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氣候變遷下島嶼生態系植群組成的變化

The shift of vegetation composition under climate change in an island ecosystem

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摘要

受全球暖化的影響，許多物種可能無法適應目前棲地的環境改變因而導致當地族群滅絕或向更適合的環境遷移，因此預測族群的變動是目前生態學急迫關切的課題之一。許多研究著重在預測個別物種分布受氣候變遷的影響，但忽略了物種不同遷移程度也可能影響物種間的交互作用網絡。台灣擁有從高海拔到低海拔的環境條件，物種將根據自身的棲位在合適的環境梯度上分佈，因此適合我們了解環境氣候的差異對於植群分佈的影響。本研究模擬氣候變遷對植群兩個面相的影響：當地原生族群受環境改變威脅的程度，及計入外來遷徙族群的群落整體改變。結果顯示，從原生地物種受威脅程度來說，低海拔地區(海拔 1,000 公尺以下)是較受威脅的地方，然而就整體改動而言，中海拔地區(海拔 1,000～2,800 公尺)是改動最大的地方。而且，在高海拔地區(海拔 2,800 公尺以上)也須面臨一定程度的非生物逆境，以及部分中海拔物種上移所帶來的競爭。此兩種迥異結果源於大量低海拔物種相較於中海拔物種有更大規模的海拔垂直遷移，使低海拔原生物種消失程度較高，而中海拔植群將受到大量低海拔物種移入造成總體群落結構改變。物種共存網路分析證實此論點：由現有分布資料歸納出代表不同林相的植物群落，彼此間的分界在未來會變得更加模糊，尤其是低海拔與中海拔群落將有更多交疊。總結來說，雖然中海拔植群的未來分布受到非生物因子影響相對較小，但生物性因子可能使原生群落結構受到改變，限制當地原生種的生存空間。此外，極端天氣是必須被納入氣候變遷的討論中，從過去歷史氣候資料區的計算出的有較高頻的極端天氣事件的地區需要多加注意。

關鍵字：

氣候變遷、族群變遷、共存網絡、植群組成、極端天氣

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Abstract

Under global warming, many species might be unable to adapt to the environmental changes, leading to extinction or migration. Predicting community changes is therefore an urgent issue. However, many studies focused on predicting the effects of climate change on individual species, ignoring that different magnitudes of climate-change-driven migration among species might affect their potential interaction. Given the limited geographical but wide altitudinal range, the island Taiwan is a suitable location to study the effects of differential altitudinal shift of species facing climate change. In this study, we modeled the impact of climate change on vegetation community from two aspects: the decline of local species and the overall community change after accounting for foreign migrating species. In terms of local species, regions in low altitude (below 1,000 m above sea level [asl]) are highly threatened. For overall community change, on the other hand, middle-altitude (1,000 - 2,800 m asl) mountains across Taiwan, has the highest community change. However, species at high altitudes (above 2,800 m asl) also face high abiotic stress, as well as competition from the upward shift of some mid-altitude species. Such discrepancy might result from the differential altitudinal migration of species: comparing to high-elevation species, those originally reside in low elevation have higher upward altitudinal shift, resulting in large local species decline in lower elevation and more immigrants causing overall

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community change in middle-altitude regions. This was supported by species co-existence network analyses: in the future, the boundaries among distinct vegetation community modules identified by their current co-existence become more obscure, especially between the modules originating from middle- and low-altitudes. Therefore, although the future distribution of middle-altitude species seems less affected by the change of abiotic climatic factors, such biotic factor of community structure disruption might restrict the living space available to local middle-altitude species. Furthermore, extreme weather must be considered in the discussion of climate change, and regions with high frequency of extreme weather events from historical climate data require more attention.

Keyword:

Climate change, Community change, Network, Vegetation composition, Extreme weather

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Introduction

Due to anthropogenic climate change [1], recent reports indicated that the global temperature has increased by 1.0 degree Celsius than pre-industrial levels [2]. If the Earth maintains the present rate of warming, the temperature rise will reach 1.5 degree Celsius in 2030-2050. Moreover, the Earth's surface temperature in 2006-2015 is higher than the observed value of 1850-1900 by 0.87 degrees, indicating that the temperature has increased more rapidly in recent years [2]. The pattern of precipitation has also been changing. The massive increase in heat may cause more intense evaporation, resulting in longer droughts in some areas. Furthermore, the air moisture content will increase by 7% as temperature increases by 1 degree Celsius. Therefore, the intensity of precipitation from typhoon rain, convective rain, and topographic rain might increase due to the increase of moisture in the atmosphere, potentially causing more flooding. In general, dry regions may become drier in the future, and humid regions may become more humid [3]. Such a drastic change in temperature and precipitation may cause many organisms to shift to more suitable locations or even extinct if they cannot shift to appropriate environments [4, 5]. Moreover, each species has a different response in face of climate change, and such differences in the rates and magnitudes of distribution shift may cause new co-existence relationships. These novel interactions may change

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ecosystem composition and function, potentially accelerating the collapse of the ecosystem [5-7].

The geographic distribution of plants is strongly influenced by climatic factors [8]. Drastic climate change therefore may have a serious impact on vegetation. In particular, montane vegetation is sensitive to climate change [9-12], since the steep topography triggers more noticeable variation. These alterations have been confirmed in several studies through repeated surveys at the same locations. By comparing the records of past and current European vegetation, researchers showed that species have moved to higher altitudes, and at the same time the richness of species in the highest altitudes has increased [13-20]. Similarly, some studies show that the richness of high mountain vegetation is gradually declining through surveys of long-term in high mountains [18, 21]. Similarly, a study comparing the current Andean vegetation composition with that from 1802 has found that the whole vegetation has shifted to higher elevations [22]. These results indicate that climate change has strongly re-shaped the vegetation and demonstrate that climate is the dominant factor controlling the difference in altitude distribution of vegetation.

In recent years, with the improvement in the accuracy of global climate datasets [23-25], there has been an increase in the number of studies modelling the species distribution [26]. These studies have unequivocally predicted that vegetation may face adaptation challenges as the changing pattern of precipitation and increasing temperature at the end of the 21st century, in particular, the alpine community in the cold and temperate zone may be the most vulnerable vegetation type under climate change [27-29]. Ecologists have also predicted the vegetation in 22 protected areas in North America and found that the original alpine communities at the highest elevations would all disappear under the most severe scenario [30]. Moreover, most high-altitude species in the tropical mountains of northeastern Australia are also predicted to lose suitable habitat, indicating that species inhabiting tropical mountaintops are equally vulnerable to threats caused by climate change [31].

While many such studies have been performed, most of these studies were conducted at high-latitudes regions, and their main conclusions focused on the changes and challenges of species at high altitudes or mountain tops (highest elevations) [13-20]. Although it has been reported that tropical vegetation is as strongly affected by climate change as high latitude areas, studies on the fate of vegetation in low altitude or low latitude are still scarce [32-37]. Therefore, in this study, we not only focused on the change of species and vegetation at higher altitudes but also described the change of vegetation along the altitudinal gradient sub-tropical mountains. With such efforts, one

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may be able to investigate the potentially distinct types of stresses that vegetation communities from different altitudes may face.

Jump *et al*. (2009) mentioned that, on average, an altitude increase of 167 meters can decrease the temperature by one degree Celsius, but the same temperature shift requires 145 km of latitudinal change [38]. Taiwan is a small island with an altitudinal difference of about 4,000 meters in an area of 36,000 square kilometers, and in the mountainous regions, such temperature shift could be achieved in less than 2 km of geographical distance. Therefore, Taiwan is an ideal site to more realistically model Furthermore, the diverse climate has led to the growth of highly diverse vegetation ecosystems including high-mountain coniferous woodlands and forests, subtropical mountain zonal forests, tropical mountain zonal forests, tropical mountain azonal forests, subtropical mountain azonal woodlands and forests, and seashore woodlands and mangroves [39], thereby allowing us to simultaneously evaluate the changes of vegetation in different altitudinal zones.

In Taiwan, Su *et al*. (1984) defined the physiognomy of forests into six different vegetation zones according to climate, altitude, and dominant tree species [40]. He also described the relationship between geo-climatic zones and vegetation distribution. Subsequently, from 2003 to 2009, the government of Taiwan conducted an island-wide vegetation inventory to investigate the composition and number of species based on 3,000 sample plots. Therefore, Li *et al*. (2013) used these detailed data to further subdivide the forest into 21 vegetation types, including zonal forest azonal forest types, providing formal definitions and describing their habitat characteristics, species composition and geographic distribution.

With the presence of data for each species, the researcher could further predict vegetation changes in the future through vegetation and climate information. Previous studies have modelled the future vegetational distribution of Taiwan [37, 41], both using the species distribution model (SDM) [42], a common tool for predicting species distribution. The results are also consistent with most of the studies mentioned above. They both mentioned that most of the vegetation might have an upward shift in altitude distribution, and the distribution of area in high-altitude vegetation may shrink in the future. This shift may cause overall community restructuring, potentially changing the interaction relationships among species, increasing the biotic stress on local vegetation, such as competition and compression niche, leading to another type of adversity. However, both studies used vegetation type as units for distribution modelling instead of species, potentially ignoring that each species has a different magnitude of altitudinal shift under climate change. To address this, here we establish a large number of species-

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level SDM and compare species distributions between current and future conditions to investigate community change.

This study aims to comprehensively analyze the different challenges that tropical mountain vegetation might encounter under climate change. We predicted alterations in vegetation composition through the multiple SDM. We also consider that each species may have different magnitudes of altitudinal shift, resulting in the restructuring of the overall community.

Materials and Methods

Study area

Taiwan is a subtropical continental island in East Asia with an area of about 36,000 km^2. More than 70% of the area contains mountains and hills with the highest peak at 3,952 m above sea level (asl) (Supplementary Figure 1). Due to the highly variable topography, Taiwan contains many climate zones from low to high elevation. Therefore, species with different niches distribute along the altitudinal gradient, resulting in a highly diverse ecosystem, including, high-mountain coniferous woodlands and forests, subtropical mountain zonal forests, tropical mountain zonal forests, tropical mountain azonal forests, subtropical mountain azonal woodlands and forests, and seashore woodlands and mangroves [39]. In addition to the altitudinal difference, the northern and southern parts of Taiwan belong to different climatic zones due to seasonal monsoon. In the north, the northeast monsoon brings cold weather and plentiful precipitation in winter, resulting in a perennial humid climate in the northern area. In contrast to the northern areas, the climate of the southern area is marked by distinct dry and wet seasons.

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Vegetation data

The First National Vegetation Inventory in Taiwan [43], which established more than 3000 permanent plots (20 × 20 m) throughout Taiwan's natural forest (no open ground) (Supplementary Figure 1). The survey was completed in 2008, and it recorded more than 65% of native vascular plant species. In this investigation, 90% of plots contain four or five sub-plots (10 × 10 m), while the remaining plots contain more than five sub-plots. For this study, we selected plots with the four or five sub-plots and averaged counting records of all subplots within the same plot. In summary, this dataset contains 3080 plots with 2569 species recorded at least once. Based on subsequent analysis needs, we separated Taiwan into four regions (East, West, South, North) by major mountain ridgeline and climate zone, where the northern region covers area facing northeastern winter monsoon, the southern region covers regions facing southwestern summer monsoon, and the remaining region was separated into east and west mainly based on the highest ridgeline of the central mountain range [44-46]. Furthermore, we removed 20 plots in Shoushan due to the geographical isolation from other plots and filtered out species that appeared in less than five plots or more than 95% of plots in a region. For analysis in each region separately, we used the above filtering criteria, and for the analyses involving whole Taiwan, species retained in each

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region were used together. Finally, we used 552 woody species and 447 herbaceous plants for follow-up analyses.

Climate data

We used climate data (1960-2009) of 5 x 5 km grid from the Taiwan Climate Change Projection Information And Adaptation Knowledge Platform (TCCIP; http://tccip.ncdr.nat.gov.tw/NCDR/main/usage.aspx). In this dataset, the climate of each grid was interpolated by summarizing data from more than one thousand weather stations, providing better local climate estimates than global databases. This dataset recorded many climate variables, including monthly mean temperature (Tmean01 to Tmean12), monthly maximum temperature (Tmax01 to Tmax12), monthly minimum temperature (Tmin01 to Tmin12), and monthly precipitation (precip01 to precip12). For future climate, TCCIP contains 49 different general circulation models (GCMs) with four different magnitudes of warming scenarios (RCP2.6, RCP4.5, RCP6.0, and RCP8.5) and three periods (2016-2035, 2046-2065, 2081-2100). Furthermore, to acquire more precise and continuous climate values across finer geographic scale, we used the climate regression method [47], which incorporates local altitudinal information (100 x 100 m)

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and spatial smoothing function. All data (100 x 100 m) were then converted to 1 x 1 km grid data by R package raster [48]. Finally, nineteen bioclimatic variables were calculated based on TCCIP data set and R function biovars in dismo packages [49] (Table 1). These 19 bioclimate variables (BIO1-BIO19) include current and future conditions, one GCM (HadGEM2-AO) which was recommended for Taiwan [50] two warming scenarios (RCP4.5, RCP8.5) and three different periods (2016-2035, 2046-2065, 2081-2100). In addition, to avoid autocorrelation, we conducted the pairwise correlation analysis between all variables (BIO1-BIO19) to eliminate highly correlated (Pearson's $r > 0.75$) variables (Supplementary Figure 2). In summary, we used eight variables including Bio1: Annual Mean Temperature, BIO2: Mean Diurnal Range, BIO4: Temperature Seasonality, BIO7: Temperature Annual Range, BIO12: Annual Precipitation, BIO15: Precipitation Seasonality, BIO16: Precipitation of Wettest Quarter, and BIO19: Precipitation of Coldest Quarter (Supplementary Figure 3, 4).

Species distribution modelling (SDM)

Species distribution modelling is a popular tool in ecology [42], and it has widely been used on predicting species distribution at different climate scenarios. Before we

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modeled the species distribution, we needed to prepare three required data, including the location of presence and absence, and environment variables. Here we used MAXENT [51], a population SDM application, and the ensemble method [52], which calculated the weighted average of eight different algorithms, including generalized linear mode [53], generalized additive model [54], support vector machine [55], Flexible Discriminant Analysis [56], multivariate adaptive regression spline [57], Random Forest [58], boosted regression trees [59], and Maxent [51]. First, we did the SDMs with 552 woody species and 447 herbaceous species by their presence records and randomly selected 1000 absence points to be background values. The models were evaluated with five runs of 5-fold cross-validation, and model accuracy was evaluated by True Skill Statistic [60, 61], recommended to be above 0.4, and AUC (The area under the ROC curve), recommended to be above 0.7 [62]. Models with these values lower than recommended were removed from the community change analyses. Finally, SDM was extrapolated to GCM and two warming scenarios on three different periods as mentioned above.

As part of the goal of this study, we estimated the altitudinal distribution of each species in current and various future climatic conditions. Since SDM reported a continuous value of suitability ranging from 0 to 1, we first identified the threshold of

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suitability value for each species to be called presence or absence in each location. Sensitivity-specificity sum maximization approach, calculated by the maximized sum of sensitivity (the proportion of real presence predicted to the presence in the model) and specificity (the proportion of real absence predicted to absence in the model), was recommended to be the threshold that transferred the probability distribution to presence distribution for each species [63-65]. Based on the predicted current and future presence locations of each species, we obtained their altitudinal distribution for further analyses. The predicted presence allowed us to calculate the number of species at each geographical grid to identify current and future biodiversity composition and the median altitude of each species' distribution. If there is no suitable area in the future for a species, it was treated as extinct.

To ensure that SDM using MAXENT algorithm was feasible for subsequent analyses, we calculated the correlation between the suitability values estimated by MAXENT and the ensemble method. From the predicted suitability map of each species, we randomly selected 10% of the grids and calculated the correlation of suitability values between MAXENT and ensemble. This was done for both the current and future SDM results. All SDM runs were produced using the package sdm in R [66, 67], and the conversion between numeric suitability and presence/absence data for each species in each grid was determined by a threshold value, determined using the sensitivity-specificity sum maximization method in the “evaluate” functions.

Community change in the future

Based on SDM, we modeled the impact of climate change on vegetation community from two aspects: the decline of local species and the overall community change after accounting for foreign migrant species. In each geographical grid, the “local species” was defined based on the threshold value above. For local decline, for each resident species we first subtracted SDM current suitability from future suitability. Since only the negative value represents decline, all positive values were substituted by zero, and absolute value was then taken for the remaining negative value. In each geographic grid, such values were averaged across all resident species. For overall community change considering the alternation involving all species, we simply averaged the absolute suitability change across time of all species without any modification, thus incorporating both the decline of local species and the increased suitability of foreign species.

In addition to the SDM-based methods, for overall community change we further employed a new algorithm, ‘’Gradient Forest’’ [68]. Such method used continuous

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abundance data instead of categorical presence and absence as in most SDMs to investigate species-environment relationship. The method was later adopted in population genetics, using the association between allele frequency and environments to identify genomic locations for environmental adaptation [69]. Fitzpatrick and Keller (2015) further extended the method to model future “genetic offset”, identifying geographic regions where local alleles are unfit to future climate change. Here we apply this method back to community ecology to model the “community offset”. However, the original investigation data has two issues. First, woody species were recorded as individual counts and herbaceous species as the percentage area covered within a sub-plot. Second, the distribution of survey plots does not appear random across Taiwan mountainous regions. We therefore did not directly use the original survey data, but instead used the aforementioned SDM results, using suitability values as numerical input into gradient forest. While standard SDM compare the future and current species distribution to estimate the impact of climate change, gradient forest first identified the environmental ranges that best distinguish the abundance records and compared current and future climates across the map to identify geographic regions with environmental changes in the sensitive ranges. Since such offset measure is based on climate rather than species distribution, one should focus the analyses only in the regions where a

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species naturally distributes. Given that northern and southern Taiwan contain unique vegetation zones and species not found elsewhere in Taiwan [36], this analysis was performed separately for the four regions of Taiwan (East, West, South, North). We randomly selected 10% grids in each region and extracted SDM suitability and environmental values for gradient forest and community offset analyses.

In addition, to understand whether different magnitudes of community change in these four regions were related to their magnitudes of environmental change, we calculated the absolute differences between current and future bioclimatic variables and visualized those on maps.

Community change of specialist and generalist species

Specialist species have a narrower niche space than generalists [70-75]. Here we aim to investigate whether specialists are more threatened than generalists in the future and whether different magnitudes of future local decline in Taiwan are associated with the abundance of restricted-distribution species. We first established the niche space of each species to define the specialist and generalist of this study. From the presence data predicted by SDM (converted from the numeric suitability data using a threshold, above), we randomly selected 50 presence 1 x 1 km grids and extracted the environmental data from these grids (re-sampling if the species has less than 50 presence grids). From the resulting 50 x 8 matrix of each species (50 presence grids and eight standardized bioclimatic variables), we built a covariance matrix among bioclimatic variables and calculated the sum (trace) and the multiplication of the eigenvalues (determinant). Since trace and determinant are measures of the space occupied by the covariance matrix, their values therefore represent the “niche breadth” of a species in the multidimensional niche space defined by the eight bioclimatic variables. Higher value means the species distributes across wide environmental ranges in Taiwan. Therefore, we defined the top 100 species with largest niche breadth as the generalist and 100 species from the other extreme as the specialist. Local decline, based on SDM, upon climate change was calculated separately for the two groups.

Identifying and characterizing plant co-existence modules

We found that those who originally reside in low or middle elevation have higher upward altitudinal shift compared with the high-elevation species. To investigate whether such differential altitudinal shift affects community structure, we first used current species distribution to identify distinct plant co-existence modules (a community) and simulated their future distribution.

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We established the co-existence network and identified plant community clusters in four regions by the weighted gene co-expression network analysis (WGCNA) [76]. In molecular biology, WGCNA was used to identify groups of genes that are highly co-expressed. We applied the same concept to identify groups of species that are highly co-existing. Here, each module is similar to a community. We used the aforementioned data for gradient forest analysis to conduct the network analysis separately for four regions (East, West, South, North). In short, the WGCNA method used pairwise correlation between species suitability records to construct a topology overlap matrix, and hierarchical clustering with the average method was used to produce a clustering tree of species. The best number of modules and species assignment into groups was determined by the dynamic tree cut algorithm. Species not having high-enough correlation with any module remained un-assigned.

We compared these WGCNA results with previous studies on the classification of Taiwan vegetation [39]. First, we calculated the average suitability of each module in its distribution region from the SDM results of species in each module. We then compared these results with previous manually curated and defined vegetation membership of 3824 plots: by taking the geographic coordinates of these 3824 plots, we extracted the predicted suitability of these points in each module. Using the criteria of Lin *et al.*

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(2020), each plot is assigned to the most probable module. In this way, we can compare our modules with the vegetation classification based on dominant woody plants.

