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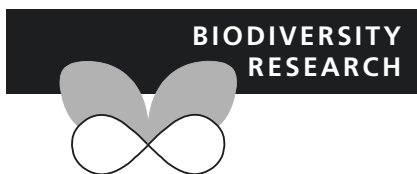
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Simulating climate change impacts on forests and associated vascular epiphytes in a subtropical island of East Asia

Rebecca C.-C. Hsu^{1*}, Wil L. M. Tamis², Niels Raes³, Geert R. de Snoo², Jan H. D. Wolf⁴, Gerard Oostermeijer⁴ and Shu-Hua Lin⁵

¹Taiwan Forestry Research Institute, No. 67, Sanyuan St., 10079 Taipei, Taiwan, ²Institute of Environmental Sciences (CML), Leiden University, PO Box 9518, 2300 RA Leiden, The Netherlands, ³Netherlands Centre for Biodiversity Naturalis (section NHN), Leiden University, PO Box 9514, 2300 RA Leiden, The Netherlands, ⁴Universiteit van Amsterdam, Institute for Biodiversity and Ecosystem Dynamics (IBED), PO Box 94248, 1090 GE Amsterdam, The Netherlands, ⁵APEC Research Center for Typhoon and Society, 9F, No. 97, Sec. 1, Roosevelt Rd., Taipei 10093, Taiwan

ABSTRACT

Aim This study aims to assess the impact of climate change on forests and vascular epiphytes, using species distribution models (SDMs).

Location Island of Taiwan, subtropical East Asia.

Methods A hierarchical modelling approach incorporating forest migration velocity and forest type–epiphyte interactions with classical SDMs was used to model the responses of eight forest types and 237 vascular epiphytes for the year 2100 under two climate change scenarios. Forest distributions were modelled and modified by dominant tree species' dispersal limitations and hypothesized persistence under unfavourable climate conditions (20 years for broad-leaved trees and 50 years for conifers). The modelled forest projections together with 16 environmental variables were used as predictors in models of epiphyte distributions. A null method was applied to validate the significance of epiphyte SDMs, and potential vulnerable species were identified by calculating range turnover rates.

Results For the year 2100, the model predicted a reduction in the range of most forest types, especially for *Picea* and cypress forests, which shifted to altitudes c. 400 and 300 m higher, respectively. The models indicated that epiphyte distributions are highly correlated with forest types, and the majority (77–78%) of epiphyte species were also projected to lose 45–58% of their current range, shifting on average to altitudes c. 400 m higher than currently. Range turnover rates suggested that insensitive epiphytes were generally lowland or widespread species, whereas sensitive species were more geographically restricted, showing a higher correlation with temperature-related factors in their distributions.

Main conclusions The hierarchical modelling approach successfully produced interpretable results, suggesting the importance of considering biotic interactions and the inclusion of terrain-related factors when developing SDMs for dependant species at a local scale. Long-term monitoring of potentially vulnerable sites is advised, especially of those sites that fall outside current conservation reserves where additional human disturbance is likely to exacerbate the effect of climate change.

Keywords

Dispersal limitation, East Asia, maximum entropy method, species distribution model (SDM), subtropical island, tree persistence.

*Correspondence: Rebecca C.-C. Hsu, Taiwan Forestry Research Institute, No. 67, Sanyuan St., 10079, Taipei Taiwan.
E-mail: ecogarden@tfri.gov.tw

INTRODUCTION

Numerous studies indicate that climate change has already altered global patterns of biodiversity by modifying the

geographical distributions of species (Root *et al.*, 2003; Walther *et al.*, 2005; Lenoir *et al.*, 2008; Harsch *et al.*, 2009; Woodall *et al.*, 2009). In the field of climate change impact research, species distribution models (SDMs) or ecological

niche models (ENMs) have been increasingly used to estimate potential species range shifts under paleontological and/or future climate change conditions (Bakkenes *et al.*, 2002; Broennimann *et al.*, 2006; Hijmans & Graham, 2006; Thuiller *et al.*, 2006; Carnaval & Moritz, 2008; Fitzpatrick *et al.*, 2008; Jensen *et al.*, 2008). SDMs attempt to recognize species' realized niche, which is used to construct potential geographical distributions by relating species occurrences to values of predictor variables across a series of observation sites (Guisan & Thuiller, 2005). However, purely climate-based models have been criticized in numerous studies because they may not contain sufficient environmental parameters to assess climate change impacts (Heikkinen *et al.*, 2006; Austin & Van Niel, 2011a,b). For example, SDMs tend to overestimate the area of suitable habitats, particularly for those species with a strong dependency on other species (Huntley *et al.*, 2010).

In wet tropics, epiphytes form a conspicuous layer in the forest canopy and are regarded as one of the groups most vulnerable to global climate change (Benzing, 1998; Nadkarni & Solano, 2002; Zotz & Bader, 2009). Canopy-dwelling plants have no vascular connection to the ground or their host plants, making them more sensitive to environmental changes than their soil-rooted counterparts (Benzing, 2004). Two decades of monitoring the lichen flora of the Netherlands indicated a dramatic change on the species composition and abundance attributed to global warming (Van Herk *et al.*, 2002). Epiphyte performance relies on the presence and characteristics of host trees. Although exceptions exist (Callaway *et al.*, 2002), most vascular epiphytes exhibit no clear host tree preference (Zimmerman & Olmsted, 1992; Hsu *et al.*, 2002; Martin *et al.*, 2007), yet, the host tree (phorophyte) composition has a significant influence on likely epiphyte assemblages (Benavides, 2010). Thus, assessing climate change impacts on epiphytes requires information on not only the regional climate but also the microclimate associated with forest types and the specific epiphyte–tree biotic interactions. Studies have indicated that the inclusion of biotic interactions significantly improved the accuracy of SDMs (Leathwick *et al.*, 1996; Araújo & Luoto, 2007; Preston *et al.*, 2008). Other studies have pointed out that the rate of climate change probably outpaces the migration capacity of many species (Svenning *et al.*, 2008; Thuiller *et al.*, 2008). However, epiphytes are adapted to highly dynamic forest canopies by producing many, mostly wind-dispersed seeds or spores (Benzing, 1990). Accordingly, the colonization of epiphytes on trees should be rapid, which, in addition to short life cycles, makes epiphytes suitable climate change indicators (Lugo & Scatena, 1992). For other forest plants, it is still crucial to take dispersal limitation into account when simulating species distributions (Engler & Guisan, 2009); a study on Cape Proteaceae indicated that, even with an optimistic migration rate scenario, the modelled species range loss closely approximated null migration (Midgley *et al.*, 2006). However, because it is difficult to obtain reliable dispersal data, especially for the tail end of the leptokurtic distribution, most studies assume either unlimited or no dispersal for the target species.

