

Assembly of nonnative floras along elevational gradients explained by directional ecological filtering

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Nonnative species richness typically declines along environmental gradients such as elevation. It is usually assumed that this is because few invaders possess the necessary adaptations to succeed under extreme environmental conditions. Here, we show that nonnative plants reaching high elevations around the world are not highly specialized stress tolerators but species with broad climatic tolerances capable of growing across a wide elevational range. These results contrast with patterns for native species, and they can be explained by the unidirectional expansion of nonnative species from anthropogenic sources at low elevations and the progressive dropping out of species with narrow elevational amplitudes—a process that we call directional ecological filtering. Independent data confirm that climatic generalists have succeeded in colonizing the more extreme environments at higher elevations. These results suggest that invasion resistance is not conferred by extreme conditions at a particular site but determined by pathways of introduction of nonnative species. In the future, increased direct introduction of nonnative species with specialized ecophysiological adaptations to mountain environments could increase the risk of invasion. As well as providing a general explanation for gradients of nonnative species richness and the importance of traits such as phenotypic plasticity for many invasive species, the concept of directional ecological filtering is useful for understanding the initial assembly of some native floras at high elevations and latitudes.

altitudinal gradient | dispersal | invasibility | nestedness | Rapoport effect

Several factors are known to shape species richness patterns along elevational gradients, notably energetic constraints on primary productivity and species–area relationships (1, 2). However, these factors are often highly correlated, making it difficult to assign causality, especially because species richness patterns are the result of both contemporary and historical ecological and evolutionary forces. High-elevation floras are typically composed of species with narrow climatic ranges and specialized ecophysiological adaptations to low temperatures, such as low stature, slow growth rates, and freezing resistance (3). Because richness gradients emerge from the overlap of individual species ranges, some authors have generated null models for richness patterns by assuming that species ranges are placed at random within a bounded elevational domain (4, 5). This usually produces a mid-domain effect, with richness peaking at mid-elevations where the overlap of species ranges is greatest. Indeed, such mid-elevation peaks do occur, and at least some of them can be explained by the overlap at ecotones of species adapted to different parts of the gradient (6).

Although there is a long tradition of studies on elevational richness patterns of native species, little is known about similar phenomena in nonnative species. Nearly 1,000 nonnative plant species have been recorded from mountains throughout the world (7), with species richness usually peaking either at low elevations or toward the middle of the elevational range (8). The decline in nonnative plant richness at higher elevations might

reflect the same factors thought to determine richness patterns in native species. A key difference, however, is that although richness patterns of native species have developed over thousands to millions of years, those of nonnative species have assembled from an ecologically diverse pool of species dispersed through human agency over, at most, a few hundred years. For this reason, evolutionary factors such as differential rates of speciation (9, 10) may be less relevant for explaining patterns of nonnative species richness than dispersal processes or preadaptation of species to novel abiotic and biotic conditions (11).

One reason why it is important to understand the assembly of nonnative species along elevational gradients is that mountain areas, many of them rich in endemic species, remain largely uninvaded (8). The usual explanation is that special adaptations are required to invade extreme environments (8, 12–15), making them inherently resistant to invasion (16, 17). Few studies, however, have explicitly quantified invasion patterns along elevational gradients, although such studies could help explain the apparently low invasibility of extreme environments and provide a basis for their future protection. In addition, understanding the assembly of nonnative species along such gradients could provide insights into the processes determining richness patterns in native floras (18).

To reach general conclusions about elevational trends in nonnative plant richness and the factors that determine them, we recorded species richness in transects placed at regular elevational intervals along roads in eight mountain regions including five continents and two oceanic islands. All regions were characterized by a steep climatic gradient spanning, on average, a 10 °C difference in mean annual temperature from bottom to top and a land use gradient from heavily modified lowland to more natural highland habitat. However, several factors differed greatly among regions, including the elevational range, available area, and density of the road network. Our study addressed three core questions. (i) How consistent are elevational richness patterns of nonnative plants around the world? (ii) How are elevational gradients of nonnative plant richness assembled? (iii) Can a

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common mechanism explain elevational gradients in nonnative plant richness in the various regions?

