

Major declines of woody plant species ranges under climate change in Yunnan, China

Ming-Gang Zhang^{1,2,3}, Zhe-Kun Zhou^{1,4}, Wen-Yun Chen⁴, Charles H. Cannon^{5,6}, Niels Raes⁷ and J. W. Ferry Slik¹*

¹Plant Geography Lab, Center for Integrated Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China, ²State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China, ³Graduate University of Chinese Academy of Sciences, 19 Yuquan Road, Beijing, China, ⁴Key Laboratory of Biogeography and Biodiversity, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650204, China, ⁵Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China, ⁶Department of Biological Sciences, Texas Tech University, Lubbock TX 79409, USA, ⁷Naturalis Biodiversity Center, Section Botany, Leiden 2333 CR, The Netherlands

*Correspondence: J. W. Ferry Slik, Plant Geography Lab, Center for Integrated Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China Email: ferryslik@hotmail.com

ABSTRACT

Aim A wide range of forests distributed across steep environmental gradients are found in Yunnan, southwest China. Climate change could profoundly change these forests by affecting species ranges. We produce predictions about species suitable habitat shifts and use these to (1) evaluate species range size change, loss and turn-over under no- and full-dispersal and nine climate change scenarios and (2) identify environmental variables responsible for current species richness and future local species losses.

Location Yunnan Province, Southwest China.

Methods Using MaxEnt, we modelled current distributions of 2319 woody plant species, corrected for collecting bias and found that 1996 had significant spatial association with environmental factors. Using three General Circulation Models (GCMs: CGCM, CSIRO and HADCM3) for the years 2070–2099 (2080s), based on three emission scenarios for each GCM (A1b, A2a and B2a), we predicted the future geographic position of suitable habitat for each species.

Results Although most species were predicted to persist within Yunnan, with a maximum extinction rate of *c*. 6% under the most extreme climate change scenario, up to 1400 species (of the 1996 tested) are expected to lose more than 30% of their current range under the most extreme climate change scenario. Assuming no- or unlimited dispersal minimally affected these outcomes. Species losses were associated with increasing temperature variability and declining precipitation during the dry season.

Main conclusions To conserve Yunnan's woody flora, management efforts should focus on providing elevational migration routes at local scales, with priority for those areas located within previously identified conservation hotspots. As almost all species show range contractions, storage of genetic diversity in seed banks and botanical gardens would be sensible. A change in Yunnan's conservation policy will be needed to counter the predicted negative impacts of climate change on its flora.

Keywords

Climate change, conservation strategies, emigrants, extinction risk, immigrants, species distribution model.

INTRODUCTION

Human-caused climate change has already begun to affect species distribution patterns (Colwell *et al.*, 2008), as global warming drives species towards the poles and upslope (Parmesan, 2006; Wilson *et al.*, 2007; Roberts & Hamann, 2012).

The effect of climate change on local species distribution patterns is central for developing proactive strategies to reduce the impact of climate change on biodiversity (Bellard *et al.*, 2012). Species distribution modelling (SDM) is an effective means to predict the possible change in species distribution patterns under different scenarios of climatic change. SDM

DOI: 10.1111/ddi.12165 http://wileyonlinelibrary.com/journal/ddi uses current associations between environmental variables and species occurrence data to derive species niche models via statistical- or machine-learning procedures (Guisan *et al.*, 2002; Phillips *et al.*, 2006; Roberts & Hamann, 2012). By combining these niche models with spatially explicit predictions for future climates, the future geographic distribution of the suitable habitat for each species can be estimated.

Yunnan province, southwest China, is one of the most diverse floristic regions on Earth and forms a major part of the Indo/Burma biodiversity hotspot (Myers et al., 2000). Yunnan is located at a transitional zone, characterized by strong environmental gradients. Previously, Yunnan was divided into five floristic regions based on surveys and expert opinion (Wu, 1987), but a more recent analysis divided Yunnan into seven floristic regions based on the modelled distribution patterns of 1996 woody plant species (Zhang et al., 2012). The seven regions currently recognized overlap mostly with the original five regions but identified two further regions on Yunnan's central plateau (Fig. 1). The strong environmental gradients and complex geological history of Yunnan have resulted in a disproportionate amount of

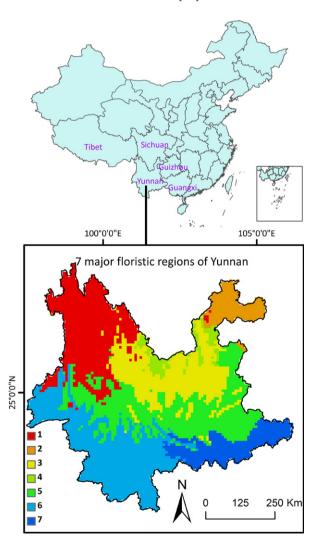


Figure 1 The seven major floristic regions of Yunnan.

China's overall floristic diversity being present in the province (Wu, 1987; Yang *et al.*, 2004), including many endemics. Due to rapid climate change, the plants of Yunnan now face significant environmental changes (Fan & Thomas, 2013). Predicting how the woody flora will respond to these changes is necessary to adapt regional conservation strategies so as to minimize or mitigate the climate change impact on the plant diversity of Yunnan.

