Protecting endemic seed plants on the Tibetan Plateau under future climate change: migration matters

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Abstract

Aims

Climate change in the near future may become a major threat to high-altitude endemics by greatly altering their distribution. Our aims are to (i) assess the potential impacts of future climate change on the diversity and distribution of seed plants endemic to the Tibetan Plateau and (ii) evaluate the conservation effectiveness of the current National Nature Reserves (NNRs) in protecting the endemic plants in the face of climate change.

Methods

We projected range shifts of 993 endemic species to the years 2050 and 2070 under two representative concentration pathway scenarios using an ensemble species distribution modeling framework and evaluated range loss, species-richness change and coverage of the current conservation network considering two dispersal scenarios.

Important Findings

In a full-dispersal scenario, 72–81% of the species would expand their distribution by 2070, but 6–20% of the species would experience >30% range loss. Most species would shift to the west. The projected species net richness would increase across the region on average. In a no-dispersal scenario, 15–59% of the species would lose >30% of their current habitat by 2070. Severe species loss may occur in the southeastern and the eastern peripheral plateau. Seventeen percent of species ranges are covered by the NNRs on average and may increase in the future if species disperse freely. We found a significant difference of species redistribution patterns between different dispersal scenarios and highlighted the importance of migration in this region.

Keywords: biodiversity, global change, impact assessment, nature reserves, species conservation, species distribution models

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INTRODUCTION

Evidence from the past has shown that plant species could mitigate the influences of environmental change through migration or adaptation (Davis and Shaw 2001). Because of the uncertainty of adaptation for plants in response to the fast-changing contemporary climate, the possibility of migration is likely to be of great importance for their survival (Davis and Shaw 2001; Jump and Peñuelas 2005) and is regulated by the dispersal ability of plants and the availability of new suitable sites (Engler *et al.* 2009).

High-altitude endemics may be the most vulnerable group to a rapidly changing climate because they tend to have a small range size and strict environmental requirements (Pauli *et al.* 2012; Svenning *et al.* 2015). Meanwhile, they represent the uniqueness of a region's biodiversity and preserve valuable genetic resources; thus, they are of high conservation value (Myers *et al.* 2000). However, the future range shift caused by climate change and the possibility of migration for high-altitude endemic species have rarely been evaluated on a large scale, especially for species limited to the Tibetan Plateau.

The Tibetan Plateau, with an average altitude >4000 m, is the highest plateau on Earth (Zhang *et al.* 2002). It is home to ~10 000 seed plants, of which ~38% are endemic to this area (Yan *et al.* 2013; Yu *et al.* 2018). An earlier and faster warming process compared with the global mean has occurred on the plateau, and the change may continue in the future at an

even faster pace (Qin *et al.* 2009; Yang *et al.* 2014). Studies have revealed that the recent warming has slightly influenced the current tree line at the edge of the plateau (Gaire *et al.* 2014; Gou *et al.* 2012; Liang *et al.* 2011). A recent case study illustrated that the distribution ranges of an endemic fungus may shrink due to future climate change (Yan *et al.* 2017), but the ranges of threatened plants in the Three River Source region may expand (Wu *et al.* 2018). Nevertheless, the general pattern of range shifts under climate change in this area is poorly understood.

To conserve the current biodiversity, 41 National Nature Reserves (NNRs) were established on the Tibetan Plateau by the end of 2014 (Zhang *et al.* 2015b). Because species may still disappear from the reserves in the future due to further climate change (Araújo *et al.* 2004), it is urgent to evaluate the effectiveness and test the possibility of mitigation of climate change in these NNRs under different climate change scenarios (Hannah 2008).

In this study, we modeled the distribution of 993 seed plants endemic to the plateau to the years 2050 and 2070 under different climate-change scenarios based on an ensemble-modeling framework (Araújo and New 2007). We asked: (i) what are the potential consequences of predicted climate change on the distribution of endemic seed plant species of the Tibetan Plateau? (ii) How would climate change affect the species diversity patterns in this region? (iii) Is the current protected area network sufficient to conserve endemic species as well as species diversity in the face of climate change?

MATERIALS AND METHODS

Study area and species distribution dataset

The Tibetan Plateau (Fig. 1) ranges from E73°29′56″ to E104°40′20″ in latitude, from N25°59′37″ to N39°49′33″ in longitude, and from ~400 to ~8500 m in altitude (Zhang *et al.* 2002).

We collected distribution data about seed-plant species endemic to the Tibetan Plateau based primarily on the latest *Red List of Chinese Higher Plants* (Ministry of Environmental Protection of the People's Republic of China 2013) and an updated county-level distribution dataset with elevation ranges of vascular plants on the Tibetan Plateau (Yan *et al.* 2013). The dataset mainly focused on the species occurring on the main body of the plateau within China. Species names were checked using the Taxonomic Name Resolution Service v4.0 (Boyle *et al.* 2013) and, if necessary, manually verified using The Plant List (2013). Subspecies and varieties were combined to species as the classification was ambiguous for many of them.

