Vascular epiphytes in Taiwan and their potential response to climate change
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Chapter 3
Regional and altitudinal patterns in vascular epiphyte richness on an East Asian island

In Taiwan, active orogenesis has created an extensive mountain system with high vegetation heterogeneity, providing diverse habitats for epiphyte growth.
CHAPTER 3

Regional and altitudinal patterns in vascular epiphyte richness on an East Asian island

Rebecca C.-C. Hsu, Jan H.D. Wolf & Wil L.M. Tamis

Abstract

The distribution of species on mountains has been related to various predictor variables, especially temperature. Thermal specialization, which is presumed to be more pronounced on tropical mountains than on temperate mountains, accounts for the elevational pattern of species richness and varies between organisms and geographic areas. In this study, the elevational and regional distribution patterns of 331 epiphyte species in Taiwan were explored using 39,084 unique botanic collections, mostly from herbaria. Species richness showed a peak in elevation between 500 and 1500 m. This peak could not be explained by a null model, the mid-domain effect, suggesting that environmental variables accounted mostly for the distribution of species on the mountains. Next, species distributions were modelled (with 30 predictor variables) to assess epiphyte regional and altitudinal distribution patterns. The model results not only corroborated the position of the mid-elevation peak in richness, they also identified two mountain areas on the island with exceptionally high species richness. These areas of high epiphyte diversity coincide with areas of high rainfall in relation to the direction of the prevailing winds. Moreover, a subsequent exploratory ordination analysis showed a varied thermal preference between epiphyte subcategories (hemiepiphytes, dicotyledons, orchids and ferns). In contrast to predictions by the Rapoport Effect hypothesis, ordination analysis also showed that the degree of thermal specialization increased with elevation, suggesting that highland species may be especially vulnerable to global warming. Finally, the partial ordination analysis controlling for all other variables suggested that typhoons exert a significant influence on the distribution of epiphytes.
Fig. 1 The geographical location of Taiwan and climatic zones in the island according to the Köppen-Trewartha climate system. Ar = tropical wet climate (coolest month > 18°C), south-eastern peninsula (< 500 m); Aw = tropical savannah climate (winter dry > two dry months), southern lowlands (< 500 m); Cfa = wet subtropical climate (warmest month > 22°C, no distinct dry season), island-wide (< 500 m); Cwa = wet subtropical -winter dry climate (warmest month > 22°C), south-western inland hills (500–1000 m); GCfa = mountain climate (warmest month > 22°C, no distinct dry season), island-wide (500–1500 m); GCfb = mountain climate (warmest month < 22°C, no distinct dry season), island-wide (1500–3000 m). The central range, with an altitude > 3000 m is unshaded.
Introduction

The distribution of species on tropical mountains has received renewed interest since high-elevation thermal specialists in the tropics could be among the most imperiled species on earth due to global warming (Laurance et al., 2011). Compared with species in temperate areas, species in the tropics experience limited annual thermal variability and presumed resulting thermal specialization may explain the generally relatively low elevation-range of species on tropical mountains (Janzen 1967). The degree of thermal specialization is nevertheless not universal, varying among taxa, elevations and geographic locations. Hence, studies with various species and from different areas are required to attain a complete picture. Moreover, the assessment of thermal specialization is obscured because, in addition to thermal factors, hydrological, biotic and other unknown factors may determine the distribution of species on mountains (Bruíjnzeel et al., 2010). Another arguably characteristic of species in tropical areas is that mountain species have less thermal specialization than lowland species as an extension of Rapoport’s latitudinal rule (Stevens 1992). Accordingly, on small continental islands such as Taiwan, overall thermal specialists are relatively rare, largely due to a paucity of upper-zone specialists (Laurance et al., 2011).

Species distribution patterns on mountains account for the variability in species richness with elevation. Many organisms show a peak in species richness at mid-elevation (Laurance et al., 2011), and this is also true for epiphytes (Wolf and Flameco-S 2003, McCain 2004, Cardelus et al., 2006). In addition to environmental factors, such as temperature, rainfall and fogs, and historical factors (Gentry and Dodson 1987a, Küper et al., 2004), the mid-elevation peak in species richness has been explained solely by applying a distribution null model (i.e. the mid-domain effect). The mid-domain effect arises from geographic constraints on species range within a bounded domain (Colwell and Lees 2000). Within a landmass boundary (e.g. from coasts to mountain tops), the null model predicts a peak in species richness at mid-elevation, simply based on overlapping species’ ranges. For epiphytic bryophytes in Colombia, the mid-elevation maximum in species richness was indeed explained by a mid-domain effect (Wolf 1993, Ah-Peng et al., 2012). In contrast, the richness of ferns on mountains was best accounted for by climatic factors (Kessler et al., 2011).