The phylogenetic structure of co-existing modules

Here we tested whether the composition of species in the same module is random with respect to their phylogenetic relationship, or whether they are concentrated in specific phylogenetic groups (but these groups are not necessarily close to each other). Specifically, for each species, we estimated the phylogenetic distance to the most closely related species within the same module. If species of the same module tend to concentrate in some phylogenetic groups, in the same module a species would tend to find its closest species within the same clade and hence smaller phylogenetic distance than random expectation. The phylogenetic tree was obtained from Phylomatic 3.0 [77], and pairwise genetic distance was estimated with function ‘’cophenetic.phylo’’ in R package ‘’ape’’ [78]. The analyses were done separately for each region of Taiwan, where the pairwise genetic distance matrix was pruned to retain only species in that region. In each module we estimated the mean of species’ phylogenetic distance to the closest species in the same module, and statistical significance was tested with 1000

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permutations, where we randomized the label denoting species membership to modules, generating the null models that modules were randomly assigned.

To investigate whether different plant communities were enriched for different taxa, we tested whether each taxon was over-represented in species number in a specific module, compared with all other modules in the same region of Taiwan. We separated all species in a region into four groups: *a* – species in this module and this family, *b* – species in this module but not this family, *c* – species not in this module and in this family, *d* – species not in this module nor this family. The fold enrichment (odds ratio) was calculated as (*a*/*b*)/(*c*/*d*), and statistical significance was estimated with Fisher's exact test.

The alteration of community structure

To visualize whether climate change alters the association among plant communities defined by current co-existence relationships, we performed dimension reduction on the spatial relationship of species' current and future suitability records. Specifically, for the aforementioned 10% random locations within each region of Taiwan, we extracted the current and future suitability of all species. For this table of suitability where rows are current and future species and columns are locations, we

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applied the un-supervised Uniform Manifold Approximation and Projection (UMAP) [79] algorithm to visualize the relationship among all current and future species based on their relationship of co-existence across the map.

Extreme weather

The climate change was not only carried with gradual changes but also caused immediate harm on vegetation community. Besides, the extreme weather has been discussed more because of the high frequency of extreme weather events in recent years [80]. Therefore, we counted the frequency of extreme weather events by the definition of previous study [81] including Heat (Extreme high temperature), Cold (Extreme low temperature), Extreme rainfall and Extreme drought. In this analysis, we used historical climate (1960-2018) of 5 x 5 km grid data from the TCCIP recorded with three different variables, including the daily maximum temperature, daily minimum temperature, and daily rainfall.

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Results

Species distribution modelling (SDM)

We performed species distribution modelling (SDM) for 999 species. The area under the ROC curve (AUC) value of most models were greater than 0.7 (Supplementary Figure 5), and the average True Skill Statistic (TSS) were above 0.6 (Supplementary Figure 6), showing that the prediction model for most species performed well. However, there are 18 species with AUC values less than 0.7 and 8 species with TSS less than 0.4. These species were excluded from subsequent analyses.

The results of important bioclimatic variables show that the most important bioclimatic variable for 70% of the species was BIO1, indicating that temperature was the main factor affecting the distribution. The second and third most important bioclimatic variables depend on the response of each species to the environment, with a certain proportion of either temperature (BIO1, BIO2, BIO4, BIO7) or precipitation (BIO12, BIO15, BIO16, BIO19) bioclimatic variables. (Table 2) In addition, similar results can be seen in the gradient forest algorithm. (Table 3)

We compared results from MAXENT with the ensemble method [52], which calculated the weighted average of eight different algorithms (see Materials and

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Methods). The correlation coefficients of predicted suitability across randomly sampled locations in Taiwan between the two algorithms are higher than 0.75 for 998 species in the current condition and 813 species in the future (Supplementary Figure 7). Since the two methods gave highly similar results, for some later analyses we mainly used results from MAXENT.

Patterns of local decline and overall community change across Taiwan

We first observed the community change through biodiversity composition. We found the vegetation composition and abundance distribution may change under future scenarios. The high richness area in current mainly concentrates at about 1500 m asl, while these areas under future scenarios may move to a higher altitude to about 2000 m asl (Figure 1). In addition, according to the vegetation composition changing in different altitudes, we also could find that the number of species in the area around 2000 m asl did not change. However, the results do not indicate that the community has not changed, since it is possible that the loss of local species might be replenished by the same number of immigrating species from other areas.

As a result, we modelled plant community alteration facing future climate change from two aspects: the decline of local species and the overall community change, incorporating local decline and effects of immigration. In terms of the decline of local species, we focused on whether local species will be able to adapt to climate change in the future if they have no shift. Therefore, we only consider whether they could adapt to future conditions at the original location. Based on the results of local decline and the altitudinal information, we roughly divided the pattern of local decline into three different altitude zones and combined the altitude distribution of vegetation from the previous study to illustrate this result [36, 39]. We can see that the local decline in altitudes below 1000 m asl (defined as low altitude in this study) is larger than in other regions, and indicating the vegetation in low altitude regions including *Drypetes-Helicia* forest, *Dysoxylum-Machilus* forest, *Illicium-Cyclobalanopsis* winter monsoon forest, *Phoebe-Machilus* forest, *Ficus-Machilus* forest, and *Pyrenaria-Machilus* winter monsoon forest may face highest local decline (Figure 2). The local decline in altitudes between 1000 and 2800 meters asl (defined as middle altitude in this study) is lower than in other regions, and this shows the vegetation in middle altitude including *Chamaecyparis* cloud forest, *Quercus* cloud forest, *Machilus-Castanopsis* forest may confront less abiotic stress (temperature or precipitation changing). However, we found that the two vegetation zones, *Fagus* cloud forest, and *Pasania-Elaeocarpus* cloud forest, have higher local decline than other cloud forests. Therefore, we checked the

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altitudinal distribution of this two vegetation and found they distribute at a lower altitude (median below 1500 m asl). Finally, the local decline in altitudes higher than 2800 m asl (defined high altitude in this study) is higher than the middle altitude. This result shows that both *Juniperus* woodland and scrub and *Abies-Tsuga* forest may face environmental adaptation stress to a certain extent. In summary, the species in mid-altitude might face relatively less environmental stress, followed by species in high-altitude, while the species in low-altitude may face the strongest stress. However, it is worth noting that the northern half of Taiwan had a higher local decline in middle altitude areas than the south half (Figure 2). This result was supported by the climate change in the northern region. The variables about precipitation (BIO12: Annual Precipitation, BIO15: Precipitation Seasonality, BIO19: Precipitation of Coldest Quarter) have more drastic change in the northern than the southern parts of Taiwan (Supplementary Figure 8).

Why does such a pattern exist? Previous studies suggested species with narrower niche space might be more vulnerable to climate change [82-85]. Therefore, we asked whether different magnitudes of future local decline in Taiwan are associated with the distribution of species with narrower niche space (niche specialists). We calculated the trace value to define the niche space of each species and selected the top 100 species

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with the highest value as generalist (max 100) and the bottom 100 species with low value as a specialist group (min 100). In terms of the number of species, both types of species have similar patterns (Figure 3A), reflecting the pattern of overall species richness across Taiwan (Figure 1).

On the other hand, in terms of the proportion of specialists and generalists among local species in each geographical grid, specialists distributed at lower and higher altitudes, while generalists distributed at lower and middle altitudes (Figure 3B). While this distribution suggests the patterns of all-species local decline across Taiwan might be driven by the uneven distribution of niche specialist, the predicted local decline patterns of specialists and generalists resemble each other, and both have very similar pattern with that obtained from all species combined (Figure 3C). Therefore, the results suggest the uneven distribution of specialists and generalists may not be the main cause of higher local decline at low and high altitudes.

In community change, we have the other viewpoint. In terms of overall change, it considered the alternation involving all species, where we incorporated both the decline of local species and the increased suitability of foreign species. All three methods (MAXENT, ensemble, gradient forest) have the consistent results that that middle altitude has the highest overall change, followed by high-altitude and low-altitude

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regions (Figure 2). This indicates that the greatest variation in the vegetation community occurred at mid-altitude. It means if there is a high overall change, they might have some issues with local communities not adapting in the future, face massive species shifts from other areas (including from other elevation ranges) or both.

Mismatch between local decline and overall community change caused by differential altitudinal shifts

While focusing on the effects of climate change on species suitability, most studies emphasized the fate of high-elevation species [21, 85-87]. However, here we found a mismatch between local decline and overall community change, each having the most severe outcomes at different altitudinal ranges. Since local decline and overall change differ by the factor of immigrant species, we further investigated whether differential altitudinal shift results in such patterns. Therefore, we estimated the altitude distribution of each species by SDM (MAXENT) and calculated the difference between the elevation distribution in present and future. We can see that species distributed under 1500 m asl have a high upward shift (Figure 4A). In contrast, species in the 1500-2800 m asl altitude range have a relatively lower shift. In addition, it is worth noting that the upward shift of species in high altitudes (higher than 2800 m asl) was also about 400 m.

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In summary, we found that different species have different magnitudes of altitude shift due to climate change, and this variation is highly associated with the original altitude of the species.

Although the highest peak of Taiwan is close to 4,000 m asl, the geographic area in high elevation is limited (area higher than 3200 m asl consists of only 0.35 percent of Taiwan). Therefore, is our prediction that low-elevation species have highest altitudinal shift merely an artefact of the landscape of Taiwan, where species originating from mid- or high-elevation regions have limited altitudinal space to climb up to? To test this, we investigated whether the upper limits of species' future altitudinal distributions reach the altitudinal limits of Taiwan. From the results, we can see that the upper 90% percentile of most of the species' distribution range do not reach the limitation of geography in Taiwan (Supplementary Figure 14), especially for the mid-altitude species, whose upper range seldom reach 3,000 m asl. This indicates our prediction that low altitude species have a higher upward shift than species in middle-altitude is not an artefact of Taiwan's topography.

However, due to geographical constraints, high-altitude species might not be able to shift to higher altitudes, and it might lead to extinction. Indeed, the result shows that high-altitude species have a high extinction risk (Figure 4B). Therefore, while the

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surviving high-altitude species have relatively low upward shift compared to species from other altitudinal ranges, we do see higher extinction rate among high-elevation species (Figure 4B), suggesting the magnitudes of upward shift for those extinct species might exceed the geographic upper limit of Taiwan. Indeed, for the surviving high-elevation species, their future altitudinal range are close to the geographic upper limit (Supplementary Figure 14).

In summary, while the middle-altitude species might face less stress from abiotic factors than low-altitude species do, resulting in less local decline and less need for an upward altitudinal shift, biotic stress from large amounts of immigrant species from a lower elevation might be an important impact. Such differential altitudinal shifts among species might disrupt the boundaries among once distinct co-occurring species groups, resulting in the restructuring of vegetation communities or even competition of habitats.

The properties of species-co-existence network

Before moving on to the restructuring of vegetation communities, we needed to understand the species co-existence groups in Taiwan. To identify these groups, we applied the weighted gene co-expression network analysis (WGCNA) [76, 88] to identify groups of highly co-existing species. Here, each identified module is similar to a vegetation community. From the results of WGCNA, each of the four regions (east, west, south, north) of Taiwan was divided into five modules. From the mean MAXENT suitability of species within the same module (Supplementary Figure 15A-E) and their altitudinal distributions (Supplementary Figure 16), we found that the distribution of modules is mainly affected by altitude, so we defined these modules from high to low altitude as module one to module five within each region. However, although the southern and northern regions were divided into five groups by WGCNA, module four and five were quite similar in their geographical and altitudinal distribution (Supplementary Figure 17). We therefore merged these two groups into module four for subsequent analyses.

In addition, we compared our modules with the expert-curated vegetation classification of 3824 survey plots from previous studies [36, 39] The result shows that our co-existence modules have different vegetation composition (Supplementary Figure 18). It is worth noting that modules three and four in the southern and northern regions might have been classified in the same group in the previous classification since they were mainly classified based on dominant woody plants. However, in our analysis, we covered more species information (including herbaceous seed plants and ferns), which contributes to the separation of these modules.

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To understand the properties of species composition of these modules, we investigated their phylogenetic composition for species within the same module and tested whether they distribute randomly across the phylogenetic tree or concentrate within specific groups. The result shows that there are seven modules in which the mean of species' phylogenetic distance to the closest species in the same module is significantly closer（p-value ＜ 0.05）than the random expectation (Table 4). Consistently, we found specific taxa are enriched in each module (Table 5). For example, most of the modules in high altitude were enriched for Gentianaceae, Pinaceae, and Poaceae. Mid-altitude modules are mostly enriched for Ericaceae and Symplocaceae, and low-altitude modules are for Euphorbiaceae, Fabaceae, Moraceae, and Rubiaceae. Eastern Taiwan

Eastern Taiwan has more modules with such property than other regions. From the phylogenetic tree of all species in eastern Taiwan (Figure 5), we can see that the highest altitude species were concentrated in gymnosperms, monocotyledons, and Asterids, and the lowest altitude module was concentrated in Rosids.

Finally, according to the elevation distribution and families enriched, we found that the species composition of the two highest modules (module one, module two) in the southern and northern regions are similar to two middle-high modules (module two,

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module three) in the eastern and western regions, indicating that the highest-elevation locations in the northern and southern regions are lower than the eastern and western regions (Supplementary Figure 16,17).

The alteration of community structure

From the above results (community change, species shift), we learnt that each species may have a different response to climate change in the future, particularly in terms of altitudinal shifts. Different magnitudes of climate-change-driven migration among species might cause the change of vegetation community. The boundaries between communities might be more obscure, and species in the original community would face competition from foreign species, eventually changing the interactions of species in the whole community. Here we used the current and future (Rcp8.5 in 2081-2100) distribution data to construct the co-existence relationship among species across time and climate change scenarios and visualized them using Uniform Manifold Approximation and Projection (UMAP). Since the species co-existence modules were constructed from their current distribution, in current conditions the boundaries between these modules are quite clear and there is no overlapping between the modules (Figure 6, first column). However, the modules may become obscure in the future (Figure 6,

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second and third columns). Moreover, we found a large number of species in the low-altitude module moving to the niche space of middle altitude module. In contrast, although the species in middle-altitude also has a certain degree of shifting to the space of high-altitude module, the magnitude is relatively less (Figure 6 third column). These results of the restructuring of the vegetation community also correspond to the above-mentioned results that low-altitude species have stronger upward shift than mid-altitude species (Figure 4A). Interestingly, not all regions of Taiwan would have similarly serious response, as the eastern and southern regions have relatively less change than the northern and western regions under the moderate warming scenario (Rcp4.5) (Figure 6 second column). From the combination of all time periods (2016-2035, 2046-2065, 2081-2100) and scenarios (Rcp4.5, Rcp8.5), we found that the restructuring of the vegetation may not be so drastic as Rcp8.5 in 2081-2100 under a lower warming scenario (Rcp4.5) before 2065 (Supplementary Figure 19, and 20).

Extreme weather

However, in addition to resulting in shifts of overall temperature or precipitation, climate change also includes extreme weather. Therefore, according to a recent study Dodd *et al.* (2021), we calculated the frequency of four different extreme weather events (extreme high temperature, extreme low temperature, extreme rainfall, and extreme drought) by the data from the past to the present 1960-2018. The highest frequency of extremely high temperature occurred in the high northern mountains, high southern mountains, and northeastern Taiwan, which are also the areas with the highest overall change or local decline (Figure 7). On the other hand, extremely low temperatures occurred in the central high mountains and eastern Taiwan. (Figure 7), but the frequency is declining in recent years (Supplementary Figure 21).

In contrast, extreme rainfall and drought occurred in the southwestern region, and the frequency of events in the southern region seems to be increasing (Supplementary Figure 21). Therefore, these areas with a high frequency of extreme weather events should be of high sensitivity.

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Discussion

In this study, we utilized interdisciplinary approaches to ecological studies and compared whether the results differ from previous works. On the topic of the restructuring of vegetation community under climate change, we investigated the changes in vegetation from two aspects and showed the vegetation community in three altitude zones (low, middle, and high) may encounter distinct fates. Moreover, each species' distinct response upon climatic change might cause the boundary between communities to become blurred and partially overlapped. Besides the warming changes, the threat of extreme weather should not be underestimated.

Novel approaches to investigate species' fate

In this study, we modeled the impact of climate change on vegetation community from two aspects: the decline of local species and the overall community change after accounting for foreign migrating species. In overall change, besides simply averaging the absolute suitability change of all species based on the species distribution model (SDM), we tried the new algorithm, gradient forest, in community change. This method has the advantage of using abundance data to directly calculate the relationship with environmental variables, presenting the species-environment relationship in the most original state. Later, Fitzpatrick and Keller (2015) extended the method to population genetics, simulating future "genetic offset" to estimate the mismatch between locally adaptive alleles and future climates. We applied this concept to vegetation ecology and named it “community offset”. However, we know that all species in a geographic region may be unsuitable or suitable for future climate. Here, the concept of community offset is equivalent to the overall change calculated by SDM-based methods.

Both gradient forest and SDM-based methods show similar results of high overall change in mid-altitude zones. In our attempt, we first used the original abundance data as input into gradient forest and calculated the community offset, which we noticed was very different from the results of SDM-based methods. We further used SDM suitability (randomly sampled from 10% of the grids), instead of the original abundance data, as input into gradient forest. In this way, the community offset is similar to the overall community change trend from SDM-based methods (Figure 2). Therefore, using different data sources (original abundance data versus SDM suitability), the same gradient forest method yielded distinct results. This discrepancy could be due to either the data source or the distinct distribution of sampling locations (original plots versus randomly chosen grids). To test this, we used SDM suitability values from the location of the original survey plots to model community offset. The result appears similar to the community offset from the abundance data of the survey plots (Supplementary Figure 22). Therefore, the pattern of community offset using abundance data from the original plots appears to result from the non-random distribution of survey plots across Taiwan, resulting in poor community offset results. If one could use environmental factors to fit a model and extrapolate the original abundance of each species across Taiwan, gradient forest using abundance from randomly selected sites might be feasible.

The other new attempt is using weighted gene co-expression network analysis (WGCNA) for identifying co-existence species modules, which was originally used in molecular biology to find genes with similar expression patterns. A co-existence species module, hence, represents a community where species have similar presence-absence patterns. By comparing the results with previous studies [36, 39] (Supplementary Figure 15-18), our classification method is also able to roughly separate different vegetation types. Moreover, we not only used the information of woody plants but also include herbs and fern species. As the result, we can further subdivide some previous groups into distinct groups (Supplementary Figure 15-18). While the previous vegetation classification methods were mostly based on supervised learning (based on pre-defined and curated vegetation groups) and classified locations into vegetation zones, here we performed un-supervised classification to group species into co-existence modules. In

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addition, each species is assigned to only one community (module), and not all species would be assigned into a module, while those that could be assigned to a module have a high probability of co-existence with the community. Compared with the traditional hierarchical clustering (h-cluster) [89] and k-means clustering (k-means) [90], WGCNA is a new attempt in ecology for clustering. The difference between WGCNA and traditional methods that it first created weighted co-expression networks by soft thresholds and weight networks [88]. Moreover, adding dynamic tree cutting in the subsequent development is more advantageous than the height cutoff method [91]. Previous studies have also compared these three clustering methods (h-cluster, k-means, WGCNA) and shown similar results [92]. Therefore, we also tried to compare the two traditional methods with WGCNA. After clustering, we defined whether the altitude distribution of the species within the community overlaps, and the range is concentrated to indicate the merit of the clustering. The results show that WGCNA is more concentrated and apparent than the other two traditional methods and has less overlap with other communities (Supplementary Figure 23). In summary, WGCNA may be a better clustering method in this study. Consequently, we further use Uniform Manifold Approximation and Projection (UMAP) to visualize the modules and their changes through different warming scenarios and time scales. In this way, not only we may

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clearly see the time periods of the change, but also which modules (communities) are changing more severely.

Community change

In this study, we only analyzed 999 species since we set the selection criteria filtered out species that appeared in less than five plots or more than 95% of plots in a region. The number of species included in the analysis represents 39% [43] of the entire dataset (2569 species) and 25% of the total number of native plant species identified in Taiwan (4077 species) [93]. It may not completely represent the change of overall vegetation in the future. However, this is unavoidable, as other species occur too infrequently in the survey, and using all data without any filter might lead to unreliable prediction results.

In addition, since SDM uses the grid climate data of the species' occurrence, even though we have improved the resolution and accuracy of the climate variables by the previous method, it is undeniable that the distribution of organisms is strongly affected by a microclimate [94, 95]. The distribution of organisms may be affected by topography, airflow, radiation, moisture interception, soil, and water conservation [96-98]. Therefore, the SDM results do not necessarily indicate the most suitable niche and

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distribution of the species. However, in this study, we want to present the whole fate of the vegetation in the future under macroscale climate and landscape patterns. In this context, we consider that SDM is still a good tool for predicting potential species distribution changes under climate change.