We first selected species that were endemic to China and distributed only in counties covered by the Tibetan Plateau. At the same time, we checked the species list against literature concerning seed plants endemic to the Tibetan Plateau,
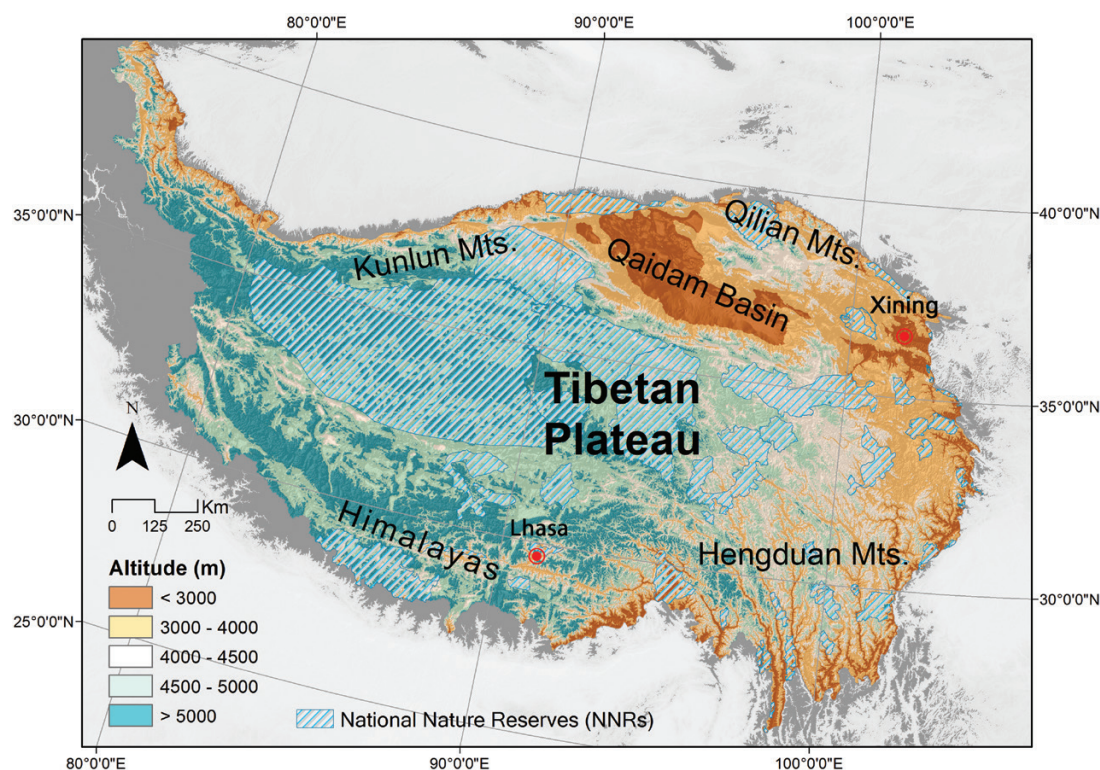
Figure 1: topographic map of the study area, with locations of major mountain ranges and NNRs.

added species that were considered endemic by species-specific studies or in at least two reports, removed species that were identified as non-endemic by experts (online supplementary Appendix 1) and finally got 1433 endemic species. For these species, we collected the species description from the *Flora of China* (Wu *et al.* 1994–2006) and Flora Reipublicae Popularis Sinicae (1959–2004) and extracted their life form as well as habitat information. We classified the habitat type into six categories, that is forest, shrub, meadow, desert, farmland and alpine vegetation in accordance with the classification system of the vegetation map of China (Editorial Board of Vegetation Map of China 2007). The conservation status was obtained from the *Red List of Chinese Higher Plants* (Ministry of Environmental Protection of the People's Republic of China 2013).

We collected occurrence data with geographical coordinates from the literature and online datasets (online supplementary Appendix 1). We included records from either direct observations or specimen records with at least one decimal digit in accuracy for latitude and longitude. We excluded records before 1950, records assigned to county centroid or city center records referring to cultivations. Considering the accuracy of the georeferenced occurrence records and the scale of our study, we used 10 km × 10 km as the study resolution and cleaned duplicate records per grid. This gave us an average of 15 records for 53% of the species. Because of the limited number of available georeferenced occurrences and possible incomplete sampling across the distribution range for most endemic species in this area, we added a pseudo-occurrence dataset for all species extracted from the literature-based species ranges to feed species distribution modeling (SDM). A previous study has proved the feasibility of this method (Fourcade 2016). The key sample steps were as follows: (i) we divided the study area into 10 km × 10 km grids in accordance with the resolution of environmental layers; (ii) we extracted the elevation intervals, major land-cover types (covering >10% of the grid) and county information for each grid based on a digital elevation model with 1 km × 1 km resolution (Shuttle Radar Topography Mission, srtm.usgs.gov/), a vegetation map of China (Editorial Board of Vegetation Map of China 2007) and a county-level administrative map of China; (iii) we assigned species to grids in accordance with their distribution elevation interval, vegetation types and counties. The central coordinates of the grids were used as occurrences for each species.