Here, we present for the first time data on the elevational distribution of epiphytes in Taiwan, an island in the western Pacific on the transition from tropical to subtropical latitudes. In Taiwan, active orogenesis has created an extensive mountain system with diverse vegetation types, ranging from alpine tundra to tropical rainforests. With approximately 4000 species of vascular plants (including ca. 600 Pteridophytes), the floristic diversity of Taiwan is exceptionally high compared with other (sub-) tropical islands (Dawson 1963, Reyes-Betancort et al., 2008, Creese et al., 2011). Taiwan is also one of the botanically best explored regions in
Southeast Asia, and digitized herbarium collections contain over 200,000 records. Despite having immense plant diversity, Taiwan may be considered relatively poor in epiphytes. There have been ca. 350 species of vascular epiphytes reported for Taiwan, comprising only eight percent of the total vascular flora (Hsu and Wolf 2009), which is less than the worldwide level of 10 percent (Benzing 1990). In some wet tropical ecosystems, the native vascular flora may consist of up to 35 percent epiphytic species (Gentry and Dodson 1987a). Epiphytes are also poorly represented on tropical islands of the Caribbean, which has been attributed to geographical isolation and large-scale disturbances by tropical cyclones (Migenis and Ackerman 1993). In south Florida, a single cyclone (hurricane) may reduce the population density of epiphytic bromeliads by 12–43 percent (Oberbauer et al., 1996). Tropical cyclones (called typhoon in Asia) may also have a dramatic influence on forest canopies, increasing understory light levels to 30 percent of outside levels (Lin et al., 2003).

The aim of this study was to assess patterns in the distribution of Taiwanese vascular epiphytes. In particular, we tested the following hypotheses: (1) epiphytes show a mid-elevation peak in species richness, (2) the peak in richness is explained by a mid-domain effect, (3) environmental forcing accounts for areas with high species richness, (4) hemiepiphytes, orchids, ferns and epiphytic dicotyledons have a different thermal preference on the mountain, (5) upper-zone thermal specialists are relatively rare in comparison with those in the lower zone, and (6) typhoons influence the distribution of epiphytes.

### Methods

#### Study site

Taiwan is a 36,000 km$^2$ tropical-subtropical transition island (21°45′–25°56′N and 119°18′E–124°34′E). About 70 percent of the island is covered by mountains (> 1,000 m above sea level [asl]; Fig. 1), including more than 50 peaks > 3000 m in altitude. Annual rainfall ranges from 1000 mm to > 6000 mm, and falls mainly during the north-east (NE) monsoon (October–January) and during typhoon-induced heavy rain events (July–September). The NE monsoon accounts for 45 percent of the total annual rainfall in north-eastern Taiwan (Kao et al., 2004). On average, 3.7 typhoons hit Taiwan every summer (July–September), of which about 80 percent land on the east coast and track westbound (Wu and Kuo 1999). The torrential precipitation associated with typhoons mainly causes catastrophic damage to human lives and natural habitats. For example, the medium (category-2) typhoon Morakot (2009) brought 2777 mm rainfall in 72 h, triggering disastrous flooding, debris flows and landslides, especially in the mountain area. The typhoon induced-heavy rain supplied by south-westerly monsoon flows usually interact with the South China Sea summer monsoon (Xie and Zhang 2012). In addition, the dominated central range on the island often has complex interaction with the typhoon
circulation, altering its structure, intensity and path, producing significant mesoscale variations in pressure, wind and precipitation distribution over Taiwan (Wang 1980). The central range may decrease the intensity of typhoons by an average of > 40 percent within 12 h of the storm centre reaching the island (Wu and Kuo 1999), thus typhoon impact is reduced in the western part of the island on the lee side of the central range.

