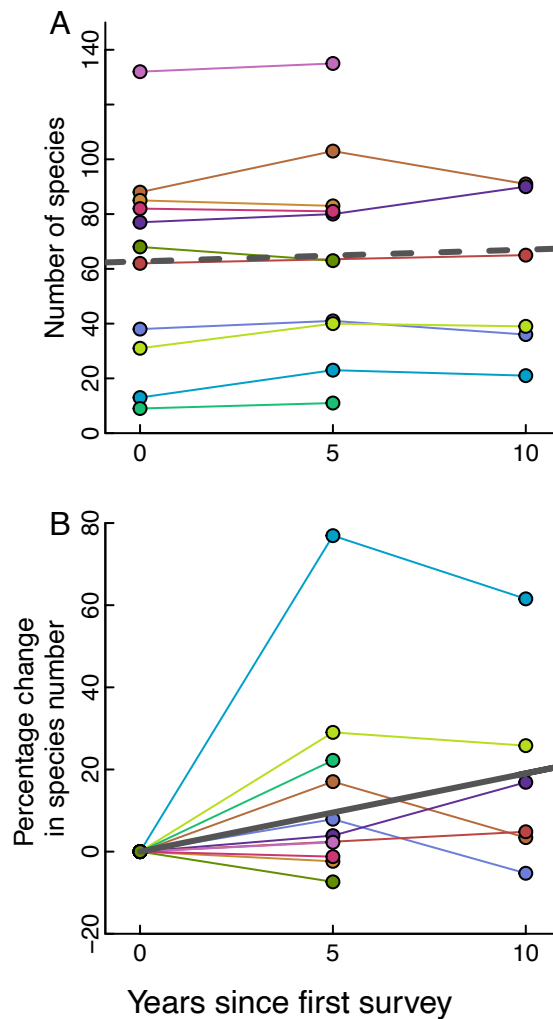


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657 **Figure 1. A null model approach to explaining species' range limit shifts across an**  
 658 **elevational gradient.** (A) Possible changes in observed upper elevation limit for eight  
 659 species (bars) shifting their upper limits upwards (green portions of bars: expansions) or  
 660 downwards (yellow portions of bars: contractions) along an elevational gradient from time  
 661 point 1 (t1; points) to time point 2 (t2; 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 t1. 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

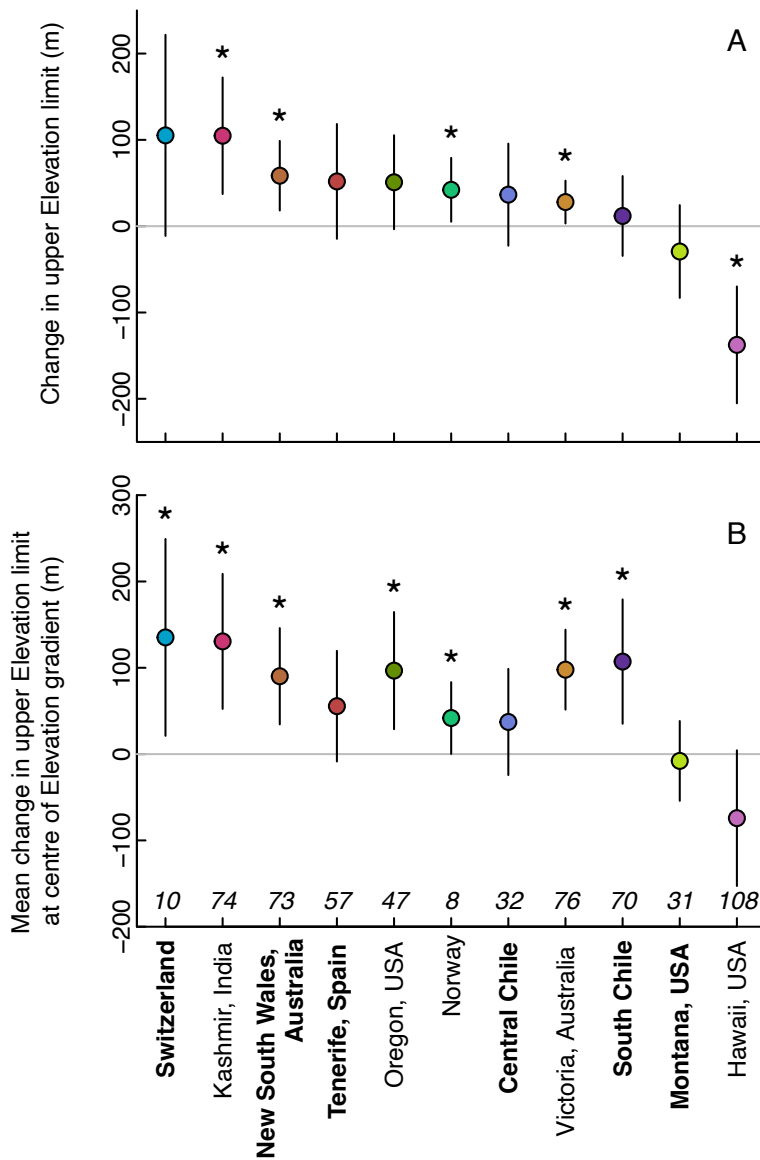
678 intervals calculated as described above, but excluding species falling in the top and bottom



