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Chapter 12

A Novel Approach to Simulate Climate Change Impacts on Vascular Epiphytes: Case Study in Taiwan

Rebecca C.-C. Hsu and Jan H.D. Wolf

Keywords Dispersal limitation • Global climate change • Maximum entropy method (MaxEnt) • Subtropical island • Tree persistence

Bullet Points

1. In comparison to terrestrial rooted plants, canopy epiphytes represent a promising model system to study the impact of climate change on living organisms because they are sensitive to the atmospheric climate, have relatively short life cycles, and show great potential for dispersal and colonization.
2. Epiphytes are adapted to highly dynamic forest canopies by producing many, mostly wind-dispersed diaspores, whereas long-lived dominant canopy trees have relatively limited dispersal ability and are more resistant to unfavorable climatic conditions. Accordingly, the response of tree-dependent epiphytes to climate change is likely slowed down by persistent forest trees and the slow immigration rate of trees into suitable new habitat.
3. The incorporation of forest trees into epiphyte species distribution models under climatic change scenarios in Taiwan confirmed that many known sensitive epiphytes (specialists) had restricted distributions (i.e., they were confined to mid-elevation/montane cloud forests), whereas insensitive species (generalists) were widespread and included several pantropical species.

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Summary

Forest vascular epiphytes have a critical influence on forest hydrology and nutrient cycling, so it is vital to assess how climate change affects these inhabitants. This study describes a novel hierarchical modeling approach, incorporating forest migration velocity and forest type–epiphyte interactions into classical species distribution models (SDMs). In Taiwan, eight major forest-type distributions were modeled under climate change scenarios and tailored to include dominant tree species' dispersal limitations and hypothesized persistence under unfavorable climate conditions. The forest projections, together with 16 environmental variables, were used to predict the likely distribution in the year 2100 of 237 vascular epiphyte species. The hierarchical modeling approach produced ecologically interpretable results. Biotic interactions must be considered when developing SDMs for dependent species, such as epiphytes.

1 Epiphytes in a Changing World

In the wet tropics, epiphytes form a conspicuous layer in the forest canopy, support abundant coexisting biota, and are known to have a critical influence on forest hydrology and nutrient cycling. Since canopy-dwelling plants have no vascular connection to the ground or their host plants, they are likely more sensitive to environmental changes than their soil-rooted counterparts (Benzing 1998), subsequently regarded as one of the groups most vulnerable to global climate change. Epiphytes have adapted to life in highly dynamic forest canopies by producing many, mostly wind-dispersed, seeds or spores. Consequently, epiphytes should colonize trees rapidly, which, in addition to atmospheric sensitivity and short life cycles, make epiphytes suitable climate change indicators. In this study, we assess the impact of climate change on Taiwanese epiphytes using a modeling approach.

2 Epiphyte Distribution Modeling

In the field of climate change impact research, species distribution models (SDMs) have been used increasingly to estimate potential species range shifts under paleontological and/or future climate change conditions. SDMs attempt to recognize species' realized niches, which are used to construct potential geographic distributions by relating species occurrences with values of predictor variables across a series of observation sites. Although classical SDMs may yield satisfactory results, modeling dependent epiphyte distributions is conducive to including additional factors. Since epiphyte performance also depends on the presence and characteristics of host trees, host tree composition probably has a significant influence on epiphyte assemblages. Other relevant factors include (1) information on regional topography and climate, (2) the microclimate associated with forest types and the specific epiphyte–tree biotic interactions, (3) the persistence of host trees (to sustain epiphyte populations under adverse climate change

conditions), and (4) the dispersal ability of host trees compared to epiphytes as linked to deceleration of epiphyte colonization of suitable new habitat. We propose a novel modeling approach tailored for epiphytes, demonstrated on subtropical island of Taiwan.

3 Methods

3.1 Data Preparation

We obtained the localities of 237 strictly arboreal epiphyte species (Hsu and Wolf 2009) from herbarium records, published plant inventories, and our own botanical observations and entered these in a database (MsAccess). The final database comprised 18,239 epiphyte records with occurrences ranging from 5 to 1,083 grid cells (1 km²). In addition, we obtained the localities of dominant canopy trees (11,700 records in total) from the third national forest resource inventory, conducted by the Taiwan Forest Bureau in 1993. Taiwanese major forest types were grouped as (1) lowland broad-leaved forest (BLL), (2) midland broad-leaved forest (BLM), (3) highland broad-leaved forest (BLH), (4) cypress forest, (5) *Pinus* forest, (6) *Tsuga* forest, (7) *Picea* forest, and (8) *Abies* forest.