Following the above limitations, we move on to discuss community change, most previous studies on vegetation shifts under climate change have focused on the fate of alpine communities in temperate regions, either through *in situ* re-investigations or model predictions. The general conclusions emphasized that alpine communities will face a severe threat in the future and that mid-altitude species will replace the original alpine communities [18, 20]. Our study is among the few conducted in tropical regions with an environmental gradient from low to high altitude [33, 99, 100], and we illustrate not only the fate of high-altitude vegetation in the future [86], but also the challenges facing mid- and low-altitude vegetation. This study used two different perspectives, local decline and overall community change, to predict alterations of vegetation communities. In an overview of all the results, we defined three main altitude zones mainly by the magnitude of community change: High-altitude (above 2800 m asl), Middle-altitude (1000-2800 m asl), and low-altitude (below 1000 m asl):

(A) High-altitude regions

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Temperature is one of the main factors affecting the distribution of high-altitude communities [101], and increasing temperatures have caused high altitude communities to be affected [102, 103]. Our study indicates that high altitude communities have the second highest local decline, suggesting that these species are unable to adapt to future environmental changes and must have relatively long shift distances. However, these species are unable to move upwards due to the topographical limitations, eventually resulting in high extinction rates.

The findings are consistent with previous studies. Hsu *et al.* (2012) mentioned that the area of suitable habitats of *Picea* and *Tsuge*, which distributed above 2500 m asl, was predicted to shrink. Similarly, Lin *et al*. (2020) predicted that two high-altitude vegetation, Juniperus woodland and scrub and Abies-Tsuga forest, would lose most of their distribution area in the future, especially Juniperus woodland and scrub (lost 92% suitable areas) [41]. Correspondingly, our study showed that the extinction rate of vegetation at the altitude of 3000 m asl was as high as 50%, indicating that nearly half of the high-altitude species will be extinct in the future (i.e., there is no suitable area). This result is consistent with other regional studies [27-29], implying that high altitude vegetation is one of the most vulnerable vegetation types facing climate change. However, our study not only indicates that species in high altitude mountains might face threats due to temperature increase, but also demonstrates that species in middle altitudes may move upwards. Therefore, the overall change is relatively high in high altitudes. Not only are there species with the high local decline due to loss of suitable area, but they also have to face competition from mid-altitude species moving upwards [104]. Therefore, for high-altitude vegetation, such a circumstance may be more severe than previous thought, which only considered environmental changes.

In our results, the number of species in high altitudes does not decrease and even increase due to the upward shift of mid-altitude species (Figure 1), which is consistent with the majority of studies [14, 17-20, 105]. However, for high-altitude mountain areas, the slope is an important factor for successful species shifting [106], and there are also studies that show that different landscapes may have different results in the upward shift of species in the future [107]. Therefore, we should be more careful when predicting the number of species in high-altitude vegetation. The factors such as geomorphology or slope should be considered.

Besides, some studies have recently reported that non-climatic variables such as winter snowmelt [108, 109] and frozen soil melt [110] due to climate warming are changing dramatically in high latitudes, and these alterations may affect the evaluation of species numbers at high altitudes. However, in tropical regions such as Taiwan,

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where winter snowfall occurs above 3000 m asl (only 0.4% of Taiwan's area) with little accumulated snow, the above issues have a low effect for evaluating the number of species in high-altitude Taiwan.

It is worth mentioning that H. Pauli *et al*. (2012) suggested that while the number of species is generally increasing in the high-altitude mountains of Europe, it is decreasing in the Mediterranean region. The main reason for this is that the local environment has a more drastic change and is drier than other areas, leading to the extinction of the vegetation composed of most endemic species. A similar pattern may occur in northern and southern Taiwan, where the number of species declined more in the northern high-elevation areas (Supplementary Figure 24), probably due to the more intense environmental changes in precipitation in the north compared to the south (Supplementary Figure 8).

(B) Middle-altitude regions

The species in middle altitude are also affected by climate change in the future [111]. However, the local decline in this zone is weaker than in other altitudes. This result is also consistent with previous studies. Lin *et al.* (2020) indicated that two vegetations, *Quercus* forset, and *Machilus-Castanopsis* forest, would be stable (less change in the area of suitable habitats) compared to other vegetation types in middle

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altitude [41], and Hsu *et al.* (2012) also mentioned that two vegetation groups, highland broad-leaved forest and *Pinus*, have the less upward shift. These vegetation types also belong to the mid-altitude group in our definition, and their overall changes are relatively stable. The cloud forest in Taiwan also happens to be located at this altitude [112], and most studies suggested the importance of cloud forests as having more specialists due to the unique environmental conditions [113, 114], which is consistent with our results (Figure 3). However, Lin *et al.* (2020) mentioned two other cloud forest types, *Fagus* cloud forest and, *Pasania-Elaeocarpus* cloud forest, will be threatened by climate change leading to vegetation loss in extreme scenario in extreme scenarios [41]. We noticed that the altitudinal distribution of this two vegetation is 1200-1600 m asl and 1000-1400 m asl, which are lower compared to other cloud forest vegetations, and consistently, they face higher degrees of abiotic adversity based on our finding in local decline. In summary, except for the two vegetation types mentioned above, the response of communities to environmental change is relatively low.

However, by using the results of overall change and the degree of species shift, we suggest that the mid-altitude communities may face stronger biotic stress. Furthermore, we show a range of altitudes between 1800-2200 m asl where species numbers may not change in the future. In fact, this is the range where overall change is highest, and

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community change is most severe. This issue highlights the advantage of using two different perspectives on community change: biological adversity can be identified from the difference between the shift of biodiversity composition and comparative local decline and overall change, rather than being considered stable simply by the fact that species richness does not change much, the suitable area does not change greatly, or shift does not move with a long distance.

(C) Low-altitude regions

Low-altitude species are also exposed to warming and changes in precipitation patterns [33, 115], which result in species that are unable to stay in the same location and must shift upward to find suitable environments [4, 22, 100]. Consistent with previous studies [37, 41], our results show that the local decline of low elevation species is quite high, consistent with the decline in the number of species, and requires a high shift distance. Hsu *et al.* (2012) mentioned that the two vegetation types distributed under 1500 elevation in the broad-leaved forest lowland and midland have the higher upward shift distance among all vegetation types. The research of Lin *et al.* (2020) also similarly suggests that vegetation groups in low altitude, *Drypetes-Helicia* forest, and *Phoebe-Machilus* forest, distributed at 500-1000 m asl, have the highest shift distance consistent with our results [41]. In contrast to previous studies, we calculated and

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compared the suitability of each species in each location both in the present and in the future. As a result, we can further indicate that low-altitude species may face a great degree of abiotic adversity and predict most species in low-altitude to be extinct in low-altitude environments. Such results are close to those of Duque *et al.* (2015), who observed the same upward trend in the distribution of species at lower elevations in tropical forests, and showed higher mortality rates in the lower elevations. Therefore, they concluded that changes in the composition of tropical forest species are not shifts or expansions but rather a concentration of their ranges to higher elevations [99, 100]. If these low-elevation species move successfully to middle altitudes in the future and the middle altitude flora does not have the same magnitudes of the upward shifting, the distribution of the vegetation may overlap. Therefore, lower altitude species may be inevitably competing with species in middle altitudes [114, 116, 117].

Generalist & specialist

Previous research indicates that generalists, the species having a wider niche and broader distribution on the environmental gradient, have higher tolerance to climate change than specialists [82-85]. There are also researches showing that specialists have been severely impacted by climate change [118, 119]. Moreover, some researchers explained that the decrease of species richness in specific regions was caused by the high ratio of the specialist in its local species composition, which led to the difference between regions while under the same effect of climate change [120].

We compared the response to climate change in the future between specialists and generalists using 999 species, including woody, herbaceous, and fern. We found that specialists are primarily in high altitude areas, while the generalists are in intermediate and low altitude areas. However, the predicted local decline patterns of specialists and generalists resemble each other, and both have very similar patterns (Figure 3C). Hsu *et al*. (2012) also indicated similar patterns by using 221 species of epiphyte to compare the specialist and the generalist. Thus, the result shows that it is a general trend, not only for epiphytes.

Community restructuring

Strong climate change will affect the distribution of species, as a result, ecologists are focusing on the effect of climate change on species. The previous forecasting was mainly focusing on the direct effect of climate change, nevertheless, the interaction between species plays a role in an individual's adaptiveness and geographical distribution as well [121]. Besides, from the result of community change, we can tell that the vegetation in the future, especially the middle-altitude community, may face

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biotic stress from the upward shift of low-altitude species, which is consistent with previous studies [114, 116, 117]. Consequently, this will probably result in the coextinction cascades, that is to say, the community will disappear due to the extinction of their dependent species then cause much more species to die out. The series of effects will contribute to the crash of the community [35, 122]. There is also research suggesting the complicated interaction network is able to stabilize the effect of the ecological community [123]. However, the interaction will definitely change in the future. Accordingly, we need a long-term investigation to determine whether this change has a positive effect on the whole community or not.

It is worth noticing that we could found some interesting patterns from the combination of other time periods (2016-2035, 2046-2065, 2081-2100) and different scenarios (Rcp4.5, Rcp8.5). For example, before 2035, we seem not to predict module overlap and the boundaries of the communities are quite clear under both the Rcp4.5 and Rcp8.5 scenarios. However, we can begin to see that the modules overlap, and the boundaries of the communities become blurred by 2065 and under the warming scenario of Rcp4.5. Therefore, if we could maintain a lower warming scenario (Rcp4.5) or even lower before 2065, the module among vegetation communities may be non-

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overlapping and may not lead to the issues mentioned above (Supplementary Figure 19-20).

Furthermore, aside from causing the plants' interaction network to change, the change of distribution of plants will also change the larger interaction network (plants & animals), which is shown in some research of phytophagous insects with plants [124-127].

In conclusion, climate change will not only affect the adaptiveness of the species. The community restructuring caused by climate change will be one of the following focusing points.

Extreme weather

With Climate Change, the occurrence of extreme climatic events is gradually increasing [128]. Extreme weather events have an impact on organisms in an ecosystem [128-131] and is even a key factor of regional biodiversity [132]. Furthermore, since the magnitude of damage and changes caused by extreme weather are immediate, the vegetation might not have enough time to adapt [129, 133]. However, as we know the prediction of the occurrence of extreme weather events is very difficult. We try to find the high-frequency occurrence of extreme weather events from the historical database.

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In our study, we informed about the frequency of extreme weather occurrences in various regions. In particular, the precipitation should be noted, as extreme precipitation and drought will cause severe threats to the southern cloud forests [41].

Conclusion

In conclusion, the vegetation in each altitude zones encounters a different challenge. We emphasized that the vegetation in the low-altitude faces the strongest abiotic stress, seconded by high-altitude, and the vegetation in middle-altitude faces the least abiotic stress. However, such differences in stress requires different degrees of altitudinal shift, resulting in an overlap in some altitude zones. Furthermore, extreme climate should be included in the discussion of climate change. The information which could show unstable regions provided additional view.

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Table 1. Formula Table for converting TCCIP data to Worldclim format.

Bioclimate	Definition
BIO1	Mean (Tavg01 + Tavg02 + … + Tavg12)
BIO2	Mean ((Tmax01-Tmin01) + (Tmax02-Tmin02) … (Tmax12- Tmin12))
BIO4	Sd (Tavg01, Tavg02, … Tavg12)
BIO7	Max (Tmax01: Tmax12) – Min (Tmin01: Tmin12)
BIO12	Sum (precip 01 + … + precip 12)
BIO15	Cv (precip 01 + 1, precip 02 + 1 …precip 12 + 1)
BIO16	Mean (Precipitation of wettest quarter)
BIO19	Mean (Precipitation of coldest quarter)

We convert the TCCIP data into Worldclim format by using the formula in the table above. The following explanation of the terms in the formula.

Mean: Calculate the average of values in parentheses

Sd: Calculate the standard deviation of values in parentheses

Max: Selects the maximum value of values in parentheses

Min: Selects the minimum value of values in parentheses

Sum: Accumulate all values in parentheses

Cv: Calculate the coefficient of variation of values in parentheses

Table 2. Proportion of the top three important bioclimatic variables across all species in all species distribution modelling.

Climatic variables	Imp1	Imp2	Imp3
BIO1	70.00%	15.00%	8.00%
BIO2	3.00%	9.00%	11.00%
BIO4	7.00%	18.00%	20.00%
BIO7	4.00%	4.00%	8.00%
BIO12	2.00%	8.00%	9.00%
BIO15	4.00%	19.00%	15.00%
BIO16	3.00%	11.00%	14.00%
BIO19	8.00%	16.00%	16.00%

We summarize the top three important bioclimatic variables across all species in all species distribution modelling.

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Table 3. Proportion of the top three important bioclimatic variables across all species in all gradient forest models.

Climatic variables	Imp1	Imp2	Imp3
BIO1	66.00%	10.00%	9.00%
BIO2	4.00%	15.00%	16.00%
BIO4	12.00%	36.00%	19.00%
BIO7	8.00%	13.00%	15.00%
BIO12	2.00%	5.00%	11.00%
BIO15	2.00%	5.00%	10.00%
BIO16	4.00%	9.00%	9.00%
BIO19	2.00%	8.00%	12.00%

We summarize the top three important bioclimatic variables across all species in all gradient forest models.

Table 4. Co-existence modules with species significantly concentrating in certain clades.

Region	**Module**				
	module1	**module2**	**module3**	**module4**	**module5**
east	**0.007***	0.123	**0.047***	**0.01***	**0.001***
west	0.096	0.424	0.217	0.067	0.115
south	0.747	**0.042***	0.518	0.104	-
north	0.127	**0.013***	**0.016***	0.724	-

Shown are the *p*-values comparing data to permuted null expectation. Significant results denote mean species' distance to nearest neighbor within the same module is closer than null expectation.

Table 5. Families with enriched number of species within each co- existence module.

Species in this module and this family	Species in this module but not this family	Species not in this module and in this family	Species not in this module nor this family	Odds	P	Family	Module
4	36	2	392	21.778	0.001	Gentianaceae	E1
5	35	6	388	9.238	0.002	Poaceae	E1
4	28	1	401	57.286	0.000	Pinaceae	E2
3	29	5	397	8.214	0.016	Asteraceae	E2
3	29	8	394	5.095	0.040	Ericaceae	E2
8	152	0	274	Inf	0.000	Symplocaceae	E3
9	151	3	271	5.384	0.011	Theaceae	E3
8	152	3	271	4.754	0.022	Fagaceae	E3
3	157	0	274	Inf	0.050	Celastraceae	E3
6	140	0	288	Inf	0.001	Zingiberaceae	E4
15	131	8	280	4.008	0.002	Rubiaceae	E4
7	49	4	374	13.357	0.000	Euphorbiaceae	E5
8	48	7	371	8.833	0.000	Moraceae	E5
5	51	4	374	9.167	0.003	Rutaceae	E5
4	52	4	374	7.192	0.012	Fabaceae	E5
6	30	10	383	7.660	0.001	Poaceae	W1
5	31	6	387	10.403	0.001	Asteraceae	W1
4	49	1	375	30.612	0.001	Pinaceae	W2
3	50	3	373	7.460	0.027	Oleaceae	W2
8	135	1	285	16.889	0.001	Symplocaceae	W3
3	140	0	286	Inf	0.037	Ranunculaceae	W3
8	135	5	281	3.330	0.037	Ericaceae	W3
5	131	0	293	Inf	0.003	Euphorbiaceae	W5
9	127	6	287	3.390	0.023	Rubiaceae	W5
5	131	2	291	5.553	0.035	Moraceae	W5
4	132	1	292	8.848	0.037	Zingiberaceae	W5
9	132	0	355	Inf	0.000	Ericaceae	S1
10	131	3	352	8.957	0.000	Rosaceae	S1
10	131	4	351	6.698	0.001	Symplocaceae	S1
13	87	23	373	2.423	0.018	Orchidaceae	S3
3	97	1	395	12.216	0.027	Begoniaceae	S3
11	89	20	376	2.324	0.037	Lauraceae	S3
9	105	2	380	16.286	0.000	Euphorbiaceae	S4
11	103	8	374	4.993	0.001	Rubiaceae	S4
8	106	4	378	7.132	0.001	Moraceae	S4
7	107	6	376	4.100	0.014	Fabaceae	S4
4	110	2	380	6.909	0.027	Araceae	S4
3	111	1	381	10.297	0.040	Ulmaceae	S4

4	73	0	363	Inf	0.001	Berberidaceae	N1
3	74	0	363	Inf	0.005	Cupressaceae	N1
3	74	0	363	Inf	0.005	Pinaceae	N1
4	73	3	360	6.575	0.020	Asteraceae	N1
6	71	8	355	3.750	0.022	Ericaceae	N1
7	70	12	351	2.925	0.033	Rosaceae	N1
4	73	4	359	4.918	0.035	Poaceae	N1
11	124	2	303	13.440	0.000	Symplocaceae	N2
3	132	0	305	Inf	0.028	Dryopteridaceae	N2
10	94	12	324	2.872	0.020	Lauraceae	N3
5	99	4	332	4.192	0.037	Smilacaceae	N3
7	117	2	314	9.393	0.003	Moraceae	N4
5	119	1	315	13.235	0.008	Fabaceae	N4
12	112	12	304	2.714	0.020	Orchidaceae	N4
12	112	12	304	2.714	0.020	Rubiaceae	N4
4	120	1	315	10.500	0.024	Euphorbiaceae	N4

We separated all species in a region into four groups: *a* – species in this module and this family, *b* – species in this module but not this family, *c* – species not in this module and in this family, *d* – species not in this module nor this family. The fold enrichment (odds ratio) was calculated as (*a*/*b*)/(*c*/*d*), and statistical significance was estimated with Fisher's exact test.

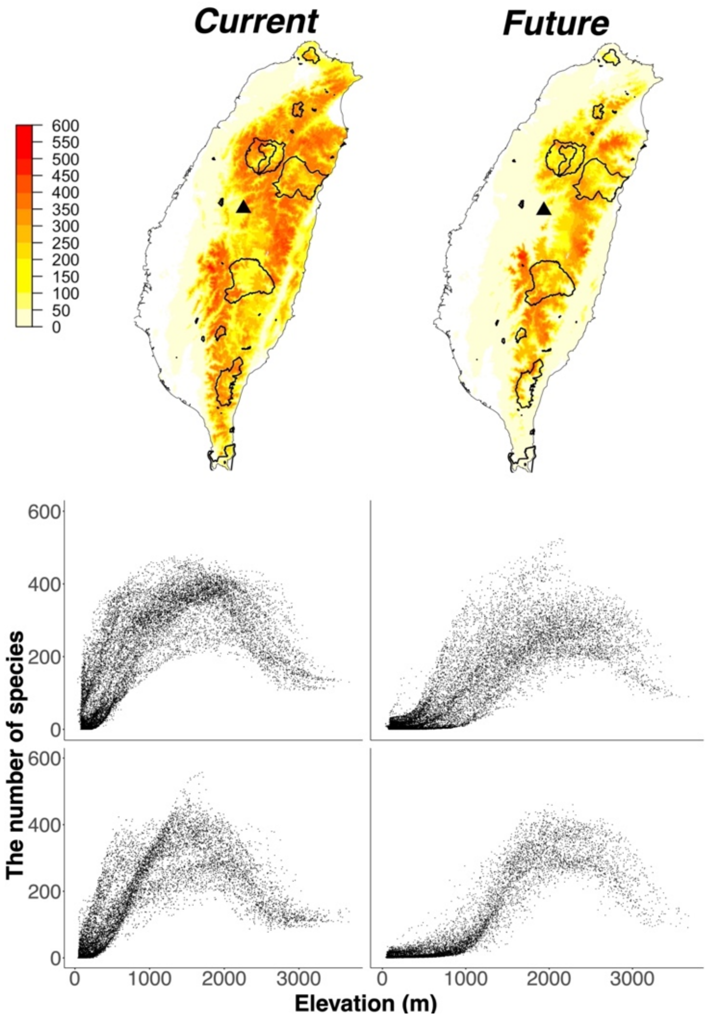

Figure 1. The biodiversity composition in current and future conditions. The figure shows the number of species on each 1x1 km grid in the current and future (Rcp8.5 at 2081-2100) climatic conditions. The triangle on the map is the Geographic Center of Taiwan (23.973875°N, 120.982024°E), used to separate Taiwan into the northern and southern parts for the scatter plots. For the top row, colors present the number of species on each grid with red areas representing predicted biodiversity composition, and regions encompassed by solid lines are national parks, nature reserves, or forest reserves. The middle and bottom rows are for northern and southern Taiwan respectively, showing the altitudinal distribution of biodiversity composition from the corresponding maps on the top row. Each dot is a 1 x 1 km grid.