Climate dataset

Current (mean of 1950–2000) and future climate data obtained from the WorldClim Version 1 dataset (Hijmans *et al.* 2005) were projected from 5 min × 5 min to 10 km × 10 km resolution. As collinearity between factors may lead to overfitting, we selected eight bioclimatic variables, namely mean annual temperature (MAT), annual precipitation (AP), mean temperature of coldest quarter (MTCQ), mean temperature of warmest quarter (MTWQ), precipitation of wettest quarter

(PWEQ), mean diurnal range (MDR), temperature seasonality (TSN) and precipitation seasonality (PSN). These variables have a known impact on the distribution of plants in this region and contributed most during the pre-modeling process. The coefficient between any pair was <0.8.

The future climate data were projected to year 2050 (average for 2041–2060) and 2070 (average for 2061–2080) according to the IPCC fifth assessment report (IPCC AR5, Kirtman *et al.* 2013), and comparable with baseline 'current' climate used in the study. To account for the difference in various general circulation models (GCMs) used in the IPCC AR5, the predictions of five GCMs which were BCC-CSM 1.1, HadGEM2-ES, IPSL-CM5A-MR, MRI-CGCM3 and NorESM1-M, were used in our study based on their performance in simulating the climate of the Tibetan Plateau (Su *et al.* 2013) and data availability. Two extreme representative concentration pathways (RCPs) representing the lowest and highest greenhouse gas emissions in the future in IPCC AR5, that is RCP 2.6 (mean temperature + ~2°C in 2070) and RCP 8.5 (mean temperature + ~4.8°C in 2070), were incorporated into the modeling process (Meinshausen *et al.* 2011). The distribution of differences between current and projected future climate (online supplementary Figs S1–S3) was consistent with the observed climate change trends (Li *et al.* 2010), showing a warmer and wetter climate for most regions in the future.

All climate data were clipped to the Tibetan Plateau and its surrounding areas (E72°–110°, N23°–44°).

Species distribution modeling and dispersal scenarios

We modeled current and future occurrence probabilities for each species using an ensemble modeling method that combined three modeling algorithms: maximum entropy (MaxEnt), random forest (RF) and generalized linear modeling (GLM) embedded in R package Biomod2 (Thuiller *et al.* 2009). Three sets of pseudo-absence data equal to the number of species presence data were randomly generated (Barbet-Massin *et al.* 2012). We calibrated the model using 85% randomly selected data units and tested the model using the remaining 15% of the data. The process was repeated three times and generated 27 models in total (three datasets × three divisions × three modeling algorithms). We then evaluated the model performances using true-skill statistics (TSS; Allouche *et al.* 2006), area under the receiver operating characteristic (AUC; Hanley and McNeil 1982) metrics and Boyce index (Breiner *et al.* 2015; Hirzel *et al.* 2006). Finally, we combined the results of models with an AUC value >0.9 through weighted average and converted the continuous habitat suitability into a binary map using ROC characteristics (Nenzén and Araújo 2011).

We compared the performance between occurrence-based SDMs and grid-based SDMs concerning modeled range-size, niche occupation and range change under climate change (online supplementary Note S1; Figs S6–S8) and mixed the grid-based data and the georeferenced occurrences to build

models. To eliminate the bias created by very small sample sizes, species with <20 records were not included in this study; this gave us 1291 species. We grouped the species into woody and herbaceous plants and compared their responses to climate change.

Two extreme dispersal scenarios, that is full-dispersal and no-dispersal, were considered. To detect the directional change and dispersal speed under full dispersal scenario, we calculated the suitability centroid change between current and projected distribution for each species (angle and distance). The suitability centroid was defined as the weighted centroid of the continuous habitat suitability map. Directional change was assigned to 16 directions. Projected dispersal speed was calculated using distance of suitability-centroid change divided by the time-period length.

Evaluation of species vulnerability, regional vulnerability and conservation

To evaluate the regional vulnerability caused by climate change, we calculated the number and percentage of immigrant, emigrant and persistent species per grid under different scenarios. Based on these, the species turnover rate of each grid cell was calculated as (Thuiller *et al.* 2005):

$$\text{Species turnover rate} = \frac{N_{\text{immigrants}} + N_{\text{emigrants}}}{N_{\text{persistents}} + \text{ current species richness}} \times 100\%$$

The boundaries of current NNRs (Fig. 1) were extracted from the nature reserves dataset of China (updated from Zhao *et al.* 2013). We calculated the protection ratio for each species following Zhang *et al.* 2015c:

$$\text{Protection ratio} = \frac{\text{distribution area within the boundary of protected areas}}{\text{distribution area on the Tibetan Plateau}} \times 100\%$$

The protection ratio was compared between species of different life forms and conservation status using *t*-test. Paired *t*-tests were used to test the significance of change under climate change scenarios.

All analysis was performed in R 3.2.4 (R Core Team, 2016) and ArcGIS 10.5 (Esri, Inc., 2016).

