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

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**Introductory Paragraph (199 words)**

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

**Keywords**

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

## Introduction

Species' distributions are being reshuffled across the globe at unprecedented rates<sup>1-5</sup>. These redistributions are particularly visible in mountain ecosystems, where species can cross large environmental gradients across relatively short distances<sup>6,7</sup>. While many native species are on the move in mountains in response to changing climate<sup>8-10</sup>, mountain ecosystems have so far experienced comparatively few invasions by non-native species<sup>11,12</sup>. Possible reasons for this include less-intense human activity and disturbance at high elevation, or that few non-native species can thrive in high-elevation conditions<sup>11,13-16</sup>. However, this situation is changing with climate warming and increasing human pressures at high elevation<sup>11,15,17</sup>. For instance, road verges in mountain ecosystems are already known to provide more suitable conditions for non-native plants at higher elevations than would be expected without disturbances<sup>14,18,19</sup>, and within individual regions, non-native plants are expanding their ranges upward faster than native species<sup>15,20</sup>.

Understanding how quickly the richness and elevational distribution of non-native species is changing in mountain regions is important if we are to react appropriately to the challenges (e.g., conservation issues) and opportunities (e.g., ecosystem services) they may pose. The few regional studies assessing temporal changes of non-native plant distributions in mountains have revealed either no average expansion over a decade (in Europe<sup>21</sup>) or upward range expansions over several decades to a century (in Europe<sup>15</sup>, Hawaii<sup>22</sup> and California<sup>20</sup>). However, we have so far lacked the necessary time-series data to assess how consistent range limit changes are worldwide or whether (and ultimately why) they differ among regions with contrasting climates, land use histories and species introductions.

Studies have shown that most non-native plant species in mountains are initially introduced at low elevation and from there spread upwards to fill their climatic niche<sup>13</sup>. As a result, species that have been introduced for a longer period tend to reach progressively higher elevations<sup>23-25</sup>. This leads to the prediction that, over time and under stable climatic conditions, upward range shifts will be most pronounced for non-native species that are found initially at low elevation and spread upwards to fill their climatic niche, and less evident for species already found at high elevation, although climate warming could contribute to accelerate upward shifts also at high elevation<sup>20</sup>. Studies of climate-induced range shifts in native plant species have repeatedly found a similar negative relationship between species' initial upper range limits and the magnitude of their upper range limit expansion (Fig. 1). Contrasting mechanisms have been proposed to explain this pattern, including: (i) stronger responses of warm-adapted (i.e. low elevation) species to climate warming<sup>15,26</sup>; (ii) changes in climatic water balance or biotic interactions driving downward migrations at higher

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

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

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

environmental gradients, these patterns should be evaluated against appropriate null models<sup>27,33,35</sup>. However, very few studies of climate-related range shifts use null models to interpret patterns of range limit shifts or to fully account for geometric constraints<sup>10,35</sup>.

Here, we analysed data from a standardized survey of non-native plant distributions (developed by the Mountain Invasion Research Network MIREN; [www.mountaininvasions.org](http://www.mountaininvasions.org)<sup>36</sup>) to quantify and compare temporal patterns of invasions in mountains across the globe. We surveyed elevational gradients along mountain roads and adjacent semi-natural vegetation in eleven mountain ranges from five continents, ranging from 68° N (Norway) to 37° S (Australia). Our data includes nearly 15000 observations of 616 non-native plant species from 651 sampling transects resurveyed every five years across a 5-year (five regions) or 10-year (six regions) period. We analyzed temporal changes in the richness and upper elevational limits of non-native plant species, introducing a null model approach to interpret patterns of range shifts across elevational gradients after accounting for geometric constraints, and compare these patterns across regions. Specifically, we ask: (1) Has the richness of non-native plant species in mountains increased during the last decade? (2) Are the upper elevation limits of non-native species moving upslope, and if so, are upslope shifts occurring faster than expected at lower elevations?

## Results and Discussion

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

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

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

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

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

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

Across regions, and as predicted, the upper range limits of non-native plants shifted upslope at low elevations with linearly decreasing magnitude across the elevational gradient, with slight average downslope shifts at high elevations in some regions (linear mixed-effects model of range shifts on initial elevation limit, weighted by species' frequencies of occurrence:  $F_{1,579.89} = 54.82$ ,  $p < 0.001$ ; Fig. 4). This relationship was significant in six regions when regressions were fitted within individual regions (Table S6). On average, upslope shifts at low elevation tended to outweigh downslope shifts at high elevation. To account for these effects of elevation on the average upper range limit shifts, we evaluated the range limit shift at the median of each elevational gradient based on the fitted values of linear regressions in each region. Retaining all species present at least twice per region, upper range limit shifts between the first and last survey were significantly upslope in seven regions (Fig. 3B, for annual shifts see Fig. S1B). Though still upslope, range limit shifts were no longer significant for Norway (filter 1) and for Switzerland (filter 2), when excluding less common species. Excluding species occurring fewer than 10 times per region and year resulted in non-significant shifts at the midpoint for South Chile and Oregon (USA) (Table S5; regions with fewer than five species remaining after filtering were excluded from the analysis). This might be due to the low sample size in some regions (Switzerland and Norway), or also reflect the expectation that more widespread species will tend to have been introduced for longer and so more likely to be in equilibrium with their climatic limits<sup>24</sup>. To conclude, accounting for the elevation-dependence of species' shifts at the upper range limit strengthened our inference that non-native plant species have rapidly expanded their ranges upslope in mountains globally.

