Vascular epiphytes in Taiwan and their potential response to climate change
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The recommended sites in Taiwan for monitoring the influence of changing climates on forests, Chi-Lan and Da-Wu reserves (blue boundaries) and on epiphytes, Mt. Chia-Li, Tai-Chi Canyon and Jin-Shuei-Ying (orange dots). Two sites (dashed circle) indicate areas with high epiphyte richness, HsuehShan and AliShan, located in the northern and central part of the island, respectively.
CHAPTER 8

Conclusions

Patterns in composition and distribution of vascular epiphytes

To investigate and explain regional patterns in species richness along gradients is one of the major challenges for ecological and biogeographical research. To date, few epiphyte studies are available from the Paleotropics. Moreover, most studies focus on tropical areas, whilst epiphyte research from sub-tropical areas remains scarce. In chapter 2, data is provided on the distribution of epiphyte diversity in Taiwan, a subtropical mountainous island in East Asia, to complement the perplexity of global patterns. Similar to the epiphyte flora in tropical areas, the epiphyte diversity in Taiwan was dominated by few higher taxa (families), mostly monocotyledons. Lacking several species-rich epiphyte families (e.g. Bromeliaceae and Marcgraviaceae) that have evolved independently in the Neotropics, the most abundant epiphytes in the checklist were ferns, followed by orchids. The taxonomic composition of the epiphyte flora demonstrated the transitional aspect of Taiwan, incorporating both tropical and sub-tropical regions, corroborating a trend of increasing proportion of epiphytic ferns and fern-allies with latitudes (Wolf and Flamenco-S, 2003; Zotz, 2005).

In addition to the latitudinal gradient, the presence of an extensive mountain system on the island provides an ideal opportunity for studying species richness patterns along an elevational gradient. Using 39,084 unique botanical collections, in chapter 3 the epiphyte richness was found to show a mid-elevation peak at ca. 1000 m asl. This often described phenomenon of a hump-shaped curve in species richness could not be explained by the mid-domain effect, as observed in some other studies, but coincided with the richness pattern of bryophytes on an island in the Indian Ocean (Cardelús et al., 2006; Ah-Peng et al., 2012). The epiphyte pattern in species richness showed a peak of substantially higher species richness and at slightly lower elevation than expected under the null model. The latter is presumably explained by the Massenerhebung effect (i.e. mountain mass elevation effect, Bruijnizeel et al., 1993). This phenomenon occurs on isolated, small coastal mountains, where floristically-similar vegetation types tend to be distributed at lower altitude than on large mountain masses, due to a steep lapse rate of temperature and cloud formation (Flenley, 1995).

The exceptional high species richness beyond the expectation of the null model can probably be attributed to a large number of species with a small range size, related to fine niche partitioning. For example, the restricted altitudinal band of Chamaecyparis-dominated “cypress” cloud forest (1800-2500 m) is inhabited by no less than 92 species of rare ferns (Moore 2000).
Moreover, extraordinary endemism has been observed in the mountains and, for instance, several epiphytic orchid genera, *Bulbophyllum* (24 spp.), *Gastrochilus* (9 spp.) and *Oberonia* (7 spp.), show a high endemism of nearly 50 percent. Further analysis in chapter 3 on the altitudinal ranges of species showed a higher degree of thermal specialization in the upper-zone of mountains than in the lowlands, which is in contrast to the Rapoport Effect hypothesis (Stevens, 1992). Interestingly, a transplant experiment suggested that also at the intraspecific (*Asplenium antiquum*) level, there was more genetic adaptation of populations at higher elevations (chapter 6). In summary, the results of above mentioned chapters suggest that environmental factors mostly account for the observed epiphyte distribution in Taiwan. In this light, the approach in chapter 7 to use species distribution models (SDMs) to assess potential range change of epiphytes under future climate conditions is reasonable.