RESULTS

Model accuracy

The SDMs of most species performed well (Table 1). After excluding species whose projected potential distribution area outside the Tibetan Plateau was larger than within and for which the models had insufficient predictive power, 993 species from 71 families and 259 genera (see online supplementary Table S1 for full species list), including 741 (74.6%) herbaceous and 252 (25.4%) woody species, remained for further analysis. TSN and MTWQ contributed most to the models of herbaceous plants, while TSN, MTWQ and MTCQ contributed most to the models of woody plants (online supplementary Table S2). The comparison between distribution of occurrences and modeled species richness is presented in online supplementary Fig. S4.

Species range shifts

On average, the species would lose 16.9–42.3% of their habitat under different periods and scenarios; however, the predicted species range shifts varied widely for different dispersal settings.

If full dispersal is considered, under the RCP 2.6 scenario, the distribution ranges of 797 species (80.3% of the total) would expand until 2050 and 2070 (Table 2). The relative proportion of species predicted to expand their range was higher for woody (94.8% and 95.2%, 239 and 240 of 252 species in 2050 and 2070, respectively) than for herbaceous plants (75.3% and 76.5%, 558 and 567 of 741 species in 2050 and 2070, respectively). Sixty-six species (3 woody and 63 herbaceous) were predicted to experience a net range loss of >30% in 2050, and the number decreased slightly to 60 species (3 woody and 57 herbaceous) in 2070 (Table 2). However, when the emission scenario became extremely high (RCP 8.5), the number of species predicted to expand their distribution

Table 1: summary of evaluation metrics of species distribution models (mean ± standard deviation)

Evaluation metrics	Algorithm	Herbaceous plants	Woody plants	All species
AUC	Total	0.97 ± 0.05	0.97 ± 0.05	0.97 ± 0.05
	GLM	0.97 ± 0.05	0.97 ± 0.04	0.97 ± 0.05
	MaxEnt	0.94 ± 0.06	0.94 ± 0.06	0.94 ± 0.06
	RF	0.99 ± 0.02	0.99 ± 0.01	0.99 ± 0.01
TSS	Total	0.92 ± 0.10	0.92 ± 0.10	0.92 ± 0.10
	GLM	0.92 ± 0.09	0.93 ± 0.09	0.92 ± 0.09
	MaxEnt	0.86 ± 0.12	0.87 ± 0.12	0.87 ± 0.11
	RF	0.96 ± 0.05	0.97 ± 0.04	0.96 ± 0.04
BI	Total	0.80 ± 0.31	0.50 ± 0.59	0.72 ± 0.42

Abbreviations: AUC = area under the curve, TSS = true statistics, BI = Boyce Index, GLM=general linear model, MaxEnt =maximum entropy, RF = random forest.

Table 2: number and percentage (within parentheses) of species with different range changes under various dispersal modes, periods and emissions scenarios

Life forms	Range change (%)	RCP2.6				RCP8.5			
		2050		2070		2050		2070	
		No dispersal	Full dispersal	No dispersal	Full dispersal	No dispersal	Full dispersal	No dispersal	Full dispersal
Herbeceous plants	>0	—	558 (75.3)	—	567 (76.5)	—	524 (70.7)	—	478 (64.5)
	−30 to 0	592 (79.9)	120 (16.2)	605 (81.6)	117 (15.8)	435 (58.7)	90 (12.1)	259 (35)	80 (10.8)
	−50 to −30	95 (12.8)	36 (4.9)	85 (11.5)	32 (4.3)	150 (20.2)	48 (6.5)	176 (23.8)	56 (7.6)
	−80 to −50	51 (6.9)	25 (3.4)	48 (6.5)	22 (3)	112 (15.1)	55 (7.4)	176 (23.8)	62 (8.4)
	−100 to −80	3 (0.4)	2 (0.3)	3 (0.4)	3 (0.4)	44 (5.9)	24 (3.2)	130 (17.5)	65 (8.8)
Woody plants	>0	—	239 (94.8)	—	240 (95.2)	—	235 (93.3)	—	232 (92.1)
	−30 to 0	234 (92.9)	10 (4)	239 (94.8)	9 (3.6)	212 (84.1)	11 (4.4)	150 (59.5)	9 (3.6)
	−50 to −30	12 (4.8)	2 (0.8)	7 (2.8)	2 (0.8)	21 (8.3)	2 (0.8)	60 (23.8)	5 (2)
	−80 to −50	5 (2)	0 (0)	6 (2.4)	1 (0.4)	14 (5.6)	3 (1.2)	24 (9.5)	2 (0.8)
	−100 to −80	1 (0.4)	1 (0.4)	0 (0)	0 (0)	5 (2)	1 (0.4)	18 (7.1)	4 (1.6)
Overall species	>0	—	797 (80.3)	—	807 (81.3)	—	759 (76.4)	—	710 (71.5)
	−30 to 0	826 (83.2)	130 (13.1)	844 (85)	126 (12.7)	647 (65.2)	101 (10.2)	409 (41.2)	89 (9)
	−50 to −30	107 (10.8)	38 (3.8)	92 (9.3)	34 (3.4)	171 (17.2)	50 (5)	236 (23.8)	61 (6.1)
	−80 to −50	56 (5.6)	25 (2.5)	54 (5.4)	23 (2.3)	126 (12.7)	58 (5.8)	200 (20.1)	64 (6.4)
	−100 to −80	4 (0.4)	3 (0.3)	3 (0.3)	3 (0.3)	49 (4.9)	25 (2.5)	148 (14.9)	69 (6.9)

