Evolutionary assembly of flowering plants into sky islands

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Although they experience cold climates, particularly in temperate mountains during winter, alpine floras (plants in the vegetation belts above the climatic treelines) are generally species-rich. Yet, whether these floras represent evolutionarily independent, but convergent, assemblages drawn from their regional floras, or they originated from particular clades pre-adapted to harsh conditions, has not been determined. Here, we analyze the evolutionary relationships of angiosperm (flowering plant) species in 63 alpine floras worldwide (~7,000 species) in comparison with their regional floras (~94,000 species) and to the entire global flora. We find that each of the alpine floras represents an assemblage of more closely related species in comparison to their respective regional floras. The degree of phylogenetic clustering of species in alpine floras in tropical mountains exceeds that in temperate mountains. However, in relation to the global flora, temperate alpine floras are phylogenetically closely-related subsets of floras that colonized cold temperate areas during inter-glacial periods. We conclude that alpine floras include a few dominant families that have evolved tolerance to low temperature, and that evolutionary niche conservatism explains their phylogenetic clustering, compared to species in their regional species pools.

The local assembly of species from a pool of regionally available species (i.e., the regional species pool) reflects an interplay between evolutionary and ecological processes[1-2]. Under strong environmental filtering, the tendency of lineages to retain ancestral ecological traits over time (phylogenetic niche conservatism[3]) will leave a signature in the phylogenetic structure of local assemblages[4].

Because most plant taxonomic orders (or higher-level taxa) originated tens of millions of years ago, when Earth experienced predominately tropical conditions[5-6], ancestral traits are likely to emphasize adaptation to warm and wet environments. Steep gradients of decreasing temperature from tropical to temperate latitudes emerged following global climate cooling since the late Eocene[7]. These more recent conditions promoted adaptation to cold climates, particularly to withstanding freezing temperatures[8]. However, many lineages have not adapted to cold climates[7,9-10], and those that did might be more closely related to each other than expected by chance due to phylogenetic niche

47 conservatism. This would likely result in phylogenetic clustering (i.e., species being more
48 closely related than expected) in areas with cold climates. That plant assemblages in cold
49 climates include phylogenetically more closely related species than those in warm
50 climates supports this argument (e.g., ref. 11). Because vegetation zonation from low to
51 high elevations parallels zonation from low to high latitudes[12], we expect plant species at
52 high elevations to be more closely related (i.e., more phylogenetically clustered) than
53 those at low elevations. However, unlike strong latitudinal gradients of temperature,
54 which originated only since the late Eocene (~34 million years ago) and thus are
55 relatively young, strong elevational gradients of temperature have existed since plants
56 have grown on mountains, well before the origin of angiosperms (flowering plants)[13].
57 Elevational gradients also occupy smaller geographical areas than latitudinal gradients,
58 and thus may structure local floras. Altogether, changes in species assemblages across
59 elevational gradients, and notably their phylogenetic structure, might thus differ from
60 variation across latitudinal gradients. Understanding those differences is essential to
61 gather a better understanding of the history of plant assembly.
62   Several studies (e.g., refs. 14-15) have shown that the phylogenetic relatedness of
63 high-elevation tree species decreases with elevation, which contrasts with the increase in
64 phylogenetic relatedness within tree assemblages with increasing latitude[16-17]. This
65 pattern suggests that niche convergence, rather than niche conservatism, has
66 characterized the assembly of tree species along tropical elevational gradients[18]. Whether
67 niche convergence is restricted to tropical mountains, and whether it characterizes
68 assemblages of both lowland and alpine vegetation (i.e., the entire regional flora), and for
69 both woody and herbaceous plants, remain open questions.
70   Here, we describe the phylogenetic structure of alpine floras across the world in
71 comparison to their regional floras and to the global flora. Specifically, we analyzed a
72 dataset of 63 alpine angiosperm floras (i.e., flowering plants occurring above the tree line)
73 compared to their regional angiosperm floras (i.e., all flowering plants present in a
74 mountain system from the lowlands to the alpine belt), from all continents except
75 Antarctica (Figure 1; Supplementary Table 1).
76
77 **Results and Discussion**
78 We constructed a phylogeny for the 94,161 species of angiosperms (more than one
79 quarter of all angiosperm species) occurring in the regional floras utilized in this study.
80 We did so by using an updated version of the largest dated phylogeny of seed plants[19] as
81 a backbone and V.PhyloMaker[20] as a tool to attach additional species to the backbone
82 phylogeny (see Methods). To capture the phylogenetic structure of the floras, we used
83 two complementary metrics[21], namely phylogenetic diversity (PD) and mean pairwise
84 distance (MPD). PD represents the sum of the branch lengths of the phylogenetic tree
85 linking all species of a particular assemblage. MPD represents the mean phylogenetic
86 distance between all pairs of species in an assemblage, the phylogenetic distance between
87 a pair of species being defined as the total branch length of the shortest path between the
88 two species. A species assemblage with a large PD or MPD represents an assemblage
89 with species from different clades far apart in the phylogeny. In contrast, a species
90 assemblage with low PD or MPD might represent an assemblage from a single clade, or a
91 few clades that recently diversified. However, because these metrics are influenced by
92 species richness, they need to be standardized to be comparable between sites. Each

93 metric was thus standardized using a set of null models to compare the phylogenetic
94 structure of each alpine flora with its regional flora, with significant differences
95 indicating elevational gradient effects. Expanding the breadth of the compared flora, up
96 to the global flora, allows comparison of the phylogenetic structure of each alpine flora
97 with that of the global pool of species. By varying the scale of the pool of species
98 considered in null models, one can test hypotheses about mechanisms that have generated
99 the phylogenetic structure of alpine assemblages[22].
100 Once corrected by these tailor-made null models (Methods), the resulting
101 standardized effect size (ses) metrics quantify the relative excess (e.g., several clades far
102 apart in the phylogeny, old and unique species) or a deficit (e.g., a single highly
103 diversified clade) in phylogenetic diversity for a given assemblage relative to the overall
104 species pool. More specifically, the standardized effect size of PD (PD_{ses}) reveals the
105 phylogenetic structure that predominates at the tips of the phylogenetic tree (recent
106 divergences), while standardized effect size of MPD (MPD_{ses}) reflects deep-branching
107 (i.e., ancient) divergences[21]. We used these two complementary metrics because different
108 processes may act over different evolutionary time scales, which would not be detectable
109 using a single metric[21].
110 Using these metrics, we test whether angiosperm species in alpine floras are
111 phylogenetically clustered (as predicted by the niche conservatism hypothesis) or
112 phylogenetically over-dispersed (as predicted by the niche convergence hypothesis) in
113 comparison to their respective regional species pools (including species in alpine belts
114 and below). We also investigate whether this phylogenetic structure differs between
115 continents and climate regions of the world. Finally, we test whether the phylogenetic
116 clustering of alpine floras differs across latitude (and thus temperature) gradients and in
117 relation to the species pool considered.
118 All 63 alpine floras analyzed here comprise groups of phylogenetically more
119 closely related species (i.e., MPD_{ses} and $PD_{ses} < 0$), compared to groups of species
120 randomly drawn from their regional species pools (Supplementary Figure 1). This result
121 was significant for 50 (79%) and 59 (94%) of the 63 alpine floras for MPD_{ses} and PD_{ses},
122 respectively (i.e., MPD_{ses} and $PD_{ses} < -1.96$) (Figure 1, Supplementary Figure 2). Thus,
123 most alpine floras represent specific phylogenetic subsets of the regional floras of the
124 mountain systems in which they occur. Interestingly, clustering due to shallow-branching
125 divergences (i.e., PD_{ses}) near the tips of the phylogenetic tree was stronger than clustering
126 due to deep-time divergences (i.e., MPD_{ses}, Supplementary Figure 2), with the exception
127 of the alpine floras in South America (Supplementary Figure 2). Thus, phylogenetic
128 clustering is rather recent for most alpine floras and characterizes shallow-branching
129 divergences within the regional phylogenies. Conversely, evolutionary divergence
130 between alpine and lowland floras in South America involves primarily deep-time splits
131 within the regional floras. This pattern might originate from ancient mountain uplifts in
132 South America that early on induced deep-time divergence of floras. We tested whether
133 phylogenetic clustering holds even when alpine floras and their respective regional
134 species pools are aggregated at continental scales. Here again, alpine floras represented
135 closely-related assemblages compared to their respective continental species pools,
136 irrespective of the metric used (Figure 2). This result was confirmed when the
137 combinations of species in all alpine floras were compared to the combinations of the
138 species in all regional species pools. In this case, values for MPD_{ses} and PD_{ses} were

139   extremely negative (MPD_{ses} = -38.6 and PD_{ses} = -35.0), demonstrating very strong
140   phylogenetic clustering for the global alpine flora examined in this study.
141   Strikingly, the strength of phylogenetic clustering of each alpine flora varies with
142   latitude (Figure 1, Figure 3), irrespective of the metric used. When each alpine flora was
143   compared to its regional flora, clustering was stronger at low latitudes than at high
144   latitudes (Figure 3a). Thus, the alpine floras of tropical mountains form distinct
145   phylogenetic groupings of species, compared to their regional floras. In contrast, species
146   in alpine floras at high latitudes, such as those in North America and Europe, are only
147   loosely clustered assemblages of species drawn from their regional floras (Figure 3a).
148   This difference might reflect the fact that high latitude floras are already a non-random
149   set of the global flora, primarily with clades adapted to cold conditions[11], with an arctic-
150   alpine affiliation. To test this hypothesis, we first compared each alpine flora to a global
151   pool of the 313,855 angiosperm species in the combination of our regional floras and The
152   Plant List (see Methods), and then compared each associated regional flora (alpine and
153   lowland species combined) to the same global angiosperm species pool. Interestingly,
154   high latitude alpine floras were still less clustered than low latitude ones when extending
155   the species pool of each alpine flora to the global species pool of angiosperms (Figure 3b).
156   However, in agreement with the hypothesis that high latitude regional floras (i.e., the
157   species in alpine belts plus lowlands) are already clustered phylogenetically compared to
158   low latitude floras, the strength of the phylogenetic clustering is strongly linked to
159   latitude but with a negative slope (Figure 3d). This clustering of the entire regional
160   mountain floras at high latitudes partly explains the lower phylogenetic clustering of their
161   individual alpine floras in contrast to that in low latitude alpine floras. When each alpine
162   flora was compared to the combination of all angiosperm species in the 63 alpine floras,
163   species in alpine floras at low latitudes tended to be more strongly clustered than those at
164   high latitudes (Figure 3c). This implies that species in each of the alpine floras at high
165   latitudes are more phylogenetically related to each other than those at low latitudes when
166   species in each alpine flora are compared to the species pool that included all species of
167   the 63 alpine floras. When latitude was substituted with growing degree days in these
168   analyses, the results were generally consistent with those based on latitude
169   (Supplementary Figure 3).
170   Overall, our analyses, based on two complementary metrics and tailored
171   definitions of the species pool, confirmed that alpine floras represent phylogenetically
172   closely-related species assemblages and that the origin of this clustering varies with
173   latitude. These observations do not reflect sampling bias since our study includes the
174   majority (~70%) of all alpine angiosperm species in the world (based on the global
175   estimate reported in ref. 23). Instead, the phylogenetic clustering appears to reflect strong
176   environmental filtering in combination with phylogenetic niche conservatism. That is,
177   owing to shared evolutionary adaptations to low temperature, species in alpine
178   environments are likely more closely related to each other, on average, than are species in
179   lowlands.
180   Biotic interactions may further increase this pattern[11]. For instance, both
181   asymmetric competition[24] and facilitation between similar species[25] can increase
182   phylogenetic clustering. However, these processes probably do not drive the observed
183   pattern for alpine plants because competitive interactions are usually reduced, and plant-
184   plant interactions are thought to be more positive due to facilitation (mutual benefits of