Table 1. Predictors that were used for modelling species distribution, including four temperature-related (1–4), 12 precipitation-related (5–16), nine topographic variables (17–25), and five landcover/vegetation indices (16–30).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Tmean*</td>
<td>Annual mean temperature</td>
<td>°C</td>
</tr>
<tr>
<td>2 TcoldM</td>
<td>Mean temperature of coldest month</td>
<td></td>
</tr>
<tr>
<td>3 TdryQ</td>
<td>Mean temperature of driest quarter</td>
<td></td>
</tr>
<tr>
<td>4 Tsd*</td>
<td>The standard deviation of the monthly mean temperatures</td>
<td>No dimension</td>
</tr>
<tr>
<td>5 Pannual*</td>
<td>Annual precipitation</td>
<td></td>
</tr>
<tr>
<td>6 PdryM</td>
<td>Precipitation of driest month</td>
<td></td>
</tr>
<tr>
<td>7 PdryQ</td>
<td>Precipitation of driest quarter</td>
<td></td>
</tr>
<tr>
<td>8 PcoldQ</td>
<td>Precipitation of coldest quarter</td>
<td></td>
</tr>
<tr>
<td>9-14 P.1, P.4, P.5, P.6 P.7*, P.10*</td>
<td>Monthly rainfall: January, April, May, June, July, October</td>
<td></td>
</tr>
<tr>
<td>15 Pdef</td>
<td>Water deficiency: monthly precipitation minus doubled monthly mean temperature</td>
<td>Millimetre</td>
</tr>
<tr>
<td>16 Pcv*</td>
<td>The coefficient of variation of the monthly mean precipitation</td>
<td>No dimension</td>
</tr>
<tr>
<td>17-18 Eastness* Northness*</td>
<td>Aspect transformed by sin(aspect rad) and cos(aspect rad)</td>
<td>Ordinal: 0–8</td>
</tr>
<tr>
<td>19 Soilcode</td>
<td>Soil category</td>
<td>Cardinal: 0–9</td>
</tr>
<tr>
<td>20 SoilPH</td>
<td>Soil alkalinity</td>
<td>Ordinal: 0–9</td>
</tr>
<tr>
<td>21 Estd</td>
<td>The standard deviation of elevation within 1-km²</td>
<td>No dimension</td>
</tr>
<tr>
<td>22 Elevation</td>
<td>Altitude above sea level</td>
<td></td>
</tr>
<tr>
<td>23 Dto3000*</td>
<td>The distance to the nearest location above 3000 m [asl]</td>
<td>Metre</td>
</tr>
<tr>
<td>24 DtoSea</td>
<td>The distance to the nearest coast</td>
<td></td>
</tr>
<tr>
<td>25 DtoRiver</td>
<td>The distance to the nearest river</td>
<td></td>
</tr>
<tr>
<td>26 Landcover*</td>
<td>Land-cover classification</td>
<td>Cardinal: 0–27</td>
</tr>
<tr>
<td>27-30 EVI.1–4</td>
<td>Monthly enhanced vegetation index, EVI.1: spring (April to May), EVI.2: summer (June to September), EVI.3: NE monsoon initiation (October to November), EVI.4: slow growth season (December to March)</td>
<td>No dimension</td>
</tr>
</tbody>
</table>

* Predictors only used in model building for species with < 80 occurrences.
Data collection

We compiled occurrences of epiphytic species in herbarium records, published plant inventories and our own botanical observations as a georeferenced epiphyte database that finally comprised 39,084 records in 331 species (24 families, 105 genera). Pteridophytes contributed most species (171), followed by orchids (120). The epiphyte species in the database were divided into four subcategories based on life form and taxonomy: hemiepiphytes, (abbreviation Hemis, e.g. Moraceae, Araceae), ferns and fern allies (Ferns), orchids (Orchids) and dicotyledons (abbreviation Dicots). For more detailed information on the species in the database, see Hsu and Wolf (2009).

To assess species richness patterns along the altitudinal gradient (Hypotheses 1 and 2), we used the entire epiphyte collection database. We computed species accumulation curves (sample-based rarefaction) and associated richness estimators (Chao 2005), using the freeware program EstimateS 8.2 (Colwell 2011). The species range midpoints were tested against the mid-domain effect hypothesis using Mid-Domain Null, a Monte Carlo based simulation programme, applying 1000 permutations without replacement (McCain 2004).