Other debates are concerned with species persistence in unfavourable climatic conditions (Loehle & LeBlanc, 1996). Common sense dictates that many species (especially long-lived trees) will not immediately perish during climate changes. Long-lived dominant canopy trees will be relatively resistant since they can tolerate years of slow growth, whilst early successional species will die rapidly if their growth rate falls below a minimum (Loehle & LeBlanc, 1996); this justifies the importance of including species persistence in SDMs. Despite aforementioned limitations, SDMs do provide valuable first-order assessments of potential climatic change impacts on biodiversity (Huntley *et al.*, 2010). Pearson & Dawson (2003) suggested a hierarchical framework for modelling species distributions at different geographical scales to improve model reliability. We have also adopted this approach and incorporated a number of non-climatic factors (such as topography).

This study aims to assess the climate change impacts on forests and vascular epiphytes in the subtropical island of Taiwan, using SDMs. We propose a stepwise hierarchical modelling approach and aim to improve model accuracy and realism by considering dispersal limitation, tree persistence and biotic interactions between epiphytes and host trees. Our study specifically addresses two questions: (1) How do environmental factors contribute to species distributions and their ecological interpretations? and (2) What areas and which species are potentially vulnerable to climate change?

METHODS

Study site, species collections and forest types

Taiwan (situated between 21°45′–25°56′N and 119°18′E–124°34′E) is an island with an area of 36,000 km² (Fig. 1). About 70% of the island area is covered by mountains (> 1000 m above sea level [a.s.l.]); Mt. Jade (3952 m) is the highest peak in Taiwan. The annual rainfall in Taiwan ranges from 1000 mm to over 6000 mm and generally falls during the NE monsoon (October–January), spring rain (February–April), plum rain (May–June) and typhoon-induced heavy rain events (July–September). The NE monsoon accounts for 45% of the total annual rainfall, mainly in east Taiwan (Kao *et al.*, 2004). Three hundred and thirty-six species of vascular epiphytes have been reported for Taiwan (Hsu & Wolf, 2009), of which 271 species are holo-epiphytes (i.e. epiphytes that complete their entire life cycle without contacting the forest floor). In this study, we applied SDMs on those 271 strictly arboreal species to assess the impact of climate change under two projected scenarios.

We identified the locations of epiphytic species from herbarium records, published plant inventories and our own botanical observations. We assigned species occurrences to 1 km² grid cells; multiple occurrences within the same cell were considered as one 'unique' record. The final database comprised 18,239 records (occurrences ranged from 5 to 1083) including 237 species; 34 species with less than five unique localities were excluded from the model. Over 90% of

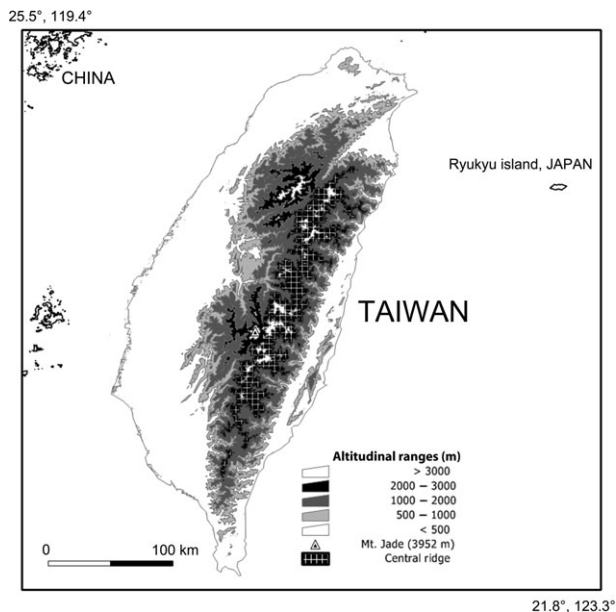


Figure 1 Location and the contour altitudes of Taiwan. The Central Ridge runs north-east to south along the island mountain chain.

modelled species were either ferns or orchids (see Appendix S1 in Supporting Information). According to the typology studies (Su, 1992; Chiou *et al.*, 2009), the Taiwanese major forest types can be 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 (see Table 1 for descriptions). Localities of the forest types (dominant canopy trees, 11,700 unique records in total) were obtained from the third national forest resource inventory, conducted by the Taiwan Forest Bureau in 1993 (Taiwan Forest Bureau, 1995).

Environmental variable preparation

Present climate data were derived from an array of weather stations (data recorded from 1900 to 1990). Future projected climate data (for the years 2050, 2080 and 2100, determined by decadal average) were obtained from the Intergovernmental Panel on Climate Change (IPCC) Third Assessment Report (IPCC, 2001). By 2100, based on Taiwan regional averaging, a greater temperature increase is predicted for scenario A2 (4.8 °C) than for scenario B2 (3.2 °C), and predicted annual rainfall increases are 193 mm for A2 and 79 mm for B2. The simulated climate data were statistically downscaled to a resolution of 1 km² to match the resolution of the present-day data (35,928 grid cells in total; Wilby & Wigley, 1997; Lin *et al.*, 2010) for the purposes of regional assessment. Based on monthly temperature and rainfall data, we calculated ecologically relevant climate variables representing annual trends (such as mean annual temperature), seasonality (for example,

temperature seasonality) and extreme or limiting climatic factors (such as water deficiency) (Nix, 1986). To avoid multicollinearity (Heikkinen *et al.*, 2006), we applied correlation tests between variables to exclude highly correlated (Pearson's $r > 0.75$) factors. Along with one edaphic and four topographic factors, 16 environmental variables with low correlation were eventually selected for model building (Table 2).

Modelling species distributions and model validation

The species distributions were modelled with the maximum entropy method (MAXENT, version 3.3.3; <http://www.cs.princeton.edu/~schapire/maxent/>). This programme was developed for modelling species' geographical distributions with presence-only data and has been shown to outperform the majority of other modelling applications, especially when sample sizes are small (Elith *et al.*, 2006; Hijmans & Graham, 2006; Pearson *et al.*, 2007; Graham *et al.*, 2008; Wisz *et al.*, 2008; Mateo *et al.*, 2010). MAXENT is particularly suited for epiphytes, since most epiphyte species (especially orchids) are notoriously rare, and it puts 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 programme also gives an estimate of the relative contribution of each environmental variable to the model by means of iterative calculations (in this study, 500 times). Furthermore, the relative magnitudes of environmental variables derived from one training set of data can be 'projected' to another set of environmental data, which enables MAXENT to model species distribution under different climate conditions, such as future climate simulations (VanDerWal *et al.*, 2009).

We applied a stepwise hierarchical modelling approach to simulate forest and epiphyte distributions under various climate change scenarios (Fig. 2). In the first step, forest distributions were modelled under present climatic conditions and subsequently projected on future scenarios (for the years 2050, 2080 and 2100). The modelled forest projections at year 2050 and 2080 were used as intermediate steps (Fig. 2), incorporating divergent persistence abilities for needle- (NL) and broad-leaved trees (BL). We randomly selected 70% of the forest occurrences for model building and reserved the remaining 30% for model testing, calculating the area under the curve (AUC) value (Phillips *et al.*, 2006). In the second step, we included species dispersal limitation as a factor affecting future forest distributions. Corlett (2009) pointed out that most plant species, depending on their dispersal vectors, probably have maximum dispersal distances of between 100 m and 1 km in tropical East Asia. In Taiwan, annual typhoons may promote long-distance (up to 1 km) dispersal of conifer winged seeds (Engler & Guisan, 2009). After carefully reviewing earlier reports (Vittoz & Engler, 2007; Engler & Guisan, 2009) and considering dispersal vectors, for our model, we hypothesized a maximum horizontal dispersal distance of

Table 1 The eight forest types, associated characters and the maximum dispersal distance at target years.