range dropped ~10% and more species (13.4–19.5%) would face moderate to severe range contraction. Sixty-nine species, including 4 woody and 65 herbaceous, would lose >80% of suitable habitat in 2070. In addition, the distribution range of 177 (17.8%) species would decrease regardless of the emission scenarios (Table 2).

If no dispersal was considered, under the RCP 2.6 scenario, most species tended to retain their original habitat and distribution range, and only 167 (16.8%) and 149 (15.0%) species would lose >30% of their current habitat in 2050 and 2070, respectively. The habitat loss for herbaceous plants was more severe than for woody plants. Under the RCP 8.5 scenario, 346 species (34.8%, 40 woody and 306 herbaceous) would experience >30% habitat shrinkage in 2050, and the number would rise to 584 species (58.8%, 102 woody and 482 herbaceous) in 2070, among which 148 (14.9%, 18 woody and 130 herbaceous) would lose >80% of their suitable habitats (Table 2).

Most species would move to the WNW or west, where the altitude is higher, at a speed of 10–30 km per decade under the RCP 2.6 scenario and 20–40 km per decade under the RCP 8.5 scenario. A few species would move to the south or east (Fig. 2).

Changes of species richness patterns under different scenarios

On average, the projected species richness increases by 17–33 species per grids across different periods and climate-change scenarios when full dispersal is considered. While species richness would increase in most places, especially in the northern part of the Hengduan Mountains and the southwestern

peripheral plateau, the southeastern peripheral plateau and eastern peripheral plateau would experience a decrease in species richness (Fig. 3a and b). We projected that areas lower than 4000 m would tend to lose species, while areas higher than 4000 m would tend to gain species (Fig. 3c).

On average, the species turnover rate was predicted to vary from 48.1% to 77.2% across the Tibetan Plateau under different scenarios and during different periods. The turnover rate of the central Hengduan Mountains and the northwestern part of the Kunlun Mountains is predicted to be relatively low across different scenarios, while that of other regions is predicted to increase substantially for the RCP 8.5 scenarios with the highest rate reaching >80%, especially around the eastern part of the Kunlun Mountains, the Karakorum Mountains, the Gangdisi Mountains and the Qaidam Basin. The species turnover rate of the western part of the plateau is higher than that of the eastern part (Fig. 3d and e).

Breaking down the richness-pattern changes to different facets, the average projected numbers of immigrants, emigrants and persistent species were 31–70 (>58.5% relative to the current richness), 14–37 (23.1–57.4%), and 45–67 (42.6–76.9%), respectively. The western peripheral plateau would have the highest percentage of immigrants, especially around the Gangdisi Mountains and the middle part of the Kunlun Mountains. With increasing greenhouse gas emissions, the Three Rivers Source Region would have an increasing number of immigrants (Fig. 3g and h). The midwestern part of the Tibetan Plateau, the Qaidam Basin and the southern edge of the plateau may have the highest percentage of emigrants in the future (Fig. 3j and k). The eastern part of the plateau and the Himalayas would have the highest
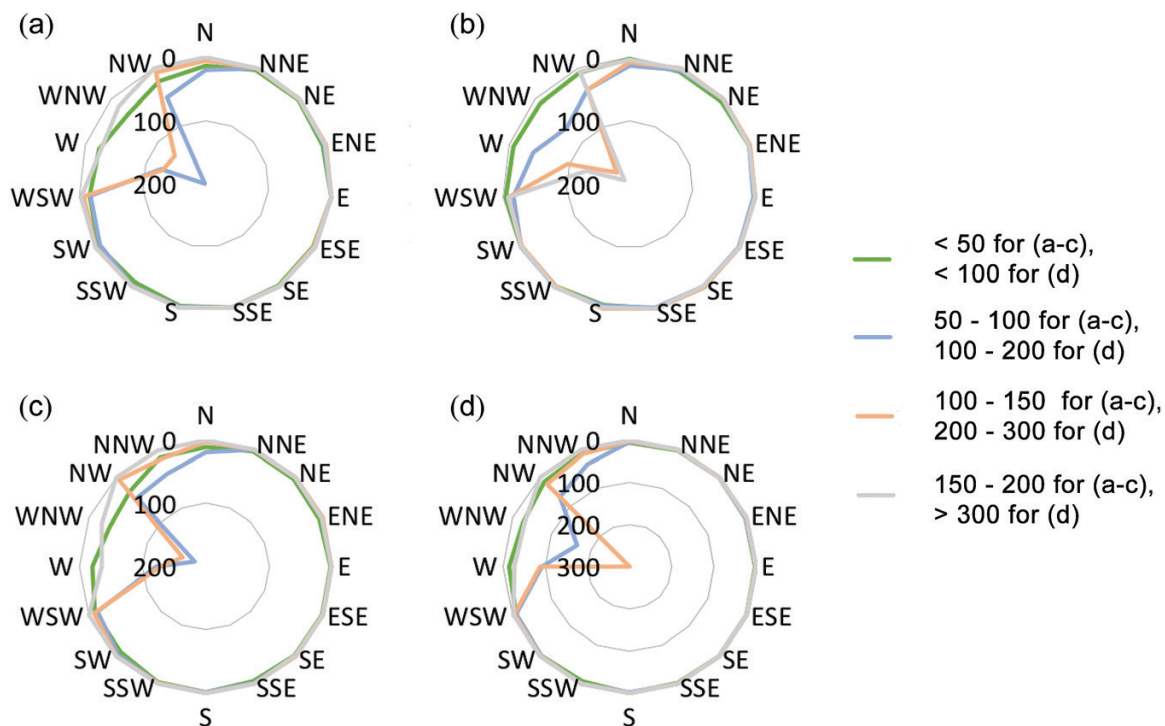
Figure 2: centroid changes in direction and distance of species ranges between the current time and the projected distributions for (**a**) year 2050, RCP 2.6; (**b**) year 2050, RCP 8.5; (**c**) year 2070, RCP 2.6; (**d**) year 2070, RCP 8.5. Centroid change was assigned to 15 directions. The colors represent shifted distance, and the distance between each line and the center represents the number of species.

