Constructing a database of alien plants in the Himalaya to test patterns structuring diversity

Suresh Rana[1], Bhawana Dangwal[2], G.S. Rawat[3], and Trevor Price[4]

[1]G.B Pant National Institute of Himalayan Environment
[2] G.B Pant National Institute of Himalayan Environment
[3]Wildlife Institute of India
[4]University of Chicago

November 9, 2023

Abstract

Differences in the number of alien plant species in different locations may reflect climatic and other controls that similarly affect native species and/or propagule pressure accompanied with delayed spread from the point of introduction. We set out to examine these alternatives for Himalayan plants, in a phylogenetic framework. We build a database of alien plant distributions for the Himalaya. Focusing on the well documented regions of Jammu & Kashmir (west) and Bhutan (east) we compare alien and native species for (1) richness patterns, (2) degree of phylogenetic clustering, (3) the extent to which species-poor regions are subsets of species-rich regions, and (4) continental and climatic affinities/source. We document 1,470 alien species (at least 600 naturalised), which comprise ~14% of the vascular plants known from the Himalaya. Alien plant species with tropical affinities decline in richness with elevation and species at high elevations form a subset of those at lower elevations, supporting location of introduction as an important driver of alien plant richness patterns. Separately, elevations which are especially rich in native plant species are also especially rich in alien plant species, suggesting an important role for climate (high productivity) in determining both native and alien richness. We find no support for the proposition that human disturbance or resistance to invasion by native species affect alien distributions. Results imply an ongoing expansion of alien species from low elevation sources, some of which are highly invasive.

1

1   **Constructing a database of alien plants in the Himalaya to test patterns**

2   **structuring diversity**

3   Suresh K. Rana[1], Bhawana Dangwal[1], Gopal S. Rawat[2], Trevor D. Price[3*]

4   [1]G.B Pant National Institute of Himalayan Environment, Almora, Uttarakhand, 263643 India.

5   [2]Wildlife Institute of India, Dehradun, Uttarakhand, 248001 India.

6   [3]Zoology 309A, Department of Ecology and Evolution, University of Chicago, 1101 East

7   57th Street, Chicago, IL 60637 USA.

8   **Correspondence**

9   [*]Trevor D. Price: Email. pricet@uchicago.edu

Abstract

Differences in the number of alien plant species in different locations may reflect climatic

and other controls that similarly affect native species and/or propagule pressure accompanied

with delayed spread from the point of introduction. We set out to examine these alternatives

for Himalayan plants, in a phylogenetic framework. We build a database of alien plant

distributions for the Himalaya. Focusing on the well documented regions of Jammu &

Kashmir (west) and Bhutan (east) we compare alien and native species for (1) richness

patterns, (2) degree of phylogenetic clustering, (3) the extent to which species-poor regions

are subsets of species-rich regions, and (4) continental and climatic affinities/source. We

document 1,470 alien species (at least 600 naturalised), which comprise ~14% of the vascular

plants known from the Himalaya. Alien plant species with tropical affinities decline in

richness with elevation and species at high elevations form a subset of those at lower

elevations, supporting location of introduction as an important driver of alien plant richness

patterns. Separately, elevations which are especially rich in native plant species are also

especially rich in alien plant species, suggesting an important role for climate (high

productivity) in determining both native and alien richness. We find no support for the

proposition that human disturbance or resistance to invasion by native species affect alien

distributions. Results imply an ongoing expansion of alien species from low elevation

sources, some of which are highly invasive.

Key words: alien species, climatic niche, directional filtering, elevational distribution,

Himalaya, species richness, seed plants.

1 | INTRODUCTION

Alien species have been introduced to new areas for centuries. The process has increased

exponentially in the past 50 years, with no signs of slowing down (Hulme et al., 2009; Sax et

al., 2007; Seebens et al., 2017; Van Kleunen et al., 2015). However, the number of alien plant

species varies across the globe, with some locations being relatively devoid of alien species,

while others are heavily dominated by them (Guo et al., 2021; Pyšek et al., 2017). Here we

evaluate the underlying causes of the distribution of alien species richness across the

Himalaya. In order to do this we compare native and alien species richness, given different

processes affect each. For example, differential rates of speciation can affect the richness

patterns of native species, but not that of aliens (Sax, 2001).

The predominant pattern for native plant species richness is that warm and wet

locations harbour more species than cold and dry ones (Francis & Currie, 2003; Kreft & Jetz,

2007). The pattern correlates with higher plant productivity (Currie et al., 2004; Hutchinson,

1959), aseasonality (Gao & Liu, 2018), and/or historical patterns of turnover (speciation and

extinction) (Igea & Tanentzap, 2020; Rana et al., 2022), all of which are correlated with each

other across space. In contrast, at a large spatial grain size, alien species richness broadly

correlates with native richness, but unlike native richness, which is highest in the tropics,

alien richness is thought to reach a maximum at mid-latitudes (Guo et al., 2021; Sax, 2001).

The alien pattern plausibly reflects a lack of knowledge of tropical introductions (Chong et

al., 2021; Nuñez et al., 2022), but postulated biological processes include invasion resistance

by species-rich tropical communities, differences in disturbance, and differences in number

of introductions (Chong et al., 2021; Guo et al., 2021). Similarly, across elevational gradients

alien richness broadly correlates with native richness because both decline towards high

altitudes (Alexander et al., 2011) but sometimes alien richness shows a steeper decline than

natives (e.g., Mallen-Cooper & Pickering, 2008). Punctuating the decline with elevation, both

aliens and natives may also show intermediate peaks in richness. The positions of the alien

and native peak may roughly correspond (e.g., Denslow et al., 2010; Khuroo et al., 2011), or

be displaced (Manish, 2021). The drivers of similarities and difference between natives and

aliens along elevational gradients have yet to be assessed.

If native and alien patterns are concordant, and both strongly correlated with climate,

a parsimonious inference is that climatic conditions in the introduced region are an important

determinant of alien distributions (Sax, 2001). A corollary of this hypothesis is that if (1)

climate *per se* is important and (2) native and alien species with similar climatic niches are

closely related, we expect to observe increased phylogenetic clustering (the extent to which

species are drawn from a few clades) when alien and native species are considered together,

rather than separately (Qian & Sandel, 2022).

Deviations of alien patterns from native patterns suggest additional forces beyond

climate are at play, which may apply to native species or to alien species. For example, native

diversity in the Himalaya is affected by differential patterns of extinction and speciation in

different climatic zones, as well as limitations on dispersal (Muellner-Riehl, 2019; Rana et

al., 2022), whereas as noted above alien patterns cannot be affected by speciation processes

(Sax, 2001). A steep decline in alien richness across space may reflect location of

introduction and the subsequent time it takes to extend range, whereas time available has

been much longer to native species. When applied to mountains, a role for location of

introduction coupled with a time delay is known as the directional filtering hypothesis,

specifically invoked to explain a decline in alien richness from low to high elevations (the

location of introduction is considered to be primarily at low elevations, Alexander et al.,

2011; Marini et al., 2013). The directional filtering hypothesis predicts a pattern of

79   nestedness, whereby species at higher elevations represent a subset of those at lower

80   elevations (Alexander et al., 2011).

81   If directional filtering operates, both biotic and abiotic factors may limit range

82   expansions. The contrasting roles of biotic and abiotic factors have been invoked to explain

83   patterns of phylogenetic distance between alien and native species across the North American

84   flora, as observed when moving from benign to harsh climates, and from small to large

85   scales. The logic is abiotic factors lead to small phylogenetic distances (relatives are similarly

86   adapted), and biotic ones to larger phylogenetic distances (close relatives exclude each other

87   (Park et al., 2020)). Finally, disturbance, by removing competitors can facilitate alien

88   establishment and is associated with introductions: e.g., exotic crops associated with

89   agriculture.

90   In this paper we study the distribution of Himalayan plants to evaluate hypothesized

91   factors that account for variation in alien species richness. First, we develop a comprehensive

92   database of Himalayan alien species, describe their source affinities, and characterize their

93   elevational ranges and geographical distributions within the Himalaya. Second, we use this

94   compilation to assess underlying correlates of alien richness patterns. We evaluate causes of

95   patterns of alien species richness across the Himalaya, as far as is possible with the resolution

96   available, which is at broad spatial grain size (200m elevational bands across large regions).

97   Because this is a large grain size, we focus on elevational distributions in two relatively small

98   geographically separated regions, one in the west (Jammu & Kashmir) and the one in the east

99   (Bhutan, north Bengal and Sikkim), which are relatively well known and provide a summary

100 of the species diversity gradients across space. Specifically, our goals are to:

101 (1) examine a role for climate in affecting the distribution of alien plant species in the

102 Himalaya by searching for correlates with climatic variables, and secondarily, by testing if

103 alien and native species when considered together show relatively high phylogenetic

104 clustering.

105 (2) evaluate the evidence for directional filtering by asking if high elevation assemblages of

106 alien species are nested within lower elevation assemblages, and if alien species show a

107 pattern of nesting that is stronger than observed for native species. We also consider a

108 possible role for a varying intensity of competition along the gradient as a driver of the

109 patterns by testing if (a) the proportion of alien species declines with the number of native

110 species, (b) increased phylogenetic clustering of alien species correlates with elevation,

111 expected if abiotic conditions become more important in harsher climates (Park et al., 2020),

112 and (c) highly disturbed areas contain more alien species.