To evaluate regional species richness, species thermal niches and the influence of typhoons (Hypotheses 3 to 6), we subsequently assembled the plotless herbarium collection localities as records in grid cells with a spatial resolution of 1 km². Multiple occurrences of the same species in a single cell were considered a ‘unique’ record. The final database comprised 28,693 records. A total of 252 species occurred in more than 10 cells, and the most widespread species occurred in 1613 cells. It is well known that systematic botanists have a bias for certain accessible localities and taxonomic groups, and the absence of species in cells is possibly due to insufficient sampling. To endeavour to fill in the distribution gaps, we used species distribution models (SDMs).

Epiphyte species distribution models

In our SDM, we used a maximum entropy method, MaxEnt (version 3.3.3k) (Phillips et al., 2006). In MaxEnt, species’ occurrences are related by predictor variables across a series of observation sites to recognize the realized niche of each species (Guisan and Thuiller 2005). Statistically speaking, the MaxEnt model minimizes the relative entropy between probability densities of species presence data and the background landscape (Elith et al., 2011). MaxEnt uses species presence-data only and we entered all species in the model that occurred in at least ten 1-km² grid cells. Since MaxEnt puts no weight on the absence of a species, it is particularly suited for high-canopy epiphytes, which are often difficult to detect from the ground (Flores-Palacios and García-Franco 2001).
Based on the ecological understanding of epiphytes, 30 environmental variables (Table 1) were selected for building SDMs at a resolution of 1-km², comprising 35,928 grid cells in total. The predictors included nine topographic variables, 16 climatic (12 precipitation-related and four temperature-related) variables and five land-cover/vegetation indices. The land-cover classification (27 categories) was derived from data of a national vegetation inventory and mapping programme (Chiou et al., 2009) combined with satellite data from a global land cover facility (Hansen et al., 1998). An enhanced vegetation index (EVI) with improved sensitivity in high biomass regions was obtained from NASA’s Land Processes Distributed Active Archive Center (see URL http://reverb.echo.nasa.gov/reverb, averages from year 2001 to 2010). The monthly EVI was further summarized and averaged to represent annual patterns for spring (April–May), summer (June–September), NE monsoon initiation (October–November) and slow growing season (December–March). There was a degree of correlation among some of our predictors, such as mean temperature of coldest month and annual mean temperature. However, visual maps of these factors indicated regional heterogeneity in spatial patterns, despite a general similarity throughout most of the island. Certain small regions may provide ‘unique’ environmental requirements for species with restricted distribution. There is a reduced need for our modelling method MaxEnt to pre-select predictors, since it is more stable than most methods when dealing with correlated variables (Elith et al., 2011). In order to extract all possible information on regional spatial patterns, we used all thirty candidate predictors to build our SDMs, unless species were represented by only a few samples (< 80 records). For these rarer species, we pre-selected the candidate predictors to avoid over-parameterizing models using correlation tests and the result of a preliminary run of the model. Ten variables (Table 1) were indentified for modelling the distribution of species with less than 80 samples. To avoid misinterpretation and ensure model reliability, we also excluded species with fewer than ten records (79 species, 24%) from the SDMs. For different sample sizes (numbers of records), we used different model validation approaches and varied the MaxEnt settings for background samples and selection of features.

**Background samples**

In MaxEnt, a finite collection of points with associated covariates (environmental predictors) from the geographic area (landscape) of interest is called a background sample (VanDerWal et al., 2009). Conceptually, the landscape used for the background sample should include the full environmental range required by the species, and exclude the areas where species are unlikely to disperse. Areas that have not been surveyed because there is no suitable habitat for the species should also be excluded (Elith et al., 2011). In this study, we used the MaxEnt program’s default setting, randomly sampled 10,000 background locations from the given 35,928 grids of covariates covering the island for the common species (≥ 80 occurrences). We restricted backgrounds sampled from preferred epiphyte habitats for species with few records.
EPIPHYTE DISTRIBUTION PATTERN

(< 80 occurrences) by deriving a set of 5000 backgrounds randomly sampled from the full set of epiphyte occurrences (29,087).

