



Climatic niche models and their consensus projections for future climates for four major forest tree species in the Asia–Pacific region [☆]



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ABSTRACT

Modeling and mapping the climatic niches of forest tree species and projecting their potential shift in geographic distribution under future climates are essential steps in assessing the impact of climate change on forests and in developing adaptive forest management strategies. It is particularly important for selecting suitable tree species to match future climates for afforestation and restoration of forest ecosystems. Large scale afforestation and reforestation projects have occurred or planned in Asia–Pacific region; however, the direct impact of climate change has not been widely considered. This has been at least partially due to the lack of availability of robust inventory data on forest vegetation and lack of access to appropriate climate data. In this study, we used our recently developed model, ClimateAP, to generate a large number of climate variables for point locations and used an ensemble modeling approach with Random Forest to overcome some limitations that exist with vegetation data. Uncertainty in future climates was incorporated into the analysis through consensus based projections using 12 climate change scenarios. We modeled the climatic niches for four economically and ecologically important forest tree species in the region and projected their shift in geographical distribution under climate change. Unusual patterns in the shift of geographic distributions of climatic niches were found in two species in Southern China. The implications of the projections in forest management for adaptation to climate change are discussed.

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1. Introduction

Climate is the primary factor regulating geographic distributions of plant species (Woodward and Williams, 1987; Davis and Shaw, 2001; McKenney and Pedlar, 2003). Most forest tree species are adapted to a range of climatic conditions, which is referred to as their climatic niche (Peterson et al., 1999; Pearson and Dawson, 2003). Due to the long lifecycle and slow rate of migration of forest trees, unprecedented rapid climate change will likely result in a mismatch between the climate that trees are historically adapted to and the climate that trees will experience in the future (Aitken et al., 2008). Individuals or populations exposed to climate conditions outside their climatic niches will likely be maladapted, resulting in compromised productivity and increased vulnerability of species to disturbance such as insects and pathogens (Hamann

and Wang, 2006; Kurz et al., 2008; Fettig et al., 2013). Therefore, understanding the climatic niches of forest tree species and projecting their potential shift in spatial distributions for the future are important to assess the vulnerability of tree species and to develop adaptive forest resources management strategies under a rapidly changing climate, including assisted migration (Huntley et al., 2010; Alfaro et al., 2014; Rehfeldt et al., 2014a).

Climatic niches can be defined as constituting the climatic component of Hutchinson's (1957) fundamental niche (Pearson and Dawson, 2003). As they are often built based on the observed distribution of the target species, these models thus reflect a realized climatic niche (i.e., resulting from climatic and biotic constraints, such as interspecific competition) (Pearson and Dawson, 2003; Holt, 2009) as opposed to the fundamental niche (i.e., solely based on the species' environmental requirements) (Hutchinson, 1957). As models of this form involves biological and ecological components, thus they are typically referred to as climatic niche models, bioclimatic envelope models or ecological niche models. We used these terms interchangeably in this study.

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The volume of literature using climatic niche models has been rapidly growing in recent years, while debate about the usefulness of the approach has also followed. A recent review suggests that the criticism has often been misplaced in regard to the objectives of the climatic niche models (Araujo and Peterson, 2012). A climatic niche model defines and predicts the suitable climatic habitat rather than the actual distribution of a species, which involves a series of evolutionary and ecological processes (Aitken et al., 2008). Therefore, a climatic niche model is technically not a species distribution model (SDM) but a habitat suitability model (Keith et al., 2008; Anderson et al., 2009). Confusion between these two kinds of models has led to unrealistic expectations about the outcomes from climatic niche models (Araujo and Peterson, 2012). As a result, many now feel that these so-called SDMs cannot meet users' expectation in adaptation decision making or species conservation strategies (Keenan, 2015).

The distribution and potential shift of climatically suitable habitats are the target of many ecosystem management activities. This information allows users to assess the vulnerability and climate change impact for species or ecosystems for adaptation and conservation (Schueler et al., 2014; Keenan, 2015). Bioclimatic envelope models are reasonably suited for informing species selection and assisted migration in reforestation or afforestation (McLane and Aitken, 2012; Gray and Hamann, 2013; Alfaro et al., 2014). Using the species that best match both current and future climates, regenerating stands will have a better chance of remaining healthy, productive and able to maximize their ecological and/or economic value under a changing climate. This is particularly important given the stated policy aim of planting 20 million hectares of forests in the Asia Pacific over the coming years (Rozelle et al., 2000). Climatic niche models, if properly established and interpreted, can provide valuable, first-order assessments of the potential impacts of climate change and provide a scientific basis for developing adaptive strategies in forest management (Huntley et al., 2010; Fetting et al., 2013; Alfaro et al., 2014; Rehfeldt et al., 2014b).

Bioclimatic envelope models have widely been used in North America (Hamann and Wang, 2006; Rehfeldt et al., 2006; McKenney et al., 2007; Wang et al., 2012a) and Europe (Araujo and New, 2007; Buisson et al., 2010; Lindner et al., 2014). However, related studies in Asia Pacific are lagging behind. This is partially due to the lack of vegetation data and limited access to high quality climate data and to a large number of projections for future climates. In this study, we chose three major forest tree species in China including Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook), Masson Pine (*Pinus massoniana*) and Chinese pine (*Pinus tabulaeformis* Carr.). We also chose a major plantation tree species in Australia, blue gum (*Eucalyptus globulus* Labill.). Chinese fir and Masson pine are the two most important subtropical coniferous species in China. Chinese fir occupies about 30% of all plantations in China accounts 25% of China's national commercial timber production, thus it plays a major role in environment, timber supply, and human society (FAO, 2006). Chinese pine is the most widely distributed conifer in North China, with a natural range that stretches from northeastern to northwestern China, between latitudes 31°00' and 44°00'N and longitudes 101°30' and 124°25'E (Xu, 1993). Within this range it grows as discrete populations in mountain areas at elevations from 100 to 2700 m (Xu et al., 1993). Blue gum, an evergreen broadleaved tree species, is one of the most widely cultivated trees native to Australia (Booth, 2013). It has four subspecies distributed across southeast Australia. The main objectives of our study is to (1) develop climatic niche models for each of the four major forest tree species in the Asia Pacific considering the limitation of vegetation data; (2) identify climate variables that are important in determining the climatic niche for each species; and (3) project climatic niches for future periods addressing the uncertainty in future climates.

2. Data and methods

2.1. Vegetation data

Presence-absence observations for Chinese fir, Masson pine and Chinese pine were obtained from the digital version of Vegetation Map of China (1:1000,000) provided by "Environmental & Ecological Science Data Center for West China, National Natural Science Foundation of China" (link: <http://westdc.westgis.ac.cn>). A shape file of the distribution for each species was generated from polygons with the species present. The shape file was then rasterized at the spatial resolution of 0.008333 arc min (approximately 1 km). Each data point (i.e., a raster pixel) within a polygon of presence was assigned as presence of the species. Similarly, a data point within a polygon of absence was assigned as absence within the range of the species distribution and expanded by 200 km in each of the four directions if possible following Barbet-Massin et al. (2012). Due to a long history of anthropogenic disturbances to forests in China the current distributions of the species are likely to be underestimated. Thus, some of the absence data points were assumed to be false absences. An adjustment was applied to our modeling process to address this consideration (see below).