113 **2 | MATERIALS AND METHODS**

114 **2.1 | Data curation**

115 We curated the information on distribution and elevational ranges of all alien species reported

116 from the Himalaya in 31 regional floras and 93 research articles (Appendix-1). To compare

117 the alien distribution patterns with natives we used our previously published dataset on

118 distributions of native plant species across the Himalaya (Rana et al., 2022; Rana, Price, et

119 al., 2019). To harmonize taxonomy across sources, we assessed all species names against the

120 updated list of botanical names available from www.worldfloraonline.org (World Flora

121 Online) and resolved every taxon to the species level. Any species whose native distribution

122 extends into the Himalayan region is considered as a native, whereas a species whose native

123 range is elsewhere is considered as alien. Native and alien distributional ranges of all species

124 were validated from various online sources including the Invasive Species Compendium

125 (www.cabi.org/isc), the Global Invasive Species database (http://www.iucngisd.org/gisd/)

126   and the USDA-GRIN (https://npgsweb.ars-grin.gov/). Complete dataset of alien species along

127   with the hyperlinks to the sources are provided for each species in Appendix-2. Species were

128   classified as cultivated (species that are cultivated by humans for food or ornaments) or

129   naturalized (a species that does not require human assistance to reproduce and maintain itself

130   in its natural environment). Note that many cultivated species may also be naturalized, but we

131   prioritize cultivated over naturalized in this compilation. We also listed each species as

132   invasive (species considered to have harmful impacts) as classified by the Global Invasive

133   Species databases (hence not necessarily invasive in the Himalaya).

134   To assess source regions we recorded the native range of alien species to the

135   continents (Africa, Australia, Europe, North America and South America; following

136   Brummitt, 2001). Tropical Asia and Temperate Asia were not separated because the

137   Himalaya acts as a boundary between these two regions and species distributions have been

138   assigned too crudely to classify them unambiguously. Plant species were also classified into

139   three biogeographic categories, i.e., tropical, temperate and cosmopolitan, based on the centre

140   of species diversity within each genus, as categorized by Wu (1991). These data are

141   unavailable for 525 species (<5%, 378 native species, 147 alien species) which we excluded

142   from relevant analyses.

143   **2.2 | Species distributions**

144   The distribution of every species was categorised into six distinct regions from east to west,

145   i.e., Arunachal Pradesh, Bhutan plus Sikkim and adjoining hill districts of West Bengal

146   (henceforth the Bhutan region), Nepal, Uttarakhand, Himachal Pradesh, and Jammu &

147   Kashmir (Fig. 1). To compare the elevational patterns between the east and west Himalaya,

148   as noted above we particularly focus on two well-known regions: Jammu & Kashmir (west)

149   and the Bhutan region (east). To help interpret elevational patterns we also assessed the

150   distribution of different life forms (i.e., trees, shrubs, herbs, woody climbers, herbaceous

151   climbers, and epiphytes).

152   We considered only angiosperms (8,765 native species and 1,470 alien species).

153   Elevational ranges of 1,141 species (845 native species and 296 alien species) are unavailable

154   and were excluded from the distributional analyses. Along elevational gradients, we

155   calculated species richness as the number of species with overlapping ranges in every 200m

156   elevational band up to 5000m in east and west Himalaya (Rana, Price, et al., 2019). To

157   interpolate species richness patterns across the Himalayan landscape, we divided a Digital

158   Elevation Model (https://srtm.csi.cgiar.org) into grids of size 0.2 degree (1140 grids). Within

159   each of the six regions, grids at 0.2º resolution are assigned the presence of a species if it is

160   recorded in that region, and its elevational range intersects the mean elevation of the cell.

161   Species richness across the Himalaya was smoothed from these data by using the inverse

162   distance weight interpolation method in the 'gstat' R package (Gräler et al., 2016).

2.3 | Climatic data

164   We confined our analysis to annual precipitation (BIO12) and minimum temperature of the

165   coldest month (BIO6), because of the apparent importance of freezing in setting the

166   altitudinal distribution of native plant in the Himalaya (Rana et al., 2022). We obtained these

167   climatic raster layers from the WorldClim (www.worldclim.org) database (Fick & Hijmans,

168   2017), using the 'raster' (Hijmans, 2017) and 'sp' (Bivand et al., 2013; Pebesma & Bivand,

169   2005) packages in R. Coordinates of the grids of size 0.2x0.2 degrees were used to extract

170   annual precipitation and minimum temperature of every grid for further analyses. For natives

171   we have previously shown that, WorldClim and the alternative Chelsa dataset (Karger et al.,

172   2017) give similar results across the Himalaya.

2.4 | Phylogenetic analysis

We evaluate patterns of phylogenetic clustering to ask if (1) clustering is higher when native and alien species are considered together than when native species are considered alone, as predicted if related species have similar climatic niches and climate is an important control on establishment (Qian & Sandel, 2022), and (2) document patterns of phylogenetic clustering of native and alien species along the elevational gradient. To do this, all species were linked to a phylogeny implemented in the 'V.PhyloMaker' R package (Jin & Qian, 2019). The phylogeny was derived from two published trees (Smith & Brown, 2018; Zanne et al., 2014) and includes 74,533 species and all families of extant vascular plants (Jin & Qian, 2019). A total of 4,579 Himalayan species are present in the backbone. To graft unresolved species (55%) and genera (26%) we used the 'scenario 3' approach implemented in 'V.PhyloMaker' (Jin & Qian, 2019). This method attaches a species of an existing genus to the basal node of the genus (if only one sequenced species is available for the genus, the basal node is generally placed half the distance from the family basal node to the tip), and any new genera to the basal node of the family branch.

Using the phylogeny and species presence/absence matrix for every 200m elevational band we calculated the Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD) (Webb et al., 2002) separately for the Bhutan region in the east and Jammu & Kashmir in the west, using the 'PhyloMeasures' R package (Tsirogiannis & Sandel, 2016). The phylogenies used for calculation of these metrics were restricted to alien species, native species, or all plants together within these two focal regions. We computed the standardised versions of MPD and MNTD, i.e. the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) respectively because these should be largely uncorrelated with species richness in null model phylogenies (Tsirogiannis et al., 2012). A positive value for NRI or NTI implies

197 clustering (i.e., relatively few lineages contribute to the species present in a particular

198 elevational belt), whereas a negative value implies over-dispersion (i.e., many lineages

199 distributed throughout the phylogeny); significance at $P = 0.05$ is equivalent to NRI (or NTI)

200 > +1.96 (or < -1.96) (Mazel et al., 2016). We also computed species to genus ratios in 200m

201 bands (high ratios would be equivalent to clustering). To remove any biases due to

202 differences in the number of genera between native species and alien species, we rarefied the

203 native genera in each band to the same number as the alien genera (100 random samples) and

204 show the mean value for both the rarefied and complete data.

205 **2.5 | Species nestedness**

206 To test for directional filtering, we computed nestedness of alien and native plant species

207 assemblages (Almeida-Neto et al., 2008; Ulrich et al., 2009). First, we calculated the NODFc

208 statistic ('Nestedness metric based on Overlap and Decreasing Fill, standardized for

209 Connectance', Song et al., 2017), using the R package 'maxnodf' (Hoeppke & Simmons,

210 2021) which is designed to control for network size. We calculated NODFc for species

211 occurrences in elevational bands of 200m as one traverses from low to high elevations in

212 Jammu & Kashmir ($N = 23$ bands) and the Bhutan region ($N = 26$ bands), as well as from

213 west to east across the Himalaya at low elevations (below 1000m). We also computed a

214 phylogenetic version of NODFc using treeNODF (Melo et al., 2014) in the R package

215 'CommEcol' (Melo, 2021) which accounts for branch lengths. We test the hypothesis that the

216 composition of species-poor, high-elevation sites are nested within the composition of

217 species-rich, low-elevation sites, and that this pattern is stronger in aliens.

218   We developed a simple statistical test to compare nestedness between alien species

219 and native species, which involved for each elevational band drawing 100 random samples

220 from the native pool in the region, and 100 samples from the alien pool in the region, with the

221   sample size set to the number of species present in a given elevational band. The sampling

222   process revealed that with such a large number of species, the probability that native and

223   alien species are drawn from a common pool is extremely low (difference in NODFc values

224   greater than 0.05 are highly significant). Confidence limits are not reported given the large

225   differences in observed NODFc values.

226   **2.6 | Disturbance measures**

227   Both large numbers of native species and low levels of disturbance have been invoked as

228   factors limiting establishment of aliens. Both operate at small grain sizes, whereas our

229   analysis is of necessity at a large grain size, so we use our results only as a guide to possible

230   limits to establishment. Following Beaury et al. (2020) we regressed the proportion of alien

231   species in an elevational band on the number of natives (a negative slope may indicate

232   inhibition of alien establishment by natives). We discuss the assumptions involved in

233   applying this across large grain sizes in the supplement (Methods S1), where we show a

234   linear model is more appropriate than the general linear model recommended by Beaury et al.

235   (2020, see Fig. S1). As a measure of disturbance, we use Venter et al.'s (2020) estimate of the

236   human footprint for 2009, which is based on quantity of pastureland, agricultural land, night

237   lights and built environments. Understory forest management, forest conversion to

238   plantations, and extensive grazing in native habitats are not recorded. We note that

239   disturbance has been ongoing for thousands of years in the Himalaya and every elevational

240   belt has been disturbed to some degree (Fig. S2). Nevertheless, disturbance is greater in the

241   west than the east Himalaya (Fig. S2), as is apparent to visitors to each area.