Features selection

MaxEnt uses the term ‘feature’ to describe the transformation of predictors. Currently, MaxEnt has six feature classes: linear, product, quadratic, hinge, threshold and categorical. The programme by default (i.e., using Auto features) restricts models to simple features if few samples were introduced. When there are at least 80 training samples, all six feature types are used; features are excluded as sample numbers decline (for example, for 15–79 samples, the product and threshold features are excluded; for 10–14 samples, the hinge feature is excluded; and for < 10 samples, only linear features are used). We ran preliminary models using 10-fold cross-validation to estimate predictive performance via held-out data (Phillips 2008). For species with ≥ 80 samples, the test statistic (the area under the receiver operating characteristic curve [AUC]) was significantly higher when using all features than when using only the hinge feature as suggested by Elith et al., (2011). However, for species with few (< 80) samples, using auto features provided a significantly lower 10-fold cross-validated AUC than the linear and hinge features (the last two features had statistically equal AUC values). Nevertheless, the hinge feature exhibited many more violations of AIC (Akaike’s Information Criterion) values than the linear feature for species with few samples. Therefore, the final models were fitted on the full data sets (i.e., all samples for model training) using all feature types for species with ≥ 80 samples and using the linear feature for species with < 80 samples.

Model validation

We used several measures to validate the resulting SDMs. We calculated AIC values using ENMtools 1.3 to determine whether the models had more parameters than samples, which would have violated the assumptions of AIC (Warren and Seifert 2010). Three SDMs (containing < 80 samples) were excluded from later analyses at this stage. Next, we used a null method to test the model significance (Raes and ter Steege 2007). Models with the same settings as described above were fitted on 29 sets (each with a thousand permutations) of randomly chosen samples (with intervals of one for 5–30 records, intervals of five for 35–55 records, and intervals of ten for 60–80 records). We applied a curve-fit through the upper limit of the 95% confidence interval (CI) on the MaxEnt generated AUC values (1000 values per set) to identify which SDMs had a significantly higher AUC value than expected by chance alone (p < 0.05). There were 94 SDMs (< 80 samples) excluded from later analyses at this stage. We did not apply the null test to species with ≥ 80 samples because it had been found previously that models based on more than 80 samples were rarely insignificant (Hsu et al., 2012).
Creating an epiphyte richness map (Hypothesis 3)

We obtained 156 validated SDMs, comprising 68 relatively rare (< 80 samples) and 88 common (≥ 80 samples) species. To create an epiphyte richness map, we applied a threshold of sensitivity-specificity sum maximization (Liu et al., 2005) to convert the MaxEnt probability distribution to a predicted presence map for each species. We then overlaid every single-species map to produce a species richness map for epiphytes in Taiwan.

Ordination analysis (Hypothesis 4-6)

We used a direct gradient ordination analysis, canonical correspondence analysis (CCA) to assess the thermal specialization of species and species groups and the influence of typhoons (Braak and Smilauer 2002). For predictor variables, we used the same 30 environmental variables that we used in MaxEnt (Table 1). For species, we used the same presence-absence data from the 156 epiphyte SDMs that we used to create the species richness map. To avoid multicollinearity, we performed a principal component analysis (PCA) on all variables. The first extracted PCA component was highly correlated with temperature: Tmean (Loading [L]: –0.27), TcoldM (L: –0.26), TwarmM (L: –0.26), TdryQ (L: –0.27) and Elevation (L: 0.26). The second PCA component was highly correlated with rainfall: Pev (L: –0.30), PdryM (L: 0.29), PdryQ (L: 0.28), PcoldQ (L: 0.29), P01 (L: 0.29), PTY (L: –0.27), and P06 (L: –0.26). The first and second component together explained 52 percent of the variation. Both components were retained in the CCA, as opposed to a third component that had little additional explanatory value (9%).

Next, the species and environmental variables (PCA component-1 and -2) were subjected to CCA We tested the significance of the first extracted CCA axis using a Monte Carlo test (999 permutations). CCA not only generates the species scores on the axes, but also their standard deviations (called tolerances in CCA), which may be seen as a measure of niche width (Lepš and Smilauer 2003). Hence, on a generated axis that is highly correlated with elevation, the species tolerance is a measure of thermal specialization.

