Original Research Article

Effects of climate change on the potential distribution of the threatened relict *Dipentodon sinicus* of subtropical forests in East Asia: Recommendations for management and conservation

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A R T I C L E   I N F O

A B S T R A C T

Dipentodon sinicus Dunn. (Dipentodonaceae) is a rare and threatened relict plant species usually found co-dominating with other relict plants in subtropical forest patches in highly fragmented habitats of southwestern China, northern Vietnam and northeastern Myanmar of East Asia. To date, its management and conservation strategies in the light of climate change have not been explored. We evaluated effects of climate change on the distribution of climatically suitable areas of *D. sinicus* as found prevailing during the last glacial maximum (LGM), the mid-Holocene and the present time, and predicted the distribution of climatically suitable habitats in 2070 throughout East Asia. The results as derived from ecological niche modeling (ENM) show the current distribution to be limited to the pre-historic (the mid-Holocene and LGM) refugia, and to indicate decreasing probability of presence and a reducing range of distribution for 2070. In addition, the suitable areas predicted with high probability (0.5−1) only account for on average 9.8% of the total area of potential habitats (threshold–1) among the models for the year 2070, thereby indicating that *D. sinicus* is highly vulnerable. Under all the future scenarios for the year 2070, 69−74.2% of potential habitats in China would be outside protected areas. We assess and propose priorities for protected areas, and provide suggestions for conservation management strategies.

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1. Introduction

During the last three decades, strong evidence has emerged indicating that increased atmospheric concentration of greenhouse gases, particularly carbon dioxide and methane linked to human activities, have already begun to modify the global climate. Significant changes are predicted in temperature, rainfall, sea-levels, CO_2 concentrations and fire patterns across the world (IPCC, 2014). The multiple components of global climate change are anticipated to affect all the levels of biodiversity, from organism to biome levels (Bellard et al., 2012), and can have profound impacts on the sustainability of various ecosystems (Liu et al., 2015). Climatic variables are important environmental factors that determine ecological niches of tree species and their patterns of distribution (Avise, 2000; IPCC, 2001; Wang et al., 2019). Studies suggest that climate change could surpass habitat destruction as the greatest global threat to biodiversity over the next few decades. Because of climate change, species may no longer be adapted to the set of environmental conditions in a given region and could therefore
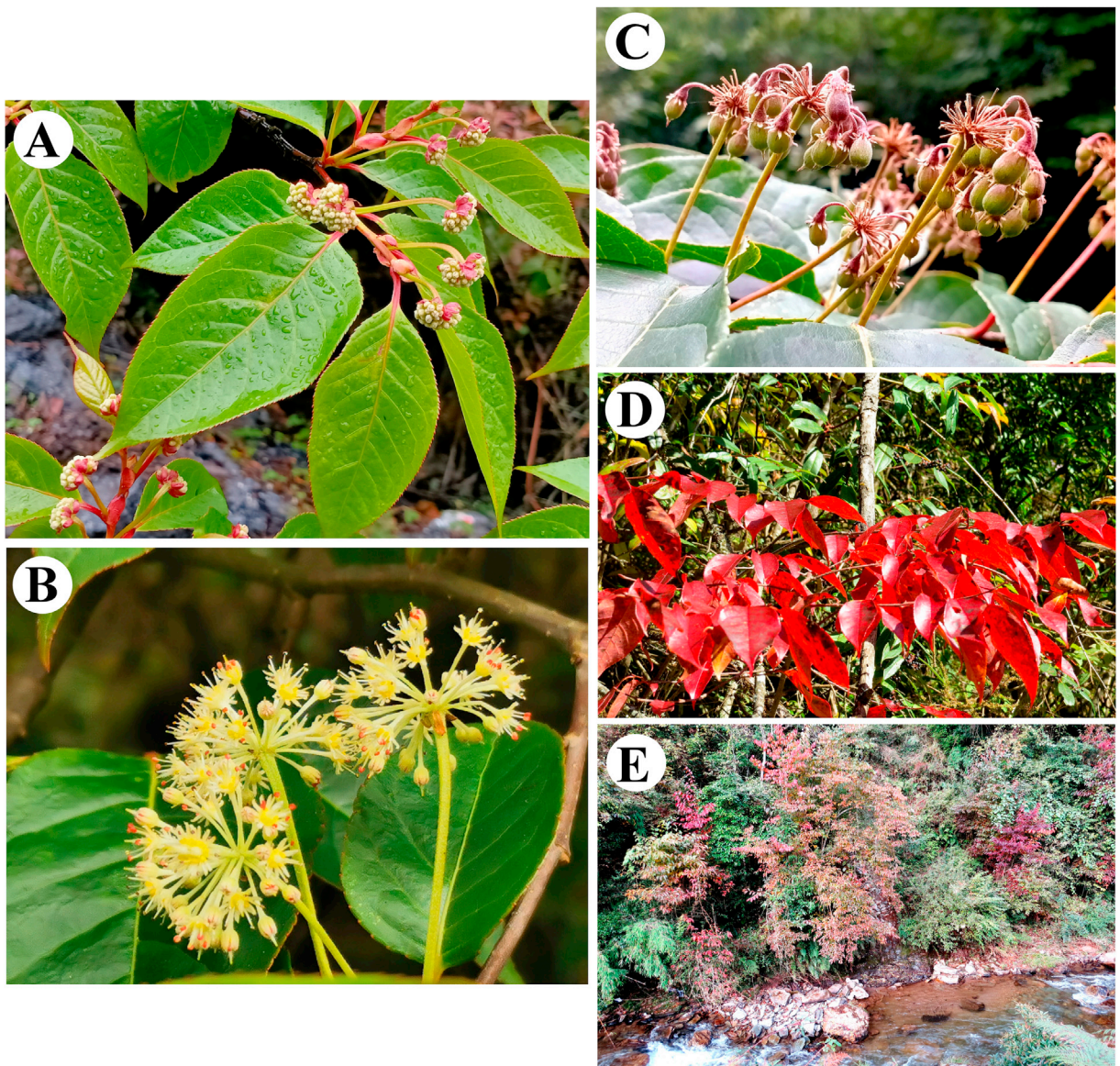

Fig. 1. Dipentodon sinicus and its habitat. (A) *D. sinicus* leaves and flower buds. (B) *D. sinicus* inflorescences. (C) *D. sinicus* fruits. (D) *D. sinicus* leaves in autumn. (E) *D. sinicus* trees (the ones with red and reddish leaves) along a stream side in Caojian Zhen, Yunlong County, Yunnan. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

fall outside its climatic niche (Leadley et al., 2010). Estimating the past and present distribution of relict plants can provide insights in identifying climatic refugia (Chen et al., 2012; Sakaguchi et al., 2012; Tsuyama et al., 2014; Tang et al., 2017, 2018). Predicting future distribution patterns can reveal regions that may face high extinction rates, thus aiding in assessing threats to the survival of species (Matsui et al., 2004; Wiens and Graham, 2005; Tsuyama et al., 2014; Tang et al., 2017, 2018). Ecological niche modeling (ENM) is a widely used method to produce spatially explicit and comprehensive maps that are particularly useful for identifying areas where conservation efforts and management strategies are most needed. There are few ecological evaluations of climate change that may threaten the survival of relict species in East Asia in future (e.g. Qin et al., 2017; Tang et al., 2017, 2018; Wang et al., 2019). It is necessary to know how species will change their spatial distribution in response to global climate change for management and conservation.

Many plant species in East Asia may have survived through the Quaternary climate change, partly thanks to the fact that ice sheets did not cover this region during the glacial periods (Clark and Lix, 2002; Ehlers and Gibbard, 2007). East Asia is found to have a high number of relict plants (Tang, 2015; Tang et al., 2018). This region also displays high endemism, particularly paleo-endemism (Qian et al., 2003; Manchester et al., 2009). Southwestern China and northern Vietnam are identified as long-term stable climatic refugia that can conserve ancient lineages, in many cases lineages that became extinct before and during the Pleistocene in North America and Europe, but persisted to the present in East Asia (Tang et al., 2018). In addition to remain ice-free, these refugia (Tang et al., 2018) would have enjoyed mild climates (with annual mean temperatures of 10−20 °C, annual precipitations of 1000−2000 mm, and moderate seasonality both in temperature and precipitation) throughout time, favoring the persistence of mesophytic relict lineages (Tang et al., 2018).