We derived present climate data from an array of weather stations (recorded from 1900 to 1990) and future projected climate data (A2 and B2 scenarios, decadal average) from the Intergovernmental Panel on Climate Change (IPCC) Third Assessment Report (http://www.grida.no/publications/other/ipcc_tar/). We statistically downscaled the latter to a resolution of 1 km² to match the present-day data. We used monthly temperature and rainfall data to calculate ecologically relevant climate variables and applied a correlation test to exclude highly correlated (Pearson's $r > 0.75$) factors. We selected one edaphic, four topographic factors, and 16 environmental variables exhibiting low correlation to build our model (Table 12.1).

3.2 Model Building

We built the SDMs of epiphytes with the maximum entropy method (MaxEnt, version 3.3.3). This program was developed to model species' geographic distributions with presence-only data and has been shown to outperform the majority of other modeling applications, especially when sample sizes are small. MaxEnt is particularly suited for epiphytes, since most epiphyte species (especially orchids) are notoriously rare and the program places no weight on the absence of an epiphyte in a forest, which is difficult to ensure, especially for high-canopy species. MaxEnt calculates a probability distribution over the grid, which may be interpreted as an index of habitat suitability for a species (Elith et al. 2011). The program also provides an estimate of the relative contribution of each environmental variable to the model and the relative magnitudes of environmental variables, which are derived from one training set of data that can be

Table 12.1 Environmental variables used in model building

No.	Environmental variable	Unit	Calculation
1	Annual mean temperature	°C	Average monthly mean temperature
2	Annual precipitation	Millimeter	Average monthly precipitation
3	Temperature seasonality	Decimal fraction	The standard deviation of the monthly mean temperatures
4	Precipitation seasonality	Decimal fraction	The coefficient of variation of the monthly mean precipitation
5	Total water deficiency	Millimeter minus °C	Monthly precipitation minus twice the monthly mean temperature
6–11	Monthly rainfall (P01, P04, P05, P06, P07, P10)	Millimeter	Monthly rainfall in January, April, May, June, July, and October
12	Inclination	Degree	Average terrain slopes of 1 km ² land area
13–14	Aspect (eastness, northness)	Ordinal numbers: 0~8	Aspect measurement transformed by sin(aspect rad), cos(aspect rad), and assigned ordinals: 0, flat; 1, (−1)−(−0.75); 2, (−0.75)−(−0.5); 3, (−0.5)−(−0.25); 4, (−0.25)−0; 5, 0−0.25; 6, 0.25−0.5; 7, 0.5−0.75; 8, 0.75−1
15	Distance to 3,000 m	Meter	The distance to the nearest location above 3,000 m asl
16	Soil category	Cardinal numbers: 0~9	No soil (0), inceptisols (1), oxisols (2), alfisols (3), spodosols (4), mollisols (5), entisols (6), ultisols (7), andisols (8), vertisols (9)

Fig. 12.1 The stepwise hierarchical modeling approach used in this study. The procedure THRESHOLD removed species distributions below thresholds. The years 2050, 2080, and 2100 are target years for our models. Solid line arrows indicate SDM modeling; broken line arrows indicate SDM projection. Framed squares indicate our final SDMs. *NL*, needle forests: *Abies*, *Picea*, *Tsuga*, cypress, and *Pinus*; *BL*, broad-leaved forests: highland (BLH), midland (BLM), and lowland (BLL); *ENVI VARs*, environmental variables; *EP* epiphyte

“projected” on another set of environmental data, thus enabling MaxEnt to model species distribution under different climate conditions such as future climate simulations. We refined the classical SDM by considering dispersal limitation, tree persistence, and biotic interactions between epiphytes and host trees using a stepwise hierarchical modeling approach (Fig. 12.1).

- *Step 1, forest species distribution modeling*: We modeled forest distributions under present climatic conditions and subsequently made projections for future scenarios (specifically A2 and B2 scenarios, for the years 2050, 2080, and 2100). We used the modeled forest projections at year 2050 and 2080 as intermediate steps, incorporating divergent persistence abilities for needle- (*NL*) and broad-leaved trees (*BL*) (see step 3).
- *Step 2, forest species dispersal limitation*: We calculated the maximum expanded range of each forest type with the age of the tree at maturity in target years (1 km y^{-1} ; Engler and Guisan 2009). The projected forest distributions were then bounded by species dispersal limitations (Fig. 12.2).