Results

Two important patterns emerged from our data. First, nonnative species richness always declined from above the lowest one-third to the upper end of the elevation gradients ($P < 0.0001$) (Fig. 1 and Table S1). This pattern was independent of the elevational range and other differences among regions. Richness patterns in the lowest one-third of the gradient were less consistent, with fewer species in the lowest elevation plots in some regions. This heterogeneity could be explained by a combination of climatic effects—for example, very dry conditions at the lowest elevations on Tenerife (19)—and patterns of human disturbance. Thus, nonnative plant richness was always highest in that part of the elevational range where human activity, using road and population density as proxies (Fig. S1), was greatest. In contrast, native plant richness showed no consistent trend with elevation in the three study regions for which data were available (Table S1 and Fig. S2).

Second, the decrease in nonnative species richness with increasing elevation was because of a progressive loss of species, and therefore, the species found at high elevations were those with the widest elevational ranges that also occurred at low elevations (Fig. 2). In all regions, the elevational range of species recorded at high elevations was significantly greater ($P < 0.05$) (Fig. 3) than would be expected if ranges were random in relation to elevation (4, 21). Additionally, the number of species restricted to the upper one-half of the gradient was significantly smaller than would be expected with random range placement and in five cases, was fewer than three (Fig. 3). Furthermore, a nestedness analysis confirmed that, in five of eight regions, the nonnative species composition of sites was significantly nested in relation to elevation, indicating that the species found at high

elevation were a subset of those found at low elevation (Fig. 2). These patterns again contrasted with those of native species, whose elevational ranges were not consistently larger than expected at high elevation (Fig. 4). Furthermore, the proportion of native species found only at high elevations was substantially greater than for nonnative species, and in two regions, the proportion was either slightly greater than or not different from that expected with a random placement of species ranges.

Discussion

In contrast to native species, which tend to be most numerous in the center of the elevational range (although a range of patterns including monotonic decreases have been reported) (1, 22, 23), numbers of nonnative plants consistently peaked at lower elevations. Significantly, the richness patterns that we observed were independent of the large differences in the elevational gradients and climates among regions. For example, in both central and southern Chile, species richness declined from ~15–25 species at the bottom to fewer than 5 species at the top, although the elevational extents of these gradients did not overlap. This strongly suggests that it is the relative difference in abiotic factors along the gradient from low to high elevation and not region-specific factors such as the available area or particular climatic conditions that drives richness patterns in nonnative plants. Furthermore, the consistency of these patterns around the world suggests that they are explained by a common mechanism.

The nesting of species elevational ranges suggests that most nonnative plant species first arrive at low elevations, where anthropogenic propagule pressure is greatest (8, 23–25), and from there, spread upwards, either naturally or through human agency. Because propagule pressure at high elevations is low, the species that reach the highest elevations must be good dispersers. However, because they are able to establish populations across the full