Dipentodon sinicus is the sole member of the monotypic genus Dipentodon. This genus, together with Perrottetia, forms the small family Dipentodonaceae (Ma and Bartholomew, 2008), which is at present placed within the small order Huerteales together with Gerrardinaceae, Petenaeaceae, and Tapisciaceae based on molecular data (Worberg et al., 2009; Christenhusz et al., 2010; APG IV (Angiosperm Phylogeny Group IV), 2016; Chen et al., 2016). Although a second species of Dipentodon has been described, D. longipedicellatus (Liu and Cheng, 1991), genetic data does not support the existence of a separate species of D. sinicus (Yuan et al., 2008). Thus, though no fossils of this species have been found, its relictual nature is beyond doubt as Dipentodonaceae is sister to Tapisciaceae (Christenhusz et al., 2010; Chen et al., 2016), and fossils of Tapiscia are known from the Eocene in Europe and North America (Manchester et al., 2009). Dipentodon sinicus is endemic to East Asia, sparsely scattered in montane forests in southwestern China, northern Vietnam, and northeastern Myanmar. It is a habitat specialist and has specific regeneration niches (Tang et al., 2019). This species is protected in China, already included in the National List of Rare and Endangered Plant Species of 1984 (listed as "second grade" nationally protected) and later in the Catalogue of the National Protected Key Wild Plants of 1999 (also as "second-grade"). The species was already included in the first (Fu and Jin, 1992) and second (Wang and Xie, 2004) red books of China (as a "rare" species and as a "vulnerable" one, respectively). But in the red list of 2013 the species is listed, surprisingly, as LC ("least concern"; MEP−CAS, 2013). Despite this, based on our previous paper and fieldwork, the species should be regarded as threatened, as over the past 20 years it has suffered rapid population declines (Yuan et al., 2008), mostly because of anthropogenic activities such as its direct cutting for fuel and the habitat loss and fragmentation of its habitats (Tang et al., 2019). Dipentodon sinicus is rare in botanical gardens, though its seeds are collected and stored in the Germplasm Bank of Wild Species in Kunming, Yunnan, China.

Conservation and management of rare, threatened and/or protected species are top priorities for the maintenance of biodiversity. Up to now no adequate studies have been carried out to estimate the potential impact of climate change on D. sinicus, and so far no conservation strategies that consider climate change have been proposed. Here we apply an ENM approach based on D. sinicus presence data and climatic surfaces at four different time points (LGM, mid-Holocene, present, and 2070) to (1) estimate the geographic distribution of D. sinicus at the LGM and mid-Holocene and present, (2) predict potential distribution of D. sinicus under future climate change (2070), and (3) propose priority protected areas and suggest conservation strategies for this relict species.

2. Material and methods

2.1. Species

Dipentodon sinicus is a small (<15 m) deciduous broad-leaved tree. The leaves are stipulate, alternate, and simple, with serrate margins. Inflorescences are globose umbels of abbreviated cymes. The fruit is a single-seeded fleshy capsule. When the fruit is mature, it begins to burst before it dries out. Then the seed is ejected. Dipentodon sinicus is usually co-dominating with other relict plants such as Tetracentron sinense, Pterocarya macroptera var. delavayi, and Liquidambar formosana in subtropical forest patches in highly fragmented habitats along streams, steep slopes, landslide sites, roadsides at elevations of ca. 1800−2900 m in subtropical mountainous area, in southwestern China, northern Vietnam and northeastern Myanmar (Tang et al., 2019) (Fig. 1A−E). Its high chromosome count ($2n = 2x = 34$) compared to the confamiliar Perrottetia racemosa ($2n = 2x = 20$) may suggest that D. sinicus may have resulted from hybridization of two ancestors with basic chromosome numbers of $x = 8$ and $x = 9$ (Yang et al., 2009).

2.2. Occurrence data and ecological niche modeling

Dipentodon sinicus occurrence data for the whole of geographic distribution range were obtained from our field investigations and the Chinese Virtual Herbarium (CVH; http://www.cvh.org.cn/). Although many records from CVH did not specify latitude and longitude, we were able to geo-reference detailed locations, using only specimens with locations specified in the label information. In total, after removing duplicate records within each pixel (2.5 arc-min, *ca.* 5 km), we obtained 199 presence records.

In order to study the distribution patterns of *D. sinicus* from the Last Glacial Maximum (LGM; *ca.* 21,000 yr BP) to mid-Holocene (*ca.* 6000 yr BP), present and future [2070 (average for 2061−2080], we carried out species distribution models using MaxEnt v. 3.3 (Phillips et al., 2006). The output is a map of habitat suitability ranging from 0 to 1 per grid cell. We compiled as baseline predictors a set of 19 WorldClim bioclimatic variables (www.worldclim.org; Hijmans et al., 2005), which were extracted for current climatic conditions (ca. 1960−1990). We designed as the study area a region considerably larger than the current species range (0−80°N and 65−180°E). Although such an approach may produce less realistic predictions of species potential distribution (Anderson and Raza, 2010), we have considered the whole East Asia as the study area, given the complexity of this region in terms of topography and Neogene biogeographic history (including substantial marine transgressions/regressions) and the possibility that suitable areas would appear far away from the present occurrence areas for any of the other time periods considered (as it sometimes occurs, with range shifts of several thousand km; e.g. Pellisier et al., 2016).

For the past (the mid-Holocene and LGM), we employed data derived from three general circulation models (GCMs) that are available in WorldClim: the Community Climate System Model Version 4 (CCSM4) (Gent et al., 2011), the Model for Interdisciplinary Research on Climate Earth System Model (MIROC-ESM) (Watanabe et al., 2011), and the New Earth System Model of the Max Planck Institute for Meteorology (MPI-ESM-P) (MPIM, 2012).

For the year 2070 (average for 2061−2080), we used three of the models that have shown excellent performance among those that have participated in the 5th Coupled Model Inter-Comparison Project (CMIP5) experiment (McSweeney et al., 2015): CCSM4, the NOAA Geophysical Fluid Dynamics Laboratory Coupled Model 3 (GFDL-CM3) (Donner et al., 2011), and MPI-ESM-LR. The three models were run in the two extreme concentration pathways (RCPs) of the Fifth Assessment IPCC report, RCP 2.6 and RCP 8.5 (Collins et al., 2013). RCP 2.6 considers a likely increase of 0.3−1.7 °C for ca. 2081−2100), whereas in RCP 8.5 the increase is of 2.6−4.8 °C for the same period. All 19 bioclimatic variables for present, past and future climate scenarios were downloaded with a resolution of 2.5 arc-min (*ca.* 5 km) from the WorldClim database.

To choose the species-specific environmental set from the 19 variables, we selected a set of candidate models after correlation analysis for environmental variables in 10,000 random points generated from background bias file (Phillips et al., 2009). First, we excluded those models that included combinations of highly correlated variables (Pearson's $r \geq |0.70|$; correlation analyses were run in R package base; R Core Team, 2017). Then, we calculated Variance Inflation Factors (VIF); datasets with VIF $\geq$ 5 were excluded to avoid multi-collinearity. VIF were estimated using the *vif* function included in the *usdm* package in R (R Core Team, 2017). By this procedure, the number of final candidate combinations of parameters was 1615. To select the most parsimonious combination of parameters, we first set the ß-multiplier at 0, and chose the best combination among the 1615 candidate parameter combinations by the corrected Akaike Information Criterion (AICc; Hurvich and Tsai, 1989). Then, we tested 31 different ß-multipliers (Morales et al., 2017) from 0 to 15 in steps of 0.5 and chose the best ß-multiplier value based on AICc. The best combination of variables (that with the lowest AICc value) was bio2 (mean diurnal range), bio8 (mean temperature of the wettest quarter), bio9 (mean temperature of the driest quarter), bio15 (precipitation seasonality), bio18 (precipitation of the warmest quarter), and bio19 (precipitation of the coldest quarter).