Forest type (abbreviation used)	Altitudinal range (m)	Dominant species	Dispersal vector	Age of maturity (years)†	Persistence (years)‡	Maximum dispersal distance for persistence trees (m)§	Maximum dispersal distance in 2100 (m)
1 Lowland broad-leaved forest (BLL)	< 500	<i>Ficus</i> spp. <i>Machilus</i> spp.	Large canopy birds, Macaques, Rodents	10	20	7759*	9699
2 Midland broad-leaved forests (BLM)	500–1500	<i>Machilu</i> spp. <i>Castanopsis</i> spp.	Large canopy birds, Macaques, Rodents	15	20	5173*	6466
3 Highland broad-leaved forest (BLH)	> 1500	<i>Quercus</i> spp.	Large canopy birds, Macaques, Rodents	20	20	3715*	4643
4 Cypress forest	1800–2500	<i>Chamaecyparis</i> spp.	Wind	30	50	1548**	3096
5 <i>Pinus</i> forest	800–3000	<i>Pinus taiwanensis</i>	Wind	15	50	3096**	6191
6 <i>Tsuga</i> Forest	2500–3200	<i>Tsuga chinensis</i> var. <i>formosana</i>	Wind	25	50	1857**	3715
7 <i>Picea</i> forest	2500–3200	<i>Picea morrisonicola</i>	Wind	30	50	1548**	3096
8 <i>Abies</i> forest	> 3200	<i>Abies kawakamii</i>	Wind	30	50	1548**	3096

†USDA Forest Service (<http://www.fs.fed.us/database/feis/plants/index.html>); He & Mladenoff (1999); Verdú (2002); Engler & Guisan (2009).

‡Engler & Guisan (2009).

§Maximum dispersal distance for the year 2080 (*) and 2050 (**).

1 km per year for each forest type. We calculated the maximum expanded range of each forest type with the age of the tree at maturity in target years (Table 1) and calibrated by average terrain inclinations (both 14° below and 22° above 1500 m a.s.l.). In step three, we included the persistence time of forests, being a measure of the time that trees can tolerate unfavourable 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*) (Table 1). Accordingly, we modified the projected forest distributions at year 2100 by incorporating BL distributions at year 2080 and NL distributions at year 2050 (Figs 2 and 3). The persistent/extended distributions were assigned threshold values (i.e. minimum habitat suitability). In step four, the resulting eight forest distributions (eight variables), together with the 16 abiotic variables (Table 2), were used to model the distribution of 237 epiphyte species. For each species, we simulated present-day conditions and then modelled projections for the year 2100 under both A2 and B2 climate change scenarios.

To validate our model, we used a null method to test the significance of the epiphyte SDMs (Raes & ter Steege, 2007). This analysis uses all presence records for model building, which is an advantage because the sample sizes of most epiphyte species were small. We created null distributions (999 permutations) for 5–30 records (with intervals of one), 35–55 records (with intervals of five) and 60–100 records (with intervals of 10) and then applied a curve-fit through the upper limit of the 95% confidence interval AUC values (see Fig. S1 in Supporting Information). We thus identified which epiphyte SDM had a significantly higher AUC value than expected by

chance ($P < 0.05$). Species with a non-significant SDM were omitted from the analyses. Null analysis was not applied on forest SDMs because each forest type had more than a hundred occurrences.

Data analysis

We calculated the number of newly appearing, remaining and disappearing epiphytes in each grid cell. The altitude of each grid cell was derived from digital terrain models (DTM). After testing for normality (Shapiro–Wilk test), pairs of means of median altitudes of the projected distributions were compared using one-way ANOVA (SPSS, version 13.0; IBM, Armonk, New York, USA). We described the dissimilarity between present and projected distributions using the Jaccard distance index (J') and calculated the range turnover rate for each species. To create a species richness map, we first 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. 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).

RESULTS

Forest transitions

The SDM-generated forest distribution patterns agreed strongly with observed data (AUC values ranging from 0.809

Table 2 All environmental variables calculated in this study. Asterisks indicate variables used in model building.

Environmental variable (abbreviation)	Unit	Calculation	Citation
1 Annual mean temperature (Tmean)*	°C	Average monthly mean temperature	
2 Annual precipitation (Pannual)*	Millimetre	Average monthly precipitation	
3 Temperature seasonality (Tsd)*	Decimal fraction	The standard deviation of the monthly mean temperatures	Hijmans <i>et al.</i> (2005)
4 Precipitation seasonality (Pcv)*	Decimal fraction	The coefficient of variation of the monthly mean precipitation	
5 Mean temperature of warmest month	°C	The monthly mean temperature of the warmest or coldest month	Nix (1986)
6 Mean temperature of coldest month			
7 Mean temperature of wettest quarter		The average monthly mean temperature of the three wettest or driest contiguous months	
8 Mean temperature of driest quarter			
9 Mean temperature of warmest quarter		The average monthly mean temperature of the three warmest or coldest contiguous months	
10 Mean temperature of coldest quarter			
11 Precipitation of wettest month	Millimetre	The monthly precipitation of the wettest or driest month	
12 Precipitation of driest month			
13 Precipitation of wettest quarter		The total precipitation of the three wettest or driest contiguous months	
14 Precipitation of driest quarter			
15 Precipitation of warmest quarter		The total precipitation of the three warmest or coldest contiguous months	
16 Precipitation of coldest quarter			
17 Temperature annual range	°C	Variable 5 minus variable 6	
18 Precipitation ratio of coldest quarter	Decimal fraction	Variable 17 as a percentage of variable 2	
19 Warmth index	°C	Sum of monthly mean temperature above 5 °C	Kira (1977)
20 Total water deficiency (Pdef)*	Millimetre minus °C	Monthly precipitation minus doubled monthly mean temperature	Lee <i>et al.</i> (1997)
21 Potential evapotranspiration ratio	Decimal fraction	Mean annual biotemperature divided by total annual precipitation	Anderson <i>et al.</i> (2002)
22 Monthly rainfall (P01–P12)	Millimetre	P01*, P04*, P05*, P06*, P07*, P10*	
23 Inclination (slope)*	Degree	Average terrain slopes of 1 km ² land area	
24 Aspect (Eastness*, Northness*)	Ordinal numbers: 0~8	Transformed by sin(aspect rad), cos(aspect rad), and assigned ordinals: 0: flat, 1: (−1) to (−0.75), 2: (−0.75) to (−0.5), 3: (−0.5) to (−0.25), 4: (−0.25) to 0, 5: 0–0.25, 6: 0.25–0.5, 7: 0.5–0.75, 8: 0.75–1	
25 (Dto3000)*	Metre	The distance to the nearest location above 3000 m a.s.l.	Lee <i>et al.</i> (1997)
26 Soil category (Soilcode)*	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)	Guo <i>et al.</i> (2005)