percentage of persistent species (Fig. 3m and n). The percentage of immigrants would increase greatly along altitude (Fig. 3i). For emigrants, low elevations (<3000 m) would encounter severe species loss (Fig. 3l). Many species would have a stable distribution in areas between 3000 and 4500 m; however, the stability would drop as greenhouse gas emissions would increase (Fig. 3o).

Conservation networks in the face of climate change

On average, NNRs covered 16.7% of the current distribution areas of the endemic species on the Tibetan Plateau. The average protection ratio was higher for herbaceous plants (17.4%) than for woody species (14.7%) (online supplementary Fig. S5). No significant difference was observed between species at low risk and threatened species (*P*-value > 0.1).

When full dispersal was considered, the protection ratio tended to increase in the future for most species (paired *t*-test *P*-value always < 0.05). The average protection ratio in 2050 and in 2070 under the RCP 2.6 scenario is 17.8 and 17.6%. The average protection ratio in 2050 and in 2070 under the RCP 8.5 scenario is 18.1 and 18.0% (Fig. 4). However, the protection ratio tends to decrease for woody species in 2070 under the RCP 8.5 scenario (*P*-value < 0.05) (online supplementary Fig. S5). No significant difference was observed for threatened species between different periods (*P*-value > 0.1).

NNRs in Sichuan and Tibet tend to preserve the most species across all periods and scenarios, with the Mt. Qomolangma National Nature Preserve in Tibet harboring the most species (online supplementary Table S4).

DISCUSSION

Regional vulnerability evaluation and the importance of dispersal

In general, the Tibetan Plateau is predicted to get warmer and wetter (online supplementary Figs S1–S3), but the impact of future climate change may be quite variable under different emissions scenarios in this area. In contrast to the studies on plant species in other mountainous regions in China (Zhang *et al.* 2014) or Europe (Engler *et al.* 2011) and on endemic plants in the Austrian Alps (Dirnböck *et al.* 2011), the distribution areas of many species in this area would be enlarged. These differences are possibly due to differences in characteristics of the studied species, the topography and the historical climate of the studied regions.