For blue gum, 7, 172 presence observations were obtained from the Atlas of Living Australia (Atlas) (<http://www.ala.org.au>). These observations were aggregated from a wide range of data providers including museums, herbaria, community groups, government departments, individuals and universities. As there were no absences demarcated in the observations, pseudo-absence data points (Elith and Leathwick, 2007; Barbet-Massin et al., 2012) were generated with the following steps: (1) generation of grid locations at the spatial resolution of 0.008333 arc min for areas within the range of the species distribution and extended by 200 km in each of the four directions if possible; (2) randomly sampling 50,000 pseudo-absence data points from the grid locations; and (3) elimination of false-absence data points in the modeling process as described below. After the presence-absence datasets were constructed, the elevation for each data point was extracted, based on its geographic coordinates, from a 90 × 90 m digital elevation model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM). The latitude, longitude and elevation of the datasets were then used to extract climate data.

2.2. Climate data

The availability of a climate data for the Asia Pacific was achieved through the development of a high-resolution climate model, ClimateAP. This model was used to generate climate data across the region. ClimateAP is a climate data downscaling tool developed for the Asia-Pacific region using the same downscaling algorithms used in ClimateWNA (Wang et al., 2012b) which extracts and downscales PRISM (Daly et al., 2008) and WorldClim (Hijmans et al., 2005) 1961–1990 monthly normal data (2.5 × 2.5 arcmin) to produce seasonal and annual climate variables for specific locations (scale-free) based on latitude, longitude and elevation. The program uses the scale-free data as a baseline, in combination with monthly anomaly data (relative to the 1961–1990 normals) from IPCC AR5 general circulation models (GCMs) to calculate and downscale (i.e., a delta downscaling approach) monthly, seasonal and annual climate variables for future periods. The output of the program includes both directly calculated and derived climate variables. For this study, we generated 66 annual and seasonal climate variables for the point locations with presence and absence of the species for the reference normal period 1961–1990. Monthly climate variables were not considered due to the large number of annual and seasonal climate variables. For the

predictions and projections of the geographic distribution of each species for the reference period (1961–1990 normal) and three future periods (2020s, 2050s and 2080s), gridded climate data were generated at the spatial resolution of 4×4 km for each of these periods for China and Australia. For future projections, the gridded climate data were generated for 12 climate change scenarios including six AR5 GCMs and 2 emission scenarios (RCP4.5 and RCP8.5) (Taylor et al., 2012). The six GCMs include: ACCESS1-3, BCC-CSM1, CanESM2, CNRM-CM5, CSIRO-Mk3-6-0, and HadGEM2-ES (<http://cmip-pcmdi.llnl.gov/cmip5/availability.html>).

2.3. Statistical analysis

We used the R version Liaw and Wiener (2002) of Breiman (2001) of the Random Forests (RF) algorithm to model relationships between climate variables for the reference period and the presence and absence of each of the four species. RF produces many classification trees, collectively called a ‘forest’, and aggregates the results over all trees. Each of these decision trees in the forest is constructed using a bootstrap sample of the input data (i.e., a random sample with replacement) so that the resulting dataset (‘bagged sample’) contains about 64% of the original observations, and the remaining observations comprise the ‘out-of-bag’ (OOB) sample. Using the trees grown from a bootstrap sample, each of the independent observations in the OOB sample is classified (assigned to either presence or absence) and a model prediction error, called the OOB error (% of incorrectly classed observations), is calculated. RF is designed for overcoming collinearity and over-fitting problems (Breiman, 2001; Dormann et al., 2013) and considered as one of the most credible statistical methods for climatic niche model building (Rehfeldt et al., 2006; Elith et al., 2008; Wang et al., 2012a).

RF works best if the samples are relatively balanced between classes (Breiman, 2001; Rehfeldt et al., 2006; Barbet-Massin et al., 2012). Our sample data were unbalanced with the number of locations for absence much greater than that for presence. One way to balance the samples was to randomly sample the data points for absence to match the number of samples for presence. However, this can lead to a poor representation of the areas for the absence of the species. We applied a multiple “forests” approach to build an ensemble of RF models; each RF model was built with randomly sampled data points for absence while the data points for presence remained the same. The final prediction was based on the ensemble of the 10 individual model predictions. This also is a recommended method when using machine-learning based modeling approaches (Barbet-Massin et al., 2012).

To remove the false-absence samples from the absence data points for the three species in China, we eliminated absence samples with an absence probability of less than 0.20 in each RF model, which removed about 10% of the absence data points. To maintain the balance in sample size between presence and absence, 10% more absence samples were taken at the initial sampling step as mentioned above. The same approach was also used to eliminate the false-absence samples from the pseudo-absence data points

for blue gum in Australia. However, we increased the threshold probability from 0.20 to 0.25 based on the assumption that there were more false-absence samples in the pseudo-absence data. This also removed about 10% of the pseudo-absence samples.

RF generates importance values for each of the predictors. We used the importance values to optimize the model and to identify the climate variables that were important for determining the climatic niche of each species. All 66 climate variables were included in the initial RF model. The least important climate variables were iteratively removed until only two climate variables remained in the model (i.e., the least possible number of predictors for RF). By comparing the accuracies of different RF models composed of a different number of climate variables the best RF model was identified and selected. The final RF models were therefore built using the optimal combination of climate variables for each of the four species.

The models were also optimized for the number of trees in each forest and the number of predictors selected at each node. We used 300 trees, which was more than adequate, for all species. The effect of the number of predictors selected at each node was minor, so we used the default square-root of the number of climate variables (Breiman, 2001).

The final RF models were then fed with climate variables for the gridded data points to generate spatial distributions of the climatic niche for each species for the reference period (1961–1990 normal period) and future periods (2020s, 2050s and 2080s). For the reference period, the ensemble predictions for presence of a species were determined from 10 forests generated for each gridded pixel. For future periods, the frequency was calculated at two levels; the first was among the 10 forests and the second was among the 12 climate change scenarios. We set it as “presence” if the number of predictions for presence was equal or larger than five (i.e., 50%), so that we only needed to count predictions for “presence” among the climate change scenarios to determine the consensus of the projections. Since blue gum was modeled at the subspecies level, we could not count the frequency for multiple categories. Instead, we used the mode of predictions as the final outputs. The final outputs were then imported into ArcGIS (v10.2.1) to generate maps.

3. Results

3.1. Climatic niches of the species and important climate variables

The overall accuracies of the models were high (>90%) for all species modeled (Table 1). The climatic niche for each species in terms of the most commonly used climatic variables (mean annual temperature and precipitation) were defined by the models (Table 1). The OOB error rate was higher for absence than for presence except for blue gum. This was expected as the sampling rate for absences was much smaller for blue gum which in turn affects the error rate.

Through the removal of the least important climate variables from the RF model each time, we identified the best combination of climate variables for the RF model for each species. The change

Table 1
Model error rates and major climate profiles for the climatic niches of the four major forest tree species.

