



## Identifying long-term stable refugia for dominant *Castanopsis* species of evergreen broad-leaved forests in East Asia: A tool for ensuring their conservation

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### ABSTRACT

Identifying and protecting refugia is a priority for conservation management under projected anthropogenic climate change. We have two main objectives: the first is to explore the spatial (East Asia) and temporal (Last Glacial Maximum to year 2070) distribution patterns of dominant *Castanopsis* species of evergreen broad-leaved forests, also the relation with their niche breadths; the second is to identify long-term stable refugia for preserving these species and provide a framework of conservation strategies. We find that there is an extraordinary richness with 32 dominant *Castanopsis* species, and they form both a geographically and climatically almost unbroken connection from ca. 5°N to 38°N, having thus ecological significance. During the Mid-Holocene and, particularly, the Last Glacial Maximum, the predicted suitable areas of the species as a whole were larger than those in the present. By 2070, potentially suitable areas with high richness of dominant *Castanopsis* species will be reduced by 94.5 % on average. No correlation between species niche breadths and distribution ranges is found, which could be due to regional climate stability. Mountains of southwestern and southern Yunnan in China are identified as climatically long-term stable refugia for 7–9 *Castanopsis* species. We recommend that these refugia have the highest priority of conservation to prevent their extinction. Our suggested urgent measures include improving the effectiveness of currently protected *Castanopsis* species and expanding the network of protected areas to cover a larger fraction of the refugia, as well as ensuring *Castanopsis* species natural regeneration potential in fragmented and natural secondary forest areas.

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## 1. Introduction

Climate change, which is now beyond dispute and unequivocally linked to man will be a major threat to biodiversity in the next decades and centuries (Masson-Delmotte et al., 2021). But we currently lack quantitative assessments that could inform the debate regarding the conservation of the natural heritage, guiding further actions and suggesting strategies for ecosystem management. Identifying and protecting refugia is a priority for conservation under projected anthropogenic climate change, because of their demonstrated ability to facilitate the survival of biota under adverse conditions (Keppel et al., 2012). The term “long-term stable refugia” is defined as the climatically suitable areas that allowed the persistence (in contrast to other areas) of ancient lineages at least since the late Pleistocene (Tang et al., 2018). These authors revealed the existence of such refugia in the mountainous humid subtropical/warm-temperate areas of East Asia, which are still home of an extraordinary assemblage of paleo-lineages that once occurred in North America and Europe (and that were extirpated from there because of the Neogene climatic deterioration; Latham and Ricklefs, 1993; Manchester et al., 2009). If Tang et al. (2018) models are valid, these relict lineages would persist there even under the worst climatic change scenarios, a concept of refugia that differs somewhat, thus, from other views advocating that refugia would only be effective at the short-term, giving species longer persistence time but not necessarily providing a permanent haven (e.g., Morelli et al., 2020).

Quantifying changes in the spatial distribution of species across time can provide valuable information regarding biogeography, paleoecology and macro-evolution (Stigall and Lieberman, 2006). Modelling these changes, using Ecological Niche Modelling (ENM), allows an opportunity to predict species' niches in changing environmental conditions which in turn can be used to generate conservation plans not only for endemic taxa but also for forests (e.g., Hijmans and Graham, 2006; Tang et al., 2017, 2018, 2020b). Determining climatic niche breadths (the range of climatic conditions that a species experiences over space and time) is also important to understand species responses to climate change (Quintero and Wiens, 2013), because species are often confined to a limited set of climatic conditions (i.e., they have narrow climatic niche breadths), and this narrowness may have important implications for species responses to global warming (e.g., Tingley et al., 2009; Sinervo et al., 2010).

About 125–130 species of *Castanopsis* (Fagaceae) are confined to the subtropics and tropics of East and Southeast Asia (south to the Yangtze River in China, Indo-China, Malay Peninsula, Malay Archipelago, and the Himalayas), and further extending to northern regions including warm-temperate Japan (Kyushu and Honshu) and the southern edge of Korea (Tang, 2023). Reliable fossil records were found in the USA in Middle Eocene (Manchester, 1994) and Pliocene (Axelrod, 1962), and in Europe and Japan in Miocene (Mai, 1989, 2001; Ozaki, 1991), indicating that the geographical distribution range of *Castanopsis* was much wider in the past than today. Despite that diversification times of *Castanopsis* infrageneric taxa (i.e., species) are not still available, the relictual character of the genus is indisputable, as it would have split from *Castanea* at least 52 Mya according to recently-discovered fossils (Wilf et al., 2019). *Castanopsis* has important ecological and economic significance. Many *Castanopsis* species are the dominant canopy trees of subtropical/warm-temperate evergreen broad-leaved forests and some tropical montane evergreen broad-leaved forests (e.g., Ohsawa, 1993; Tang, 2015; Tang, 2023). They are also significant ecological components of the evergreen broad-leaved forests in East Asia (Kremer et al., 2007; Tang, 2023). Most species of *Castanopsis* are used for timber, firewood and charcoal, and the nuts of some species are edible (Huang et al., 1999). In addition, they also have high cultural values (e.g., Watanabe et al., 2021).

Whether and how climate change affects spatial and temporal distribution patterns of all dominant *Castanopsis* species of evergreen broad-leaved forests (hereafter dominant *Castanopsis* species) in East

Asia has not been fully clarified, though recent modeling under future climate change scenarios predicted potential range reductions or expansions of some *Castanopsis* species (Cheuk and Fischer, 2021). Up to now the climatic long-term stable refugia for dominant *Castanopsis* species have not been identified and conservation evidence for the stable refugia is not available. The aims of this study are (1) to explore spatial and temporal distribution patterns of all the 32 dominant *Castanopsis* species of the evergreen broad-leaved forests at a large geographic scale—East Asia—for the past (Mid-Holocene and Last Glacial Maximum), present and future (2070); (2) to explore the possible correlations between niche breadths and distribution ranges; (3) to identify long-term stable refugia for the dominant *Castanopsis* species; and (4) to see whether the current network of protected areas is effective in preserving the identified *Castanopsis* refugia, and to provide suggestions for conservation management strategies.