As method of replication to construct MaxEnt models, we used the cross-validation approach by running 10 replicates to obtain more robust modeling results. In *k*-fold cross-validation, occurrence data is divided randomly into *k* equal-size groups, and models are built using $k − 1$ bins for calibration in each iteration, with the left-out bin used for evaluation; background data are sampled by Maxent from the entire study region (Radosavljevic and Anderson, 2014). Predictive performance of models was evaluated by using the continuous Boyce index (CBI; Boyce et al., 2002; Hirzel et al., 2006). To distinguish between suitable and not suitable areas in the models, we chose the maximum sensitivity plus specificity (MSS) logistic threshold, which is very robust with all types of data (Liu et al., 2016). Finally, to overcome the uncertainty associated to the variability in the predicted suitable areas among all generated models, we employed the methodology described in Tang et al. (2017). Following this method, once the "standard" model was obtained, we removed the pixels that were regarded as suitable by <95% of the replicate models; the resulting map was regarded as "refined" map (i.e., that depicting predicted areas with a very high level of confidence; Tang et al., 2017).

All ENM predictions were visualized in ArcGIS v. 10.2 (ESRI, Redlands, CA, USA). The suitable area (in km^2) for all models at each time slice for *D. sinicus* was also calculated in ArcGIS. To estimate suitable area gains or losses (or unchanged areas) for both past and future scenarios with respect to the present, binary output maps were overlapped with the Intersect Tool of ArcGIS. To provide conservation advice on *D. sinicus*, the digitized map of Chinese protected areas was overlapped with the species occurrences and both binary maps of the present and future scenarios. The climate data under various scenarios for the three time periods (present, mid-Holocene, LGM) are provided in the Supplementary Tables S1−S2.

3. Results

3.1. Model performance and present potential distribution

The present distribution area of *D. sinicus* is confined to mountainous regions in southwestern China including Yunnan, Guizhou, Guangxi and southeastern Tibet, but also northern Vietnam and northeastern Myanmar (Fig. 2A).

We projected possible distribution of climatically suitable areas (potential habitats) for *D. sinicus* as expressed by occurrence probability (Fig. 2B). Our model showed excellent performance (CBI = 0.904 ± 0.028). Bio9 (mean temperature of the driest quarter) was the most important variable determining the potential distribution of the species, followed by bio18 (precipitation of the warmest quarter), bio8 (mean temperature of the wettest quarter), and bio19 (precipitation of the coldest quarter); their percent contributions were 47.83%, 40.57%, 4.25%, and 4.05%, respectively.

Present-day records are located in potential habitats under current climate (Fig. 2B). The area of potential habitats, after accounting for uncertainty, is 1,719,604 km^2 using the threshold of 0.137, but the potential habitats under high probability (0.5−1) only account for 16.8% of the total suitable area (threshold−1) (Table 1). The potential areas for *D. sinicus* in southern Korea and southern Japan show low probability (threshold−0.3), as also occurs for southeastern China. Taiwan, southeastern Sichuan Basin, southeastern Hubei, and the Himalayan region (i.e. from Nepal to Arunachal Pradesh in the Himalayas) appear as highly potential habitats but *D. sinicus* is not found there at present (Fig. 2B). These so-called "empty habitats" are results of conditions other than the climate.
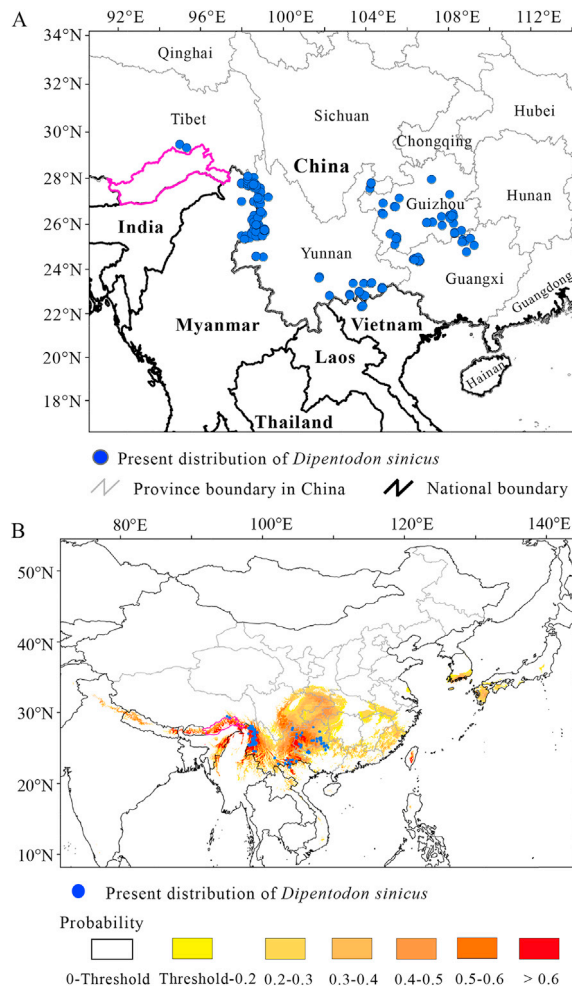

Fig. 2. *Dipentodon sinicus* current occurrences and occurrence probabilities under present climate in East Asia. (A) Current occurrences. (B) Occurrence probabilities under present climate. Purple lines: national boundaries between China and India (at issue). Maps were generated using the software ArcGIS v. 10.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Predicted potential distribution of *Dipentodon sinicus*.

Model	Total Predicted area (km^2)	Predicted area (km^2) from threshold−0.5	Predicted area (km^2) from 0.5 to 1	Difference respect to present (km^2 and %)	Overlap with present (km^2 and %)	Overlap of the present with each model (%)
Present	1,719,604	1,430,708	288,896			
Mid-Holocene-CCSM	1,703,062	1,543,955	159,107	16,542 (−0.96)	1,388,019 (81.50)	80.72
Mid-Holocene-MIROC	1,840,903	1,382,304	458,599	121,299 (+7.05)	1,287,737 (69.95)	74.89
Mid-Holocene-MPI	2,179,728	1,831,928	347,800	460,124 (+26.76)	1,523,156 (69.88)	88.58
Average Holocene	*1,907,897*	*1,586,062*	*321,835*	*188,293,67 (+10.95)*	*1,399,637 (73.78)*	*81.39*
LGM-CCSM	2,923,421	2,234,830	688,591	1,203,817 (+70.01)	1,407,005 (48.13)	81.82
LGM-MIROC	2,717,306	2,139,745	577,561	997,702 (+58.02)	1,224,628 (45.07)	71.22
LGM-MPI	2,568,936	1,712,342	856,594	849,332 (+49.39)	1,304,940 (50.80)	75.89
Average LGM	*2,736,554*	*2,028,972*	*707,582*	*1,016,950 (+59.14)*	*1,312,191 (47.95)*	*76.31*
2070-CCSM-RCP 2.6	1,729,506	1,509,157	220,349	9902 (+0.58)	1,458,872 (84.35)	84.84
2070-GFDL-RCP 2.6	1,038,689	937,669	101,020	680,915 (−39.60)	906,596 (87.28)	52.72
2070-MPI-RCP 2.6	1,153,224	1,045,898	107,326	566,380 (−32.94)	1,094,284 (94.89)	63.64
2070-CCSM-RCP 8.5	1,375,836	1,238,079	137,757	343,768 (−19.99)	1,041,465 (75.70)	60.56
2070-GFDL-RCP 8.5	536,112	485,406	50,706	1,183,492 (−68.82)	349,888 (65.26)	20.35
2070-MPI-RCP 8.5	783,963	752,414	31,549	935,641 (−54.41)	660,083 (84.20)	38.39
Average 2070	*1,102,888*	*994,770*	*108,117*	*616,715 (−35.86)*	*918,531 (83.28)*	*53.42*

3.2. Projected distribution during the mid-Holocene (ca. 6000 yr BP) and LGM (ca. 21,000 yr BP)

We used scenarios mid-Holocene-CCSM, mid-Holocene-MIROC and mid-Holocene-MPI to model potential climatic habitats of *D. sinicus* during the -mid-Holocene (*ca.* 6000 yr BP). Under the three scenarios (Fig. 3), potential habitats were increased with respect to the present (about 10.95% on average; Table 1), and were mainly located in Guizhou, Yunnan, eastern Sichuan Basin, northern Vietnam, east-central Myanmar, the boundary between northwestern Yunnan and Myanmar and the boundary between Myanmar and northeastern India. Southern Korea and southern Japan (for southern Japan, mid-Holocene-MIROC) were, in contrast, generally not potential habitats during the mid-Holocene. The potential habitats during the mid-Holocene were mostly included within the current potential habitats (73.78% on average; Fig. 3 and Table 1). Potential areas for the mid-Holocene not included in the current ones were limited to east-central Myanmar (Fig. 3C, E and G).