to 0.967; Table 3). Although our models suggested that the total forest area would decrease by 27% and 4% (scenarios A2 and B2, respectively), most forest types exhibited larger area reductions (Table 3), with the exception of the BLL forest, which was projected to expand by 37% from its current extension under scenario B2. The largest projected reductions in range were for the *Picea* forest, which decreased by 77% in scenario A2 and 81% in scenario B2, followed by the cypress forest (−52% and −54%, respectively). Moreover, projected forest distributions indicated a general tendency to move to higher altitudes (Table 3). *Picea*, cypress and BLM forests showed more significant movement to higher altitudes than other forest types under both scenarios, whereas *Pinus* forests had the most stable distribution. According to the top three factors contributing to each forest model, all forest types were sensitive to annual mean temperature (Tmean; Table 3). We also found that the factor distance to elevations above 3000 m

(Dto3000) and temperature-related factors (such as Tmean and Tsd) were relatively important for *Picea* forests, whilst cypress forest was also sensitive to moisture-related factors (such as Pdef and Pcv). October rainfall (P10) was a contributing factor to BLM forest distributions.

In addition to the shifting distribution patterns of the eight forest types, the relative extent of each forest type was also projected to change under climate change. Currently, the ratio (in terms of area occupied) of broad-leaved forests to coniferous forests is nearly 1:1. By the year 2100, our models suggest this ratio will be 1.5:1 under scenario A2 and 2:1 under scenario B2. Vegetation maps (Fig. 4) provided a visual indicator of predicted changes in forest type, notably in the north-east of Taiwan, especially under scenario A2 (Fig. 4b). Isolated *Tsuga* and *Picea* forests at the southern end of the Central Ridge (Fig. 1) were projected to disappear under both scenarios. The projections suggested a large decline and

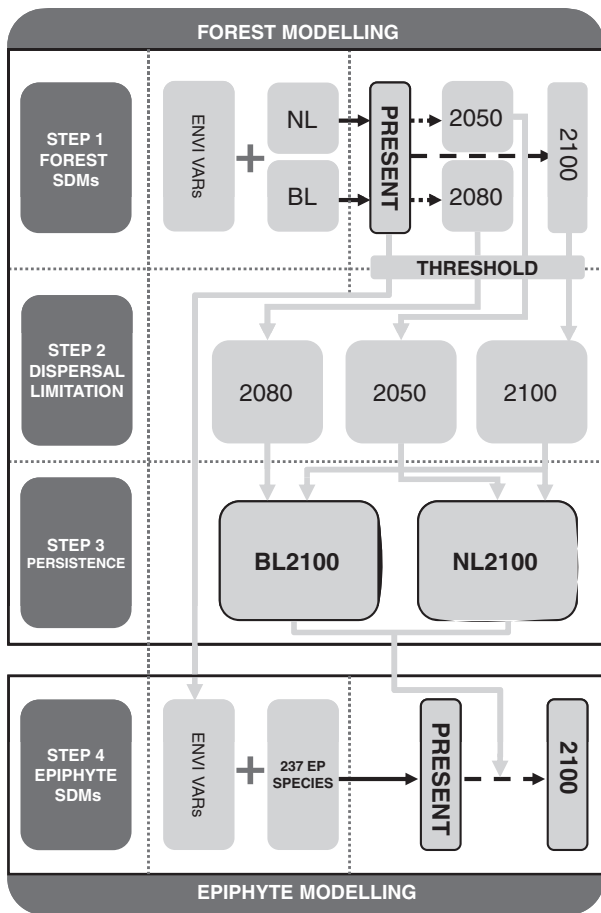


Figure 2 The stepwise hierarchical modelling approach used in this study. The procedure THRESHOLD removed species distributions below thresholds. The years 2050, 2080 and 2100 are target years for our models. Solid-line arrows indicate SDM modelling; broken-line arrows indicate SDM projection. Framed 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.

fragment of the cypress forest on the eastern side of the Central Ridge under scenario B2.

Epiphyte transitions

After testing SDMs against null distributions, we excluded 26 non-significant SDMs (see Fig. S1). The 211 modelled epiphyte species consisted of 83 orchids, 111 ferns and 17 species belonging to other taxa (see Appendix S1). We identified the top 10 most and least sensitive epiphytes to the two climate change scenarios by ranking their Jaccard distance index (J' , i.e. range turnover rate) and the three most contributing factors to the modelled distribution of each epiphyte (Table 4). Generally, relatively insensitive (low J') species correlated with lowland forest (BLL), whilst more sensitive (high J') species were associated with mid-elevation forests (cypress and BLM).

Table 3 The range changes (%) and altitudinal change (in metres) for each forest type under two climate change scenarios (scenarios A2 and B2; IPCC, 2001), the area under curve (AUC) values for the forest models and the top three factors sorted in descending order according to their relative contributions to each species distribution model. Broad-leaved forest: lowland (BLL), midland (BLM), highland (BLH).

Forest type	Range change (%)		Altitudinal change (m)		AUC	Top three factors
	A2	B2	A2	B2		
<i>Abies</i>	-46	-49	217	239	0.9595	Tmean, Dto3000, Eastness
<i>Picea</i>	-77	-81	403	428	0.9606	Dto3000, Tmean, Tsd
<i>Tsuga</i>	-48	-53	250	279	0.9124	Tmean, Tsd, Dto3000
Cypress	-54	-52	322	329	0.9113	Tmean, Pcv, Pdef
<i>Pinus</i>	-29	-29	130	148	0.8878	Tmean, Dto3000, Pdef
BLH	-44	-34	378	282	0.8428	Tmean, Pdef, Tsd
BLM	-20	-2	578	364	0.8091	Tmean, slope, P10
BLL	-12	37	470	268	0.8406	Tmean, P10, Eastness

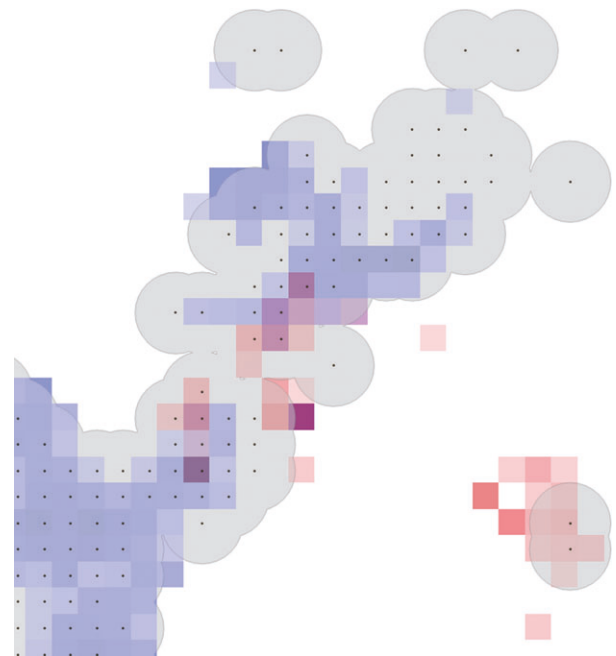


Figure 3 An example of a model incorporating dispersal limitation and tree persistence. The modelled distributions (year 2050 = blue, and year 2100 = red) outside dispersal ranges (grey bubbles) were removed from the result. Black dots indicate present-day plant occurrence. Considering tree persistence, the tree distribution in year 2050 (blue grids) was assigned a threshold value (lowest suitability) and added to the 2100 distribution (red grids).

