

A global analysis of elevational distribution of non-native versus native plants

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Abstract

Aim: Much is known about the elevational diversity patterns of native species and about the mechanisms that drive these patterns. A similar level of understanding is needed for non-native species. Using published data, we examine elevational diversity patterns of non-native plants and compare the resulting patterns with those observed for native plants.

Location: Global.

Methods: We compiled data from 65 case studies on elevational diversity patterns of non-native plants around the world (including 32 cases in which both non-native and native plants were sampled). We compared the elevational distributions (upper and lower limits, and extents) and diversity patterns of non-native and native species.

Results: Compared to native plant species, the elevational diversity patterns of non-native plant species were more negative (47% vs. 13%) and less unimodal (44% vs. 84%). That is, non-native species richness tended to be highest at lower elevations, whereas native species richness peaked at mid-elevations. In cases where species richness for both non-native and native species on the same mountains showed unimodal patterns in relation to elevation, maximum values in species richness occurred at lower elevations for non-native species.

Main conclusions: At present levels of invasion, non-native and native species show different patterns in both distribution and diversity along elevational gradients worldwide. However, our observations constitute a snapshot of ongoing, long-term invasion processes. As non-native species typically show strong associations with human activities, future changes in human population (e.g. growth and migration), land use and climate change may promote upward spread of non-native species and may thus increase risks of impact on native species and communities.

KEYWORDS

diversity, elevational patterns, global change, human, non-native, plant invasions, species richness

1 | INTRODUCTION

Elevational gradients offer perspectives on the mechanisms underlying spatial variations in biodiversity that complement those provided

by latitudinal gradients. Unlike latitudinal gradients, seasonality and day length change little over a given elevational gradient (Bertuzzo et al., 2016; Merckx et al., 2015; Vetaas, 2002), and in many cases regional species pools are similar within a given elevational gradient

(Bertuzzo et al., 2016; Colwell et al., 2009). In consequence, elevational gradients have long formed a basis for macroecological studies (Brown, 2001; Rahbek, 1995) and continue to do so. Much of this work has focused on species indigenous to the focal elevational gradients, often for conservation purposes (Grytnes, Beaman, Romdal, & Rahbek, 2008; Guo et al., 2013; Rahbek, 1995).

Recently, however, elevational gradients in non-native species have garnered much attention (Steinbauer et al., 2016). There are two likely reasons for this increased interest. First, understanding elevational limits in non-native species enables independent tests to be made of macroecological mechanisms (Cadotte, Murray, & Lovett-Doust, 2006). Second, evidence is mounting of the upward spread of non-native species (e.g. Alexander, Naylor, Poll, Edwards, & Dietz, 2009; Alexander et al., 2011; Arevalo et al., 2005; Averett et al., 2016; Chown et al., 2013; Loarie et al., 2009; Pauchard et al., 2009; Seipel et al., 2012; Zhang et al., 2015), likely a consequence both of climate change and of changing land use associated with growth in human activities (Alexander et al., 2016; Jakobs, Kueffer, & Daehler, 2010; Marini, Gaston, Prosser, & Hulme, 2009). Therefore, much interest exists in understanding how these changes in non-native elevational ranges may impact native species and communities.

Indeed, the upward shift or range extension of many native and non-native species, at least partly due to climate warming, either has, or is expected to, significantly alter patterns of native species diversity, potentially having profound conservation and management implications (Pauchard et al., 2009, 2016). Thus, native species, especially rare and endangered ones that are endemic to high elevations (e.g. mountaintop or sky-island species) may face threats from both climate change and biological invasions (Figure 1). Climate warming may in many cases lead to upward range extensions, resulting in displacement of previous habitat occupants, leaving those at the highest elevation with literally no place to go, and thus at risk from