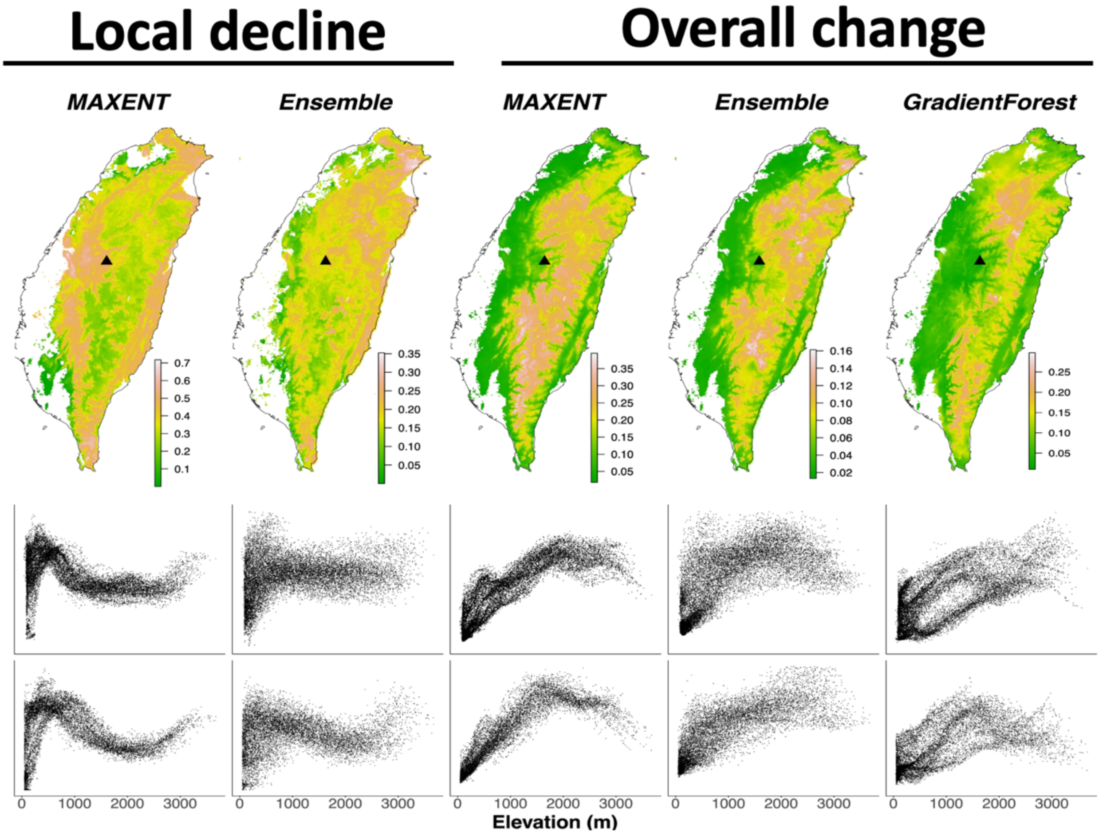

Figure 2. The change of plant communities in Taiwan. The top row shows two different perspectives of community change calculated by multiple algorithms, shown separately in the five columns of this figure. The triangle on the map is the Geographic Center of Taiwan (23.973875°N, 120.982024°E), used to separate Taiwan into the northern and southern parts for the scatter plots. Panels in the middle row show, for northern Taiwan, relationships between elevation and local decline or overall change values from the corresponding maps on the top row. Each dot in the scatter plots represents one 1 x 1 km geographic grid, and the range of the vertical axis corresponds to the colored legend for the map. Panels in the bottom row are for southern Taiwan.

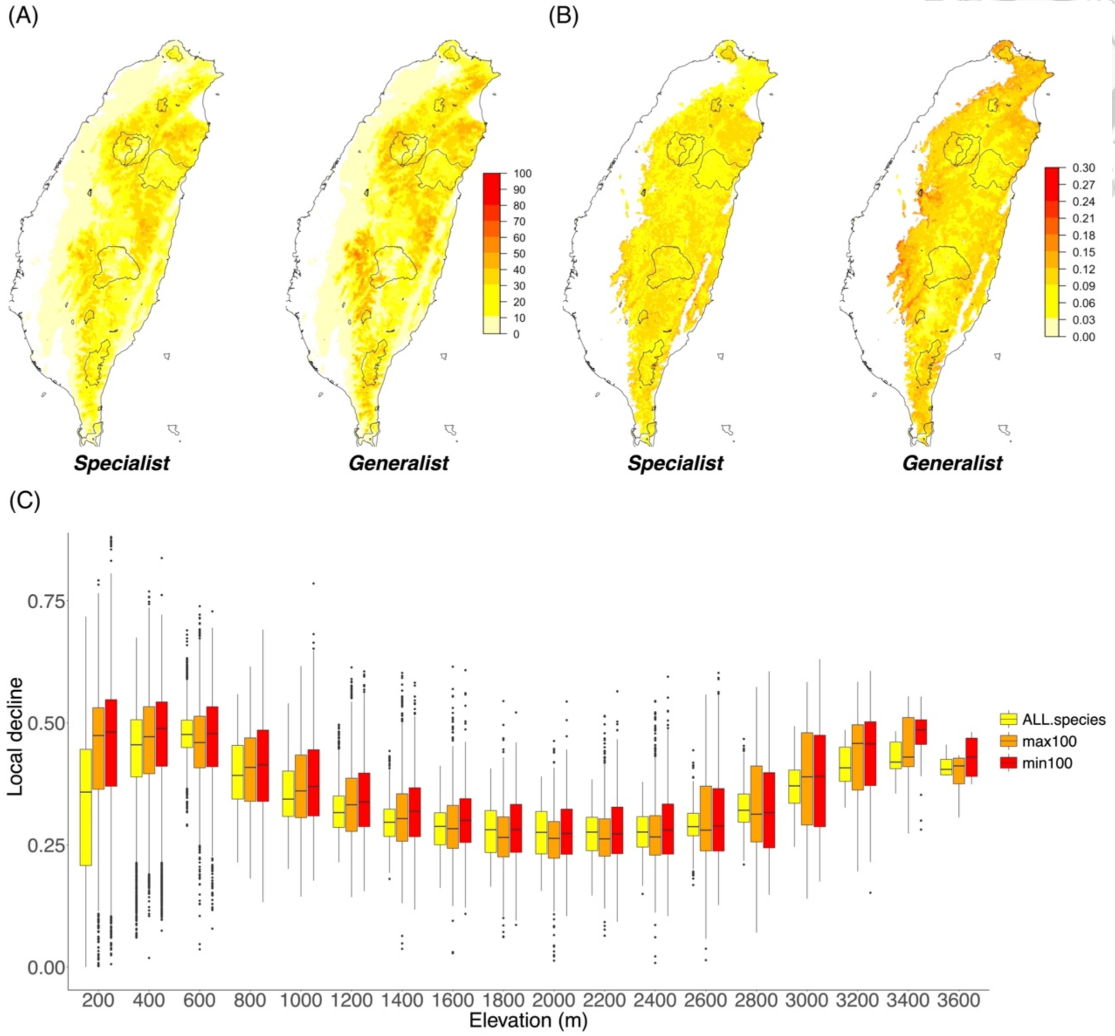

Figure 3. The local decline of plant community in species of different niche space. Panel A shows number of specialist and generalist species across Taiwan, and panel B shows their proportion over local species in each 1 x 1 km geographical grid. Panel C shows the magnitude of local decline upon climate change (Rcp8.5, MAXENT, 2081-2100) in three different groups, comparing all species, the top 100 species with broadest niche space (max100), and the top 100 species with narrowest niche space (min100).

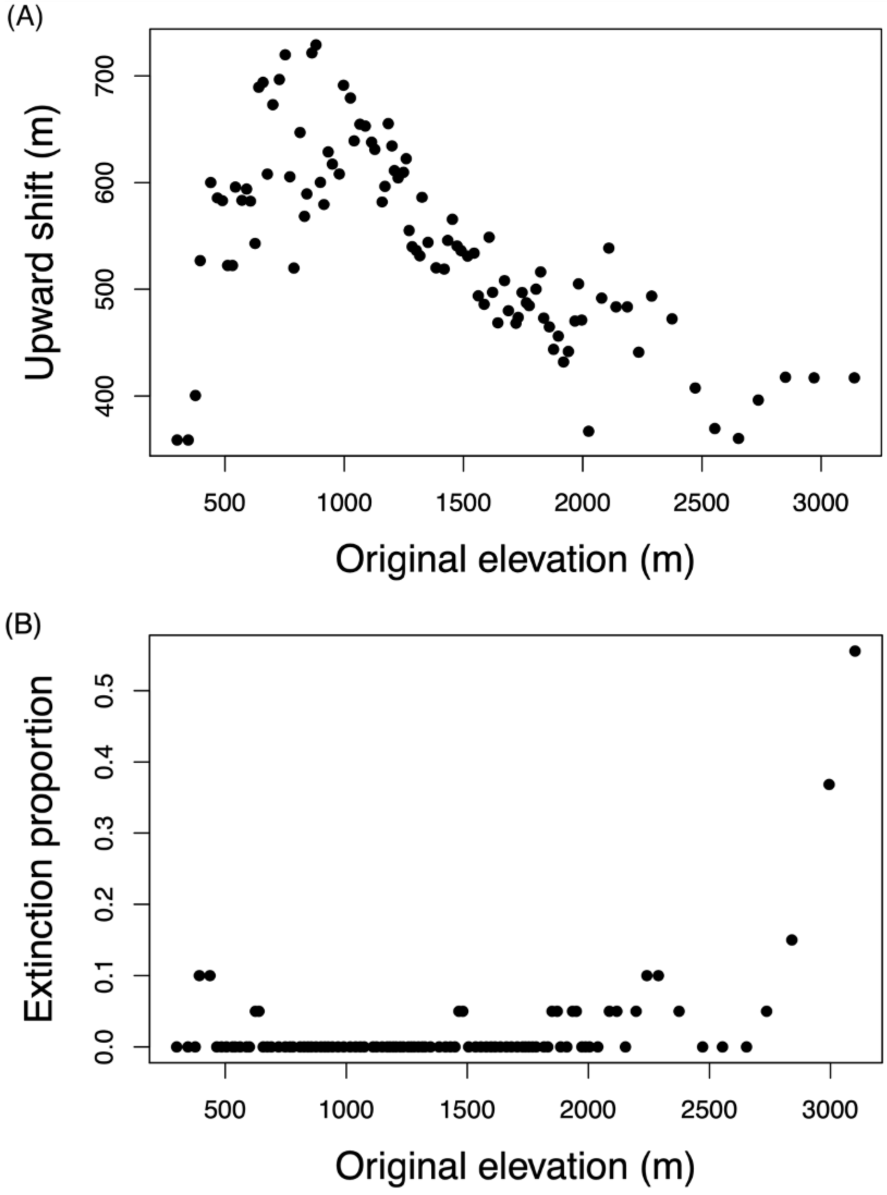

Figure 4. The elevation shift (A) and extinction proportion (B) of plants. Species were first ranked by their original elevation, and each point represents a sliding widow with size of 20 and step size of 10 species, taking the median value of all 20 species within.

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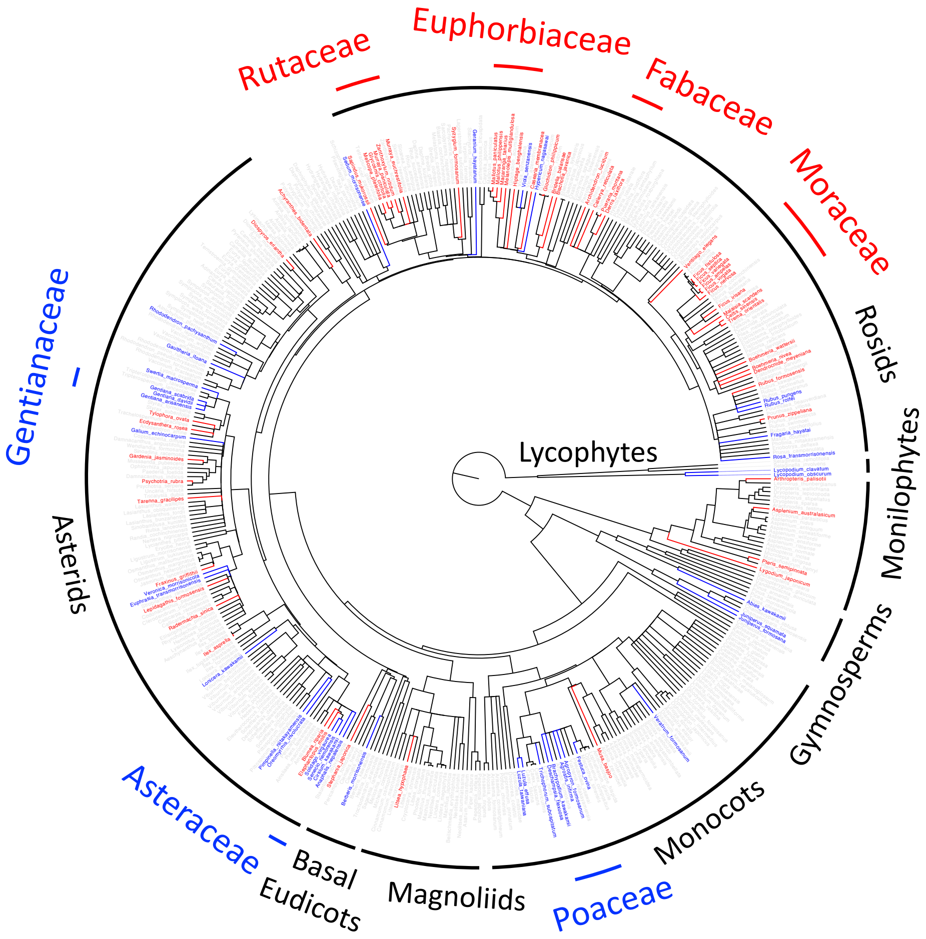

Figure 5. The phylogenetic tree of all species used for analyses in eastern Taiwan. The tree was obtained from Phylomatic [78] with major clades noted by black curves and labels. The names and terminal branches of species belonging to the highest-elevation co-existence community (east module 1) were labeled blue, and those from lowest-elevation community (module 5) were labeled red. In the outer ring, colored curves and labels denote families with enriched number of species in the corresponding modules.

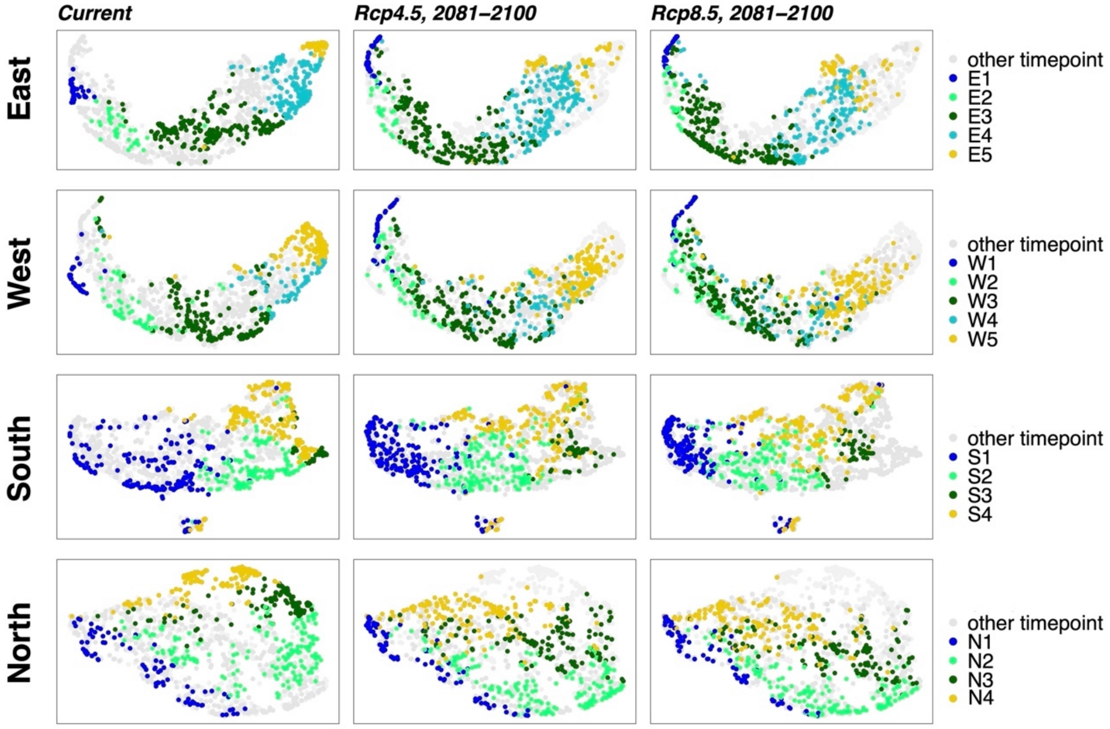

Figure 6. Change of community structure between current and future conditions in the eastern (A), western (B), southern (C), and northern (D) regions of Taiwan. Shown are the Uniform Manifold Approximation and Projection (UMAP) dimension reduction of species suitability across Taiwan, presenting the co-existence relationship among species across time and climate change scenarios. On UMAP, each species is represented by three dots, presenting its distribution patterns across Taiwan for current and two future conditions (Rcp4.5 and Rcp8.5 in 2081-2100). Within the same region, the three graphs are the same except modules were painted for species in different time points or climate change scenarios (left to right: Current, Rcp4.5, and Rcp8.5).

