

1 **Rapid altitudinal migration of mountain plants in Taiwan and its implications**
2 **for high altitude biodiversity**

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15 **Abstract**

16

17 Mountain systems throughout the globe are characterized by high levels of species
18 richness and species endemism. Biodiversity, however, is not distributed evenly with
19 altitude, but often declines from mid to high altitudes. Conversely, endemic species
20 may be over-represented at high altitudes. Upward elevational range shifts of
21 mountain species have been reported in response to ongoing changes in climate, yet
22 the reports are dominated by studies on woody species and mountains at high
23 latitudes. We investigated spatial and temporal changes in the mountain biodiversity
24 in the subtropical island of Taiwan, based on historical survey and resurvey data
25 during the period 1906-2006. We found that upper altitudinal limits of mountain plant
26 distributions have risen by approximately 3.6 m y^{-1} during the last century, in parallel
27 with rising temperatures in the region. Although species, genus, and family richness
28 decline with altitude, approximately 55 % of species at the highest altitudes are
29 endemic to the island. Given the steep decline in land area with increasing elevation,
30 these high altitude areas are disproportionately important for plant biodiversity when
31 richness and endemism are standardized by available land area. We argue that the
32 distributional shift that we report, in combination with the altitudinal distribution of
33 plant diversity, is likely to pose a major threat to high mountain species of this highly
34 biodiverse island, a threat that is becoming increasingly evident for high mountain
35 plants throughout the globe.

36 **Introduction**

37

38 Climate poses strong limitations on the geographical distribution of species
39 (Woodward 1987). Rising temperatures linked to escalating anthropogenic
40 greenhouse gas emissions are, therefore, expected to alter species distributions due to
41 geographical displacement of the climates to which they are adapted (IPCC 2007a,
42 IPCC 2007b). There is increasing evidence that altitudinal and latitudinal
43 distributional shifts are occurring in response to ongoing anthropogenic climate
44 change (Sturm et al. 2001, Walther et al. 2002, Lloyd and Fastie 2003, Parmesan and
45 Yohe 2003, Walther 2004, Parmesan 2006, Lenoir et al. 2008). Given the continuous
46 increase in emissions of greenhouse gasses (IPCC 2007a), temperature changes and
47 biotic responses to them will continue long in the future (IPCC 2007b). However,
48 species can be constrained in their migration responses to changing climate by
49 intrinsically slow migration speeds and lack of habitat availability due to
50 anthropogenic degradation or modification (Williams et al. 2003, Feeley and Silman
51 2010) or reduced land area availability (Opdam and Wascher 2004, La Sorte and Jetz
52 2010). Such migration lags are predicted to lead to novel species assemblages but also
53 the extinction of populations and species throughout the globe (Huntley 1991,
54 Thomas et al. 2004, Walther 2004, Aitken et al. 2008, Colwell et al. 2008, La Sorte
55 and Jetz 2010).

56

57 Mountains harbour high levels of biodiversity and are often rich in endemic species
58 (Lomolino 2001, Ozenda and Borel 2003, Cox and Moore 2010). Although rapid
59 changes in temperature are driving migrations of species to higher elevations
60 (Grabherr et al. 1994, Walther et al. 2005, le Roux and McGeoch 2008, Lenoir et al.
61 2008, Raxworthy et al. 2008, Chen et al. 2009), the potential for migration between
62 mountains is often severely restricted due to the natural isolation of high mountain
63 regions (La Sorte and Jetz 2010). For many mountain species, therefore, the only way
64 to track a warming climate is by upward migration. Given the persistent rise in global
65 temperatures, many such species face decreasing population sizes and increased
66 extinction risk as land area and, therefore, habitat availability declines (Körner 2007,
67 Colwell et al. 2008, Sekercioglu et al. 2008, La Sorte and Jetz 2010), with the
68 endemic species of high mountain regions being particularly vulnerable (Raxworthy
69 et al. 2008, Dirnböck et al. 2011). Since high altitudes and latitudes are expected to
70 experience above average warming (IPCC 2007a), the assessment and prediction of
71 climatic change impacts on the distribution of biota of high mountain regions should
72 be a high priority (Shoo et al. 2006).