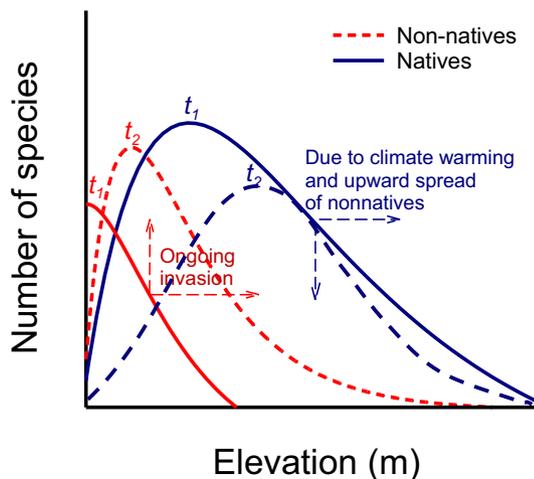


FIGURE 1 Diagram showing theoretical predictions of shifts of both native versus non-native species along elevational gradients from t_1 (current—solid line) to t_2 (future). Dashed lines are projections of future trends under ongoing species invasion coupled with climate change [Colour figure can be viewed at wileyonlinelibrary.com]

extinction (Pauchard et al., 2016). In addition, species invasions extending upward from lower elevational anthropogenic landscapes (Small & Cohen, 2004) may also limit the abundance of native plants through several mechanisms, such as competition and herbivory, and in doing so greatly alter the characteristics of mountain plant communities (but see Davis, 2003). The velocity of such change also appears to be increasing (Marini et al., 2009; Pauchard et al., 2009). Montane areas have typically been less prone to invasion than other regions due not only to climate, but also to lower human populations, lower trade and travel, and larger physical barriers (Marini, Bona, Kunin, & Gaston, 2011; Wilson, Dormontt, Prentis, Lowe, & Richardson, 2009). This situation, however, is now changing with growing human populations more often using lands at higher elevations (Pauchard et al., 2016).

Thus, understanding the current patterns of non-native species richness in response to elevational gradients is of much interest from the macroecological and the conservation perspectives (Alexander et al., 2011). While general patterns in the form of elevational diversity gradients, and their underlying mechanisms, have been assessed for different groups of indigenous species and for all native species as a whole (Rahbek, 1995), similar assessments for non-native biotas are limited.

Here, using a global dataset based on distributions of non-native species across 65 elevational gradients, we examine variability in non-native species richness along elevational gradients and compare these patterns to those of native species. Based on the knowledge that (1) non-native species usually spread in relation to the expansion of human populations, which usually have lower densities at higher elevations (Nogues-Bravo, Araujo, Romdal, & Rahbek, 2008; Cohen & Small, 1998), and (2) native species have had more time to occupy geographical space than non-natives (Wilson et al., 2009), we test the following four hypotheses. (1) Non-native species tend to exhibit negative species richness–elevation relationships, whereas native species tend to have more unimodal/hump-shaped relationships. (2) The mean elevation of diversity peaks and mean elevational limits are lower for non-native than for native species. (3) The mean elevation of diversity peaks for non-native species is more strongly correlated with mean lower than mean upper elevational limits. (4) The mean elevational extent over which non-native species occur is smaller than that of native species. We also discuss the potential role of human activities in influencing the elevational distribution and diversity patterns of non-native species.

2 | MATERIALS AND METHODS

To examine the distributional extents, diversity peaks, and upper and lower limits of non-native plant species along elevational gradients, we searched Google Scholar using the following terms in Boolean combinations: elevation(all), altitude/altitudinal, native, non-native (exotic, alien, introduced, non-indigenous), diversity and richness. The search included papers published up to December 31, 2015. We compiled and examined published studies on elevational diversity

gradients of plants from 65 qualified case studies distributed globally that met our criteria (out of 314 search results; see Figure 2, Table S1 and Appendix 1 for sampling locations of investigations). In order to be included in our analysis, published studies need to investigate plants and document study location (region, mountain range and latitude/longitude), lower and upper elevations of where sampling occurred (thus elevational extent), diversity patterns (e.g. unimodal, negative) and elevation of the diversity peak. Of the 65 cases that met these criteria, 32 included data for both native and non-native species (i.e. both groups of species were sampled along the same elevational gradients). While some case studies were from the same mountain ranges (e.g. Alps, Himalayas), they were located far away from one another, in different countries and/or on different topographic aspects.

To test the first hypothesis, that non-native species richness is more likely to exhibit negative relationships with elevation while native species richness is more likely to exhibit unimodal (hump-shaped) relationships, we classified elevational diversity relationships from all studies ($N = 65$) and from those having both native and non-native species sampled ($N = 32$) into the following categories: unimodal, linear negative, polymodal (with two or more peaks) and none (no clear pattern). Pattern classification was based on the analyses and descriptions in the original literature.