185   shelter) in alpine environments[26]. For example, plant species with a cushion habit (e.g.,
186   an androsace, or rock jasmine) can facilitate the establishment of individuals of species
187   that would otherwise be less successful at such locations[27]. Such a mechanism should
188   lead to phylogenetic overdispersion (androsace and grass are far apart on the phylogeny
189   of angiosperms), rather than phylogenetic clustering. It is also unlikely that, within each
190   mountain system, dispersal limitation has caused phylogenetic clustering of alpine
191   species compared to the whole flora of the mountain system. This is because
192   geographical distances across elevational gradients are relatively small, and major
193   dispersal barriers are unlikely across such small geographical extents[28]. However,
194   dispersal limitation might explain, to some degree, the stronger phylogenetic clustering
195   observed when an alpine flora is compared to the global species pool. This is because
196   defining the global species pool to include species from different biogeographic realms,
197   i.e., on different continents, would likely over-extend the breadth of the phylogenetic tree
198   used to standardize the phylogenetic metrics of a given alpine flora. In other words, the
199   global species pool includes some lineages (e.g., families or even orders) that are absent
200   from the biogeographic realm of any particular focal alpine flora, which tend to
201   'artificially' increase the relative phylogenetic clustering of the alpine flora, compared to
202   the global species pool. This is supported by our major result, i.e., the average MPD_{ses} of
203   the 63 alpine floras was less negative when their respective regional floras were used as
204   species pools, compared to that when the global species pool was used as species pools
205   for each alpine flora (-4.76 and -5.91, respectively). In other words, the larger the
206   reference species pool, the more deficient in phylogenetic diversity the alpine flora
207   becomes. This pattern reflects the dominance of few clades in the alpine flora of the
208   world compared to the global angiosperm flora.
209   Interestingly, while the phylogenetic clustering of alpine floras presents a general
210   pattern, its strength varies with latitude, with temperate alpine floras less clustered than
211   tropical alpine floras compared to their respective lowland regional floras. This difference
212   might result, at least in part, from the fact that ecological gradients (particularly
213   temperature) are shorter in high latitude mountains with fewer altitudinal life belts than in
214   low latitude mountains[28] (e.g., a tropical mountain has a tropical vegetation belt at low
215   elevations, but this belt is lacking in temperate mountains). However, this general pattern
216   is reversed when the overall angiosperm flora of a mountain area (including both alpine
217   and lowland elevations) is compared to the global species pool of angiosperms. This
218   simply confirms that species in temperate floras are already a clustered, rather than
219   random, subset of the entire angiosperm flora of the world[11]. In other words, tropical
220   alpine floras represent primarily clades that have diverged early in flowering plant
221   evolution, while temperate alpine floras are recent clustered assemblages of temperate
222   floras (i.e., mostly herbaceous species), which are particular, closely-related species
223   groups of the global angiosperm flora.
224   Nonetheless, these relationships cannot fully explain the overall patterns. Indeed,
225   when comparing each alpine flora to the angiosperm flora of the world, low latitude
226   alpine floras remained more clustered than high latitude ones (Figure 3b). A
227   complementary hypothesis is that ecological gradients are shorter in high latitude
228   mountains with fewer life belts than in low latitude mountains, as noted above. Because
229   genera and families are generally similar among all alpine floras of the world (e.g., 88%
230   of angiosperm families in tropical-latitude alpine floras examined in this study also occur

231 in temperate-latitude alpine floras), including more tropical taxa (families, genera, and
232 species) in regional species pools of low latitude regions would necessarily cause
233 stronger phylogenetic clustering for their alpine floras, compared to their regional species
234 pools.
235   Interestingly, when each alpine flora is compared to the species pool that includes
236 only the species of the 63 alpine floras, species in low latitude alpine floras remain more
237 strongly clustered than those in high latitude alpine floras (Figure 3c). The following
238 hypothesis might account for this pattern. Angiosperms originated in, and spread from,
239 the tropics[29]. Some early tropical lineages became adapted to tropical montane climates,
240 forming clustered assemblages compared to lowland tropical floras. While species in
241 tropical alpine belts, as a whole, might be clustered compared to the global species pool,
242 species adapted to tropical alpine belts within different continents or major mountain
243 systems might belong to different major lineages, and thus might be further clustered,
244 because dispersal among mountains within and between continents is particularly limited
245 within tropical latitudes[30]. This would cause 'double-clustering' for tropical alpine floras.
246 In contrast, although species in temperate alpine floras are also clustered compared to the
247 global species pool, glacial-interglacial cycles during the Pleistocene repeatedly mixed
248 species of alpine floras at low elevation among different regions and continents,
249 particularly in the Northern Hemisphere. This would have tended to homogenize alpine
250 floras across continental regions. Overall, these processes would have resulted in stronger
251 phylogenetic clustering in tropical than in temperate alpine floras, in comparison with the
252 global alpine species pool.
253
254 **Methods**
255 **Alpine belt**
256 We defined the alpine belt in a mountain system as the area located above the natural
257 climatic limit of trees (alpine treeline). Because alpine belts of different mountains are
258 commonly separated by extensive forested or rangeland areas below alpine treelines,
259 alpine belts are often considered as 'sky islands'[31-32]. Alpine vegetation represents the
260 only terrestrial biogeographic unit that occurs at all latitudes worldwide[23], a remarkable
261 fact first documented by Alexander von Humbolt[33]. Vegetation above the alpine
262 (elevational) treeline resembles that north of the arctic (latitudinal) treeline[23,34]. Although
263 the total area of alpine vegetation represents only 2.6 % of the Earth's terrestrial surface
264 outside Antarctica[23,35], and only half as much area as arctic vegetation (c. 5% of the land
265 area), global species diversity of vascular plants in alpine vegetation is ca. six-fold higher
266 than that in arctic vegetation (ca. 10,000 species in alpine vegetation; vs. ca. 1,500 arctic
267 species; ref. 36). Alpine belts present severe environmental challenges to plant life,
268 including low temperatures and high ultraviolet radiation[21].
269
270 **Floras**
271 The latitudinal range of this study was confined between 50°N and 50°S. We did not
272 include higher latitudes because elevational gradients below alpine treelines at these
273 latitudes are generally short, with few vegetation belts, which would have weakened
274 comparisons with other alpine belts. We assembled 63 alpine floras worldwide (Figure 1).
275 Of these 63 alpine floras, 62 are typical alpine floras located above climate treelines. No
276 true alpine flora exists in southeastern North America; to represent this broad region in

277 our study, we included one plant assemblage from the highest mountain peaks for this
278 region (maximum elevation 2037 m) (we call it an "alpine" flora for convenience of
279 discussion). The 63 alpine floras represent the major mountain systems across the world,
280 including Mount Kenya and the Drakensberg Escarpment in Africa, the Himalayas in
281 Asia, the Andes in South America, the Rocky Mountains in North America, and the
282 European Alps. We assigned each of the 63 alpine floras to either temperate or tropical
283 latitudes, using 23.5°N and 23.5°S as the temperate-tropical boundaries.
284   We then assembled a regional species pool for each alpine flora. These regional
285 species pools included all angiosperm species along the entire elevational gradient (from
286 the lowest to highest elevations) within the region. For example, the regional species pool
287 for the alpine flora of Nepal included all angiosperm species recorded in Nepal from 59
288 to 6,400 m in elevation (i.e., the entire elevation range of Nepal over which angiosperms
289 are distributed). Details about each alpine flora and its regional species pool are available
290 in Supplementary Table 1. The species of the alpine floras included in this study are
291 restricted to non-tree species. Botanical nomenclature was standardized according to The
292 Plant List (version 1.1, www.theplantlist.org). Infraspecific taxa were combined with
293 their respective species. Non-native species in each flora were excluded. In total, the
294 regional species pools of the 63 alpine floras included 94,161 species in 369 families of
295 angiosperms (more than one quarter of angiosperm species in the world). Of these, 6,918
296 species in 140 families) comprised the 63 alpine floras. Each species was assigned to a
297 family recognized in APG IV[37], based on information on the relationships between
298 genera and families provided by the Angiosperm Phylogeny Website
299 (http://www.mobot.org/MOBOT/research/APweb/).
300   For the 63 alpine floras, on average, each regional species pool included 3,867 (±
301 4,709 SD) angiosperm species, and each alpine flora included 171 (± 124) angiosperm
302 species; on average, 9.1% of species in a regional species pool were present in its alpine
303 flora. When the 63 sites were considered together, 7.3% of the 94,161 species in the
304 regional species pools occurred in the 63 alpine floras.
305
306 **Phylogeny reconstruction**
307 We used a recently generated time-calibrated megatree for vascular plants,
308 GBOTB_extended.tre[20], as a backbone to generate a phylogeny for the 94,161 species.
309 The megatree included an updated version of the phylogeny for pteridophytes (ref. 8) and
310 an updated version of GBOTB for seed plants (ref. 19). The megatree includes all
311 families of vascular plants worldwide, including families that are absent from the
312 phylogenies of refs. 8 and 19. Of the 8,341 genera in our data set, 80% (6,673) were
313 present in the megatree. We added the genera and species in our data set that were absent
314 from the megatree to their respective families and genera using the Phylomatic and
315 BLADJ approaches[38] implemented in the V.PhyloMaker software[20]. V.PhyloMaker sets
316 branch lengths of added taxa in a family by placing the nodes evenly between dated
317 nodes and terminals within the family and placing a missing species at the mid-point of
318 the branch length of its genus (e.g., ref. 14). A recent study (ref. 39) showed that for the
319 two phylogenetic metrics used in our present study (see below), values of a phylogenetic
320 metric derived from a phylogenetic tree resolved only at the genus level are nearly
321 perfectly correlated to those derived from a phylogenetic tree resolved fully at the species
322 level (Pearson's correlation coefficient is 1.000 for one phylogenetic metric and 0.992 for

323   the other phylogenetic metric), suggesting that patterns of phylogenetic structure
324   measured with the two phylogenetic metrics would be similar or identical regardless of
325   whether a phylogenetic tree resolved at the species or genus level is used to calculate
326   these phylogenetic metrics. Finally, we pruned the megatree to generate a phylogenetic
327   tree for each of the regional species pools, retaining only the species present in the
328   regional species pool.
329   We also used V.PhyloMaker, and the approach described above, to build a
330   phylogeny for angiosperm species worldwide, which included all angiosperm species in
331   the regional floras included in this study, plus angiosperm species in The Plant List that
332   can be directly assigned to the families of APG IV. We considered the 313,855 species in
333   this phylogeny as a global species pool of angiosperms for the analyses in this study.
334
335   **Phylogenetic structure metrics**
336   We analyzed the phylogenetic structure of the alpine floras using two complementary
337   metrics, namely phylogenetic diversity (PD; ref. 40) and mean pairwise distance (MPD).
338   Because PD and MPD are positively correlated with species richness, in order to make
339   them comparable between sites, it is necessary to standardize their values by accounting
340   for species richness. This is commonly done with the use of a null model that keeps
341   species richness constant while randomizing the phylogenetic relationships between
342   species. Using this null model, the standardized effect size, which gives the relative
343   position of an observed value with respect to the null distribution, can be calculated as:
344
345         $Metric_{ses} = [Metric_{obs} − mean(Metric_{null})]/sd(Metric_{null})$,
346
347   where $Metric_{ses}$ is the standardized effect size of PD or MPD (i.e., PD_{ses} or MPD_{ses},
348   respectively), $Metric_{obs}$ is the observed phylogenetic structure metric in a given alpine
349   flora, and $Metric_{null}$ is the same metric calculated n times with n randomized assemblages
350   drawn from a species pool (see below for the definition of the species pool). Both PD_{ses}
351   and MPD_{ses} quantify the relative excess (overdispersion) or deficit (clustering) in
352   phylogenetic structure for a given alpine flora relatively to the species pool. In other
353   words, a negative PD_{ses} or MPD_{ses} reflects relative phylogenetic clustering of species
354   while a positive PD_{ses} or MPD_{ses} reflects relative phylogenetic overdispersion of species.
355   PD_{ses} and MPD_{ses} measure the phylogenetic structure of assemblages at different
356   evolutionary depths: MPD_{ses} is linked to the more basal structure of the phylogenetic tree,
357   whereas PD_{ses} describes the more terminal structure of the phylogenetic tree[41]. It is
358   important to use metrics that can assess phylogenetic structure at both basal and shallow
359   depths of evolutionary history across a phylogeny because some processes produce basal
360   clustering while others create terminal overdispersion, generating 'clusters of
361   overdispersion'[21].
362   The two metrics were calculated using computationally efficient algorithms[42-43]
363   based on exact solutions given a particular phylogenetic tree and species richness (rather
364   than being based on a resampling approximation of the mean and variance), using a null
365   model that considers all possible combinations of S species from the species pool (where
366   S is the number of species in a sample under investigation) to be equally likely[44]. To
367   determine whether MPD_{ses} and PD_{ses} values for a particular alpine flora were significantly
368   smaller (i.e., more clustering and lower phylogenetic diversity) or larger (i.e., more

369 overdispersion and higher phylogenetic diversity) compared to null assemblages
370 randomly drawn from its species pool, we generated 999 null assemblages from the given
371 species pool with the number of species in each null assemblage being equal to the
372 number of species in the alpine flora. The position of the observed value relative to the
373 null distribution was computed as the proportion of null values that are lower or higher
374 than the observed value, which corresponds to a p-value. For normally distributed data,
375 significance at p-value < 0.05 is equivalent to a standardized effect size > 1.96 (or $< -$
376 1.96).
377
378 **Phylogenetic structure and defined species pools**
379 To depict the evolutionary structure of alpine floras around the world, we considered
380 several ways to define the species pools and associated alpine floras. First, we used three
381 species pools to calculate values of MPD_{ses} and PD_{ses} for each alpine flora: (1) a species
382 pool that included all angiosperm species in the region within which the focal alpine flora
383 was located (the 'regional species pool', see below for details; Supplementary Table 1),
384 (2) a species pool that included all angiosperm species in the 63 alpine floras, and (3) a
385 global species pool for angiosperms, which included 313,855 species (see above for
386 details). For each alpine flora, the regional species pool was defined as all the species in
387 the published flora of the mountain region (Supplementary Table 1). When several
388 independent regional species pools could be retrieved from the literature, we chose the
389 one that maximized the elevation range while minimizing the area of the region. This
390 strategy provided a good representation of the area while minimizing the effects of
391 dispersal limitation. On average, the geographic distance from the alpine belt of a region
392 to the edge of the region was less than 250 km in our study. Because the distributions of
393 most plant species exceed this distance within a region, we suggest that plant species
394 distributions across different elevation belts within a mountain region are primarily a
395 result of environmental sorting, rather than dispersal limitation.
396   Second, to test whether the phylogenetic structure of alpine floras varied
397 significantly between climate zones across latitudes (tropical and temperate) and between
398 continents, we combined the 63 alpine floras, and their respective regional species pools,
399 into 12 climato-continental species pools (temperate versus tropical across continents).
400 For each of the 12 species pools, we generated a species list of alpine plants by
401 combining all alpine plant species in the alpine floras belonging to each pool
402 (Supplementary Table 2). These species pools allowed us to strictly compare MPD_{ses} and
403 PD_{ses} values across continents and climates. We also generated a global alpine flora and a
404 single associated species pool.
405   Finally, to test whether species in temperate regional floras are more closely
406 related (clustered) than species in tropical regional floras, compared to the global flora of
407 angiosperms, we measured phylogenetic structure for each of the 63 regional floras based
408 on the global angiosperm species pool.
409
410 **Data availability**
411 The data used in this study have been published and are accessible. Details about data
412 sources are provided in Supplementary Table 1 or cited in the article. The data on which
413 the analyses of this study were based are available at
414 https://github.com/Kifir0411/NATECOLEVOL-200610646.