**Common features of vulnerable epiphyte species and biomes to climate change**

In chapter 7, the SDMs indicated a large proportion of epiphytes that were projected to have a high range turnover rate under climate change scenarios (referred to here as “sensitive” species) presently have restricted distributions in the mountain area (e.g. *Bulbophyllum chitouense*, *Grammitis nuda*, *Flickingeria taimbounia*, *Saxiglossum angustissimum*), whereas species with a low range turnover (“insensitive”) are generally widespread lowland species, including several pantropical species (e.g. *Hoya carnosa*, *Psilotum nudum*). Corroborated by the findings of chapter 3, presumably the sensitivity and/or vulnerability of species under climate change is mostly correlated with thermal specialisation. The SDMs did indicate that temperature-related factors (Tmean and Tsd, appendix) had an important effect on the modelled distributions of sensitive epiphytes, and many of them occurred only in the mid-elevation cloud forests (e.g. cypress forest). The SDMs projected a distinct decline of cypress forest under future climates, and showed that here rainfall seasonality (Pcv) and water deficiency (Pdef) were the most contributing factors to the distribution of cypress forest. This forest is typically enveloped in clouds during the afternoon and characterized by cool temperatures and continuously moist and dim conditions (Still *et al.*, 1999; Lai *et al.*, 2006). Many epiphytes with restricted distributions (e.g. *Bulbophyllum chitouense* and *Gastrochilus raraensis*) are specialized to this particular thermal and hydrological regime (chapter 3). In addition, the SDM result in chapter 3 showed that species with a narrow niche-width (specialists) often have a scattered distribution. Under future warming scenarios, most species were projected to shift to higher altitudes (chapter 7), which may result in increased habitat fragmentation due to isolation of deep ravines at higher elevations. High elevation specialist species, having a relatively small range size and fragmented population, are likely most susceptible to global warming.
In agreement with many prior studies, the ordination analysis in chapter 3 suggested that, next to light conditions, temperature and water availability were most crucial for epiphyte distribution (Gentry and Dodson, 1987a, Benzing, 1990, Wolf, 1994). In chapter 4, the experiment on *Hoya carnosa* indicated that even in a wet subtropical forest, water conservation was the likely ecophysiological significance of CAM instead of CO₂ availability. In fact, there exists a positive correlation between air humidity and CAM/C3 species ratio (Monteiro *et al.*, 2008). The drought-tolerance adaptation might be beneficial under future climate change of increasing seasonal variation and weather extreme. A contrasting example was represented by the filmy fern *Mecodium badium*. Although presently widespread, this epiphytic fern was projected to have a high range turnover rate under climate change scenarios (chapter 7). Since the fern's frond consists of only a single layer of cells, absorbing moisture from the air, this species may be particularly susceptible to atmospheric drying in a warming climate. However, many epiphytes may be more tolerant to drought stress than usual expectations. For example, the widespread and abundant population of bird's nest ferns on the island suggests their successful adaptation to the canopy environment, especially in some dry forests at the highlands. In chapter 5, an experiment to explore the physiological plasticity of *Asplenium nidus* revealed its flexibility in photosynthetic capacity to diverse microclimates. The experiment accidentally found that *A. nidus* lacked stomata on the adaxial surface of leaf blades, which likely also is a morphological adaptation to drought stress. Moreover, drought tolerance may vary amongst populations of the same species. A transplant experiment with altitudinally widespread *Asplenium antiquum* indicated intraspecific variation of drought tolerance (chapter 6).

**Species distribution modelling: what can we learn from the MaxEnt approach?**

Despite some uncertainties (Barry and Elith, 2006; Pearson *et al.*, 2006), present studies (chapter 3 and 7) demonstrated that species distribution modelling or ecological niche modelling was a practical tool for assessing species richness patterns or evaluating the impact of climate change. Consistent with field observations, the models indicated that epiphyte distributions were strongly correlated with forest type, suggesting the importance of considering biotic interactions for modelling dependent species such as epiphytes. Moreover, SDMs confirmed that terrain-related factors (e.g. aspect, inclination) were influential when projecting species' response to climate change at a local scale. Incorporating stable topographic or edaphic factors into models might prevent overestimating range reduction and may help to recognize potential landscape-defined refugia when assessing climate change impacts (Austin and Van Niel, 2011).
CONCLUSIONS