We defined typhoon disturbance as the frequency of historical typhoons on the same 1 × 1 km grid (35,928 cells) as the other environmental predictors. Recorded traces and eyes of typhoons from 1958 to 2006 were plotted as circles with radii of Beaufort scale 7 and 10 (wind speed = 17.1 and 28.3 m/sec, respectively), and the accumulated numbers of typhoons per cell were calculated (Lin et al., 2006). To establish whether typhoon influenced the distribution of epiphytes, we performed a separate CCA analysis using our typhoon frequency data and 156 epiphyte SDMs, entering the PCA components of our 30 environmental predictors as covariables. Due to the complex interaction between the central range and typhoon circulation, which causes unpredictable changes in typhoon structure on the lee side of the central range, we excluded cells from the western part of the island. Therefore, we only considered cells east of the central ridge (10,725 grids) and past typhoons landing on the east coast of Taiwan to
explore the influence of typhoons on epiphyte vegetation. The ordination analyses were performed in R with vegan, a community ecology package (Oksanen et al., 2012, R Core Team 2012).

**Results**

Epiphyte species richness showed a peak in species richness between 500 and 1500 m (Table 2; Fig. 2). Although the difference between the species richness at < 500 m and richness at 500–1000 m was small, it was significant (M = 306.03, SD = 8.53 and M = 308.33, SD = 9.47, respectively; paired t(24740) = 20.1, p < 0.05). Species richness showed a more rapid decrease above 1500 m. The elevation-species richness curve fell outside the 95% CI curves of the mid-domain null model curve (Fig. 3); hence the mid-elevation peak in richness could not be explained by a mid-domain effect.

![Graph](image-url)

**Fig. 2** Epiphyte species accumulation curves based on sample-based rarefaction (software program EstimateS 7). Collections per altitudinal interval: 12,944 (< 500 m), 11,798 (500–1000 m), 7,198 (1000–1500 m), 4,024 (1500–2000 m), 2,197 (2000–2500 m) and 923 (> 2500 m).
Table 2. Number of epiphyte species per altitudinal interval in Taiwan; n = number of records, Sobs = the number of observed species, singletons = number of species that were only recorded once and Schao = estimated number of species for 95% CI and standard deviations (SD).

<table>
<thead>
<tr>
<th>Altitudinal interval</th>
<th>n</th>
<th>Sobs</th>
<th>Singletons</th>
<th>S_{chao}</th>
<th>S_{chao} 95% CI</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 500m</td>
<td>12944</td>
<td>286</td>
<td>39</td>
<td>306.03</td>
<td>(294.99, 330.59)</td>
<td>8.53</td>
</tr>
<tr>
<td>500–1000m</td>
<td>11798</td>
<td>289</td>
<td>29</td>
<td>308.33</td>
<td>(296.79, 336.98)</td>
<td>9.47</td>
</tr>
<tr>
<td>1000–1500m</td>
<td>7198</td>
<td>281</td>
<td>28</td>
<td>293.6</td>
<td>(285.91, 313.32)</td>
<td>6.42</td>
</tr>
<tr>
<td>1500–2000m</td>
<td>4024</td>
<td>235</td>
<td>39</td>
<td>276.17</td>
<td>(253.47, 326.76)</td>
<td>17.56</td>
</tr>
<tr>
<td>2000–2500m</td>
<td>2197</td>
<td>205</td>
<td>39</td>
<td>232.44</td>
<td>(217.43, 265.590)</td>
<td>11.56</td>
</tr>
<tr>
<td>&gt; 2500m</td>
<td>923</td>
<td>165</td>
<td>37</td>
<td>185.81</td>
<td>(174.2, 212.08)</td>
<td>9.06</td>
</tr>
</tbody>
</table>

Fig. 3 The species richness curve (with data points), based on 39,084 collections and 331 epiphytic species, and the 95% CI null model prediction curves sampled without replacement (software program Mid-Domain Null, 1000 simulations).
The mid-elevation peak in species richness was also shown by the epiphyte SDMs; most epiphyte species being found in the mild mountain climate of the GCfa Köppen-Trewartha climate zone between 500 and 1500 m (Fig. 1). The SDMs also identified two regions with high diversity on the western slope of the central range at mid-elevations: HsuehShan in northern Taiwan and AliShan in central Taiwan (Fig. 4A). Both areas are sheltered from east-coast landing typhoons and receive high amounts of annual rainfall under the influence of NE monsoons and SW flows, respectively. SDMs also showed considerable variation in distribution patterns between epiphyte subcategories. The most south-eastern tip of Taiwan (Fig. 1, HenChun peninsula) is characterized by a tropical wet lowland climate (Ar), and contained the highest percentage (11%) of hemiepiphytes (Hemis) of all the climatic zones. Epiphytic ferns were most often found in the cool mountain climate of the Köppen-Trewartha GCfb climate zone (67%), at an altitude of 1500–2500 m.