415
Code availability
This study used codes in published R packages, which were cited in the article.

References
1. Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. Annual Review of Ecology, Evolution and Systematics, 41, 321-350.
2. Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. Science, 235, 167-171.
3. Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics, 36, 519-539.
4. Münkemüller, T., Boucher, F., Thuiller, W. & Lavergne, S. (2015) Common conceptual and methodological pitfalls in the analysis of phylogenetic niche conservatism. Functional Ecology, 29, 627-639.
5. Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D., & Wing, S.L., eds. (1992) Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago.
6. Graham, A. (1999) Late Cretaceous and Cenozoic history of North American vegetation north of Mexico Oxford University Press, New York.
7. Latham, R.E. & Ricklefs, R.E. (1993). Continental comparisons of temperate-zone tree species diversity. In Species Diversity in Ecological Communities (eds R.E. Ricklefs & D. Schluter), pp. 294-314. University of Chicago Press, Chicago.
8. Zanne, AE, et al. (2014) Three keys to the radiation of angiosperms into freezing environments. Nature 506:89-92.
9. Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology, and species richness. Trends in Ecology and Evolution, 19, 639-644.
10. Ricklefs, R.E. (2006) Evolutionary diversification and the origin of the diversity-environment relationship. Ecology, 87, S3-S13.
11. Qian, H. & Sandel, B. (2017) Phylogenetic structure of regional angiosperm assemblages across latitudinal and climatic gradients in North America. Global Ecology and Biogeography, 26, 1258-1269.
12. Körner, C. (2000) Why are there global gradients in species richness? Mountains might hold the answer. Trends in Ecology & Evolution, 15, 513-514.
13. Pulsipher, L.M. & Pulsipher, A. (2014) World Regional Geography: Global Patterns, Local Lives, 6th edn. W.H. Freeman and Company, New York.
14. Culmsee, H. & Leuschner, C. (2013) Consistent patterns of elevational change in tree taxonomic and phylogenetic diversity across Malesian mountain forests. Journal of Biogeography, 40, 1997-2010.
15. González-Caro, S., Umaña, M.N., Álvarez, E., Stevenson, P.R., & Swenson, N.G. (2014) Phylogenetic alpha and beta diversity in tropical tree assemblages along regional scale environmental gradients in Northwest South America. Journal of Plant Ecology, 7, 145-153.

460 16. Qian, H., Zhang, Y., Zhang, J., & Wang, X. (2013) Latitudinal gradients in
461   phylogenetic relatedness of angiosperm trees in North America. Global Ecology
462   and Biogeography, 22, 1183-1191.
463 17. Qian, H., Field, R., Zhang, J., Zhang, J., & Chen, S. (2016) Phylogenetic structure
464   and ecological and evolutionary determinants of species richness for angiosperm
465   trees in forest communities in China. Journal of Biogeography, 43, 603-615.
466 18. Qian, H. & Ricklefs, R.E. (2016) Out of the tropical lowlands: latitude versus
467   elevation. Trends in Ecology and Evolution, 31, 738-741.
468 19. Smith, S.A. & Brown, J.W. (2018) Constructing a broadly inclusive seed plant
469   phylogeny. American Journal of Botany, 105, 302-314.
470 20. Jin, Y. & H. Qian. 2019. V.PhyloMaker: an R package that can generate very large
471   phylogenies for vascular plants. Ecography DOI: 10.1111/ecog.04434.
472 21. Mazel, F., Davies, T.J., Gallien, L., Renaud, J., Groussin, M., Münkemüller, T., &
473   Thuiller, W. (2016) Influence of tree shape and evolutionary time-scale on
474   phylogenetic diversity metrics. Ecography, 39, 913-920.
475 22. Thuiller, W., Gallien, L., Boulangeat, I., de Bello, F., Münkemüller, T., Roquet-Ruiz,
476   C. & Lavergne, S. (2010) Resolving Darwin's naturalization conundrum: a quest
477   for evidence. Diversity and Distributions, 16, 461–475.
478 23. Körner, C. (2003) Alpine Plant Life: Functional Plant Ecology of High Mountain, 2nd
479   edn. Springer.
480 24. Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on
481   the phylogenetic structure of communities. Ecology Letters, 13, 1085-1093.
482 25. Gallien, L., Zurell, D., & Zimmermann, N. E. (2018). Frequency and intensity of
483   facilitation reveal opposing patterns along a stress gradient. Ecology and
484   Evolution, 8(4), 2171- 2181.
485 26. Choler, P., Michalet, R., & Callaway, R.M. (2001) Facilitation and competition on
486   gradients in alpine plant communities. Ecology, 82, 3295–3308.
487 27. Butterfield, B.J., Cavieres, L.A., Callaway, R.M., Cook, B.J., Kikvidze, Z., Lortie,
488   C.J., Michalet, R., Pugnaire, F.I., Schöb, C., Xiao, S., Zaitchek, B., Anthelme, F.,
489   Björk, R.G., Dickinson, K., Gavilán, R., Kanka, R., Maalouf, J.-P., Noroozi, J.,
490   Parajuli, R., Phoenix, G.K., Reid, A., Ridenour, W., Rixen, C., Wipf, S., Zhao, L.,
491   & Brooker, R.W. (2013) Alpine cushion plants inhibit the loss of phylogenetic
492   diversity in severe environments. Ecology Letters, 16, 478–486.
493 28. Steinbauer et al. (2016) Topography-driven isolation, speciation and a global increase
494   of endemism with elevation. Global Ecology and Biogeography, 25:1097-1107.
495 29. Takhtajan, A.L. (1969) Flowering plants: origin and dispersal Oliver & Boyd,
496   Edinburgh.
497 30. Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006) Are
498   mountain passes higher in the tropics? Janzen's hypothesis revisited. Integrative
499   and Comparative Biology, 46:5-17.
500 31. Heald, W. (1967) Sky Island. Princeton, New Jersey.
501 32. Marx, H.E., Dentant, C., Renaud, J., Delunel, R., Tank, D.C., & Lavergne, S. (2017)
502   Riders in the sky (islands): using a mega-phylogenetic approach to understand
503   plant species distribution and coexistence at the altitudinal limits of angiosperm
504   plant life. Journal of Biogeography, 44, 2618-2630.

505 33. Humboldt, A.v. & Bonpland, A. (1807) Essai sur la géographie des plantes:
506   accompagné d'un tableau physique des régions équinoxiales. Schoell, Paris;
507   reprint Arno Press, New York, 1977.
508 34. Qian, H., White, P.S., Klinka, K., & Chourmouzis, C. (1999) Phytogeographical and
509   community similarities of alpine tundras of Changbaishan Summit, China, and
510   Indian Peaks, USA. Journal of Vegetation Science, 10, 869-882.
511 35. Körner, C., Paulsen, J., & Spehn, E.M. (2011) A definition of mountains and their
512   bioclimatic belts for global comparisons of biodiversity data. Alpine Botany, 121,
513   73-78.
514 36. Chapin, F.S. III. & Körner, C. (1995). Patterns, changes, and consequences of
515   biodiversity in arctic and alpine ecosystems. In: Arctic and alpine biodiversity:
516   patterns, causes and ecosystem consequences (eds F.S.I. Chapin & C. Körner), pp.
517   313-320. Springer.
518 37. Angiosperm Phylogeny Group (2016) An update of the Angiosperm Phylogeny
519   Group classification for the orders and families of flowering plants: APG IV.
520   Botanical Journal of the Linnean Society, 181, 1-20.
521 38. Webb C, Ackerly D, & Kembel S (2011) Phylocom: Software for the Analysis of
522   Phylogenetic Community Structure and Character Evolution, with Phylomatic,
523   version: 4.2.
524 39. Qian, H. & Jin, Y. (2021) Are phylogenies resolved at the genus level appropriate for
525   studies on phylogenetic structure of species assemblages? Plant Diversity,
526   https://doi.org/10.1016/j.pld.2020.11.005.
527 40. Faith D.P. (1992) Conservation evaluation and phylogenetic diversity. Biological
528   Conservation 61:1-10.
529 41. Webb, C.O., Ackerly, D.D., McPeek, M.A., & Donoghue, M.J. (2002) Phylogenies
530   and community ecology. Annual Review of Ecology and Systematics, 33, 475-
531   505.
532 42. Tsirogiannis, C., Sandel, B., & Cheliotis, D. (2012) Efficient computation of popular
533   phylogenetic tree measures. Lecture Notes in Computer Science 7534:30-43.
534 43. Tsirogiannis, C., Sandel, B., & Kalvisa, A. (2014) New algorithms for computing
535   phylogenetic biodiversity. Lecture Notes in Computer Science 8701:187-203.
536 44. Tsirogiannis, C. & Sandel, B. (2016) PhyloMeasures: A package for computing
537   phylogenetic biodiversity measures and their statistical moments. Ecography
538   39:709-714.
539

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547
548 **Competing interests**
549 The authors declare no competing interests.
550

Figure Legends

Figure 1 Geographic patterns of standardized effect size of mean pairwise distance (MPD_{ses}, upper panel) and standardized effect size of phylogenetic diversity (PD_{ses}, lower panel) for the 63 alpine floras used in this study. MPD_{ses} and PD_{ses} of each alpine flora were calculated in regard to its regional flora. Filled symbols are significant ($p<0.05$). A more negative value represents a stronger degree of phylogenetic clustering among species within an alpine flora compared to its regional flora. Note that the location of a dot represents the location of the mid-point of a region, for which its alpine flora was analyzed in this study, i.e., the center of a regional flora (species pool), not a place where an alpine flora was located.

Figure 2. Comparisons of standardized effect size of mean pairwise distance (MPD_{ses}, red triangles) and standardized effect size of phylogenetic diversity (PD_{ses}, blue triangles) with histograms for distributions of these two phylogenetic metrics derived from null assemblages (see Methods for details) for different climates (temperate versus tropical) and continents, and the globe. Each histogram represents the frequency (Freq.) of MPD_{ses} or PD_{ses} values derived from 999 null assemblages randomly drawn from the species pool defined at the climato-continental or global scale. A more negative value of MPD_{ses} or PD_{ses} (indicated by a red or blue triangle) represents a stronger degree of phylogenetic clustering among alpine species compared to the reference species pool.