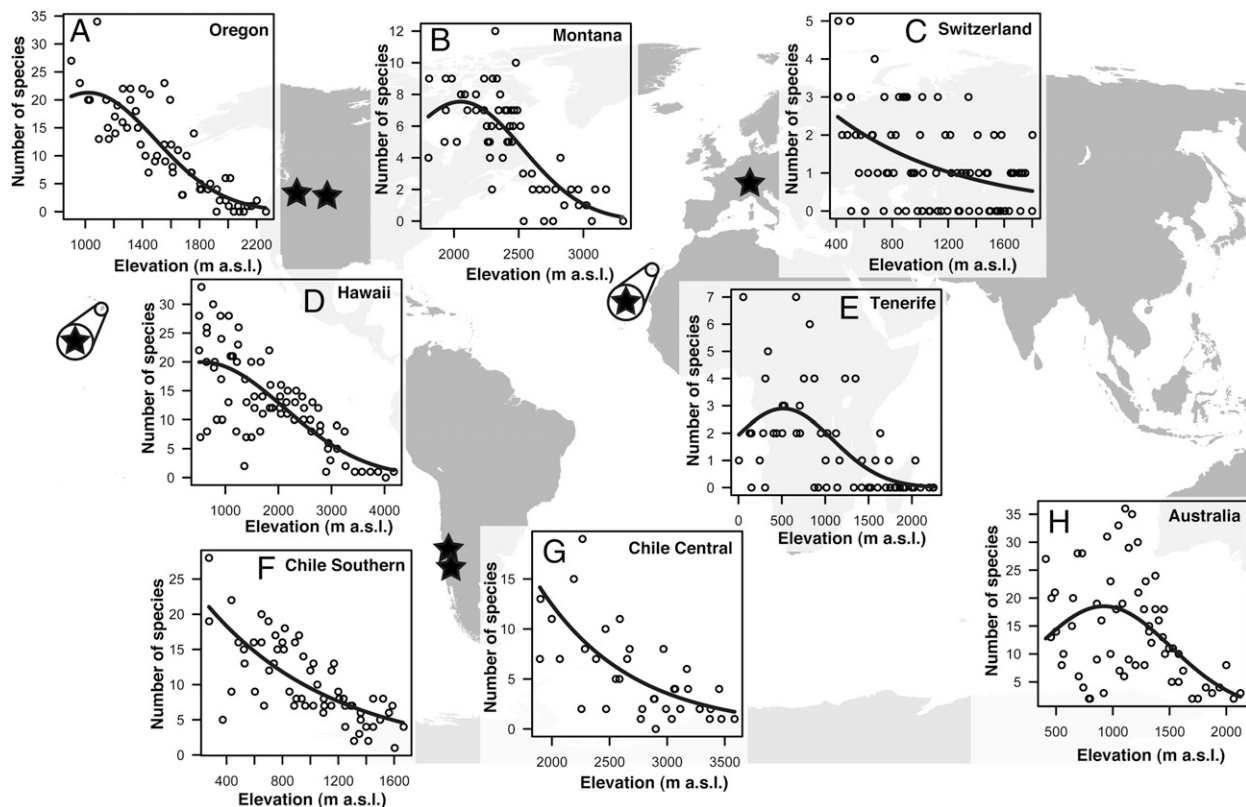


Fig. 1. Global decreases in nonnative species richness with elevation. The relationship between nonnative species richness in plots along roadsides and elevation in eight mountain regions (stars) around the world. For model parameters and statistics, see Table S1.