## 2. Materials and methods

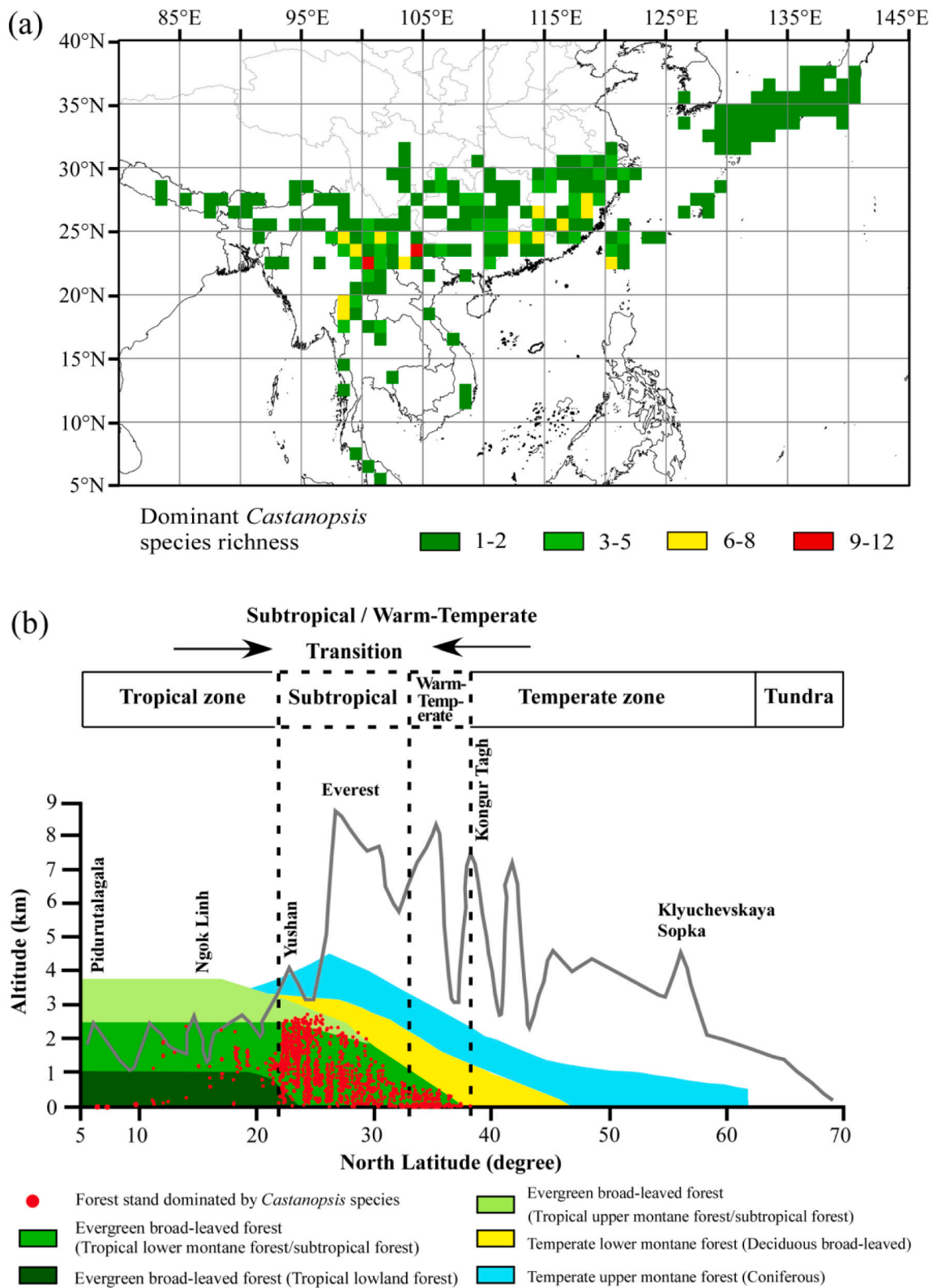
### 2.1. Data collection and notations

We selected 32 *Castanopsis* species that each of them is the 1st dominant of evergreen broad-leaved forests in an area approximately delimited by a rectangle with coordinates of 5°N/80°E in the SW corner and 40°N/145°E in the NE one (Fig. 1a). This area is aimed to represent the range of dominant *Castanopsis* species of East Asia, including large parts of China, Japan, and Korea, the eastern and central Himalayas (northern Myanmar, north-eastern India, Bhutan, Nepal), the deltaic plain of Bangladesh, southern Myanmar, Thailand, Vietnam, Laos and Cambodia (but excluding areas of Malaysia, Indonesia and neighboring islands).

Within this area, occurrence records of these 32 *Castanopsis* species were gathered only when they were the dominant species in that location in terms of importance value [IV = (Relative density + Relative basal area) / 2] (Tang et al., 2020a). The species with the highest IV in each location was determined as the 1st dominant. We were able to compile a total of 1515 occurrences (the number of occurrences per species is detailed in Appendix Table S1), which should be regarded as locations with dominant *Castanopsis* species of evergreen broad-leaved forests (or, simply, “dominant *Castanopsis* species”). Occurrence data for the 32 dominant *Castanopsis* species were based on field records mostly (but not exclusively) derived from our own extensive fieldwork during recent decades. Further data were drawn from a large number of printed sources including monographs and journal articles pertinent to the evergreen broad-leaved forests of East Asia (the data sources are detailed in Appendix Additional Occurrence Data Sources). Data were scrutinized for misidentified, possibly inaccurate or duplicate records by the expertise and further field work of plant ecologists and botanists who have contributed to this paper. We georeferenced localities based on the descriptions of the sites where the dominant *Castanopsis* species exist; we considered only those descriptions that allowed georeferencing with the accuracy required for ecological niche modeling (2.5 arc-min, ~5 km).

### 2.2. Ecological niche modeling

For the ecological niche modeling, we employed the maximum entropy algorithm implemented in MaxEnt v. 3.3 (Phillips et al., 2006). We used as baseline predictors a set of 19 bioclimatic variables (for current climatic conditions; ca. 1960–1990) downloaded from WorldClim v. 1.4 ([www.worldclim.org](http://www.worldclim.org); Hijmans et al., 2005) at a resolution of 2.5 arc-min (~5 km). Distribution models have been projected to two past [Mid-Holocene (MH, ca. 6000 yr BP) and Last Glacial Maximum (LGM, ca. 21,000 yr BP)] and one future (year 2070, average for 2061–2080) time slices. We designed as the ENM background area a region considerably larger than the current species range of the study area (0–80°N and 65–180°E vs. 5–40°N and 80–145°E). Although such an approach may produce less realistic predictions of species potential distribution



**Fig. 1.** Dominant *Castanopsis* species richness and distributions in East Asia. (a) Dominant *Castanopsis* species richness in East Asia; (b) latitudinal and altitudinal distribution of dominant *Castanopsis* species. The potential forest vegetation zone model is modified from (Ohsawa, 1993).

(Anderson and Raza, 2010), we have considered a very large part of Asia as the ENM background area; reasons include 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; Pellissier et al., 2016).

For the past (MH and LGM), we used paleoclimatic layers derived from three general circulation models (GCMs) that are available in

WorldClim v. 1.4: CCSM4 (Gent et al., 2011), MIROC-ESM (Watanabe et al., 2011), and MPI-ESM-P (MPI, 2012). For the future, we used three of the models that have shown excellent performance among the various available ones that have participated in the 5th Coupled Model Inter-Comparison Project (CMIP5) experiment (McSweeney et al., 2015), also available in WorldClim v. 1.4: CCSM4, GFDL-CM3 (Donner et al., 2011), and MPI-ESM-LR. The three future 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). Both past and future layers had a resolution of 2.5 arc-min.

For avoiding problems associated with multicollinearity, a combination of relatively uncorrelated (Pearson's  $r < |0.70|$ ) bioclimatic variables were chosen for each species (Appendix Table S1), following the methodology described in Tang et al. (2018) [i.e., by estimating Variance Inflation Factors (VIF) and using the Akaike Information Criterion (AICc)]. We used two methods of replication to build MaxEnt models: jackknife for those species with 5–29 occurrence records, and cross-validation for those with >30 occurrences (the number of occurrences per species is detailed in Appendix Table S1). Predictive performance of models was tested with a jackknife (or “leave-one-out”) procedure (Pearson et al., 2007), through success rate ( $q$ , which is the proportion of right predictions) and statistical significance (a  $p$ -value computed across the set of jackknife predictions); additionally, for those species with >30 occurrences, model performance was assessed using the continuous Boyce index (CBI) (Boyce et al., 2002; Hirzel et al., 2006). A third metric to evaluate model performance was also estimated for all species, the area under the curve of the receiver operating characteristic curve (AUC). All ecological niche models performed well with jackknife (mean probability of success = 0.891; range = 0.571–0.995), continuous Boyce index (mean CBI = 0.739; range = 0.542–0.939), and AUC (mean AUC = 0.972; range = 0.791–0.997) approaches. For more details, see Appendix Extended Materials and Methods.