Figure 3. Relationships (Pearson's correlation coefficient, *r*) between latitude (in absolute terms) and standardized effect size of mean pairwise distance (MPD_{ses}) for (**a**) species in alpine floras with MPD_{ses} being calculated using the regional species pool of each of the alpine floras, (**b**) species in alpine floras with MPD_{ses} being calculated using the global species pool of angiosperm species in the combination of our regional floras and The Plant List (Methods), (**c**) species in alpine floras with MPD_{ses} being calculated using all species in the 63 alpine floras as a species pool, and (**d**) species in the regional floras of the alpine sites with MPD_{ses} being calculated using the global species pool of angiosperm species in the combination of our regional floras and The Plant List. Lines are linear least squares best fits; we used them to show linear trends, not for statistical tests.
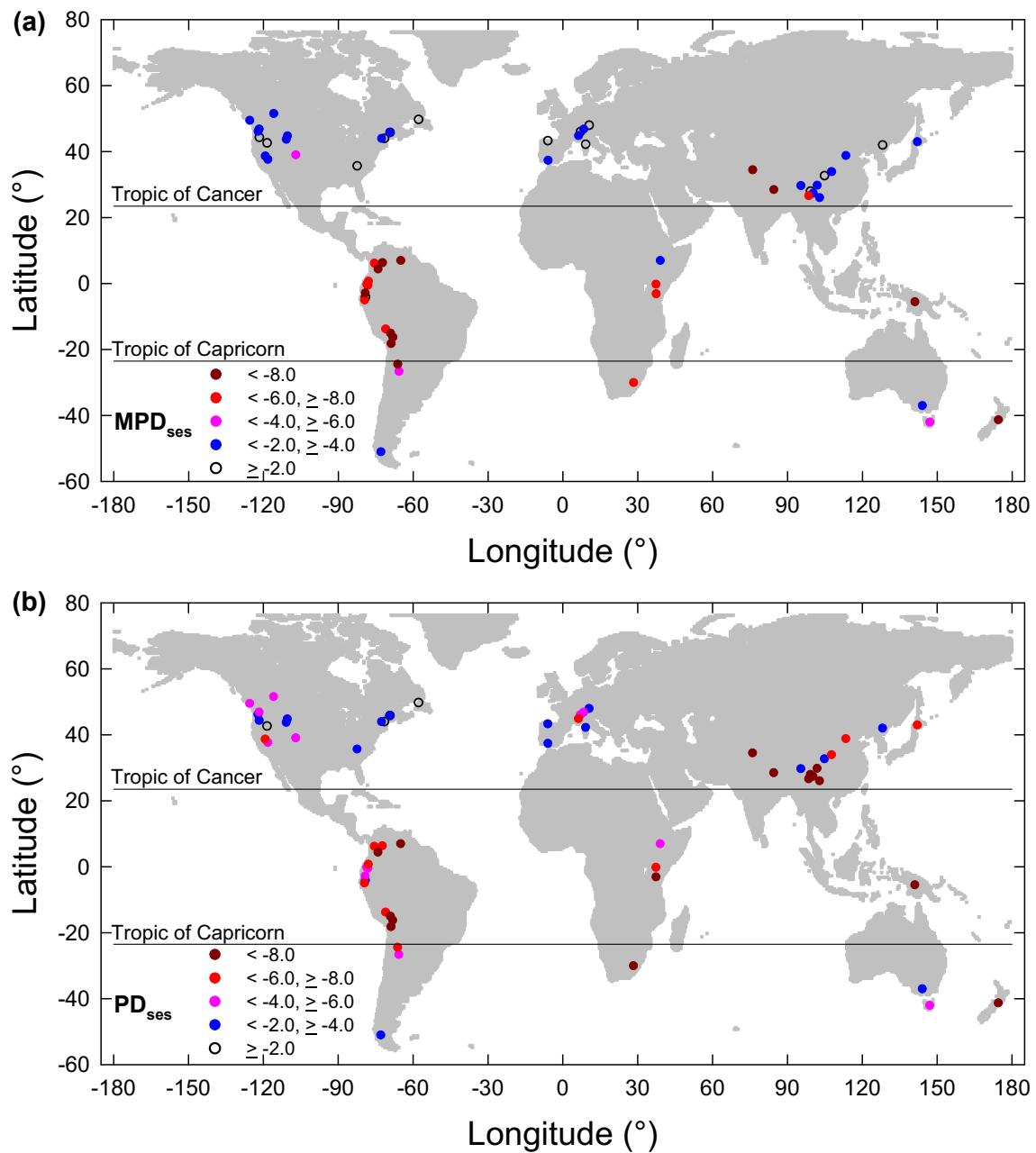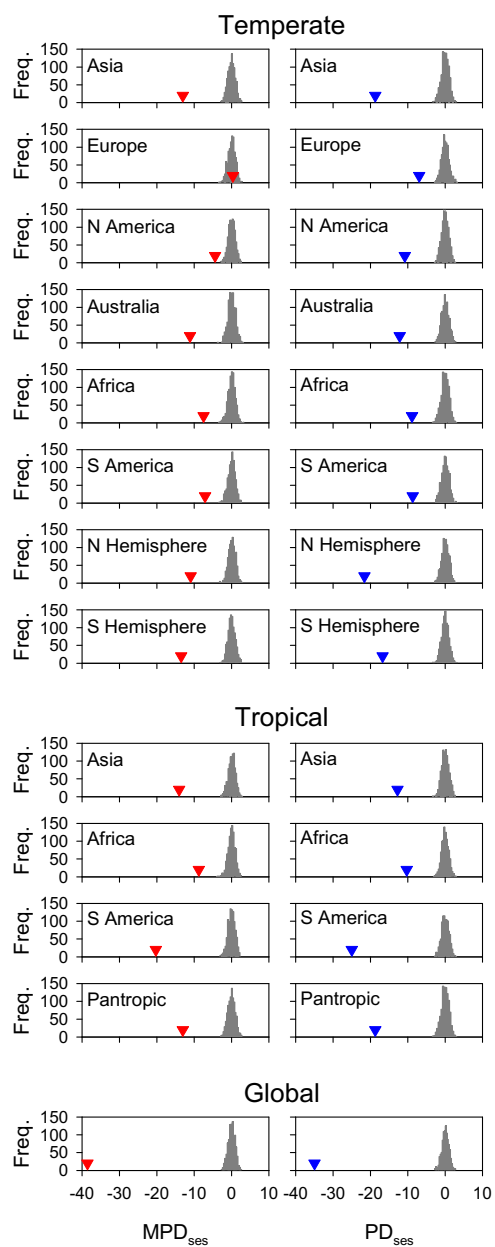
584
585   Figure 1
586

Temperate

Tropical

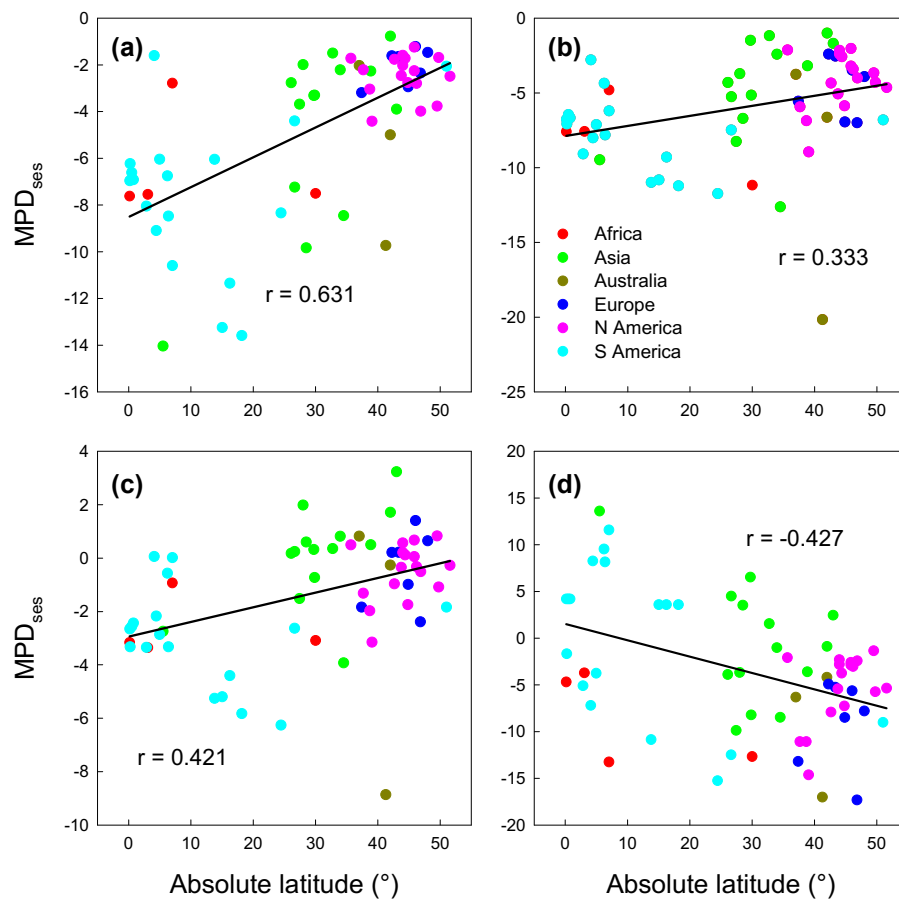
Global

MPD_{ses} PD_{ses}

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588   Figure 2
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Supplementary Information

Supplementary Table 1. Alpine floras and their regional species pools used in this study.

Supplementary Table 2. Alpine floras and their species pools in broad geographical regions.

Supplementary Figure 1. Standardized effect size of mean pairwise distance (MPD_{ses}, red triangles) and standardized effect size of phylogenetic diversity (PD_{ses}, blue triangles) in the 63 alpine floras examined in this study.

Supplementary Figure 2. Standardized effect size of mean pairwise distance (MPD_{ses}) and the standardized effect size of phylogenetic diversity (PD_{ses}) for the 63 alpine floras examined in this study.

Supplementary Figure 3. Relationships between growing degree days and standardized effect size of mean pairwise distance (MPD_{ses}).

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Supplementary Table 1 Alpine floras and their regional species pools used in this study.

Site ID	Continent	Country [region]	Alpine flora	Regional species pool	Data source
1	Africa	Ethiopia	Alpine flora of Mt Galama	Flora of Ethiopia	1, 63
2	Africa	Kenya	Alpine flora of Mt. Kenya	Flora of Kenya	2, 63
3	Africa	South Africa and Lesotho	Alpine flora of Drakensberg Mountains	Flora of KwaZulu-Natal Province of South Africa and Lesotho	3, 64, 101
4	Africa	Tanzania	Alpine flora of Mount Kilimanjaro	Flora of Tanzania	4, 53, 63
5	Asia	China	Alpine flora of Baima Snow Mountains	Flora of Baima Snow Mountains	5
6	Asia	China	Alpine flora of Big Bend Gorge of Yalu Tsangpo	Flora of Big Bend Gorge of Yalu Tsangpo	6
7	Asia	China	Alpine flora of Changbai Mountains	Flora of Changbai Moutains	7, 65
8	Asia	China	Alpine flora of Gaoligong Mountains	Flora of Gaoligong Mountains	8
9	Asia	China	Alpine flora of Gongga Mountains	Flora of grid cell #1616 in ref. 66	9, 66
10	Asia	China	Alpine flora of Jiaozi Mountains	Flora of Jiaozi Mountains	10, 54
11	Asia	China	Alpine flora of Motianling	Flora of Baishuijiang Nature Reserve	11
12	Asia	China	Alpine flora of Taibai Mountains	Flora of Taibai Mountains	12, 67
13	Asia	China	Alpine flora of Wutai Mountains	Flora of grid cell #990 in ref. 66	13, 66
14	Asia	China	Alpine flora of Yulong Snow Mountains	Flora of Yulong Snow Mountains	14, 55, 61
15	Asia	India	Alpine flora of Kashmir Himalaya	Flora of Jammu and Kashmir	15, 68
16	Asia	Japan	Alpine flora of Hokkaido	Flora of Hokkaido	16, 69
17	Asia	Nepal	Alpine flora of Nepal	Flora of Nepal	17
18	Asia	[New Guinea]	Alipine flora of New Guinea	Flora of New Guinea	18, 56, 70, 96
19	Australia	Australia	Alpine flora of Tasmania	Flora of Tasmania	19, 71
20	Australia	Australia	Alpine flora of Victoria	Flora of Victoria	20, 71
21	Australia	New Zealand	Alpine flora of New Zealand	Flora of New Zealand	21, 72
22	Europe	France	Alpine flora of Corsica	Flora of Corsica	22
23	Europe	France	Alpine flora of Écrins National Park	Flora of Écrins National Park	23
24	Europe	Germany	Alpine flora of Germany	Flora of Baden-Württemberg and Bavaria States	24, 57, 73
25	Europe	Spain	Alpine flora of Rasón and San Isidro	Flora of Asturias	25, 74
26	Europe	Spain	Alpine flora of Sierra Nevada	Flora of Andalusia	26, 74
27	Europe	Switzerland	Alpine flora of Switzerland	Flora of Switzerland	27, 75

28	Europe	Switzerland	Alpine flora of Valais (Western Alps)	Flora of Valais	28, 76
29	North America	Canada	Alpine flora of Banff National Park	Flora of Banff and Jasper National Park	29, 77, 97, 100
30	North America	Canada	Alpine flora of Gros Morne National Park	Flora of Gros Morne National Park	30, 78
31	North America	Canada	Alpine flora of Vancouver Island	Flora of Vancouver Island	31, 58, 79
32	North America	USA	Alpine flora of Adirondack Mountains	Flora of Adirondack Mountains (Adirondack Park) - 5 northeastern counties	32, 59, 62, 80
33	North America	USA	Alpine flora of Baxter State Park	Flora of Piscataquis County	33, 81, 98
34	North America	USA	Alpine flora of Elk Mountains	Flora of Colorado	34, 82
35	North America	USA	Alpine flora of Mount Hood	Flora of Clackamas and Hood River counties of Oregon State	35, 83
36	North America	USA	Alpine flora of Mount Rainier National Park	Flora of Mount Rainier National Park	36, 84
37	North America	USA	Alpine flora of Mount St. Helens	Flora of Skamania County	37, 83, 99
38	North America	USA	Alpine flora of Mount Washburn	Flora of Yellowstone National Park in Wyoming	38, 85
39	North America	USA	Alpine flora of New Hampshire State	Flora of New Hampshire State	39, 86
40	North America	USA	Alpine flora of Appalachian Mountains in North Carolina	Flora of Blue Ridge Mountains in North Carolina	40, 87
41	North America	USA	Alpine flora of Steens Mountain	Flora of Steens Mountain	41, 88
42	North America	USA	Alpine flora of Sweetwater Mountains	Flora of Mono County	42, 89
43	North America	USA	Alpine flora of Teton Range	Flora of Teton County	43, 90
44	North America	USA	Alpine flora of Vermont State	Flora of Vermont State	44, 85
45	North America	USA	Alpine flora of White Mountains	Flora of Mono County	45, 89
46	South America	Argentina	Alpine flora of Monumento Natural Abra del Acay	Flora of Salta Province	46, 91
47	South America	Argentina	Alpine flora of Parque Provincial Cumbres Calchaquíes	Flora of Tucumán Province	46, 91
48	South America	Bolivia	Alpine flora of Área Natural de Manejo Integrado Apolobamba	Flora of Bolivia	46, 92
49	South America	Bolivia	Alpine flora of Parque Nacional Sajama	Flora of Bolivia	46, 92
50	South America	Bolivia	Alpine flora of Parque Nacional Tuni Condoriri	Flora of Bolivia	46, 92