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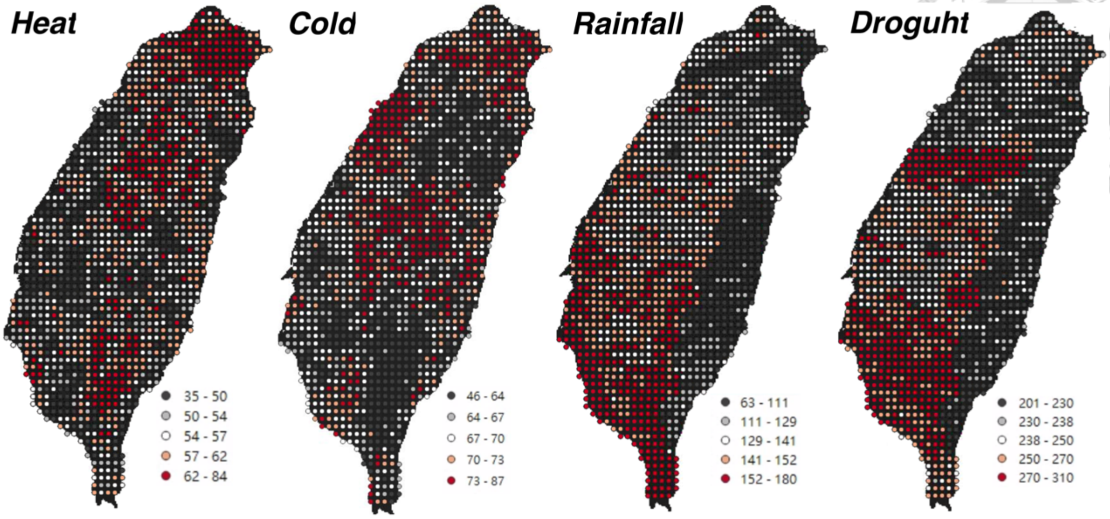
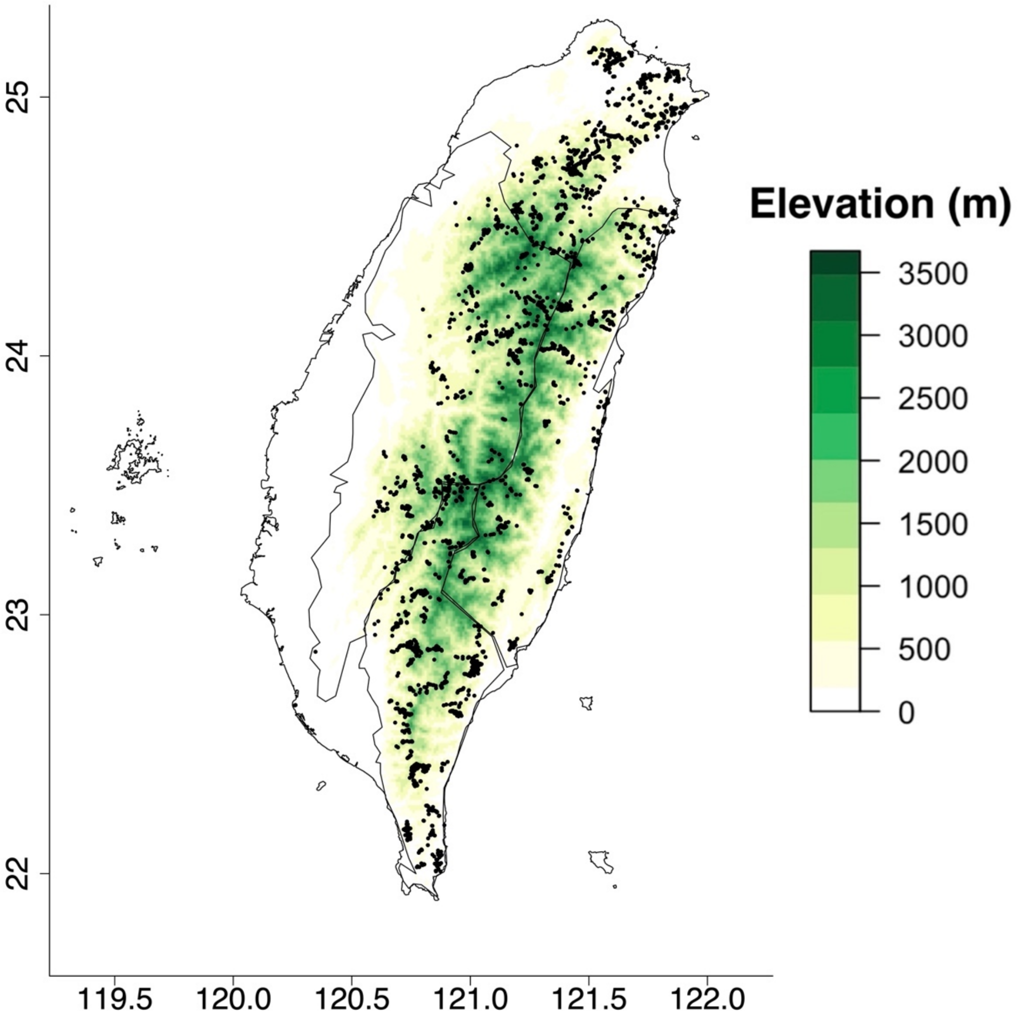
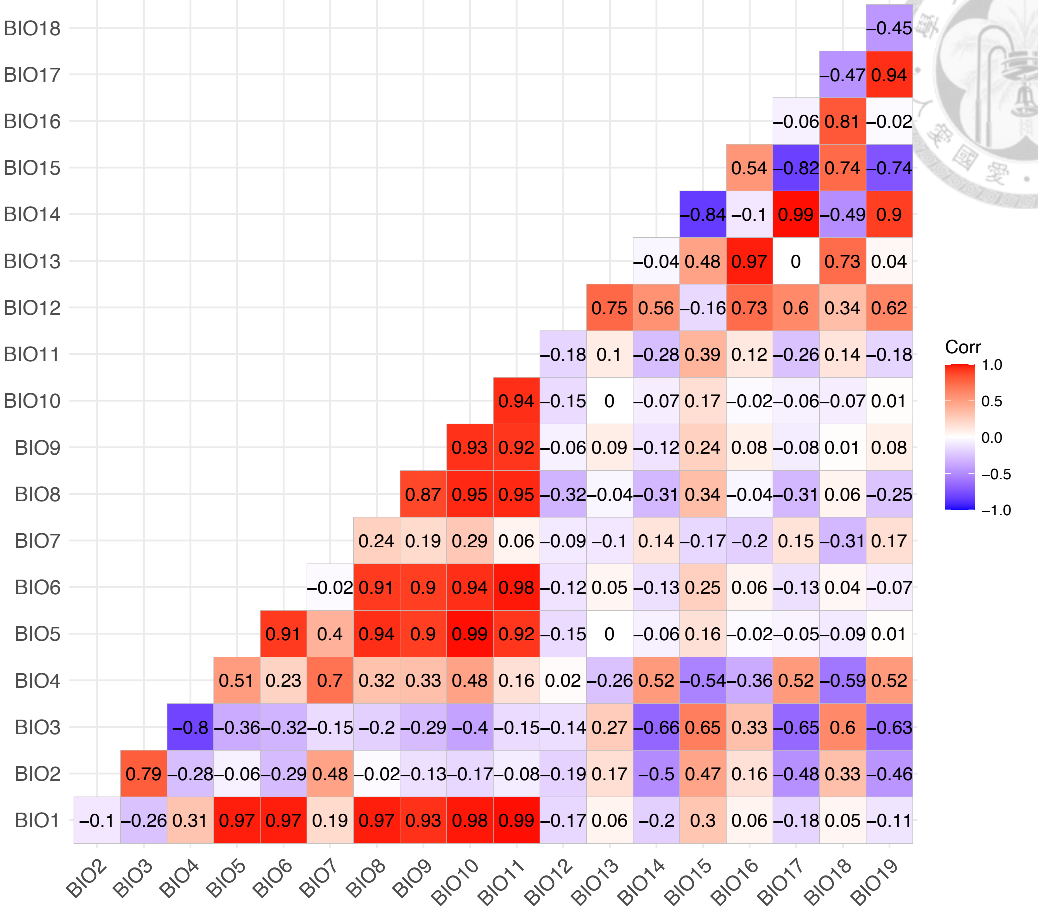


Figure 7. The frequency of four types of extreme weather events in Taiwan. The figure shows the frequency of extreme weather events. Each point is a data grid (5 x 5 km) that records three different variables: daily maximum temperature, daily minimum temperature, and daily rainfall. The legend shows the frequency of events in different colors.

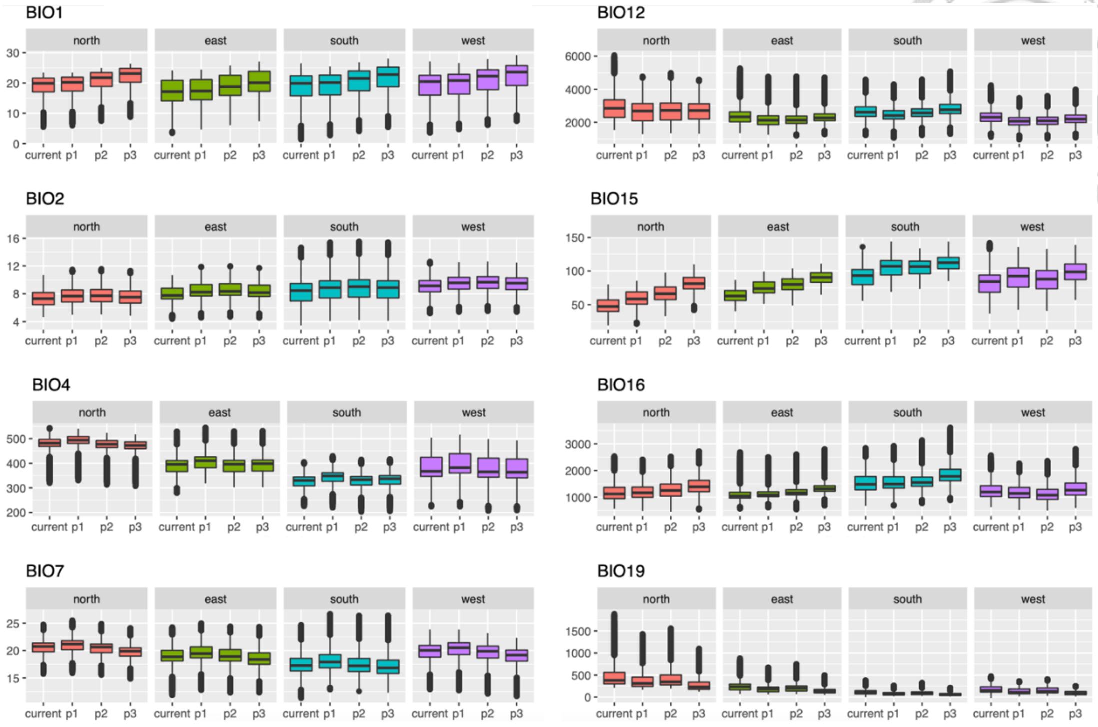


Supplementary Figure 1. All study sites in four regions of Taiwan. This figure shown 3060 plots (black point) in four regions (separated by solid lines within Taiwan). All plots are set in the natural forest of Taiwan (no open ground). We separated Taiwan into four regions (East, West, South, North) by major mountain ridgelines and climatic zones.

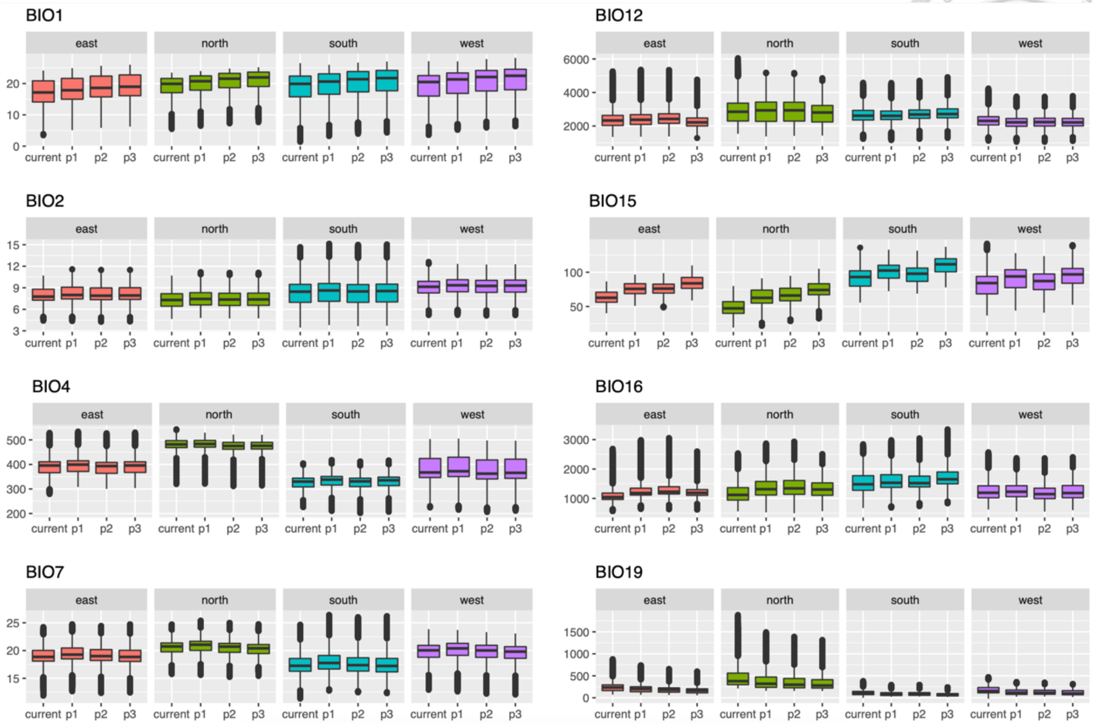


	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19
BIO18																		−0.45
BIO17																	−0.47	0.94
BIO16																−0.06	0.81	−0.02
BIO15															0.54	−0.82	0.74	−0.74
BIO14														−0.84	−0.1	0.99	−0.49	0.9
BIO13													−0.04	0.48	0.97	0	0.73	0.04
BIO12												0.75	0.56	−0.16	0.73	0.6	0.34	0.62
BIO11											−0.18	0.1	−0.28	0.39	0.12	−0.26	0.14	−0.18
BIO10										0.94	−0.15	0	−0.07	0.17	−0.02	−0.06	−0.07	0.01
BIO9									0.93	0.92	−0.06	0.09	−0.12	0.24	0.08	−0.08	0.01	0.08
BIO8								0.87	0.95	0.95	−0.32	−0.04	−0.31	0.34	−0.04	−0.31	0.06	−0.25
BIO7							0.24	0.19	0.29	0.06	−0.09	−0.1	0.14	−0.17	−0.2	0.15	−0.31	0.17
BIO6						−0.02	0.91	0.9	0.94	0.98	−0.12	0.05	−0.13	0.25	0.06	−0.13	0.04	−0.07
BIO5					0.91	0.4	0.94	0.9	0.99	0.92	−0.15	0	−0.06	0.16	−0.02	−0.05	−0.09	0.01
BIO4				0.51	0.23	0.7	0.32	0.33	0.48	0.16	0.02	−0.26	0.52	−0.54	−0.36	0.52	−0.59	0.52
BIO3			−0.8	−0.36	−0.32	−0.15	−0.2	−0.29	−0.4	−0.15	−0.14	0.27	−0.66	0.65	0.33	−0.65	0.6	−0.63
BIO2		0.79	−0.28	−0.06	−0.29	0.48	−0.02	−0.13	−0.17	−0.08	−0.19	0.17	−0.5	0.47	0.16	−0.48	0.33	−0.46
BIO1	−0.1	−0.26	0.31	0.97	0.97	0.19	0.97	0.93	0.98	0.99	−0.17	0.06	−0.2	0.3	0.06	−0.18	0.05	−0.11

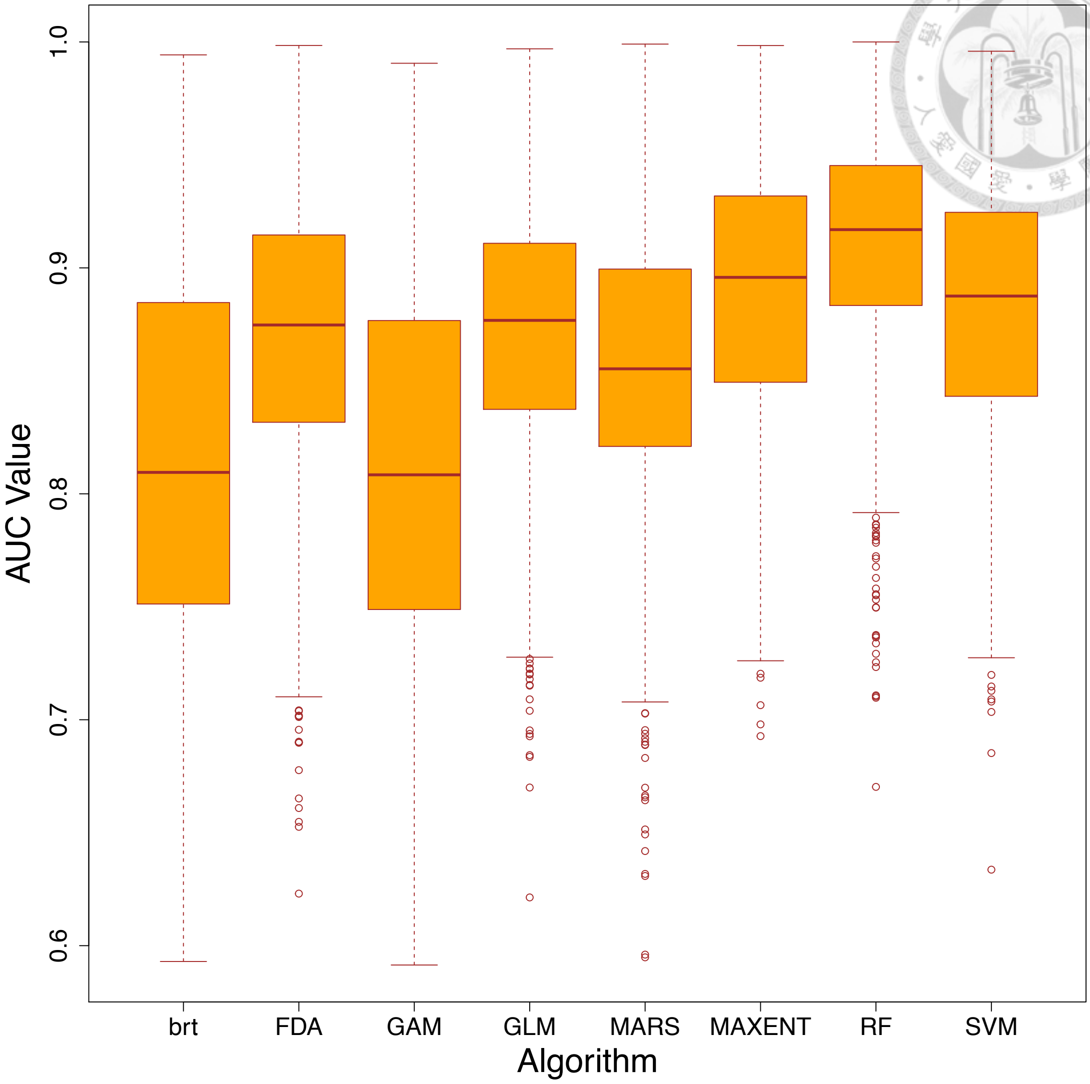
Supplementary Figure 2. Pairwise correlation of 19 bioclimatic variables. We calculated the pairwise correlation for 19 climatic variables to remove highly correlation variables (Pearson's r > 0.75). Finally, we selected BIO1: Annual Mean Temperature, BIO2: Mean Diurnal Range, BIO4: Temperature Seasonality, BIO7: Temperature Annual Range, BIO12: Annual Precipitation, BIO15: Precipitation Seasonality, BIO16: Precipitation of Wettest Quarter, and BIO19: Precipitation of Coldest Quarter for our analyses.



Supplementary Figure 3. Change of climatic variables in four regions under Rcp8.5 scenario and HadGEM2-AO general circulation models (GCMs). This figure shows the eight climatic variables (BIO1: Annual Mean Temperature, BIO2: Mean Diurnal Range, BIO4: Temperature Seasonality, BIO7: Temperature Annual Range, BIO12: Annual Precipitation, BIO15: Precipitation Seasonality, BIO16: Precipitation of Wettest Quarter, and BIO19: Precipitation of Coldest Quarter) simulated in three periods (P1: 2016-2035, p2:2046-2065, p3:2081-2100).



Supplementary Figure 4. Change of climatic variables in four regions under Rcp4.5 scenario and HadGEM2-AO general circulation models (GCMs). This figure shows the eight climatic variables (BIO1: Annual Mean Temperature, BIO2: Mean Diurnal Range, BIO4: Temperature Seasonality, BIO7: Temperature Annual Range, BIO12: Annual Precipitation, BIO15: Precipitation Seasonality, BIO16: Precipitation of Wettest Quarter, and BIO19: Precipitation of Coldest Quarter) simulated in three periods (p1: 2016-2035, p2:2046-2065, p3:2081-2100).



Supplementary Figure 5. The area under the ROC curve (AUC) of eight different algorithms. We established the species distribution models (SDMs) with eight different algorithms. In each algorithm, each data point is the mean AUC value of 25 independent runs of a species.

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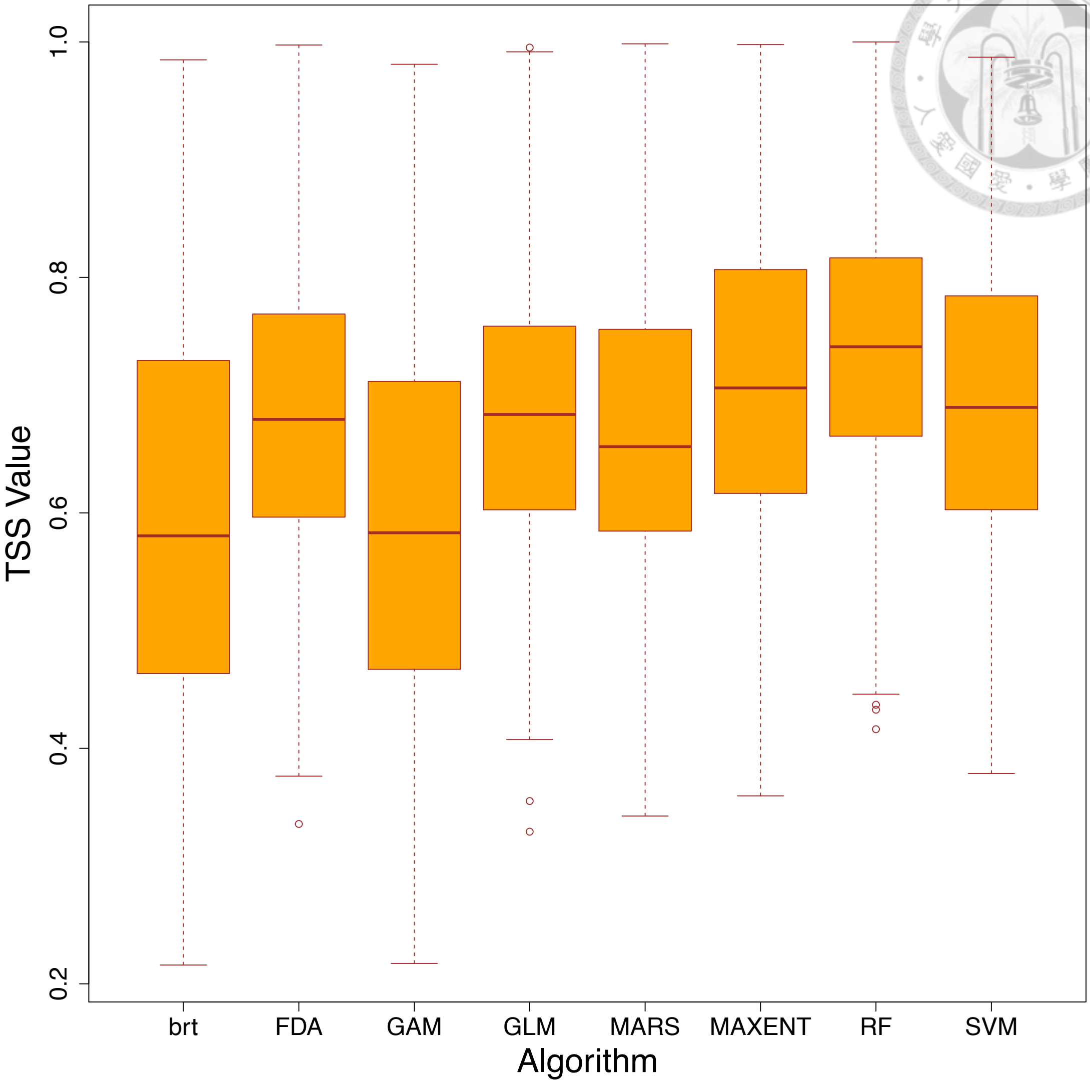

Supplementary Figure 6. True Skill Statistic (TSS) evaluation of eight different algorithms. We established the species distribution models (SDMs) by eight different algorithms. In each algorithm, each data point is the mean TSS value of 25 independent runs of a species.