Fig. 12.2 An example of a model incorporating dispersal limitation and tree persistence. The modeled distributions (year 2050 = blue; year 2100 = red) outside dispersal ranges (grey bubbles) were removed from the result. Black dots indicate present-day plant occurrence. Considering tree persistence, the tree distribution in year 2050 (blue grids) was assigned a threshold value (lowest suitability) and added to the 2100 distribution (red grids)

- *Step 3, forest species persistence:* We included the persistence ability of forests, as a measure of the time that trees can tolerate unfavorable climate conditions. We hypothesized a persistence of 20 years for broad-leaved trees (BLL, BLM, and BLH) and 50 years for needle trees (*Abies*, cypress, *Picea*, *Pinus*, and *Tsuga*). Accordingly, we modified the projected forest distributions at year 2100 by incorporating BL distributions at year 2080 and NL distributions at year 2050 (Fig. 12.2). The persistent/extended distributions were assigned threshold values of distribution probability (i.e., minimum habitat suitability).
- *Step 4, epiphyte species distribution modeling:* We used the resulting eight forest distributions (eight variables) together with the 16 abiotic variables (Table 12.1) to model the distribution of 237 epiphyte species. For each species, we simulated present-day conditions and then modeled projections for the year 2100 under both A2 and B2 climate change scenarios.

3.3 Species Richness Map

To create a species richness map, we first applied a threshold of sensitivity-specificity sum maximization to convert the MaxEnt probability distribution to a predicted presence map for each species. Next, every single species map was overlaid to produce a species richness map for epiphytes. The richness map was corrected for land-use change to eliminate species distributions in urbanized regions (assuming this remains unchanged in 2100).

4 Results, Applications, and Prospects

The SDM-generated forest distribution patterns agreed strongly with observed data (area under curve [AUC] values ranging from 0.809 to 0.967). All forest types were highly sensitive to mean annual temperature: this is expected because mean annual temperature is a driving force for altitudinal vegetation stratification in Taiwan. Consistent with observations, the models indicated that epiphyte distribution was strongly correlated with forest type; forest type was one of the three most significant factors contributing to the modeled distribution of each epiphyte species. The projected epiphyte richness map suggested a notable future shift in the altitudinal distribution of epiphytes. Epiphyte diversity is currently greatest at 1,000–1,500 m above sea level (asl) (nearly 100 species per 1 km²), but, under simulated climate change conditions, our model indicated that this belt of maximum species richness would shift to elevations of 1,500–2,000 m asl (Fig. 12.3).

We also identified the epiphytes that were most and least sensitive to the climate change scenarios by ranking their range turnover rates. Generally, relatively insensitive species were correlated with lowland forest (BLL), while species that were more sensitive to climate change were associated with mid-elevation forests (cypress and BLM). Moreover, our projection also inferred a distinct decline in cypress forest, a major component of montane cloud forest at mid-altitudes (1,800–2,500 m asl). Tropical montane cloud forests are unique among terrestrial ecosystems for their particular hydrological regime and typically occur in narrow altitude belts characterized by high endemism and abundant epiphytes (Bruijnzeel et al. 2010). Our model results showed that many

Fig. 12.3 The species richness maps of epiphytes in Taiwan under present and climate change conditions (values are the average of scenarios A2 and B2, IPCC)

epiphytes of the mid-elevation cloud forests (e.g., *Bulbophyllum chitouense* and *Mecodium badium*) are relatively sensitive to climate change conditions and may thus be suitable indicators for climate change. Conversely, our models suggested that species that were insensitive were generally widespread; these included several pantropical species (e.g., *Psilotum nudum* and *Hoya carnosa*) that are likely to demonstrate broader tolerances to climate change than species with a more restricted distribution (for a detailed species list and model results, see Hsu et al. 2012).

Finally, our model indicated a considerable decline in the surface area covered by mid-elevation forests and their associated epiphytic species under both climate change scenarios. Despite this perceived threat, most mid-altitude forests currently fall outside established protective reserves. We recommend establishing long-term plots for epiphyte monitoring outside and inside conservation areas, especially in those areas where climate change is projected to result in dramatic species composition changes.

The prediction of future species distributions is challenging because the species range shift is an ongoing process, reflecting dynamic relationships with environmental parameters, both biotic and abiotic (Elith et al. 2010). Our approach integrates knowledge on forest dynamics and host tree–epiphyte relationships and yielded easily interpretable results that will be crucial to building reliable and realistic species distribution models for dependent species such as epiphytes.

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