To overcome the uncertainty associated with the variability in the predicted suitable areas among all generated models, we employed the methodology described in Tang et al. (2017); this method, that is based in removing the pixels that are regarded as suitable by <95 % of the replicate models, has been proved to be effective (e.g., Tang et al., 2018). Suitability maps for each species were drawn with ArcGIS v. 10.5 (ESRI, Redlands, CA, USA) for all time periods (present, MH, LGM, year 2070) using all GCMs.

### 2.3. Data analyses

We followed the workflow of Tang et al. (2018) where individual species at different time scenarios were intersected, with only the suitable areas that overlap across time being retained (as a way to identify “long-term stable refugia” for individual species). We assessed five different types of time combinations: (1) present with all past models (expressed as Present–Past); (2) present with all future models of RCP 2.6 (expressed as Present–Future RCP 2.6); (3) present with all future models of RCP 8.5 (expressed as Present–Future RCP 8.5); (4) present with all past and future models of RCP 2.6 (expressed as Present–Past–Future RCP 2.6); and (5) present with all past and future models of RCP 8.5 (expressed as Present–Past–Future RCP 8.5). This assessment strategy is schematized in Appendix Fig. S1 and, for the first case (Present–Past), we did it as follows: firstly, we intersected the three MH GCMs (model 1) and the three LGM GCMs (model 2) and, secondly, we intersected model 1, model 2, and the present model (model 3) to get the “Present–Past” model.

Once the intersection step was completed, the maps for each species were stacked (i.e., summed) (Guisan and Rahbek, 2011) to generate maps of species richness (as a way to delineate long-term stable refugia for *Castanopsis*), and this was done for each of the five time combinations. The stacked maps were generated using *raster* package in R (Hijmans et al., 2021) and drawn with ArcGIS. Suitable area gains or losses (or unchanged areas) for both past and future scenarios with respect to

the present were estimated by means of overlapping presence/absence maps (details in Appendix Extended Materials and Methods). Suitable areas (in km<sup>2</sup>) were estimated for several species richness categories (co-occurrence of 1–3 species of *Castanopsis*, 4–6, 7–9, 10–12, 13–17, and 1–17) separately for each time scenario and also for the five different types of time combinations.

For conservation purposes, the digitized map of protected areas (PAs) for the studied region [combining the official boundaries of PAs in China—as they were in late 2010s version (Ministry of Ecology and Environment) with maps recently got from Protected Planet; <http://www.protectedplanet.net>] was overlapped with the map of Present–Past–Future RCP 2.6 and Present–Past–Future RCP 8.5, to see whether those areas with large numbers of *Castanopsis* species (i.e., the long-term stable refugia) are adequately protected.

In order to characterize the climatic niche of dominant *Castanopsis* species, and to see whether there are niche differences among them, we firstly performed a principal component analysis (PCA) using the 19 bioclimatic variables. We standardized (scaled) them in order to assign equal weights to all variables. We employed the mean values of the principal components (PCs) with eigenvalues  $\geq 1$  to calculate a distance matrix using the squared Euclidean distance with the *dist* function of *stats* package in R (R Core Team, 2017). A simple agglomerative hierarchical clustering method (UPGMA) was finally used to group the species according to their climatic niche. Climatic groups were defined by placing the UPGMA dissimilarity cut at one-third.

We determined the niche breadth by calculating the standard deviation (SD) for each bioclimatic variable and summing all SD for each species (Appendix Extended Materials and Methods). Aimed to shed light on the climate niche patterns of dominant *Castanopsis* species, niche breadths were also estimated for each of the groups identified based on their climatic affinities, but also for three groups after classifying the 32 *Castanopsis* species according to the geographic distribution, i.e., range size [widespread (EOO, extent of occurrence sensu IUCN > 1,000,000 km<sup>2</sup>), intermediate (100,000–1,000,000 km<sup>2</sup>), narrow (<100,000 km<sup>2</sup>)] and the altitudinal range [large (>2000 m), intermediate (1000–2000 m), small (<1000 m)]; see details in Appendix Extended Materials and Methods. We searched for possible correlations between niche breadth and distribution range and also between niche breadth and altitudinal range using *cor.test* function of *stats* package in R (R Core Team, 2017) with the Pearson correlation coefficient. Comparisons among groups based on climatic affinities, geographic distribution range, and altitudinal range, were also statistically tested by the non-parametric analysis of Wilcoxon-Mann-Whitney (Appendix Extended Materials and Methods).

## 3. Results

### 3.1. Dominant *Castanopsis* species in East Asia today: richness and distribution patterns

According to our field work and our summarized additional data sources from literature, the dominant *Castanopsis* species were widely distributed in East Asia, ranging from ca. 83°30'E to 141°E, 5°47'N to 38°6'N, crossing, thus, 57°30' of longitudes and 32°19' of latitudes (Fig. 1a). Yunnan of China was the richest region in dominant *Castanopsis* species (Fig. 1a). Although the altitudinal distribution of dominant *Castanopsis* species in East Asia was very wide (from the sea level to nearly 2700 m), there was a trend of altitudinal ranges to become smaller with increasing latitude in the subtropical and warm-temperate regions (Fig. 1b); at latitudes above 32°N (i.e., Japan and Korea) the *Castanopsis* species were never reaching 700 m, just below the upper altitudinal limit of the evergreen broad-leaved forests (Fig. 1b).