We used scenarios LGM-CCSM, LGM-MIROC and LGM-MPI to model potential climatic habitats of *D. sinicus* during the LGM (*ca.* 21,000 yr BP). Under each of the three scenarios, the potential area greatly increased with respect to the present (59.14% on average), and overlap areas were about 48% (47.95% of the LGM with the present; Fig. 4 and Table 1). Area gains with respect to the present were mainly concentrated in northwestern and east-central Myanmar, northern Laos, Vietnam and, from China, the southern margins of Guangdong, as well as Fujian and Zhejiang provinces (including also some emerged lands in both the South and East China Seas; Fig. 4C, E and G). The potential habitats were continuously distributed from the boundary between southeastern Yunnan and northern Vietnam to Yunnan, Guizhou and eastern Sichuan Basin in southwestern China, and east-central and northeastern Myanmar.

3.3. Projected distribution under future climate (2070)

Climate change effects on the geographic range of *D. sinicus* in 2070 are predicted under 2070-CCSM RCP 2.6, 2070-GFDL RCP 2.6, 2070-MPI RCP 2.6, 2070-CCSM RCP 8.5, 2070-GFDL RCP 8.5, and 2070-MPI RCP 8.5 scenarios (Figs. 5 and 6).

Under the 2070-GFDL RCP 2.6 and 2070-MPI RCP 2.6 scenarios the area of potential habitat for *D. sinucus* would be somewhat diminished (39.60% and 32.94%, respectively), whereas it would not change under the 2070-CCSM RCP 2.6 scenario (Table 1). Most of the potential habitats for the year 2070 are included among those of the present time (84.35−94.89%; Fig. 5B–G and Table 1). The only exception would be the northwest to the Sichuan Basin under the 2070-GFDL RCP 2.6 scenario (Fig. 5E). The predicted suitable habitats having high probability (0.5−1) would account for only 9.31%−12.74% of all the area of potential habitats (threshold–1) (Fig. 5 and Table 1).
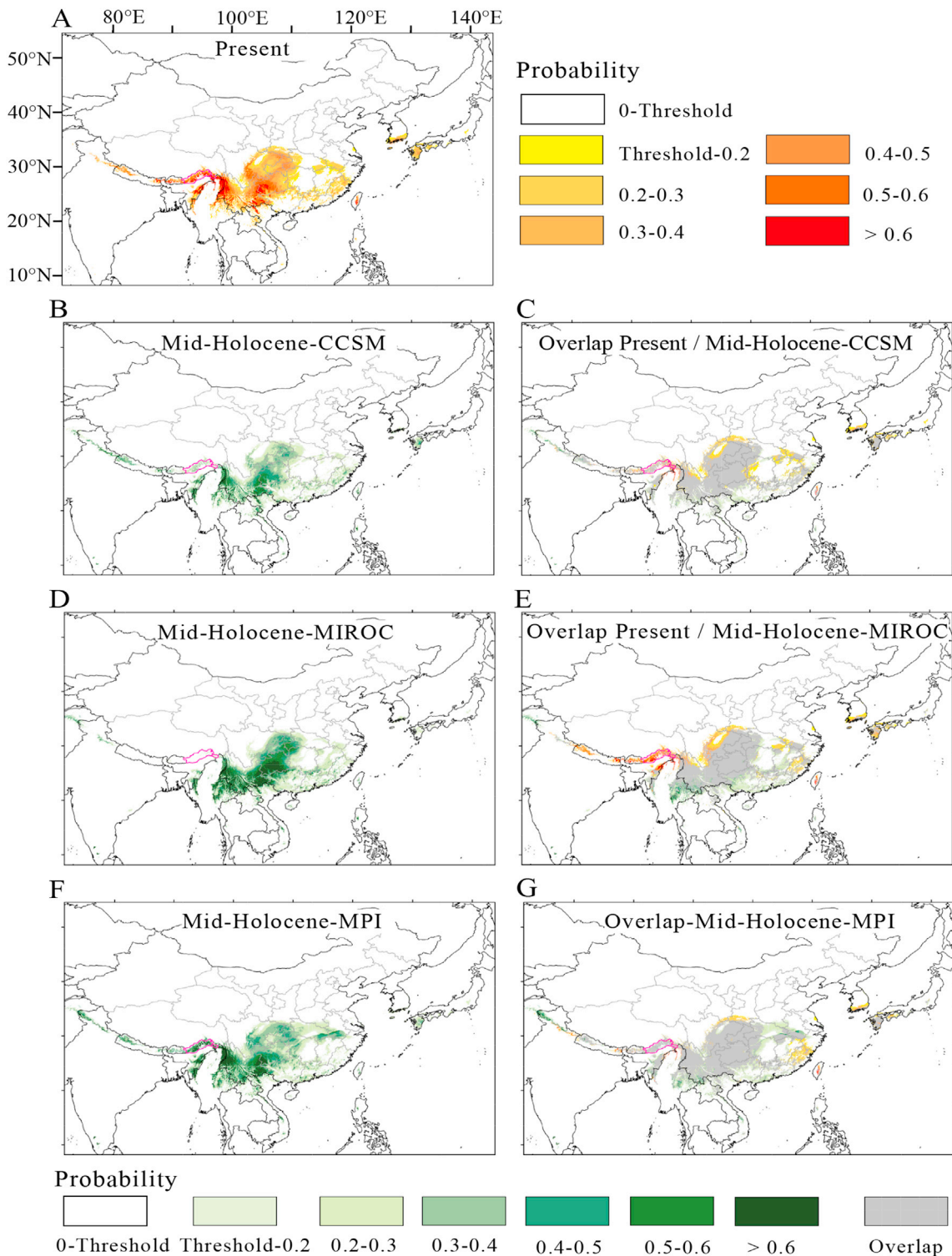
Fig. 3. A comparison of potential habitats under the present climate and three climatic scenarios in the mid-Holocene. (A) Potential habitats under the present climate; (B) Potential habitats under the climatic scenario mid-Holocene-CCSM; (C) Overlap areas of the mid-Holocene-CCSM and the present. (D) Potential habitats under the climatic scenario mid-Holocene-MIROC; (E) Overlap areas of the mid Holocene-MIROC and the present. (F) Potential habitats under the climatic scenario mid-Holocene-MPI. (G) Overlap areas of the mid-Holocene-MPI and the present. Purple lines: national boundaries between China and India (at issue). Maps were generated using the software ArcGIS v. 10.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
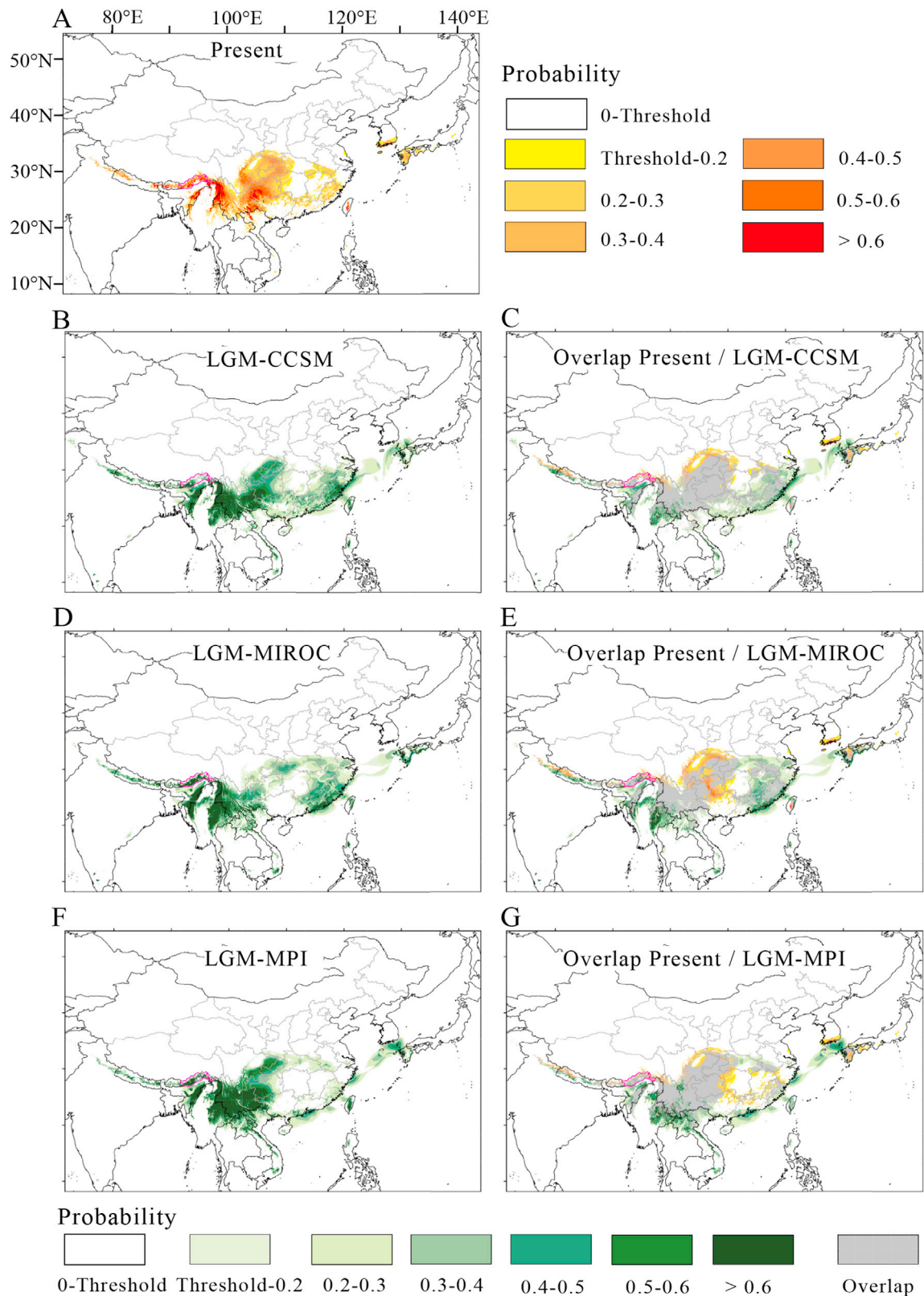