Species	Model error rate (%)			Mean annual temperature (°C)	Mean annual precipitation (mm)
	Presence	Absence	Overall		
Chinese fir	5.4	11.8	8.6	16.9 (9.2–22.6)	1637 (834–3062)
Masson pine	3.0	9.7	6.4	17.6 (6.4–23.5)	1553 (650–3199)
Chinese pine	7.1	12.4	9.8	7.3 (0.4–14.7)	620 (228–1122)
Blue gum	9.7	6.8	8.1	12.0 (4.6–18.4)	887 (455–2928)

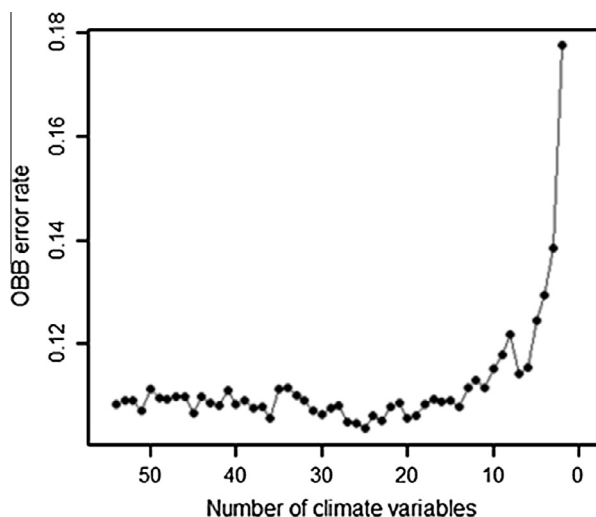


Fig. 1. Changes in error rate of RF model prediction for out-of-box (OOB) samples with the least importance climate variable removed step by step.

in the OOB error rate with various number of climate variables is illustrated for Chinese fir in Fig. 1. The level of the change was not substantial when the number of climate variables was greater than 20. The 10 most important climate variables for each species are listed in Table 2.

The ensemble predictions of the geographic distribution of the climatic niche for each species are illustrated in Figs. 2a, 3a, 4a and 5a. The predictions of the 10 RF models using random samples for absence agreed for vast majority of the areas, while the disagreement only occurred at margins of the climatic niches for all the four species. The predicted geographic distribution of each species climatic niche was larger but congruent with its current distribution. This was particularly the case for Chinese fir.

3.2. Consensus projections of the geographic distribution of the climatic niches for future periods

Consensus based projections of the future geographic distribution of the climatic niches among the four species shared some common features (Figs. 2–5). The projections were highly consistent among the 12 different climate change scenarios for the 2020s, suggesting that the uncertainty in projections of the change in species geographic distribution is relatively low for the near future. However, the consistency declined in the 2050s and

2080s scenarios. Another common feature, was the upward shift in elevation of the projected distribution for each species. The magnitude of the shift was substantial (up to 1100 m by the 2050s). Interestingly, no clear shift in latitude was projected as commonly expected for species with the exception of blue gum, which showed a slight southward shift. The size of the climatic niches were projected to contract for most of the species (3 out of 4) and ranged between 24% and 34% by the 2050s.

For Chinese fir and Masson pine, contractions along the trailing edge of their climatic niches were projected (Figs. 2 and 3). Surprisingly, the expansion of their climatic niche along the leading edges was not predicted. For Chinese pine (Fig. 4), the expansion of its climatic niche was substantial (47% by the 2050s) (Table 3). Interestingly, the expansion was predicted to occur westward instead of northward. For blue gum, the projected shift under future climates was southward towards the edge of the continent, resulting in a considerable contraction of its geographic distribution (–24% by the 2050s) (Fig. 5 and Table 3). Projected changes in the area of the climatic niches varied considerably among sub-species (Table 4). The distribution of the climatic niche of *E. globulus* ssp. *pseudoglobulus* was projected to nearly disappear by 2050s. In contrast, the size of projected climatic niche for *E. globulus* ssp. *globulus* remained almost the same. The contraction for *E. globulus* ssp. *bicostata* was also substantial (–50%).

4. Discussion

4.1. Climatic niches of the species

Our results suggest that the climatic niches of the major forest species in the Asia-Pacific region can be modeled with a combination of climate variables at an accuracy consistent with other regions (Rehfeldt et al., 2006; Gray et al., 2011; Rehfeldt et al., 2014a). The application of following approaches in this study contributed to the low error rates observed in the climatic niche models for the four tree species. These approaches included: (1) the removal of false-absence samples; (2) the optimization of the combination of climate variables; and (3) the use of multiple forests to address the issue of an unbalanced dataset. The developed climatic niche models thereby produced credible predictions of the current geographic distributions for four important tree species in the Asia Pacific (Figs. 2a, 3a, 4a, and 5a). The predicted distribution of the climatic niche included both the areas where the species are currently occupied and areas where the climatic conditions are suitable for the species, but where they may not be present due to various factors including physical barriers, adaptational lag and/or human interference. The models do not consider the role of soil

Table 2

The 10 most important climate variables for each of the four forest species based on the importance values (Imp. value) generated from the Random Forest models.

Chinese fir		Masson pine		Chinese pine		Blue gum	
Climate variable	Imp. value	Climate variable	Imp. value	Climate variable	Imp. value	Climate variable	Imp. value
PPT_MAM ^a	40.6	TD	33.8	CMD_JJA	39.9	PPT_DJF	41.1
TD	35.6	PPT_MAM	32.8	PPT_JJA	37.8	Eref_MAM	32.1
Tmin_JJA	34.6	CMD_DJF	31.4	Tmin_JJA	32.6	PPT_JJA	39.3
PPT_SON	30.4	PPT_JJA	26.9	TD	31.1	Eref_JJA	26.6
Tmin_DJF	29.6	PPT_DJF	22.9	DD5_SON	25.4	TD	30.7
Eref_MAM	29.1	DD5_JJA	22.2	MAP	24.0	CMD_DJF	27.7
PPT_JJA	28.9	Tmax_MAM	22.0	MWMT	23.8	DD5_DJF	26.6
CMD_SON	27.8	CMD_SON	20.5	CMD_SON	23.7	EXT	28.7
Tmin_SON	27.7	Eref_JJA	19.8	DD5_JJA	23.1	PPT_SON	26.5
DD5_JJA	27.6	Tmin_JJA	19.2	CMD	22.8	Tmin_MAM	27.5

^a PPT = precipitation; Tmin = mean minimum temperature; Tmax = mean maximum temperature; MAP = mean annual precipitation; EXT = extreme maximum temperature over 30 years; Eref = Hargreaves reference evaporation; CMD = Hargreaves climatic moisture deficit; MWMT = mean warmest month temperature; MCMT = mean coldest month temperature; TD = the difference between MWMT and MCMT, also referred to as continentality; DD5 = degree-days above 5 °C, growing degree-days; MAM = March–May; JJA = June–August; SON = September–November; DJF = December–February.