To test the second and third hypotheses, that native and non-native species differ in their upper and lower elevational limits, and in their elevational extents, t tests were used except where distributions were not normal (as detected using Shapiro–Wilk tests), in which case Mann–Whitney Rank Sum Tests were used. Only datasets containing both native and non-native species ($N = 32$) were

used in this analysis. The lower and upper sampling limits were used as surrogates to represent the length and start/end limits of elevational gradients. However, in many cases, the sampling limits did not always represent the actual mountain elevational limits. For example, agricultural lands at lower elevations and areas above the tree- or vegetation-lines at higher elevations can limit the elevational extents that can be sampled. For these reasons, in addition to the fact that environmental conditions at a given elevation can vary drastically across different elevational gradients, we were unable to standardize elevation across the 65 case studies.

We used linear mixed-effects models to test whether the native and non-native species show evidence of the same or similar distributional constraints along the elevational gradients. That is, whether non-natives and natives occurring within the same mountain range have similar lower and upper elevational limits or overall elevational extents. Because native and non-native species richness within a given mountain range are not statistically independent, sampling location was treated as a random effect. The diversity peak and the lower and upper elevational limits of non-native and native species were modelled as linear functions of either their lower elevational limit, upper limit (Grytnes & Vetaas, 2002), or extent, and as interactions between these variables and species status (native versus non-native). Statistically significant interaction terms would provide evidence to support our hypothesis that native and non-native species differ in their responses to elevation. For this analysis, we only used the data from mountain locations having both native and non-native species ($N = 32$).

To examine the possible effects of sampling methods on elevational diversity patterns, we classified the data collection techniques for the 32 cases with both native and non-native species into three