73

74 In order to predict the impacts that rapid climate change will have on the distribution
75 and diversity of species worldwide, a globally coherent assessment of biogeographical
76 impacts of rising temperatures is necessary. However, the currently available data on
77 plant range shifts is strongly biased by the dominance of studies of (often woody)
78 plants in boreal and temperate and Mediterranean latitudes (Walther 2004, Harsch et
79 al. 2009, Jump et al. 2009). Little information on potential range changes is available
80 from tropical and subtropical areas (although Colwell et al. (2008) and Feeley et al.
81 (In press) provide notable examples), despite the particularly high importance of these
82 regions for biodiversity, including high numbers of narrowly distributed endemic
83 species (Laurance et al. 2011).

84

85 In this investigation, we sought to identify if changes in the distribution of alpine

86 plant species are occurring in the Central Mountain Range of the island of Taiwan, a
87 subtropical island covering some 36,000 km². Approximately one third of the island is
88 occupied by mountains over 1000 meters above sea level (m a.s.l.) with more than
89 200 peaks exceeding 3000 m a.s.l., and the highest peak, Yushan, reaching 3952 m
90 a.s.l. (Guan et al. 2009). The treeline in the Central Mountain range occurs at
91 approximately 2800-2900 m a.s.l. (S. Greenwood, pers. obs.). The island supports
92 some 4077 vascular plant species, of which approximately 26 % are believed to be
93 endemic (Huang 2002). Beginning in the latter part of the 19thth Century, Taiwan
94 was the target of extensive biological exploration by Japanese botanists, culminating
95 in the publication of a comprehensive biological inventory of the high mountain areas
96 in 1908 (Hayata 1908). This work continued throughout the first half of the 20th
97 Century (Ito 1927, 1928), leading to the deposition of substantial botanical reference
98 collections in the herbaria of the Universities of Tokyo, Kyoto and National Taiwan
99 University, and has been continued by local botanists during the last 50 years.

100
101 Climate data from the Alishan meteorological station, which holds the longest
102 uninterrupted instrumental data record in the Central Mountain Range (23° 30' 37" N,
103 120° 48' 18 E", 2413 m a.s.l.), demonstrate that temperatures in the region have risen
104 by approximately 1.05 °C in comparison with the 1934-1970 mean, whilst
105 precipitation during this period is similar to that in recent years (Fig. 1). This
106 temperature increase would be predicted to result in an upward shift of isotherms of
107 approximately 210 m based on the regional altitudinal temperature lapse rate of -0.5
108 °C 100 m⁻¹ (Guan et al. 2009). Consequently, we expected that the upper range limits
109 of the distribution of species might also have increased in elevation, assuming that
110 these limits are at least in part determined by temperature.

111
112 Altitudinal gradients in diversity and species endemism are commonly reported in
113 mountain systems (Kessler 2000, Vetaas and Grytnes 2002, Ozenda and Borel 2003,
114 Wang et al. 2007, Cox and Moore 2010) and rising species range limits have the
115 potential to alter these patterns by increasing diversity at higher altitudes and reducing
116 the proportion of endemic species (McKinney and Lockwood 2001, Jurasinski and
117 Kreyling 2007, Britton et al. 2009). Given the high species richness and endemism of
118 Taiwan's flora and the threat posed to the island's biodiversity by rapid changes in
119 climate, we also discuss the potential consequences of any such changes for the
120 island's high altitude flora based on current patterns of altitudinal variation in plant
121 richness and endemism in the region.

122 123 124 **Materials and Methods**

125 126 **Comparison of recent and historical upper altitudinal range limits**

127 Databases maintained by the Biodiversity Research Center of Academia Sinica, Taipei
128 (BRC/AS) (<http://hast.sinica.edu.tw/>), the National Taiwan University
129 (<http://tai2.ntu.edu.tw>), Taiwan Forestry Research Institute (<http://taif.tfri.gov.tw>), and
130 the Taiwan Endemic Species Research Institute (<http://plant.tesri.gov.tw/plant>) were
131 interrogated to identify the upper altitudinal range limits of alpine plant species on the
132 mountains Yushan (3952 m), Hehuanshan (3422 m) and the Alishan area (2663 m), all
133 of which were well documented during early botanical exploration (Hayata 1908).
134 Additionally, historical and recent plant voucher specimens were examined at the
135 Universities of Tokyo, Kyoto, the National Taiwan University, Academia Sinica, and

136 Taiwan Forestry Research Institute. Available data, therefore, comprised of a
137 combination of distributional range records detailing species presence and upper
138 altitudinal limit on individual mountain peaks and geographically referenced point
139 records of species presence. Upper range limit records were only used in this
140 investigation if initial and re-survey data were available for the same species for the
141 same mountain peak. Data were discarded if the locations of historical and recent data
142 differed or could not be verified.

