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Vascular Epiphytes in Taiwan and Their Potential Response to Climate Change

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SUMMARY

From 1997 to 1998, a strong El Niño event caused a dramatic decline of epiphytic populations in NE Taiwan (pers. observ.). Looking back, this incident has triggered my interest in the response of epiphytes to climate change, which is the main topic of this dissertation. At the time of the El Niño event, for Taiwan virtually no information was available yet on the floristic composition of the epiphyte flora, the biogeography of epiphytes, and the regional epiphyte distribution patterns. Moreover, the ecophysiology of Taiwanese epiphytes had been little studied, in particular in relation to global warming with presumed accompanying changes in CO_2 availability and solar insulation. Hence, conservationists were far removed from making a dependable assessment of the impact of climatic change on epiphyte communities in Taiwan.

Taiwan is a 36,000 km^2 island in East Asia (21°45'–25°56'N and 119°18'E–124°34'E). About 70% of the island is covered by mountains of 1000 up to 3952 m asl in height, with a dominant central range along the island's long axis. Annual rainfall ranges from 1,000 to over 6,000 mm depending on the prevailing wind directions.

The general aim of this study is to get insight in the response of Taiwanese epiphytes to climate change. More in detail, the following hypotheses were tested: 1) the composition of epiphyte flora is similar to other tropical areas; 2) the epiphyte flora is a mixture of that of adjacent floristic regions, influenced by prevailing winds; 3) epiphytes show a mid-elevation peak in richness that is better explained by environmental factors than by the mid-domain effect; 4) The evolution of Crassulacean Acid Metabolism (CAM) in humid forest epiphytes occurred in response to CO_2 availability; 5) in *Asplenium nidus*, the photosynthetic capacity is greater for the leaf surface that receives more insolation during a day; 6) there exists intraspecific variation of a widespread epiphytic fern *Asplenium antiquum* which determines its responses to changing climate; 7) epiphyte distribution are correlated with forest types; 8) certain epiphytic species and forest types are relatively susceptible to climate change.

To test the various hypotheses, descriptive, experimental (laboratory and field), and modelling studies were performed. A descriptive study, based on botanical collections in herbaria, helped to obtain insight in the current floristic composition, distribution and richness patterns of vascular epiphytes (hypothesis 1-3, chapters 2,3). Laboratory experiments and *in situ* measurements gained insight in the hypothesized evolution of CAM in response to diurnal changes in air CO_2 concentration (*Hoya carnosa*) and in the photosynthetic capacity of fern leaves (*Asplenium nidus*) under different conditions (hypothesis 4,5, chapters 4,5). A field experiment assessed the occurrence of adaptation of populations of a widespread epiphytic fern (*Asplenium antiquum*) to simulated climate-change conditions (hypothesis 6, chapter 6). Finally, a modelling approach was performed to assess epiphyte distribution patterns

(hypothesis 3, chapter 3) and climate change impacts on forests and associated vascular epiphytes (hypothesis 7,8, chapter 7).

Chapter 2. Composition and phytogeography of the epiphyte flora

By consulting herbarium specimens, literature records, and field observations, an epiphyte checklist was compiled comprising 336 vascular species (105 genera of 24 families). The Epiphyte-Quotient (i.e. the proportion of epiphytic species) was only 8%. Presumably, frequent tropical storms (typhoons) have contributed to the reduced epiphyte diversity in Taiwan. Similar to epiphytic flora's in other tropical regions, our checklist is dominated by few families, especially ferns (171 spp) and orchids (120 spp). Epiphyte endemism was high (21.3%), with half of the endemic species being orchids. Regarding epiphyte phytogeography, the total epiphyte flora exhibited a similar affinity to Malesian, Eastern Asiatic and Indochinese regions, yet epiphytic orchids shared most species with Indo-China, which likely may be attributed to prevailing winds.

Chapter 3. Epiphyte distribution pattern and explanatory factors

Using 39,084 unique botanical records, the elevational distribution pattern of over 300 epiphytic species was explored. The result showed a richness peak between 500 and 1500m asl that could not be explained by the mid-domain effect, suggesting environmental factors mostly accounting for epiphyte distribution. The overall epiphyte richness patterns were modelled using species distribution models, software MaxEnt. The modelled result not only corroborated the position of the mid-elevation peak in epiphyte richness, it also identified two regions with exceptionally high species richness in mid-elevations. The epiphyte hotspots are probably related to the direction of prevailing winds. Exploratory ordination analyses indicated two factors, elevation-related temperature and precipitation, which were most influential for epiphyte distribution. However, subcategories demonstrated different thermal preferences; for instance, hemi-epiphytes were most abundant in the lowland tropical forest whilst epiphytic ferns showed a preference for increasing elevations. In contrast to predictions by the Rapoport Effect hypothesis, the ordination analysis also showed that the degree of thermal specialisation increased with elevation, suggesting that highland species are especially vulnerable to global warming. Finally, in a partial ordination analysis controlling for all other variables, typhoons were shown to exert a significant influence on the distribution of epiphytes.