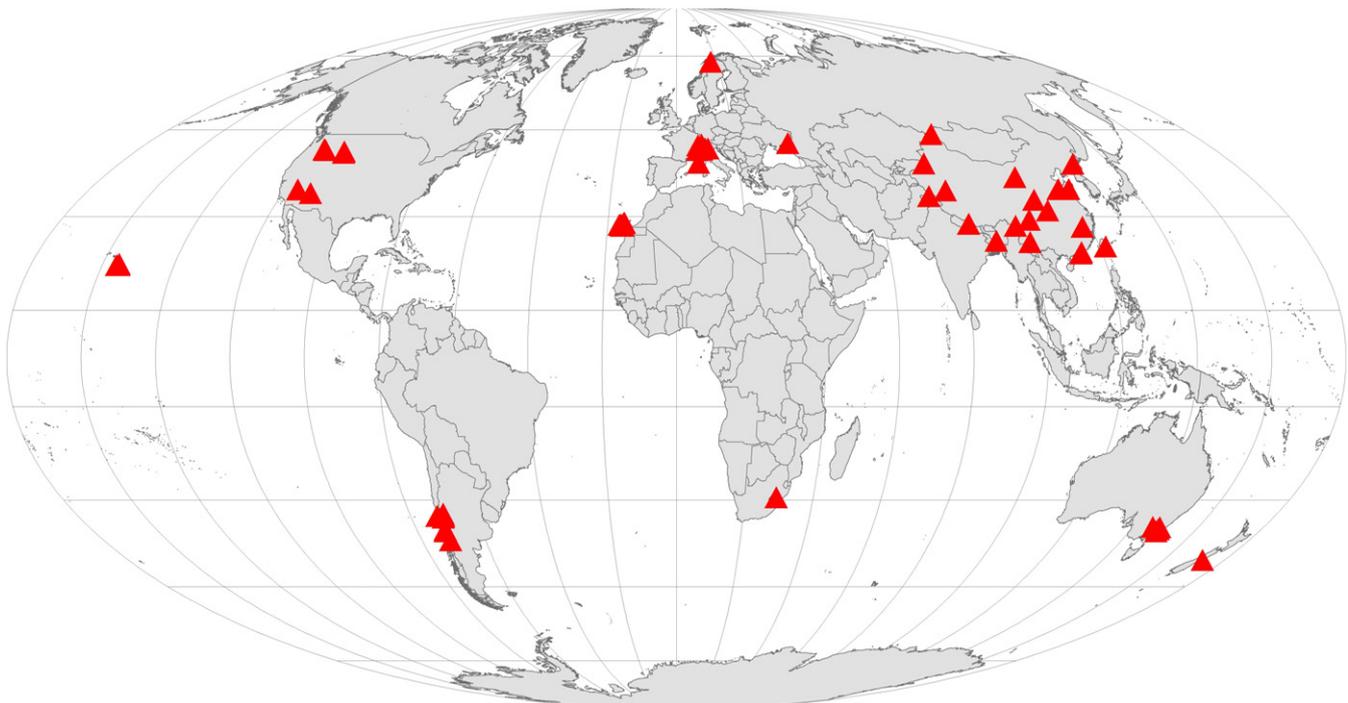


FIGURE 2 Locations of the 65 case studies on elevational distribution of non-native plants around world's mountains [Colour figure can be viewed at wileyonlinelibrary.com]

main categories: field transect (plot-based data), regional flora (interpolated species richness based on only presence point data) and raster grid data (see Guo et al., 2013). The regional floras category also included herbarium and museum records (specimens) from floristic and vegetation surveys. However, because the raster/grid category included only six cases, which are similar to many flora data collections, we combined these two methods to ensure an adequate sample size for statistical analysis.

To examine how elevational diversity patterns may change with latitude, we also classified the 32 cases containing both native and non-native plants into two latitudinal zones (i.e. 0–35° and >35°). We used these two groups to ensure sufficient sample sizes for statistical analysis (only three cases were below 20°, and only one case was above 50° in latitude). We also tested for differences in elevational diversity relationship between studies conducted in the Northern and Southern Hemispheres.

We used G-tests for the above comparative analyses of sampling approach, latitudinal gradient, Southern and Northern Hemispheres. To ensure sufficient sample sizes, we limited these analyses to the two dominant elevational diversity patterns—negative versus unimodal.

3 | RESULTS

Non-native and native species clearly exhibited different elevational diversity patterns ($\chi^2 = 11.82$, $df = 3$, $p = .008$). Among the 32 cases where both non-native and native species were sampled, 15 cases (47%) showed declines of non-native species with elevation, and 14 cases (44%) showed unimodal patterns. For native species, only four cases (13%) showed declines with elevation, but 27 (84%) showed unimodal patterns (Table 1).

Among the 65 cases worldwide, non-native species richness declined with increasing elevation (or better described as “negative exponential” distribution; 32/65 = 49%), with fewer of the gradients showing a unimodal form (25/65 = 39%). The rest were positive ($N = 3$), bimodal ($N = 2$), polymodal ($N = 2$) or had no clear pattern ($N = 1$). These observations generally support our first hypothesis.

All 25 unimodal gradients for non-native species were right-skewed (i.e. peak diversity below the elevational midpoint); whereas,

TABLE 1 The classification of the relationships between species richness and elevation for both non-native and native plant species sampled on the same mountains ($N = 32$). Shapes of elevation-diversity relationships differed significantly between non-native and native species

Category	Description	No. cases (%)	
		Non-native	Native
Unimodal	Hump-shaped	14 (44)	27 (84)
Negative	Decreasing with elevation	15 (47)	4 (13)
Polymodal	Multi-peaks	2 (6)	1 (3)
None	No clear pattern	1 (3)	0 (0)

three of the 27 unimodal patterns for native species were negatively or left-skewed. However, among the 27 cases where native species showed a unimodal pattern, 11 (41%) cases were non-unimodal for co-occurring non-native species along the same elevational range. Thus, the two groups showed low concordance in their elevational distribution and diversity patterns on the same mountains (e.g. Table 2 and S2).

Our observations support our second, third and fourth hypotheses. Regarding hypothesis 2, on average and across the elevational gradients examined, the richness of non-native species peaked at lower elevations than that of native species (Mann–Whitney Rank Sum Test, $U = 742$, $T = 1,995$, $p = .013$, $r = .29$). Regarding hypothesis 3, the mean upper, but not the lower distribution limits of non-native species were lower than those of natives (Mann–Whitney Rank Sum Test for upper, $U = 555$, $T = 1,677$, $p = .87$, $r = .03$; Mann–Whitney Rank Sum Test for lower, $U = 444.5$, $T = 1,039$, $p = .037$, $r = .21$). Finally, regarding hypothesis 4, non-native species also occupied smaller mean elevational ranges than natives (Mann–Whitney Rank Sum Test, $U = 319.5$, $T = 880.5$, $p = .002$, $r = .36$).

