

# Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity

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

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

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

In order to predict the impacts that rapid climate change will have on the distribution and diversity of species

worldwide, a globally coherent assessment of biogeographical impacts of rising temperatures is necessary. However, the currently available data on plant range shifts is strongly biased by the dominance of studies of (often woody) plants in boreal and temperate and Mediterranean latitudes (Walther 2004, Harsch et al. 2009, Jump et al. 2009). Little information on potential range changes is available from tropical and subtropical areas (although Colwell et al. (2008) and Feeley et al. (2011) provide notable examples), despite the particularly high importance of these regions for biodiversity, including high numbers of narrowly distributed endemic species (Laurance et al. 2011).

In this investigation, we sought to identify if changes in the distribution of alpine plant species are occurring in the Central Mountain Range of the island of Taiwan, a subtropical island covering some 36 000 km<sup>2</sup>. Approximately one third of the island is occupied by mountains over 1000 m a.s.l. with more than 200 peaks exceeding 3000 m a.s.l., and the highest peak, Yushan, reaching 3952 m a.s.l. (Guan et al. 2009). The treeline in the Central Mountain range occurs at ca 2900–3200 m a.s.l. (S. Greenwood pers. comm.). The island supports some 4077 vascular plant species, of which ca 26% are believed to be endemic (Huang 2002). Beginning in the latter part of the 19th century, Taiwan was the target of extensive biological exploration by Japanese botanists, culminating in the publication of a comprehensive biological inventory of the high mountain areas in 1908 (Hayata 1908). This work continued throughout the first half of the 20th century (Ito 1927, 1928), leading to the deposition of substantial botanical reference collections in the herbaria of the Univ. of Tokyo, Kyoto and National Taiwan Univ., and has been continued by local botanists during the last 50 yr.

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

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

## Material and methods

### Comparison of recent and historical upper altitudinal range limits

Databases maintained by the Biodiversity Research Center of Academia Sinica, Taipei (BRC/AS) (<<http://hast.sinica.edu.tw/>>), the National Taiwan Univ. (<<http://tai2.ntu.edu.tw/>>), Taiwan Forestry Research Inst. (<<http://taif.tfri.gov.tw/>>), and the Taiwan Endemic Species Research Inst. (<<http://plant.tesri.gov.tw/plant/>>) were interrogated to identify the upper altitudinal range limits of alpine plant species on the mountains Yushan (3952 m), Hehuanshan (3422 m) and the Alishan area (2663 m), all of which were well documented during early botanical exploration (Hayata 1908). Additionally, historical and recent plant voucher specimens were examined at the Univ. of Tokyo, Kyoto, the National Taiwan Univ., Academia Sinica, and Taiwan Forestry Research Inst. Available data, therefore, comprised of a combination of distributional range records detailing species presence and upper altitudinal limit on individual mountain peaks and geographically referenced point records of species presence. Upper range limit records were only used in this investigation if initial and re-survey data were available for the same species for the same mountain peak. Data were discarded if the locations of historical and recent data differed or could not be verified.

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

### Altitudinal patterns in richness of plant taxa

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

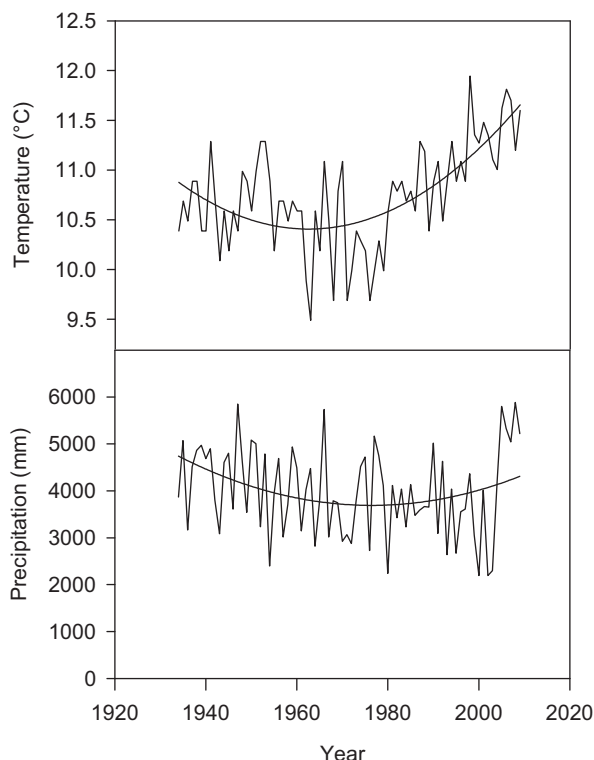


Figure 1. Mean annual temperature (top) and total annual precipitation (bottom) during the period 1934–2009 from the Alishan meteorological station. Temperature shows a significant warming trend ( $y = 2233.74 - 2.27x + 0.0006x^2$ ,  $p < 0.0001$ ), beginning approximately 1970. Precipitation also shows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