### 3.2. Richness of dominant *Castanopsis* species shaped by climate change

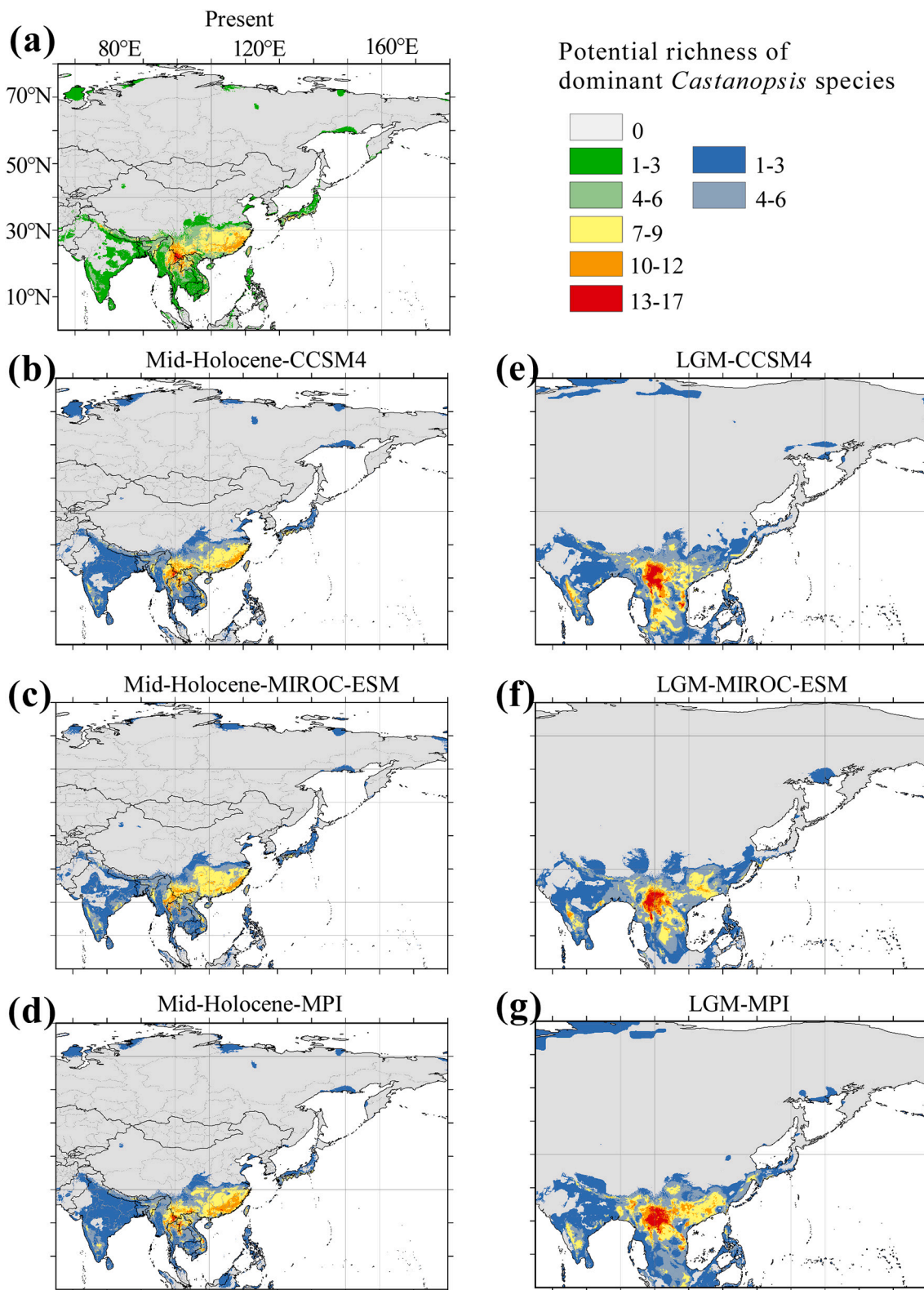
The predicted suitable areas under the present climate for the highest



richness (rank 13–17) of dominant *Castanopsis* species were only located in southern, southeastern and southwestern Yunnan, and in eastern Myanmar. The next high richness (rank 10–12) were mainly in Yunnan, the Nanling Mountains on the boundaries of Guangdong, Guangxi and

Hunan, Fujian, eastern Jiangxi of China, eastern Myanmar and north-western Laos (Fig. 2a).

By the MH, the predicted suitable areas of dominant *Castanopsis* species as a whole were larger by 9.9 % on average than the present,



**Fig. 2.** A comparison of potential richness of dominant *Castanopsis* species under the present climate and climatic scenarios in the past. (a) Under the present climate; (b–d) under scenarios Mid-Holocene-CCSM4, Mid-Holocene-MIROC-ESM, Mid-Holocene-MPI, respectively; (e–g) under scenarios LGM-CCSM4, LGM-MIROC-ESM, LGM-MPI, respectively.

although the predicted areas for the highest richness (ranks 13–17 and 10–12) were smaller by 38.8 % and 18.6 % on average, respectively (Fig. 2b–d, Appendix Table S3). In the LGM, the areas as a whole increased by 53.9 % on average, with ranks 13–17 and 10–12 being 5.2 and 1.1 times larger than those in the present, respectively (Fig. 2e–g, Appendix Table S3). When the *Castanopsis* species were considered individually, the same patterns were also found; the average individual gains were 6.93 % and 75.96 % for the MH and LGM, respectively, compared to the present (Appendix Table S4).

As compared to the present, in the future (2070) under six scenarios (the three GCMs under two RCPs) there was a clear trend of decreasing suitability with increasing the highest richness of dominant *Castanopsis* species (rank 13–17 will be reduced by 94.5 % on average, rank 10–12 by 54.3 %, rank 7–9 by 34 %, and rank 4–6 by 1.6 %). In contrast, areas with the lowest richness (rank 1–3) will expand (increase by 43.4 % on average), mostly in the northern areas, i.e., Russia (Fig. 3a–g; Appendix Table S3).

### 3.3. Niche groups and niche breadths of dominant *Castanopsis* species

In the PCA, the first three PCs accounted for 92.7 % of the total climatic variance (PC1 = 44.7 %, PC2 = 27.2 % and PC3 = 20.8 %). The first component (PC1) was mainly explained by bio3 (isothermality) and bio4 (temperature seasonality), the second (PC2) by bio12 (annual precipitation) and bio13 (precipitation of the wettest month), and finally the third (PC3) by bio5 (maximum temperature of the warmest month) and bio18 (precipitation of the warmest quarter) (Appendix Table S2). According to both UPGMA and the graphical output of PCA, five groups of dominant *Castanopsis* species could be defined based on their climatic niches (Fig. 4a, Appendix Fig. S2). Groups 1, 3, and 4 showed wide latitudinal ranges (Appendix Fig. S3), the first two covering tropical and subtropical regions (5–28°N and 12–32°N, respectively) and the latter mostly subtropical ones (18–38°N). Groups 2 and 5 had narrower latitudinal ranges (ca. 17–30°N and 22–30°N, respectively; Appendix Fig. S3), although the former was the group containing the species with the largest geographic range (mean EOO = 1,662,744 km<sup>2</sup>); *Castanopsis* species in Group 1 (which had the widest latitudinal range) showed the smallest distribution ranges (mean EOO = 284,140 km<sup>2</sup>; Appendix Table S4).

The responses of the five climatic niche groups to climate change were varied, though highly consistent with the species individual responses or when the species were stacked ( $N = 32$ ) (Fig. 4b). However, only group 4 showed a statistically narrower niche breadth compared to groups 1–3 ( $p < 0.05$ ), while for the rest of comparisons the differences were not significant. Overall, the dominant *Castanopsis* species mostly showed net increases for past scenarios (for three and four out of the five groups at the MH and the LGM, respectively) but net losses for future scenarios (for three and four out of the five groups at the year 2070 RCP 2.6 and RCP 8.5, respectively; Appendix Table S4).

No correlation between the niche breadth and the geographic distribution range size for the 32 dominant *Castanopsis* species ( $r = 0.096$ ,  $p = 0.601$ ) was found. In addition, there was also no relationship between the niche breadth and the altitudinal range ( $r = 0.029$ ,  $p = 0.876$ ). This lack of relationship in *Castanopsis* was also confirmed when the 32 species were sorted into three groups according to the range size and altitudinal range (range  $p$  values = 0.097–0.805; Fig. 4c, d).