**Fig. 4** (A) Modelled richness of pooled epiphytes (156 spp.) and two regions with exceptional high epiphyte diversity, namely HsuehShan and AliShan, both located at mid-elevation (800–2000 m asl). (B) Richness pattern for the half of the modelled species (78 spp.) that had lower thermal tolerance values (i.e. the species with the highest thermal specialization). (C) Richness pattern for the other half of the modelled species that possessed higher thermal tolerance values.
The thermal preference of the subcategories was also indicated by the CCA analysis. The distribution of the species on a significant first axis (explained variance 15.0%, Monte Carlo, \( p = 0.001 \)) constrained by elevation, PCA component-1, indicated that hemiepiphytes (e.g. *Ficus* spp.) were predominately found at lower elevations, whilst epiphytic ferns (e.g. *Crypsinus quasidivaricatus*, *Lepisorus clathratus* and *L. suboligolepidus*) were the most prominent low temperature specialists (Fig. 5). Epiphytic orchids were found from low elevations (e.g. *Liparis grossa* and *Appendicula reflexa*) to upper mountains (*Gastrochilus hoii*). The thermal specialization (inverse niche-width) of the 156 analysed species was higher with increasing elevation, particularly for some epiphytic ferns and orchids (Pearson’s \( R = -0.39, p < 0.001 \), Fig. 6). Moreover, the half of the species (78 species) possessing relatively high thermal specialization (low tolerance values) exhibited an obvious mid-elevational pattern (Fig. 4B) in comparison to the indistinct distribution of the other half of species with a higher tolerance value (Fig. 4C).

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**Fig. 5** CCA ordination diagram of the species scores (156 spp.) on the first two axes with epiphyte species arranged by subcategory: orchids (open squares), ferns (open triangles), hemiepiphytes (black diamonds) and dicotyledons (black circles). The first axis (eigenvalue 0.4534, explaining 15% of total variance; Monte Carlo \( p < 0.001 \)), is highly correlated with temperature (elevation), with higher elevation shown towards the right. The second axis (eigenvalue 0.1173, explaining 4% of variance) is related to water availability, with reduced water availability shown towards the top.
Fig. 6 Species scores (156 spp.) on the first constrained canonical axis generated by CCA and standard deviations. The first axis is highly correlated with temperature (elevation), and thus its standard deviation (i.e. tolerance) may be interpreted as a measure of niche-width. The thermal tolerance of the species is lower (i.e. higher thermal specialization) with increasing elevation towards the right (Pearson’s $R = -0.39$, $p < 0.001$). Epiphyte species are arranged by subcategory: orchids (open squares), ferns (open triangles), hemiepiphytes (black diamonds), and dicotyledons (black circles).

Independent of thermal and rainfall influences (PCA component-1 and component-2), partial CCA showed that typhoons also exert an influence on the distribution of epiphytes (explained variance 1.6%, Monte Carlo $p < 0.001$; Fig.7). The two typhoon intensities that we analysed (scales 7 and 10) had largely opposing effects on the epiphyte community.

Discussion

In agreement with many tropical epiphyte studies from the American continent (Gentry and Dodson 1987a, Wolf 1993, Wolf and Flamenco-S. 2003, Krömer et al., 2005, but see Ibisch et al., 1996), our analyses, which used both empirical collections and SDMs, showed that vascular epiphytes had a peak in species richness at a mid-elevation on mountains. Recognizing that botanic collections are essentially non-random, we nevertheless presume that, for our data, a meaningful assessment of the observed distribution and diversity patterns is possible because of the extremely high number of unique records in the database (39,084).
The mid-elevational peak in species richness could not be explained by a null model. The result indicated a substantially higher species richness, and a richness peak at slightly lower elevations than expected by the null test. A similar pattern has also been described for an Indian Ocean island (Ah-Peng et al., 2012). Such a pattern is probably explained by the Massenerhebung effect (i.e. mountain mass elevation effect; Schroeter 1908, Bruijnzeel et al., 1993). This phenomenon occurs on isolated, small coastal mountains, where floristically-similar vegetation types tend to distribute at lower altitudes than on large mountain masses due to climatic compression. Moreover, the exceptionally high species richness observed at island mid-elevation may be augmented by a large number of species with a small range size in relation to fine niche partitioning. For instance, the restricted altitudinal band of *Chamaecyparis*-dominated cloud forest (1800–2500 m), characterized by low temperatures and continuously moist and dim conditions, is inhabited by no less than 92 species of rare ferns (Moore 2000). Environmental factors may thus account for the observed epiphyte distribution and, with this in mind, our approach using SDMs to complement grid cells with absent species is not unreasonable.