Chapter 4. CO_2 availability and the evolution of CAM in the epiphyte *Hoya carnosa*

Twenty CAM plants of *Hoya carnosa* were selected to compare the acid accumulations and stable carbon isotope ratios of their leaves under two habitat conditions. Ten in host trees that grow in intact, dense stands of forest (closed canopies), and ten in hosts with few neighbour trees (open canopies). We found that the air CO_2 concentration was significantly higher (40-60 μmol mol^{-1}) at night than during the day, and was higher in closed canopies than in open canopies at night, presumably the result of host-respired CO_2 added to the canopy air. However, the carbon isotope ratio of *H. carnosa* was not substantially lower than those of many other CAM plants, suggesting that the surplus CO_2 released by host trees to the atmosphere at night was not an importance CO_2 source for these CAM plants. In addition, *in vitro* experiment showed an appreciable daytime CO_2 uptake in *H. carnosa*, which should even lower the carbon isotope values of the species. Overall, the results indicated that host-respired CO_2 does not contribute CO_2 budget of canopy epiphytes, hence does not support the hypothesis that CAM has evolved in epiphytes in response to diurnal changes in air CO_2 concentration rather than water conservation.

Chapter 5. Plasticity of photosynthetic capacity in the epiphytic fern *Asplenium nidus*

CO_2 exchange rates of leaves in an epiphytic ferns were measured *in situ* to compare the difference of photosynthetic capacity between two leaf sides in relation to sunlight exposure. Three orientations of leaves with different patterns in sunlight exposure were selected, namely, vertical, angled and horizontal leaves spacing from inner to outer rings in *Asplenium nidus*, a fern of a rosette growth form. Except the vertically oriented leaves, the results indicated that photosynthetic rates were higher when the side of the leaf that typically received more direct isolation was illuminated during the measurement. Judging from equal stomatal conductances and accompanying transpiration rates, the higher CO_2 uptake rates were attributed to a greater biochemical capacity for photosynthesis. The study revealed the physiological plasticity within epiphytes in relation to their diverse microclimate conditions.

Chapter 6. Adaptation of a widespread epiphytic fern, *Asplenium antiquum,* to simulated climate change

A two-year reciprocal transplant field experiment along an altitudinal gradient was conducted to investigate the adaptive response of juvenile plants of the widespread epiphytic fern *Asplenium antiquum* to simulated climate change conditions. The experiment results showed a strong site effect between the three altitudinal sites at 600, 1100 and 1950 m asl on both the growth and survivorship of juvenile *A. antiquum*. Under the more extreme climate conditions at the highland site, the local population was clearly better adapted, evidenced by their significantly higher survival than the other two populations. The results suggested that intraspecific genetic diversity should be considered when assessing the potential impact of climate change on species.

Chapter 7. Modelling climate change impacts on forests and associated epiphytes

Hierarchical species distribution models (SDMs) were used to assess climate change impacts on forests and 237 vascular epiphyte species in Taiwan. By (1) incorporating dispersal limitation, tree persistence, and non-climatic factors into models, and (2) considering biotic interactions between epiphytes and host trees, a novel approach was developed to improve SDMs' accuracy and realism. The modelled results suggested that epiphyte distributions highly depended on forest compositions. In the model results, the annual means and the variances of the climate variables exerted an equal influence on species distributions, and non-climatic factors tended to retain their influence under climate change conditions. Our model also indicated certain forest types (e.g. Cypress and *Picea* forests) and certain thermal- or hydro-sensitive species are relatively more vulnerable to projected scenarios of climate change on the island.

In conclusion, the descriptive study of epiphytes on Taiwan has shown that its epiphyte flora is typical for tropical island biota, having relatively low diversity compared to mainland areas, yet showing high endemism, and sharing a low number of dominating groups, especially ferns and orchids. The relatively low diversity and the low contribution of epiphytes to the total vascular flora is, presumably, at least partly, explained by frequent large scale typhoon disturbances. Modelling showed that the altitudinal epiphyte distribution pattern was mostly accounted for by environmental factors rather than a null model of geometric constraints. However, laboratory experiments also showed that epiphytes may have a substantial degree of physiological plasticity in response to the diverse habitat of forest canopies. In addition, a field experiment indicated an intraspecific genetic adaptation to elevation for a widespread species. Information on physiological plasticity along with genetic adaptation is essential for assessing the climate change impacts on epiphyte biodiversity. Lastly, it is concluded that the mid-elevation Cypress and *Picea* forests that have a large number of niche-specialized epiphytic species deserve special attention for conservation purposes.