242   **2.7 | Multivariate analyses**

243 Having conducted the tests of hypotheses separately, we evaluated roles for some of the

244 variables after statistically holding the others fixed, as many, including both climatic

245 variables and disturbance correlate with elevation (Table S1). We asked if disturbance

246 remained an important predictor of alien success after including number of native species and

247 climate variables in a linear model assuming normal errors, and if climate or elevation *per se*

248 better predict alien richness. In these analyses we also included tests for interactions. We

249 confirmed residuals were approximately normally distributed and homoscedastic through

250 visual plots. Multi-collinearity is not a problem in these tests (Table S1). We conducted

251 various analyses to evaluate the robustness of the results to spatial area and connectivity,

252 including using 1,140 grids of 0.2º resolution across the entire dataset, and random sampling

253 down to just 10-20 grids of 0.2º. All analyses gave similar results, and here we present

254 regressions of numbers of alien species for entire 200m elevational belts below 4,000m in the

255 Bhutan region and Jammu & Kashmir. We excluded the 4,000m to 5,000m belt because very

256 few alien species are present at these elevations.

257 **3 | RESULTS**

258 **3.1 | Species richness patterns**

259 In total we documented 1,470 alien angiosperm species, or approximately 14% of the known

260 Himalayan flora. Of these, 614 are considered completely naturalized, which is twice the

261 number in a global database (van Kleunen et al., 2019), but similar to that that which comes

262 from a recent study based on checklists from the relevant states (Wani et al., 2023). The van

263 Kleunen *et al.* (2019) database reports 606 naturalized alien species in the Himalaya, but in

264 our appraisal only ~50% of these species are alien, and the remainder are native.

265   Among associations with different continents, North America provides the most alien

266   species (402), followed by South America (388), Europe (368), Africa (310) and Australia

267   (106). Note that the total is greater than 1,470 because some alien species are native to

268   multiple continents. The pattern for alien species is almost the inverse of that for native

269   species (native species: Africa [519 species] followed by Europe [341], Australia [347],

270   North America [132] and South America [88]).

271   Species richness for both aliens and natives decreases from the east to the west

272   Himalaya (Figs 1 b,c, 2). Jammu & Kashmir contains 70% fewer native species than the

273   Bhutan region (1,649 vs 5,452 respectively (Rana, Price, et al., 2019) but only 16% fewer

274   alien species (556 versus 634). Along elevational gradients in belts of 200m, native and alien

275   species shows a strong positive correlation both in the west and the east Himalaya i.e., $r =$

276   0.79 (Jammu & Kashmir) and $r = 0.92$ (Bhutan region, see Fig. 2). Alien species richness

277   remains approximately constant up to 2,000m, and then declines with elevation (Fig. 2), a

278   feature common to both naturalized and cultivated alien species (Fig. S3), as well as different

279   life forms (trees, shrubs, herbs; Fig. S4). The elevational decline associated with the 762

280   cultivated alien species, many of which are naturalized as well, may reflect the large number

281   of species cultivated across the plains of India, which are also present in the Himalayan

282   foothills. However, the 614 completely naturalized species show a similar decline (Fig. S3).
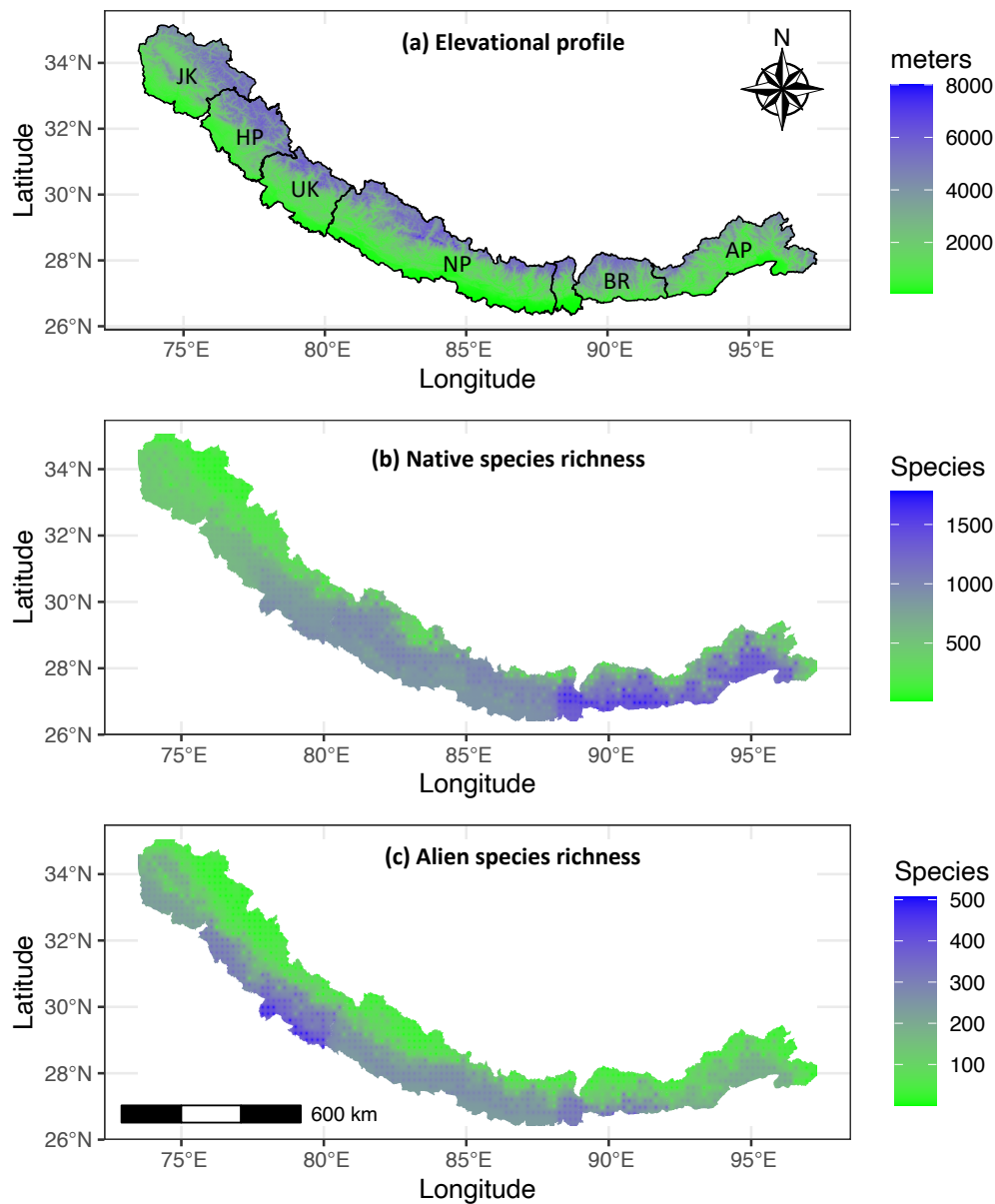
FIGURE 1 Maps of the Himalaya showing (a) elevations, with boundaries of the six regions we studied (JK: Jammu & Kashmir, HP: Himachal Pradesh, UK: Uttarakhand, NP: Nepal, BR: Bhutan region, AP: Arunachal Pradesh), (b) richness of native plant species, (c) richness of alien plant species.
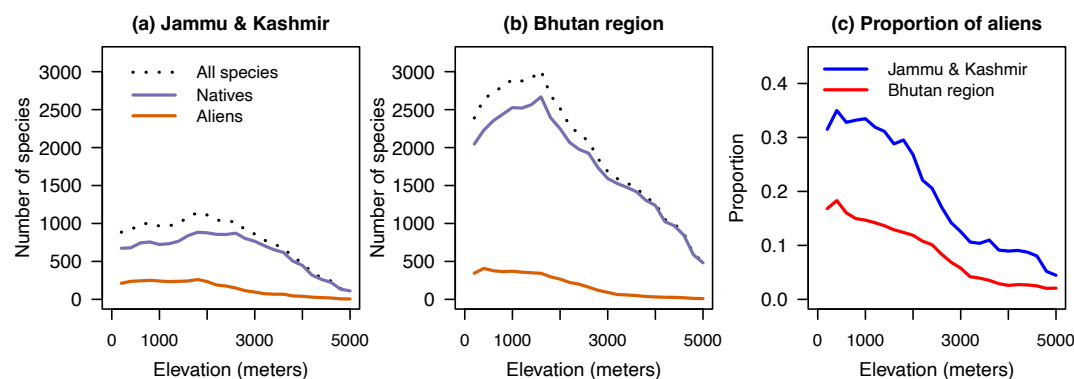
288

FIGURE 2 Species richness pattern of all species, native and alien species in 200m

elevational belts in Bhutan region and Jammu & Kashmir, and, *left,* the proportion of alien
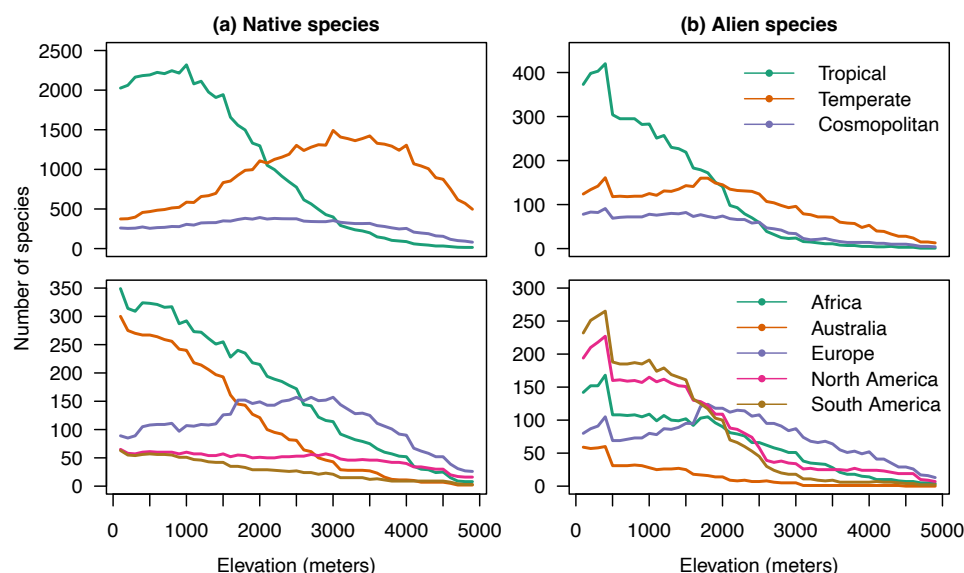
species in each belt.