Fig. 4. A comparison of potential habitats under the present climate and three climatic scenarios in the LGM. (A) Potential habitats under the present climate; (B) Potential habitats under the climatic scenario LGM-CCSM; (C) Overlap areas of the LGM-CCSM and the present. (D) Potential habitats under the climatic scenario LGM-MIROC; (E) Overlap areas of the LGM-MIROC and the present. (F) Potential habitats under the climatic scenario LGM-MPI. (G) Overlap areas of the LGM-MPI and the present. Purple lines: national boundaries between China and India (at issue). Maps were generated using the software ArcGIS v. 10.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
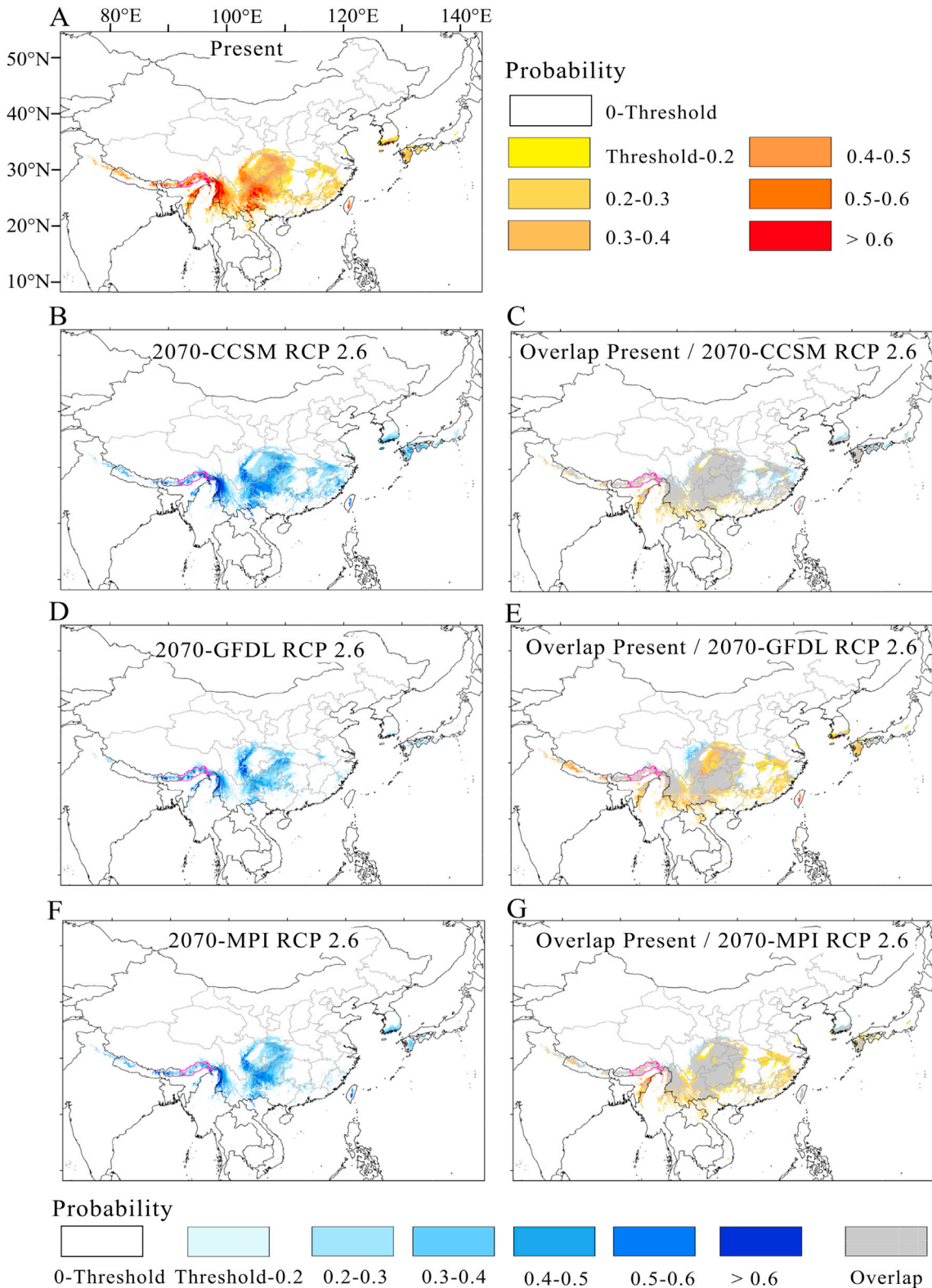
Fig. 5. A comparison of potential habitats under the present climate and three climatic scenarios in future (2070). (A) Potential habitats under the present climate; (B) Potential habitats under the climatic scenario 2070-CCSM RCP 2.6; (C) Overlap areas of the 2070-CCSM RCP 2.6 and the present; (D) Potential habitats under the climatic scenario 2070-GFDL RCP 2.6; (E) Overlap areas of the 2070-GFDL RCP 2.6 and the present; (F) Potential habitats under the climatic scenario 2070-MPI RCP 2.6; (G) Overlap areas of the 2070-MPI RCP 2.6 and the present. Purple lines: national boundaries between China and India (at issue). Maps were generated using the software ArcGIS v.10.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
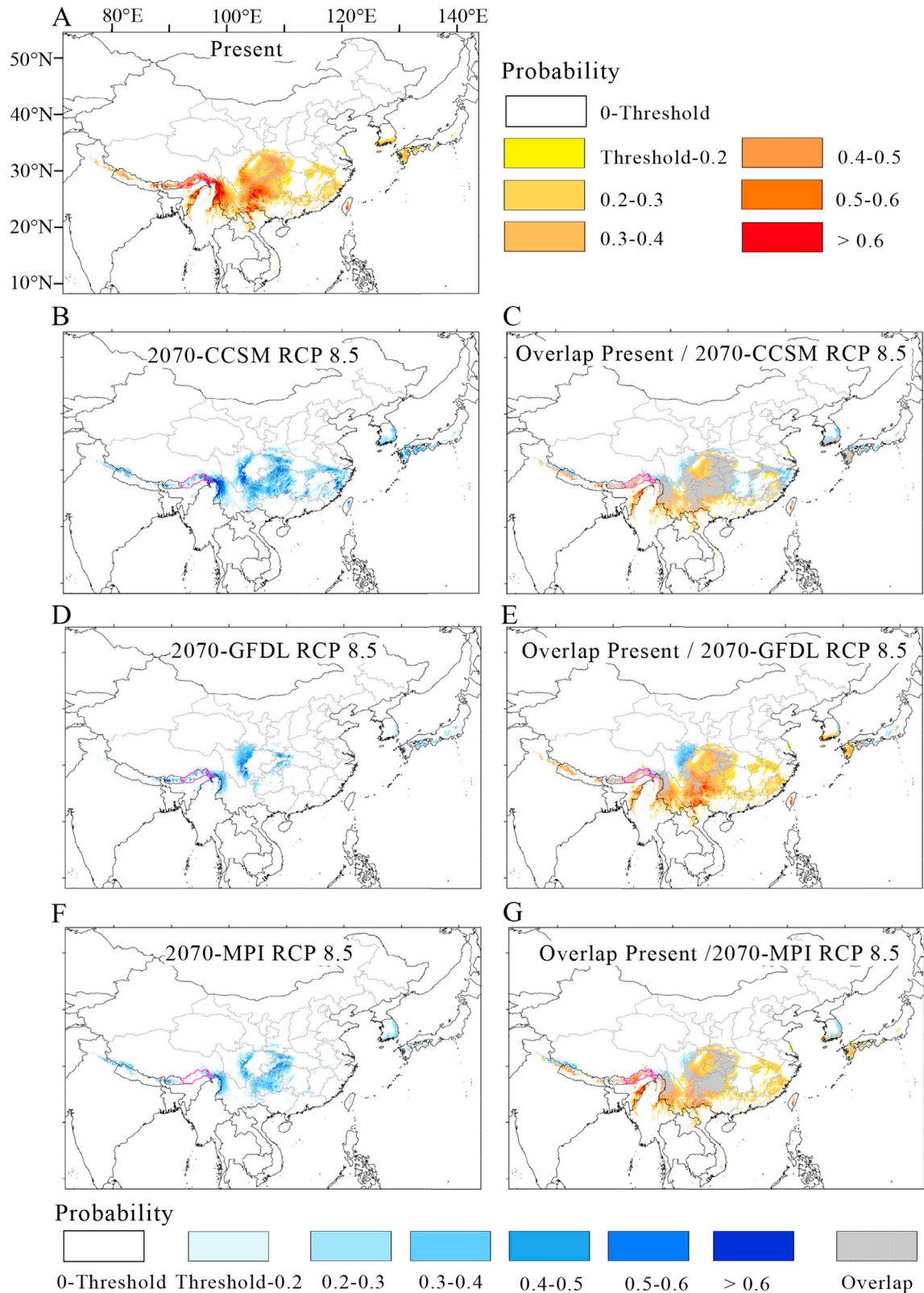
Fig. 6. A comparison of potential habitats under the present climate and three climatic scenarios in future (2070). (A) Potential habitats under the present climate; (B) Potential habitats under the climatic scenario 2070-CCSM RCP 8.5; (C) Overlap areas of the 2070-CCSM RCP 8.5 and the present; (D) Potential habitats under the climatic scenario 2070-GFDL RCP 8.5; (E) Overlap areas of the 2070-GFDL RCP 8.5 and the present; (F) Potential habitats under the climatic scenario 2070-MPI RCP 8.5; (G) Overlap areas of the 2070-MPI RCP 8.5 and the present. Purple lines: national boundaries between China and India (at issue). Maps were generated using the software ArcGIS v. 10.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Under the 2070-CCSM RCP 8.5, 2070-GFDL RCP 8.5, and 2070-MPI RCP 8.5 scenarios, the area of potential habitats would show a big loss (19.99−68.82%) compared to the present one (Table 1); suitable areas in Yunnan, Guizhou, the Sichuan Basin, eastern China, northern Vietnam, and Myanmar would be largely reduced (Fig. 6B, D, F). The area overlapping with the present potential habitats is still high (65.26−84.2%), and non-overlapping areas would be limited to the northwest to the Sichuan Basin. (Fig. 6C, E, G and Table 1). The suitable habitats with high probability (0.5−1) would account for only 4.02−10.0% of all the area of potential habitats (threshold−1) (Fig. 6 and Table 1).