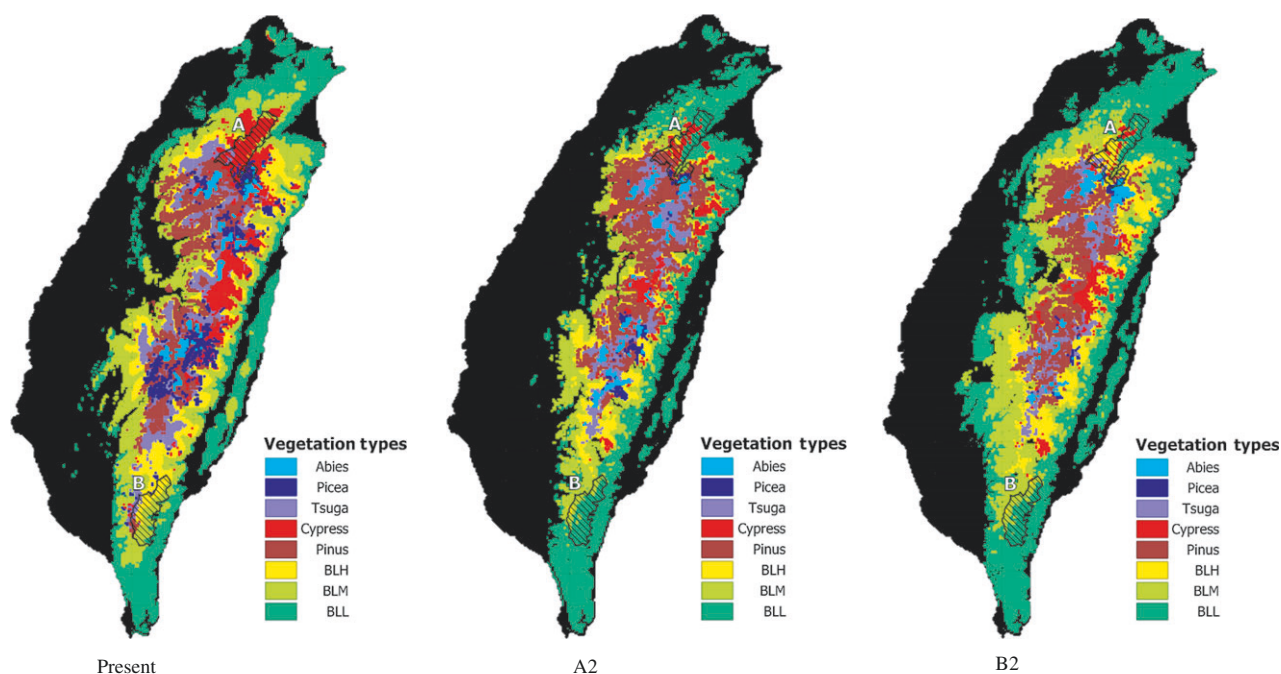


Figure 4 The potential distributions of eight forest types under present and climate change conditions (scenario A2, B2; IPCC, 2001) in Taiwan. Since more than one forest type exist within several altitudinal zones (*Abies*, *Picea* and *Tsuga* > 2500 m; cypress, *Pinus* and BLH > 1500 m; BLM and BLL < 1500 m), the resulting habitat suitability of grids is compared to visually present the major forest type. Slashed boundaries indicate reserves suggested for forest monitoring. A = Chi-Lan reserve, B = Da-Wu reserve.

and temperature-related factors (T_{mean} and T_{sd}). Insensitive epiphytes were generally lowland or widespread species (those with greater occurrence; see Appendix S1), whereas sensitive species were more geographically restricted (Fig. 5a,c). Under scenario A2, 83% of epiphyte species had shifted to higher altitudes by 2100; this figure was 90% for scenario B2 (see Appendix S1). In our projections, high J' species were more likely to shift to higher altitudes than low J' species (Table 4). The average median altitude increased by c. 400 m under both climate change scenarios (Fig. 6). On average, 78% of epiphyte species were projected to lose 58% of their currently occupied area under scenario A2, and 77% of species were projected to lose 45% of their area under scenario B2 (see Appendix S1). Our models showed that the remainder of the species (about 20%) expanded their range size by on average 210% and 170% under scenarios A2 and B2, respectively.

At the community level, projected altitudinal shifts in epiphyte distributions brought about changing spatial patterns of epiphyte richness. At present, epiphyte diversity is highest at 1000–1500 m a.s.l. (nearly 100 species per 1 km²). Under climate change conditions, our model indicated that this belt of maximum species richness would shift to 1500–2000 m a.s.l. (Fig. 7). On average, 28 epiphytic species are projected to disappear from each grid cell under scenario A2 and 24 species under scenario B2 (Fig. 5a); the most stable species number was generally found at 1000–1500 m a.s.l. (Fig. 5c). Our models suggested a dramatic decrease in species richness in the north of Taiwan, which was more pronounced under scenario A2 than B2 (Fig. 7). In general, newly appearing species

occurred in the southern mountains (1500–2000 m a.s.l.) of Taiwan (Fig. 5b).

DISCUSSION

Modelled species responses and possible ecological interpretations

The massive sample size of the tree occurrence data may partially contribute to the high quality of the forest models. All forest types were highly sensitive to mean annual temperature; this is expected because mean annual temperature strongly correlates with elevation, driving vegetation stratification in Taiwan (Su, 1992). Our results showed that most species, both trees and epiphytes, are projected to shift to higher altitudes. This would probably lead to increased habitat fragmentation, since landscapes are dissected by deep ravines at higher elevations. In Taiwan, *Picea morrisonicola* currently has a scattered distribution between 2500 and 3200 m a.s.l., and our model indicates that a major factor in *Picea*'s distribution is distance to elevations above 3000 m (Dto3000), producing two discrete populations separated by a depression in the middle of the Taiwan Central Ridge (Fig. 4a). Variable Dto3000 is related to Massenerhebung effect which explains the variation in altitudinal limits of forest types based on mountain sizes and locations. In Taiwan, the forest type on the main ridges of major ranges generally have higher altitudinal limits because of heat retention and wind shadowing, a phenomenon that has often been noted on small coastal islands (Grubb, 1971; Foster,

Table 4 The top 10 (grey shading) and lowest 10 (white background) species for the two scenarios (A2 and B2; IPCC, 2001) sorted by their Jaccard distance index (J'), and the top three factors sorted in descending order according to their relative contributions to each species distribution model. Asterisks indicate species endemic to Taiwan.