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



an appropriate null model before they can be interpreted ecologically<sup>35</sup>. Our null-model approach (Methods; Fig. 1) revealed that the observed negative relationships between initial upper elevation limits and range limit shifts fell outside of the 95% confidence intervals of null expectations in seven regions (both Australian regions, South Chile, Tenerife, Hawaii, Kashmir [India] and Montana [USA]; Fig. 4). In all seven cases, observed relationships fell above the confidence intervals of expected relationships in the lower part of the elevational gradients (or in the middle part of the gradient in Kashmir [India]), indicating that species initially restricted to lower (or middle) elevations spread upwards significantly more than expected by chance alone. Greater downward shifts than expected by chance were also observed at high elevation in Tenerife and Montana (Fig. 4). Alternative null models (differing in the vectors of initial elevation limits used to derive expected relationships; see Methods for further details) supported an additional significantly greater upward range shift at low elevation than expected by chance in Oregon (USA) (Fig. S2, S3). Support for greater downward shifts than expected by chance also differed depending on the null model used (zero to three regions; Fig. 4, S2, S3).

Non-native plant species distributions along elevational gradients tend to display a nested pattern, with species with small ranges mainly restricted to lower elevation sites, where human population density and corresponding opportunities for introduction and establishment are greatest<sup>13,15</sup>. Greater upward shifts in elevation limits for species previously restricted to lower or middle elevations are therefore consistent with a scenario of ongoing dispersal, in which many of these species have only recently been introduced to lower elevation sites. On average, we would not expect recently introduced species to be in equilibrium with their climatic limits, but rather to be in a phase of active range expansion (i.e. climatic niche filling), in contrast to species that have already established at higher elevations and are closer to their cold limit. Consistent with this hypothesis, recently-introduced non-native species in Tenerife tend to have narrower elevation ranges than older introductions<sup>24</sup>, while time since introduction of non-native plant species in Central Europe is positively related to their maximum elevation<sup>23</sup>, elevation range<sup>25</sup> and to the magnitude of upward range shifts<sup>15</sup>. Conditions at lower elevation might also be more conducive to spread, with longer growing seasons, at least in temperate regions, and greater anthropogenic disturbances and propagule pressure associated with settlements, agriculture and industry. Similar reasons have been proposed to explain the more pronounced elevational shifts and abundance increases of native plants in the European Alps at lower elevation<sup>29</sup>. We hypothesize that a combination of these mechanisms is responsible for the rapid (within 5 to 10 years) expansion of species' upper elevation limits that we document in most of our study regions. While climate warming might also have contributed to the upward

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

In contrast to upward shifts at low elevation, significant deviations from the downward shifts at high elevation predicted by the null model were more scarce. Possible explanations for the few cases of significant downslope shifts might be active removal of non-native species at high elevation in some regions, pushing their upper limits to lower sites<sup>38</sup>, or harsh environmental conditions preceding the final survey (e.g. a greater probability of mortality or failed reproduction due to cooler temperatures or severe frost events<sup>21,39</sup>). Downward shifts might also have arisen stochastically, especially if species reaching high elevation tended to be rare and assuming that rarer species are more prone to large range contractions due to stochastic local extinction events<sup>21,27</sup>. Our models partly accounted for this by weighting species based on their frequency of occurrence. In unweighted models, negative relationships between initial elevation limits and range limit shifts were more pronounced in eight regions (Table S7), suggesting that stochasticity in colonization and extinction events contribute at least partly to the magnitude of upward and downward shifts.

In summary, the different lines of evidence we have presented collectively reveal that non-native plant species are expanding their upper elevation limits in 10 out of the 11 surveyed regions. Specifically, upward shifts were chiefly represented by average upper limit changes within regions either before (four regions; Fig. 3A) or after (additional three regions; Fig. 3B) accounting for elevation, or more than expected by chance for species at low/mid elevation (additional three regions; Fig. 4). The only region showing no evidence of significant changes in non-native species' upper range limits was Central Chile. That these upper range limit changes were observed after just five years in five of the regions indicates how rapidly non-native plant species are spreading upwards in mountains around the world, especially along road corridors. By comparison, native plants in the European Alps are moving upslope on average by 28.2 m per decade<sup>40</sup>, which is substantially less than what we report for non-