In sum, under the six future climate scenarios D. sinicus would have considerable losses of potential habitats (with an average of 35.86%), particularly focused on Yunnan, Guizhou, the Sichuan Basin, eastern China, northern Vietnam and northeastern Myanmar. The remaining suitable areas for the year 2070 are mostly included within the current potential distribution area (Figs. 5 and 6, Table 1). We must expect a decline in area of suitable habitats for this species as global climate change progresses, although some populations of D. sinicus would shift to the high mountains in the northwest to the Sichuan Basin (Figs. 5E and 6C, E and G).

3.4. Priority protected areas for management and conservation

Because of different policies of nature reserve management in different countries, and because the current distribution range of D. sinicus is mainly in China, also because 80.3% of future (2070) potential distribution range of this species is within China, we only assess priority protected areas in China in this study. Up to 50.3% of the present-day presence points of this species are outside the present protected areas (nature reserves) of China (Fig. 7A). The result of the spatial distribution model shows that 73.8% of potential habitats are outside the existing protected areas (nature reserves) under the present climate (Figs. 7B and 8, Supplementary Table S3). Under the future 2070-GFDL RCP 2.6 scenario, 70.5% of potential habitats in China would be outside the protected areas (nature reserves) (Figs. 7C and 8, and Supplementary Table S3). On an average of all the six predicted models for the year 2070, 70.8% of potential habitats in China would be outside the network of nature reserves (Figs. 7C and 8, and Supplementary Fig. S2 and Table S3). These currently unprotected areas are as priority for management and conservation, and particularly the highest priority protected areas for the most suitable habitats (i.e., the high-probability ones, 0.5−1).