### 3.4. Climatically long-term stable refugia

The overlap of the past (LGM and MH) and the present showed that areas (147,314 km<sup>2</sup> for rank 7–9, 9479 km<sup>2</sup> for rank 10–12; there was no overlap area for rank 13–17) in southwestern, southern and south-eastern Yunnan (China) and in eastern Myanmar have been suitable for dominant *Castanopsis* species since the LGM (Fig. 5a, Appendix Table S5). The overlap of present–future (2070) showed rather smaller potential areas with the highest richness [rank 10–12, 9102 km<sup>2</sup> on

average (18,144 and 59 km<sup>2</sup> for the RCP 2.6 and 8.5, respectively); Fig. 5b, c, Appendix Table S5]. With the overlap of present–past–future (2070) we were only able to detect suitable areas with moderate to low richness [ranks 7–9 and 4–6, with respectively 6050 km<sup>2</sup> (11,937 km<sup>2</sup>/162 km<sup>2</sup> for RCP2.6/RCP 8.5) and 313,317 km<sup>2</sup> (446,509 km<sup>2</sup>/180,125 km<sup>2</sup> for RCP2.6/RCP 8.5) on average]. The overlap areas (the areas in yellow in Fig. 5d, e) with the moderate richness (rank 7–9) were located in southwestern and southern Yunnan (Fig. 5d, e, Appendix Table S5); the *Castanopsis* species most frequently found in these areas with moderate richness were *C. calathiformis*, *C. echinocarpa*, *C. fleuryi*, *C. hystrix*, and *C. indica*. This reveals that mountains in southwestern (the Lincang and southern Boashan areas) and southern (the Simao and Xishuangbanna areas) Yunnan of China can be regarded as climatic long-term stable refugia for *Castanopsis*, with moderate richness (rank 7–9) of dominant *Castanopsis* species. Up to 78.3 % and 66.8 % of the long-term stable refugia (rank 7–9) areas were outside the existing PAs under Present–Past–Future RCP 2.6 and Present–Past–Future RCP 8.5 scenarios, respectively (Fig. 6).

## 4. Discussion

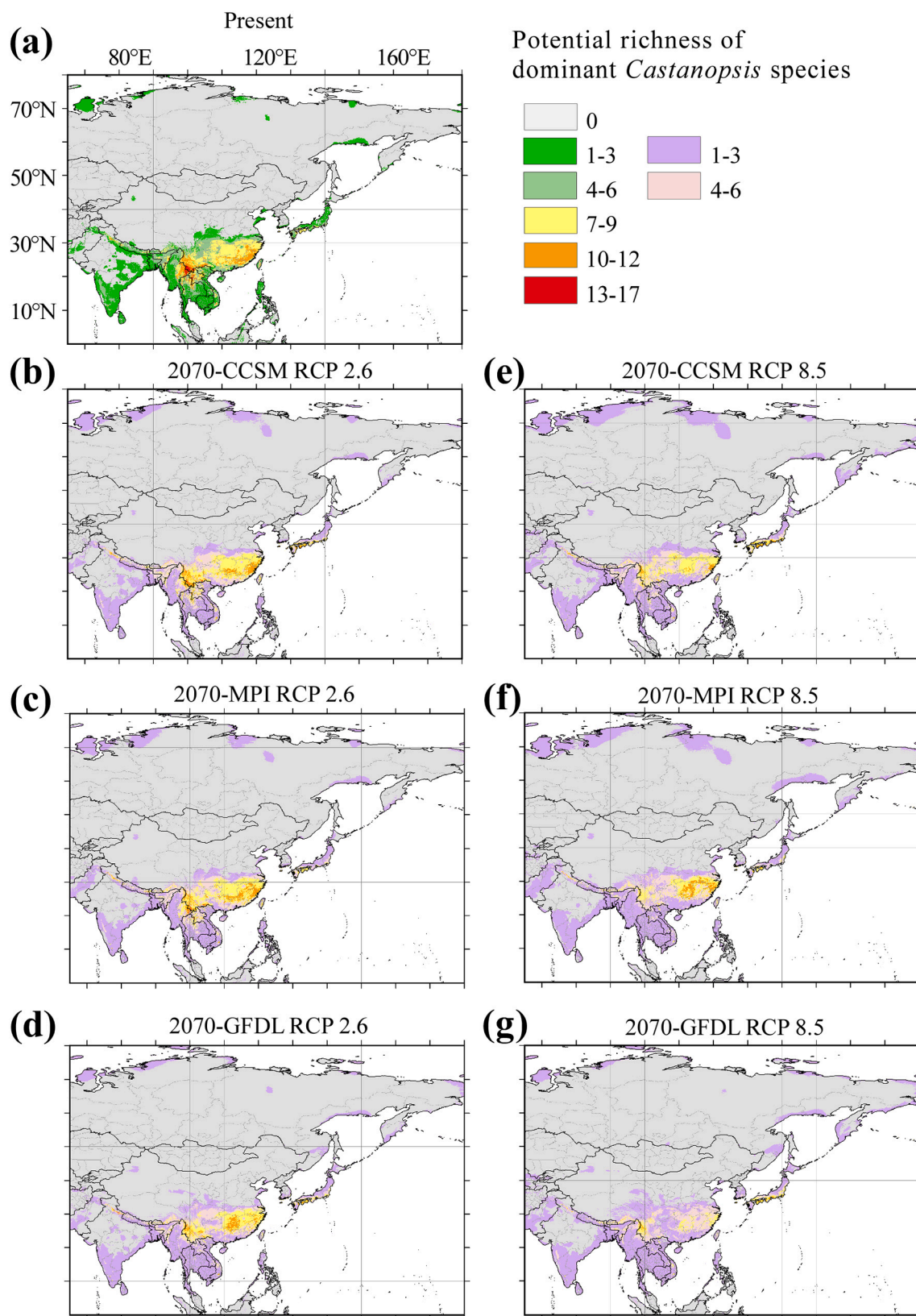
### 4.1. Richness of dominant *Castanopsis* species shaped by climate change

The potential distribution (Fig. 2a) of dominant *Castanopsis* species is generally consistent with the observed present spatial patterns (Fig. 1a). Only for the rank 1–3 there is some predicted range in areas where dominant *Castanopsis* species do not occur (western India, Sri Lanka, Pakistan, Russia, Xinjiang, and Shandong and Liaoning Provinces of northern China), which may result from conditions other than species' climatic requirements, such as soils or insurmountable physical barriers (e.g., mountains, oceans, rivers).