51	South America	Chile	Alpine flora of Paine National Park	Flora of Region XII of Chile	47, 91
52	South America	Colombia	Alpine flora of Antioquia Department	Flora of Antioquia Department	48
53	South America	Colombia	Alpine flora of Parque Nacional Natural Cocuy	Flora of Colombia	46, 93
54	South America	Colombia	Alpine flora of Chisacá	Flora of Colombia	49, 93
55	South America	Ecuador	Alpine flora of Complejo Volcánico Pichincha	Flora of northwestern Ecuador (incl. the provinces of Esmeraldas, Carch, Imbabura, Pichincha)	46, 92
56	South America	Ecuador	Alpine flora of El Cajas	Flora of Azuay Province	50, 60, 92
57	South America	Ecuador	Alpine flora of Parque Nacional Podocarpus	Flora of Loja Province	46, 92
58	South America	Ecuador	Alpine flora of Quito	Flora of Pichincha Province	51, 92
59	South America	Ecuador	Alpine flora of Reserva Ecológica Antisana	Flora of northwestern Ecuador (incl. the provinces of Esmeraldas, Carch, Imbabura, Pichincha)	46, 92
60	South America	Ecuador	Alpine flora of Reserva Ecológica El Ángel	Flora of northwestern Ecuador (incl. the provinces of Esmeraldas, Carch, Imbabura, Pichincha)	46, 92
61	South America	Peru	Alpine flora of Cordillera de Vilcanota - Laguna de Sibinacocha	Flora of Cuzco Department (Region)	46, 94
62	South America	Peru	Alpine flora of Páramos de Pacaipampa	Flora of Piura Department (Region)	46, 94
63	South America	Venezuela	Alpine flora of Venezuela	Flora of Venezuela	52, 95

Data sources

1. Hedberg, O. 1971. The high mountain flora of the Galama Mountain in Arussic Province, Ethiopia. Webbia, 26, 101-128.
2. Rehder, H., Beck, E. & Kokwaro, J.O. 1988. The Afroalpine plant communities of Mt. Kenya (Kenya). Phytocoenologia 16: 433−463.
3. Killick, D.J.B.. 1978. The Afro-alpine Region. In: Werger M.J.A. (eds) Biogeography and Ecology of Southern Africa. Monographiae Biologicae, vol 31. Springer, Dordrecht.
4. Beck, E., Scheibe, R. & Senser, M. 1983. The vegetation of the Shira Plateau and the western slopes of Kibo (Mount Kilimanjaro, Tanzania). Phytocoenologia, 11:1 – 30.
5. Li, H.-W. 2003. Baima Snow Mountain National Nature Reserve. Yunnan Nationalities Publishing House.
6. Sun, H. and Z. Zhou. 2002. Seed plants of the Big Bend Gorge of Yalu Tsangpo in SE Tibet, E Himalayas. Yunnan Science and Technology Press, Kunming.
7. Qian, H. 1989. Alpine Tundra of Mt. Changbai: Phytotaxonomy, Florology and Phytoecology. Ph.D. dissertation. Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang.
8. Li, H. et al. (eds.). 2000. Flora of Gaoligong Mountains. Science Press, Beijing.
9. Liu, Z.-G. 1985. Vegetation of Gongga Mountains. Sichuan Science and Technology Press.
10. Zhang, L.-S. 2006. Yunnan Jiaozishan Nature Reserve. Yunnan Science and Technology Press.

11. Wu, G.H. & Zhang, K.R. 1997. Scientific Survey of Gansu Baishui River Nature Reserve. Gansu Scientific and Technology Press, Lanzhou.
12. Cui, H.-T., H.-Y. Liu and J.-H. Dai. 2005. Studies of montane ecology and alpine treelines. Science Press.
13. Cao, Y.-L. 1999. Vegetation landscape at the alpine treeline of Wutai Mountains in Shanxi. M.S. Thesis. Peking University.
14. Yang, Q.-E. 1987. Study of Seed Plant Floristics in Yulong Mountains, Lijiang, northwestern Yunnan. M.S. thesis. Kunming Institute of Botany, Chinese Academy of Sciences.
15. Dhar, U. and P. Kachroo. 1983. Alpine flora of Kashmir Himalaya. Jodhpur, India : Scientific Publishers : Distributors, United Book Traders.
16. Shimizu, T. 1982-1983. The new alpine flora of Japan in color , vol. 2. Osaka: Hoikusha.
17. Press, J. K., Shrestha, K. K., & Sutton, D. A. (2000). Annotated checklist of the flowering plants of Nepal. London: Natural History Museum.
18. Hoogland, R. D. 1958. The Alpine flora of Mount Wilhelm (New Guinea). Blumea (suppl. IV) vol. 2.X, 220-238
19. Kirkpatrick, J. B., Dombrovskis, P., Davis, G. and Eberhard, J. 1997. Alpine Tasmania : an illustrated guide to the flora and vegetation. Melbourne : Oxford University Press.
20. Horrocks, G. F. B. . 1987. Flora and fauna of the Beloka and Gibbo River forest blocks, Alpine area, Victoria. Melbourne : Dept. of Conservation, Forests and Lands.
21. Mark, A. F. and N. M. Adams. 1995. New Zealand alpine plants. Birkenhead, Auckland, N.Z. : Godwit.
22. Jeanmonod, D. and Gamisans, J. 2007. Flora Corsica. Edisud.
23. Marx, H. E., Dentant, C., Renaud, J., Delunel, R., Tank, D. C., & Lavergne, S. (2017) Riders in the sky (islands): using a mega-phylogenetic approach to understand plant species distribution and coexistence at the altitudinal limits of angiosperm plant life. Journal of Biogeography, 44, 2618-2630.
24. Reisigl, H. and Keller, R., 1987. Alpenpflanzen im Lebensraum : alpine Rasen, Schutt- und Felsvegetation : Vegetationsökologische Informationen für Studien Exkursionen und Wanderungen. (German edition)
25. González, J. M. C. and T. E. D. González. 1992. Flora, vegetación y fauna de los Puertos del Rasón [= Alpine flora and fauna of Rasón and San Isidro]. [Asturias] : Servicio de Publicaciones del Principado de Asturias.
26. Fernandez Calzado, M. R., Molero Mesa, J., Merzouki, A. et al. 2012. Vascular plant diversity and climate change in the upper zone of Sierra Nevada, Spain. PLANT BIOSYSTEMS Volume: 146 Issue: 4 Pages: 1044-1053 Published.
27. Schröter, L., Lüdi, W., Botaniker, Schröter, C., Botaniker. 1963. Schröter's coloured vade-mecum to the Alpine Flora. Zürich : Schumann.
28. Theurillat, J.-P., A. Schlüssel, P. Geissler, A. Guisan, C. Velluti, and L. Wiget. 2003. Vascular plant and bryophyte diversity along elevational gradients in the Alps. In: Alpine biodiversity in Europe (eds. Nagy, L., Grabherr, G., Körner, C., Thompson, D.B.A.). Berlin ; New York : Springer.
29. Kuchar, P. 1975. Alpine tundra communities and *Dryas octapetala* ssp. *hookeriana* in the Bald Hills, Jasper National Park. Ph.D. thesis. Edmonton.
30. Brouillet, L., Hay, S., Turcotte, P. et al. 1998. The alpine vascular flora of the Big Level Plateau, Gros Morne National Park, Newfoundland. GEOGRAPHIE PHYSIQUE ET QUATERNAIRE Volume: 52 Issue: 2 Pages: 175-193 Published.
31. Brett, R. B., K. Klinka, and H. Qian. 2001. Classification of high-elevation, non-forested plant communities in coastal British Columbia. Scientia Silvica Extension Series, Number 29. Forest Sciences Department, University of British Columbia.

32. Robinson, S. C.. Ketchledge, E. H., Fitzgerald, B. T. et al. 2010. A 23-Year Assessment of Vegetation Composition and Change in the Adirondack Alpine Zone, New York State. Rhodora 112:355-377.

33. Urban, A. J., Mittelhauser, G. H., Dickinson, M. et al. 2017. The Alpine Vascular Plants of Baxter State Park, Maine, USA. Rhodora 119:110-131.

34. Seagrist, R.V. and Taylor, K. J. 1998. Alpine vascular flora of Hasley Basin, Elk Mountains, Colorado, USA. Madroño 45, 310-318.

35. Hall, L. 1967. A survey of the vascular plants above timberline on Mt. Hood, Oregon. Madroño 19, 130-133.

36. Edwards, O. M. 1980. The alpine vegetation of Mount Rainier National Park: structure, development and constraints. Ph.D. Dissertation, University of Washington.

37. del Moral, R. and D. M. Wood. 1988. The high elevation flora of Mount St. Helens, Washington. Madroño 35:309-319.

38. Aho, K. and J. Bala. 2012. Vascular Alpine Flora of Mount Washburn, Yellowstone National Park, USA. Madroño 59(1):2-13.

39. Slack, N. G., Bell, A. W., Slack, N. G. 2013. Field guide to the New England alpine summits :mountaintop flora and fauna in Maine, New Hampshire, and Vermont. Boston, Massachusetts : Appalachian Mountain Club Books.

40. Wiser, S. K., Peet, R. K. and White, P. S. 1996. High-elevation rock outcrop vegetation of the Southern Appalachian Mountains. Journal of Vegetation Science. 7:703-722

41. Collins, P. 1978. Alpine vegetation of Steens Mountain. M.S. Thesis, Portland State University, Portland.

42. Hunter, K. B. and Johnson, R. E. 1983. Alpine flora of the Sweetwater Mountains, Mono County, California. Madroño 30, 89-105.

43. Spence, J. R. and Shaw, R. J. 1981. A checklist of the alpine vascular flora of the Teton Range, Wyoming, with notes on biology and habitat preferences. Great Basin Naturalist 41, 232-242.

44. Slack, N. G. and Bell, A. W. 2013. Field guide to the New England alpine summits: mountaintop flora and fauna in Maine, New Hampshire, and Vermont. Boston, Massachusetts: Appalachian Mountain Club Books.

45. Rundel, P. W., Gibson, A. C., Sharifi, M. R. 2008. The alpine flora of the White Mountains, California. Madroño 55, 202-215.

46. Cuesta, F., Muriel, P., Llambí, L.D., Halloy, S., Aguirre, N., Beck, S., Carilla, J., Meneses, R.I., Cuello, S., Grau, A., Gámez, L.E., Irazábal, J., Jácome, J., Jaramillo, R., Ramírez, L., Samaniego, N., Suárez- Duque, D., Thompson, N., Tupayachi, A., Viñas, P., Yager, K., Becerra, M.T., Pauli, H., & Gosling, W.D. (2017) Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes. Ecography, 40, 1381-1394.

47. Arroyo, M.T.K., Von Bohlen, C. P., Cavieres, L. and Marticorena, C. 1992. Survey of the alpine flora of Torres del Paine National Park, Chile. Gayana Botánica 49(1-4):47-70.

48. Idárraga, A., R. del C. Ortiz, R. Callejas & M. Merello (eds.) 2011. Flora de Antioquia: Catálogo de las Plantas Vasculares del Departamento de Antioquia (Colombia) [= Catalogue of the Vascular Plants of the Department of Antioquia (Colombia)]. 2 vols. Medellín, Colombia : Universidad de Antioguia : Governación de Antioquia : Missouri Botanical Garden

49. Pedraza Peñalosa, P., Franco Roselli, P., Betancur, J. 2004. Chisacá, un recorrido por los Páramos Andinos. Bogotá, D.C. : Universidad Nacional de Colombia, Instituto de Ciencias Naturales.

50. Minga, D., Ansaloni, R., Verdugo, A. and Ulloa Ulloa, C. 2016. Flora del páramo del Cajas [= Flora of the Páramo of El Cajas Azuay, Ecuador]. Cuenca : Universidad del Azuay.