292

FIGURE 3 Elevational richness patterns of angiosperm plant species in the Himalaya

assessed every 200m, as the number of species whose range overlaps that elevation, split by

biogeographical affinities. Top panels refer to species categorized by Wu (1991) as belonging

to tropical or temperate genera, and lower panels to species shared between the Himalaya and

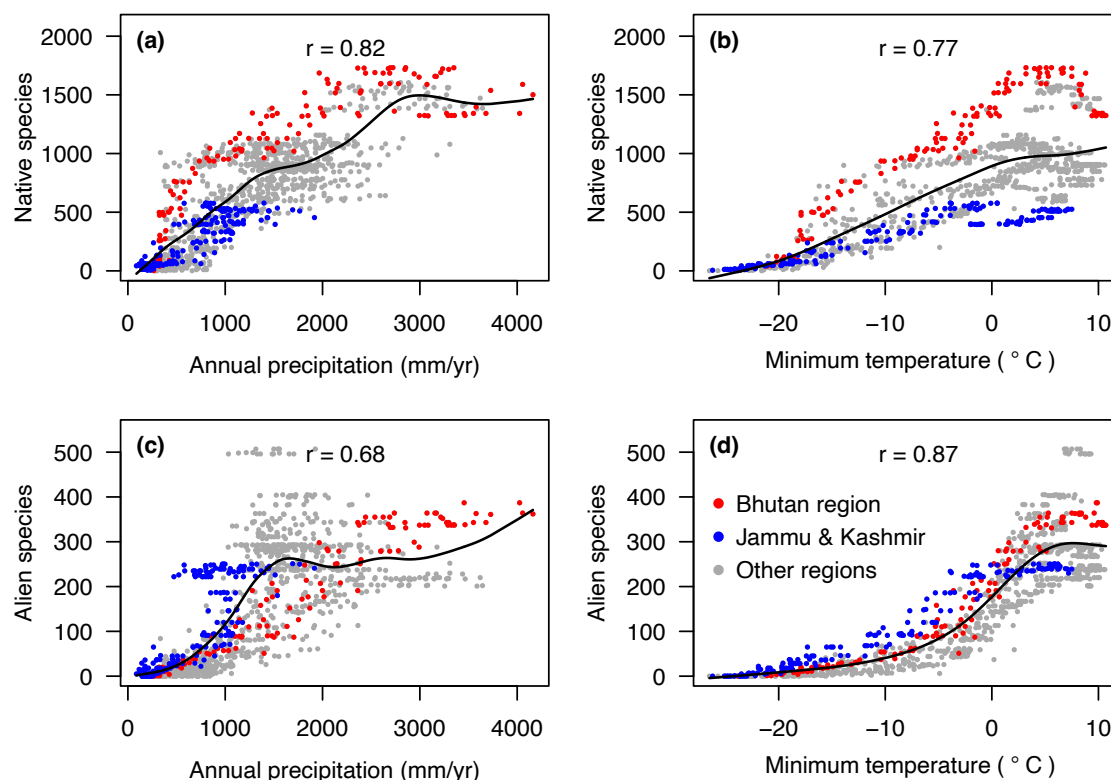other regions. *Left:* native species, *right:* alien species.

FIGURE 4 Scatter plot of species richness verses climatic variables (annual precipitation and mean minimum temperature of the coldest month) for 1140 grids of 0.2° resolution across the Himalaya, based on species richness maps in Fig. 1. Alien species lower row, native species upper row. Lines are non-parametric spline fits.

Alien species richness declines with elevation for taxa with tropical affinities, whereas those with European/temperate affinities show a peak at 2,000m - 3,000m (Fig. 3). Native species with tropical affinities show a mild peak at 1,000m, and those with temperate affinities a more pronounced peak above 3,000m. Thus, the peak is about 1,000m higher for native species than for alien species, both for species with tropical and temperate affinities.

3.2 | Climatic control

Correlations between alien and native richness are at least in part a result of both being correlated with climate (Fig. 4). Climatic controls are particularly apparent from the

311   distribution of species with tropical and temperate affinities. In the subtropical Bhutan region,

312   48% of the native species and 52% of the naturalized alien species have tropical affinities,

313   whereas in the drier and more temperate Jammu & Kashmir the corresponding figures are

314   31% and 32%. The similarity between the native and alien species is striking and suggests

315   that present climate is an important determinant of alien species richness.

316   A possible additional test of a role for climate comes from assessment of the net

317   relatedness index, which is predicted to increase in a combined dataset as compared to only

318   native species, under the assumption that those alien species with similar climatic niches to

319   native species are also closely related to them (e.g., Qian & Sandel, 2022). In fact, the net

320   relatedness index of native species across elevational gradients barely differs from that of

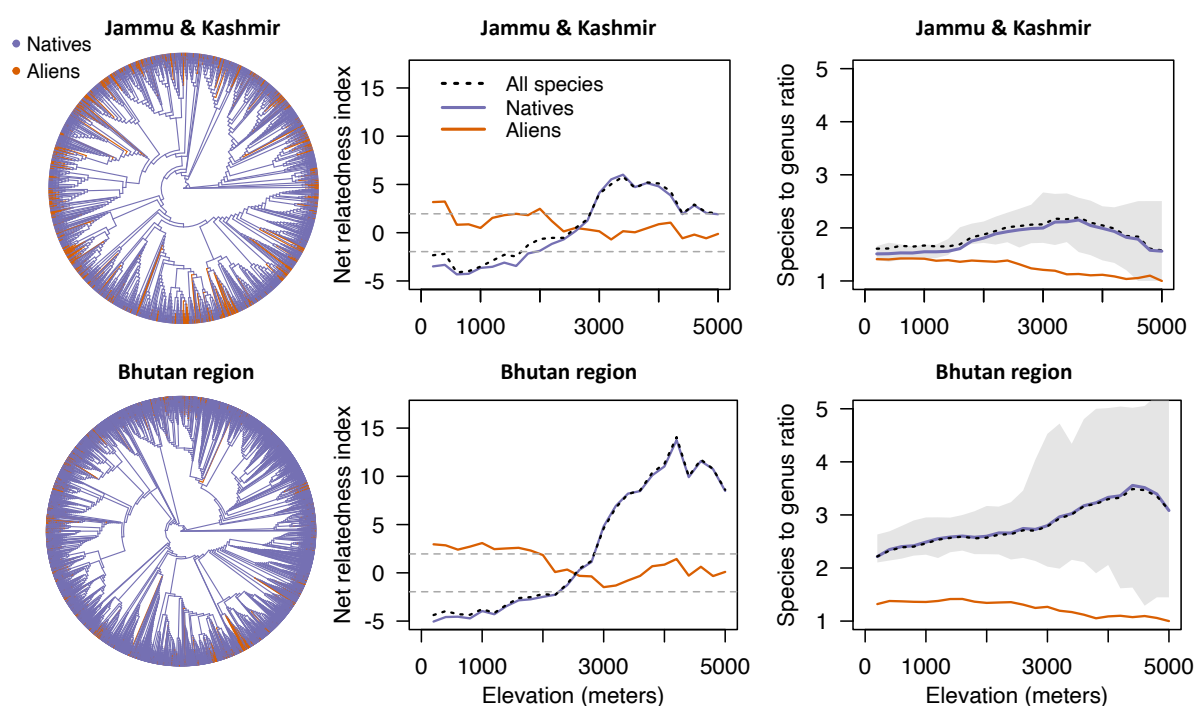321   alien species plus native species combined (Fig. 5).

322

323   **FIGURE 5** *Left:* Phylogenies of 5,452 native and 634 alien species in Bhutan and 1,649

324   native and 556 alien species in Jammu & Kashmir showing tips of the two groups in different

325   colours. *Center:* Net Relatedness Index of all species, native species, and alien species

326   separately along 200m elevational belts in Jammu & Kashmir (alien: native correlation, r = -

327   0.64) and Bhutan region (alien: native correlation, r = -0.65). Dashed lines are $\pm$ 1.96, i.e.,

328   values outside this limit are putatively significant at P = 0.05 (ignoring multiple testing

329   issues). Native and alien indices are based on subsets of the phylogenies on the right (for

330   similar Nearest Taxon Indices, see Figure S5). *Right:* Species to genus ratios for native and

331   alien species along 200m elevational belts in Jammu & Kashmir and Bhutan region. Black

332   dotted line is the mean based on subsampling the native species pool down to that of the alien

333   species numbers in the belt (shading indicates 95% confidence limits). Figure S6 shows

334   species:genus ratios subset according to tropical and temperate affinities.