Recent reviews on effective conservation strategies under climate change (Heller & Zavaleta, 2009; Game et al., 2011) give some sensible recommendations, such as enlarging the extent of protected areas, designating new natural areas to incorporate the effects of predicted climate change and add or protect corridors that could facilitate migration between regions. In this study, we focus on how climate change will affect the woody plant species distribution patterns of Yunnan in the context of developing conservation strategies. Our aims are to (1) evaluate species extinction risk and range change under two extreme assumptions about species dispersal (no dispersal vs. full dispersal); (2) examine the vulnerability of the different floristic regions of Yunnan to climate change; and (3) determine which environmental variables are responsible for current species richness and future local extinction. These results can provide a rigorous basis for regional conservation management of the woody plants of Yunnan.

METHODS

Species data

Our data included all woody species (except Fagaceae) collected in Yunnan Province that were present in the herbaria of the Kunming Institute of Botany (KIB), Chinese Academy of Sciences. Because most of these specimens had no latitude and longitude data, all collections were georeferenced using the location descriptions as provided on the labels. Of the 85,289 collections, we were able to georeference 60,552 specimens. Subsequently, species presences were scored in 5 arc-minute grid cells (ca. 10 × 10 km), avoiding duplicate species records in each grid cell. The 5 arc-minute spatial resolution matched the environmental data resolution (WorldClim and FAO soil properties). Species that were present in fewer than 5 grid cells were removed from the analysis. Of the 60,552 georeferenced specimens, 42,114 records belonging to 118 plant families representing 2319 species possessed adequate data for further modelling.

Current and future environmental predictors

We initially selected 35 environmental predictors to model the current and future species distribution patterns. These included 19 bioclimatic predictors (1950–2000) plus elevation of the WORLDCLIM dataset (www.worldclim.org) for Yunnan at 5 arc-minute resolutions, and 15 soil variables selected from the FAO database for poverty and insecurity mapping (FAO, 2002). The resolution of 5-arc minutes resulted in 4936 grid cells covering whole Yunnan.

A problem with species distribution modelling is formed by multicollinearity of variables that can result in model over-fitting (Graham, 2003; Pearson et al., 2006). To avoid this problem, we removed highly correlated environmental predictors. For both current bio-climatic and soil predictors, we used Spearman's rank correlation test to select the least correlated variables (spearman's < 0.75) (Tables S1 & S2 in Supporting Information). From correlated variables with Spearman rho higher than 0.75, only the ecologically most important factors were kept. For the current bio-climate predictors, the following variables were included in the analyses: (1) Bio01: Annual Mean Temperature; (2) Bio02: Mean Diurnal Temperature Range; (3) Bio04: Temperature Seasonality; (4) Bio07: Temperature Annual Range; (5) Bio12: Annual Precipitation; (6) Bio14; Precipitation of Driest Month; (7) Bio15: Precipitation Seasonality (Table. S1). Of the current soil predictors, the following variables were included in the analysis: (1) CE-T: cation-exchange capacity (CEC) of clay topsoil; (2) CN-T: C:N-ratio class topsoil; (3) CP-T: organic carbon pool topsoil; (4) Depth: effective soil depth; (5) Drain: soil drainage class; (6) NN-T: nitrogen% topsoil; (7) PH-T: pH top soil; (8) Prod: soil production index; (9) Text.: textural class subsoil (Fig. S1). In total, 16 of the original 35 predictors were kept to model the species distributions. Most of the selected variables have repeatedly been identified as ecologically important in studies across the tropics (Amazon: Raes, 2012; Sundaland: Raes & terSteege, 2007; Raes et al., 2009, in press; Yunnan: Zhang et al., 2012).

The future climate data were downloaded from the International Centre for Tropical Agriculture (CIAT) (www.ccafs-climate.org) which is based on the Intergovernmental Panel on Climate Change Fourth Assessment Report (2007). Our projection included the bioclimatic data created by three General Circulation Models (CGCM, CSIRO, and HADCM3) for the years 2070–2099 (2080s). For each GCM, we included three emission scenarios (A1b, A2a and B2a), A1: Maximum energy requirements, A2: High-energy requirements, B2: Lower energy requirements.

Species distribution modelling and significance testing

To model the current and future species distributions pattern, we used the modelling application Maxent (ver. 3.3.1; www.cs.princeton.edu/~schapire/maxent/) (Phillips *et al.*, 2006). Maxent was specifically developed to model species distributions with presence-only data. Of available species distribution modelling algorithms, Maxent has been shown to perform best, especially when few presence records are available, while it is also the least affected by location errors in occurrences (Graham *et al.*, 2007). Maxent was run with the following modelling rules: (1) for species with 5–10 collection records, linear features were applied, (2) for species with 10–14 records, quadratic features were applied, while

(3) for species with > 15 records, hinge features were applied (for a detailed explanation for choosing these modelling rules see Raes & terSteege, 2007).