51. Ulloa Ulloa, C. & D. Fernández (eds.). 2015. Plantas de los páramos del Distrito Metropolitano de Quito, Ecuador [= Plants of the páramos around Quito, Ecuador]. Serie de publicaciones Museo Ecuatoriano de Ciencias Naturales del Instituto Nacional de Biodiversidad. Publicación Patrimonio Natural del Ecuador No. 2.
52. Vareschi, V. 1970. Flora de Los Paramos de Venezuela. Universidad de Los Andes, Merida.
53. Beck, E., Scheibe, R. & Schulze, E.-D. 1986. Recovery from fire: observations in the alpine vegetation of western Kilimanjaro (Tanzania). Phytocoenologia, 14 , 55 – 77.
54. Peng, H. and E.-D. Liu. 2015. Yunnan Jiaozishan Nnational Nature Reserve. Chinese Forestry Publishing House.
55. Lv, Z.-W. 1999. Alpine garden and seed plant checklist of Lijiang region. Yunnan Nationalities Publishing House.
56. Royen, P. van. 1979-1983. The alpine flora of New Guinea. 4 vols. Vaduz : J. Cramer
57. Hegi, G. and Merxmüller, H. 1976. Alpenflora : die wichtigeren Alpenpflanzen Bayerns, Österreichs und der Schweiz. 24th ed. Berlin : P. Parey.
58. Ogilvie,R. T. and A. Ceska. 1984. Alpine plants of phytogeographic interest on northwestern Vancouver Island. Canadian Journal of Botany 62(11): 2356-2362
59. Slack, N. G. and A. W. Bell. 2006. Adirondack Alpine Summits: An Ecological Field Guide. Adirondack Mountain Club.
60. Ulloa Ulloa, C., S. Álvarez Molina, P.M. Jørgensen & D. Minga. 2009. Guía de 100 plantas silvestres del páramo del Parque Nacional Cajas [= Cajas National Park field guide of 100 wild plants of the páramo]. Spanish/English edition. Pp. 1-90. ETAPA, Cuenca. [Second edition]
61. Xu, B., Z.-M. Li and H. Sun. 2014. Seed plants of the alpine subnival belt from the Hengduan Mountains, SW China. Science Press.
62. DeNunzio, M. G. 1972. A vegetational survey of the alpine zone of the Adirondack Mountains, New York. M.S. thesis, College of Environmental Science and Forestry, State Univ. New York, Syracuse, NY.
63. Conservatoire et Jardin botaniques & South African National Biodiversity Institute. online. African Plant Database [http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php]
64. Killick, D.J.B.. 1963. An Account of the Plant Ecology of the Cathedral Peak Area of the Natal Drakensberg. Thesis. University of Natal.
65. Cao, W. and J.-Y. Li. 2003. Natural distribution for plant of Changbai Shan in China. Northwest University Press. Shengyang.
66. Lu, L.-M. et al. 2018. Evolutionary history of the angiosperm flora of China. Nature 554, 234-238.
67. Ren, Y. 2006. Biodiversity, conservation and management of Taibaishan Nature Reserve. Chinese Forestry Publishing House.
68. Rana, S. K. and G. S. Rawat. 2017. Database of Himalayan Plants Based on Published Floras during a Century. Data 2017, 2, 36; doi:10.3390/data2040036
69. Check List of Vascular Plants in Hokkaido. [http://www.hinoma.com/maps]
70. GBIF. online. Global Biodiversity Information Facility. [https://www.gbif.org]
71. Council of Heads of Australasian Herbaria. online. Australian Plant Census (APC). https://www.anbg.gov.au/chah/apc/
72. Wilton, A. D., Schönberger, I., Boardman, K. F., Breitwieser, I., Cochrane, M., Dawson, M. I., de Lange, P. J., de Pauw, B., Fife, A. J., Ford, K. A., Gibb, E. S., Glenny, D. S., Heenan, P. B., Korver, M. A., Novis, P. M., Redmond, D. N., Smissen, R. D., Tawiri, K. (2016) Checklist of the New Zealand Flora – Seed Plants. Lincoln, Manaaki Whenua-Landcare Research. [http://dx.doi.org/10.7931/P1PP42]
73. Buttler, K. P., M. Thieme und Mitarbeiter. online. Florenliste (List of species for each federal state). [http://www.kp-buttler.de/florenliste/]
74. Anthos. online. Spanish plants information system. [http://www.anthos.es/index.php?lang=en]

75. Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M., & Webb, D. A. (1964-1980) Flora Europaea, vols. 1-5. Cambridge University Press, Cambridge.

76. D'Angreville, J. E. 1863. La flore Vallaisanne. Genève : M. Mehling.

77. Kojima, S. 1977. A Preliminary Checklist of Vascular Plants of Banff National Park. Canadian Forestry Service, Northern Forest Research Centre, Edmonton.

78. Bouchard, A., Hay, S., Bergeron, Y., Leduc, A. 1991. The vascular flora of Gros Morne National Park, Newfoundland: a habitat classification approach based on floristic, biogeographical and life-form data. In: Quantitative approaches to phytogeography. (Eds: Nimis, P. L.; Crovello, T. J.) Kluwer Academic Publishers

79. Klinkenberg, B. (Editor) 2018. E-Flora BC: Electronic Atlas of the Flora of British Columbia [eflora.bc.ca]. Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia, Vancouver. [http://a100.gov.bc.ca/pub/eswp/html/moeRegMap.htm]

80. New York Flora Association. online. New York Flora Atlas. Five northeastern counties (Clinton, Essex, Franklin, Hamilton, Warren). [http://newyork.plantatlas.usf.edu/]

81. Hudson, W. D. 1988. The preliminary vascular flora of Baxter State Park. (Critical Areas Miscellaneous Report, 37.) Maine State Planning Office, Augusta, Maine.

82. Wittmann, R. C., Weber, W. A., Johnston, B. C. 1988. Flora of Colorado: Computer Generated Catalog. University of Colorado, Boulder.

83. USDA, NRCS. 2019. The PLANTS Database (http://plants.usda.gov, 30 January 2019). National Plant Data Team, Greensboro, NC 27401-4901 USA.

84. Biek, D. 2000. Flora of Mount Rainier National Park. Oregon State University Press, Corvallis.

85. Snow, N. 1992-1994. The vascular flora of southeastern Yellowstone National Park and the Headwaters Region of the Yellowstone River, Wyoming. The Wasmann Journal of Biology 50, 52-95.

86. Angelo, R. 2018. Atlas of the Flora of New England. [http://neatlas.org/index.html]

87. Wofford, B. E. 1989. Guide to the Vascular Plants of the Blue Ridge. University of Georgia Press, Athens, Georgia.

88. Mansfield, D. H. 2000. Flora of Steens Mountain. Oregon State University Press, Corvallis.

89. Anonymous. online. CalFlora. [https://www.calflora.org/]

90. Shaw, R. J. 1992. Annotated checklist of the vascular plants of Grand Teton National Park and Teton County, Wyoming. Grand Teton Natural History Association, Moose, Wyoming.

91. Zuloaga F., Morrone O. & Belgrano M. 2008. Catálogo De Las Plantas Vasculares Del Cono Sur. 3 vols. Monographs in Systematic Botany 107. Missouri Botanical Garden Press, St. Louis.

92. Jørgensen, P. M.; Nee, M. H. & Beck, S. G. (eds.). 2014. Catálogo de plantas vasculares de Bolivia, Monographs in Systematic Botany from the Missouri Botanical Garden 127: i-viii, 1-1744.

93. Ulloa, C. U., Acevedo-Rodríguez, P., Beck, S., Belgrano, M. J., Bernal, R., Berry, P. E., Brako, L., Celis, M., Davidse, G., Forzza, R. C., Gradstein, S. R., Hokche, O., León, B., León-Yánez, S., Magill, R. E., Neill, D. A., Nee, M., Raven, P. H., Stimmel, H., Strong, M. T., Villaseñor, J. L., Zarucchi, J. L., Zuloaga, F. O., & Jørgensen, P. M. (2017) An integrated assessment of the vascular plant species of the Americas. Science, 358, 1614-1617.

94. Brako, L., Zarucchi, J. L. 1993. Catalogue of the flowering plants and gymnosperms of Peru [= Catálogo de las angiospermas y gimnospermas del Perú]. St. Louis, Mo.: Missouri Botanical Garden

95. Hokche, O., P. E. Berry & O. Huber (ed.) 2008. Nuevo catálogo de la flora vascular de Venezuela. Fundación Instituto Botánico de Venezuela, Caracas.

96. BGCI. online. GlobalTreeSearch online database. Botanic Gardens Conservation International. Richmond, UK.

97. Achuff, P. L., and Corns, I. G. W. 1982. Appendix A: Plant Checklists. In: Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. 2: Soil and vegetation resources. (Eds: Holland,WD; Coen,GM) Alberta Institute of Pedology Publication SS-82-44, Edmonton, 515-530.

98. Angelo, R. 2018. Atlas of the Flora of New England. [http://neatlas.org/index.html]

99. St. John, H. 1976. The flora of Mt. St. Helens, Washington. Mountaineer 70, 65-77.

100. Porsild, A. E. 1959. Botanical excursion to Jasper and Banff National Parks, Alberta: alpine and subalpine flora. Natl. Mus. Can., Ottawa, Ont. Dept. of Northern Affairs and National Resources.

101. Germishuizen, G. & Meyer, N. L. (eds) 2003. Plants of southern Africa: an annotated checklist. Strelitzia 14. National Botanical Institute, Pretoria.

Supplementary Table 2 Alpine floras and their species pools in broad geographical regions.

Group of alpine floras	Number of alpine species	Number of species in species pool
Temperate Asia	2314	14984
Temperate Europe	668	5318
Temperate North America	894	5996
Temperate Australia	1078	4981
Temperate Africa	435	4925
Temperate South America	331	4158
Temperate Northern Hemisphere	3665	25072
Temperate Southern Hemisphere	1839	13871
Tropical Asia	290	13347
Tropical Africa	190	8590
Tropical South America	1088	40892
Pantropic	1562	61390
Globe	6918	94161

Supplementary Table 3 The numbers of species and genera (in parentheses) for the ten largest families in the alpine floras examined in this study for each of the 12 geographic regions shown in Supplementary Table 2.

(a)

| temp.Asia	temp.Europe	temp.N.America	temp.Australia
Asteraceae 305 (56)	Asteraceae 94 (40)	Asteraceae 148 (46)	Asteraceae 193 (36)
Ranunculaceae 139 (20)	Poaceae 66 (22)	Cyperaceae 77 (5)	Poaceae 133 (25)
Primulaceae 109 (6)	Caryophyllaceae 41 (13)	Poaceae 73 (23)	Plantaginaceae 78 (8)
Rosaceae 105 (23)	Rosaceae 33 (12)	Brassicaceae 51 (14)	Ericaceae 76 (19)
Brassicaceae 104 (35)	Brassicaceae 32 (20)	Rosaceae 49 (16)	Apiaceae 72 (12)
Ericaceae 103 (17)	Fabaceae 32 (10)	Ericaceae 45 (18)	Cyperaceae 64 (11)
Saxifragaceae 101 (4)	Cyperaceae 29 (4)	Fabaceae 35 (5)	Ranunculaceae 38 (4)
Gentianaceae 99 (9)	Ranunculaceae 25 (11)	Ranunculaceae 30 (12)	Juncaceae 32 (4)
Caryophyllaceae 98 (14)	Saxifragaceae 22 (1)	Orobanchaceae 29 (6)	Rubiaceae 25 (4)
Cyperaceae 97 (10)	Plantaginaceae 22 (7)	Caryophyllaceae 28 (8)	Fabaceae 21 (14)

(b)

| temp.Africa	temp.S.America	temp.N.hemisphere	temp.S.hemisphere
Asteraceae 107 (31)	Asteraceae 87 (29)	Asteraceae 531 (107)	Asteraceae 387 (88)
Poaceae 35 (21)	Poaceae 47 (16)	Poaceae 219 (43)	Poaceae 213 (45)
Scrophulariaceae 34 (11)	Brassicaceae 24 (15)	Ranunculaceae 186 (24)	Apiaceae 93 (22)
Iridaceae 25 (6)	Fabaceae 23 (5)	Brassicaceae 182 (52)	Ericaceae 85 (21)
Crassulaceae 24 (3)	Caryophyllaceae 18 (8)	Rosaceae 176 (28)	Plantaginaceae 83 (8)
Aizoaceae 22 (3)	Apiaceae 11 (6)	Cyperaceae 176 (10)	Cyperaceae 81 (13)
Orchidaceae 21 (10)	Rosaceae 10 (4)	Caryophyllaceae 157 (19)	Fabaceae 54 (26)
Asparagaceae 14 (8)	Ranunculaceae 10 (4)	Ericaceae 147 (28)	Ranunculaceae 52 (5)
Cyperaceae 13 (6)	Iridaceae 7 (3)	Fabaceae 143 (26)	Brassicaceae 42 (21)
Campanulaceae 13 (5)	Juncaceae 7 (3)	Saxifragaceae 141 (8)	Juncaceae 41 (4)

(c)

trop.Asia	trop.Africa	trop.S.America	pantropic
Asteraceae 53 (22)	Asteraceae 44 (16)	Asteraceae 244 (63)	Asteraceae 244 (93)
Poaceae 41 (13)	Poaceae 28 (13)	Poaceae 125 (32)	Poaceae 125 (43)
Ericaceae 33 (9)	Apiaceae 10 (6)	Brassicaceae 43 (12)	Ericaceae 29 (20)
Cyperaceae 19 (7)	Lamiaceae 9 (5)	Caryophyllaceae 38 (8)	Rosaceae 36 (9)
Plantaginaceae 16 (5)	Rosaceae 8 (2)	Rosaceae 36 (9)	Cyperaceae 32 (12)
Rosaceae 14 (3)	Cyperaceae 7 (2)	Orchidaceae 35 (13)	Brassicaceae 43 (15)
Ranunculaceae 12 (1)	Caryophyllaceae 7 (5)	Gentianaceae 34 (4)	Caryophyllaceae 38 (11)
Orchidaceae 11 (7)	Brassicaceae 6 (5)	Cyperaceae 32 (10)	Orchidaceae 35 (21)
Orobanchaceae 10 (1)	Iridaceae 6 (4)	Caprifoliaceae 31 (5)	Plantaginaceae 23 (10)
Urticaceae 9 (2)	Crassulaceae 6 (3)	Ericaceae 29 (12)	Apiaceae 27 (17)