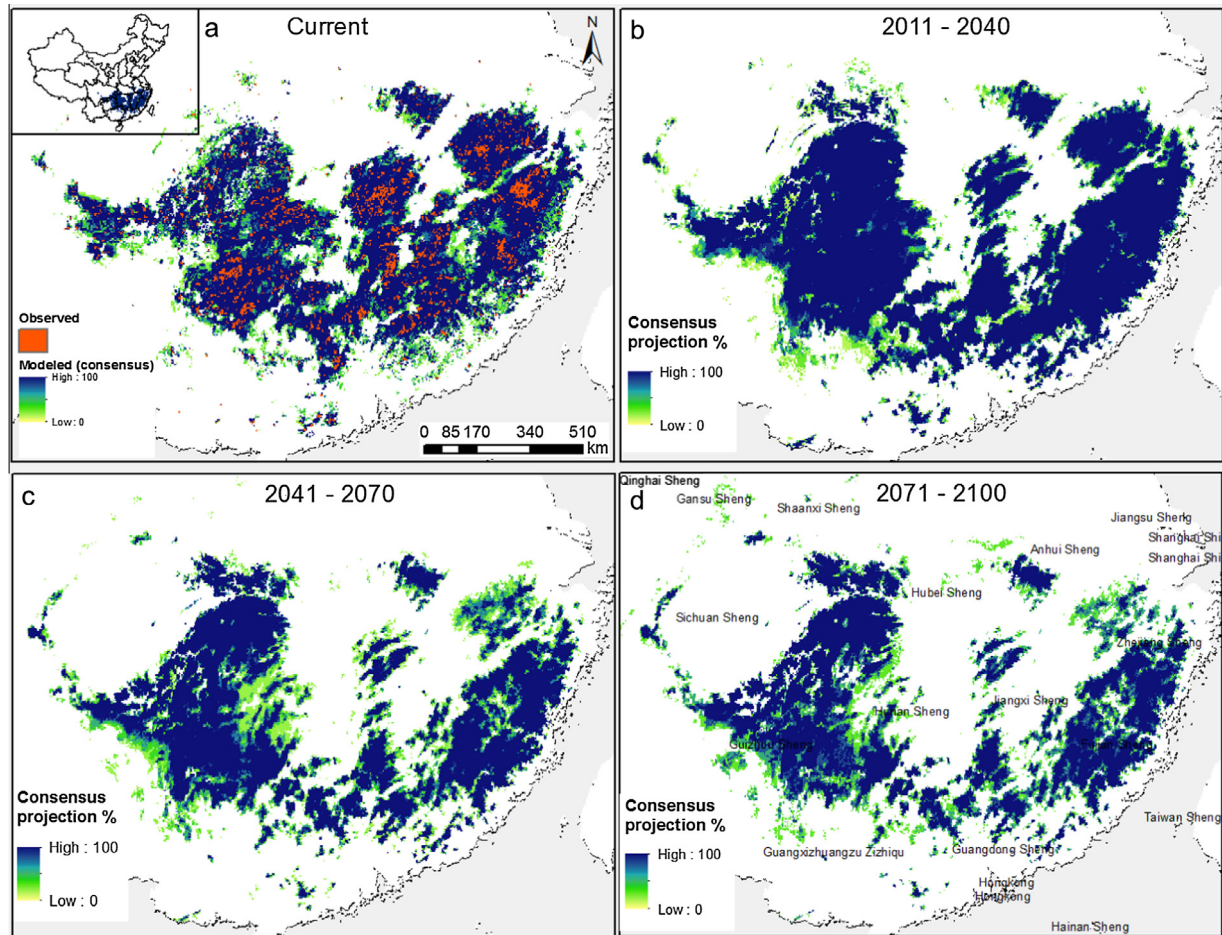


Fig. 2. Geographic distributions of current and potential climatic niches for Chinese fir based on ensemble predictions for the current (1961–1990) and consensus projections for the three future periods 2020s, 2050s and 2080s.

properties and the incidences of disease, insects or fire regimes that may limit a species occurrence/expansion into climatically suitable areas.

4.2. Consensus projections for the future

Uncertainty in future climate is probably the greatest challenge in assessment of the impact of climate change on forest ecosystems and tree species and therefore in developing adaptive strategies in forest management for the future. There are four greenhouse gas emission scenarios and over 20 general circulation models (GCMs) in the latest IPCC report (IPCC, 2014). For a given period, there are over 80 (4 scenarios \times 20 GCMs climate change scenarios) different projections of climate conditions. From a modeler's point of view, projections for a large number of climate change scenarios are resource demanding and time consuming as the spatial datasets are usually huge. Therefore, most of the future projections involve only a small number of climate change scenarios. Some studies used ensembles by averaging over GCMs or emission scenarios. However, such ensembles may cancel out the spatial and seasonal patterns of specific GCMs as discussed in Wang et al. (2012a). From a practitioner's point of view, the large range of scenarios makes it almost impossible to develop multiple adaptive options to accommodate a range of potential futures. Consensus projections that aggregate multiple individual projections provide an effective option for practical applications (Wang et al., 2012a). We believe that the consensus projections provide a solid basis for the assessment of climate change impacts on species and for

the development of adaptive strategies in forest resources management under a changing climate. Specific characteristics of the consensus projections for each species are described below.

4.3. Chinese fir

Our results suggest that the geographic distribution for Chinese fir may substantially contract under predicted climate change. The contraction in its current distribution, particularly in the south, was not a surprise as warmer climate conditions are projected to occur in the southern parts of its current distribution (Fig. 2). What was a surprise was the lack of a predicted northward shift for this wide spread species. The northward expansion of trees in response to climate change is commonly predicted in other studies (Hamann and Wang, 2006; McKenney et al., 2007; Rehfeldt et al., 2014a). The limited northward expansion is likely attributable to the spatial pattern of precipitation in China. Current species distribution and its predicted current climatic niche occur in areas with a mean annual precipitation (MAP) above 830 mm. Under future climates, the geographic distribution of temperatures suitable for this species is projected to move northward; however, the geographic distribution of mean annual precipitation is projected to remain about the same as for the reference period (Fig. 6). The areas with MAP above 830 mm are mostly south of the Yangzi River. The sharp contrast in precipitation between northern and southern China appears to play an important role in the direction of future projections and may limit the northward expansion of this species. In addition, the new combinations of temperature