As a measure of the accuracy of the SDMs, we used the area under the curve (AUC) of the receiver operating characteristic (ROC) plot produced by Maxent. All measures of SDM accuracy require absences. When these are lacking, as is the case here, they are replaced by pseudo-absences or sites randomly selected at localities where no species presence was recorded (Phillips et al., 2006). However, when SDM accuracy measures are based on presence-only data and pseudoabsences, the standard measures of accuracy (e.g. the often used measure AUC > 0.7) do not apply (Raes & terSteege, 2007). Therefore, we applied the bias-corrected null-model developed by Raes & terSteege (2007) to test the AUC value of an SDM developed with all presence records against the AUC values expected by chance. However, this assumes that collection localities represent a random subset of the study areas environmental space. In many cases, this is not a valid assumption due to collecting biases (Kleidon & Mooney, 2000; Tsoar et al., 2007).

To check for collecting bias in our dataset, we tested whether our 1406 collection localities were random subsamples of the environmental predictor space. To do this, we divided each of the 16 environmental predictors into 10 equal-interval bins based on the ranges observed for Yunnan (Loiselle et al., 2008). We then tested whether the observed frequency distributions represented by the 1406 collection localities differed from those observed for whole Yunnan using a Chi-square test. This showed that for 10 of the 16 environmental predictors, our collection locations represented non-random subsamples of Yunnan's environmental predictor space. To correct for this bias, we developed a bias-corrected null model by testing each species modelled AUC value against 1000 AUC values that were generated randomly by subsampling from all the available collection localities only. When the observed AUC value fell in the top 95% of randomly generated AUC values (for the same sample size as the observed value), it was considered to have a significant non-random distribution and was used in our further analyses. For all the 2319 available species of Yunnan, 1996 species showed a significantly non-random distribution (AUC value \geq 95% CI).

Species migration patterns and extinction risk evaluation

To determine the current and future species distribution patterns of Yunnan, a threshold is required to convert the continuous Maxent prediction values to discrete presence or absence for each grid cell. For SDMs represented by ≥ 10 records, we used the 'conservative' fixed '10 percentile presence' threshold (Raes *et al.*, 2009). For species represented by 5–9 records, we used either the 'sensitivity specificity equality' or the 'sum maximization' threshold, whereby the sensitivity specificity equality threshold means that the absolute

value of the difference between sensitivity and specificity is minimized, and the sum maximization means that the sum of sensitivity and specificity is maximized (Liu et al., 2005, 2011). Once the thresholds were set, the presence/absence of models of all the significant species became available resulting in; (1) a set of presence/absence of models under current climate conditions, and (2) nine sets of projected the presence/absence of models under three emissions scenarios (A1b, A2a and B2a) for each of the three GCMs (CGCM2, CSIRO and HADCM3) for the years 2070–2099 (2080s). Using these sets of models, we created 10 presence/absence matrixes (1 current and 9 future) with the rows representing the 4936 grid cells covering Yunnan and the columns representing the presence/absence of the 1996 modelled species.

We used modelled temporal changes in the composition of species in each grid cell to determine grid cell migration statistics (Hole et al., 2011). Species that were modelled as present under current climatic conditions but as absent under future climate were defined as emigrants; Species that were modelled as present in grid cells under future climatic conditions but were absent under present climate were defined as immigrants; and species that were modelled as present both under current climate and future climate were defined as persistent species. The number of immigrants (I), emigrants (E), persistent species (P) and turnover were calculated for each grid cell (10 × 10 km). Species turnover by pixel was defined as $T = 100 \times (I + E)/(SD + I)$ (Thuiller et al., 2005), where SD means the current species diversity in each grid cell. Grid cells that have a high value of turnover have a large change in species composition.

Extinction risks were evaluated under two extreme species dispersal assumptions (no dispersal and full dispersal). We calculated the percentage of range loss and gain for each species under these two dispersal scenarios and then assigned each species to an International Union for Conservation of Nature and Natural Resources (IUCN) threat category (IUCN, 2001; Thuiller et al., 2005) and classified species into different groups based on the simulated reduction in range size from present to the 2080s. We used the following rules to assign a species to a threat category (IUCN, 2001): Extinct when a species projected loss comprised 100% of its range size, critically endangered when a species was projected lost in > 80% of its range size, endangered when a species was projected lost in > 50% of its range size, vulnerable when a species was projected lost in > 30% of its range size, and low risk when a species was projected to lose less than 30% of its range. Current and future range size (number of grid cells occupied) for each species was calculated based on the differences in predicted presences between the current presence/ absence matrix and the 9 future presence/absence matrixes. The major spatial patterns are similar over all scenarios, but the scenarios with largest change show the most significant changes in spatial pattern. The scenarios with largest change were identified by estimated percentage of emigrants and turnover by pixel. Under this scenario, we first calculated the number of immigrants, emigrants, persistent species and the turnover value of each grid cell (Fig. S2). Subsequently, the sensitivity to climate change of the different floristic regions of Yunnan at the species level was determined using the mean percentage of immigrants, emigrants, persistent species and species turnover (full dispersal).