native species (Fig. 3). Roads provide favourable habitat and anthropogenic dispersal routes for many non-native plant species, and range expansion along roads are therefore expected to be more rapid than in undisturbed habitats. Non-native plant species spreading away from roads into the surrounding undisturbed vegetation has so far been limited at higher elevation<sup>11,16</sup>, but this might change with increasing anthropogenic disturbance and changing climate. Roadside surveys like ours<sup>36</sup> might therefore be valuable for the early detection of possible emerging threats to native species and ecosystems. To support such measures, future work should continue to interrogate which species traits promote fastest rates of spread<sup>15,16,29,41,42</sup>, which species have the potential for greatest impacts, and which features of high elevation ecosystems (e.g. native community structure, disturbance regimes, rates of climatic or land use changes) are associated with greater levels of invasion<sup>16,43</sup>. Additionally, while negative relationships between historical range positions and range shifts are pervasive, our simulations demonstrate that such patterns can also emerge in the absence of biological changes. As time-series data of species' distribution changes become increasingly available<sup>2</sup>, null models can be powerful tools for evaluating the magnitude and direction of range shifts within given observational constraints and will become crucial to support robust interpretation of range shift dynamics across environmental gradients<sup>35</sup>. Finally, this study suggests that in an era of local and global anthropogenic changes, non-native plant species in mountains will continue to expand upwards regardless of their introduction point. Therefore, any threat posed by non-native species to higher elevation ecosystems will likely increase, making it even more necessary to enact monitoring and management plans in mountain regions around the world.

## Methods

### *Data collection*

Data were collected by the Mountain Invasion Research Network (MIREN) using a standard protocol<sup>36</sup>. Sampling started in 2007/ 2008, is repeated every five years and is still ongoing. We used data from 11 mountainous regions around the world: the Australian Alps (two regions, New South Wales and Victoria); the Swiss Alps; the Andes (two regions, Central and South Chile); the Montana-Yellowstone National Park (USA); the Blue Mountains (Oregon, USA); Hawaii (USA); Tenerife (Canary Islands, Spain); Kashmir (India); and the Northern Scandes (Norway). For information about geolocation, climate, elevational range and sampling period, see Table S4. In each region, three roads were selected (two in Central Chile, four in Hawaii, five in Victoria), all of them open to vehicle traffic for at least part of the year. The bottom of each road was defined as the point below which no major elevational change occurred, while the top was set by the highest point of the road<sup>36</sup>. Each road was evenly stratified by elevation into 20 sampling transects (i.e. 60 per region, though

this varied due to local logistics; see Table S4), totaling 651 sampling transects. At each location, three 2 × 50 m plots were placed in a T-shape, with one plot parallel to the road and two plots placed adjacent and perpendicular to the first plot, to distinguish between disturbed habitats directly next to the road and more semi-natural habitats away from the road (i.e. up to 50 and 100 m away from road verges). The two perpendicular plots were only surveyed when there were no impassable barriers such as cliffs and rivers, resulting in unequal numbers of plots per sampling transect (respectively 651, 481 and 440 plots at 0, 50 and 100 m from the road). Sampling was repeated during the peak growing season at 5-year intervals (Table S4). The identity of non-native vascular plant species according to the World Flora Online<sup>44</sup> and their abundance (scale 1 = 1-10 individuals or ramets, 2 = 11-100 individuals and 3 > 100 individuals) was recorded in every plot. Data from the three plots at each sample transect (elevation) were combined to presence-absence data for each transect for the analyses presented here. The two semi-natural plots together accounted for only 35% of the total observations of non-native plant species across years, and only 11% of unique observations of non-native plant species within sample transects (i.e. observations of species away from but not at the roadside). Further, analyses conducted with data separated into road and semi-natural plots revealed no consistent differences in average upper limit shifts (Table S9). Species not identified to species level were excluded, as were species that were only recorded once in a given region.

#### *Data analysis*

All analyses were carried out in R, version 4.0.3, using the lme4 package<sup>45</sup>. All models were checked for compliance with model assumptions. To explore changes in non-native species richness over time, the total number of non-native plant species was calculated for each region and year ( $N = 27$  observations of regions/years). Species richness was fitted with linear mixed-effects models (LMMs; Gaussian error distribution). Year since first survey (0, 5 or 10 years) was used as a linear predictor and region included as a random intercept term to account for the spatial nestedness of the data. Subsequently, these models were compared to an intercept-only model, but still including the same random effect, with a likelihood ratio test. We also fitted LMMs to the percentage change in richness, setting the intercept to zero (i.e. percentage change in species richness is always zero in the first year of the survey).

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

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

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

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

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#### **Data Availability Statement**

All datasets generated before 2016 (except two roads in Victoria, Australia) and analysed during the current study are available through the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org/publisher/76388ab6-61ca-439a-ab09-e1fe73eb224a>) and the complete data set is available on Zenodo (<https://doi.org/10.5281/zenodo.5529072>). Environmental data and a summary file containing all species and range shifts are provided as supplementary files.

#### **Code Availability Statement**

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

#### **Author Contributions**

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. designed the study. S.H., T.S. and D.R. managed the data collected by S.H., T.S., J.J.L., K.M., 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., 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 the manuscript with feedback from J.L. on statistical analyses and the Regression Towards 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., A.P., A.R.B., D.R. and N.W. edited and commented the paper.