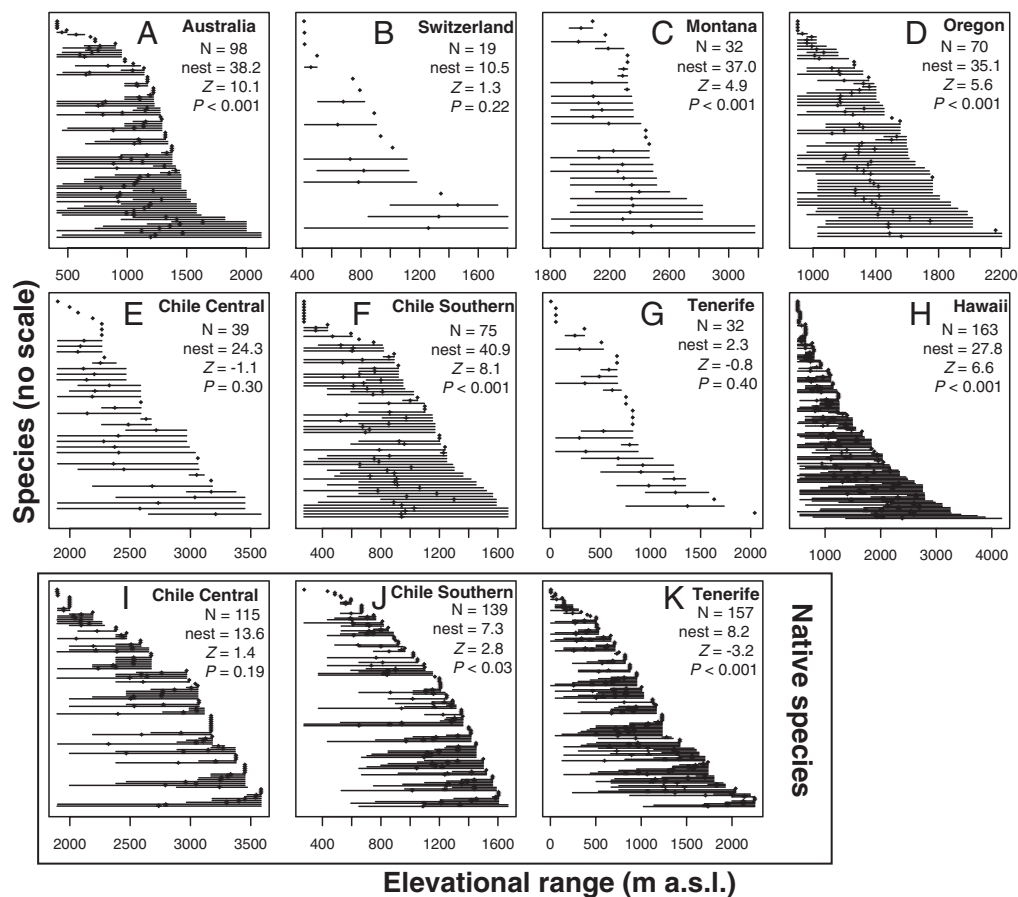


Fig. 2. The elevational ranges (lines) and mean elevation of occurrence (points) of the nonnative and native (box) species recorded in each mountain region ordered by elevation of maximum occurrence. Also shown are the results of a nestedness analysis of species composition in relation to elevation in each region. The analysis tests the hypothesis that the compositions of species-poor, high-elevation sites are nested subsets of the composition of species-rich, low-elevation sites. Only results for the nestedness (nest) of sites and their Z scores are presented (values increase with increasing nestedness). Note that significantly negative Z scores indicate that species composition is less nested than would be expected by chance (20). Note also that the analysis was performed on the presence-absence matrices and not the species ranges shown in the figure.

elevational gradient, they must also be species with the widest climatic tolerances or the greatest capacity to adapt genetically to novel conditions (24, 26, 27). The nested patterns, therefore, arise from a combination of decreasing anthropogenic propagule pressure and a corresponding increase in the proportion of climatically generalist species with increasing elevation. This could explain why residence time is sometimes correlated with the elevational limits of nonnative species, because time is needed for either dispersal or genetic adaptation (11, 19).

To obtain an independent measure of the ecological range of the species, we extracted data from the BiolFlor database (28) on the number of floristic zones of eight (arctic, boreal, temperate, submeridional, meridional, subtropical, tropical, and austral) occupied by European species native to Germany. In the New World regions, there was a positive relationship between the maximum elevation reached by a European species and the number of floristic zones occupied in its native range ($F_{1,264} = 9.63, P < 0.003$). Although this relationship varied among regions (significant interaction of elevation \times region; $F_{5,264} = 2.49, P < 0.033$) (Fig. 5A), it provides clear evidence that nonnative species at high elevation are climatic generalists. An analysis of Landolt temperature indicator values (1, arctic-alpine; 2, subalpine-boreal; 3, montane; 4, colline; 5, lowland/southern European) (29) for the same species also revealed that climatic generalists invaded high elevations, whereas there was a loss of lowland, warm-adapted species with elevation in each region ($F_{1,258} = 16.12, P < 0.001$) (Fig. 5B).

According to Landolt's classification, only one species, *Phleum alpinum* (recorded from central Chile), could be considered cold-adapted, and none were classified arctic-alpine.

We conclude that the decline in nonnative plant richness with elevation is caused by a successive filtering of the lowland species pools. These pools comprise species that vary widely in their potential elevational amplitude, including some (e.g., *Cynodon dactylon*, *Megathyrsus maximus*, and *Amaranthus* spp.) restricted to warmer conditions at low elevation and others (e.g., *Hypochaeris radicata*, *Plantago lanceolata*, and *Rumex acetosella*) capable of establishing viable populations at the highest elevations. Independent data show that this latter group is largely composed of species with broad climatic amplitudes (28, 30–32). As a result, the nonnative floras of higher elevations are composed of nested sets of species with increasingly wide elevational amplitudes, a process we call directional ecological filtering. This same mechanism could also explain the low nonnative species richness and predominance of climatically generalist species at the extremes of other environmental gradients. For example, nonnative species on sub-Antarctic islands are mainly species with wide environmental tolerances (33), whereas in the northern hemisphere, the latitudinal extents of several nonnative taxa increase with increasing latitude (18). Additionally, similar trends also apply at smaller scales to nonclimatic gradients; for example, several woody species that invade the understory of tropical forests are plastic in response to light availability and