Environmental variables responsible for current species richness and future local extinction

To identify the environmental factors responsible for current species richness and future local extinction, we explained the current species diversity and percentage of emigrants using variation partitioning (Legendre, 2007). This method is useful when two sets (environmental and spatial predictors) of independent explanatory variables are involved in explaining the variation of an ecologically dependent variable. Because environmental gradients are often spatially autocorrelated spatial predictors alone can explain part of the observed patterns. The nine terms of the trend-surface analysis regression equation $(b_1LAT + b_2LON + b_3LAT^2 + b_4LAT \times LON +$ $b_5 \text{LON}^2 + b_6 \text{LAT}^3 + b_7 \text{LAT}^2 \times \text{LON} + b_8 \text{LAT} \times \text{LON}^2 + b_9$ LON³) were used to describe this spatial pattern in current species richness and future percentage of emigrants (Lobo & Martin-Piera, 2002; Legendre, 2007). The variation in current species richness and future percentage of emigrants was partitioned by performing stepwise multiple regressions. For the current species diversity, we used the current climate and soil predictors. For the percentage of emigrants under climate change, we used the combination of current climate predictors and climate anomalies (climate in 2080 - current climate). Both current climate and climate anomalies were included because the consequences of climate change are dependent on where they occur in environmental space (Araújo et al., 2008; Fitzpatrick et al., 2008).

The stepwise multiple regression analysis, as applied to spatially structured biological processes may result in residual spatial autocorrelation (RSA). This violates the statistical independence of observations and may inflate the type I errors (Dormann *et al.*, 2007; Raes *et al.*, 2009). To test whether RSA was present, we obtained the Moran's I values of the residuals using SAM – spatial analysis in macroecology – software (Rangel *et al.*, 2010). Because the current species diversity and future percentage of emigrants was mostly explained by environmental predictors, we estimated the regression coefficients for the significant environmental predictors only.

Because of the political, rather than biological boundary in southern Yunnan, we assume that the number of immigrants in the southern part of Yunnan will be underestimated because species south of the border that may move northwards under climate change were not included in the analysis. On the other hand, species emigration is a more trustworthy parameter because it depends on species already present in Yunnan, so we applied the environmental correlation analysis on the emigrants only. Because the absolute number of emigrations is strongly linked to overall diversity of grid cells, we used percentage instead of absolute values.

RESULTS

Depending on the climate change scenario, between c. 2-40% of the species will become critically endangered or extinct in Yunnan by the year 2080, with similar outcomes for both unlimited and no dispersal (Figs. 2 & 3). The rates of species emigration and turnover by pixel varied considerably across scenarios (Fig. 4), with the largest change occurring under the CGCM-A2a scenario, with a mean percentage of species emigrating per grid cell of 62.4% and a turnover of 70.9%. Turnover in species composition under the extreme climate change scenario (CGCM-A2a) was greatest in the central and eastern portions of Yunnan (Fig. 5; Table 1) mainly because of the high levels of emigrants in that region. The north and south of Yunnan show the lowest amounts of immigrant species, the southwest and extreme northern parts of Yunnan show the lowest number of emigrants combined with highest number of persistent species (Fig. 5; Table 1). Only in floristic region four is the turnover in species composition mainly driven by immigration, while in all other regions emigration is the main driver of species turnover (Table 1).

The current species diversity and future percentage of emigrants was best explained by spatially structured environmental predictors in the variation partitioning analysis (Fig. S3). The environmental predictors explained 75.9% of the spatial patterns of current species diversity in Yunnan (Table 2; Fig. S3), with the most important environmental variables (highest β -values) being soil texture (negative, i.e. diversity declined on finer grained soils) and annual precipitation (positive). The environmental predictors explained 68% of the emigration patterns, with the most important factors being annual mean temperature (negative), increase in temperature annual range (positive) and increase in temperature seasonality (positive).

DISCUSSION

Spatial patterns in species turnover under climate change

For species to track climate change, long-distance dispersal (dispersal distance ≥ 10 km) often plays an important role (Nathan, 2006; Corlett, 2009; Corlett & Westcott, 2013), even

Table 1 Mean percentage of grid cells with immigrants, emigrants, persistent species and turnover value in each floristic region (Region code can be found in Fig. 1).

	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6	Region 7
Immigrants (%)	14.9	28.3	28.6	122.1	39.4	33.2	20.3
Emigrants (%)	60.7	44.5	80.9	41.0	78.0	42.0	66.4
Persistent species (%)	39.3	55.5	19.1	58.0	22.0	59.0	33.6
Mean value of turnover (%)	65.7	56.7	85.3	72.6	84.8	55.1	72.1

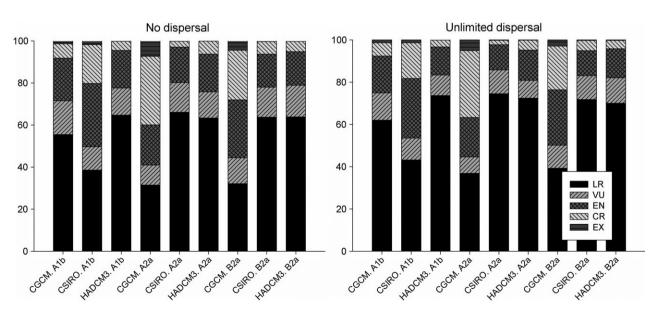


Figure 2 Extinction threat of the current woody plant species in Yunnan under different climate change and dispersal scenarios for the year 2080. Species threat classification (proportional) as based on the IUCN guidelines: Extinct (EX) 100% range lost, Critically endangered (CR) > 80% range lost, Endangered (EN) > 50% range lost, Vulnerable (VU) > 30% range lost, Least concern (LR) not listed.