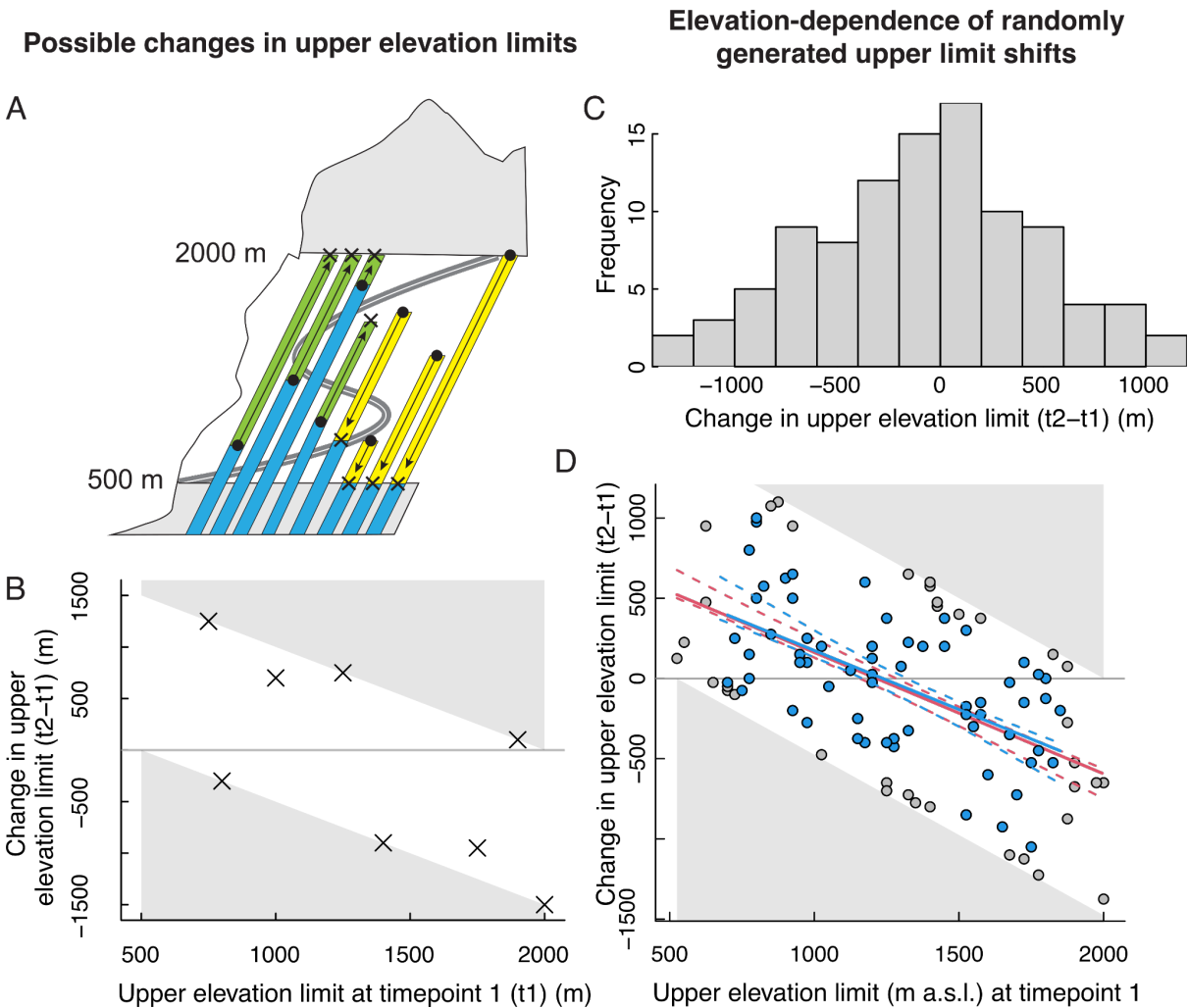
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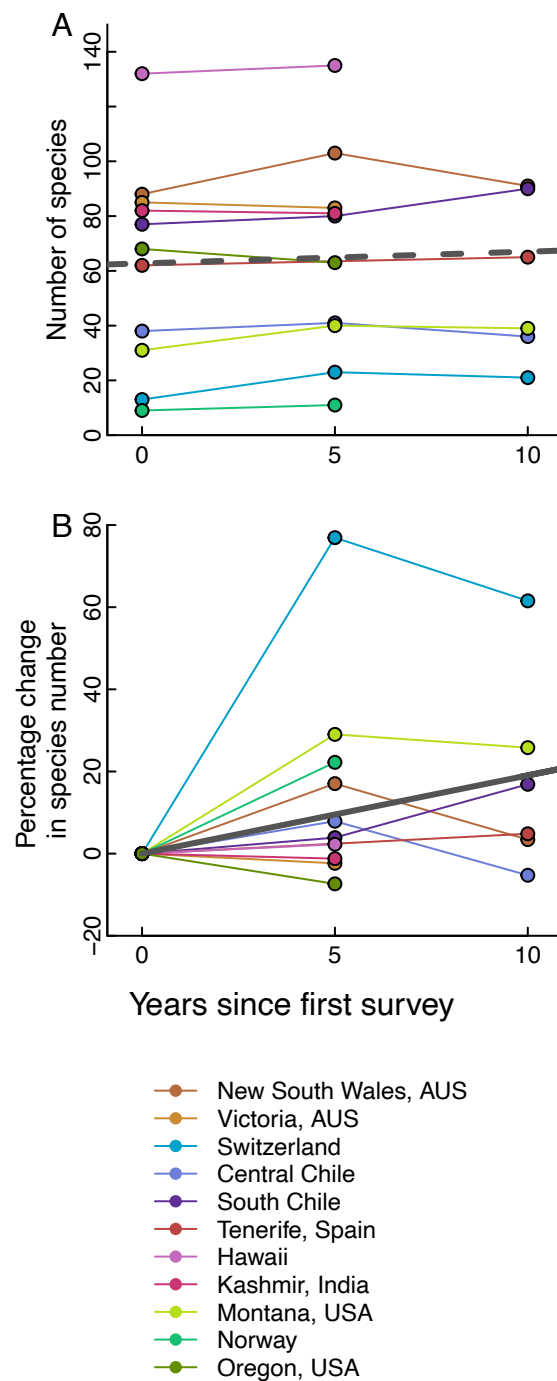
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**Figure 1. A null model approach to explaining species' range limit shifts across an elevational gradient.** (A) Possible changes in observed upper elevation limit for eight species (bars) shifting their upper limits upwards (green portions of bars: expansions) or downwards (yellow portions of bars: contractions) along an elevational gradient from time point 1 ( $t_1$ ; points) to time point 2 ( $t_2$ ; crosses). The species' distributions are surveyed at sites along a hypothetical mountain road between 500-2000 m a.s.l. (i.e., within the unshaded region), although all of them also occur at lower elevations below the surveyed elevational window. (B) The observed range shifts of the upper elevation limit for the eight example species (crosses) are plotted against their upper elevation limits at  $t_1$ . The grey triangles delimit the boundaries of the surveyed elevational gradient (cf. grey shaded regions in A), and hence represent "non-observable" shifts in elevation limits. (C) Histogram of upper limit shifts for 100 species, generated randomly within the constraints imposed by the boundaries of the observed elevational gradient (cf. panel B). (D) The boundaries of the 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