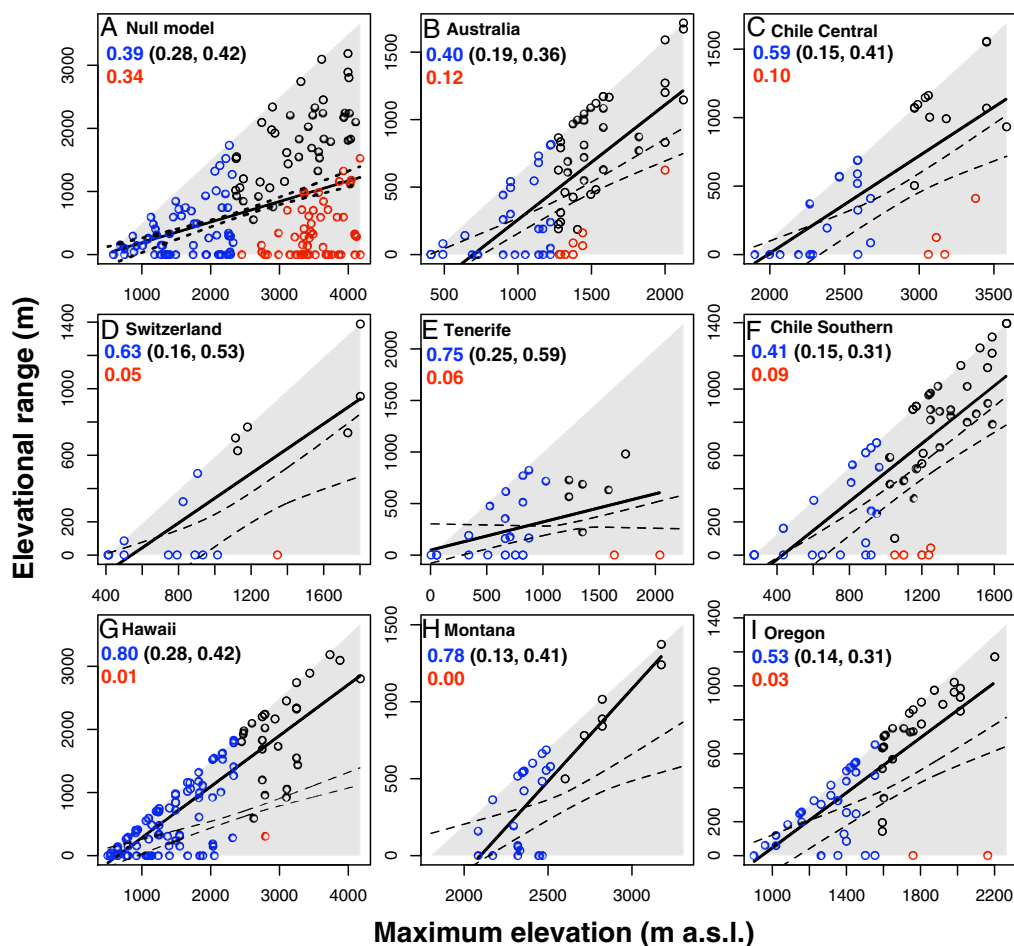


Fig. 3. The relationship between elevational range and the maximum elevation reached by nonnative species (circles and solid lines) in each region (B–I). Note that the circles are logically constrained to the gray-shaded one-half of the plots. Colored circles indicate species with ranges that fall exclusively within the lower (blue) or upper (red) halves of the elevational gradient in each region, whereas black circles indicate species whose ranges occupy both halves. The proportion of species in each category is given as colored numbers. A shows the expected relationship if species elevational ranges are distributed randomly along the elevational gradient, with approximately equal proportions of species ranges at low and high elevations; 95% confidence intervals for this expectation in each region are indicated by dashed lines and by black numbers for the proportion of species with ranges exclusively at high and low elevations. In all regions, note the lack of species with ranges falling exclusively at high elevation and the significantly steeper increase in range size with elevation than expected with random range placement. For N values, see Fig. 2.

also perform well under full sunlight typical of anthropogenic source habitats (34). Directional ecological filtering could, therefore, explain why traits such as phenotypic plasticity, capacity for rapid genetic change, and broad physiological tolerances are so frequently associated with invasive species (35–37).