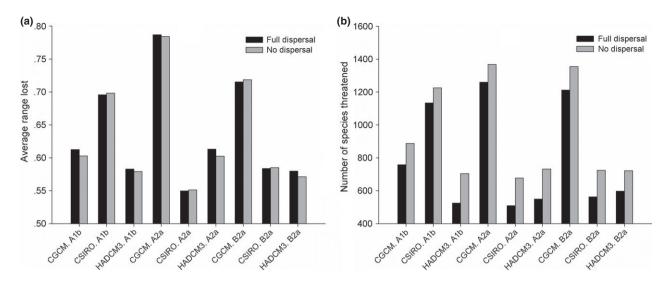


Figure 3 (a) Average range loss of present species in the year 2080 under two dispersal and nine climate change scenarios; (b) Number of threatened species in the year 2080 (species with a range loss > 30%) under two dispersal and nine climate change scenarios.

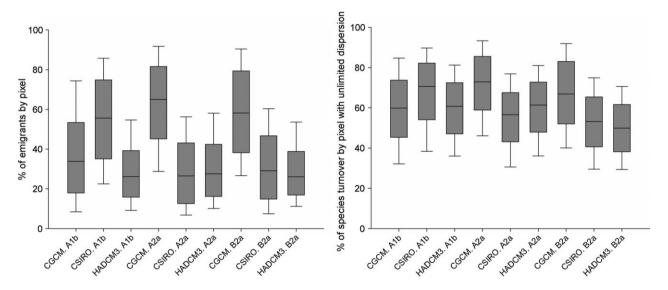


Figure 4 Percentage emigrants and species turnover per c. 10×10 km pixel in Yunnan in the year 2080 compared with present based on nine climate change scenarios. The box plots indicate the range of the projected change per pixel, with the lower and the upper boundary of the box indicating the lower and upper quartile, the line in the middle indicating the median, and the whisker above and below the box indicating the 95th and 5th percentiles value.

though such long-distance dispersal is generally accidental and rare for most plants (Cain *et al.*, 2000), especially for woody species (Corlett, 2009). Therefore, most studies focusing on the mitigation of climate change effects on biodiversity emphasize the importance of landscape connectivity to enable and enhance species latitudinal dispersal (Heller & Zavaleta, 2009; Beier *et al.*, 2011; Game *et al.*, 2011). Our modelling exercise for Yunnan province, however, showed that species vulnerability to climate change was almost identical for models with no and unlimited dispersal, indicating that latitudinal dispersal did not contribute much to species future persistence. This outcome is for a large part driven by Yunnan's peculiar combination of steeply increasing

elevation with increasing latitude leading to limited range expansion possibilities in northern direction, that is, climate change results in compressed rather than northwards shifting vegetation zones. As a result, local loss of species was the major driver of species turnover in Yunnan province.

The combination of high local species losses (emigration) with low levels of local species gains (immigration) spells a rather gloomy future for Yunnan's flora. Although most species are predicted to persist within the province, with a maximum extinction rate of c. 6% under the most extreme climate change scenario, average predicted species range losses vary between 55% and 80%, with up to 1400 species (of the 1996 tested) expected to lose more than 30% of their

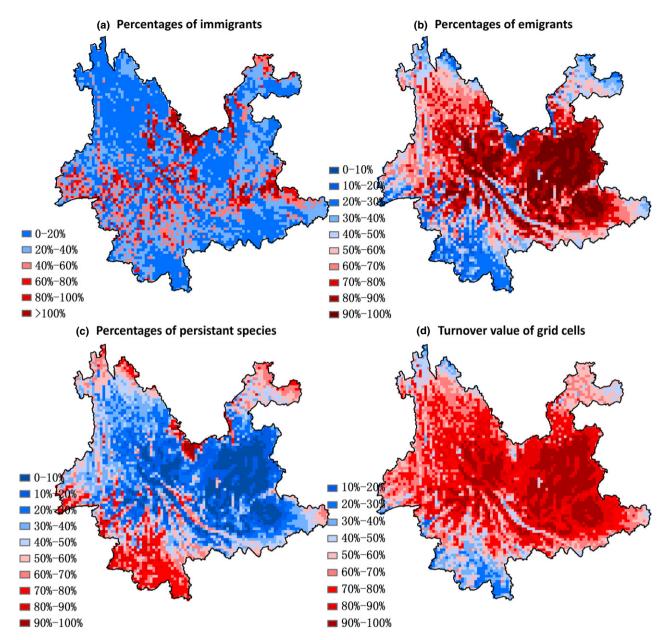


Figure 5 Vulnerability of Yunnan's seven floristic regions to climate change based on the most severe climate change scenario (CGCM-A2a) for the year 2080 under full dispersal. (a) Percentage immigrants per grid cell; (b) Percentage emigrants per grid cell; (c) Percentage persistent species per grid cell; (d) Percentage turnover per grid cell.