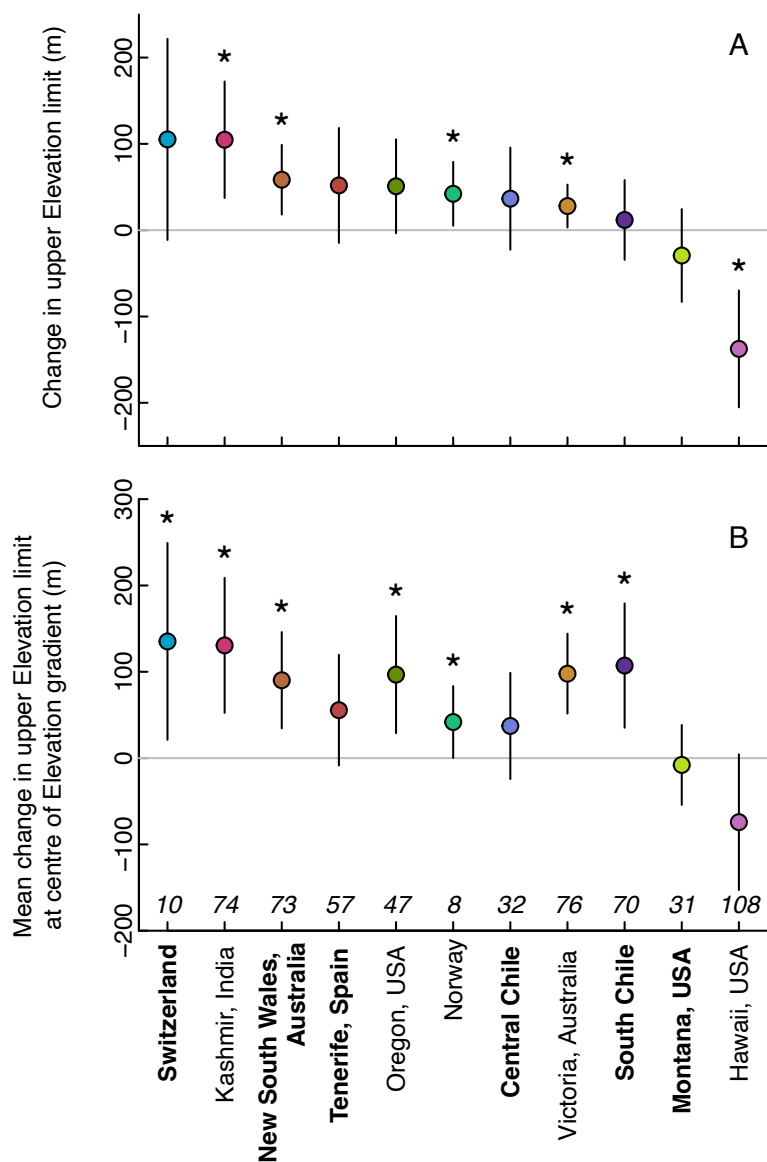
678 intervals calculated as described above, but excluding species falling in the top and bottom



679 10% of the gradient.