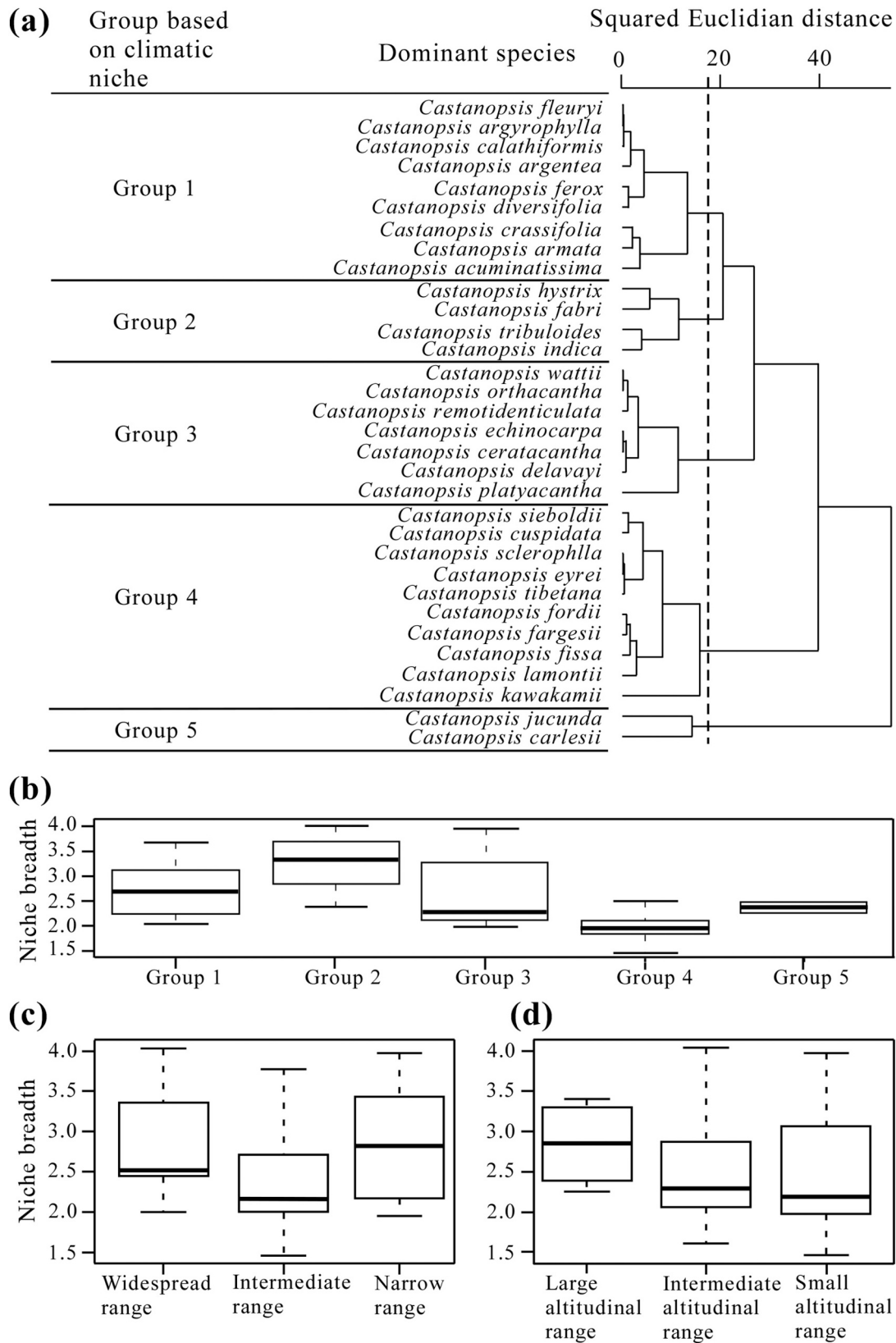
While the small changes for the MH agree with the paleoecological reconstructions for Asia (Dallmeyer et al., 2017), the considerable LGM gains are unexpected, as paleoecological data mostly suggest a general contraction of subtropical and warm-temperate forests in East Asia—at least in its central and northern regions (e.g., Ni et al., 2010; Prentice et al., 2011). Our results could be explained by the considerable expansion of lands because of LGM sea regressions, with many new areas that would have been colonized by *Castanopsis* (Sundaland [Fig. 2e–g]). According to Cannon et al. (2009), Sundaland would have sustained very large extensions of evergreen broad-leaved forests, in agreement with the modeled range expansion for the most “tropical” *Castanopsis* species (those belonging to Group 1 in Appendix Table S4, with 201.72 % of range gains on average; see also below). Indeed, the net range gains of *Castanopsis* species in the central and northernmost parts of the study area (Group 3 but especially groups 4 and 5) are more moderate or even there are losses instead of gains (Appendix Table S4).

Ongoing climate change is predicted to have unprecedented effects on the forest ecosystems of East Asia and alter the geographic distribution of forest tree species (e.g., Tang et al., 2018; Li et al., 2020). For example, using a sample of 111 tree species, a recent study found that about 52 % of the Chinese trees will show net losses of their distribution areas by 2070 (recalculated from raw data in Li et al., 2020), with some trees having lost almost completely their potential areas; however, not all trees were negatively affected, as some species will considerably expand their ranges. Our results in *Castanopsis* species for the whole East Asia are showing even more concerning results; 65.6 % and 68.8 % of the species will show net range losses for the RCP 2.6 and 8.5 scenarios, respectively, with averaged individual percentages of –10.95 % and –17.85 %, respectively (Appendix Table S2).

*Castanopsis* species have weak dispersal capacity, because their diaspores are cupulate nuts, and their dispersal depends on gravity and transportation by rodents, with a very limited dispersal distance (e.g., Xiao et al., 2005; Chou et al., 2011). Thus, *Castanopsis* species will have difficulty to migrate to new sites. This means that, in the context of ongoing climate change and from a conservation point of view, the 2070