335   **3.3 | Directional filtering**

336   We compared nestedness in species composition across elevations. In all comparisons, alien

337   species are much more nested than native species, with differences ranging from one-third to

338   twice as much (Fig. 6; Table S2). Alien plant species with tropical affinities have values of

339   nestedness 20% higher than species with temperate affinities (Table S2), which is expected if

340   sources of introduction for those with tropical affinities are from the bottom of the mountain,

341   but those with temperate affinities often at higher elevations.

342   While it is not straightforward to include the nestedness metric in the regression

343   models, we find that in a model with climate and elevation together, the significance of

344   climate is greatly reduced (Tables S3, S4), which we interpret to be because elevation

345   integrates the combined effects of both directional filtering and climate on alien richness.

(a) Jammu & Kashmir

Native species

N = 1568
NODFc = 0.64
phyloNODF = 57.3

Alien species

N = 418
NODFc = 0.96
phyloNODF = 72.3

(b) Bhutan region

Native species

N = 5330
NODFc = 0.57
phyloNODF = 57.6

Alien species

N = 606
NODFc = 1.06
phyloNODF = 81.5
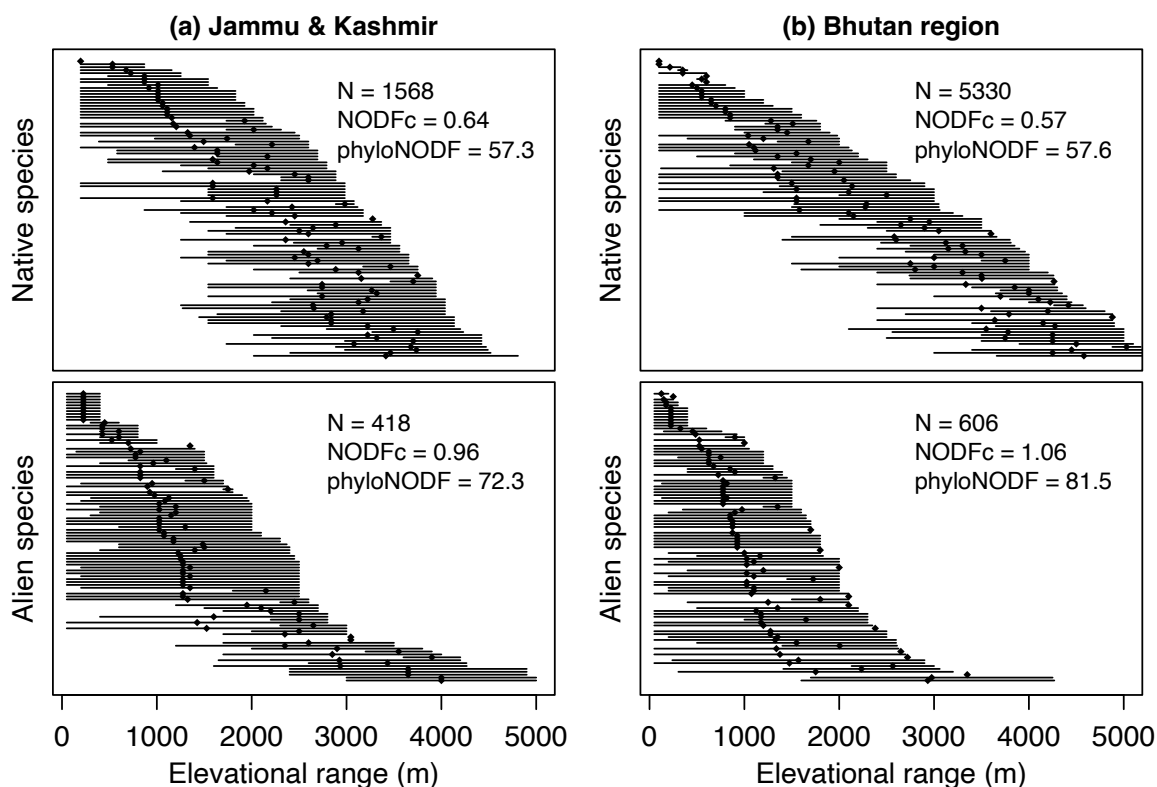
Elevational range (m)

Elevational range (m)

FIGURE 6 Elevational ranges of 100 randomly drawn species (lines) and mean elevation of occurrence (points). The nestedness statistic is calculated for all species *(N)* in each region (as in Table S1). Statistics include both phylogenetic and non-phylogenetic measures.

3.4 | Limits to establishment

The proportion of alien species weakly increases with disturbance (Table S1) but disturbance disappears as a factor when elevation is included in multiple regression models (Table S3). The proportion of alien species increases with number of native species (Fig. S7), providing no evidence that number of native species inhibits establishment of aliens.

4 | DISCUSSION

4.1 | Species richness patterns

Here we have presented a comprehensive database of alien plant species in the Himalaya, extending a recently published database which documents 771 alien species, and shows that

359   they have wider geographical ranges, on average, than natives (Wani et al., 2022, 2023). We

360   document 1,471 alien species (14% of the described flora), and add estimates of elevational

361   ranges. Of the alien species, one-third are entirely naturalized, and half of the naturalized

362   species are considered invasive at least somewhere in the world, according to the Global

363   Invasive Species database (235 invasive species). Our results suggest some previous

364   generalities might need re-evaluation, at least for Asia, such as the presence of more alien

365   species in temperate relative to tropical climates (e.g., Richardson & Pyšek, 2012; Van

366   Kleunen et al., 2015).

367   A striking finding is that the highest number of Himalayan alien species come from

368   the Americas, whereas the highest number of native species are shared with Africa, Europe

369   and Australia (as reported for a subset of alien species in India (Khuroo et al., 2012; Pandit,

370   2017, pp. 243-245) and China (Feng et al., 2011; Liu et al., 2006)). It is possible that the

371   record of relatively few alien species from Africa and Australia represents misclassification

372   of alien species as native species, given the long periods of time over which human exchange

373   has been ongoing (e.g., Boivin et al., 2016; Demske et al., 2016) but the disparity in numbers

374   seems too great to account for the alien/native species difference in sources and affinities. We

375   presume that the preponderance of alien species from the Americas is a consequence of

376   introduction biases. That presumption is supported by the global analysis of Turbelin et al.

377   (2017), who noted that about two-thirds of >880 invasive plant species had been deliberately

378   introduced for agriculture or horticulture. Other species have been carried along as weeds

379   (Boivin et al., 2016). Khuroo et al. (2012) briefly review historical trade since the 16th

380   century that might have led to the large number of introductions from the Americas. Present

381   global databases classify many Himalayan natives as aliens, and this plus the different

382   affinities of natives and aliens suggest that inferred historical drivers of alien presence need to

383   be re-appraised (cf. Lenzner *et al.*, 2022).

384   All biogeographical studies depend on accurate assessment of not only richness

385   patterns among known species, but on the plant species themselves having been described.

386   Arunachal Pradesh is particularly under-studied with fewer native species recorded than the

387   neighbouring Bhutan region, despite being larger (Rana, Price, et al., 2019). However,

388   Bhutan and Jammu & Kashmir's floras are now relatively well known, and our own on-site

389   sampling of the flora of these specific regions gives concordant results with those based on

390   the literature survey we report here (Rana et al., 2022; Rana, Gross, et al., 2019). Hence, we

391   focused on these two regions. We find that warmer and wetter areas harbour relatively more

392   alien species and suggest that filtering slows, or even may prevent, many alien species from

393   range expansions. Our findings resemble those for geographical gradients north of Himalaya

394   in China, where a latitudinal gradient in alien richness is tempered by especially high species

395   numbers along the coasts, reflecting points of introduction (Li & Shen 2020).

396   In summary, we attribute the high numbers of established alien plant species at low to

397   mid elevations to a combination of climate at these elevations favouring high species

398   diversity in general, and many introductions occurring at these elevations. Mid-elevation

399   peaks are found when we restrict our analysis to alien floras with temperate affinities, which

400   we attribute to a similar combination of introductions of species from temperate regions, and

401   climates favourable to temperate species. Elsewhere, exceptions to declines of alien species

402   richness with elevation, such as a mid-elevation peak observed in the Canary Islands

403   (Alexander et al., 2011; Haider et al., 2010) have been linked to more favourable climates at

404   these elevations (higher precipitation), as well as human disturbance, rather than site of

405   introduction. In the case of the Himalaya, a role of introduction is likely, given many early

406   settlements at 1500m (e.g., at least 4,500 years ago in the Kashmir valley, Yatoo et al., 2020).