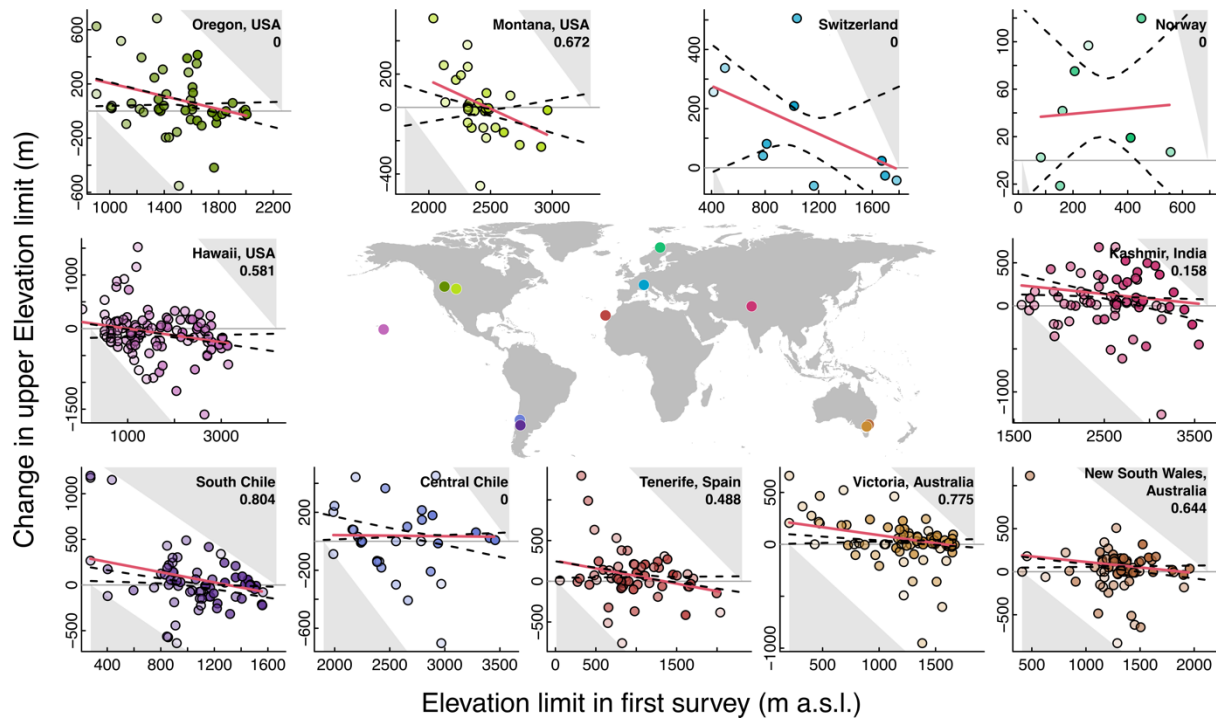
680 **Figure 2. Temporal changes of non-native plant species in 11 mountain regions.** Total  
681 species richness (A) and percentage change in species richness (B) over the 10-year  
682 sampling period. Solid and dashed heavy grey lines indicate significant and non-significant  
683 fits, respectively,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

all regions were sampled in all years.



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

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



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

## Supplemental Information

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

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



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

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

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

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

	<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

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

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

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

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

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

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

	<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

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

	Semi-natural plot $\pm$ standard error	Effect roadplot $\pm$ standard error	<i>F</i>	df	<i>p</i>
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