143
144 Typically, two records were available for each species at each location, one in the
145 early part of the 20th Century and one in the later part of this century or in the first
146 decade of the 21st Century. We classed these as records before and during/after (here
147 termed ‘historical’ and ‘recent’ records) the recent rise in temperature shown in Fig. 1.
148 For species where multiple recent and historical distributional records were available,
149 the upper altitudinal range limit for the historical and recent period was estimated by
150 calculating the mean upper altitudinal limit and survey year from the combined
151 records from these collections. We restricted analyses to those species that showed a
152 minimum period of 20 years between the historical and recent survey. For each
153 remaining species, we calculated mean historical and recent maximum elevation
154 records by averaging the maximum elevation records for year and altitude over
155 occurrences within the three mountains. Nomenclature of plant species follows the
156 Flora of Taiwan (Huang 2002).

157

158 **Altitudinal patterns in richness of plant taxa.**

159 Land area above 2000 m was arbitrarily divided into eight elevational zones of 250 m:
160 2000-2249 m, 2250-2499 m etc. with the uppermost band at 3750-3952 m. The
161 richness of plant families, genera, and species was determined by summing the
162 records of presence of individual species within each zone. Altitudinal variation in
163 land area in the Central Mountain Range was estimated from a Digital Terrain Model
164 using ArcGIS 9.3 (Esri, Redlands CA.). Land area above 2000 m was assessed for the
165 same eight altitudinal zones as for diversity and endemism. To assess implications of
166 a loss of land area for taxon richness, taxon density was calculated by dividing taxon
167 richness by untransformed land area within each zone.

168

169 **Statistical analysis**

170 A repeated measures analysis using SAS PROC MIXED (SAS System v. 9.1.3, SAS
171 Institute, Cary, NC, USA) was performed to analyse the overall change in altitude
172 observed for the different species in several time measures, with two observations for
173 each species. Species was considered as a random factor and year of measurement as
174 a quantitative explanatory variable. Model assumptions were verified through the
175 analysis of residuals. All statistical decisions were made using the value 0.05 as the
176 significance level. Ordinary least-squares regression was used to investigate
177 temperature and precipitation trends, patterns of taxon richness with altitude and
178 relationships between initial survey year and initial survey altitude and rate of
179 altitudinal shift (independent of sign). Rate of altitudinal shift was log-transformed in
180 order to improve normality, with all values being increased by 1 prior to
181 transformation due to the presence of rates of 0 m y⁻¹ in the untransformed data.

182

183

184

185 **Results**

186

187 **Climate trends**

188 Mean annual temperature measured at Alishan shows a significant rising trend over
189 time ($P < 0.0001$, Fig. 1 upper panel) indicating a $1.05\text{ }^{\circ}\text{C}$ increase when compared
190 with the 1934-1970 mean. Total annual precipitation also shows a significant trend (P
191 $= 0.032$, Fig. 1 lower panel), however, the decline in precipitation prior to 1970 has
192 been reversed in recent decades such that the 1990-2009 bi-decadal mean ($3943.06 \pm$
193 270.29 mm [SE]) is similar to that of first twenty years of the measurement period
194 ($4404.78 \pm 172.37\text{ mm}$).

195

196 **Changes in upper altitudinal limits**

197 Of the 1442 species present in the area above 2000 m, we identified a total of 24
198 species for which multiple records of upper altitudinal limits were available from
199 survey data. These 24 species were comprised of 16 forbs, seven shrubs and one rush;
200 they represented 12 plant families, 23 genera and included 13 species endemic to
201 Taiwan. Records spanned the period 1906-2006 and the altitudinal range 2210 m to
202 3952 m (Table 1). The upper altitudinal limit of species distributions showed a
203 significant positive association with year ($F = 10.31$, $df = 23$, $P = 0.0039$) with an
204 increase of $3.55 \pm 1.11\text{ m y}^{-1}$ (Fig. 2). Considering movements between the broad
205 altitudinal zones delineated in this study, 58 % species shifted upward to a higher
206 zone, 13 % shifted downwards and 29 % stayed within the same 250 m zone (Table 1).
207 There was no relationship between the initial survey year and rate of altitudinal shift
208 ($r^2 = 0.12$, $P = 0.103$), however, the rate of altitudinal shift showed a weak and
209 marginally significant negative relationship with the initial altitudinal limit of the
210 species ($r^2 = 0.15$, $P = 0.057$).