Species	Scenario	J'	J'	Altitudinal shift (m)		Factor
		A2	B2	A2	B2	
<i>Bulbophyllum chitouense</i> *	A2	1.00	0.90	496	430	Tsd, BLM, Cypress
<i>Elaphoglossum luzonicum</i>	A2, B2	1.00	0.97	−654	−160	BLM, Dto3000, soil_code
<i>Grammitis nuda</i> *	A2, B2	1.00	1.00	944	885	BLM, Dto3000, Pdef
<i>Dendrobium falconeri</i>	A2	1.00	0.82	−36	196	P10, slope, soil_code
<i>Mecodium oligosorum</i>	A2, B2	1.00	0.99	585	−162	Pdef, P01, slope
<i>Goodyera bilamellata</i> *	B2	0.97	1.00	845	530	Tmean, slope, Tsd
<i>Flickingeria tairukounia</i> *	B2	0.99	1.00	793	715	BLL, Eastness, P05
<i>Pyrrosia matsudae</i> *	A2	1.00	0.77	383	270	P10, Dto3000, Pinus
<i>Saxiglossum angustissimum</i>	A2	1.00	0.93	661	−127	Northernness, Tsd, P10
<i>Bulbophyllum electrinum</i>	A2, B2	1.00	1.00	−731	717	BLM, Pdef, Pinus
<i>Microtatorchis compacta</i>	A2	1.00	0.89	830	471	Tmean, BLL, Pdef
<i>Humata chrysanthemifolia</i>	A2	1.00	0.86	549	304	P05, P07, BLH
<i>Cleisostoma paniculatum</i>	B2	0.98	0.97	745	579	P10, BLH, slope
<i>Scleroglossum pusillum</i>	B2	0.95	0.96	−742	−775	Pdef, Pinus, Tsd
<i>Gastrochilus raraensis</i> *	B2	0.97	0.96	660	738	Pdef, Cypress, BLL
<i>Mecodium badium</i>	B2	0.96	0.96	1151	742	Tmean, Tsd, Pannual
<i>Psilotum nudum</i>	A2	0.73	0.61	385	197	slope, Pdef, BLL
<i>Vaginularia paradoxa</i>	A2	0.71	0.71	−54	−18	P06, BLL, BLH
<i>Davallia solida</i>	A2	0.68	0.78	−53	−128	Dto3000, Tsd, BLL
<i>Thrixspermum fantasticum</i>	A2, B2	0.66	0.47	9	56	Pdef, BLH, Pinus
<i>Vittaria taeniophylla</i>	A2, B2	0.64	0.42	−22	22	Pinus, slope, Tsuga
<i>Luisia cordata</i> *	A2, B2	0.61	0.31	12	23	soil_code, Dto3000, BLL
<i>Oberonia rosea</i>	A2, B2	0.61	0.41	24	11	Dto3000, Eastness, BLH
<i>Medinilla formosana</i> *	A2	0.55	0.59	−99	227	BLL, Dto3000, P07
<i>Oberonia gigantea</i> *	B2	0.79	0.51	535	431	Pdef, Pinus, slope
<i>Pentapanax castanopsicola</i> *	B2	0.84	0.51	158	243	Pdef, BLL, P05
<i>Calymmodon cucullatus</i>	A2	0.50	0.56	−173	−61	Dto3000, P06, BLM
<i>Pomatocalpa acuminata</i> *	B2	0.84	0.48	203	135	BLH, P06, Northernness
<i>Thrixspermum formosanum</i>	B2	0.80	0.48	203	182	BLH, Eastness, Dto3000
<i>Hoya carnosa</i>	B2	0.75	0.46	269	217	BLL, slope, BLH
<i>Schoenorchis vanoverberghii</i>	A2, B2	0.31	0.32	−3	−17	Dto3000, BLL, slope

2001). The relatively small and fragmented population of *Picea* is thus more sensitive to global warming than the other forest types.

The model indicated a distinct decline in cypress forest, a major component of montane cloud forest in Taiwan. Cypress forest is characterized by cool temperatures, continuously moist and dim conditions, typically enveloped in clouds during the afternoon (Lai *et al.*, 2006). Many epiphytes with restricted distributions are specialized to this particular thermal and hydrological regime. Consistent with observations, the models indicated that epiphyte distributions were strongly correlated with forest type (Table 4). Cypress forest was an important factor in the distribution of two sensitive endemic orchids (*Bulbophyllum chitouense* and *Gastrochilus raraensis*). Rainfall seasonality (Pcv) and water deficiency (Pdef) were apparently the most contributing factors to cypress forest distribution. The climate change scenarios suggest increased precipitation variability in time and space, and future weakening of the NE monsoon (Lin *et al.*, 2010), which

accounts for a substantial proportion of Taiwan's annual rainfall, especially in the north-east. These factors are probably responsible for the projected general decline of the cypress forests and associated epiphytic species (Fig. 4b,c). October is the onset of the NE monsoon season; thus, species distributions correlating closely with October rainfall (P10) are projected to have high range turnover rates (high J') under future climate conditions (Table 4).

The sensitivity of species to global climate change is often related to differences in ecological properties (Broennimann *et al.*, 2006). Past studies suggested that generalists (i.e. species with wider niche breadths and hence larger range sizes on the environmental gradient) are expected to demonstrate broader tolerances to climate changes than specialists (Brown *et al.*, 1995; Benzing, 1998; Thuiller *et al.*, 2004; Broennimann *et al.*, 2006). In other words, the species with the more critical habitat demands are probably more sensitive to climate change and may thus be suitable indicator species. Our model results confirm that many sensitive (high J') epiphytes presently have