407   We now turn to consider factors affecting alien distributions in more detail.

408 **4.2 | Climatic control**

409 Climatic affinities of species in their native range correlate with successful establishment

410 (Hayes & Barry, 2008; Sax, 2001). In our case regional source pools (i.e., tropical/temperate

411 affinities of genera) match both elevational and geographical distributions of alien species in

412 the Himalaya and imply climatic controls on establishment. Elsewhere, a similarity of

413 climatic niche between related alien species and native species has been inferred from an

414 increase in phylogenetic clustering when alien species are added to native species, expected

415 because closely related species are expected to share similar niches (Qian & Sandel, 2022). In

416 the Himalaya, addition of alien species does not increase the clustering metric. In this case,

417 increased clustering may not be expected, even if climatic affinity is an important correlate of

418 establishment, because many species from the Americas and other distant locations are likely

419 to share climatic niches by convergence, rather than shared ancestry (Qian et al., 2022).

420 Alien and native richness patterns are correlated with each other, and both are

421 correlated strongly with climatic variables in the Himalaya (Tables S1 and S4). Sax (2001)

422 noted that climatic correlations of alien species cannot result from speciation/extinction

423 dynamics and instead may reflect direct climatic controls (e.g. productivity) on the number of

424 species that can persist in an area, or possibly the number available to be introduced from

425 climatically similar source areas.

426 **4.3 | Directional filtering**

427 In addition to favourable climates, the location of introduction plus elapsed time since

428 introduction have been invoked to explain distributions of alien species along mountainsides

429 (Alexander et al., 2011; Haider et al., 2010; Marini et al., 2013). Across 10 elevational

430 gradients in temperate regions and in tropical Hawaii, Alexander *et al.* (2011) demonstrated a

431   widespread pattern of declines in alien species richness with elevation, associated with a

432   nested pattern, whereby higher elevation alien species are subsets of low elevation alien

433   species. They interpreted the declines to be a consequence of introductions occurring

434   primarily at low elevations, with only some generalist species able to expand ranges to higher

435   elevations (directional filtering).

436   Our findings from the Himalaya support this pattern. First, especially among those

437   species with tropical affinities, we observe steeper declines in alien species than native

438   species along the elevational gradient (Fig. 2), which can be explained if introductions

439   primarily occurred in lowlands, and it takes time to expand into novel climates. Second, we

440   find peaks in alien species richness at about 1000m below those for native richness (Fig. 2),

441   which applies separately for both groups with tropical and temperate affinities, suggesting

442   that with time they could expand their ranges upslope. Alien species with temperate affinities

443   show a peak at mid elevations, but as noted above this likely reflects introductions occurring

444   at these elevations (e.g., *Prunus, Ranunculus*). Finally, we find a pattern of nestedness as one

445   proceeds from base to higher elevations (Fig. 6), matching the main result of Alexander *et al.*

446   (2011).

447   **4.4 | Limits to range expansions**

448   Directional filtering implies an inferred time delay in range expansions by aliens, which may

449   reflect ability to enter different climates, especially in the face of competition from native

450   species, and previously established alien species. Even for native species, the crossing of the

451   freezing line appears to be difficult (Rana et al., 2022): relatively few genera contribute the

452   bulk of the species above the freezing line, as indicated by the high phylogenetic clustering

453   metric of native species at higher elevations (Fig. 5), i.e., speciation rather than dispersal

454   contributes importantly to native species richness at high elevations, an option yet to be

455   realised by alien species.

456   Other features that could contribute to delayed range expansions are lower

457   disturbance at higher elevations, or relatively high numbers of native species. Both these may

458   operate at relatively small spatial grain sizes, but at the larger grain sizes of this study, we

459   find patterns inconsistent with either of these factors, and instead propose climate and

460   incumbency are the main limiting factors (see further discussion in the supplement). In the

461   plains of India at a spatial scale of 700 m^2, richness along a moisture gradient from dry scrub

462   to moist evergreen forest is affected by high levels of disturbance and introductions, both of

463   which are highest in native deciduous forests (Mungi et al., 2021). The spatial grain of that

464   work and a focus on habitat rather than region differ from the present study.

465   The top three globally invasive plant species listed by Turbelin et al. (2017) are all

466   found in the Himalaya and cover large areas. While it may be the case that on a regional

467   scale, alien species increase species richness (Fig. S7, Qian & Sandel, 2022; Stohlgren et al.,

468   2003), at local grain sizes, this is not the case. Swathes of *Lantana camara, Ageratum*

469   *conyzoides* and *Parthenium hysterophorus* cover many Himalayan locations, especially

470   below 2,000m (Chaudhary et al., 2021; Lamsal et al., 2018; Mungi et al., 2020). Further

471   expansion of *Lantana* and other alien species is to be expected (Mungi *et al.*, 2018; Lamsal *et*

472   *al.*, 2018). Like the Himalayan region, alpine regions of America and Europe are also

473   relatively free of alien species but likely to be increasingly invaded over time (Alexander et

474   al., 2016). Our inference of a role for directional filtering implies range expansions are taking

475   time to overcome, which we attribute to climate, and presumed climate-associated

476   competition. In consequence, we expect ongoing invasions of higher altitudes to be

477   accelerated by climate change (Wani et al., 2023).

478 **ACKNOWLEDGEMENTS**

484 **CONFLICTS OF INTERESTS**

485 The authors declare no conflict of interest.

486 **AUTHORS CONTRIBUTIONS**

487 SKR and TDP conceived the idea and designed the methodology, BD and SKR compiled the

488 data, SKR and GSR reviewed the alien status of the species in the Himalaya, SKR analysed

489 the data and wrote the first draft, TDP revised the manuscript substantially and all authors

490 contributed to manuscript revisions and gave final approval for publication.

491 **ORCID**

492 *Suresh K. Rana* https://orcid.org/0000-0002-2386-216X

493 *Bhawana Dangwal* https://orcid.org/0000-0002-3361-3490

494 *Gopal S. Rawat* https://orcid.org/0000-0002-5743-5035

495 *Trevor D. Price* https://orcid.org/0000-0002-4423-8999

496

497

498 **Data availability**

499 Data on alien species distributions are obtained from regional floras and the published

500 literature in the Himalaya (Appendix-1) and is provided as a supplement with this paper

501 (Appendix-2).

502 **References**

503 Alexander, J. M., Kueffer, C., Daehler, C. C., Edwards, P. J., Pauchard, A., Seipel, T.,

504   Arevalo, J., Cavieres, L., Dietz, H., Jakobs, G., McDougall, K., Naylor, B., Otto, R.,

505   Parks, C. G., Rew, L., & Walsh, N. (2011). Assembly of nonnative floras along

506   elevational gradients explained by directional ecological filtering. *Proceedings of the*

507   *National Academy of Sciences*, *108*(2), 656–661.

508   https://doi.org/10.1073/pnas.1013136108

509 Alexander, J. M., Lembrechts, J. J., Cavieres, L. A., Daehler, C., Haider, S., Kueffer, C., Liu,

510   G., McDougall, K., Milbau, A., Pauchard, A., Rew, L. J., & Seipel, T. (2016). Plant

511   invasions into mountains and alpine ecosystems: Current status and future challenges.

512   *Alpine Botany*, *126*(2), 89–103. https://doi.org/10.1007/s00035-016-0172-8

513 Almeida-Neto, M., Guimarães, P., Guimarães Jr, P. R., Loyola, R. D., & Ulrich, W. (2008).

514   A consistent metric for nestedness analysis in ecological systems: Reconciling

515   concept and measurement. *Oikos*, *117*(8), 1227–1239. https://doi.org/10.1111/j.0030-

516   1299.2008.16644.x

517 Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V., & Bradley, B. A. (2020). Biotic resistance

518   to invasion is ubiquitous across ecosystems of the United States. *Ecology Letters*,

519   *23*(3), 476–482. https://doi.org/10.1111/ele.13446

520 Bivand, R. S., Pebesma, E., & Gómez-Rubio, V. (2013). *Applied Spatial Data Analysis with*

521   *R* (2nd ed.). Springer-Verlag. https://doi.org/10.1007/978-1-4614-7618-4

522   Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M.,

523   Denham, T., & Petraglia, M. D. (2016). Ecological consequences of human niche

524   construction: Examining long-term anthropogenic shaping of global species

525   distributions. *Proceedings of the National Academy of Sciences*, *113*(23), 6388–6396.

526   https://doi.org/10.1073/pnas.1525200113

527   Brummitt, R. K. (2001). *World Geographical Scheme for Recording Plant Distributions*

528   *Edition 2*. https://doi.org/10.1043/0363-6445-28.4.807

529   Chaudhary, A., Sarkar, M. S., Adhikari, B. S., & Rawat, G. S. (2021). Ageratina adenophora

530   and Lantana camara in Kailash Sacred Landscape, India: Current distribution and

531   future climatic scenarios through modeling. *PLOS ONE*, *16*(5), e0239690.

532   https://doi.org/10.1371/journal.pone.0239690

533   Chong, K. Y., Corlett, R. T., Nuñez, M. A., Chiu, J. H., Courchamp, F., Dawson, W.,

534   Kuebbing, S., Liebhold, A. M., Padmanaba, M., Souza, L., Andersen, K. M., Fei, S.,

535   Lee, B. P. Y.-H., Lum, S., Luskin, M. S., Ngo, K. M., & Wardle, D. A. (2021). Are

536   terrestrial biological invasions different in the tropics? *Annual Review of Ecology,*

537   *Evolution, and Systematics*, *52*(1), 291–314. https://doi.org/10.1146/annurev-ecolsys-

538   012021-095454

539   Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A.,

540   Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E., & Turner, J. R. G. (2004).