Linear mixed-effects models revealed that the mean elevational peaks of diversity, elevational extents, and lower and upper elevational limits were all positively correlated between native and non-native species occurring across the same mountains (Figure 3). Unlike the mean lower limits, that were similar between native and non-native species, the mean elevational extents and upper limits of non-native species were all, respectively, smaller than or lower than those of native species (Figure 3). While mean elevations of diversity peaks and lower limits were positively correlated to each other for both native and non-native species, mean diversity peaks and upper limits were only positively correlated for native species (Table S2). In addition, relationships among mean diversity peaks, elevation extents, and upper and lower limits did not differ between native and non-native species as determined by non-significant interaction terms (Table 2).

Despite the general patterns described above, the relative positions of non-native versus native species varied across the mountains and regions around the globe. For example, relative to the overall patterns described above when all studied mountains were considered together, the mean upper elevational limits and extents, and diversity peaks of non-natives were much lower than those of natives (Figure 3). In Hawaii, however, non-native species already exceed native species in terms of richness ($T = -4.81$, $p = .0002$), and in both Hawaii and New Zealand, non-native species have reached the same elevational extents of native species (Fig. S1).

The mountains at higher latitudes (>35°) had higher proportions of negative than unimodal elevational diversity patterns for non-native species across latitudes, but no difference was detected for native species (Table 3). The proportion of negative elevational diversity patterns tended to be higher for non-native plants in Northern than in Southern Hemispheres, but no difference was found for native species. No difference in the proportions of negative versus unimodal elevational diversity patterns for both non-native and native species was found between islands and continents (Table 3). There were marginally higher proportions of unimodal

TABLE 2 ANOVA style analysis of mixed-effects models to test for interactions between native and non-native plant species ("Status") based on their lower and upper elevational limits and elevational extent. Data from 32 mountain locations where both native and non-native plant data were used. Site location was treated as a random effect to account for the lack of independence between native and non-native status. Note that lower limit and diversity peak were transformed prior to analysis [$\sqrt{x + 1}$]

	χ^2	df	P
(1) Diversity peak (m)—Lower limit (m)			
ANOVA (Type III): Response: Diversity peak (m)			
Intercept	46.933	1	<.0001***
Lower limit (m)	26.422	1	<.0001***
Status	5.339	1	.021*
Lower limit (m) × Status	0.023	1	.879
(2) Diversity peak (m)—Upper limit (m)			
ANOVA (Type III): Response: Diversity peak (m)			
Intercept	11.54	1	.0007***
Status	5.596	1	.018*
Upper limit (m)	18.306	1	<.0001***
Status × Upper limit (m)	0.235	1	.628
(3) Diversity peak (m)—Elevation extent (m)			
ANOVA (Type III): Response: Diversity peak (m)			
Intercept	39.44	1	<.0001***
Status	1.444	1	.23
Elev. Extent (m)	1.394	1	.238
Status × Elev. Extent (m)	0.001	1	.982
(4) Lower limit (m)—Upper limit (m)			
ANOVA (Type III): Response: Lower limit (m)			
Intercept	1.573	1	.21
Status	0.087	1	.768
Upper limit (m)	10.652	1	.001**
Status × Upper limit (m)	0.602	1	.438
(5) Lower limit (m)—Elevation extent (m)			
ANOVA (Type III): Response: Lower limit (m)			
Intercept	14.586	1	.0001***
Status	0.179	1	.673
Elev. Extent (m)	2.194	1	.139
Status × Elev. Extent (m)	0.395	1	.53
(6) Upper limit (m)—Elevation extent (m)			
ANOVA (Type III): Response: Upper limit (m)			
Intercept	36.204	1	<.0001***
Status	0.44	1	.507
Elev. Extent (m)	100.499	1	<.0001***
Status × Extent (m)	1.376	1	.241

patterns for non-native species using data from regional floras than that from field transects, but no such difference for native species. Finally, we found no effect of roadside versus other sampling methods on elevational diversity patterns for either native or non-native species (Table 3).