4. Discussion

4.1. Effects of climate change on spatial distribution patterns of D. sinicus

To understand spatial distribution of species under climate change, identifying and characterizing climate refugia is important (Davis and Shaw, 2001; Jansson and Dynesius, 2002; Petit et al., 2005). The past refugia of D. sinicus were restricted to the same locations as contemporary populations, in a similar way to many relict plant taxa in East Asia (Tang et al., 2017, 2018). During the LGM, over 76% of the current potential distribution area would have been suitable for the persistence of the species, and some new areas would have been added as potential habitats (such as east-central Myanmar and the southern margin of eastern China, including some areas in the emerged platform of both the South and East China Seas) (Fig. 4). During the mid-Holocene, compared to the LGM, even more (over 81%) of the current potential distribution area would have been suitable for the persistence for D. sinicus (Fig. S1; Tables S1 and S2, Fig. 3). Interestingly, most of the areas suitable for both past and present time periods considered (LGM, mid-Holocene, and present) in D. sinicus coincide with those recovered from nearly 450 East Asia relict species (Tang et al., 2018). As demonstrated by these authors, central and southwestern China (and contiguous regions of Vietnam and Myanmar) would have been long-term stable refugia for paleo-species, because these areas would have maintained through time the climatic conditions favorable for the growth of thermophilic, moisture-loving relict lineages; this is probably one of the main reasons of why some of these species disappeared from other parts of the Northern Hemisphere (including the famous "living fossils" Gingko biloba or Metasequoia glyptostroboides) (Manchester et al., 2009). As in other parts of China (Tian and Jiang, 2016), elsewhere in Asia (Chabangborn et al., 2014) and the entire world (Alder and Hostetler, 2014) the climate was in general much cooler and drier at the LGM than at present; so it appears that not only the avoidance of a large drops of temperature but also the availability of moisture is a prerequisite for the survival of species through the Pleistocene climatic cycles (Tzedakis et al., 2002; Birks and Willis, 2008; Chung et al., 2017). If we compare the past–present climate conditions between the localities of D. sinicus (which are mainly located within the long-term stable refugia for paleo-species of Tang et al., 2018) and the study area (which is much larger, 0−80°N and 65−180°E), such conditions would have kept much more stable in the first compared to the second (Supplementary Fig. S1; Tables S1 and S2). Taking as examples the annual mean temperature (bio1) and the annual precipitation (bio12) they were, on average, 10.19 °C/1316 mm and 13.68 °C/1339 mm at the LGM and at present, respectively (i.e. a drop of about 3.5 °C and of just 1.7% of the year's total rainfall), for the localities of D. sinicus. For the study area, in contrast, these would be −7.28 °C/536 mm and 1.05 °C/606 mm (i.e. a drop of about 8.3 °C and of 11.6% of the year's total rainfall).

Under future rapid climate warming, however, only part (Figs. 5 and 6, Table 1) of the current refugia for D. sinicus will continue to have a suitable climate for this species, a result that has also been found with another relict species of East Asia, Davidia involucrata. As reported by Tang et al. (2018), the areas maintaining a relatively high climatic stability through time (i.e., the long-term refugia for relict lineages), which are located in central and southwestern China and in northern Vietnam, will significantly shrink in 2070. Thus, assuming that D. sinicus would not be able to shift its niche in this short time (see
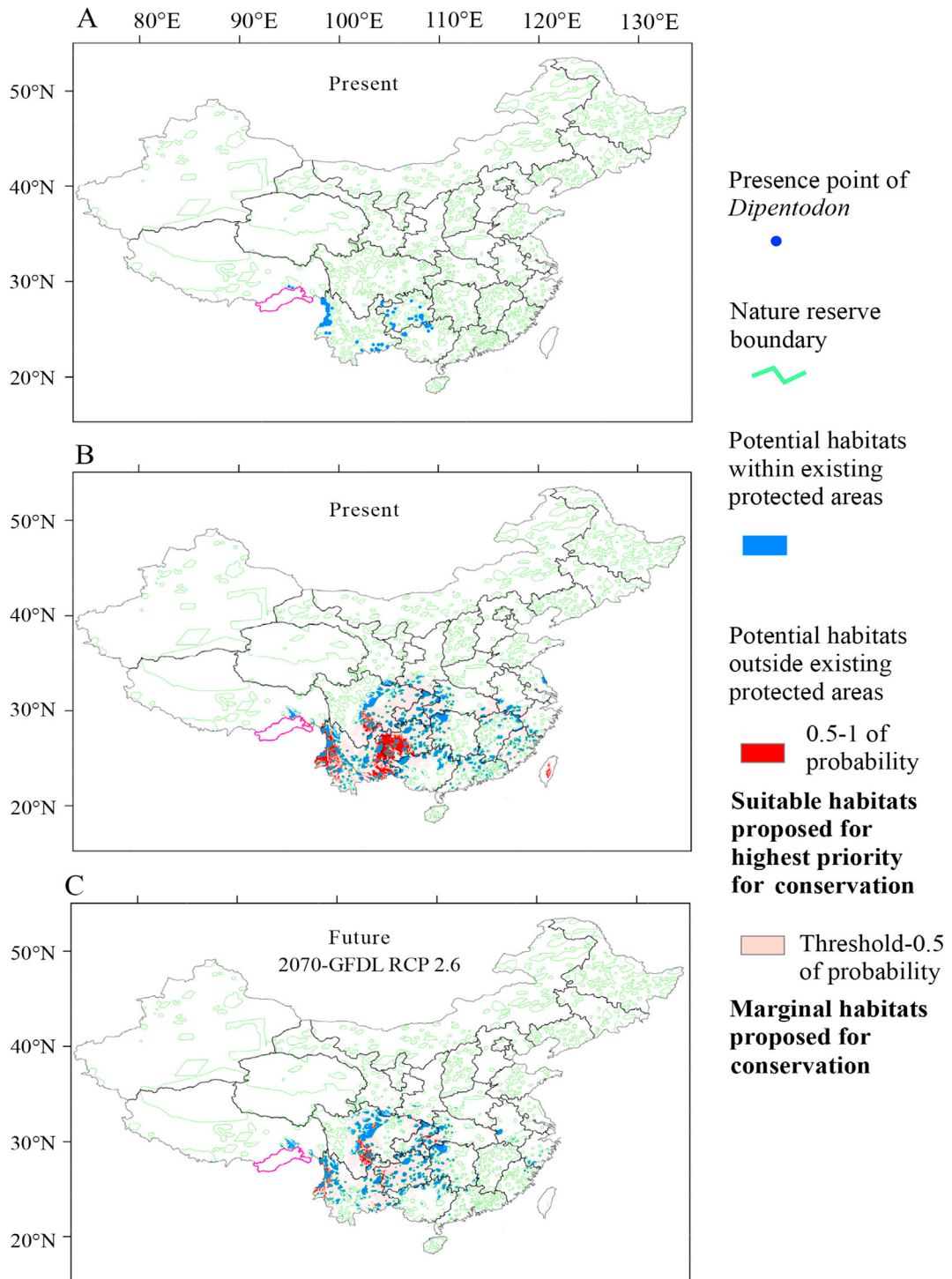
Fig. 7. Current presence points and modeled potential habitats of *Dipentodon sinicus* with and without protection in China. (A) Current presence points within and outside existing protected areas (nature reserves) of China. (B) Modeled potential habitats with and without protection under the present climate in China, with areas proposed for conservation. (C) Predicted potential habitats with and without protection under a future 2070 climate in China, with areas proposed for conservation, exemplified by the scenario 2070-GFDL RCP 2.6. Purple lines: national boundaries between China and India (at issue). Maps were generated using the software ArcGIS v. 10.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
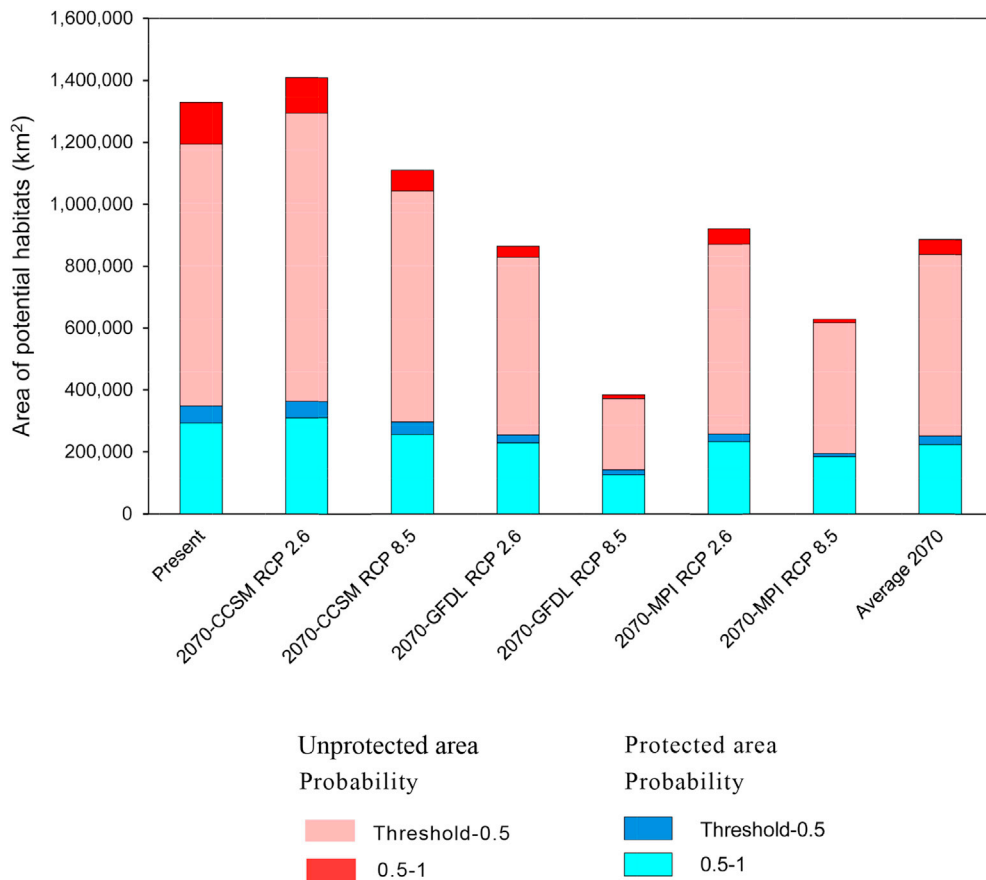
Fig. 8. Area of potential habitats of *Dipentodon sinicus* with and without protection in China.