679 10% of the gradient.

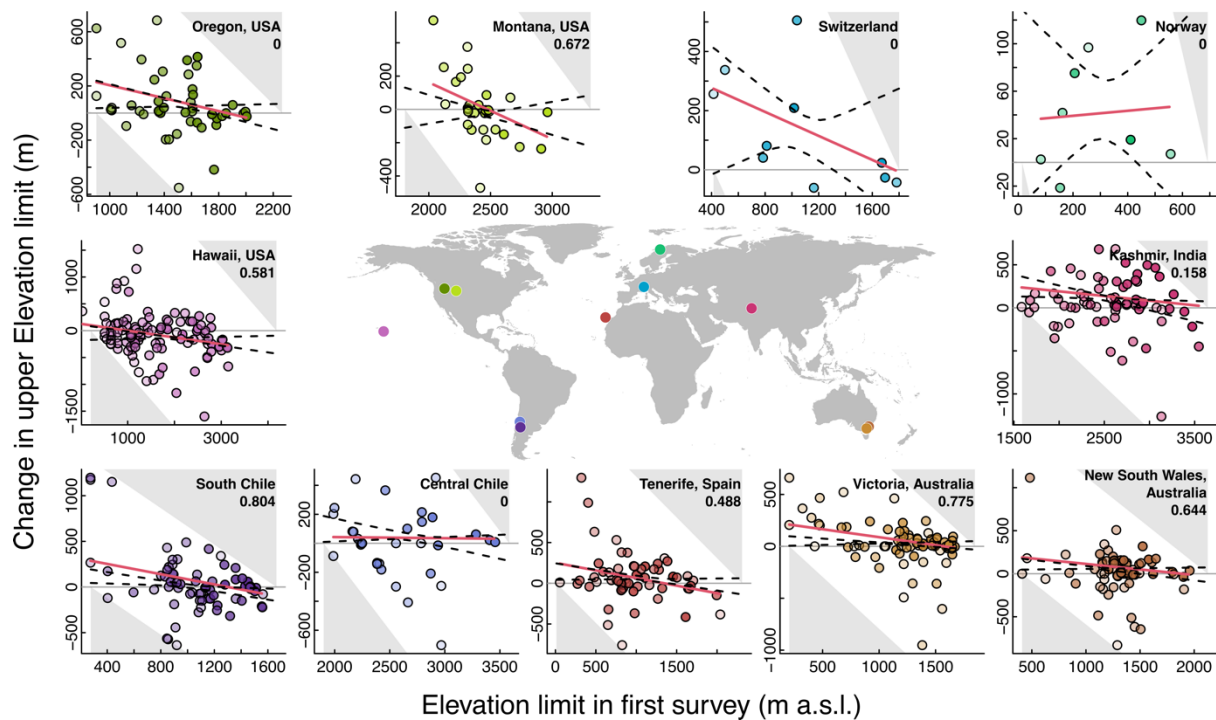
680 **Figure 2. Temporal changes of non-native plant species in 11 mountain regions.** Total  
 681 species richness (A) and percentage change in species richness (B) over the 10-year  
 682 sampling period. Solid and dashed heavy grey lines indicate significant and non-significant  
 683 fits, respectively, 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 (90<sup>th</sup> 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