Temperature stability and the mean temperature of the warmest quarter are the two most important factors controlling the distribution of endemic plant species on the Tibetan Plateau (online supplementary Table S2). Most endemic species tend to concentrate in relatively low elevations in the southern and eastern parts of the plateau, where the climate
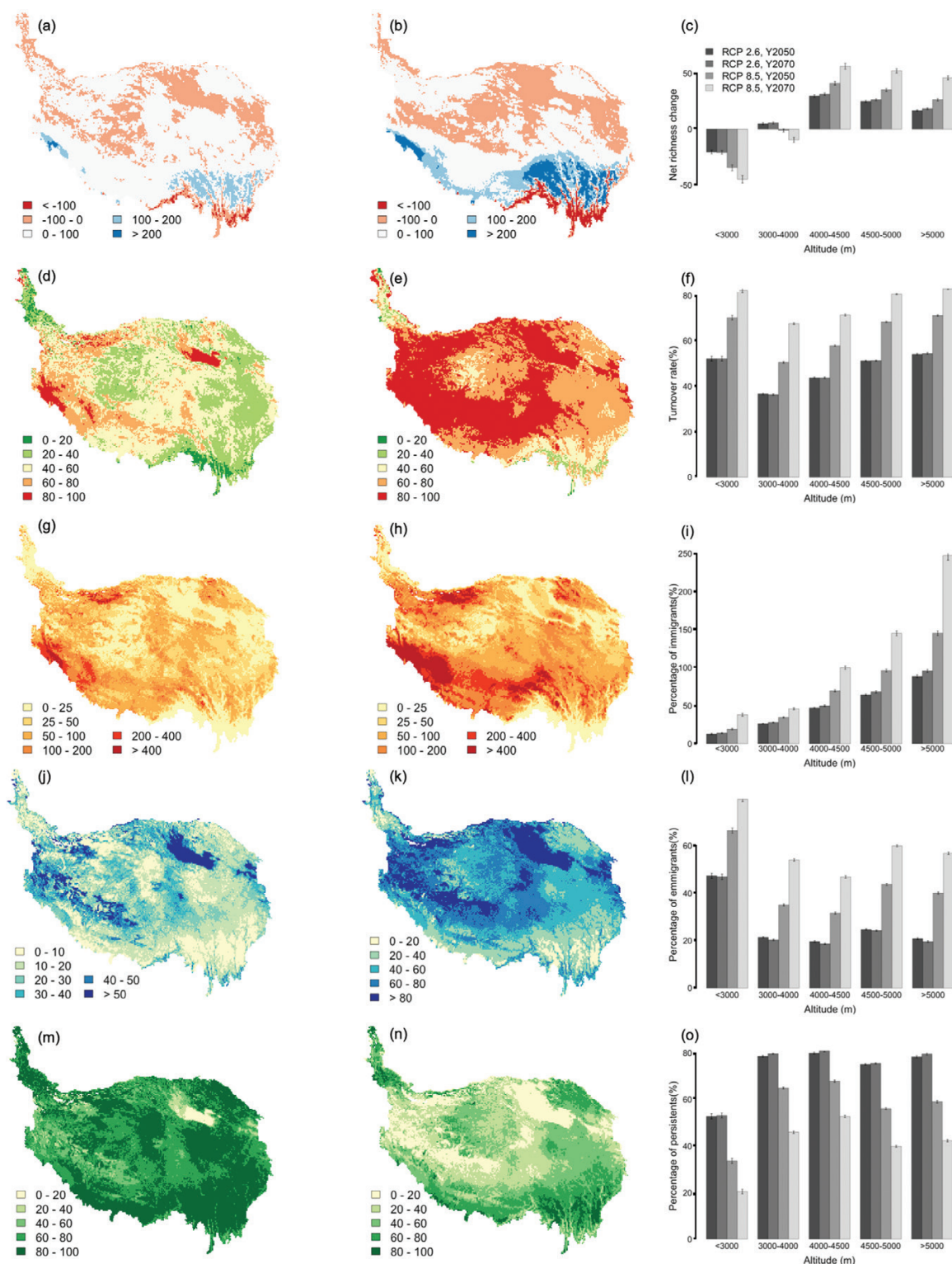
Figure 3: the spatial distribution and elevation patterns for species richness (**a–c**), turnover rate (**d–f**), proportion of emigrants (**g–i**), immigrants (**j–l**), and persistence (**m–o**) of endemic plant species in the year 2070 under the RCP 2.6 (left column) and RCP 8.5 (middle column) scenarios.

is warmer, more humid and more stable than in the interior plateau (online supplementary Fig. S4). Therefore, the future warming of the plateau may not exceed most species' upper temperature endurance, and the fast warming in the higher-altitude areas may even foster their survival. In our study, the distribution of more than half of the species
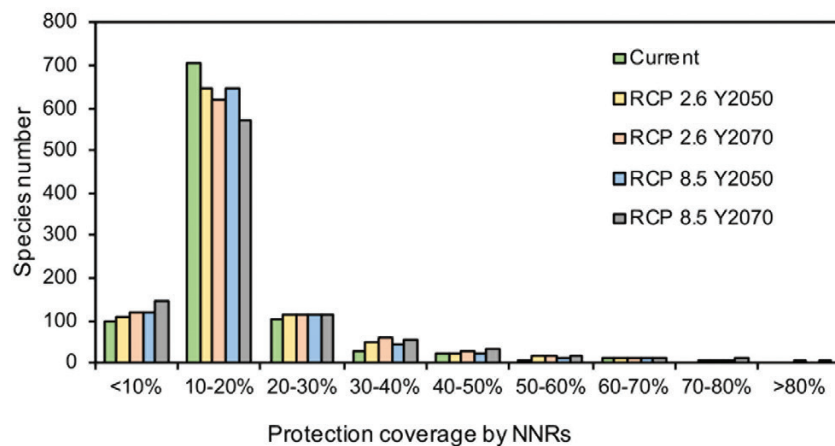
Figure 4: frequency distribution of protection coverage of NNRs under future climate change.