## Statistical analysis

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

## Results

### Climate trends

Mean annual temperature measured at Alishan shows a significant rising trend over time ( $p < 0.0001$ , Fig. 1

upper panel) indicating a 1.05°C increase when compared with the 1934–1970 mean. Total annual precipitation also shows a significant trend ( $p = 0.032$ , Fig. 1 lower panel), however, the decline in precipitation prior to 1970 has been reversed in recent decades such that the 1990–2009 bi-decadal mean ( $3943.06 \pm 270.29$  mm [SE]) is similar to that of first twenty years of the measurement period ( $4404.78 \pm 172.37$  mm).

### Changes in upper altitudinal limits

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

### Altitudinal patterns in alpine plant diversity

25 000 specimens were present in the area above 2000 m a.s.l. corresponding to 135 families, 557 genera, and 1442 species. Plant species richness shows a significant decline with increasing elevation ( $y = 2500 - 0.64x$ ,  $r^2 = 0.98$ ,  $p < 0.0001$ ), falling from 1224 species in the 2000–2249 m zone to 96 species above 3750 m. Richness of endemic plant species ( $y = 576 - 0.13x$ ,  $r^2 = 0.91$ ,  $p = 0.0002$ ), plant genera ( $y = 1043 - 0.26x$ ,  $r^2 = 0.99$ ,  $p < 0.0001$ ) and families ( $y = 267 - 0.06x$ ,  $r^2 = 0.99$ ,  $p < 0.0001$ ) shows a similar pattern (Fig. 3). 372 (26%) of the plant species found in the total mountain area are endemic, this percentage increases significantly with altitude ( $y = -19.17 + 0.02x$ ,  $r^2 = 0.99$ ,  $p < 0.0001$ ) such that endemic species account for 55% of all species in the highest altitudinal zone (Fig. 3).

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

Table 1. Mean survey year and altitude during repeated identification of the upper altitudinal limits of plant species in historical and recent 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 nitakayamensis</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>Sweetia 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

## Discussion

Comparison of historical and recent distributional data indicate that the upper distributional limits of the studied plant species in the Central Mountain Range have shifted upward in elevation (Fig. 3) by  $3.6 \text{ m yr}^{-1}$  based on repeated measures analysis, in parallel with the rise in temperatures of  $1.05^\circ\text{C}$  experienced in this region during the latter part of the last century (Fig. 1). This rate of change is rapid, but not

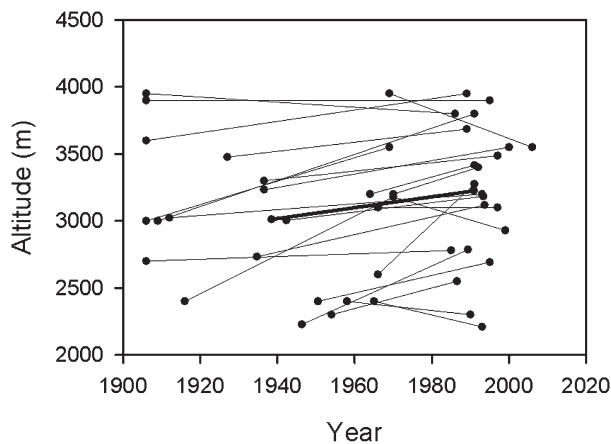


Figure 2. Maximum reported elevation for 24 species of alpine plants across the mountains Hehuanshan, Yushan and Alishan in central Taiwan. Species are listed in Table 1. Upper altitudinal limit of species distributions shows a significant increase with survey year ( $p = 0.0039$ , repeated measures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

unprecedented in studies of recent range shifts in mountain plant species. Kullman (2006) reports a mean rise of up to  $4.5 \text{ m yr}^{-1}$  from sites in the southern Scandes Mountains in Sweden, while le Roux and McGeoch (2008) and Parolo and Rossi (2008) report rate of altitudinal shift of  $3.4 \text{ m yr}^{-1}$  for plant species occurring on the sub-Antarctic Marion Island and the Alps, respectively. In a recent investigation of elevational shifts in the mean distribution of 38 Andean tree genera, Feeley et al. (2011) report a mean migration rate of  $2.5\text{--}3.5 \text{ m yr}^{-1}$ . In some cases, however, rates have been much slower (le Roux and McGeoch 2008), such as the rate of  $0.1 \text{ m yr}^{-1}$  reported by Grabherr et al. (1994), although this example may be an underestimate, given the work of Parolo and Rossi (2008) from the same region.