The mean elevations of non-native diversity peaks were higher using roadside sampling than other sampling methods ($t = 1.92$, $df = 61$, $p = .029$). However, no difference was observed in elevational diversity patterns, mean upper elevational limits ($t = 0.224$, $df = 57$, $p = .412$) and sampling elevational extents ($t = 0.551$, $df = 63$, $p = .292$) for non-native species between these two sampling methods. For native species, no difference was found in elevational diversity patterns and mean diversity peaks ($t = -0.18$, $df = 30$, $p = .427$), but mean upper limits were marginally different ($t = 1.36$, $df = 27$, $p = .093$) and the sampled extents were shorter using roadside sampling than using other methods ($t = 3.494$, $df = 31$, $p = .0007$).

4 | DISCUSSION

Non-native species richness is expected to be lower than that of native species along elevational gradients, and concentrated at lower elevations, because of fewer human activities at high elevation sites. Human activity leads to increased numbers of non-native species (Hulme, 2009; Pyšek et al., 2004), although the contribution of subsequent dispersal remains to be examined (Wilson et al., 2009). Our results—that non-native species typically exhibit negative species richness–elevation relationships whereas these relationships for native species tend to be unimodal/hump-shaped—confirm this outcome for elevational gradients globally, providing support for the first hypothesis.

Although the shapes of the diversity patterns of non-native and native species along the elevational gradients are mostly different, the absence of statistically significant interaction terms in the mixed-effects models indicate that these patterns seem to be framed in similar ways by the geological features of the mountains or sampling extents (i.e. lower and higher limits and elevational extents) regardless of native or non-native status. At the present level of invasion, however, the elevational distribution patterns of non-native species as a whole seem to be more strongly linked to lower than higher elevational limits. This also suggests that, in most cases, non-native species usually reach the lower elevations first and then spread upward with time (in contrast, most native species have already occupied their potential elevational gradients). Indeed, overall, our data support the hypotheses that mean elevations of diversity peaks and mean elevational limits are lower for non-native than for native species (hypothesis 2); mean elevations of diversity peaks for non-native species are more strongly correlated with mean lower than mean upper elevational limits (hypothesis 3); mean elevational extents over which non-native species occur are smaller than those for native species (hypothesis 4).

Although most human populations and activities have been concentrated at low elevations (Small & Cohen, 2004; Koh, Lee, & Lin, 2006; Bu, Tan, Li, & Zhang, 2010), human activities are increasingly shifting upwards and some preferentially onto mountaintops due to tourism, mining and skiing, among others. These activities provide an opportunity for increased propagule pressure of non-native species