current range under the most extreme climate change scenario. Such strong range reductions will likely present problems for the long-term viability of many species populations, potentially leading to higher extinction rates than predicted by our models. On the other hand, our models may have overestimated species losses and range declines because they were based on environmental data layers with a spatial resolution of ca. 10×10 km. Yunnan province has an extremely rugged topography, with some areas near Tibet showing elevational gradients of several kilometres over very short spatial scales. This local scale elevational heterogeneity (within grid cells) was lost in our modelling approach but may turn out to be essential for local species persistence

under changing climates (Scherrer et al., 2010; Gillingham et al., 2012) as species may be able to move upslope, over relatively short distances of several hundred meters, into suitable habitat. However, even under these conditions, the general trend of species range decline, as predicted by our models, will persist as available habitat area also declines with elevation. Furthermore, the upward migration of species may eventually result in patchy and genetically isolated species populations on mountain slopes, thus changing the population structure of many species which originally formed continuous populations.

In the southern, tropical regions of Yunnan, the political rather than biological cut-off of our analysis may have

Table 2 Result of the stepwise multiple regressions between current species richness and future (the year 2080) percentage of emigrants (response variables) and environmental predictors.

Species diversity				Percentage of emigrants				
Pred.	R²-adj	β	t	Pred.	R ² -adj	β	t	
Bio07	0.233	-0.231	-8.528	F-bio14	0.154	-0.178	-18.11	
Text.	0.384	-0.500	-33.784	F-bio07	0.312	0.353	13.58	
Bio12	0.513	0.541	40.321	Bio01	0.380	-0.566	-31.36	
Bio01	0.577	-0.286	-23.595	F-bio04	0.498	0.311	11.58	
pH-T	0.759	-0.040	-2.283	Drain	0.681	-0.031	-2.56	

Pred: the significant predictors that were included in the regression equations; R^2 -adj: cumulative amount of explained variation for addition of each variable in the model; β : standardized coefficient; t: t-value for the full regression model. Bio01: annual mean temperature; Bio07: temperature annual range; Bio12: Annual precipitation; Bio14: precipitation in driest month; F-Bio04: change in temperature seasonality; F-Bio07: change in temperature annual range; F-Bio14: change in driest month precipitation; Drain: soil drainage class; pH-T: top soil pH; Text.: subsoil texture class. Climate anomalies (F-Bio values) are based on change in climate between present and the year 2080.

resulted in biased migration estimates. Species gains through immigration may have been underestimated as species occurring south of Yunnan may migrate north into Yunnan with changing climate. However, it is likely that this effect is limited because of the same combination of increasing elevation with increasing latitude that limits northwards migration of species within Yunnan itself. A larger effect on our predicted migration rates in southern Yunnan is related to the exclusion of the southern range extension into Indochina of many species presently found in southern Yunnan. By not being able to include these records, a large part of the climate tolerance of these species was ignored in our models. This may have led our models to underestimate the upper temperature tolerance of these species (Raes, 2012), resulting in inflated species losses through emigration combined with underestimated species persistence in tropical Yunnan. On the other hand, many studies suggest that local species populations are adapted to local environmental conditions and even though a species range may extend into warmer climates, this does not automatically mean that local populations can tolerate increasing temperatures (Aitken et al., 2008; Alberto et al., 2013). So unless these southern, more heat-tolerant populations can migrate north into southern Yunnan, our results may still reflect the future spatial patterns in species turnover to a reasonable degree.

Environmental factors associated with species turnover

Current spatial distribution of woody plant diversity was strongly linked to spatially structured environmental variables. Our analysis showed that high-diversity areas in Yunnan are characterized by stable, but relatively cool annual temperatures, high annual rainfall and relatively coarse textured acidic soils. Similar patterns have also been detected in Borneo (Raes *et al.*, 2009; Slik *et al.*, 2009), and it supports the hypothesis that climate stability, in combination with sufficient rainfall and the right soil type can promote high biodiversity (Jetz *et al.*, 2004; Araújo *et al.*, 2008). At the

same time, the areas that were predicted to lose high percentages of species (emigrants) due to climate change were characterized by low current temperatures and increasing temperature instability (annual), combined with declining driest month precipitation and good soil drainage. Similar patterns were recently predicted for the western Australian flora (Fitzpatrick et al., 2008), suggesting that increasing climate instability and drought stress associated with climate change will be the main determinants of local species losses. Most of the area on Yunnan's central plateau will witness such changes in climate variability and increased dry season drought stress, corresponding to highest predicted species losses and turnover in this region.

CONCLUSIONS

Low impact of latitudinal migration possibility on species future persistence in Yunnan

This result has important implications for conservation planning in Yunnan as it implies that establishment of latitudinal migration corridors would not make a large contribution to woody plant species conservation into the future under changing climate. Instead focus will have to be placed on local scale in situ management of vegetation types. Recently, Zhang et al. (2012) identified the major woody plant conservation hotspots in Yunnan which can serve as a basis for such a conservation approach. However, a serious mismatch persists between the identified conservation hotspots and the areas in Yunnan that are actually protected (Zhang et al., 2012), and some urgency is needed in reformulating the conservation priorities of Yunnan at the provincial level given the fast land use changes that are currently taking place outside the existing nature reserves.