	<b>Estimate ± standard error</b>	<b>t-value</b>	<b>p</b>	<b>N</b>	<b>Sampling period (years)</b>
Switzerland	105.2 ± 51.49	2.04	0.071	10	10
Kashmir, India	104.77 ± 33.86	3.09	<b>0.003</b>	74	5
New South Wales, Australia	58.48 ± 20.24	2.89	<b>0.005</b>	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	<b>0.031</b>	8	5
Central Chile	36.52 ± 29.01	1.26	0.217	32	10
Victoria, Australia	27.94 ± 12.45	2.25	<b>0.028</b>	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	<b>&lt; 0.001</b>	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	<b>0.003</b>	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	<b>0.031</b>	8	5
New South Wales, Australia	5.85 ± 2.02	2.89	<b>0.005</b>	73	10
Victoria, Australia	5.59 ± 2.49	2.25	<b>0.028</b>	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	<b>&lt; 0.001</b>	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	<b>0.006</b>	66	59.7 ± 23.56	<b>0.014</b>	52	74.96 ± 19.33	<b>0.001</b>	24
Victoria, Australia	29.32 ± 11.75	<b>0.016</b>	55	28.29 ± 11.57	<b>0.018</b>	48	31.73 ± 12.02	<b>0.013</b>	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	<b>0.001</b>	66	-175.72 ± 53.29	<b>0.002</b>	40	-172.75 ± 60.11	<b>0.018</b>	10
Kashmir, India	111.05 ± 43.48	<b>0.014</b>	47	149.29 ± 49.35	<b>0.005</b>	29	184.44 ± 60.44	<b>0.009</b>	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

	<b>Geolocation (units)</b>	<b>Climate</b>	<b>Roads (transects)</b>	<b>Elevational range (m) (<math>\bar{x}</math> distance between transects)</b>	<b>Species richness</b>	<b>Sampling years</b>
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	<b>(36.12; 146.67)</b>	66	90.91	<b>(27.1; 154.72)</b>	52	70.62	<b>(29.98; 111.25)</b>	24
Victoria, Australia	77.59	<b>(38.06; 117.13)</b>	55	55.3	<b>(23.18; 87.42)</b>	48	74.54	<b>(40.4; 108.68)</b>	33
Switzerland	126.91	<b>(3.83; 250)</b>	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	<b>(16.79; 170.9)</b>	58	99.41	<b>(19.21; 179.61)</b>	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	<b>(-200.81; -25.77)</b>	66	-145	<b>(-259.92; -30.08)</b>	40	-131.76	(-276.41; 12.88)	10
Kashmir, India	143.8	<b>(50.79; 236.81)</b>	47	216.9	<b>(105.09; 328.7)</b>	29	170.53	<b>(50.04; 291.01)</b>	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	<b>(23.84; 172.83)</b>	40	69.59	<b>(8.03; 131.15)</b>	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

	<b>Intercept ± standard error</b>	<b>Slope ± standard error</b>	<b>F</b>	<b>df</b>	<b>p</b>
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	<b>0.001</b>
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	<b>0.002</b>
Tenerife, Spain	251.19 ± 91.08	-0.187 ± 0.08	5.46	55	<b>0.023</b>
Hawaii, USA	127.36 ± 97.49	-0.127 ± 0.044	8.34	106	<b>0.005</b>
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	<b>0.001</b>
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	<b>0.038</b>

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

	<b>Intercept ± standard error</b>	<b>Slope ± standard error</b>	<b>F</b>	<b>df</b>	<b>p</b>
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	<b>&lt; 0.001</b>
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	<b>&lt; 0.001</b>
Tenerife, Spain	268.27 ± 98.01	-0.206 ± 0.091	5.08	55	<b>0.028</b>
Hawaii, USA	145.79 ± 87.75	-0.143 ± 0.05	8.27	106	<b>0.005</b>
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	<b>0.001</b>
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	<b>0.047</b>

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<sup>1,2</sup> 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

	<b>Estimate ± standard error</b>	<b>Temperature increase over 17 years</b>	<b><i>p</i></b>	<b><i>N</i></b>
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

	<b>Semi-natural plot <math>\pm</math> standard error</b>	<b>Effect roadplot <math>\pm</math> standard error</b>	<b>F</b>	<b>df</b>	<b>p</b>
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	<b>0.02</b>
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