211

212 **Altitudinal patterns in alpine plant diversity.**

213 25000 specimens were present in the area above 2000 m ASL corresponding to 135
214 families, 557 genera, and 1442 species. Plant species richness shows a significant
215 decline with increasing elevation ($y = 2500 - 0.64x$, $r^2 = 0.98$, $P < 0.0001$), falling
216 from 1224 species in the 2000-2249 m zone to 96 species above 3750 m. Richness of
217 endemic plant species ($y = 576 - 0.13x$, $r^2 = 0.91$, $P = 0.0002$), plant genera ($y =$
218 $1043 - 0.26x$, $r^2 = 0.99$, $P < 0.0001$) and families ($y = 267 - 0.06x$, $r^2 = 0.99$, P
219 < 0.0001) shows a similar pattern (Fig. 3). 372 (26 %) of the plant species found in the
220 total mountain area are endemic, this percentage increases significantly with altitude
221 ($y = -19.17 + 0.02x$, $r^2 = 0.99$, $P < 0.0001$) such that endemic species account for 55 %
222 of all species in the highest altitudinal zone (Fig. 3).

223

224 Land area declines steeply with increasing elevation above 2000 m. At the highest
225 altitudinal zone, land area is only 98.2 ha, 0.5 % of that in the 2000 – 2249 m zone
226 (Fig. 3). When diversity data are standardized according to available land area in
227 each zone to show family/genus/species density (taxa ha^{-1}), density for all taxonomic
228 ranks is broadly constant from 2000 to 3000 meters and then increases gradually
229 before a rapid increase to the last altitudinal zone (Fig. 3). Density is 19 to 46 times
230 higher at the highest altitudes when compared to the 2000 m to 3000 m mean (family,
231 46.3 times higher; genus, 28.8; species, 18.8; endemic species, 36.2).

232

233

234

235 Discussion

236

237 Comparison of historical and recent distributional data indicate that the upper
238 distributional limits of the studied plant species in the Central Mountain Range have
239 shifted upward in elevation (Fig. 3) by 3.6 m y^{-1} based on repeated measures analysis,
240 in parallel with the rise in temperatures of $1.05 \text{ }^\circ\text{C}$ experienced in this region during
241 the latter part of the last century (Fig. 1). This rate of change is rapid, but not
242 unprecedented in studies of recent range shifts in mountain plant species. Kullman
243 (2006) reports a mean rise of up to 4.5 m y^{-1} from sites in the southern Scandes
244 Mountains in Sweden, while le Roux and McGeoch (2008) and Parolo and Rossi
245 (2008) report rate of altitudinal shift of 3.4 m y^{-1} for plant species occurring on the
246 sub-Antarctic Marion Island and the Alps, respectively. In a recent investigation of
247 elevational shifts in the mean distribution of 38 Andean tree genera, Feeley et al. (In
248 press) report a mean migration rate of $2.5\text{-}3.5 \text{ m y}^{-1}$. In some cases, however, rates
249 have been much slower (le Roux and McGeoch 2008), such as the rate of 0.1 m y^{-1}
250 reported by Grabherr et al. (1994), although this example may be an underestimate,
251 given the work of Parolo and Rossi (2008) from the same region.

252

253 Although shifts in plant distribution have been reported only rarely for tropical
254 mountains, reports of distributional shifts in other organisms demonstrate that changes
255 in climate are having a significant impact on the altitudinal distribution of biota in
256 these regions. The upward shift in the mean distribution of tree genera reported by
257 Feeley et al. (In press) is paralleled by upward shifts of the distributional limits of
258 tropical Lepidoptera (Chen et al. 2009) as well as reptiles and amphibians (Raxworthy
259 et al. 2008), although retractions in the upper distributional limits of tropical
260 Lepidoptera have also been recorded, potentially as a result of reduced cloud cover
261 linked to elevated temperatures (Chen et al. 2011).