Supplementary Figure 1. Standardized effect size of mean pairwise distance (MPD_ses, red triangles) and standardized effect size of phylogenetic diversity (PD_ses, blue triangles) in the 63 alpine floras examined in this study. The first twelve alpine floras included two representative alpine floras for each continent, and the remaining 51 alpine floras are shown in the rest of this appendix. Each histogram represents frequency of MPD_ses and PD_ses values derived from 999 null assemblages randomly drawn from its respective regional species pool. Details about each site are available in Supplementary Table 1.
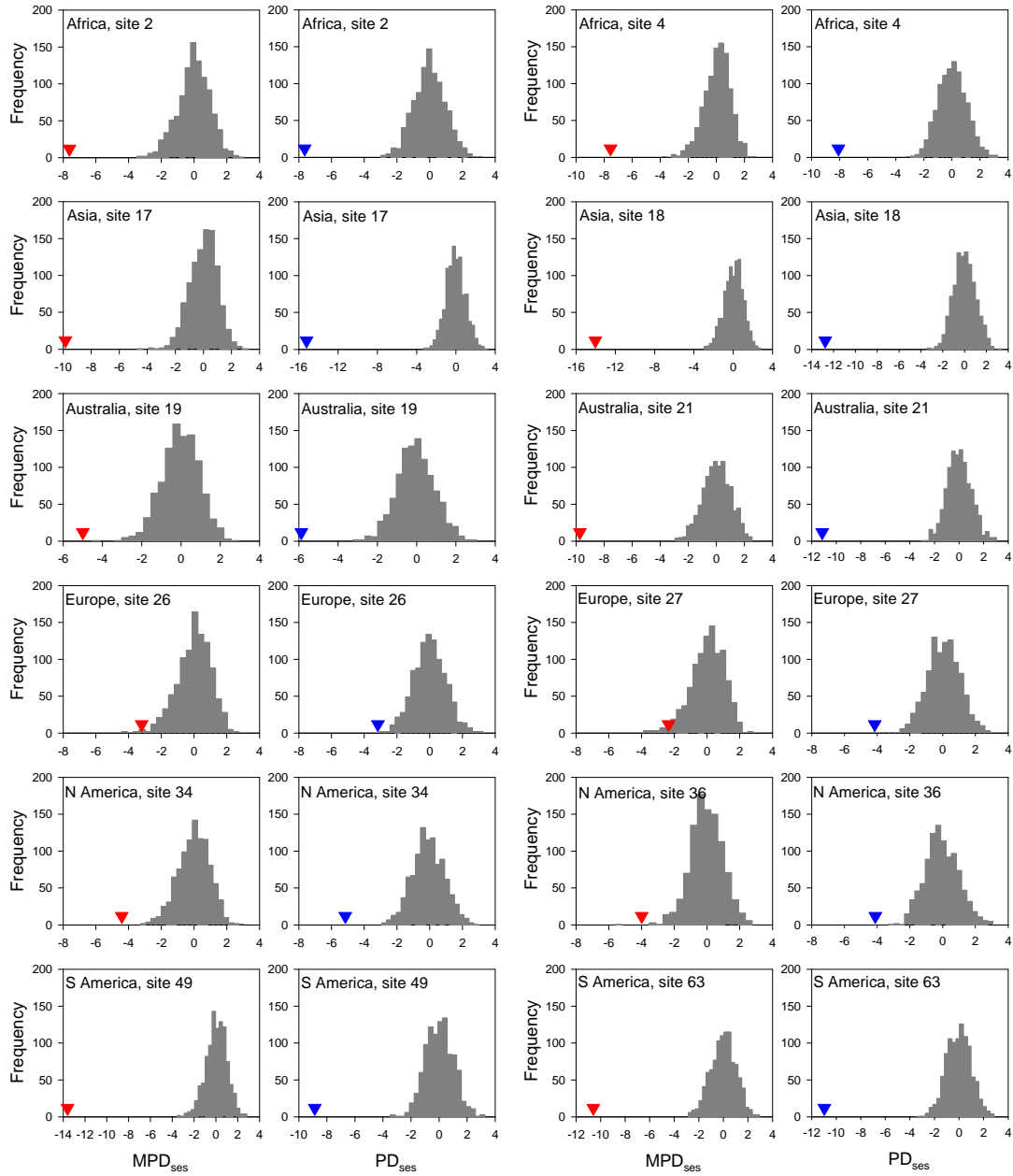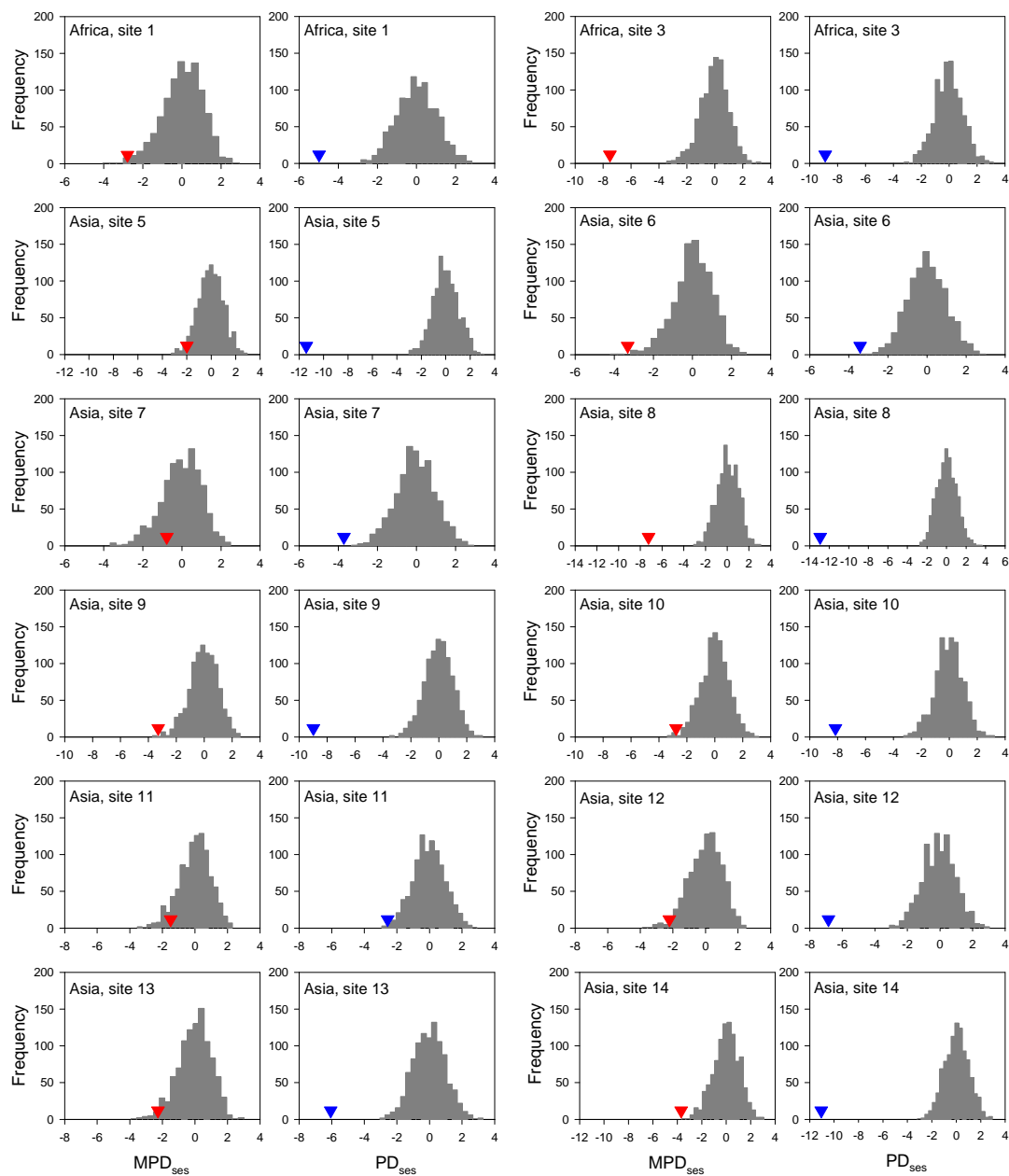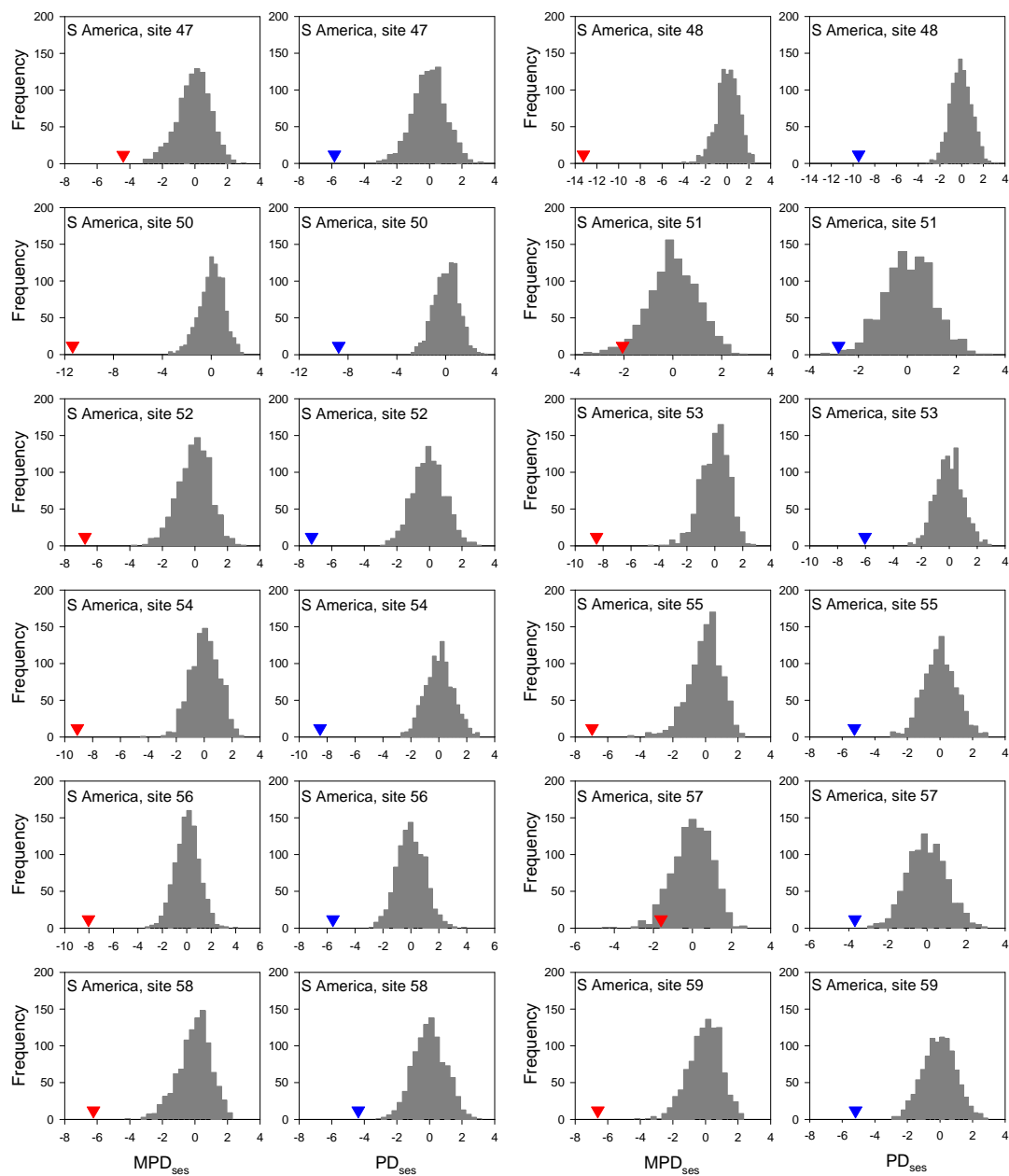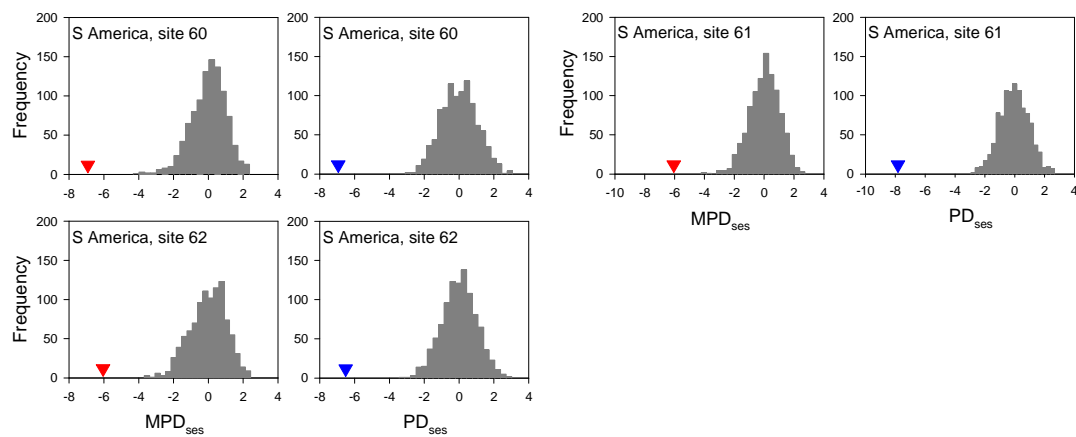
Supplementary Figure 1 (continued, 1).
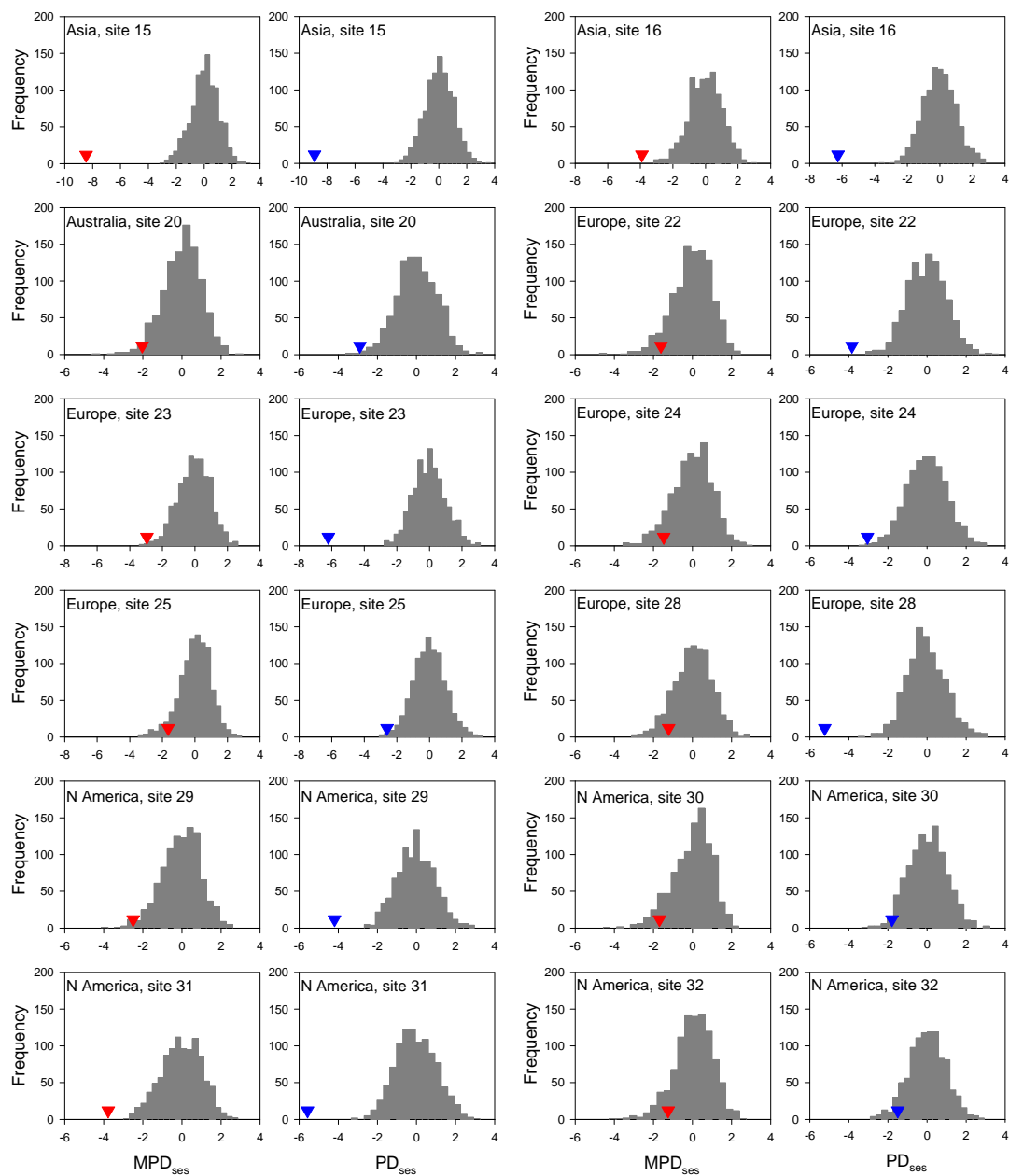
Supplementary Figure 1 (continued, 2).
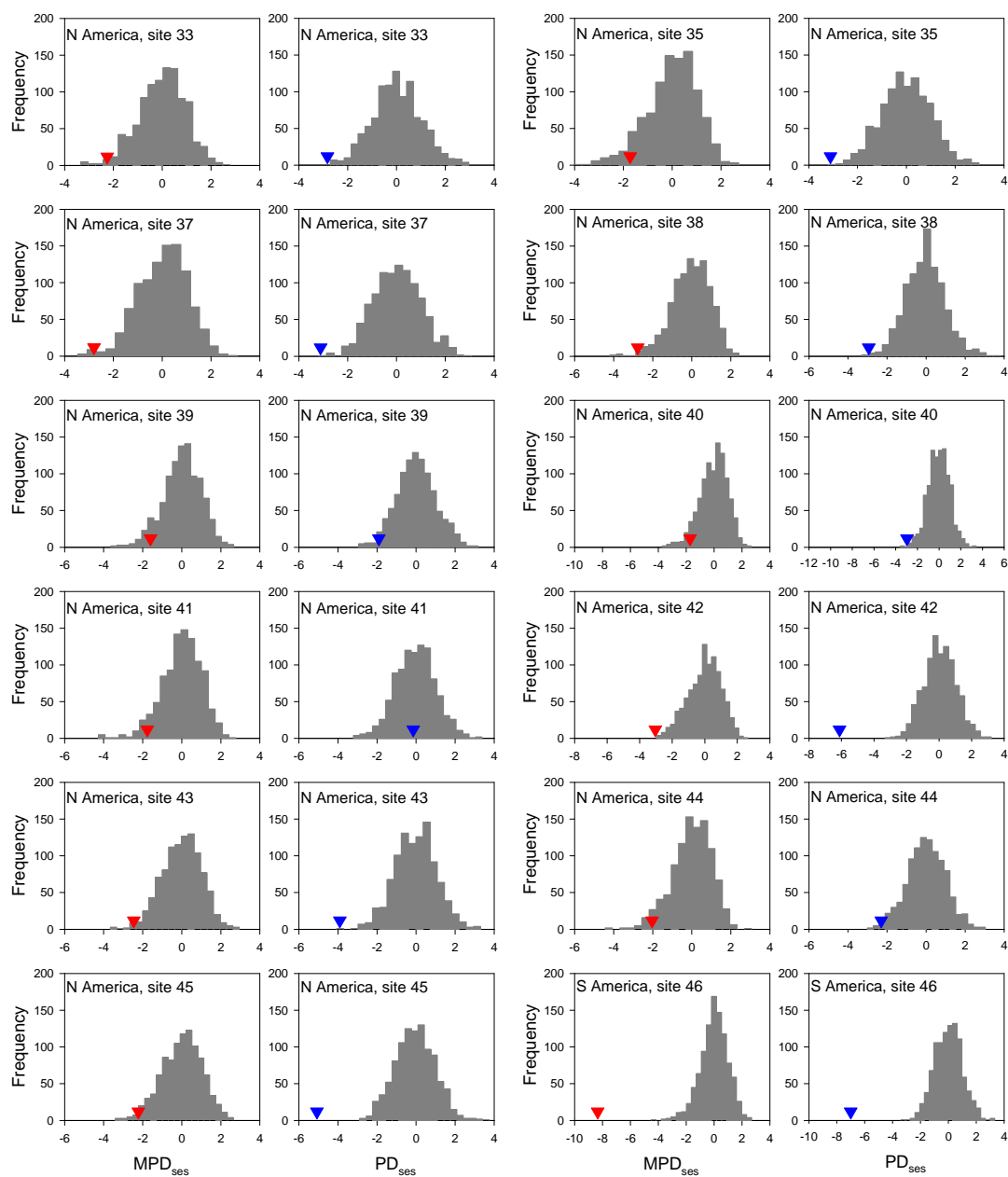
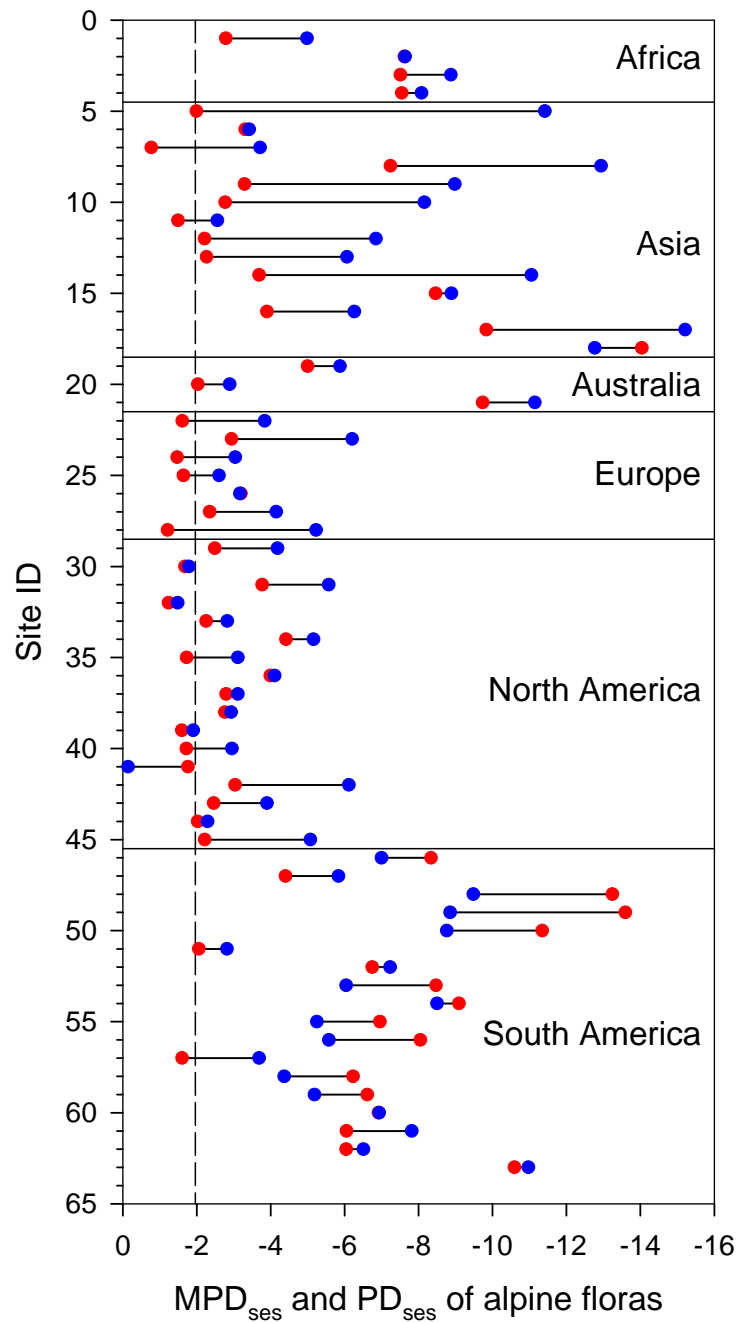Supplementary Figure 1 (continued, 3).