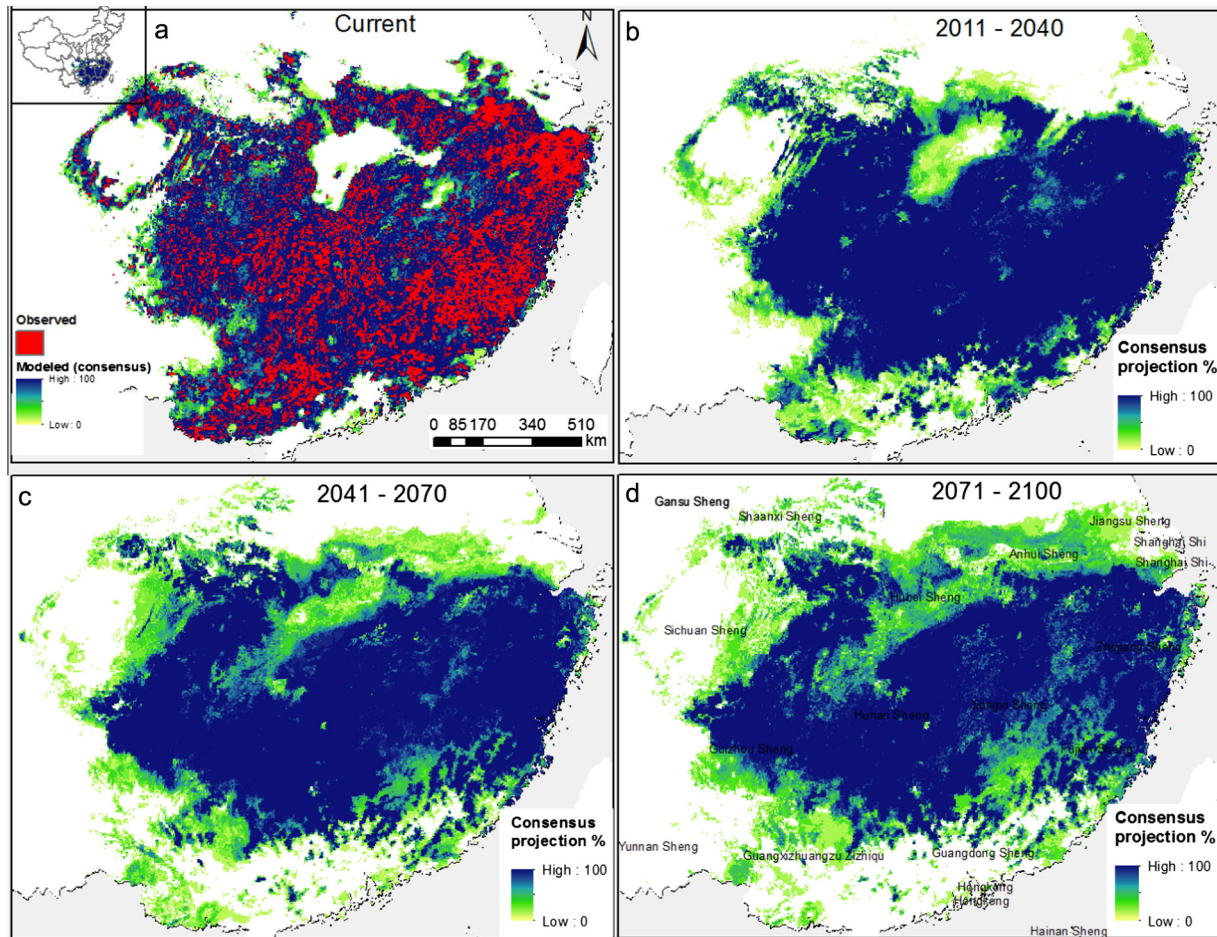


Fig. 3. Geographic distributions of current and potential climatic niches for Masson pine based on ensemble predictions for the current (1961–1990) and consensus projections for the three future periods 2020s, 2050s and 2080s.

and precipitation may represent some novel climates (Williams and Jackson, 2007) in the region and impose new challenges to model predictions.

It is worth noting however that the climatic niche modeled in this study (or in the vast majority of other studies) is a realized climatic niche. It reflects the climate conditions currently occupied by the species. Whether or not Chinese fir can grow outside of the current climatic niche is unknown and needs to be further explored through field experiments, such as provenance tests. A recent study using a process-based model 3-PG (Physiological Principles to Predict Growth) reported a northward expansion for this species, but the projected growth potential was extremely low (Lu et al., 2015). The limiting factor appeared to be the soil water content. The findings of Lu et al. (2015) are therefore in agreement with our realized niche-based projections.

The dramatic decline in the area suitable for Chinese fir projected in this study is concerning as this species is one of the most important forest species in China in term of both its economic value and role in ecosystem functioning (FAO, 2006; Jiang et al., 2011). Our results should provide an early warning for policy makers and practitioners to develop adaptive strategies in species selection and forest management practices in order to adapt the management of Chinese fir forests/plantations to future climate. Managing this species within its current geographical distribution will become increasingly problematic as its current climatic niche becomes fragmented which may lead to a loss in economic value of plantations and impair forest ecosystem functioning.

4.4. Masson pine

The climatic niche of Masson pine almost entirely overlaps that of Chinese fir, but it has a broader range in term of both temperature and precipitation (Table 1 and Fig. 3). Projected contraction in its current distributions was much less (–17%) than that of its counterpart Chinese fir (–34%). Like Chinese fir, Masson pine exhibited no substantial northward expansion under future climate conditions. The contraction of its geographic distribution was projected to mostly occur along the trailing end of its current distribution in the south of China. This is in contrast to the projections for Chinese fir, for which a contraction was also projected to occur in the central areas of its distribution. This is probably attributable to the broader climatic niche of this species compared to Chinese fir. Masson pine may therefore provide a good alternative to Chinese fir for reforestation and afforestation under a future climate in these regions of China.

4.5. Chinese pine

The consensus projections for Chinese pine falls into line with our expectations of species response to climate change. This species' distribution was modeled to contract along the trailing edges and expanded along the leading edges of its range. Instead of shifting northward, our projected distribution for this species showed a westward expansion. This is not a surprise as the topography in China is characterized by an increase in elevation as one moves