262

263 The upward shift in isotherms in the central Mountain Range is approximately 210 m
264 based on the 1.05°C temperature rise shown in Fig. 1 and the regional altitudinal
265 temperature lapse rate of $-0.5 \text{ }^\circ\text{C } 100 \text{ m}^{-1}$ (Guan et al. 2009). According to the data
266 shown in Fig. 2, the mean altitude shift (bold line) of the upper range limit of the 24
267 species assessed rose 213 m during the survey period, broadly in line with the range
268 change that might be expected based on the temperature increase noted above if we
269 assume that upper range limits can track shifting temperatures without a lag. This
270 apparent equilibrium of the mean shift in upper range limits of these 24 species with
271 climate is unlike that reported by le Roux and McGeoch (2008) and Feeley et al. (In
272 press) who found that, even despite the rapid altitudinal migration detected, the
273 majority of taxa were still unable to keep pace with the observed changes in regional
274 climate. However, it should be noted that using the mean resample interval and extent
275 of range change for the assessed species might overestimate the rate of shift (4.1 m y^{-1})
276 when compared with the rate calculated from the repeated measures analysis (3.6 m y^{-1}).
277

278

279 Plant biodiversity often shows a hump-shaped relationship with altitude, increasing
280 initially at low altitudes and then declining from approximately 1500 - 2000 m a.s.l.
281 (Rahbek 1995, Kessler 2000, Vetaas and Grytnes 2002, Grau et al. 2007, Wang et al.
282 2007, Nogués-Bravo et al. 2008). The support for declining diversity with increasing
283 elevation beyond 2000 m in the Central Mountain Range is clear (Fig. 3), although
284 our data do not allow us to comment on patterns at lower altitudes. Species richness

285 of the highest altitudinal zone (3750-3952 m) is only 8 % of that found in the lowest
286 zone investigated (2000-2249 m). This pattern of declining diversity with elevation is
287 also seen at the genus and family levels where diversity at the highest altitudinal zone
288 falls to 12 % and 22 % of the values reported from the lowest altitudes respectively.
289 The rate of decline of richness between different taxonomic ranks is not equal, such
290 that the mean number of species per represented family declines with increasing
291 elevation from 9.1 at 2000-2249 m to 3.2 at 3750-3952 m, in support of the
292 observation that families typically include more species at lower altitudes (Gaston
293 2000).

294
295 When standardized by land availability (untransformed land area), diversity remains
296 roughly constant across the first four altitudinal zones and then increases slowly
297 before rising rapidly at high altitudes. The degree of endemism of the flora also rises
298 with increasing altitude (Fig. 3), with species endemism more than doubling from 23
299 % to 55 % between the lowest and highest zones investigated. A positive correlation
300 between species endemism and altitude has been reported for other mountain regions
301 throughout the world, including the Himalayas (Vetaas and Grytnes 2002, Grau et al.
302 2007), Gaoligong Mountains (Wang et al. 2007), Andes (Kessler 2000) and the Alps
303 (Ozenda and Borel 2003), although this proportion may plateau or even decline at the
304 highest altitudes (Vetaas and Grytnes 2002, Grau et al. 2007, Wang et al. 2007).

305
306 The upward elevational shift that we report raises particular concerns given the
307 distribution of diversity with altitude in Taiwan (Fig. 3). Given that plant diversity
308 decreases with increasing elevation, upward shifts in the distribution of species is
309 likely to lead to increased biodiversity at higher altitudes (Grabherr et al. 1994,
310 Klanderud and Birks 2003, Walther et al. 2005, Pauli et al. 2007). However, whilst
311 species richness declines with altitude, species endemism shows the opposite
312 relationship. The upward migration of species from lower altitudes is, therefore, more
313 likely to include widespread species, resulting in a reduction of the proportion of
314 endemic species found at higher altitudes. The net effect of such a change is likely to
315 be that survey sites at higher altitude will increase in their floristic similarity, the
316 process of biological homogenization described by McKinney and Lockwood (2001).
317 Indeed, evidence of this proposed homogenization of alpine floras has been reported
318 recently based on comparison of recent and historical floristic surveys in Scottish
319 mountains (Britton et al. 2009) and the Swiss Alps (Jurasinski and Kreyling 2007).

320
321 A further threat to the endemic flora of the high mountain areas comes from the
322 interaction between the effects of rising temperatures on the distribution of species
323 and the decrease in land area with increasing elevation. As species are pushed up in
324 elevation, whether directly by climate or by increased elevation of competitors,
325 numbers of populations and population sizes decline as the availability of suitable
326 habitat falls, rendering the species more susceptible to stochastic extinction
327 (McDonald and Brown 1992, Pauli et al. 2007, Sekercioglu et al. 2008, Chen et al.
328 2009).