Almost all species will show range contractions

Our results show that most woody plant species in Yunnan will lose considerable amounts of their range due to the difficulty of moving northwards to track climate change. This may lead to considerable genetic erosion of these plant populations over time. Although this will be difficult to counter, an effort to collect and store specimens from species entire current ranges in seed banks and living collections could be sensible as an insurance against such future genetic losses in the wild populations. Yunnan already has some excellent research facilities and botanical gardens that could realize this aim if given priority funding. At the same time, protection of current conservation hotspots as identified by Zhang et al. (2012) will be essential for maintaining most of Yunnan's woody plant diversity into the future.

Elevational migration will be key

At the local scale, in those areas that have been identified as essential for the conservation of Yunnan's woody plant flora (the conservation hotspots), conservation efforts should focus on providing ample elevational migration possibilities. Elevational migration will be one of the main strategies that plants can realistically employ to track climate change in Yunnan, both because migration distances will be relatively small and thus feasible, and because most regions in Yunnan are extremely topographically heterogeneous thus providing elevational escape. Currently, most land use change is taking place at lower elevations, resulting in severe habitat loss and fragmentation of lowland vegetation types and associated species. A serious effort will be needed to slow this lowland habitat degradation and reconnect lowland vegetations, via corridors or stepping stones (fragment islands), with forests at higher elevations.

The main climatic drivers of species loss will be increasing climate instability and drought

Yunnan's woody plant flora is already shaped, for a large part, by climate variability and rainfall regimes due to its monsoonal climate (Zhang et al., 2012). However, several regions in Yunnan will see a considerable increase in temperature seasonality and drought stress during the dry season in the near future. Although these changes will be difficult to counter, the presence of a continuous vegetation cover generally helps in mitigating the more extreme impacts of climate variability (Chazdon, 2008; Sheil & Murdiyarso, 2009). Strategic reforestation in areas predicted to suffer most from increasing climate instability should therefore be considered to prevent a negative feedback between climate change and habitat degradation as has been observed in many other regions in the world.

ACKNOWLEDGEMENTS

We thank the herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences for providing the digital information of all the woody specimens, and the research assistant Lu Yun for geo-referencing all the specimens. Ke-Ping Ma provided valuable suggestions for this study. NR was funded by NWO – ALW grant 819.01.014.

REFERENCES

- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111.
- Alberto, F.J., Aitken, S.N., Alia, R., Gonzalez-Martinez, S.C., Hanninen, H., Kremer, A., Lefevre, F., Lenormand, T., Yeaman, S., Whetten, R. & Savolainen, O. (2013) Potential for evolutionary responses to climate change evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.
- Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8–15.
- Beier, P., Spencer, W., Baldwin, R.F. & McRae, B.H. (2011) Toward best practices for developing regional connectivity maps. *Conservation Biology*, **25**, 879–892.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377.
- Cain, M.L., Milligan, B.G. & Strand, A.E. (2000) Long-distance seed dispersal in plant populations. *American Journal of Botany*, **87**, 1217–1227.
- Chazdon, R.L. (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, **320**, 1458–1460.
- Colwell, R.K., Brehm, G., Cardelus, C.L., Gilman, A.C. & Longino, J.T. (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, **322**, 258–261.
- Corlett, R.T. (2009) Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica*, 41, 592–598.
- Corlett, R.T. & Westcott, D.A. (2013) Will plant movements keep up with climate change? *Trends in Ecology and Evolution*, **28**, 482–488.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.
- Fan, Z.-X. & Thomas, A. (2013) Spatiotemporal variability of reference evapotranspiration and its contributing climatic factors in Yunnan Province, SW China, 1961–2004. *Climatic Change*, 116, 309–325.
- FAO (2002). Terrastat; global land resources GIS models and databases for poverty and food insecurity mapping. Land and Water Digital Media Series 20.
- Fitzpatrick, M.C., Gove, A.D., Sanders, N.J. & Dunn, R.R. (2008) Climate change, plant migration, and range collapse in a global biodiversity hotspot: the Banksia (Proteaceae)