Since the presence-only tool MaxEnt puts no weight on the absence of a species, it is particularly suitable for modelling distribution of canopy epiphytes that are often difficult to detect from the ground (Flores-Palacios and García-Franco, 2001). In addition, MaxEnt has been proved to outperform most current SDM approaches, especially when a sample size is small (Elith et al., 2006; Hernandez et al., 2006). Although a large sample size is beneficial for accurately mapping of species ranges (Feeley and Silman, 2011), most species deserving special attention in conservation are inherently rare (Pearson et al., 2007). Thus, caution should especially be taken when modelling species with relatively few collections. In addition, it is advisable that SDM’s adopt the natural boundary of the studied species, rather than an artificial one, to prevent under-prediction of range sizes (Raes, 2012). In this respect, the island biome of this study is therefore convenient for applying a SDM approach. Another particularly important decision of presence-only SDMs is how to select background samples (pseudo-absences) for parameterizing models (VanDerWal et al., 2009). This issue becomes even more relevant since more than half of the epiphyte species in this study were present with less than 50 collections. It is advised that background sample should include the full environmental range required by the species, and exclude the areas where species might not disperse to or that are unsuitable for the species (Elith et al., 2011). In chapter 3, by using a full set of data comprising unique epiphyte occurrences (29,087 out of 35,928 of the total island area) for backgrounds sampling, the model reliability was improved substantially.

MaxEnt is known to be more robust than most methods when dealing with correlated variables, thus there is less necessity to pre-select predictors for this approach (Elith et al., 2011). However, when correlated predictor variables are used, variable contributions should be interpreted with care (Phillip, 2006). In addition, it is advisable to use correlation tests or ordination analyses for pre-selection of the candidate predictors to avoid over-parameterizing models if the sample size is small, thus providing limited information on the distribution of species and their environment. The transformation of predictors in MaxEnt is termed feature, which determines model complexity. 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 (linear feature at < 10 samples, linear and quadratic at 10–14 samples, linear, quadratic and hinge at 15–79, all six features at > 79 samples). The hinge feature is recommended for substantially improving model performance (Phillips and Dudik, 2008; Elith et al., 2011), however a simple feature may be sufficient for an adequate sample as being found in chapter 3 (Syfert et al., 2013).

For a species presence-only model such as MaxEnt, it is unclear what particularly diagnostic tool should be used for model validation. It is advisable that with presence-only data multiple evaluation measures are used to determine the accuracy of the produced models.
MaxEnt also generates the commonly used statistical area under the ROC curve (AUC) for the assessment of prediction errors in conventional presence/absence models. Yet, instead of the standard commission rate (i.e. false positive rate or fraction of true absences being predicted false present), the fraction of total predicted study area present is used in MaxEnt. Therefore, the AUC values tend to be higher for species with narrow ranges than widespread species, and a high AUC value necessarily does not suggest a better model. Consequently, in chapter 3 and 7 a null method was adopted to test the significances of the SDMs (Raes and ter Steege, 2007). A thousand random-permutation SDMs were generally performed for sample sizes of less than 100 occurrences, and those SDMs that had a significantly higher AUC value than expected by chance ($p<0.05$) were identified. In chapter 3, additional AIC values (Akaike’s Information Criterion) were calculated to determine whether the models had more parameters than samples, which would violate the assumptions of AIC (Warren and Seifert, 2010). Finally, it is noted that MaxEnt provides several options for repeat sampling and cross-validation, which makes it especially appropriate for small sample sizes, avoiding the use single training/test splits.