329
330 Although we have no evidence of such extinctions occurring from these data, the high
331 proportion of endemic species and area-standardized levels of plant diversity (Fig. 3)
332 that occur at high altitude in the Central Mountain Range should give significant
333 cause for concern. The highest altitudes in these mountains are particularly species
334 dense and disproportionately important for the conservation of the endemic species of

335 Taiwan. Consequently, any reduction in area, due to rising lower distributional limits
336 increased presence of competitors from lower altitudes, or other forms of habitat
337 degradation and destruction will threaten particularly high extinction risks in this area,
338 with the loss of a disproportionately high number of endemic species (Pauli et al.
339 2007, Dirnböck et al. 2011). This risk demonstrates the pressing need for an effective
340 network of monitoring plots to be established throughout the mountains of the island
341 in order to identify fine scale changes in the presence and abundance of alpine plants
342 and to determine which species are likely to show the greatest vulnerability to
343 extinction.

344
345 Our assessment of range shifts in this analysis is based on historical and recent re-
346 survey data of defined localities but not re-survey of intensively sampled historical
347 plots or transects as reported in some other studies of alpine range shifts (Klanderud
348 and Birks 2003, Walther et al. 2005, le Roux and McGeoch 2008). Consequently, we
349 take a cautious approach, analyzing the direction of implied movement and the mean
350 overall shift, rather than the magnitude of the shift of individual species. We argue
351 that an altitudinal survey bias that would favour finding species at higher altitude in
352 recent years is unlikely, given that the highest altitudes had already been well
353 explored botanically during the early part of the 20th Century (Hayata 1908, Ito 1927,
354 Ito 1928). If, however, recent records of altitudinal ranges result from surveying areas
355 of the peaks that were less well explored in previous decades, then we should be
356 equally likely to identify altitudinal limits as lower, thereby finding an overall fall in
357 range limits or confirming the null hypothesis of no overall shift. Nevertheless, it
358 must be noted that the documented range shifts concern only 24 species, 1.7% of the
359 vascular plant species recorded above 2000 m in the study area; thus, we urge caution
360 in extrapolating our findings to the entire flora of these mountains.

361
362 In addition to changes in climate, other forms of environmental change through
363 increased anthropogenic activity can alter species distributions in mountain regions
364 (Körner 2003). Although the rapid shift in upper altitudinal limits that we report is
365 broadly in line with temperature changes experienced in the region and with range
366 shifts reported in other studies, it is possible that factors other than climate change
367 may be at least partially responsible. We have no reason to believe that fire frequency
368 or grazing pressure by wild herbivores has changed over the period and the high
369 altitude grasslands are not used for grazing domesticated animals. However, many of
370 the peaks in the Central Mountain Range are now popular locations for
371 mountaineering and mountain tourism, activities that, along with better road access
372 and increased road usage are likely to impact the distribution of species and increase
373 realized altitudinal migration rates (McKinney and Lockwood 2001).

374
375 Although the majority of the 24 species for which upper distributional limits were
376 assessed in this study are increasing in elevation, some 20% demonstrate a decline
377 (Table 1). Species might increase in abundance at lower elevations if changes in
378 precipitation lead to increased water availability (Crimmins et al. 2011). However,
379 downslope movement of the upper elevational limit is less likely in such a scenario
380 and is unlikely to apply to the system studied here, given the changes in climate that
381 we report (Fig. 1). However, it should not be assumed that elevated temperatures will
382 automatically result in environments at high altitude becoming more favourable for
383 species currently occurring at lower elevations. Low resource ability can restrict
384 elevational increases for some species whilst changing conditions might negatively

385 impact current populations if drought stress is increased by higher temperatures
386 (Grant 1984, Montesinos et al. 2010, Chen et al. 2011). Moreover, high altitude
387 populations might be particularly vulnerable to direct extirpation through increased
388 human visitation of the highest peaks.