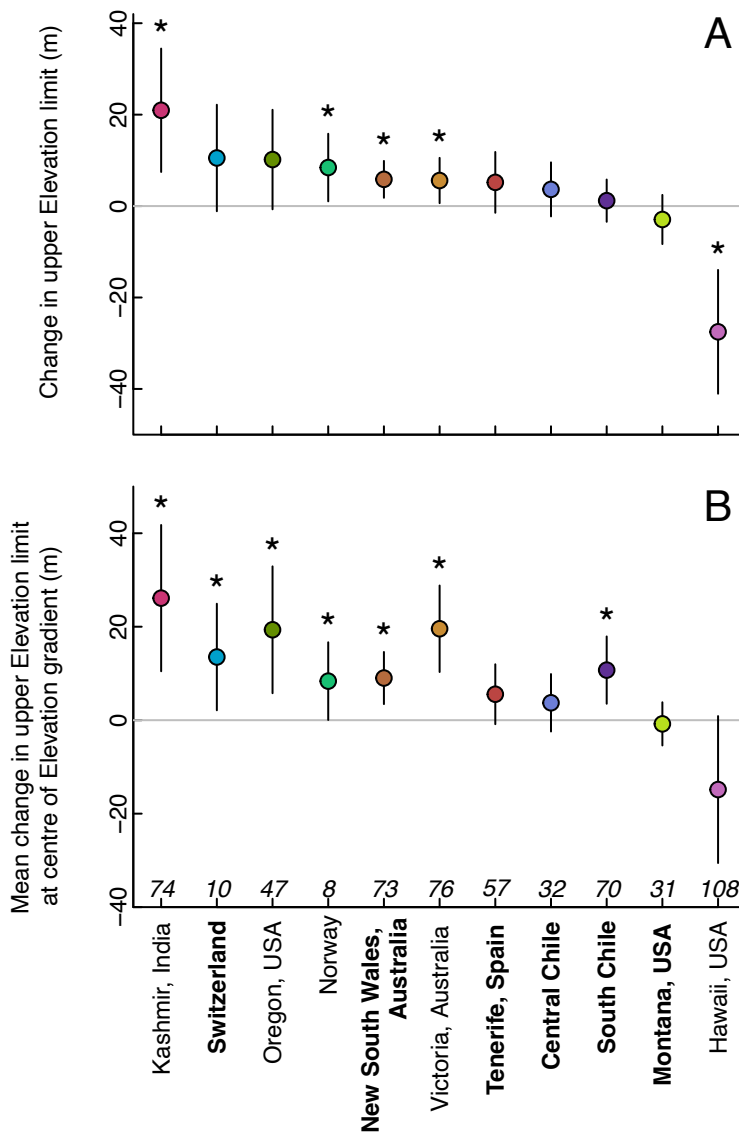
	<b>Proportion of fitted values falling outside of 95% confidence interval</b>	
	<b>Years 0 to 5</b>	<b>Years 5 to 10</b>
New South Wales, Australia	0.633	0.54
Switzerland	0	0
Central Chile	0	0.789
South Chile	0.174	0.73
Montana, USA	0.59	0.649

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 Galton<sup>3</sup>. 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<sup>4,5</sup>, there has been reported to be less  
 811 awareness of this phenomenon in ecology<sup>6</sup> (but see ref. <sup>7</sup>). In order to correct for RTM,  
 812 Mazalla<sup>6</sup> 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