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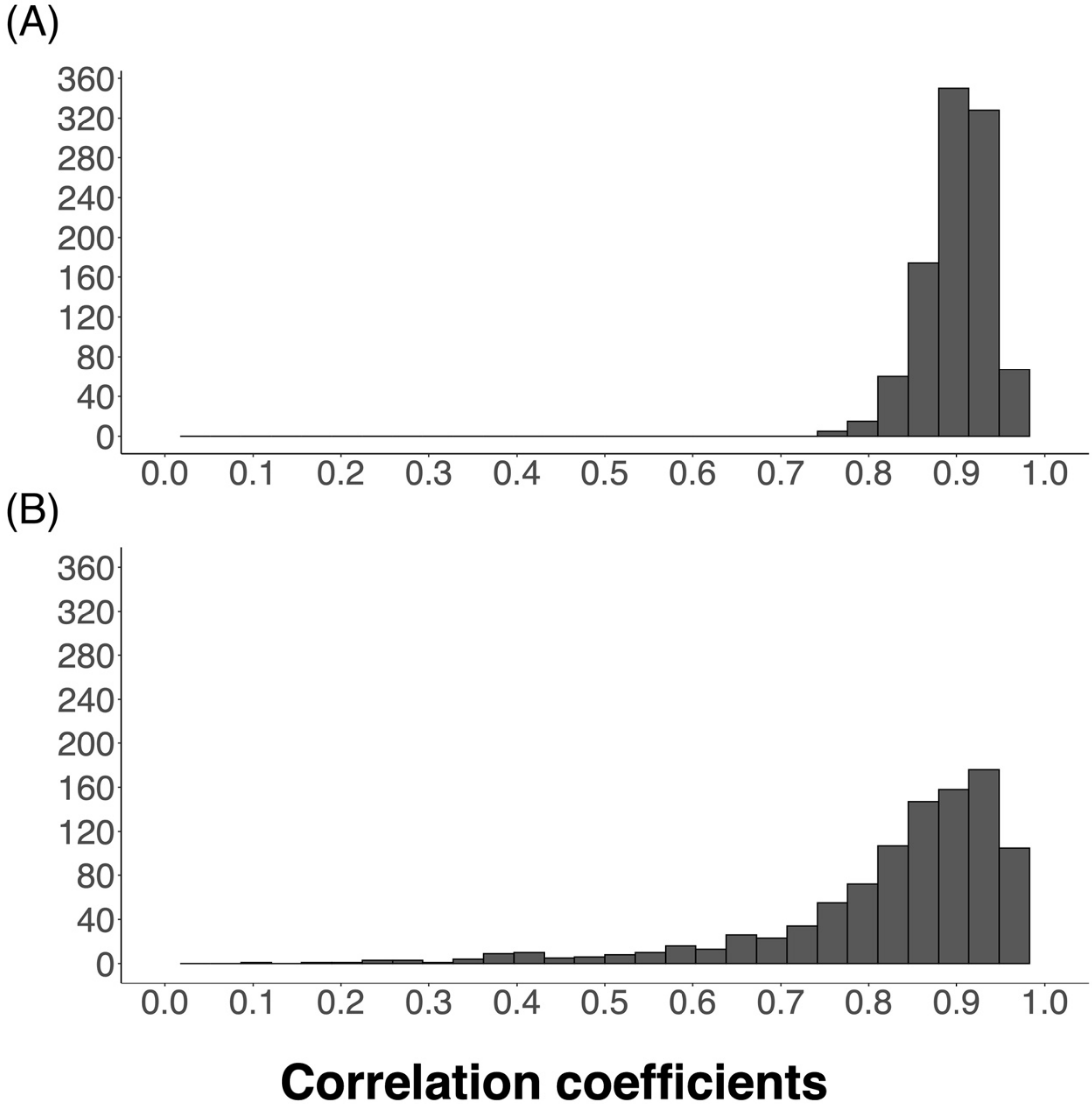

Supplementary Figure 7. The correlation of suitability values between MAXENT and ensemble methods in the current (A) and the future (B) conditions (Rcp8.5 in 2081-2100). For each species' MAXENT and ensemble prediction results, we randomly sampled geographical grids and estimated the correlation of suitability between the two methods. Show is the distribution for all 999 species used in this study.

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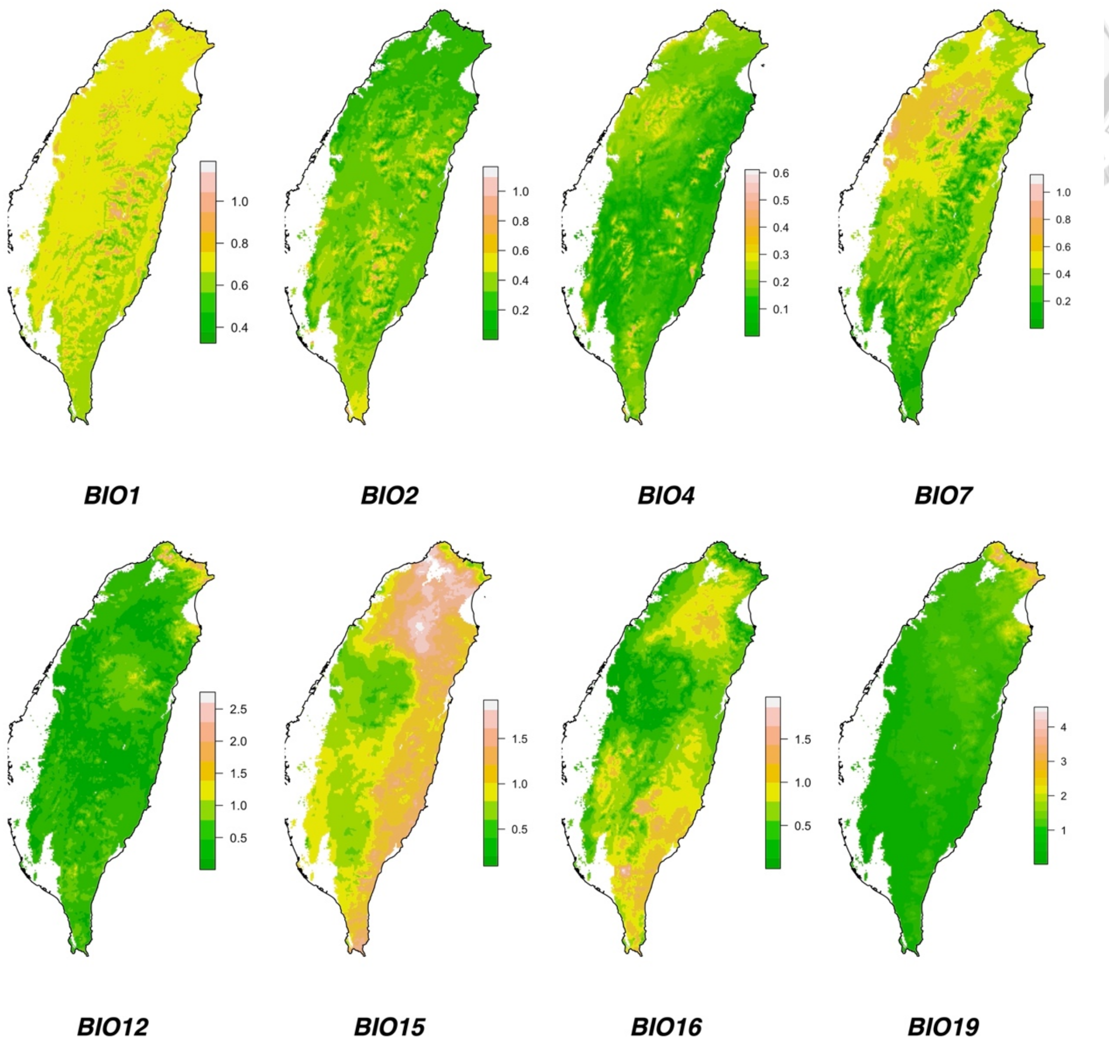
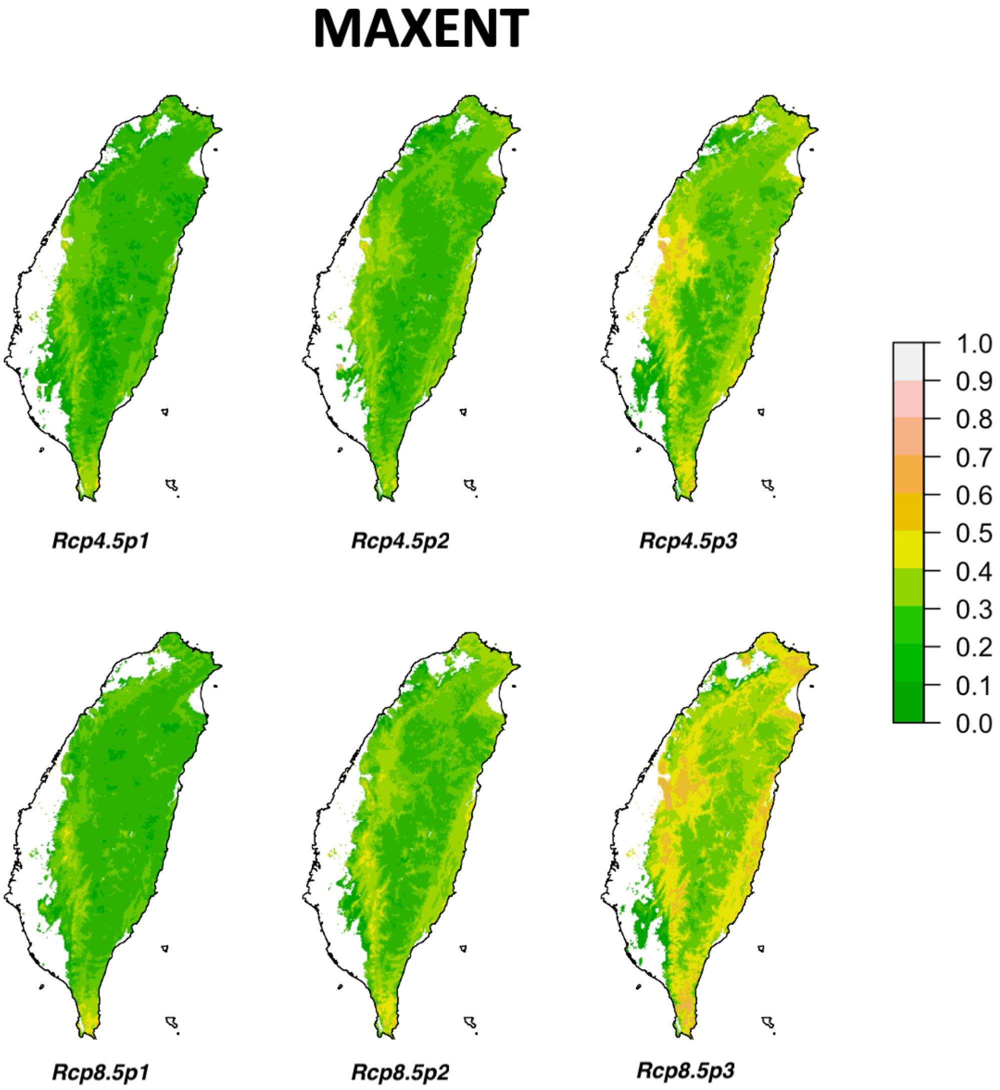
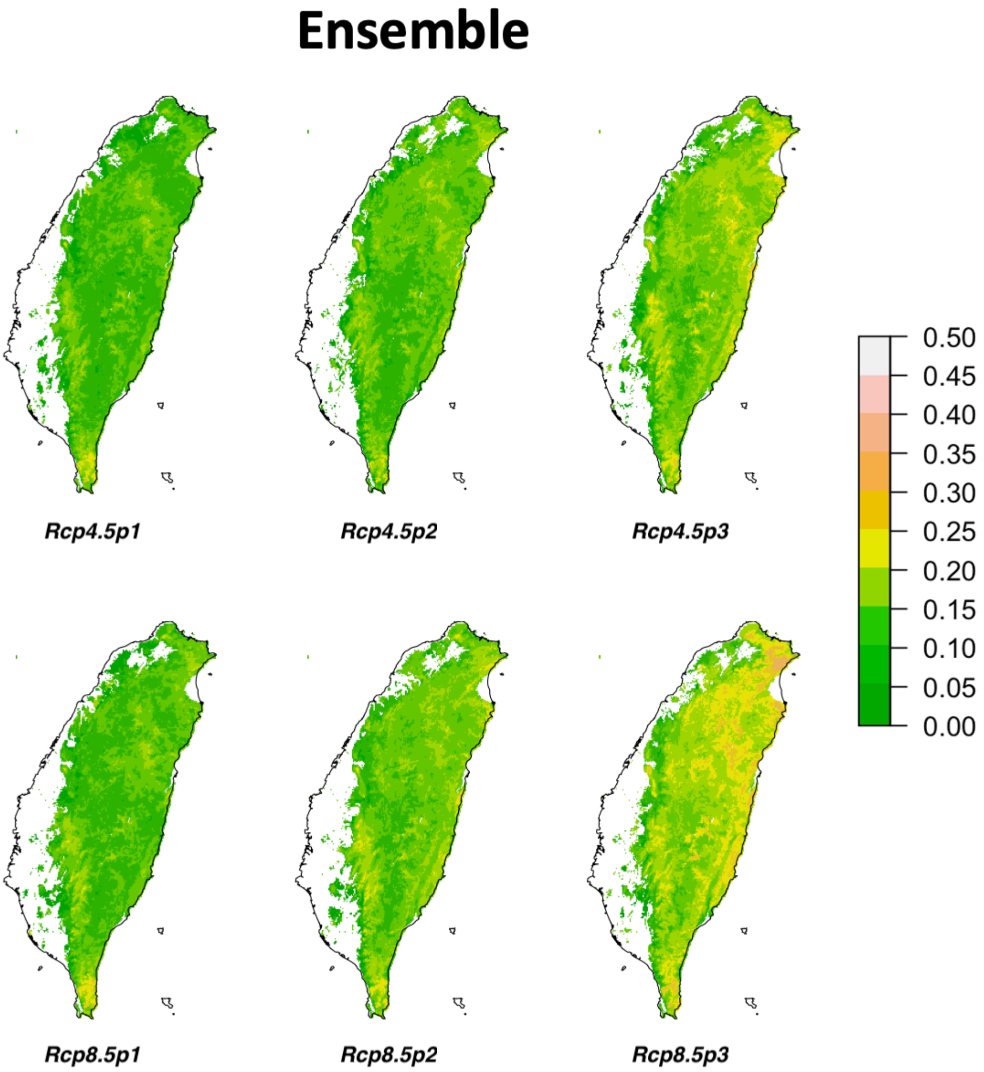


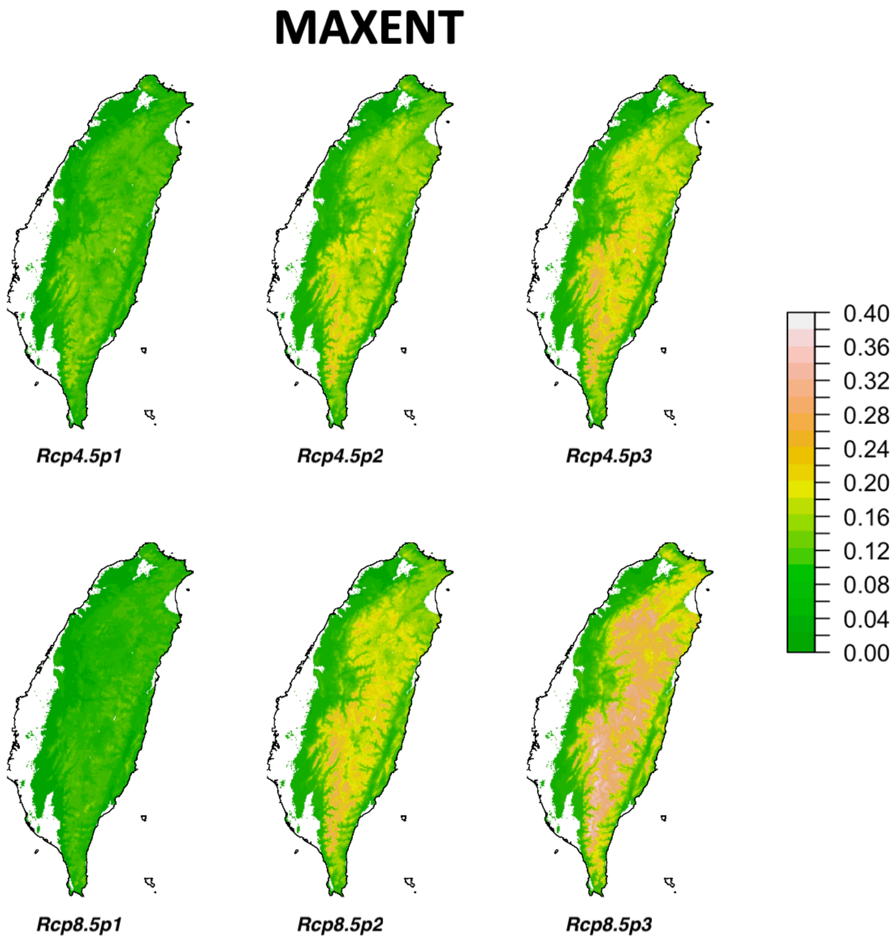
Supplementary Figure 8. The change of climatic variable in Rcp8.5 at 2081-2100. We calculated the absolute changes of eight climatic variables between current and future conditions. The legends show the change of climatic variables with different colors. BIO1: Annual Mean Temperature, BIO2: Mean Diurnal Range, BIO4: Temperature Seasonality, BIO7: Temperature Annual Range, BIO12: Annual Precipitation, BIO15: Precipitation Seasonality, BIO16: Precipitation of Wettest Quarter, and BIO19: Precipitation of Coldest Quarter for our analyses. The values are in units of standard deviation of current climatic variations across Taiwan.