389

390

391 **Conclusions**

392

393 Rising temperatures in the region are driving a rapid change in the upper elevational
394 limits of plant species in the Central Mountain Range. Plant diversity in this region
395 shows a strong relationship with altitude, with families, genera and species declining
396 with increasing elevation. Area standardized levels of diversity, however, are
397 substantially higher at the highest elevations than at other altitudes investigated, since
398 land area at high altitudes is markedly reduced. At the highest altitudes, endemic
399 species comprise approximately 55% of the flora. Given steeply declining land area
400 with elevation and a disproportionate importance of the highest altitudes for the
401 islands endemic species, rapid elevational shifts in plant distribution may represent a
402 significant threat to the plant biodiversity of Taiwan. Our work provides a vital case
403 study from mountains in the subtropical zone that adds to a growing body of evidence
404 demonstrating the impact of rising temperatures on the distribution of mountain plants
405 and the consequent threat to mountain biodiversity throughout the globe.

406

407

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409

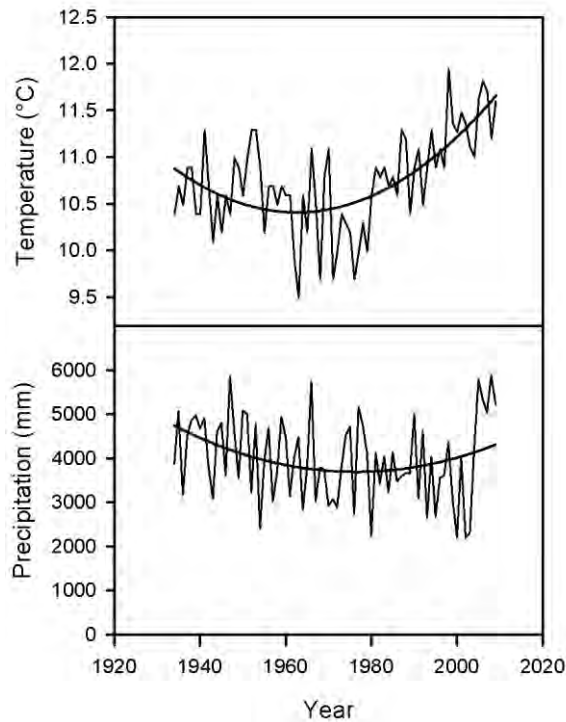
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417 Table 1. Mean survey year and altitude during repeated identification of the upper altitudinal limits of plant species in historical and recent
 418 surveys in the Central Mountain Range of Taiwan. Nomenclature follows Huang (2002).

Family	Species	Plant type	Historical survey		Recent survey	
			Year	Altitude	Year	Altitude
Apiaceae	<i>Angelica morrisonicola</i>	Forb (endemic)	1969	3952	2006	3550
Apiaceae	<i>Hydrocotyle setulosa</i>	Forb (endemic)	1966	3100	1997	3100
Apiaceae	<i>Pimpinella niitakayamensis</i>	Forb (endemic)	1937	3233	2000	3550
Asteraceae	<i>Anaphalis morrisonicola</i>	Forb	1942	3005	1993	3184
Asteraceae	<i>Artemisia morrisonensis</i>	Forb (endemic)	1927	3476	1989	3686
Asteraceae	<i>Aster taiwanensis</i>	Forb	1906	2700	1985	2780
Asteraceae	<i>Cirsium arisanense</i>	Forb (endemic)	1951	2400	1995	2693
Asteraceae	<i>Eupatorium formosanum</i>	Forb	1946	2228	1989	2786
Asteraceae	<i>Picris hieracioides</i> subsp. <i>morrisonensis</i>	Forb (endemic)	1912	3024	1993	3200
Caryophyllaceae	<i>Dianthus pygmaeus</i>	Forb (endemic)	1906	3900	1995	3900
Clusiaceae	<i>Hypericum nagasawai</i>	Forb (endemic)	1906	3600	1989	3950
Crassulaceae	<i>Sedum morrisonense</i>	Forb (endemic)	1906	3952	1986	3800
Ericaceae	<i>Gaultheria itoana</i>	Shrub	1964	3200	1991	3416
Ericaceae	<i>Lyonia ovalifolia</i>	Shrub	1954	2300	1987	2550
Ericaceae	<i>Rhododendron rubropilosum</i> var. <i>rubropilosum</i>	Shrub (endemic)	1935	2733	1994	3118
Gentianaceae	<i>Swertia randaiensis</i>	Forb	1909	3000	1991	3800
Juncaceae	<i>Luzula taiwaniana</i>	Rush (endemic)	1937	3300	1997	3488
Ericaceae	<i>Pyrola morrisonensis</i>	Forb (endemic)	1966	2600	1991	3275
Rosaceae	<i>Rubus rolfei</i>	Shrub	1970	3200	1992	3400