All these patterns, however, are contingent on past human introduction pathways (38). Thus, the absence of cold-adapted nonnative species at high elevations is expected if introductions are predominantly at low elevations. Either cold-adapted species are not introduced at all or they fail to naturalize under climatic conditions to which they are not preadapted. For instance, alpine species of genera such as *Primula*, *Meconopsis*, or *Gentiana* are often cultivated at low elevation but are rarely recorded outside the artificial abiotic and biotic conditions of gardens (7, 39). A key insight from this is that the resistance of high-elevation environments to invasion might not be inherent but rather conferred by their separation from lowland sources of potential invasive species by steep environmental gradients. This could change if species with specialized ecophysiological adaptations to low temperatures were deliberately introduced to high-elevation environments—for example, by planting ornamental alpine plants in high-elevation tourist resorts (40). This might be particularly important for

invaders of more natural habitats away from roadsides. Indeed, some of the most problematic invaders are habitat specialists that have been deliberately introduced, for example, on oceanic islands (41) and in forests (42). Where extreme environments are not separated from introduction sources by steep environmental gradients, a mixture of specialized and generalist species may become problematic invaders, which has happened in deserts (43). Thus, the degree of resistance of certain extreme environments to invasion, such as at high elevation, might depend on the introduction pathways of the nonnative flora. Furthermore, it might not be possible to predict traits of invaders in such environments without considering how they become introduced (25, 38).

In addition to its value in predicting the spread of invasive species, directional ecological filtering offers a useful model for understanding some patterns of native species richness, especially those where the biota must have assembled by immigration from one end of an environmental gradient. According to the taxon cycle concept (44), species colonizing oceanic islands first establish at low elevations, and subsequent adaptation may enable them to spread into other habitats at higher elevations. This sequence may help explain why the percentage of habitat specialists in the Hawaiian archipelago is lowest in high-elevation habitats (45). A

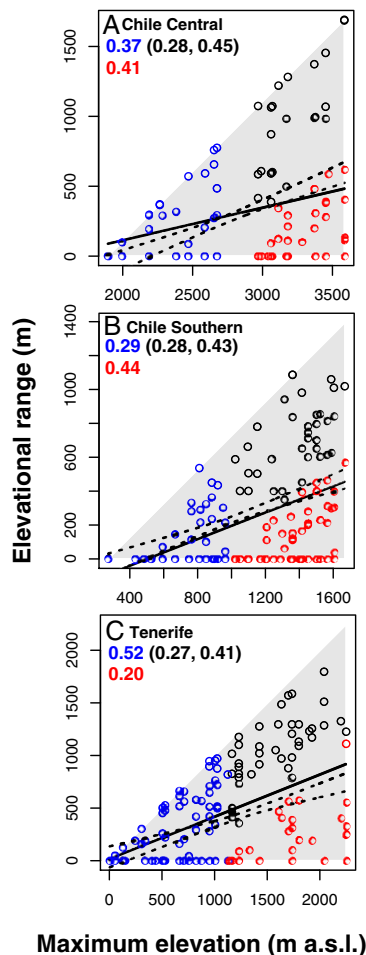


Fig. 4. The relationship between elevational range size and the maximum elevation reached by native species (circles and solid lines). Note the much higher proportion of species found exclusively in the upper one-half of the gradients compared with nonnative species (Fig. 3). For N values, see Fig. 2, and for an explanation of symbols, see Fig. 3.

similar process of directional immigration may explain why species ranges tend to increase in size with latitude in regions above 40°N subjected to Pleistocene glaciations (the Rapoport effect) (46–48). Furthermore, this process is consistent with the observation that some species specialized to habitats at the extremes of environmental gradients have clearly evolved from taxa with broader environmental tolerances (44, 49, 50), which has been suggested for *Nesotes* beetles adapting to novel habitats in the Canary Islands (51). Thus, directional ecological filtering might be a pervasive process contributing to biogeographical patterns in both nonnative and native species.