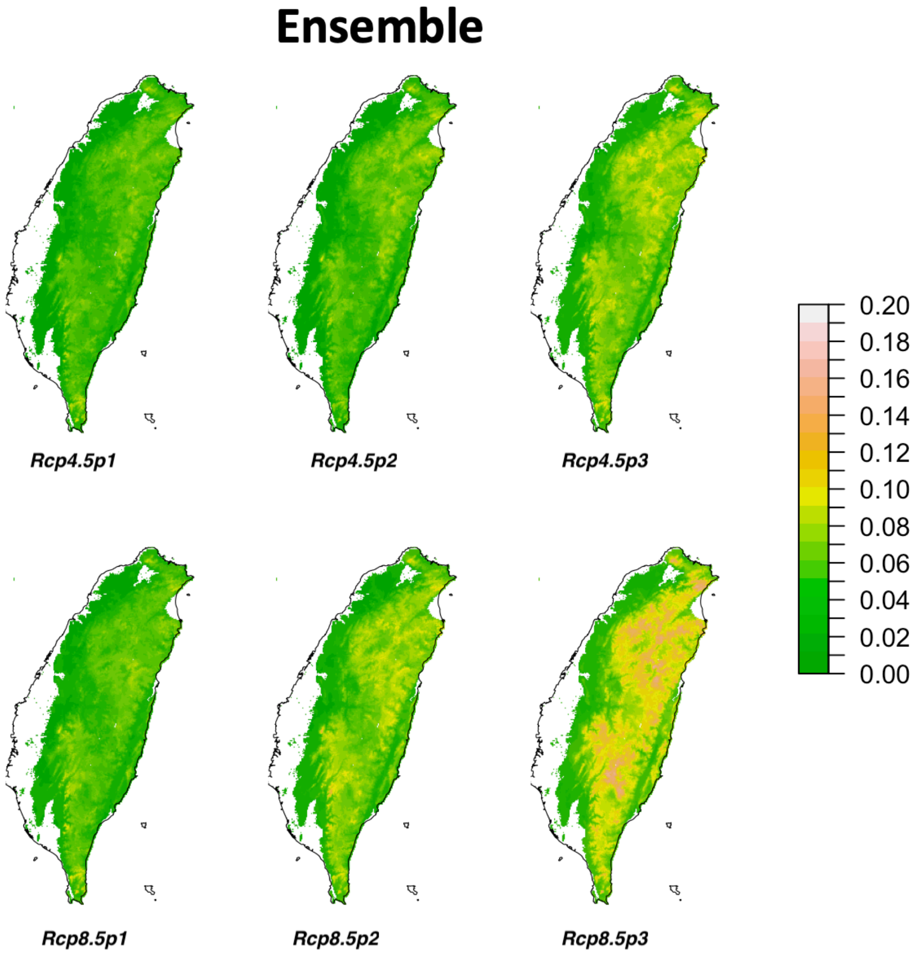
Supplementary Figure 9. The local decline of plant communities in Taiwan with two scenarios (Rcp4.5 and 8.5) and three time periods (p1: 2016-2035, p2: 2046-2065, p3: 2081-2100). We simulated species distribution with MAXENT algorithm and estimated the decline of suitability of future compared to current conditions. See Materials and Methods for detail. The value on the graph represents local decline. High value of local decline means that local community cannot adapt to climate change in the future, while the lower value means they are less affected in the future.



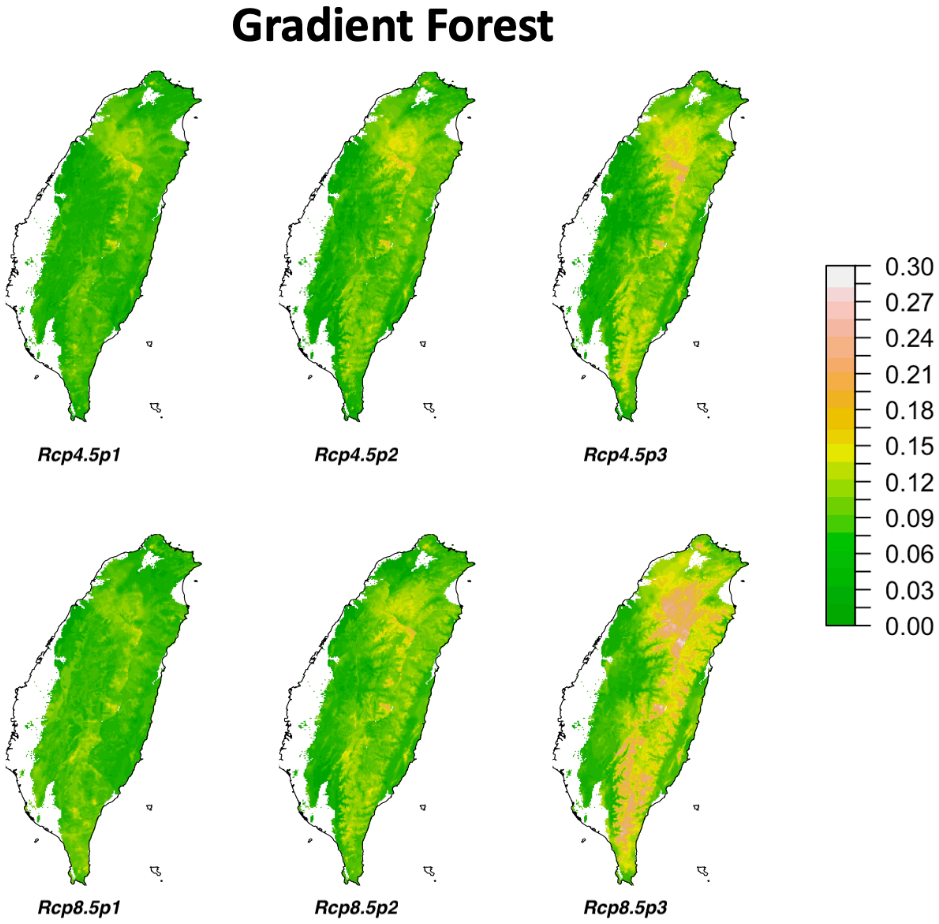
Supplementary Figure 10. The local decline of plant communities in Taiwan with two scenarios (Rcp4.5 and 8.5) and three time periods (p1: 2016-2035, p2: 2046-2065, p3: 2081-2100). We simulated the species distribution with ensemble algorithm and estimated the decline of suitability of future compare to current conditions. See Materials and Methods for detail. The value on the graph represents local decline. High value of local decline means the local community cannot adapt to climate change in the future, while the lower value means they are less affected in the future.



Supplementary Figure 11. The overall change of plant communities in Taiwan with two scenarios (Rcp4.5 and 85) and three time periods (p1: 2016-2035, p2: 2046-2065, p3: 2081-2100). We simulated the species distribution with MAXENT algorithm and estimated the overall change of suitability of future compared to current conditions. See Materials and Methods for detail. The value on the graph represents the overall change, which considers the alternation involving all species, thus incorporating both the decline of local species and the increased suitability of foreign species. High value of overall change means the community has a high decline of local species, increased suitability of foreign species, or both.



Supplementary Figure 12. The overall change of plant communities in Taiwan with two scenarios (Rcp4.5 and 8.5) and three time periods (p1: 2016-2035, p2: 2046-2065, p3: 2081-2100). We simulated the species distribution with ensemble algorithm and estimated the overall change of suitability of future compared to current conditions. See Materials and Methods for detail. The value on the graph represents the overall change, which considers the alternation involving all species, thus incorporating both the decline of local species and the increased suitability of foreign species. High value of overall change means the community has a high decline of local species, increased suitability of foreign species, or both.



Supplementary Figure 13. The overall cahange of plant communities in Taiwan with two scenarios (Rcp4.5 and 8.5) and three time periods (p1: 2016-2035, p2: 2046-2065, p3: 2081-2100). Gradient forest first identified the environmental ranges that best distinguish the suitability value and compared current and future climates across the map to identify geographic regions with environmental changes in the sensitive ranges. See Materials and Methods for detail. The value on the graph represents the overall change, which considers the alternation involving all species, thus incorporating both the decline of local species and the increased suitability of foreign species. High value of overall change means the community has a high decline of local species, increased suitability of foreign species, or both.

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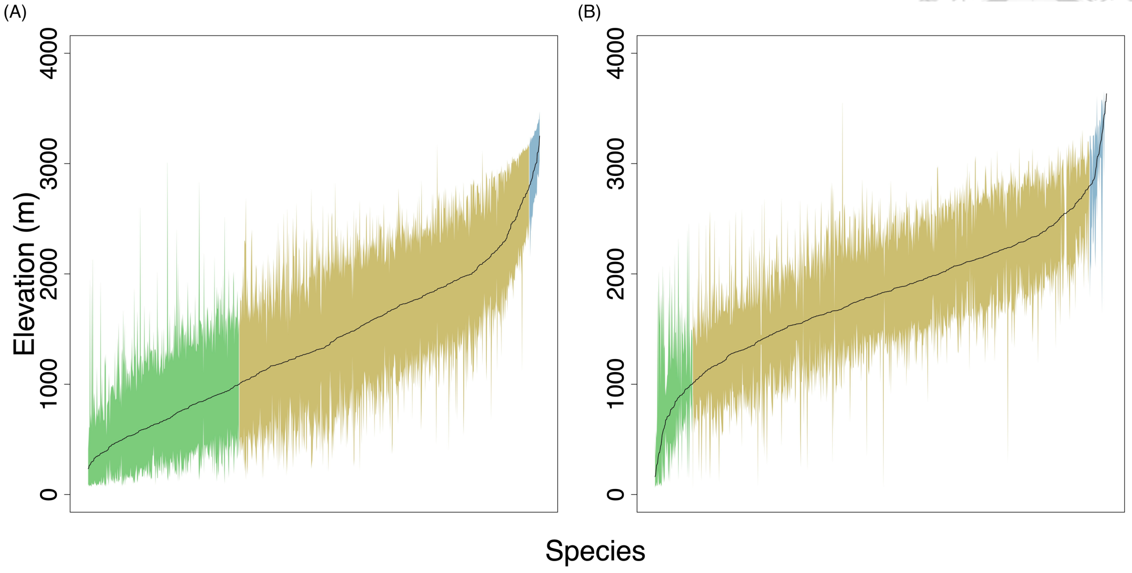

Supplementary Figure 14. The current (A) and future (B) altitudinal distribution of each species. Species were ordered along the horizontal axis based on their median elevation distribution. The black line connects the median elevation of each species, and grey shades represent the range between 10% and 90% percentiles of the distribution in each species. Different colors represent different altitude regions, and the green color is low- altitude, the yellow color is middle- altitude, and the blue color is high altitude.

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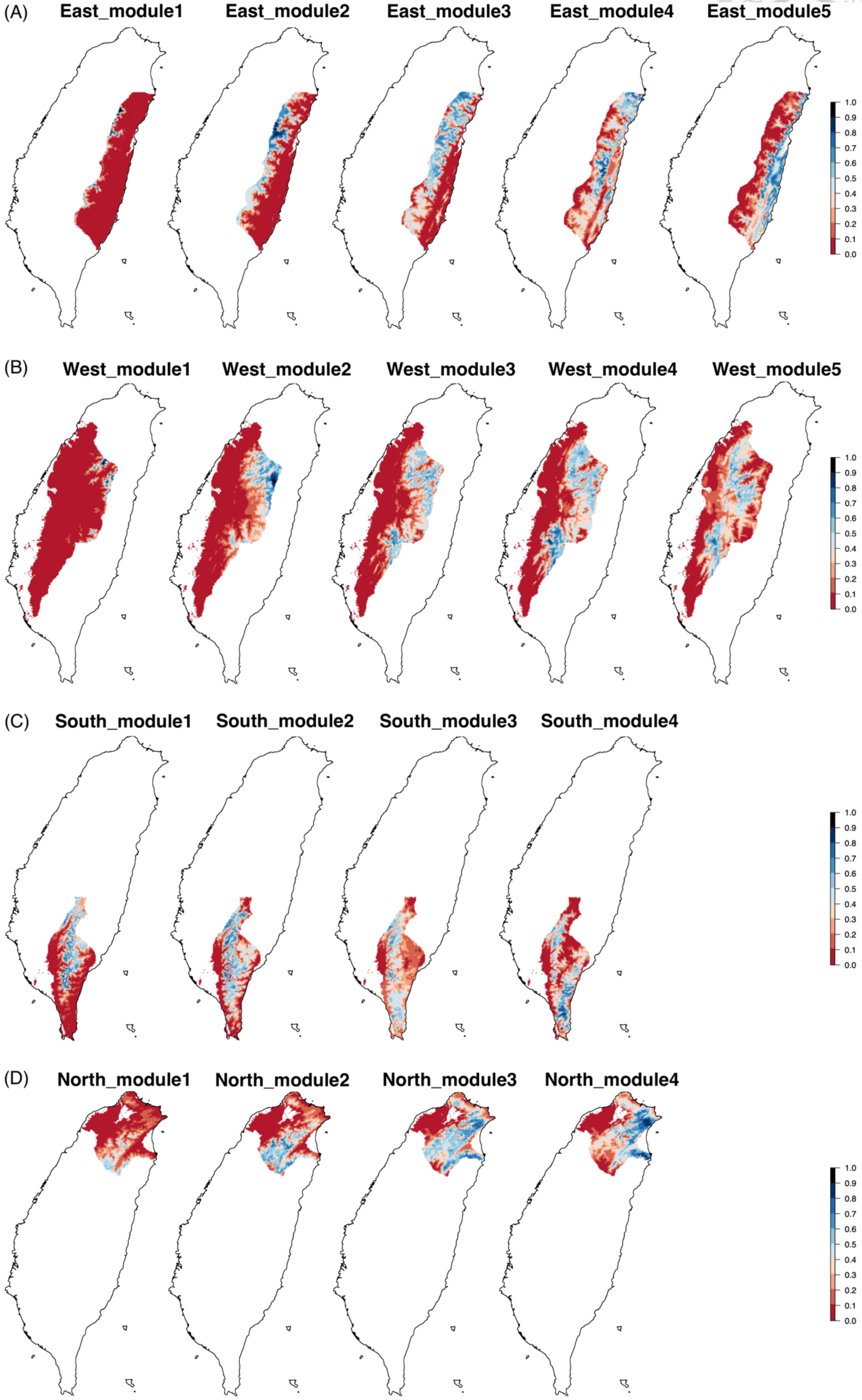

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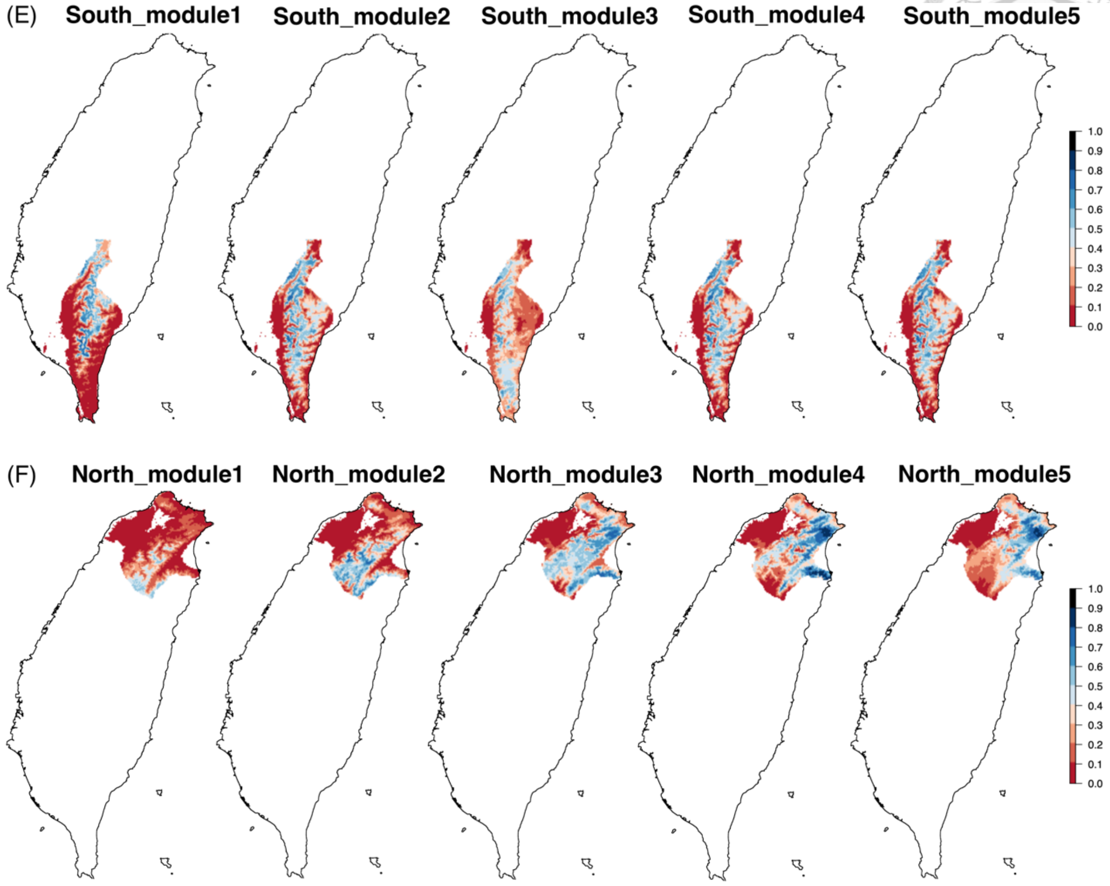
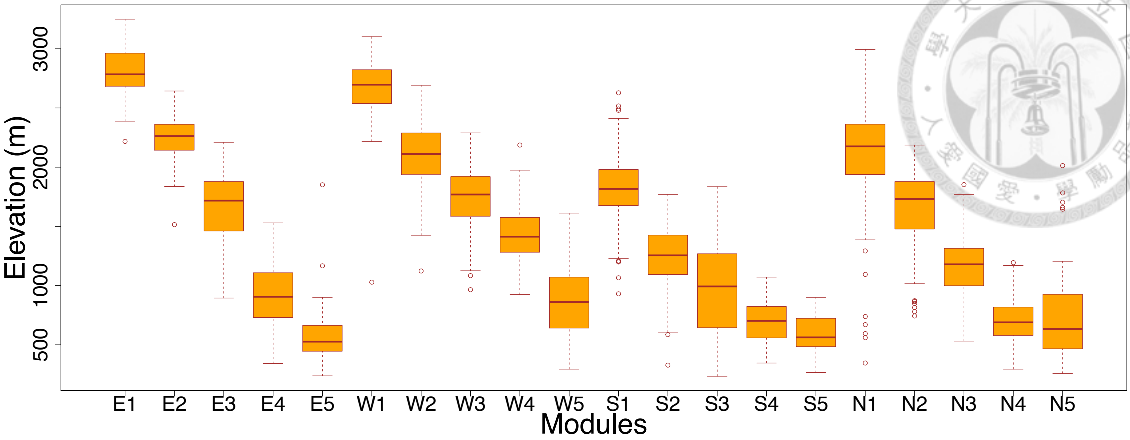


Supplementary Figure 15. The modules' distribution in the eastern (A), western (B), southern (C), northern (D), southern (before merge) (E), northern (before merge) (E) regions of Taiwan. We used Maxent to calculate the distribution of species in each module, and averaged the suitability value to indicate module distribution. Thus, high value means the species in the module have a high probability of presence.



Supplementary Figure 16. The altitudinal distribution of different modules before merge. The boxplots show altitudinal distribution of species in each module. Each data point is the median of a species' altitudinal range.

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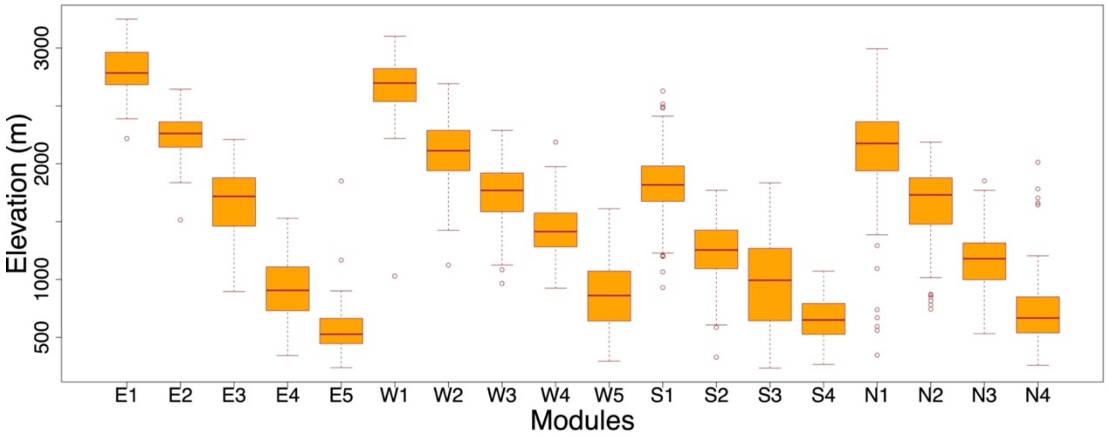

Supplementary Figure 17. The altitudinal distribution of different modules. The boxplots show altitudinal distribution of species in each module. Each data point is the median of a species' altitudinal range.