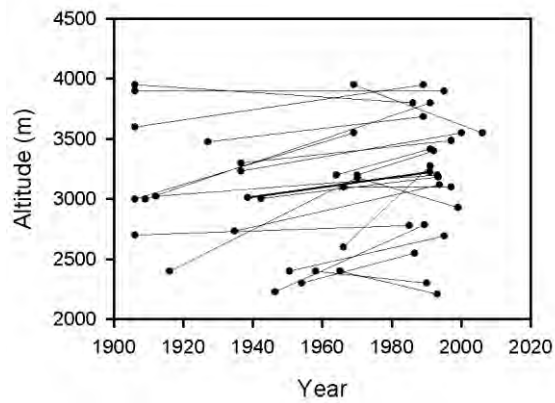
Rosaceae	<i>Spiraea formosana</i>	Shrub (endemic)	1958	2400	1990	2300
Rosaceae	<i>Spiraea prunifolia</i> var. <i>pseudoprunifolia</i>	Shrub	1916	2400	1970	3179
Saxifragaceae	<i>Deutzia pulchra</i>	Shrub	1965	2400	1993	2210
Scrophulariaceae	<i>Hemiphragma heterophyllum</i>	Forb	1970	3179	1999	2930
Valerianaceae	<i>Triplostegia glandulifera</i>	Forb	1906	3000	1969	3550

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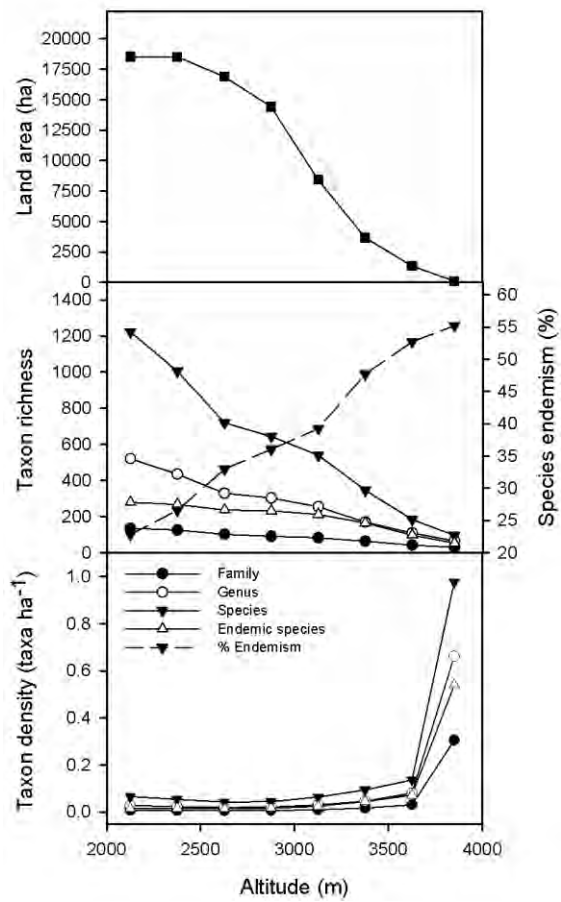
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Figure 1. Mean annual temperature (top) and total annual precipitation (bottom) during the period 1934-2009 from the Alishan meteorological station. Temperature shows a significant warming trend ($y = 2233.74 - 2.27x + 0.0006x^2$, $P < 0.0001$), beginning approximately 1970. Precipitation also shows a significant relationship with measurement year ($y = 2282540.20 - 2306.03x + 0.5834x^2$, $P = 0.032$), although the earliest and most recent 20-year periods remain similar (see text).



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Figure 2. Maximum reported elevation for 24 species of alpine plants across the mountains Hehuanshan, Yushan and Alishan in central Taiwan. Species are listed in table 1. Upper altitudinal limit of species distributions shows a significant increase with survey year ($P = 0.0039$, repeated measures analysis). The bold line indicates the mean change in altitude of all species during the survey period.



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Figure 3. Altitudinal variation in land area (top), plant taxon richness and species endemism (centre) and plant taxon density (bottom) in the Central Mountain Range of Taiwan.

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