Materials and Methods

Sampling Protocol. Surveys were conducted along roadsides in the eight study regions (Fig. 1) between October 2006 and May 2008. The regions varied greatly in climate, elevational range and extent (Fig. S3 and Table S2), human history, and current land use. They included two pairs of regions (central and southern Chile and Oregon and Montana) that were geographically close but with little or no overlap of elevational ranges. Roadsides were sampled to control for effects of differences in habitat type/disturbance along the climatic gradients and because roadside habitat is relatively homogenous around the world (52). In each region, three roads were selected that spanned a broad elevational range, were open to vehicular traffic, and captured the range of regional environmental heterogeneity. Each road was divided into 19 bands of equal elevational width between the bottom, defined as the point where there was no more substantial change in elevation (i.e., near sea

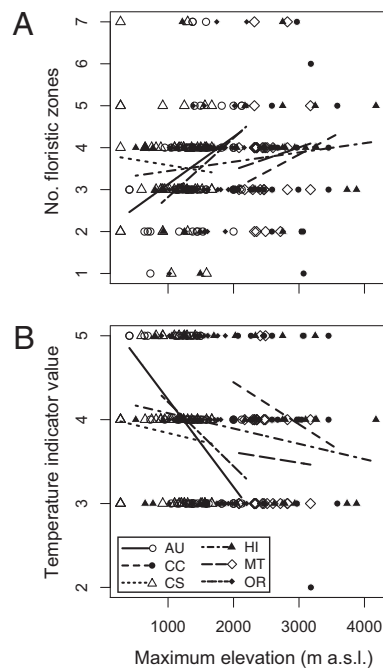


Fig. 5. The relationship in the six New World regions between the maximum elevation reached by European species and (A) the number of floristic zones that they occupy in Europe and (B) their Landolt temperature indicator values (1, arctic-alpine; 2, subalpine-boreal; 3, montane; 4, colline; 5, lowland/southern European; $n = 276$ and $n = 270$ for A and B, respectively). AU, Australia; CC, central Chile; CS, southern Chile; HI, Hawaii; MT, Montana; OR, Oregon.

level, the valley bottom, or surrounding table land), and the highest elevation reached by the road. A plot (2×50 m) was placed along the verge on one side of the road at the border of each band [$n = 60$ per region, except Switzerland ($n = 84$; four roads), central Chile ($n = 41$; three roads), and Hawaii ($n = 73$; four roads)], with the long edge parallel to the roadside, to the first occurrence of the vegetation on the verge. All nonnative species were recorded in each plot, and native species were recorded in three regions—central and southern Chile and on Tenerife. Based on local floras and expert knowledge, species were classified as nonnative if introduced from another region since 1492. Taxonomy was standardized according to the Germplasm Resources Information Network database (<http://www.ars-grin.gov>). Road density (total length/area) in 100-m elevational bands was used as a proxy for the intensity of human activities. Road length (<http://www.diva-gis.org/gData>) and area (53) were extracted from a 1° radius buffer around the geographic center of the sampled plots in each region. Additionally, data on human population density were extracted for each sample location (54).

Statistical Analyses. The relationship between nonnative species richness in plots and elevation was fitted using generalized linear models, with the retention of second-order polynomial effects of elevation determined based on likelihood ratio tests (Table S1). The maximum elevation and elevational ranges were summarized for each species recorded within a region (excluding nine undetermined species), and the relationship between these variables was described by linear regression (55). The expected relationship in each region was simulated by permuting the placement of the observed species ranges assuming (1) that species ranges are randomly placed along elevational gradients and (2) that the permuted ranges fall fully within the elevational domain (i.e., the domain is constrained by hard boundaries) (4). Permutations were performed 10,000 times to generate 95% confidence intervals for the regression of range size on maximum recorded elevation as well as for the proportion of species whose ranges fell entirely within the upper or lower one-half of the elevational domain. All analyses were performed in R (56).

A nestedness analysis (57) was also conducted for each region using the nestedness metric based on overlap and decreasing fill (NODF) by Almeida-Neto et al. (58) to test the hypothesis that the compositions of species-poor, high-elevation sites are nested within the compositions of species-rich, low-elevation sites. Rather than analyzing a maximally packed matrix of species and sites, we ordered sites (matrix rows) by increasing elevation of the site and species (col-

umns) by decreasing frequency of occurrence; 1,000 random matrices were generated using a null model that constrained species richness within sites (row totals) while randomizing the occurrence of species within sites (method R1) (59). Original species frequencies were simulated in randomized matrices by sampling occurrences using column frequencies as probabilities (59), although these were not strictly constrained. The ordering of rows and columns of the randomized matrices was also maintained before calculating the test statistics. Analyses were performed using the vegan package (60) in R (56).

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