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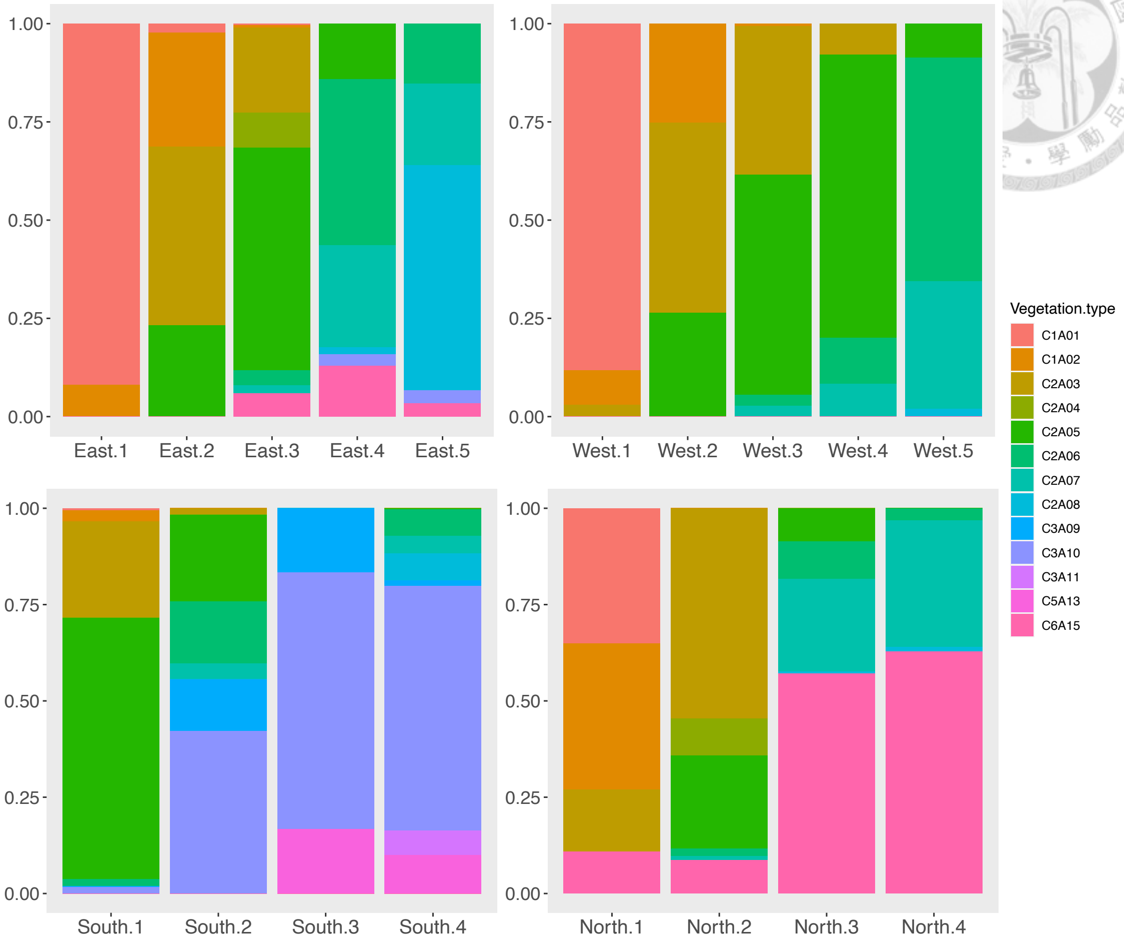
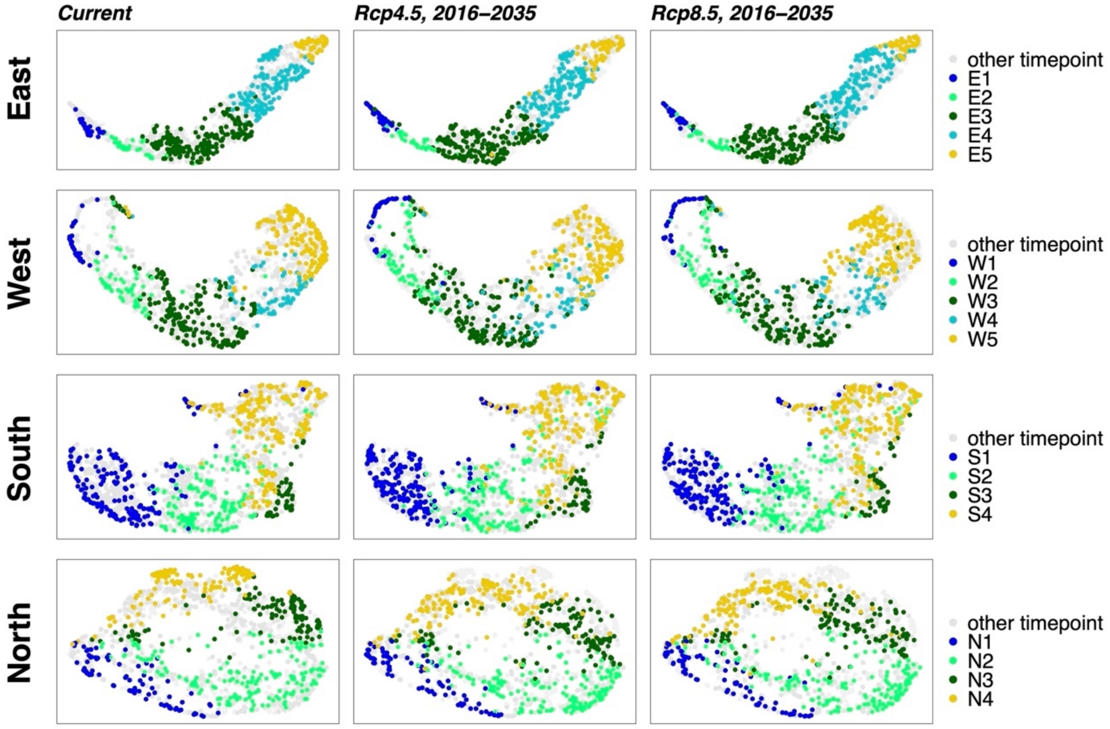
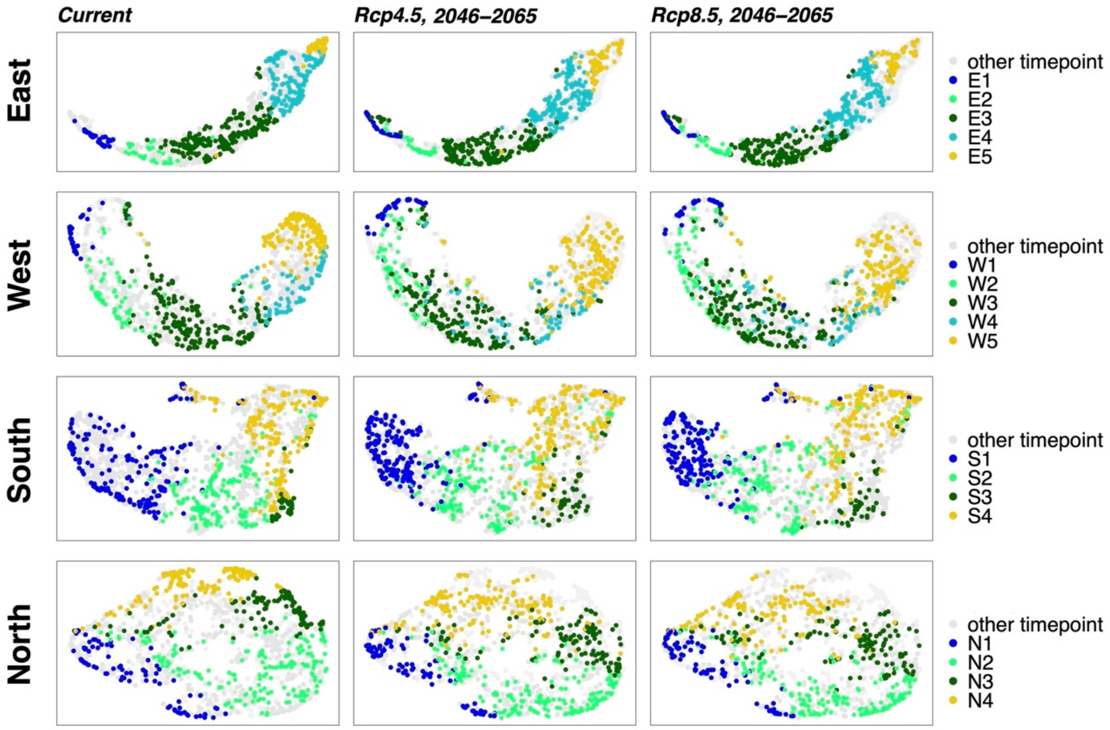


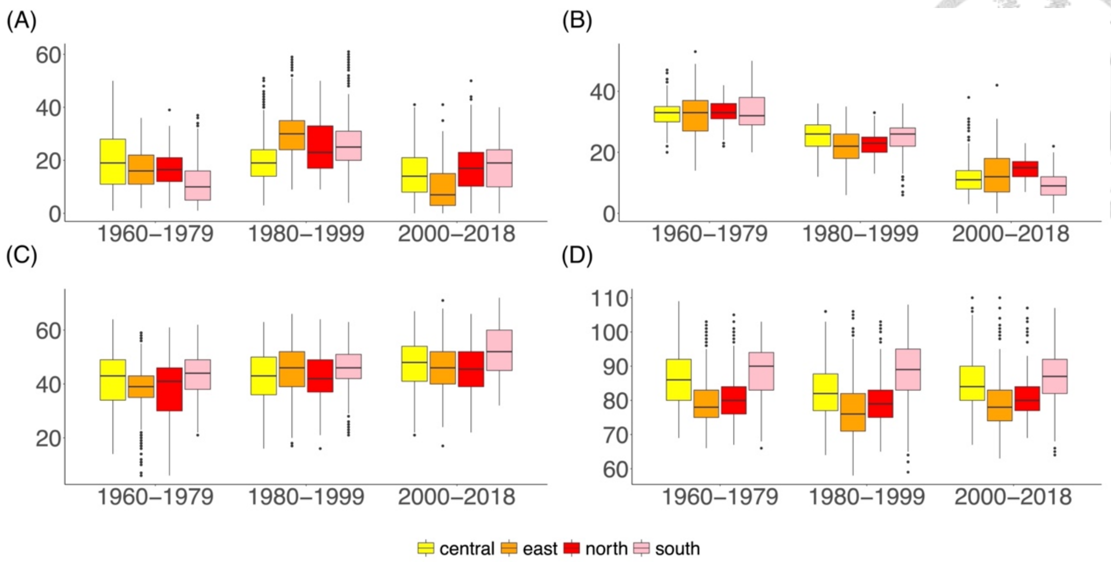
Supplementary Figure 18. The percentage of different vegetation types in different modules. This bar plots show the association between previously defined forest types (Li *et al*., 2013; Lin *et al*., 2020) and modules identified in this study.



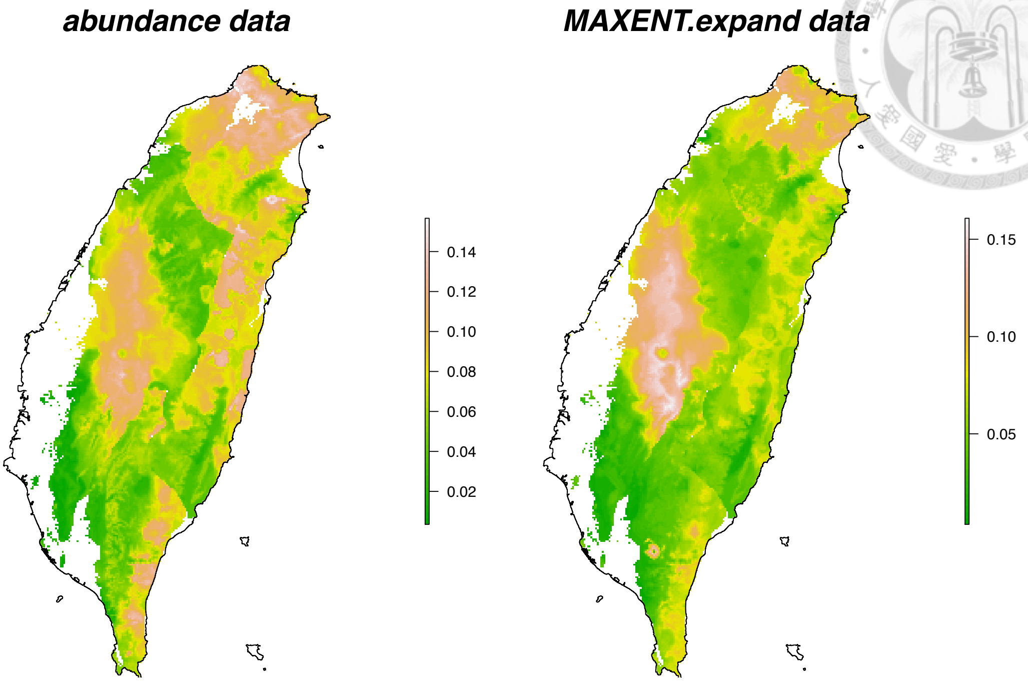
Supplementary Figure 19. The community structure change in current and future conditions in the eastern (A), western (B), southern (C), and northern (D) regions of Taiwan. Shown are the UMAP dimension reduction of species suitability across Taiwan, presenting the co-existence relationship among species across time and climate change scenarios. On UMAP, each species is represented by three dots, presenting its distribution patterns across Taiwan for current and two future conditions (Rcp4.5 and Rcp8.5 in 2016-2035). Within the same region, the three graphs are the same except modules were painted for species in different time points or climate change scenarios (left to right: Current, Rcp4.5, and Rcp8.5).



Supplementary Figure 20. The community structure change in current and future conditions in the eastern (A), western (B), southern (C), and northern (D) regions of Taiwan. Shown are the UMAP dimension reduction of species suitability across Taiwan, presenting the co-existence relationship among species across time and climate change scenarios. On UMAP, each species is represented by three dots, presenting its distribution patterns across Taiwan for current and two future conditions (Rcp4.5 and Rcp8.5 in 2046-2065). Within the same region, the three graphs are the same except modules were painted for species in different time points or climate change scenarios (left to right: Current, Rcp4.5, and Rcp8.5).



Supplementary Figure 21. The frequency of extreme high-temperature (A) low-temperature (B) high-rainfall (C), and drought (D) events in three time periods. Each box shows the frequency of extreme climate events, and different colors represent four regions of Taiwan.



Supplementary Figure 22. The community offset from two data form. The left figure shows the result of using abundance data for gradient forest and community offset analyses, and the right one is we selected grids in the original site and extracted SDM suitability and environmental values for gradient forest and community offset analyses.

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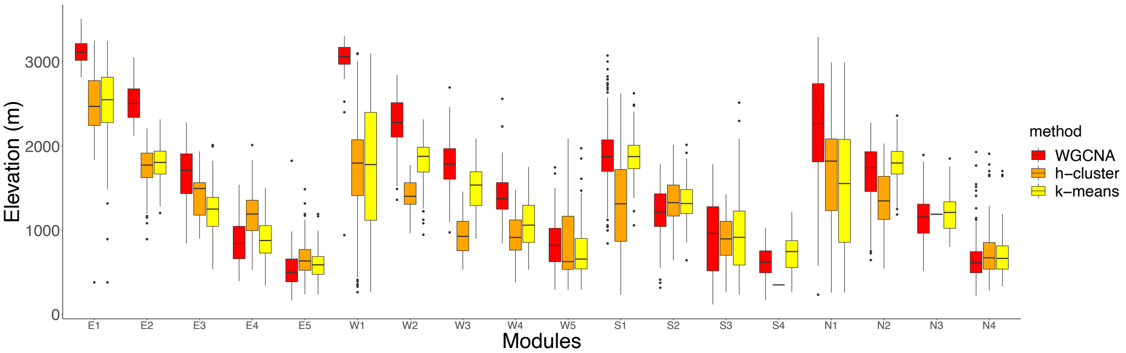

Supplementary Figure 23. The altitudinal distribution of different modules with three different methods. We used three different clustering methods, which were the weighted gene co-expression network analysis (WGCNA), hierarchical clustering (h-cluster), and k-means clustering (k-means). The boxplots show the altitudinal distribution of species in each module. Each data point is the median of a species' altitudinal range.

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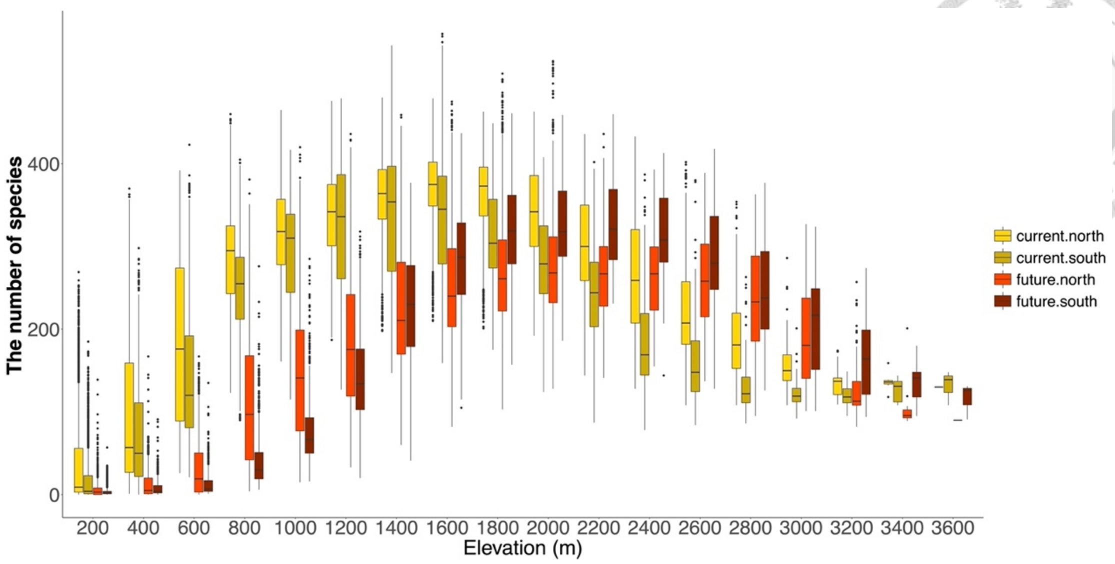

Supplementary Figure 24. The number of species in current and upon climate change (Rcp8.5, MAXENT, 2081-2100). This figure shows the number of species relationships between elevation in current and upon climate change (Rcp8.5, MAXENT, 2081-2100), and we used the Geographic Center of Taiwan (23.973875°N, 120.982024°E) to separate the result of biodiversity composition into the northern and southern parts for the box plots, then compare these two parts.

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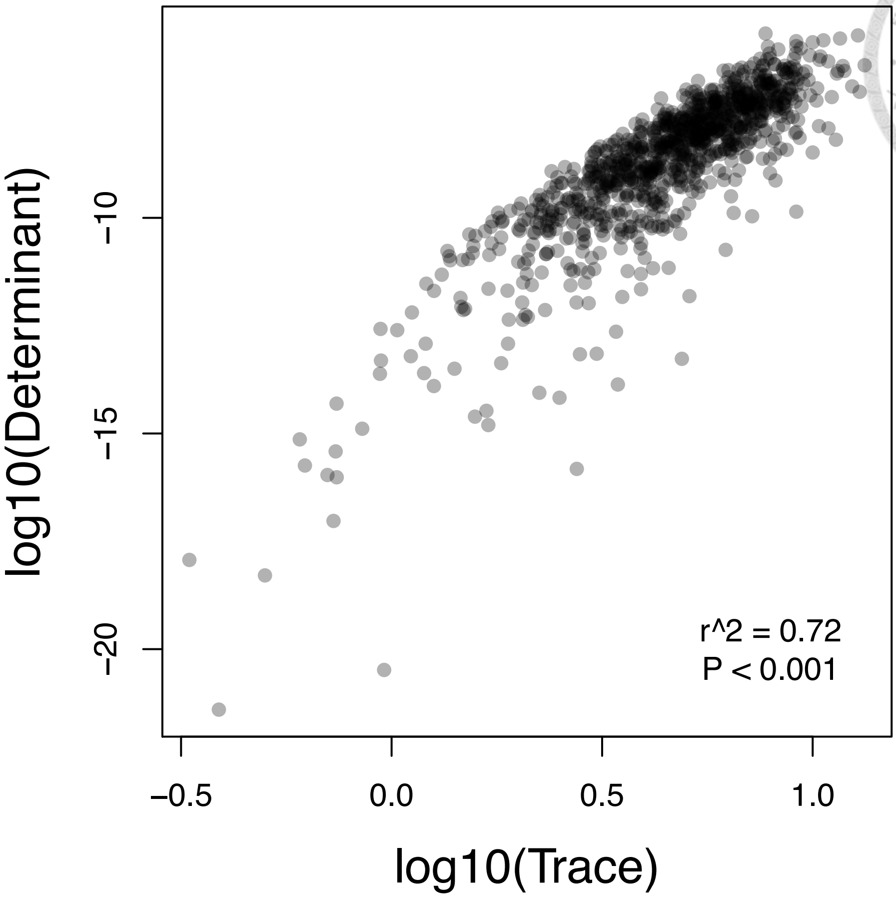

Supplementary Figure 25. The correlation between trace and determinant of species' niche space. Each data point is a species.

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