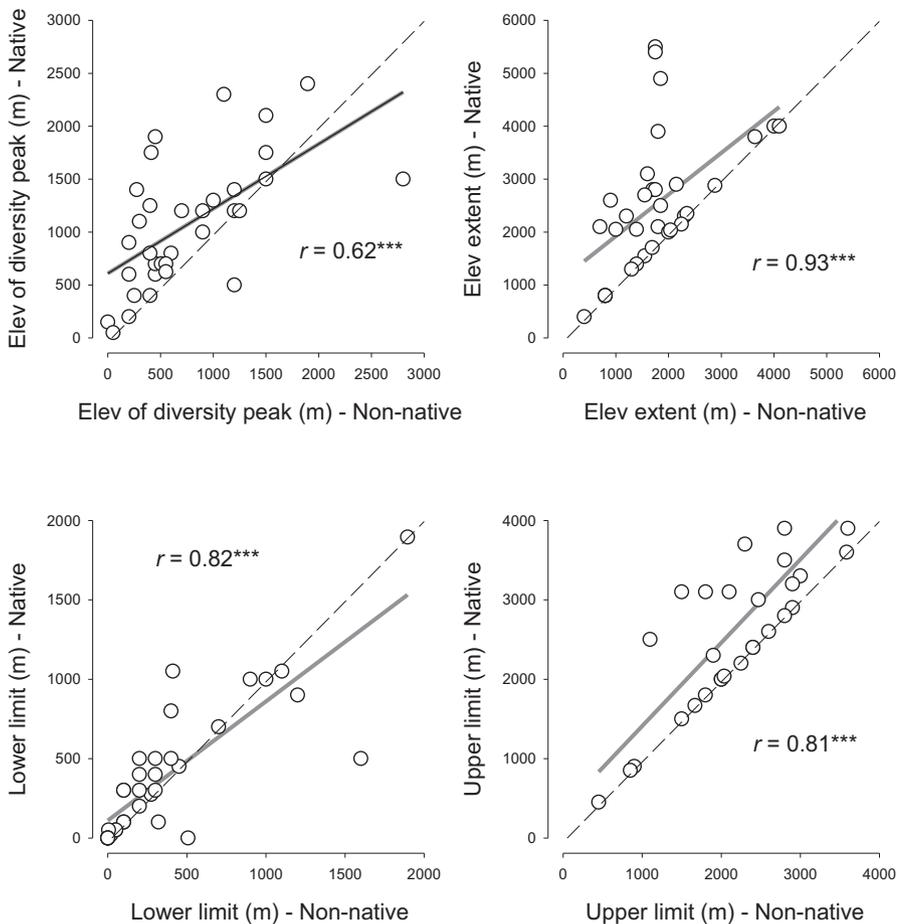


FIGURE 3 The correlations in elevation of diversity peaks, elevational lower/upper limits, and extents between non-native and native species on the same mountains ($N = 32$). The differences between the two groups of species can be seen in the intercepts and slopes in regression. * $p < .05$, ** $p < .01$, *** $p < .001$. The dashed lines serve as comparative references ($y = x$ or slope = 1)

in high elevation areas, as well as for disturbances that may promote invasion (Pauchard et al., 2016). Higher elevations are also predicted to experience greater impacts from climate warming (McDougall et al., 2011), which may further promote the upward expansion of non-native species. Indeed, with increasing human expansion and ongoing climate warming, more opportunities are being created for non-native species to spread into higher elevations (Barni, Bacaro, Falzoi, Spanna, & Siniscalco, 2012; le Roux et al., 2013). Our data from Hawaii and New Zealand illustrate how this potential for increased human activity needs future

consideration. In these regions, species richness for non-native species already exceeds that of native species across elevational gradients (Daehler, 2005; Marini et al., 2009; Sandel & Corbin, 2010; Seipel et al., 2012). These results suggest that lower elevational distributions of non-native species on other mountains do not reflect a preference of non-natives for lower elevations, but rather are indicative of limited time for upslope dispersal, and currently smaller species pools for non-native species in most cases. Moreover, they suggest that processes associated with the expansion of humans may not only increase into the future, but also be exacerbated by climate change.

Two caveats should, however, be kept in mind. First, in some areas, humans have historically utilized high elevation area in the past as a pastoral resource due to high protein quality of herbs and forbs in the alpine landscape. This pastoral use of high elevations occurred across large geographic area and likely had great impacts on plant dispersal and communities. In contrast, agricultural use of high elevation ecosystems is decreasing globally (e.g. Andes, Alps and in most Asian mountains; Baud & Ypeij, 2009). This change has the potential to limit the impacts from certain land use traditions (MacDonald et al., 2000) and complicate forecasts of future spread by non-native into high elevation ecosystems. Second, some studies on elevational distribution of non-native species included in this synthesis were conducted along roadsides (e.g. Arevalo et al., 2005;

TABLE 3 The results of G-tests showing the effects of sampling locations and techniques on elevational diversity patterns (negative versus unimodal) of non-native versus native plant species along the same elevational gradients ($N = 32$). Bold face = significant difference at $p < .05$.

	Non-native		Native	
	G	P	G	P
Hemisphere (N vs. S)	2.801	.094	0.272	.602
Islands vs. mainland	1.910	.167	0.094	.760
Latitude ($\leq 35^\circ$ vs. $> 35^\circ$)	8.222	.004	1.495	.221
Regional flora vs. field transects	3.621	.057	0.913	.339
Roadside vs. other methods	0.500	.481	0.002	.967

Seipel et al., 2012), which could overestimate the distributions of non-native species on mountain regions. The rationale is that although the non-native species are found along the roadside, many of them may not have invaded communities farther away from the roadside (Averett et al., 2016).