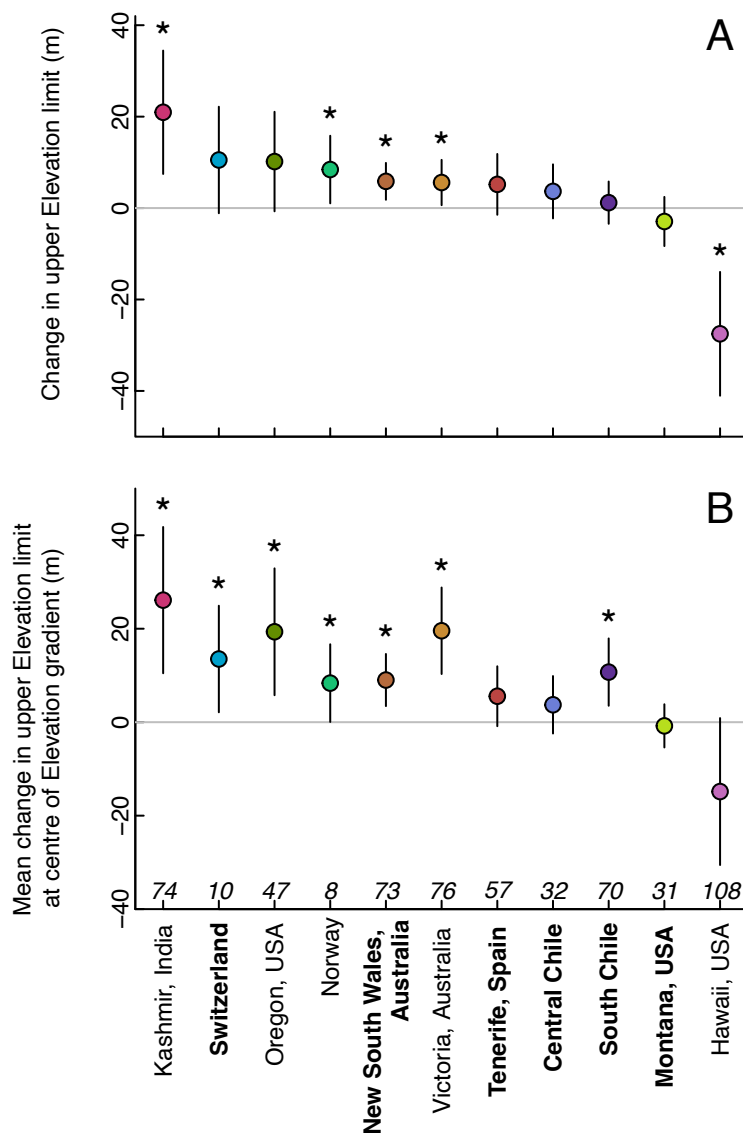


**Table S10.** Proportions of fitted values that fall above or below the 95% confidence interval for the expected null relationship between initial upper elevation limit and change in upper elevation limit after accounting for the geometric constraint (see Fig. 1; the calculations are based on the original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

	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

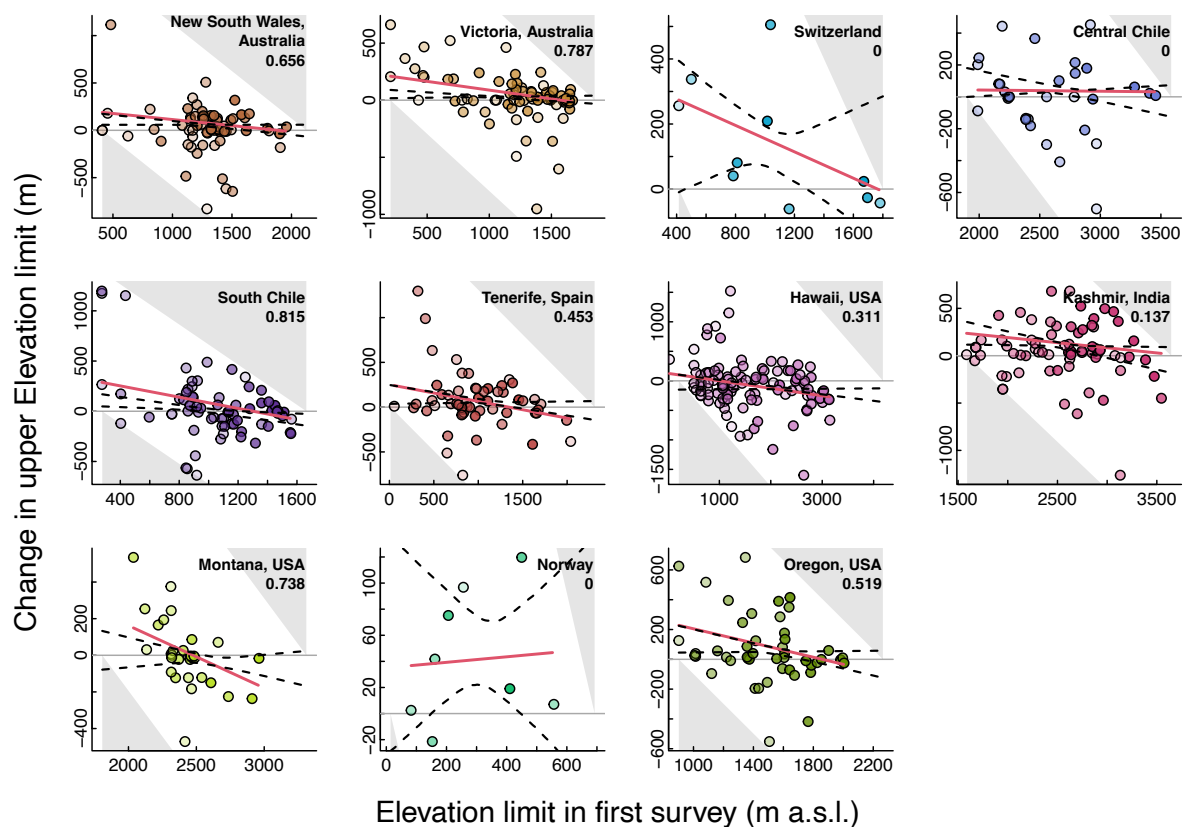
## Supplementary Methods: Regression Toward the Mean