- of Western Australia. Global Change Biology, 14, 1337–1352.
- Game, E.T., Lipsett-Moore, G., Saxon, E., Peterson, N. & Sheppard, S. (2011) Incorporating climate change adaptation into national conservation assessments. *Global Change Biology*, 17, 3150–3160.
- Gillingham, P.K., Huntley, B., Kuning, W.E. & Thomas, C.D. (2012) The effect of spatial resolution on projected responses to climate warming. *Diversity and Distributions*, **18**, 990–1000.
- Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology Letters*, **84**, 2809–2815.
- Graham, C.H., Elith, J., Hijmans, R.J., Guisan, A., Townsend Peterson, A. & Loiselle, B.A. (2007) The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology*, **45**, 239–247.
- Guisan, A., Edwards, T.C. & Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, **157**, 89–100.
- Heller, N.E. & Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.
- Hole, D.G., Huntley, B., Arinaitwe, J., Butchart, S.H.M., Collingham, Y.C., Fishpool, L.D.C., Pain, D.J. & Willis, S.G. (2011) Toward a management framework for networks of protected areas in the face of climate change. *Conservation Biology*, 25, 305–315.
- IPCC (2007) IPCC Fourth Assessment Report: Climate Change 2007. Intergovernmental Panel on Climate Change, Geneva.
- IUCN (2001). IUCN Red List Categories and Criteria, Version 3.1. Species Survival Commission, Cambridge, UK.
- Jetz, W., Rahbek, C. & Colwell, R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, 7, 1180–1191.
- Kleidon, A. & Mooney, H.A. (2000) A global distribution of biodiversity inferred from climatic constraints: result from a process-based modelling study. *Global Change Biology*, **6**, 507–523.
- Legendre, P. (2007) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, 1, 3–8.
- Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.
- Liu, C., White, M. & Newell, G. (2011) Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography*, **34**, 232–243.
- Lobo, J.M. & Martin-Piera, F. (2002) Searching for a predictive model for species richness of iberian dung beetle based on spatial and environmental variables. *Conservation Biology*, 16, 158–173.
- Loiselle, B.A., Jørgensen, P.M., Consiglio, T., Jiménez, I., Blake, J.G., Lohmann, L.G. & Montiel, O.M. (2008) Predicting species distributions from herbarium collections:

- does climate bias in collection sampling influence model outcomes? *Journal of Biogeography*, **35**, 105–116.
- Myers, N., Mittermeier, R.A. & Mittermeier, C.G. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, T. (2006) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Raes, N. (2012) Partial versus full species distribution models. *Natureza & Conservação*, **10**, 1–12.
- Raes, N. & terSteege, H. (2007) A null-model for significance testing of presence-only species distribution models. *Ecography*, **30**, 727–736.
- Raes, N., Roos, M.C., Slik, J.W.F., Van Loon, E.E. & terSteege, H. (2009) Botanical richness and endemicity patterns of Borneo derived from species distribution models. *Ecography*, 32, 180–192.
- Raes, N., Saw, L.G., van Welzen, P.C. & Yahara, T. (in press) Legume diversity as indicator for botanical diversity on Sundaland, South East Asia. South African Journal of Botany, http://dx.doi.org/10.1016/j.sajb.2013.06.004.
- Rangel, T.F., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, 33, 46–50.
- Roberts, D.R. & Hamann, A. (2012) Predicting potential climate change impacts with bioclimate envelope models: a palaeoecological perspective. *Global Ecology and Biogeography*, **21**, 121–133.
- Scherrer, D., Schmid, S. & Korner, C. (2010) Elevational species shifts in a warmer climate are overestimated when based on weather station data. *International Journal of Bio*meteorology, 55, 645–654.
- Sheil, D. & Murdiyarso, D. (2009) How forests attract rain: an examination of a new hypothesis. *BioScience*, **59**, 341–347.
- Slik, J.W.F., Raes, N., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Meijaard, E., Nagamasu, H., Nilus, R., Paoli, G., Poulsen, A.D., Sheil, D., Suzuki, E., van Valkenburg, J.L.C.H., Webb, C.O., Wilkie, P. & Wulffraat, S. (2009) Environmental correlates for tropical tree diversity and distribution patterns in Borneo. *Diversity and Distributions*, 15, 523–532.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.
- Tsoar, A., Allouche, O., Steinitz, O., Rotem, D. & Kadmon, R. (2007) A comparative evaluation of presence-only

methods for modelling species distribution. *Diversity and Distributions*, **13**, 397–405.

Wilson, R.J., Gutierrez, D., Gutierrez, J. & Monserrat, V.J. (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, **13**, 1873–1887.

Wu, Z.Y., Ed. (1987). Flora of Yunnan. Science Press, Beijing (in Chinese).

Yang, Y., Tian, K., Hao, J., Pei, S. & Yang, Y. (2004) Biodiversity and biodiversity conservation in Yunnan, China. *Biodiversity and Conservation*, **13**, 813–826.

Zhang, M.-G., Zhou, Z.-K., Chen, W.-Y., Slik, J.W.F., Cannon, C.H. & Raes, N. (2012) Using species distribution modeling to improve conservation and land use planning of Yunnan, China. *Biological Conservation*, **153**, 257–264.

SUPPORTING INFORMATION

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

Figure S1 Maps of Yunnan with detailed environmental data.

Figure S2 Maps of Yunnan with detailed species data.

Figure S3 Variance in species patterns explained by environmental and spatial variables.

Table S1 Spearman's rank correlation coefficients (r) for the 7 bio-climate predictors.

Table S2 Spearman's rank correlation coefficients (r) for the nine soil predictors.

BIOSKETCH

Ming-Gang Zhang is currently a post doc at the Institute of Botany in Beijing. He is interested in explaining species distribution patterns in relation to the environment and how these patterns will possibly be affected by climate change.

Author contributions: M.-G.Z., J.W.F.S. and C.H.C. conceived the ideas; Z.K.Z. and W.Y.C. provided the basic data sets; M.-G.Z. and N.R. analysed the data; M.-G.Z., J.W.F.S. and C.H.C. led the writing.

Editor: Bethany Bradley