541   Predictions and tests of climate-based hypotheses of broad-scale variation in

542   taxonomic richness. *Ecology Letters*, *7*(12), 1121–1134.

543   https://doi.org/10.1111/j.1461-0248.2004.00671.x

544   Demske, D., Tarasov, P. E., Leipe, C., Kotlia, B. S., Joshi, L. M., & Long, T. (2016). Record

545   of vegetation, climate change, human impact and retting of hemp in Garhwal

546   Himalaya (India) during the past 4600 years. *Holocene*, *26*(10), 1661–1675.

547   https://doi.org/10.1177/0959683616650267

548 Denslow, M. W., Palmer, M. W., & Murrell, Z. E. (2010). Patterns of native and exotic

549   vascular plant richness along an elevational gradient from sea level to the summit of

550   the Appalachian Mountains, U.S.A. *The Journal of the Torrey Botanical Society*,

551   *137*(1), 67–80. https://doi.org/10.3159/09-RA-045.1

552 Feng, J., Zhang, Z., & Nan, R. (2011). The roles of climatic factors in spatial patterns of alien

553   invasive plants from America into China. *Biodiversity and Conservation*, *20*(14),

554   3385–3391. https://doi.org/10.1007/s10531-011-0122-0

555 Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate

556   surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–

557   4315. https://doi.org/10.1002/joc.5086

558 Francis, A. P., & Currie, D. J. (2003). A Globally Consistent Richness-Climate Relationship

559   for Angiosperms. *The American Naturalist*, *161*(4), 523–536.

560   https://doi.org/10.1086/368223

561 Gao, J., & Liu, Y. (2018). Climate stability is more important than water–energy variables in

562   shaping the elevational variation in species richness. *Ecology and Evolution*, *8*(14),

563   6872–6879. https://doi.org/10.1002/ece3.4202

564 Gräler, B., Pebesma, E., & Heuvelink, G. (2016). Spatio-Temporal Interpolation using gstat.

565   *The R Journal*, *8*(1), 204–218.

566 Guo, Q., Cade, B. S., Dawson, W., Essl, F., Kreft, H., Pergl, J., van Kleunen, M., Weigelt, P.,

567   Winter, M., & Pyšek, P. (2021). Latitudinal patterns of alien plant invasions. *Journal*

568   *of Biogeography*, *48*(2), 253–262. https://doi.org/10.1111/jbi.13943

569 Haider, S., Alexander, J., Dietz, H., Trepl, L., Edwards, P. J., & Kueffer, C. (2010). The role

570   of bioclimatic origin, residence time and habitat context in shaping non-native plant

571   distributions along an altitudinal gradient. *Biological Invasions*, *12*(12), 4003–4018.

572   https://doi.org/10.1007/s10530-010-9815-7

573   Hayes, K. R., & Barry, S. C. (2008). Are there any consistent predictors of invasion success?

574   *Biological Invasions*, *10*(4), 483–506. https://doi.org/10.1007/s10530-007-9146-5

575   Hijmans, R. J. (2017). *Raster: Geographic Data Analysis and Modeling. R package version*

576   *2.6-7.* https://CRAN.R-project.org/package=raster

577   Hoeppke, C., & Simmons, B. I. (2021). maxnodf: An R package for fair and fast comparisons

578   of nestedness between networks. *Methods in Ecology and Evolution*, *12*(4), 580–585.

579   https://doi.org/10.1111/2041-210X.13545

580   Hulme, P. E., Pyšek, P., Nentwig, W., & Vilà, M. (2009). Will Threat of Biological Invasions

581   Unite the European Union? *Science*, *324*(5923), 40–41.

582   https://doi.org/10.1126/science.1171111

583   Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why Are There So Many Kinds of

584   Animals? *The American Naturalist*, *93*(870), 145–159.

585   https://doi.org/10.1086/282070

586   Igea, J., & Tanentzap, A. J. (2020). Angiosperm speciation cools down in the tropics.

587   *Ecology Letters*, *23*(4), 692–700. https://doi.org/10.1111/ele.13476

588   Jin, Y., & Qian, H. (2019). V.PhyloMaker: An R package that can generate very large

589   phylogenies for vascular plants. *Ecography*, *42*(0), 1353–1359.

590   https://doi.org/10.1111/ecog.04434

591   Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W.,

592   Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high

593   resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 170122.

594   https://doi.org/10.1038/sdata.2017.122

595   Khuroo, A. A., Reshi, Z. A., Malik, A. H., Weber, E., Rashid, I., & Dar, G. H. (2012). Alien

596   flora of India: Taxonomic composition, invasion status and biogeographic affiliations.

597   *Biological Invasions*, *14*(1), 99–113. https://doi.org/10.1007/s10530-011-9981-2

598   Khuroo, A. A., Weber, E., Malik, A. H., Reshi, Z. A., & Dar, G. H. (2011). Altitudinal

599   distribution patterns of the native and alien woody flora in Kashmir Himalaya, India.

600   *Environmental Research*, *111*(7), 967–977.

601   https://doi.org/10.1016/j.envres.2011.05.006

602   Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity.

603   *Proceedings of the National Academy of Sciences*, *104*(14), 5925–5930.

604   https://doi.org/10.1073/pnas.0608361104

605   Lamsal, P., Kumar, L., Aryal, A., & Atreya, K. (2018). Invasive alien plant species dynamics

606   in the Himalayan region under climate change. *Ambio*, *47*(6), 697–710.

607   https://doi.org/10.1007/s13280-018-1017-z

608   Lenzner, B., Latombe, G., Schertler, A., Seebens, H., Yang, Q., Winter, M., Weigelt, P., van

609   Kleunen, M., Pyšek, P., Pergl, J., Kreft, H., Dawson, W., Dullinger, S., & Essl, F.

610   (2022). Naturalized alien floras still carry the legacy of European colonialism. *Nature

611   Ecology & Evolution*, *6*(11), 1723–1732. https://doi.org/10.1038/s41559-022-01865-1

612   Liu, J., Dong, M., Miao, S. L., Li, Z. Y., Song, M. H., & Wang, R. Q. (2006). Invasive alien

613   plants in China: Role of clonality and geographical origin. *Biological Invasions*, *8*(7),

614   1461–1470. https://doi.org/10.1007/s10530-005-5838-x

615   Mallen-Cooper, J., & Pickering, C. M. (2008). Linear declines in exotic and native plant

616   species richness along an increasing altitudinal gradient in the Snowy Mountains,

617   Australia. *Austral Ecology*, *33*(5), 684–690. https://doi.org/10.1111/j.1442-

618   9993.2008.01835.x

619   Manish, K. (2021). Species richness, phylogenetic diversity and phylogenetic structure

620   patterns of exotic and native plants along an elevational gradient in the Himalaya.

621   *Ecological Processes*, *10*(1), 64. https://doi.org/10.1186/s13717-021-00335-z

622   Marini, L., Bertolli, A., Bona, E., Federici, G., Martini, F., Prosser, F., & Bommarco, R.

623   (2013). Beta-diversity patterns elucidate mechanisms of alien plant invasion in

624   mountains. *Global Ecology and Biogeography*, *22*(4), 450–460.

625   https://doi.org/10.1111/geb.12006

626   Mazel, F., Davies, T. J., Gallien, L., Renaud, J., Groussin, M., Münkemüller, T., & Thuiller,

627   W. (2016). Influence of tree shape and evolutionary time-scale on phylogenetic

628   diversity metrics. *Ecography*, *39*(10), 913–920. https://doi.org/10.1111/ecog.01694

629   Melo, A. S. (2021). *CommEcol: Community Ecology Analyses. R package version 1.7.1.*

630   https://CRAN.R-project.org/package=CommEcol

631   Melo, A. S., Cianciaruso, M. V., & Almeida-Neto, M. (2014). treeNODF: Nestedness to

632   phylogenetic, functional and other tree-based diversity metrics. *Methods in Ecology*

633   *and Evolution*, *5*(6), 563–572. https://doi.org/10.1111/2041-210X.12185

634   Muellner-Riehl, A. N. (2019). Mountains as evolutionary arenas: Patterns, emerging

635   approaches, paradigm shifts, and their implications for plant phylogeographic

636   research in the Tibeto-Himalayan Region. *Frontiers in Plant Science*, *10*, 1–18.

637   https://doi.org/10.3389/fpls.2019.00195

638   Mungi, N. A., Coops, N. C., Ramesh, K., & Rawat, G. S. (2018). How global climate change

639   and regional disturbance can expand the invasion risk? Case study of Lantana camara

640   invasion in the Himalaya. *Biological Invasions*, *20*(7), 1849–1863.

641   https://doi.org/10.1007/s10530-018-1666-7

642 Mungi, N. A., Qureshi, Q., & Jhala, Y. V. (2020). Expanding niche and degrading forests:

643   Key to the successful global invasion of Lantana camara (sensu lato). *Global Ecology*

644   *and Conservation*, *23*, e01080. https://doi.org/10.1016/j.gecco.2020.e01080

645 Mungi, N. A., Qureshi, Q., & Jhala, Y. V. (2021). Role of species richness and human

646   impacts in resisting invasive species in tropical forests. *Journal of Ecology*, *109*(9),

647   3308–3321. https://doi.org/10.1111/1365-2745.13751

648 Nuñez, M. A., Chiuffo, M. C., Seebens, H., Kuebbing, S., McCary, M. A., Lieurance, D.,

649   Zhang, B., Simberloff, D., & Meyerson, L. A. (2022). Two decades of data reveal that

650   Biological Invasions needs to increase participation beyond North America, Europe,

651   and Australasia. *Biological Invasions*, *24*(2), 333–340.