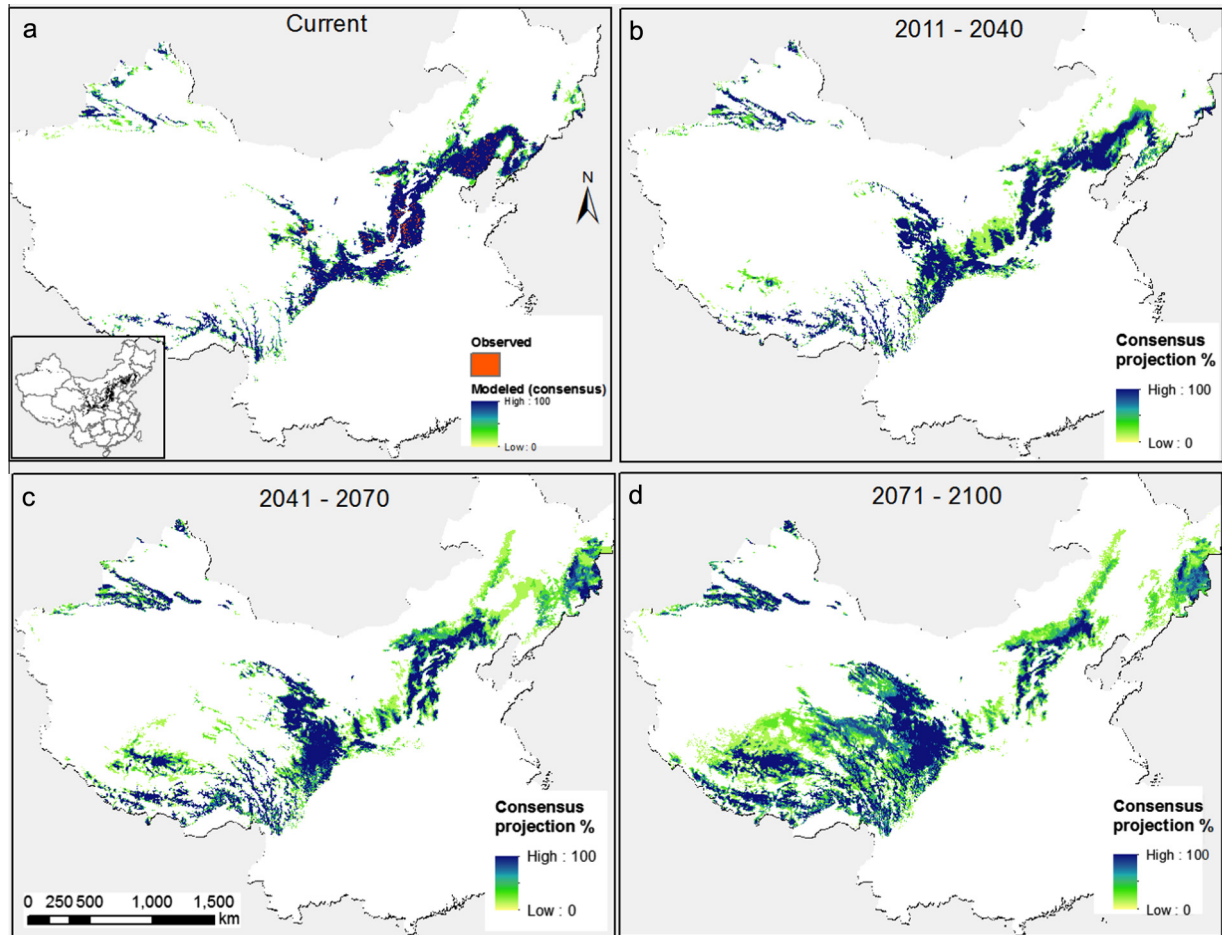


Fig. 4. Geographic distributions of current and potential climatic niches for Chinese pine based on ensemble predictions for the current (1961–1990) and consensus projections for the three future periods 2020s, 2050s and 2080s.

from the east to the west. A dramatic increase in elevation (+1100 m) was projected for the distribution of this species' climatic niche by the 2050s. The potential distribution of the climatic niche for this species is projected to increase substantially (~50%). Chinese pine is a drought tolerant forest tree species with a relatively fast growth rate (Farjon, 2013). Drought is projected to be more frequent in northern and western China under climate change (IPCC Fifth report (<http://www.ipcc.ch/report/ar5/>)). These trends, together with our projected increase in areas suitable for Chinese pine, suggest that Chinese pine could play an important role in afforestation/reforestation in north and western China in the future. Assisted migration to help the species expand westward to new locations in the future could be an option in adaptive forest resource management.

4.6. Blue gum

As a whole species, the geographic distribution of climatic niche for blue gum is projected to shift southward towards cooler conditions. The shift pole ward will be constrained by the Tasman Sea at the leading edge and likely result in a contraction of its total distribution under future climates (by 24% in 2050s, Table 3). The level of the contraction varied considerably among subspecies. The most impacted subspecies were *E. globulus* ssp. *pseudoglobulus* and *E. globulus* ssp. *bicostata*. The climatic niches of these two subspecies are predicted to almost completely disappear and contract by 50% by the 2050s, respectively (Table 4). This clearly indicates that

climate change could bring in new challenges in maintaining the current level of genetic diversity within this species. However, *E. globulus* ssp. *bicostata* is regarded as being better adaptive to drought than other subspecies (Wang et al., 1988). It will be interesting to observe the response of this subspecies to the impact. In contrast, the total distribution of the climatic niche for the major subspecies *E. globulus* ssp. *globulus* is projected to exhibit little change in overall area; however, contraction is predicted to occur on the mainland with expansion in Tasmania compensating for this loss.

The contraction in the overall climatic niche of blue gum on the mainland of southeast Australia could have negative implications for the productivity and vitality of blue gum plantations into the future but positive outcomes for plantation and forest managers in Tasmania. However, the adaptive capacity of eucalypt plantations is considered high with many eucalypts grown on short rotations (<ten years). This provides managers with opportunities to adapt their silvicultural practices and/or plant different genotypes or species to match changing climatic conditions with relative ease (Booth, 2013).

It is important to keep in mind that climatic niche models predict the realized climatic niche rather than the fundamental climatic niche or the actual distribution of a species. The realized climatic niche represents a range of climate conditions currently occupied by a species within its fundamental niche. It is a result of a long term evolutionary and ecological processes of the species involving migration, local adaptation and its interactions with

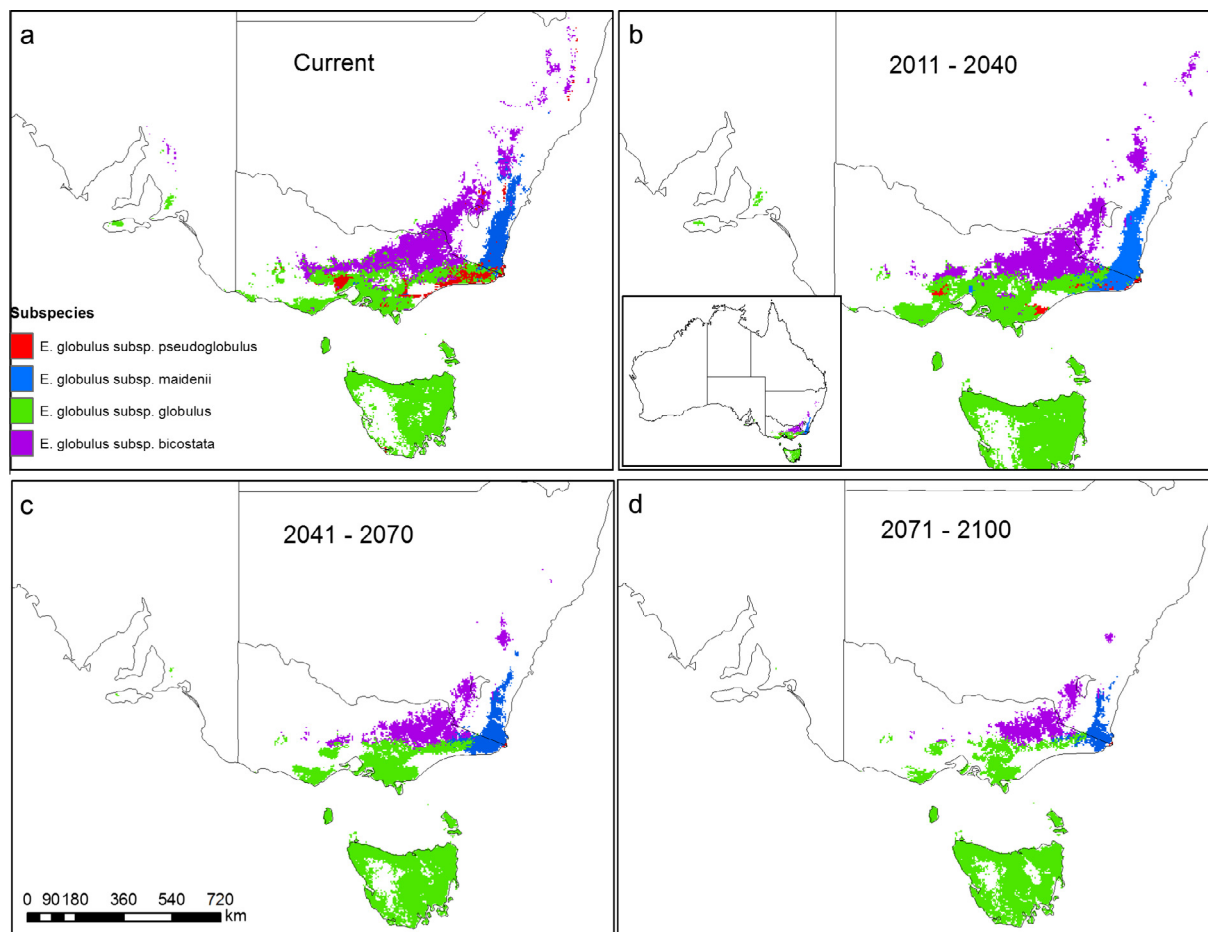


Fig. 5. Geographic distributions of current and potential climatic niches for the four subspecies of blue gum based on ensemble predictions for the current (1961–1990) and consensus projections for the three future periods 2020s, 2050s and 2080s.