would expand if they could disperse freely (Table 2). Similar predictions have been made for threatened plants in the Three River Source region (Wu *et al.* 2018). In the Alps and mountain ranges in western North America, plants at high elevations may face a nowhere-to-go situation under the warming process and encounter 'mountaintop extinction' because the elevation is not high enough to engender more climatically suitable future sites (Bell *et al.* 2014; Dirnböck *et al.* 2011; Gottfried *et al.* 2012). In contrast, on the Tibetan Plateau, where the elevation is much higher than that of the montane areas in Europe and North America, new climatically suitable sites may appear to the northwest of most species' current habitats (Fig. 2). Moreover, several north-south- and east-west-oriented valleys (such as the Yarlung Zangbo Grand Canyon, valleys the in Hengduan Mountains) could serve as ideal corridors for species to migrate under climate change, as they did during past climatic oscillations (Yu *et al.* 2014, 2017). These future colonization patterns are in concordance with the post-glacial recolonization patterns during the Quaternary Period found by previous studies (e.g. Zhang *et al.* 2005; Chen *et al.* 2008), indicating the possibility of mitigating the impact of climate change through migration.

To reach the patterns predicted under the full-dispersal scenario, species need to disperse at an average speed of 17.4 km/decade (a range of 0.1–40.9 km/decade) until 2050 and 13.0 km/decade (a range of 0.5–41.2 km/decade) until 2070 under the RCP 2.6 scenario, or 26.4 km/decade (a range of 0.3 km–64.8 km/decade) until 2050 and 28.1 km/decade (a range of 2.2–66.7 km/decade) until 2070 under the RCP 8.5 scenario (online supplementary Table S3). However, whether plants can keep up with the current velocity of climate change is still in doubt (Corlett and Westcott 2013). Given that many non-endemic plants have already been observed to be lagging behind the recent pace of warming (Essl *et al.* 2015) and are projected to fall behind in the future (Dullinger *et al.* 2012), it may be unrealistic to expect endemic plants to keep pace with the changing climate because most of them are habitat

specialists and poor dispersers (Pearson 2006). Studies about tree-line shifts on the Tibetan Plateau also reported that the population density has changed under 200 years of warming, but the change in position may need longer time (Liang *et al.* 2011). In addition, habitat destruction and fragmentation caused by human activity in this area may create barriers to the dispersal process (Cui and Graf 2009). If species could disperse freely, the notably high turnover rate across the plateau could lead to unprecedented composition changes in the current plant communities.

Herbaceous plants may face a higher extinction risk than woody plants

The predicted extinction risk for herbaceous plants is higher than that for woody species, possibly due to the differences in climate tolerance and favored habitat. Woody plants tend to favor warm areas in the lowlands and are distributed mainly in deep valleys, while herbaceous plants tend to be distributed in rather flat areas at high altitude (online supplementary Fig. S4). The expected near-future climate change will increase the climatically suitable area for woody plants and increase the possibility of woody plants expansion.

Conservation network: insufficient for current biodiversity but effective under changing climate

Although the area of the NNRs on the Tibetan Plateau is extensive, the average ratio of current habitat of endemic plant species is 2.1% lower than that for Chinese threatened plants (Zhang *et al.* 2015a) and no significant difference was observed for the average protection ratio between threatened species and species at low risk. These results indicate a need to optimize the design of the conservation network in this region. Ideally, nature reserves should be able to maintain a long-term dynamic of biodiversity (Pressey *et al.* 2007). It is interesting that climate change would drive species into nature reserves, in contrast to the findings in Europe (Araújo *et al.* 2004), showing the effectiveness of nature reserves on the plateau under climate change.

Sampling bias, projection limitations and other sources of uncertainty

Several potential sources of bias may have influenced some aspects of our results but should not invalidate the major conclusions at large-scale in the long term. Limited by the occurrence data and study resolution, species with small distribution ranges or very few distribution records were underrepresented in our study, and most of them occur in the Hengduan Mountains and some in southeastern Tibet. However, compared with other endemic species listed for this region, our sample was in accordance with 82% of endemic species identified in the shared species list of Zhang *et al.* (2016) and Yu *et al.* (2018) after excluding species non-endemic to China and endemic to Hengduan Mountains. There was no difference in the ratio between herbaceous and woody plants or all seed plants endemic to the Tibetan Plateau, indicating a relatively balanced sampling. For Hengduan Mountains and southeastern Tibet, the magnitude of climate change is predicted to be smaller than for other regions on the plateau (online supplementary Figs S1 and S2) and we predicted the potential range of many species in the former would stay stable or increase in the future. However, whether it would be the case for species with extremely small ranges still needs to be explored at finer scale, which requires more efforts in field investigations.

CONCLUSION

In conclusion, we predict significant range shifts for endemic seed plants on the Tibetan Plateau and highlight the importance of landscape connectivity for dispersal in this region. The southeastern part of the plateau harbors most of the endemic plants, and the high habitat heterogeneity there could alleviate the threat of climate change. Most species would move west and north in the future, and species occurring on the interior plateau may face great habitat loss and invasive risk. The extinction risk for herbaceous plants is higher than for woody plants. The coverage of the conservation network for current biodiversity is not satisfying, but species tend to move into the protected areas under climate change if allowing migration. Our study should facilitate practical conservation planning for this region by identifying key processes and vulnerable areas and providing thoughts about the future of high-altitude endemics in a changing world.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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