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

The upward shift in isotherms in the central Mountain Range is ca 210 m based on the  $1.05^\circ\text{C}$  temperature rise shown in Fig. 1 and the regional altitudinal temperature lapse rate of  $-0.5^\circ\text{C } 100 \text{ m}^{-1}$  (Guan et al. 2009). According to the data shown in Fig. 2, the mean altitude shift (bold line) of the upper range limit of the 24 species assessed rose 213 m



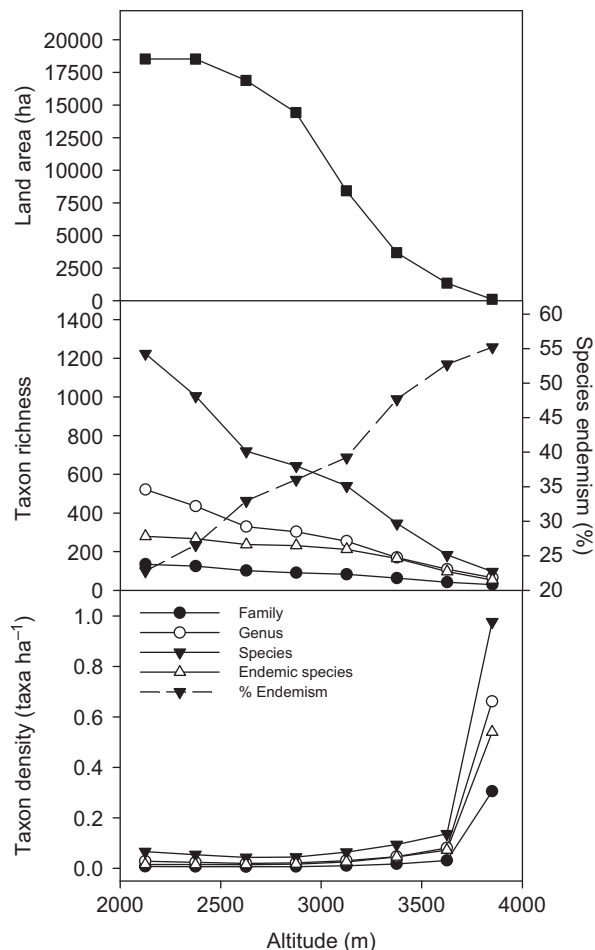


Figure 3. Altitudinal variation in land area (top), plant taxon richness and species endemism (centre) and plant taxon density (bottom) in the Central Mountain Range of Taiwan.

during the survey period, broadly in line with the range change that might be expected based on the temperature increase noted above if we assume that upper range limits can track shifting temperatures without a lag. This apparent equilibrium of the mean shift in upper range limits of these 24 species with climate is unlike that reported by le Roux and McGeoch (2008) and Feeley et al. (2011) who found that, even despite the rapid altitudinal migration detected, the majority of taxa were still unable to keep pace with the observed changes in regional climate. However, it should be noted that using the mean resample interval and extent of range change for the assessed species might overestimate the rate of shift ( $4.1 \text{ m yr}^{-1}$ ) when compared with the rate calculated from the repeated measures analysis ( $3.6 \text{ m yr}^{-1}$ ).

Plant biodiversity often shows a hump-shaped relationship with altitude, increasing initially at low altitudes and then declining from ca 1500–2000 m a.s.l. (Rahbek 1995, Kessler 2000, Vetaas and Grytnes 2002, Grau et al. 2007, Wang et al. 2007, Nogués-Bravo et al. 2008). The support for declining diversity with increasing elevation beyond 2000 m in the Central Mountain Range is clear (Fig. 3), although our data do not allow us to comment on patterns at lower altitudes. Species richness of the highest altitudinal zone (3750–3952 m) is only 8% of that found in the lowest zone investigated (2000–2249 m). This pattern of declining

diversity with elevation is also seen at the genus and family levels where diversity at the highest altitudinal zone falls to 12 and 22% of the values reported from the lowest altitudes respectively. The rate of decline of richness between different taxonomic ranks is not equal, such that the mean number of species per represented family declines with increasing elevation from 9.1 at 2000–2249 m to 3.2 at 3750–3952 m, in support of the observation that families typically include more species at lower altitudes (Gaston 2000).

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

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

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

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

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

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

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

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

lower elevations. Low resource ability can restrict elevational increases for some species whilst changing conditions might negatively impact current populations if drought stress is increased by higher temperatures (Grant 1984, Montesinos et al. 2010, Chen et al. 2011). Moreover, high altitude populations might be particularly vulnerable to direct extirpation through increased human visitation of the highest peaks.

## Conclusions

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

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