Table 3

Changes in average latitude, longitude, elevation and areas of climatic niches for each species by 2050s relative to the reference period 1970s.

Species	Latitude (°)	Longitude (°)	Elevation (m)	Area (%)
Chinese fir	0.1	−0.7	244	−34.2
Masson pine	0.4	0.5	61	−17.0
Chinese pine	−0.7	−5.6	1129	46.8
Blue gum	−1.2	−0.1	3	−24.3

Table 4

Changes in average latitude, longitude, elevation and areas of climatic niches for subspecies of blue gum by 2050s relative to the reference period 1970s.

Subspecies	Latitude (°)	Longitude (°)	Elevation (m)	Area (%)
<i>bicostata</i>	−6.8	−9.6	230	−50.7
<i>maidenii</i>	−0.9	−0.4	3	−10.9
<i>globulus</i>	−0.6	0.3	−1	−1.4
<i>pseudoglobulus</i>	−0.2	−2.1	−224	−99.0

other species and perturbations (Rosenzweig, 1995; Wiens and Graham, 2005). The process is complicated and remains a challenge to be fully understood. However, the objective of climatic niche models is to model a range of climate conditions rather than to model the process and to predict the actual species distributions as is done by species distribution models (Elith and Leathwick, 2009). The projected expansion in the geographic distribution of a species climatic niche at the leading edges of its distribution is

therefore a conservative estimate of its potential distribution based on climate, not other factors. It provides baseline information to aid in decision making around assisted migration for a given species (Gray et al., 2011; McLane and Aitken, 2012; Gray and Hamann, 2013). It is up to the forest managers to consider other factors such as soil and disturbance agents that can constraint the predicted climatic niche. Compared to a changing climate, the factors can be static (i.e. soil) and so simple to consider or stochastic (i.e., insects, disease, fire) and therefore difficult to consider.

An additional utility of the climatic niche approach is the identification of areas of a species distribution where they are more vulnerable to climate change. For example, the predicted changes at the trailing edge of a species distribution suggests that there may be populations that will occur outside their climatic niche which lead to maladaptation. Under these conditions the productivity, resilience and competitive advantage of a species may be compromised, which in turn will increase the species vulnerability to abiotic and biotic disturbances (Fettig et al., 2013; Gray and Hamann, 2013). Monitoring and genetic conservation (Hamann and Aitken, 2013) should be a priority for these areas. However, if these populations are still within their fundamental niches, which were not modeled, these problems related to their survival or even productivity may not eventuate.

In this study, the climatic niches of four economically and ecologically important tree species in the Asia Pacific were modeled and their geographic distributions estimated with a high level of accuracy. This was achieved despite a paucity of vegetation and

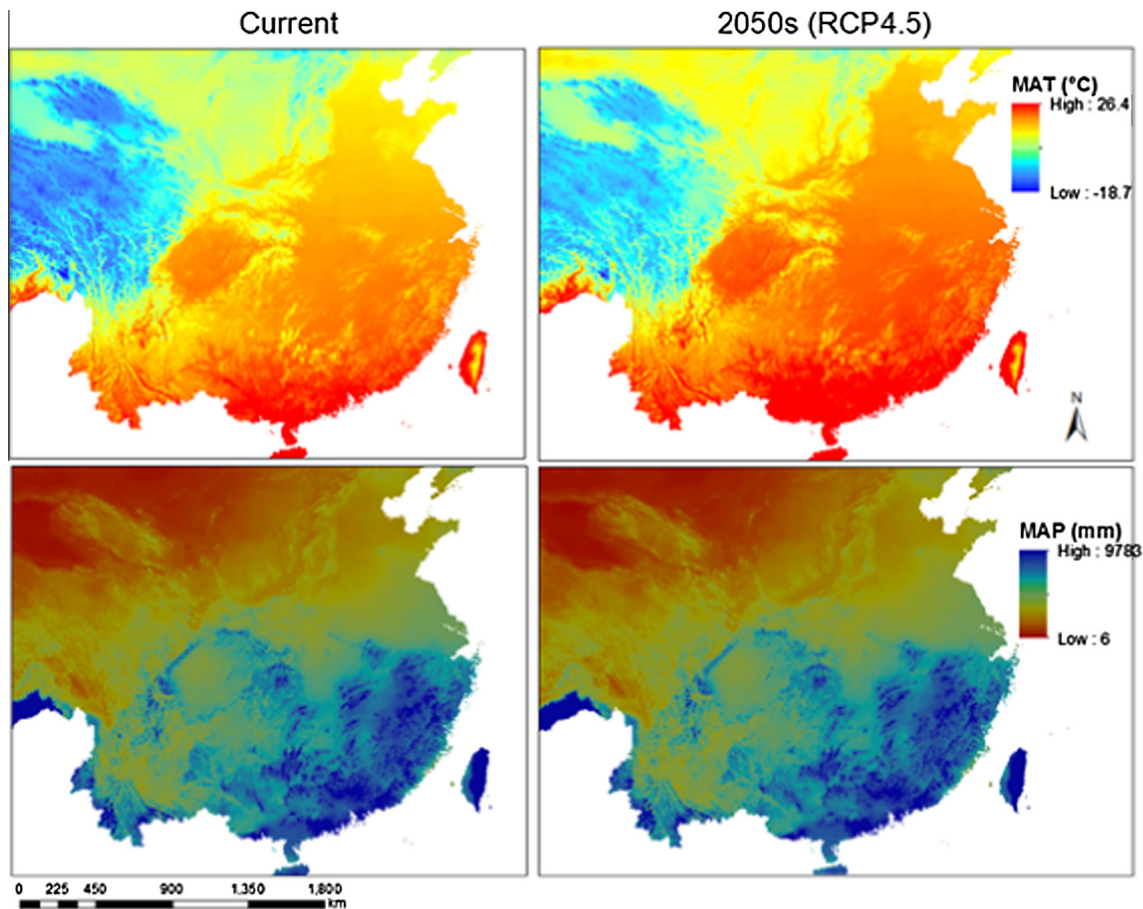


Fig. 6. Distribution of mean annual precipitation (MAP) for 1961–1990 (left) and 2080s (right) projected by one of the AR5 GCM: HadGEM2.

climate data highlighting that the methodology developed for this study is robust and useful for assessing the impacts of climate change on forests in other regions of the Asia Pacific where similar data issues exist. Understanding how the climatic niches and future distributions of these tree species may change should be useful for informing managers undertaking afforestation and ecosystem restoration in the studied regions. The consensus based projection approach for aggregating multiple climate change projections in this study provides a solid basis for the assessment of climate change impact on tree species and for developing adaptive strategies around species selection in consideration of the uncertainty of future climates.