In addition to those findings described above, we also found that non-native species data collected using regional floras and at higher latitudes, especially in the Northern Hemisphere, tend to exhibit proportionally more unimodal patterns than data based on field transects (a result similar to trends for native species found in a more extensive, previous study ($N = 443$; Guo et al., 2013). Yet, this trend was not detected for native species in this study possibly due to a smaller sample size or greater sensitivity of non-native species to sampling effects. On a related note, we presently cannot assess regional differences (e.g. Europe versus America versus Asia) in elevational diversity patterns for non-native species because of the relatively small number of mountains that have been surveyed within each region. Furthermore, this detection of regional differences could be complicated by latitude, sampling techniques and the true height of the mountain ranges versus the actual sampled elevational extents, among many other factors that are unique to each region.

The currently observed spatial patterns constitute a snapshot of ongoing processes and are likely to change with time. Thus, long-term field observations and experimental studies are needed to monitor future invasions across elevational gradients. Such efforts would be most effective when coupled with theoretical projections and simulations. In addition, the vertical patterns of invasion along elevational gradients seem to reflect the overall horizontal patterns in degree of invasion (DI) across the globe. For example, in heavily invaded regions or mountains, such as Hawaii and New Zealand, although the peaks of non-natives are still lower than those of natives, the elevational extents of both native and non-native species are equivalent. Furthermore, mountains containing extensive road networks deserve special attention given the known effects of transportation on the spread of non-native invasive species (e.g. Kalwij, Robertson, & van Rensburg, 2015).

From a conservation perspective, in most cases examined in this study, both non-native species richness and human population density (Appendix S1) decline with elevation, while native species usually exhibit hump-shaped curves. These patterns imply a strong association of human populations with the distribution of non-native species. Evidence that more non-native, but especially invasive species, tend to prefer disturbed habitats than native species (e.g. Pyšek et al., 2005) provides a potential mechanism for the pattern. The vertical spread of non-native species, as investigations of Hawaii and New Zealand suggest might occur, and the facilitation by climate change (warming) of upslope range extensions of non-native species (Pauchard et al., 2016) are likely to pose a significant ecological threat to native species at higher elevations. Although, with warming climates, both native and non-native species are expected to shift to higher elevations in tracking optimal temperatures (Dainese et al., 2017; Petitpierre et al., 2015), native

species on mountaintops are likely to be most at risk from local extirpation because no other habitat is available to them (Hellmann, Byers, Bierwagen, & Dukes, 2008; Nogues-Bravo et al., 2008). While there is some debate about the outcomes of competition among native and non-native species (e.g. Davis, 2003), a range of conditions (such as resource limitation) has been shown to enable competitive displacement of native species by non-native invaders (Alexander et al., 2016; Pauchard & Alaback, 2004). Such changes could ultimately have significant impacts on native sky-island floras globally.

Finally, it is clear that further studies to explore and understand the form of non-native versus native plant elevational distributions, their mechanistic basis, and their conservation implications are necessary. Studies occurring along the same elevational gradients and across multiple sampling periods will be particularly beneficial (Fig. S2; Seipel et al., 2012; Chown et al., 2013; Marini et al., 2013). For example, in this study, despite similar sampling approaches (methods, time and location), non-native and native plants exhibit clearly different elevational diversity patterns. The sampling locations (e.g. N. versus S. Hemisphere, islands versus mainland, low versus high latitudes) and techniques (regional floras versus field transects; roadside versus other sampling) impose greater effects on non-native than on native plants. Sampling along the same elevational gradients would help to control for this variability and in doing so help to determine the extent to which different mechanisms may be involved in determining the elevational distributions of native versus non-native species. That is, native species appear to be less strongly associated with human settlement patterns and activities than non-native species. Long-term monitoring of the changes in the distributions of non-native species along elevational gradients (e.g. through repeated sampling of the same transects/plots; Kalwij et al., 2015), by helping to determine temporal movement patterns, would help to inform native species conservation and non-native species management.

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DATA ACCESSIBILITY

Data related to this paper are available in the Purdue University Research Repository, an archive (<https://purr.purdue.edu/>; <https://doi.org/10.4231/r7610xhr>).

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BIOSKETCH

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Author contributions: Q.G. conceived the project, S.F., Z.S., Q.G. and J.K. collected/provided the data; Q.G., B.I. and J.K. analysed the data; and all authors contributed to the writing.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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APPENDIX 1

LIST OF DATA SOURCES OF SPECIES RICHNESS AND DISTRIBUTION ALONG THE ELEVATIONAL GRADIENTS FOR THE 65 WORLDWIDE CASE STUDIES

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