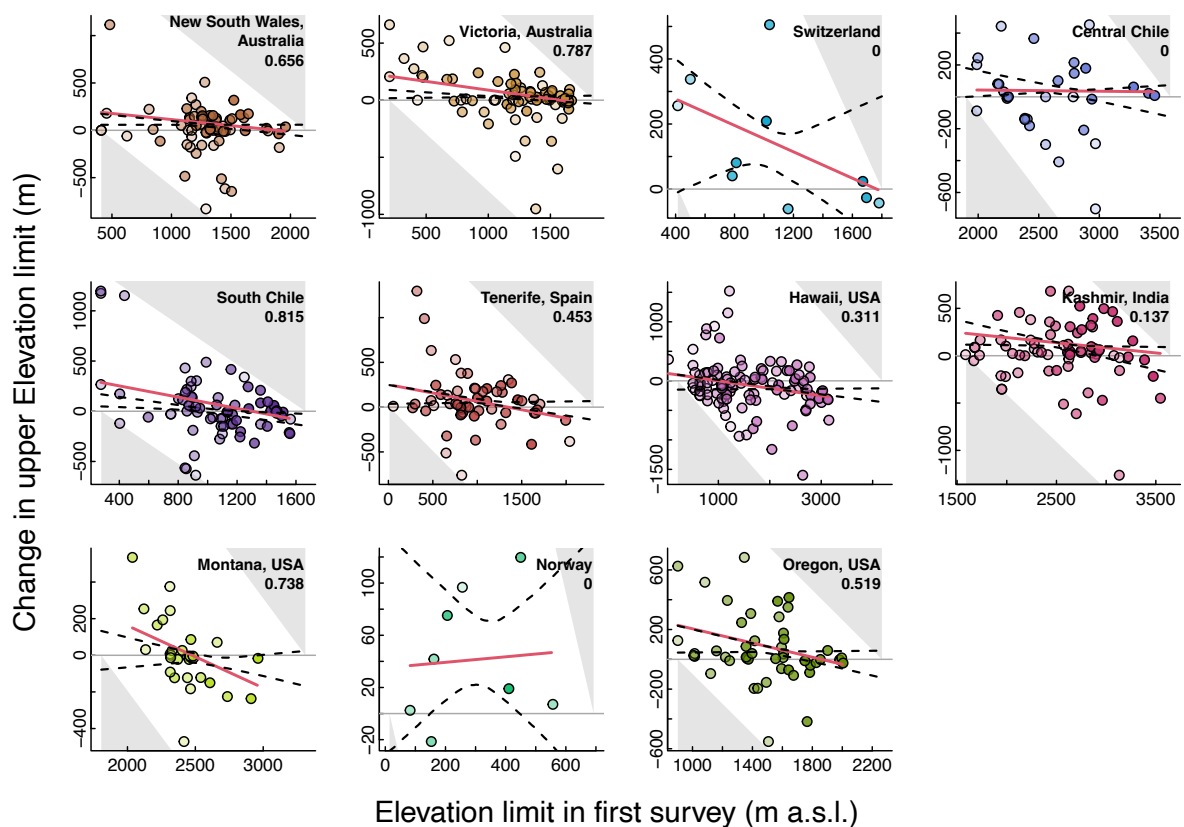


814

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

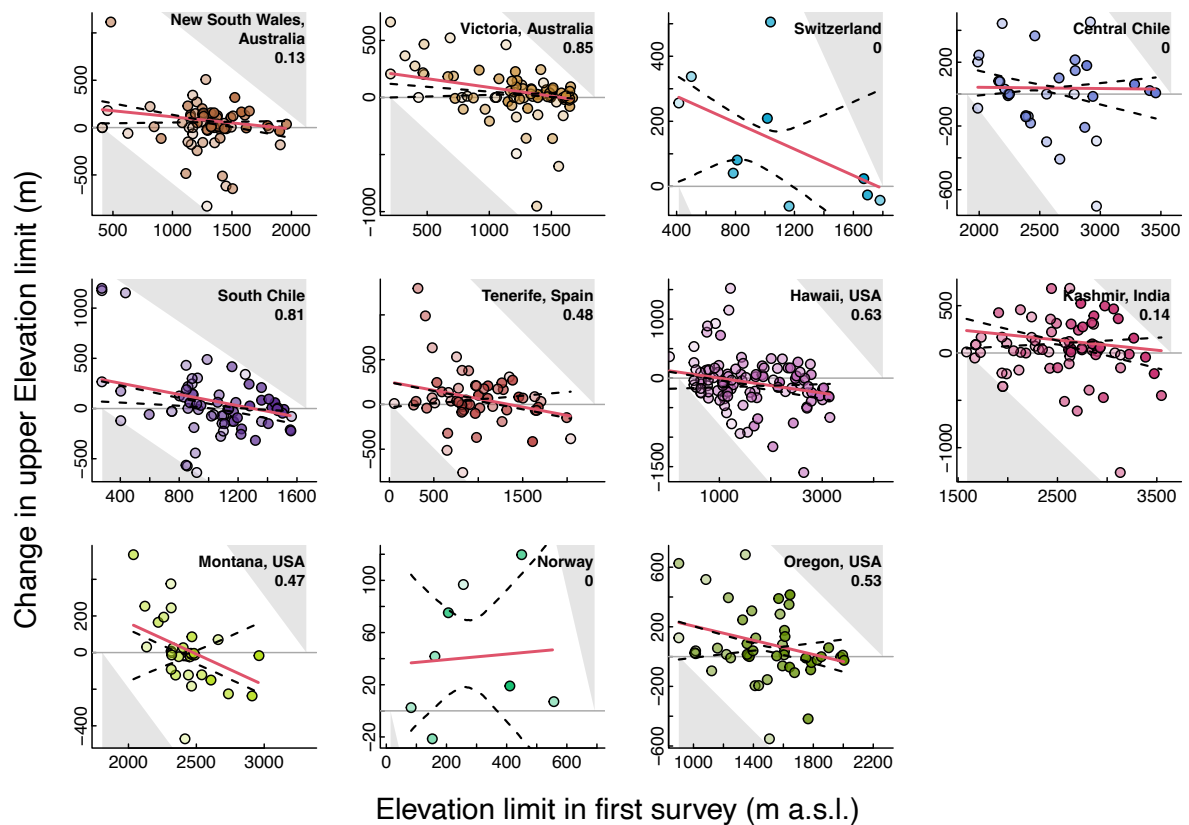
818 that weight species by their total frequency of occurrence in both years and are fitted to data  
 819 from each region separately. Panel A shows results of intercept-only models (i.e. grand  
 820 mean shifts per region), while panel B shows results of models that correct for elevation by  
 821 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 (90<sup>th</sup> 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 (90<sup>th</sup> 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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