**Recommendations on conservation and management of forests and associated epiphytes**

The SDMs in chapter 7 projected a dramatic decline of several forests under future changing climates. To confirm this result, the establishment of two permanent forest research sites is recommended for monitoring the trend on forest composition change, for example, by recording seedling establishment and the trunk diameter growth of adult trees. The two sites, Chi-Lan (棲蘭) and Da-Wu (大武) reserves, are located in the northern and southern island at similar elevations (ca. 1500-2000 m asl), yet comprising distinct tree species due to regional climate dissimilarity (Fig 1). The Chi-Lan site is a primary forest, dominated by old-growth cypress and *Picea* trees, receiving substantial influence from NE monsoon. The future climate change scenario projects weakening of the NE monsoon, and consequently a substantial decrease in annual rainfall of this area, which might account for the prediction of major decline for the local forests (Lin et al., 2010). Accordingly, Chi-Lan may provide the first-order information on the climate change impacts on forests in the relatively near future. Despite sharing a common feature of cloud forests with Chi-Lan, the Da-Wu site mainly comprises broad-leaved trees (e.g. Fagaceae) due to less influence from NE monsoon and its relatively southern latitude. Here the common coniferous tree *Tsuga chinensis* var. *formosana* was projected to be replaced by broad-leaved forests which might in turn favour shade-tolerant epiphytic species. Since broad-leaved trees and associated epiphytes are characterized by a shorter generation time than coniferous trees, the Da-Wu site is a promising site for observing climate change influence in a relatively short period of time.
CONCLUSIONS

The SDMs of chapter 3 identified two areas, HsuehShan (雪山) and AliShan (阿里山), with high epiphyte diversity and endemism that deserve special attention in conservation (title figure). Receiving adequate precipitation from SW flows, these two epiphyte hotspots harbour many epiphytic orchids. It was reported recently that terrestrial species in the Alishan area showed an upward-shift of ca. 3.6 m yr\(^{-1}\) in their range by comparing recorded upper range limits in 1906 with those of 2006 (Jump et al., 2012). However, no study concerning the dynamic of abundant epiphyte populations here is known to date. In chapter 7, many sensitive species that are projected to have a high range-turnover rate under climate change also occurred in these two areas. Considering present species diversity and the severity of anthropogenic disturbance (e.g. climate change, land-use change), three sites (title figure), Mt. Chia-Li (棲蘭山), Tai-Chi Canyon (太極峽谷) and Jin-Shuei-Ying (浸水營), are prioritized for epiphyte conservation, requiring in-depth investigations. The former two sites, Mt. Chia-Li (ca. 1000-2000 m asl) and Tai-Chi Canyon (ca. 1000 asl), are located in HsuehShan and AliShan respectively. Both sites are near human settlements and currently lie outside conservation areas. Consequently, both sites are prone to species extinction. Several rare epiphytic orchids here (e.g. *Bulbophyllum rubrolabellum*, *Bulbophyllum tokioi*, *Cymbidium floribundum*, *Dendrobium falconeri*, *Eria javanica*, *Gastrochilus ciliaris*, *Gastrochilus fuscopunctatus*, *Gastrochilus raraensis*, *Thelasis pygmaea*, *Pleione bulbocodioides*, *Thrixspermum pensile*) are potential indicators for monitoring anthropogenic influences, including climate change. The last site, Jin-Shuei-Ying (ca. 500−1500 m asl) is located in the very south of Taiwan, characterized by a primary tropical montane cloud forest and an high endemism in epiphytic ferns (e.g. *Grammitis nuda*, *Crepidomanes palmifolium*). Many epiphytic ferns here are notorious rare and particularly hydro-sensitive (e.g. Hymenophyllaceae, Grammitidaceae), thus Jin-Shuei-Ying is an ideal site for monitoring climate change influence on water regime (e.g. cloud formation) and population dynamics of climate-sensitive epiphytes.

Global warming effects seem to be less pronounced in undisturbed forests, and present centres of species diversity might retain their importance into the future (Aptroot and van Herk, 2007; Venter et al., 2010). Thus, conserving old-growth forests as in above mentioned sites is crucial in supporting species to resist climate change, particularly those epiphytes that depend on old-growth trees for establishment (Ellis et al., 2009). SDMs showed that mid-elevation forests will remain relatively rich in epiphyte species, yet become more fragmented under future climate change (chapter 7). The combination of anthropogenic habitat disturbance and destruction, over-collection, and the ongoing climate change will likely increase the risk for extinction, particularly for mid-elevation tree species and their associated epiphytes. The present study on the ecology and distribution of epiphytes provides a framework for future conservation strategies and highlights the urgency of conservation actions under global climate change. Future conservation strategies should enable conservation authorities to evaluate the effectiveness of conservation and management efforts.