Supplementary Figure 1 (continued, 4).

Supplementary Figure 1 (continued, 5).

Supplementary Figure 2. Standardized effect size of mean pairwise distance (MPD_{ses}, red dots) and the standardized effect size of phylogenetic diversity (PD_{ses}, blue dots) for the 63 alpine floras examined in this study. Each pair of dots represents an alpine flora. The dash line represents -1.96 of MPD_{ses} and PD_{ses}.

Supplementary Figure 3. Relationships between growing degree days (GDD) and standardized effect size of mean pairwise distance (MPD_{ses}) for (**a**) species in alpine floras with MPD_{ses} being calculated using the regional species pool of each of the alpine floras, (**b**) species in alpine floras with MPD_{ses} being calculated using the global species pool of angiosperm species in The Plant List (Methods), (**c**) species in alpine floras with MPD_{ses} being calculated using all species in the 63 alpine floras as a species pool, and (**d**) species in the regional floras of the alpine floras with MPD_{ses} being calculated using the global species pool of angiosperm species in The Plant List. GDD for each site represents the average value of annual growing degree days above 5°C calculated for an area of nine squares of half-degree latitude and longitude (with the centroid of the focal site being located in the center square of the frame work of 3 by 3 squares) using climate data obtained from IIASA (https://iiasa.ac.at). GDD was standardized to vary from 0 to 1. Lines are linear least squares best fits; we used them to show linear trends, not for statistical tests.