Regression toward the mean (RTM) occurs whenever there is a non-perfect correlation between measurements of observational units over time and was first described by Sir Francis Galton<sup>3</sup>. Galton observed that unusually large or small values on average tend to be followed by measurements closer to the mean. This results in a negative correlation between the change in measurements over time and their initial state. While RTM is widely discussed in other fields, such as medicine and psychology<sup>4,5</sup>, there has been reported to be less awareness of this phenomenon in ecology<sup>6</sup> (but see ref. <sup>7</sup>). In order to correct for RTM, Mazalla<sup>6</sup> proposes to always include initial measurements in analyses on temporal change. In our study, the geometric constraint of a finite environmental gradient adds another layer of



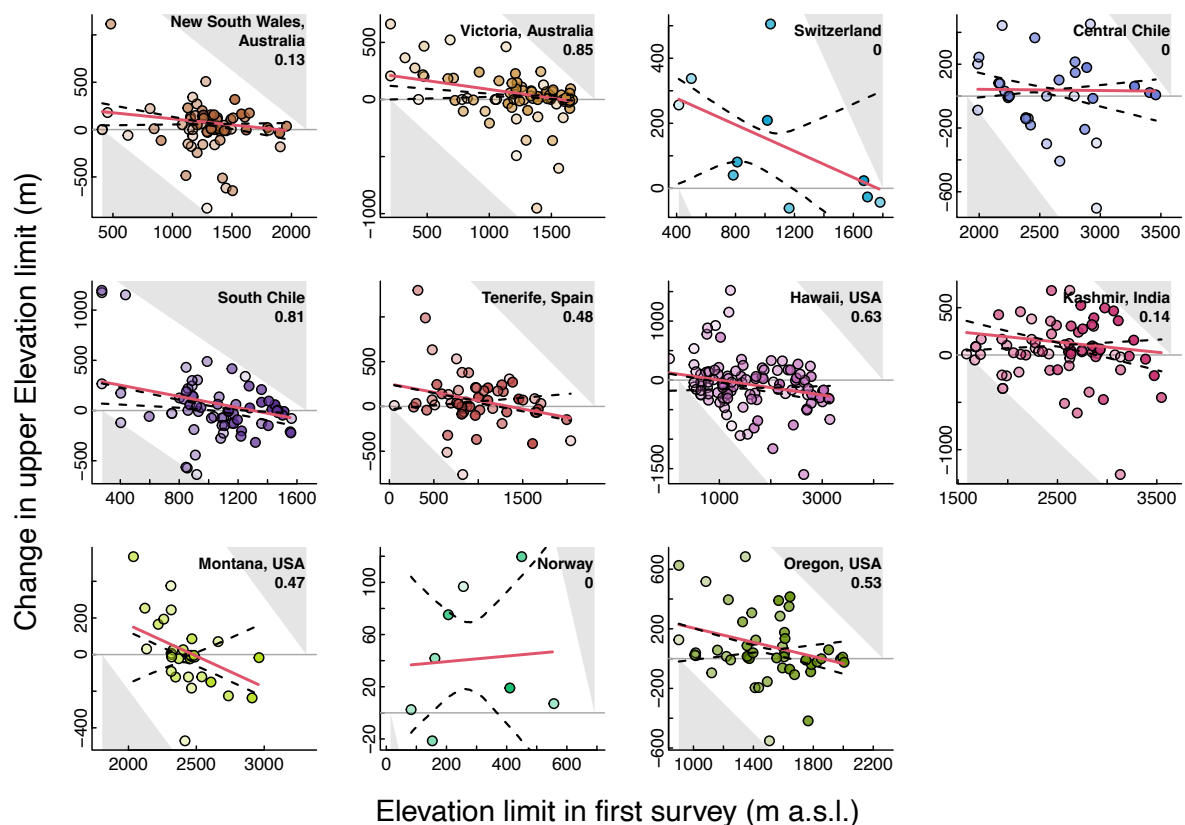
**Fig. S1. Observed annual changes in species' upper elevational limits ( $\pm 95\%$  confidence intervals). Both panels show mean annual shifts, estimated from linear models**

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



**Fig. S2. Null-model tests of elevation-dependent shifts in upper elevation limit of non-native plants in 11 mountain regions.** Each point shows the change in upper elevation limit (90<sup>th</sup> quantile of elevational distribution) of a single species, as a function of its limit in the first survey (darker shading corresponds to greater total log[frequency of occurrence] of a species in both surveys). Dashed lines are 95% confidence intervals for the expected null relationship between initial upper elevation limit and change in upper elevation limit after 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.



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

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