652   https://doi.org/10.1007/s10530-021-02666-6

653 Pandit, M. K. (2017). *Life in the Himalaya: An Ecosystem at Risk*. Harvard University Press.

654   https://www.jstor.org/stable/j.ctt1qd8zx8

655 Park, D. S., Feng, X., Maitner, B. S., Ernst, K. C., & Enquist, B. J. (2020). Darwin's

656   naturalization conundrum can be explained by spatial scale. *Proceedings of the*

657   *National Academy of Sciences*, *117*(20), 10904–10910.

658   https://doi.org/10.1073/pnas.1918100117

659 Pebesma, E. J., & Bivand, R. S. (2005). *Classes and methods for spatial data in R. R News 5*

660   *(2)*. https://cran.r-project.org/doc/Rnews/

661 Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., Weigelt, P., Winter, M.,

662   Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabesaz, F. J., Cárdenas,

663   D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Dullinger, S., …

664   Kleunen, M. van. (2017). Naturalized alien flora of the world: Species diversity,

665   taxonomic and phylogenetic patterns, geographic distribution and global hotspots of

666   plant invasion. *Preslia*, *89*(3), 203–274. https://doi.org/10.23855/preslia.2017.203

667   Qian, H., Qian, S., & Sandel, B. (2022). Phylogenetic structure of alien and native species in

668   regional plant assemblages across China: Testing niche conservatism hypothesis

669   versus niche convergence hypothesis. *Global Ecology and Biogeography*, geb.13566.

670   https://doi.org/10.1111/geb.13566

671   Qian, H., & Sandel, B. (2022). Darwin's preadaptation hypothesis and the phylogenetic

672   structure of native and alien regional plant assemblages across North America. *Global*

673   *Ecology and Biogeography*, *31*(3), 531–545. https://doi.org/10.1111/geb.13445

674   Rana, S. K., Gross, K., & Price, T. D. (2019). Drivers of elevational richness peaks, evaluated

675   for trees in the east Himalaya. *Ecology*, *100*(1), e02548.

676   https://doi.org/10.1002/ecy.2548

677   Rana, S. K., Price, T. D., & Qian, H. (2019). Plant species richness across the Himalaya

678   driven by evolutionary history and current climate. *Ecosphere*, *10*(11), e02945.

679   https://doi.org/10.1002/ecs2.2945

680   Rana, S. K., White, A. E., & Price, T. D. (2022). Key roles for the freezing line and

681   disturbance in driving the low plant species richness of temperate regions. *Global*

682   *Ecology and Biogeography*, *31*(2), 280–293. https://doi.org/10.1111/geb.13427

683   Richardson, D. M., & Pyšek, P. (2012). Naturalization of introduced plants: Ecological

684   drivers of biogeographical patterns. *New Phytologist*, *196*(2), 383–396.

685   https://doi.org/10.1111/j.1469-8137.2012.04292.x

686   Sax, D. F. (2001). Latitudinal gradients and geographic ranges of exotic species: Implications

687   for biogeography. *Journal of Biogeography*, *28*(1), 139–150.

688   https://doi.org/10.1046/j.1365-2699.2001.00536.x

689   Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D.,

690   Grosberg, R. K., Hastings, A., Holt, R. D., Mayfield, M. M., O'Connor, M. I., & Rice,

691   W. R. (2007). Ecological and evolutionary insights from species invasions. *Trends in*

692   *Ecology and Evolution*, *22*(9), 465–471. https://doi.org/10.1016/j.tree.2007.06.009

693 Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M.,

694   Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu,

695   G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger,

696   H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide.

697   *Nature Communications*, *8*, 1–9. https://doi.org/10.1038/ncomms14435

698 Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny.

699   *American Journal of Botany*, *105*(3), 302–314. https://doi.org/10.1002/ajb2.1019

700 Song, C., Rohr, R. P., & Saavedra, S. (2017). Why are some plant–pollinator networks more

701   nested than others? *Journal of Animal Ecology*, *86*(6), 1417–1424.

702   https://doi.org/10.1111/1365-2656.12749

703 Stohlgren, T. J., Barnett, D. T., & Kartesz, J. T. (2003). The rich get richer: Patterns of plant

704   invasions in the United States. *Frontiers in Ecology and the Environment*, *1*(1), 11–

705   14. https://doi.org/10.1890/1540-9295(2003)001[0011:TRGRPO]2.0.CO;2

706 Tsirogiannis, C., & Sandel, B. (2016). Fast computations for measures of phylogenetic beta

707   diversity. *PLoS ONE*, *11*(4), 1–16. https://doi.org/10.1371/journal.pone.0151167

708 Tsirogiannis, C., Sandel, B., & Cheliotis, D. (2012). Efficient computation of popular

709   phylogenetic tree measures. *Lecture Notes Comput. Sci.*, *7534*, 30–43.

710 Turbelin, A. J., Malamud, B. D., & Francis, R. A. (2017). Mapping the global state of

711   invasive alien species: Patterns of invasion and policy responses. *Global Ecology and*

712   *Biogeography*, *26*(1), 78–92. https://doi.org/10.1111/geb.12517

713 Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness

714   analysis. *Oikos*, *118*(1), 3–17. https://doi.org/10.1111/j.1600-0706.2008.17053.x

715 Van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt,

716   P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J.,

717   Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A. L.,

718   … Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*,

719   *525*(7567), 100–103. https://doi.org/10.1038/nature14910

720 van Kleunen, M., Pyšek, P., Dawson, W., Essl, F., Kreft, H., Pergl, J., Weigelt, P., Stein, A.,

721   Dullinger, S., König, C., Lenzner, B., Maurel, N., Moser, D., Seebens, H., Kartesz, J.,

722   Nishino, M., Aleksanyan, A., Ansong, M., Antonova, L. A., … Winter, M. (2019).

723   The Global Naturalized Alien Flora (GloNAF) database. *Ecology*, *100*(1), e02542.

724   https://doi.org/10.1002/ecy.2542

725 Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., Possingham,

726   H. P., Laurance, W. F., Wood, P., Fekete, B. aacute zs M., Levy, M. A., & Watson, J.

727   E. M. (2016). Sixteen years of change in the global terrestrial human footprint and

728   implications for biodiversity conservation. *Nature Communications*, *7*, 12558.

729 Wani, S. A., Ahmad, R., Gulzar, R., Rashid, I., & Khuroo, A. A. (2023). Alien flora causes

730   biotic homogenization in the biodiversity hotspot regions of India. *Science of The*

731   *Total Environment*, *884*, 163856. https://doi.org/10.1016/j.scitotenv.2023.163856

732 Wani, S. A., Ahmad, R., Gulzar, R., Rashid, I., Malik, A. H., Rashid, I., & Khuroo, A. A.

733   (2022). Diversity, distribution and drivers of alien flora in the Indian Himalayan

734   region. *Global Ecology and Conservation*, *38*, e02246.

735   https://doi.org/10.1016/j.gecco.2022.e02246

736 Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and

737   Community Ecology. *Annual Review of Ecology and Systematics*, *33*, 475–505.

738 Wu, Z. (1991). *The areal-types of Chinese genera of seed plants* (Vol. 13).

739   Yatoo, M. A., Spate, M., Betts, A., Pokharia, A. K., & Shah, M. A. (2020). New evidence

740   from the Kashmir Valley indicates the adoption of East and West Asian crops in the

741   western Himalayas by 4400 years ago. *Quaternary Science Advances*, *2*, 100011.

742   https://doi.org/10.1016/j.qsa.2020.100011

743   Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., Fitzjohn, R. G.,

744   McGlinn, D. J., O'Meara, B. C., Moles, A. T., Reich, P. B., Royer, D. L., Soltis, D.

745   E., Stevens, P. F., Westoby, M., Wright, I. J., Aarssen, L., Bertin, R. I., Calaminus,

746   A., Govaerts, R., … Beaulieu, J. M. (2014). Three keys to the radiation of

747   angiosperms into freezing environments. *Nature*, *506*(7486), 89–92.

748   https://doi.org/10.1038/nature12872

749

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information
section at the end of the article.

Fig S1. Testing models of biotic interactions on Himalayan plants.

Fig S2. Elevational patterns of disturbance in the Himalayan landscape.

Fig S3. Elevational patterns of naturalized, cultivated and invasive alien species in the Bhutan
region and Jammu & Kashmir.

Fig. S4 Elevational patterns of trees, shrubs and herbs for the native and alien species in
Jammu & Kashmir and the Bhutan region.

Fig. S5 Elevational patterns of Nearest Taxon Index in Jammu & Kashmir and the Bhutan
region in the Himalaya.

Fig. S6 Elevational patterns of species to genus ratios separated into species with tropical and
temperate affinities.

Fig. S7 The proportion of aliens is high where native richness is high.

Table S1 Correlation matrix for major variables along elevational gradients.

Table S2 Nestedness metric (NODFc) for alien and native species along elevational
gradients.

Table S3 Multiple regression of alien species richness along elevational gradients in Jammu
& Kashmir and the Bhutan region.

769   **Table S4** Multiple regression of total alien species richness for three variables i.e. elevation,

770   region and number of natives and their interactions.

771   **Methods S1** Assessing impact of native species richness on alien establishment.