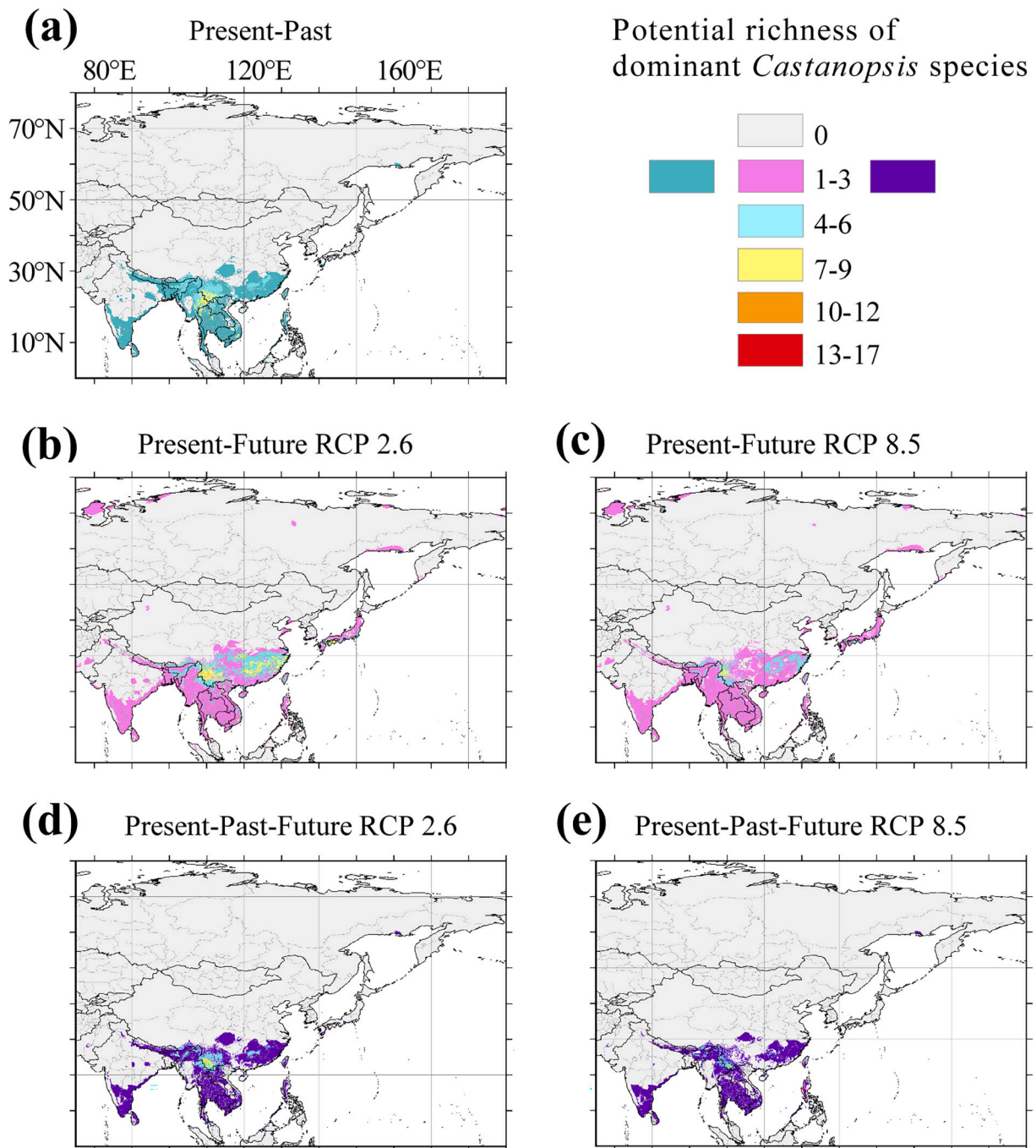


**Fig. 3.** A comparison of potential richness of dominant *Castanopsis* species under the present climate and climatic scenarios in the future (2070). (a) Under the present climate; (b–d) under scenarios 2070-CCSM RCP 2.6, 2070-GFDL RCP 2.6, 2070-MPI RCP 2.6, respectively; (e–g) under scenarios 2070-CCSM RCP 8.5, 2070-GFDL RCP 8.5, 2070-MPI RCP 8.5, respectively.



**Fig. 4.** Climatic niche groups and niche breadth of dominant *Castanopsis* species groups. (a) Climatic niche groups according to UPGMA clustering analysis; note that up to five groups can be defined when the dissimilarity cut is placed at about one-third (dashed line); (b) the niche breadth of forest groups based on climatic niches of dominant *Castanopsis* species; (c) the niche breadth of forest groups based on geographic distribution ranges (expressed as EOO; extent of occurrence) of dominant *Castanopsis* species; (d) the niche breadth of forest groups based on altitudinal distribution ranges of dominant *Castanopsis* species.



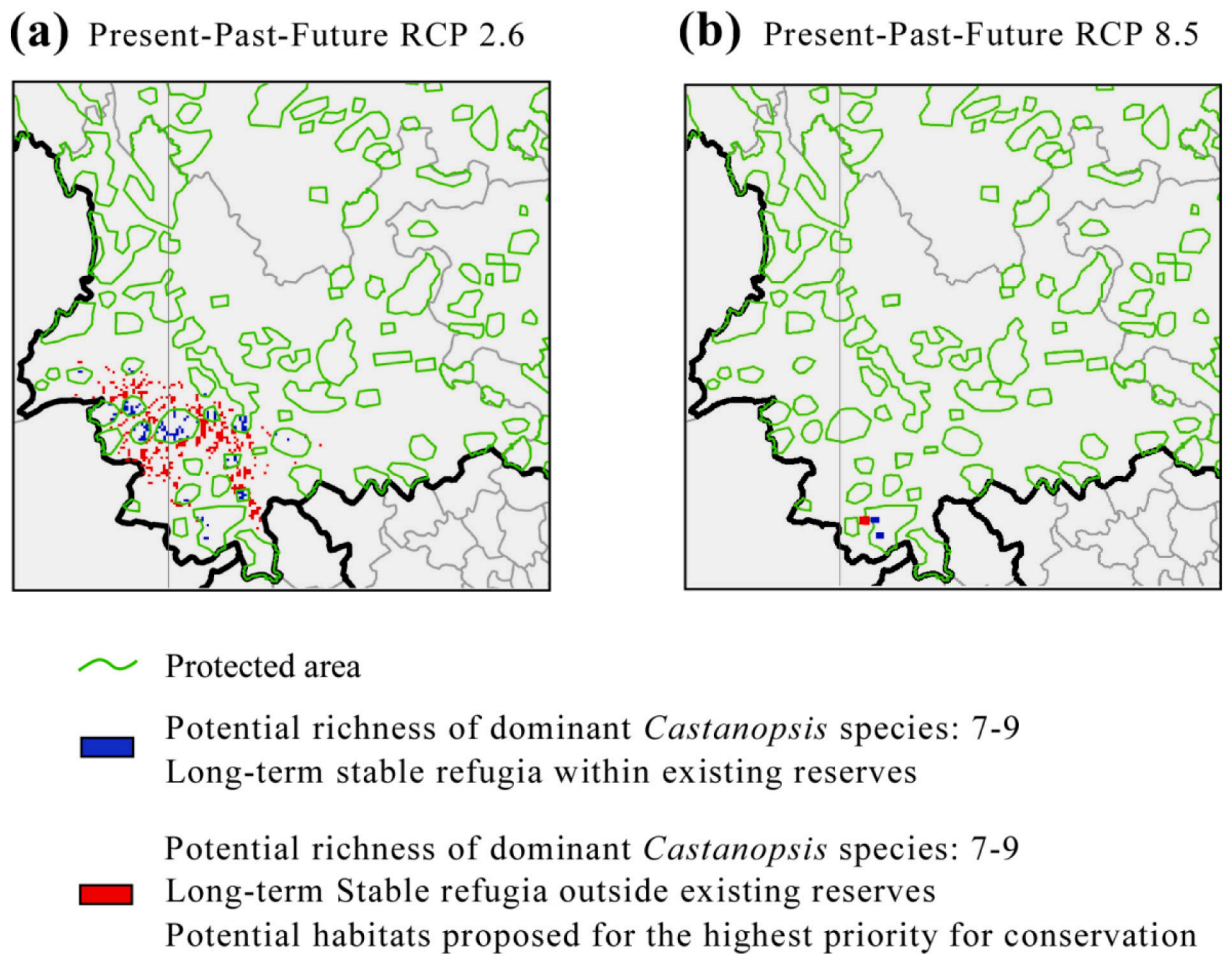


**Fig. 5.** Overlap of potential richness of dominant *Castanopsis* species of the four time frames climatic scenarios. (a) Overlap of the present and the past (LGM, Mid-Holocene); (b, c) overlap of the present and the future (2070) (under scenarios of RCP 2.6 for B, RCP 8.5 for C); (d, e) overlap of the present, the past and the future (under scenarios of RCP 2.6 for D, RCP 8.5 for E).

scenario would be worse than our predictions of net range losses, as we are assuming “universal” (full) migration (i.e., that species will be capable to colonize all new gained areas). Nevertheless, this seems to be unrealistic and, for most cases, *Castanopsis* 2070-ranges would just be the overlap areas present–future; thus, net losses could reach nearly 36 % and ca. 53 % instead of the projected losses of 10.95 % and 17.85 %, for the RCP 2.6 and 8.5 scenarios, respectively (Appendix Table S4).