discussion below), the potential areas of overlap between the current and future distribution of this tree are likely, thus, *in situ* refugia of this species from ongoing climate change. Only the northwest to the Sichuan Basin is identified as new climate refugia looking into the future (Figs. 5 and 6), a scenario that, again, has also been identified in *Davidia involucrata* (Tang et al., 2017).

The effects of climate change on trees can be complicated, as different combinations of alterations in temperature and precipitation can result in different impacts (Parmesan, 2006) and different tree species can have different responses to climate change (Hanson and Weltzin, 2000). Reductions in distribution are particularly expected for species with weak dispersal capacity, long maturation time, and/or slow growth rate (Gill et al., 2013). *Dipentodon sinicus* has persisted in the mountains in Yunnan, Guizhou and northern Guangxi, southeastern Tibet, and the boundary between southeastern Yunnan and northern Vietnam, also northeastern Myanmar. However, given future distribution under six possible climate scenarios, only some parts of the current distribution range of *D. sinicus* in southwestern China would be maintained, while the range of distribution would considerably shrink and some populations would shift to high mountains in the northwest to the Sichuan Basin by 2070 under future RCP 2.6 and RCP 8.5 scenarios. The ratio of seed-setting of this species is very low (4.31%; Zhang et al., 2017), which might be consistent with the low levels of within-population genetic diversity ($h_S = 0.047$). This species shows, however, a very high genetic differentiation ($G_{ST} = 0.948$; Yuan et al., 2008), which may be related with its short distance dispersal (seed dispersal is through ejecting from capsules; Yuan, 2007). Such a genetic pattern is unfavorable for the persistence of *D. sinicus* under a scenario of global warming, as low within-population genetic diversity may decrease the ability of species to survive to changing environments while high genetic differentiation may reflect strong local adaptation to current conditions (Falk et al., 2006). Moreover, it has slow growth, and it is found in highly fragmented habitats at limited elevations (1800−2900 m) (Tang et al., 2019). All these traits are associated with low adaptive capacity to climate change.

There is evidence of niche and evolutionary conservatism in many plants (Huntley et al., 1989; Royer et al., 2003; Romdal et al., 2013), including the relict ones (Svenning, 2003). Romdal et al. (2013) tested the niche conservatism hypothesis by comparing slopes of latitudinal diversity gradients in a wide sample of taxonomic groups—both terrestrial and aquatic—from across the 'tree of life', and found that these gradients were steeper for clades originated in periods of warm climates (and, thus, with a strong tropical affinity) than those originating in cold periods (i.e., no tropical affinity). The authors concluded that higher diversities have arisen among tropical clades because the Earth has been predominantly tropical throughout most

of its history. Aligned with the tropical niche conservatism hypothesis, Tang et al. (2018) attributed the occurrence of long-term refugia for relict lineages in the mountainous areas of southwestern China and northern Vietnam because these would have retained the pre-Quaternary mild (warm, humid, and moderately seasonal) climates till the present. However, the global warming would mean the disappearance of most of these refugia (Tang et al., 2018). Therefore, most East Asian paleoendemic species including *D. sinicus*, which generally are habitat specialists with no much potential for niche evolution, might have many difficulties to incorporate new adaptations or disperse to new localities in the time projected for climate change, nor can they compete with non-paleoendemic evergreen broad-leaved species; instead, a retraction in their distributions is the most likely scenario (e.g., Tang et al., 2017). In East Asia, most relict plants are usually found in a narrow range of altitudes (ca. 1500−2700 m) in the complex habitat mosaics of mountainous topography, subtropical/warm-temperate areas, especially southwestern China, and thrive in special habitats including stream sides, steep and scree slopes, and limestone areas where competition usually is less intense and the regeneration potential of non-relict species is lower (Tang, 2015; Tang et al., 2018). All the relict plant species that occur in the *D. sinicus* community (e.g. *Tetracentron sinense*, *Pterocarya macroptera* var. *delavayi,* or *Liquidambar formosana*) will be threatened by rapid global climate change.

5. Recommendations for future conservation efforts and management

The use of scenario planning has been advocated on climate change management adaptations (e.g., Theoharides et al., 2009; Glick et al., 2011). Climate change may reduce habitat suitability of threatened plant species within Chinese nature reserves (Wang et al., 2016; Tang et al., 2017, 2018). Establishment and management of protected areas (nature reserves) should include consideration of all the current distributed sites of *D. sinicus*, and must recognize the species' future distribution in response to future climate conditions. It is worrisome that about half of the current localities of the species in China, as well as about three quarters of its potential habitats, are not included within the network of protected areas. Moreover, this lack of *in situ* protection would continue in the future: on an average of all the six predicted models for the year 2070, 70.8% of potential habitats in China would be outside the network of nature reserves (Figs. 7 and 8, and Supplementary Fig. S2 and Table S3). As seen in Fig. 7 and Supplementary Fig. S2, the most urgent needs for new nature reserves are in the mountains of the southwestern margin of the Sichuan Basin. We especially recommend extending existing nature reserve coverage to include the threat areas in western Guizhou, southeastern and western Yunnan. If they are isolated, other categories of *in situ* conservation such as a forest park or non-logging area are recommended; establishing 'plant micro-reserves' (PMRs), which are small sites ideal for preserving endemic and endangered plants, could be a good complement for the protection provided by large protected areas (Fos et al., 2017). It is important to note that these projections are only based on climate change. In reality, more dangers are created by human activities such as encroachment and fuel wood collection. *Dipentodon sinicus* are found in very fragmented habitats (Tang et al., 2019) and according to our field survey some populations of this species outside the nature reserves are small and lack regeneration, suggesting increased risk of local extinction. Therefore, *ex situ* conservation strategies such as seed banking and reintroduction are needed for this species' genetic resources and survival. The combination of low genetic diversity and high differentiation is the worst scenario in terms of management efforts, as seeds should be taken from as many populations as possible, and special care should be paid to translocations between populations in order to minimize potential outbreeding depression. In addition, planting seedlings of *D. sinicus* in suitable habitats under future climatic conditions could also be a successful conservation strategy (Chung et al., 2020).

Declaration of competing interest

We declare there are no conflicts of interest in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01192.

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