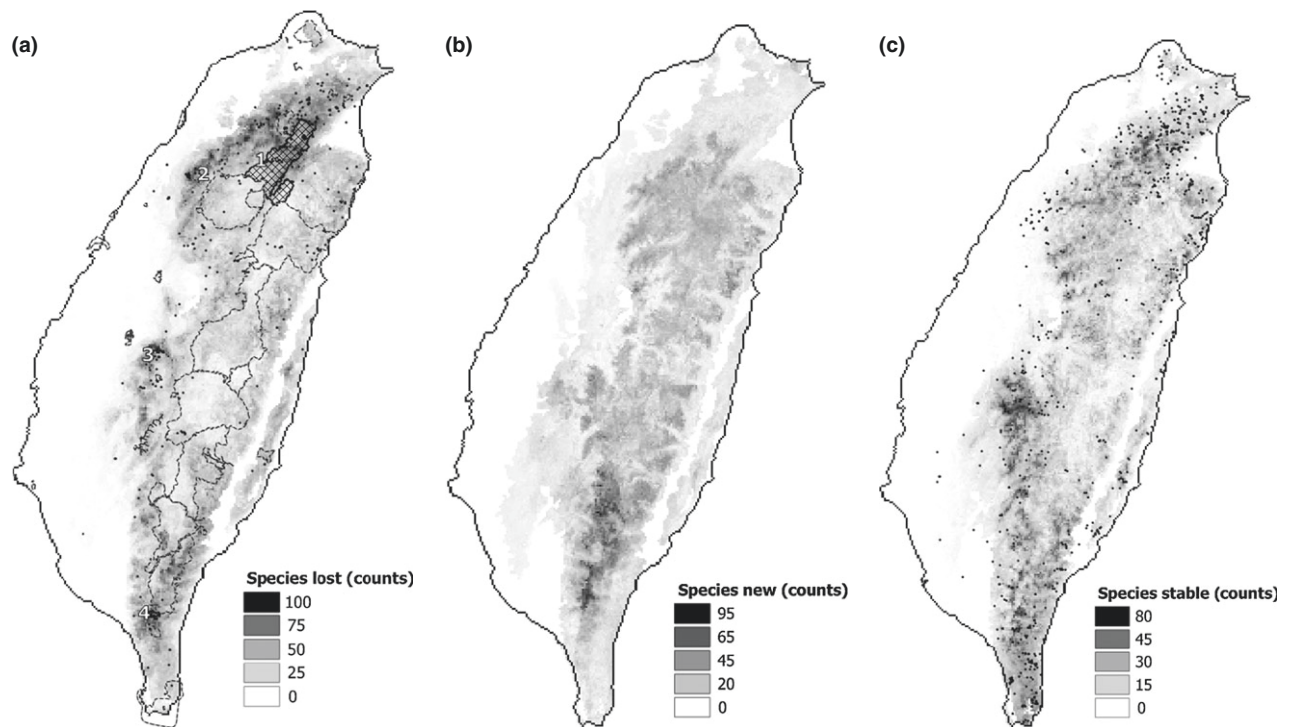


Figure 5 The modelled number of species lost (a), newly appearing (b) and remaining stable (c) under climate change conditions (values are the average of scenarios A2 and B2, IPCC, 2001). (a) Boundaries of present reserves in Taiwan and suggested monitoring sites for epiphytes: (1) Chi-Lan reserve, (2) Mt. Chia-Li, (3) Tai-Chi Canyon and (4) Jin-Shuei-Ying reserve. Occurrence of high J' and low J' species listed in Table 4 plotted as dots in a and c, respectively.

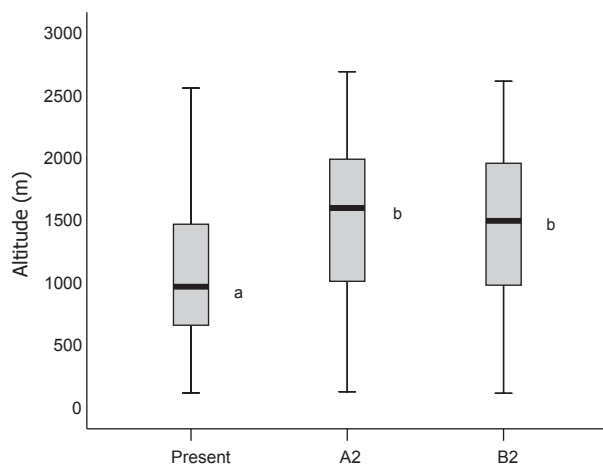


Figure 6 Box plot of median altitudes of 211 species distribution models for present climate conditions and two scenarios of climate change (A2 and B2; IPCC, 2001). The plots present median, lower quartile, upper quartile, maximum and minimum observations. Different letters indicate significant differences ($P < 0.01$).

restricted distributions (for example, *Bulbophyllum chitounense*, *Grammitis nuda*, *Flickingeria tairukounia* and *Saxiglossum angustissimum*), whereas insensitive species (low J') are widespread, and include several pantropical species (such as *Psilotum nudum* or *Hoya carnos*) (Table 4). Insensitive

epiphytes are usually lowland species, distributed in southern Taiwan, and less sensitive to temperature-related factors (Fig. 5c and Table 4). Conversely, our results indicated that temperature-related factors (T_{mean} and T_{sd}) had an important effect on the modelled distributions of sensitive epiphytes that grew in the mid-elevation/montane cloud forests (cypress, BLM and the lower altitude ranges of BLH; Fig. 5a and Table 4). Tropical montane cloud forests are unique among terrestrial ecosystems for their particular hydroregime (Still *et al.*, 1999) and typically occur in narrow altitude belts characterized by high endemism and abundant epiphytes (Foster, 2001). Accordingly, the epiphytes specialized in this ecotone are probably thermal or hydro-specialists. Among high J' species, *Mecodium badium* is relatively widespread, yet was projected to have a high range turnover rate under climate change conditions. This filmy fern occurs widely at mid-altitudes, and its occurrence correlates strongly with climate factors (i.e. annual mean temperature, T_{mean} ; temperature seasonality, T_{sd} ; and annual rainfall, P_{annual}) in the distribution model; thus, this species may be more susceptible to atmospheric drying in a warming climate.

In addition to climate variables, the models indicated that stable topographic or edaphic factors should be considered when modelling species distributions under climate change. Eastness was identified as an important predictor of *Abies* and BLL forest distributions (Table 3). During the NE monsoon, precipitation (in the form of snow at high altitudes) is greater