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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 Appl.* 1, 95–111.
- Alfaro, R.I., Fady, B., Vendramin, G.G., Dawson, I.K., Fleming, R.A., Saenz-Romero, C., Lindig-Cisneros, R.A., Murdock, T., Vinceti, B., Navarro, C.M., Skroppa, T., Baldinelli, G., El-Kassaby, Y.A., Loo, J., 2014. The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. *For. Ecol. Manage.* 333, 76–87.
- Anderson, B.J., Akcakaya, H.R., Araujo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W., Brook, B.W., 2009. Dynamics of range margins for metapopulations under climate change. *Proc. R. Soc. B-Biol. Sci.* 276, 1415–1420.
- Araujo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47.
- Araujo, M.B., Peterson, A.T., 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93, 1527–1539.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol. Evol.* 3, 327–338.
- Booth, T.H., 2013. Eucalypt plantations and climate change. *For. Ecol. Manage.* 301, 28–34.
- Breiman, L., 2001. Random forests. *Mach. Learning* 45, 5–32.
- Buisson, L., Thuiller, W., Casajus, N., Lek, S., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. *Global Change Biol.* 16, 1145–1157.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* 28, 2031–2064.
- Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to quaternary climate change. *Science* 292, 673–679.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquez, J.R.G., Gruber, B., Lafourcade, B., Leita, P.J., Munkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46.
- Elith, J., Leathwick, J., 2007. Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity Distributions* 13, 265–275.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Ann. Rev. Ecol. Evol. System.*, 677–697.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813.
- FAO, 2006. Global forest resource assessment 2005. In: Food and Agricultural Organization of the United Nations, Rome.
- Farjon, A., 2013. *Pinus tabulaeformis* var. *tabulaeformis*. The IUCN Red List of Threatened Species. Version 2015.2.

- Fettig, C.J., Reid, M.L., Bentz, B.J., Sevanto, S., Spittlehouse, D.L., Wang, T.L., 2013. Changing climates, changing forests: a western North American perspective. *J. For.* 111, 214–228.
- Gray, L.K., Gylander, T., Mbogga, M.S., Chen, P.Y., Hamann, A., 2011. Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecol. Appl.* 21, 1591–1603.
- Gray, L.K., Hamann, A., 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Clim. Change* 117, 289–303.
- Hamann, A., Aitken, S.N., 2013. Conservation planning under climate change: accounting for adaptive potential and migration capacity in species distribution models. *Diversity Distributions* 19, 268–280.
- Hamann, A., Wang, T.L., 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* 87, 2773–2786.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Holt, R.D., 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19659–19665.
- Huntley, B., Barnard, P., Altwegg, R., Chambers, L., Coetzee, B.W.T., Gibson, L., Hockey, P.A.R., Hole, D.G., Midgley, G.F., Underhill, L.G., Willis, S.G., 2010. Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change. *Ecography* 33, 621–626.
- Hutchinson, G.E., 1957. Population studies – animal ecology and demography – concluding remarks. *Cold Spring Harbor Symposia Quantitative Biol.* 22, 415–427.
- IPCC, 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. In: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jiang, P.K., Meng, C.F., Zhou, G.M., Xu, Q.F., 2011. Comparative study of carbon storage in different forest stands in subtropical China. *Bot. Rev.* 77, 242–251.
- Keenan, R.J., 2015. Climate change impacts and adaptation in forest management: a review. *Ann. Forest Sci.* 72, 145–167.
- Keith, D.A., Akcakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araujo, M.B., Rebelo, T.G., 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* 4, 560–563.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., Safranyik, L., 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452, 987–990.
- Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. *R News* 2, 18–22.
- Lindner, M., Fitzgerald, J.B., Zimmermann, N.E., Rey, C., Delzon, S., van der Maaten, E., Schelhaas, M.J., Lasch, P., Eggers, J., van der Maaten-Theunissen, M., Suckow, F., Psomas, A., Poulter, B., Hanewinkel, M., 2014. Climate change and European forests: What do we know, what are the uncertainties, and what are the implications for forest management? *J. Environ. Manage.* 146, 69–83.
- Lu, Y., Coops, N., Wang, T., Wang, G., 2015. A process-based approach to estimate Chinese fir (*Cunninghamia lanceolata*) distribution and productivity in southern China under climate change. *Forests* (In press).
- McKenney, D.W., Pedlar, J.H., 2003. Spatial models of site index based on climate and soil properties for two boreal tree species in Ontario. *Canada. For. Ecol. Manage.* 175, 497–507.
- McKenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K., Hutchinson, M.F., 2007. Potential impacts of climate change on the distribution of North American trees. *BioScience* 57, 939–948.
- McLane, S.C., Aitken, S.N., 2012. Whitebark pine (*Pinus albicaulis*) assisted migration potential: testing establishment north of the species range. *Ecol. Appl.* 22, 142–153.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeography* 12, 361–371.
- Peterson, A.T., Soberon, J., Sanchez-Cordero, V., 1999. Conservatism of ecological niches in evolutionary time. *Science* 285, 1265–1267.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analyses of plant–climate relationships for the western United States. *Int. J. Plant Sci.* 167, 1123–1150.
- Rehfeldt, G.E., Jaquish, B.C., Lopez-Upton, J., Saenz-Romero, C., St Clair, J.B., Leites, L.P., Joyce, D.G., 2014a. Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: realized climate niches. *For. Ecol. Manage.* 324, 126–137.
- Rehfeldt, G.E., Jaquish, B.C., Saenz-Romero, C., Joyce, D.G., Leites, L.P., St Clair, J.B., Lopez-Upton, J., 2014b. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: reforestation. *For. Ecol. Manage.* 324, 147–157.
- Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge Univ. Press, Cambridge.
- Rozelle, S., Huang, J., Syed Arif, H., Aaron, Z., 2000. China – from afforestation to poverty alleviation and natural forest management. In: OED Evaluation Country Case Study Series; Forestry. World Bank Group, Washington, DC.
- Schueler, S., Falk, W., Koskela, J., Lefevre, F., Bozzano, M., Hubert, J., Kraigher, H., Longauer, R., Olrik, D.C., 2014. Vulnerability of dynamic genetic conservation units of forest trees in Europe to climate change. *Global Change Biol.* 20, 1498–1511.
- Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experiment design. *Bull. Am. Meteorol. Soc.* 93, 485–498.
- Wang, D., Bachelard, E.P., Bankss, J.C.G., 1988. Growth and water relations of seedlings of two subspecies of *Eucalyptus globulus*. *Tree Physiol.* 4, 129–138.
- Wang, T.L., Campbell, E.M., O'Neill, G.A., Aitken, S.N., 2012a. Projecting future distributions of ecosystem climate niches: uncertainties and management applications. *For. Ecol. Manage.* 279, 128–140.
- Wang, T.L., Hamann, A., Spittlehouse, D.L., Murdock, T.Q., 2012b. ClimateWNA-high-resolution spatial climate data for western North America. *J. Appl. Meteorol. Climatol.* 51, 16–29.
- Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Ann. Rev. Ecol. Evol. System.* 36, 519–539.
- Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers Ecol. Environ.* 5, 475–482.
- Woodward, F.I., Williams, B.G., 1987. Climate and plant-distribution at global and local scales. *Vegetatio* 69, 189–197.
- Xu, H.C., Zhai, M.P., Ma, Q.Y., Dong, S.R., Shen, X.H., Yan, J.J., Zhang, Z.C., Shen, R.X., Shen, G.F., Yang, J.J., 1993. Chinese pine (*Pinus tabulaeformis* Carr.). China Forest Press, Beijing, p. 480.