The SDMs identified two centres of epiphyte diversity, one in the north (HsuehShan) and another in central Taiwan (AliShan). Both areas are at a mid-elevation (800–2500 m asl)
and are also subject to significant precipitation, being under the influence of the NE monsoon in the winter or the SW rains that follow typhoons in the summer, respectively. Prevailing winds probably import diaspores to these two regions, since the majority of epiphytes in Taiwan (89%) are wind dispersed (Hsu and Wolf 2009); the ferns *Asplenium bondense* and *A. pekinense*, which have an affinity with temperate East Asia and Japan, are only found in small regions under the influence of the NE monsoon (Moore 2000). Humid conditions and accessibility probably both contribute to the presence of areas of high epiphyte richness and endemism. Accordingly, the HsuehShan and AliShan regions merit special attention from conservationists.

The SDMs also showed that whilst epiphytic ferns were relatively common in northern Taiwan, central Taiwan has a relatively high number of epiphytic orchids. Central Taiwan receives little influence from the NE monsoon and is therefore relatively dry and warm in winter. Thus, in agreement with many other epiphyte studies (Gentry and Dodson 1987a, Benzing 1990, Wolf 1994), the SDMs confirmed that, of all environmental predictors that were used in the models, elevation and water availability accounted to great extent for the distribution of epiphytes in Taiwan.

The relative importance of temperature (elevation) and water availability was also demonstrated by the exploratory multivariate ordination analysis, where temperature was identified as the most important variable. In agreement with patterns in the neotropics (Wolf and Flamenco-S. 2003, Benavides *et al.*, 2010), hemiepiphytes such as aroids and Ficus species dominated moist stream valleys in the lowlands (< 1000 m asl), especially in the south-eastern peninsula where monthly mean temperature was > 18 °C. As in the Andes, epiphytic ferns were particularly adapted to mountain climates (Kessler 2011); the epiphytic fern *Crypsinus quasidivaricatus* (Hayata) Copel was recorded near the timberline (3500 m asl).

Interestingly, our results showed that thermal specialization or inverse thermal niche-width was not uniform along the elevational gradient, but increased with altitudes. Epiphytic ferns in Bolivia show a similar pattern (Kessler 2011). However, this pattern contrasts with the Rapoport effect hypothesis, which suggests that the elevational ranges of species are greatest at higher altitudes, and consequently thermal-specialist species are more likely to colonize lower altitudes than higher altitudes (Stevens 1992, Laurance *et al.*, 2011). Studies on thermal specialization in tropical mountains are clearly not conclusive. Our study identified several montane cloud forests at mid-elevations with many epiphytic thermal specialists. In mid-elevational cloud forests, the frequently occurring fog events lead to little diurnal (and seasonal) thermal variation, which according to the Rapoport effect promotes thermal specialization and susceptibility to global climate change (Foster 2001, Mulligan 2010, Ah-Peng *et al.*, 2012).
The ordination analysis also suggested for the first time that typhoons have a significant influence on the distribution of epiphytes, independent of the temperature- and humidity-related variables that were used in our analysis. Typhoons may directly blow epiphytes of their hosts, or indirectly alter the microclimate through mechanical defoliation of canopies (Mabry et al., 1998). Hemiepiphytes, such as strangler figs and aroids, seem relatively resistant to direct wind-blow in terms of their tightly-attached adventitious roots on hosts, which may explain why they are largely found on the south-eastern peninsula of Taiwan, despite ca. 11 percent of all typhoons landing in this region. Whereas powerful typhoons can be damaging to epiphytes, moderate typhoons are likely less damaging or may even promote epiphyte proliferation because of the significant accompanying precipitation. This may explain why Beaufort scale 10 and scale 7 typhoons have differing effects on epiphyte distributions. Further field studies are necessary to properly identify how typhoon may affect epiphyte distribution, which currently remains elusive.