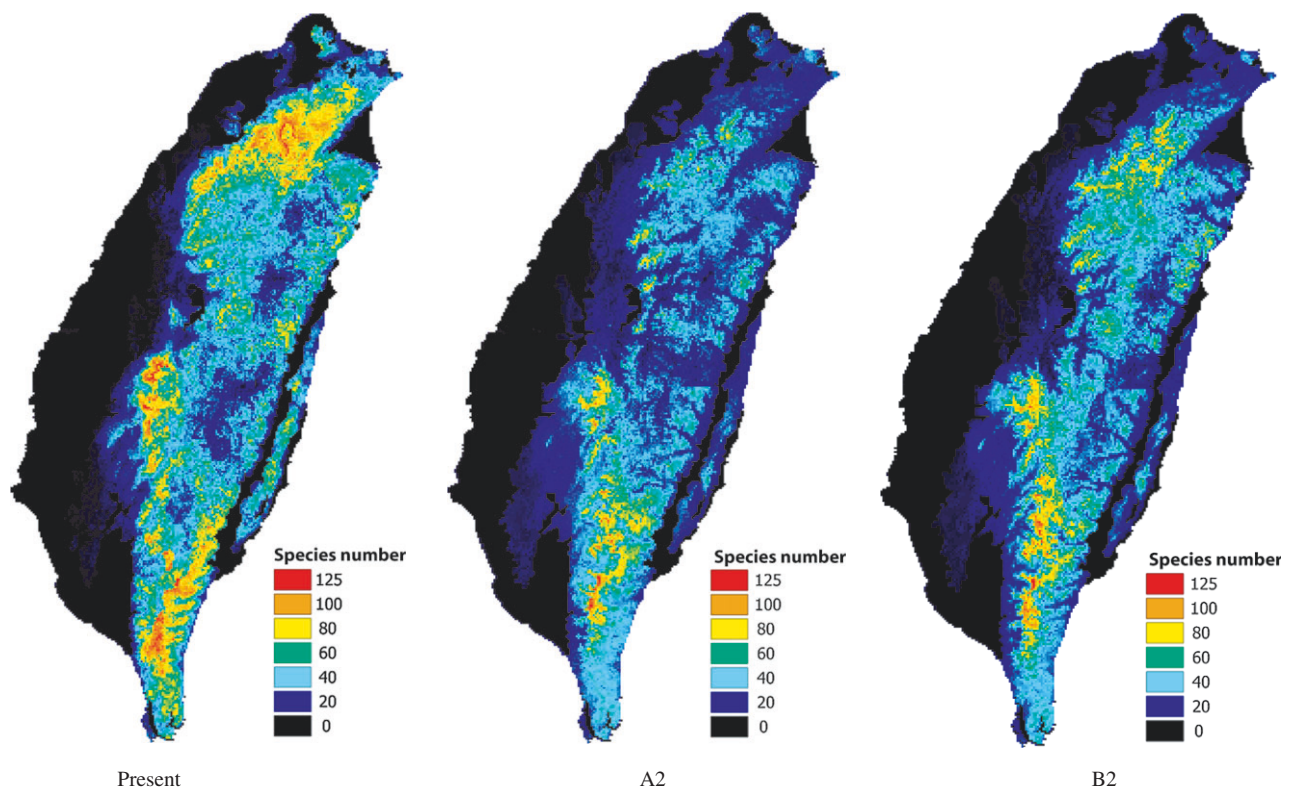


Figure 7 The species richness maps of epiphytes under present and climate change conditions (scenario A2, B2; IPCC, 2001).

on east-facing slopes than those of other aspects, exerting a significant influence on forest distributions. Austin & Van Niel (2011a) noted similar climate regime differences between north- and south-facing aspects in temperate latitudes. Soil category is a contributing factor to some epiphyte distribution models (see Appendix S1); terrestrial soil fertilities may affect nutrient availability in the canopy and hence epiphyte species compositions (Gentry & Dodson, 1987; Benner & Vitousek, 2007). SDMs using climate-only predictors often overestimate range reduction and fail to recognize potential landscape-defined refugia when assessing climate change impacts (Austin & Van Niel, 2011b). Our study confirms terrain-related factors must be incorporated when projecting species response to climate change at a local scale.

Migration velocity

Dispersal limitation and persistence induce a lag in modelled tree displacement, but forest transition may be unexpectedly rapid. Pollen records from the Andes indicated that during the last glacial maximum, the forest belt shifted by *c.* 1000 m and a massive replacement of ecotone forests occurred, implying a rapid altitudinal displacement of trees on tropical mountains (Hooghiemstra & van der Hammen, 2004; Groot *et al.*, 2010). Clark (1998) combined field data with a population growth model to prove that plant dispersal was compatible with the rapid spread shown by paleontological records. An investigation of 13 tree species in the French mountains found that the

low altitude limits of seedlings were on average 29 m higher than the adult parent trees, in response to the warming trend of the past two decades (Lenoir *et al.*, 2009). An analysis of 60,000 long-term forest inventory plots in the eastern USA suggested an approximately northward tree migration rate of 100 km per century (Woodall *et al.*, 2009); in the Alps, the altitudinal shift may have been as much as 340 m over the past 50 years; this speed correlated with the species wind dispersal (Parolo & Rossi, 2008). However, for some species and areas, establishment limits distributions more than dispersal (Alsos *et al.*, 2007). Most epiphytes produce highly mobile propagules capable of long-distance dispersal, yet recruitment of phorophyte-dependent epiphytes inevitably lags behind the trees, particularly of those epiphytes that depend on old-growth trees for establishment. Considering the biotic interaction between epiphytes and forest trees, we used forest habitat suitability as the predictor for epiphyte modelling. This approach had the additional advantage that the range boundary of forests with low habitat suitability for trees, hence, for epiphytes, was also assessed in the model.

Conservation implications

Our model indicated a considerable decline in the area extent of mid-elevation forests and associated epiphytic species under the two climate change scenarios. Many mid-altitude species fall outside current reserves because of their proximity to aboriginal villages (Fig. 5a). We recommend establishing two long-term

forest monitoring sites in the Chi-Lan and Da-Wu reserves (Fig. 4). Chi-Lan is dominated by primitive cypress and *Picea* forests and is an ideal site for monitoring forest type change. In south Taiwan, Da-Wu reserve lies in a region where coniferous forests are projected to be replaced by shadier broad-leaved forests, thus favouring an increase in shade-tolerant epiphytes. We anticipate that tree and epiphyte populations will change relatively rapidly at Da-Wu. Second, we recommend that three mid-altitude sites be established for epiphyte monitoring, at Mt. Chia-Li, Tai-Chi Canyon and Jin-Shuei-Ying reserves (Fig. 5a). Jin-Shuei-Ying reserve is characterized by a rich diversity of epiphytic ferns and is thus an ideal site for monitoring climate-sensitive species, including two locally rare epiphytic ferns (*Elaphoglossum luzonicum* and *Grammitis nuda*; Table 4). Mt. Chia-Li and Tai-Chi Canyon are near human settlements and currently lie outside conservation areas, but both areas are rich in epiphytic orchids and contain the majority of the local sensitive species (Table 4). Long-term plots in these locations can be used to investigate the effects of anthropogenic disturbance on sensitive epiphytes in a changing climate, thus evaluating the effectiveness of the present conservation reserves.

Global warming effects seem to be less pronounced in undisturbed forests; human disturbance may produce vacant niches for invasive species (Aptroot & van Herk, 2007). Thus, conserving old-growth forests may be crucial in supporting species to resist climate change (Ellis *et al.*, 2009). Our climate change models showed that midlands are likely to remain richer in epiphyte species than higher or lower altitudes (Fig. 5c); thus, present centres of species diversity will probably retain their importance into the future (Venter *et al.*, 2010). On a regional scale, a mountainous island such as Taiwan may act as a potential refuge during climate change; high mountains provide the space for species migration, as most likely occurred after the Quaternary glaciations (Hsu & Wolf, 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 The modelled epiphyte species and their predicted changes in median altitude and area.

Figure S1 The area under the curve values of species distribution models.

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BIOSKETCH

Rebecca Hsu is a researcher at Taiwan Forestry Research Institute and a Ph.D. student at UvA and Leiden University, studying the epiphyte communities in Taiwan, with general research interests in plant biogeography and ecophysiology (CV site: http://rebecca.ecogarden.tw/2006/03/cv_hsu_chiachun.html).

Author contributions: W.L.M.T., N.R. and R.C.-C.H. conceived the ideas. J.H.D.W., G.R.D., and G.O. involved in drafting manuscript and supervised the study. S.-H.L. provided future climate information. R.C.-C.H. collected and analysed the data and led the writing.

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