Our results highlight that climate change threatens *Castanopsis* species' persistence via range reductions or widespread shift. As anticipated, the worst scenario predicts the largest range-size losses. Although the extent of these (net) losses will remain relatively limited even in the worst scenario when individual values for *Castanopsis* species are

averaged (−17.85 % for RCP 8.5; Appendix Table S4), range shifts for individual species will be very large. The mean overlap areas present–2070 for RCP 8.5 [the value of OA (overlap area) in Appendix Table S4] is below 50 %; in other words, the species will suffer great range changes but with new area gains nearly compensating area losses. These low values of overlap areas present–2070 is the reason why the predicted suitable areas for the highest (rank 13–17) and high (rank 10–12) richness of dominant *Castanopsis* species will be reduced by percentages much higher than mean individual losses (−17.85 %) in 2070 with respect to the present: 99.46 % and 73.15 % for RCP 8.5 (calculated from Appendix Table S3).



**Fig. 6.** Modeled long-term stable refugia within and outside existing protected areas under climatic scenarios, with areas proposed for conservation. (a) Under scenarios of present-past-future RCP 2.6; (b) under scenarios of present-past-future RCP 8.5.

#### 4.2. Niche groups and niche breadths of dominant *Castanopsis* species

To our knowledge, this is the first time that the current extension of all dominant *Castanopsis* species in the whole East Asia is precisely determined. Our results show that dominant *Castanopsis* species occur continuously from fully tropical (e.g., *C. acuminatissima*) to truly warm-temperate latitudes (*C. sieboldii* is found at nearly 38°N in northern Honshu). This geographic unbroken connection (Fig. 1a, Appendix Fig. S3) is also climatic: in Appendix Fig. S2 there are no large empty climatic spaces between the species, while the five climatic groups are not sharply delimited. These patterns make dominant *Castanopsis* species in East Asia to be extremely valuable from an ecological perspective and, thus, an asset that should merit strong protection. The forests dominated by East Asian *Castanopsis* species would actually constitute, if habitat fragmentation is not progressing, a huge ecological corridor or, more precisely, an ecological network for conservation sensu IUCN (Hilty et al., 2020), the most up-to-date conservation initiative with inspiring examples around the world (e.g., the Yellowstone to Yukon Conservation Initiative or the Great Eastern Ranges of Australia).

Niche breadth is an important mechanism in shaping the distribution–abundance relationship (Borregaard and Rahbek, 2010). Species with a limited niche breadth are considered to experience a higher risk of extinction than generalist species (Boulangeat et al., 2012), partly because of the positive relationship that is expected between niche breadths and geographical range sizes (Brown, 1984; Slatyer et al., 2013; Kambach et al., 2019); so, specialist species (i.e., with narrow niche breadths) might be disproportionately vulnerable to climate change (cf. Slatyer et al., 2013). Assuming that net range losses

for the year 2070 could be an indicator of vulnerability to climate change, it does not seem that the *Castanopsis* species with narrow tolerances will be particularly at risk (correlation between individual niche breadth and net range losses:  $r = -0.101$  and  $p = 0.583$  for RCP 2.6, and  $r = -0.010$  and  $p = 0.957$  for RCP 8.5).

We found no correlation between the niche breadth and the geographic distribution range size, and between the niche breadth and the altitudinal range; the altitudinal range is often correlated with range size and, thus, could also be viewed—in some circumstances (see Langford et al., 2001)—as a proxy of niche breadth (e.g., Essl et al., 2009). There were also no differences when the 32 *Castanopsis* species were sorted into three groups according to their range size and altitudinal range. Leaving aside questions such as the inaccuracy of our niche breadth measures (we have only estimated the climate-derived niche breadth; other estimates might include resource-based and co-occurrence-based niche breadth; e.g., Pannek et al., 2016), the lack of a relationship between niche breadth and range size in *Castanopsis* indicates that the latter could be determined, instead, by other factors such as the geographic configuration (e.g., topography, mountains, altitudes) of specialized habitats and climate stability (e.g., Morueta-Holme et al., 2013) or the genetic structure and colonization ability of species (e.g., Lowry and Lester, 2006). Certainly, climate stability has been demonstrated to be an important factor in shaping the present distribution of East Asia plant relict species (Tang et al., 2018) and seems to play also an important role in *Castanopsis* (discussed below).

As a general trend, the northernmost-distributed *Castanopsis* species (i.e., the subtropical/warm-temperate species) seem to have narrower niches than the southernmost-distributed ones, contrary to the

expectation that when climates become more variable (towards the poles), the species are broadening their physiological tolerance and thus, niche breadth (MacArthur, 1972). A meta-analysis has shown that empirical results do not always support the prediction and even in some cases there is the reverse relationship (Vázquez and Stevens, 2004). This, coupled with more recent studies (e.g., Slove and Janz, 2010; Kostikova et al., 2013), suggest that a latitudinal gradient in niche breadth may only occur in some circumstances and could be specific of certain taxonomic groups. A technical limitation in our study could also account for the equivocal results in *Castanopsis*; our niche breadth measure is a composite of both temperature and precipitation variables and, according to Liu et al. (2020), temperature niches are wider at higher latitudes, whereas precipitation niches are wider at lower latitudes.

#### 4.3. Long-term stable refugia and conservation strategies

The overlap areas across *Castanopsis* species and time (present–past–future), despite being small (6050 km<sup>2</sup> on average; Fig. 5d, e, Appendix Table S5), should be regarded as long-term stable refugia for dominant *Castanopsis* species. The importance of climate stability for the persistence of relict plant species in East Asia, particularly in the mountainous humid subtropical/warm-temperate areas, was recently demonstrated (Tang et al., 2018). Many, if not most, species of *Castanopsis* (a genus that could date from early Eocene; Wilf et al., 2019) would have persisted in East Asia during the Pleistocene climate oscillations and, notably, there is close match between the long-term stable refugia for relict plants (Tang et al., 2018) and those for *Castanopsis*

(Fig. 5). Certainly, Yunnan has been a climatically stable region since the late Pliocene, and would continue to be stable at least till the year 2070 according to the high-resolution world-scale climate stability maps of Herrando-Moraira et al. (2022). Highest priority for conservation should be given to the long-term stable refugia.

Demographic patterns that are indicative of long-term, viable populations may also provide a tool for validating modeled climate-change refugia. As the surrounding climate becomes increasingly less suitable, populations within refugia would be expected to have higher successful recruitment rates than populations outside such areas. Empirical approaches in validation support management actions (Barrows et al., 2020). For validating the identified long-term stable refugia, based on the data on investigated seedlings/saplings as well as monitoring mortalities of dominant *Castanopsis* species inside and outside the refugia, there are more established seedlings/saplings and low mortality rates in the refugia (Tang, 2023).

Establishment and management of PAs (protected areas) must include, thus, consideration of the identified stable refugia (Fig. 6), including the Lincang and southern Baoshan areas of southwestern Yunnan, the Simao and Xishuangbannan areas of southern Yunnan for dominant *Castanopsis* species. Regrettably, up to 78.3 % and 66.8 % of the long-term stable refugia areas are outside the existing PAs under Present–Past–Future RCP 2.6 and Present–Past–Future RCP 8.5 scenarios, respectively. Conservation actions are needed to preserve the long-term viability of dominant *Castanopsis* species. First of all, we need to ensure that the current fraction of species occurring within PAs [21.7 % and 33.2 % under the two scenarios, respectively; Fig. 6a, b]) are effectively protected, as this sometimes does not occur in China (Guo

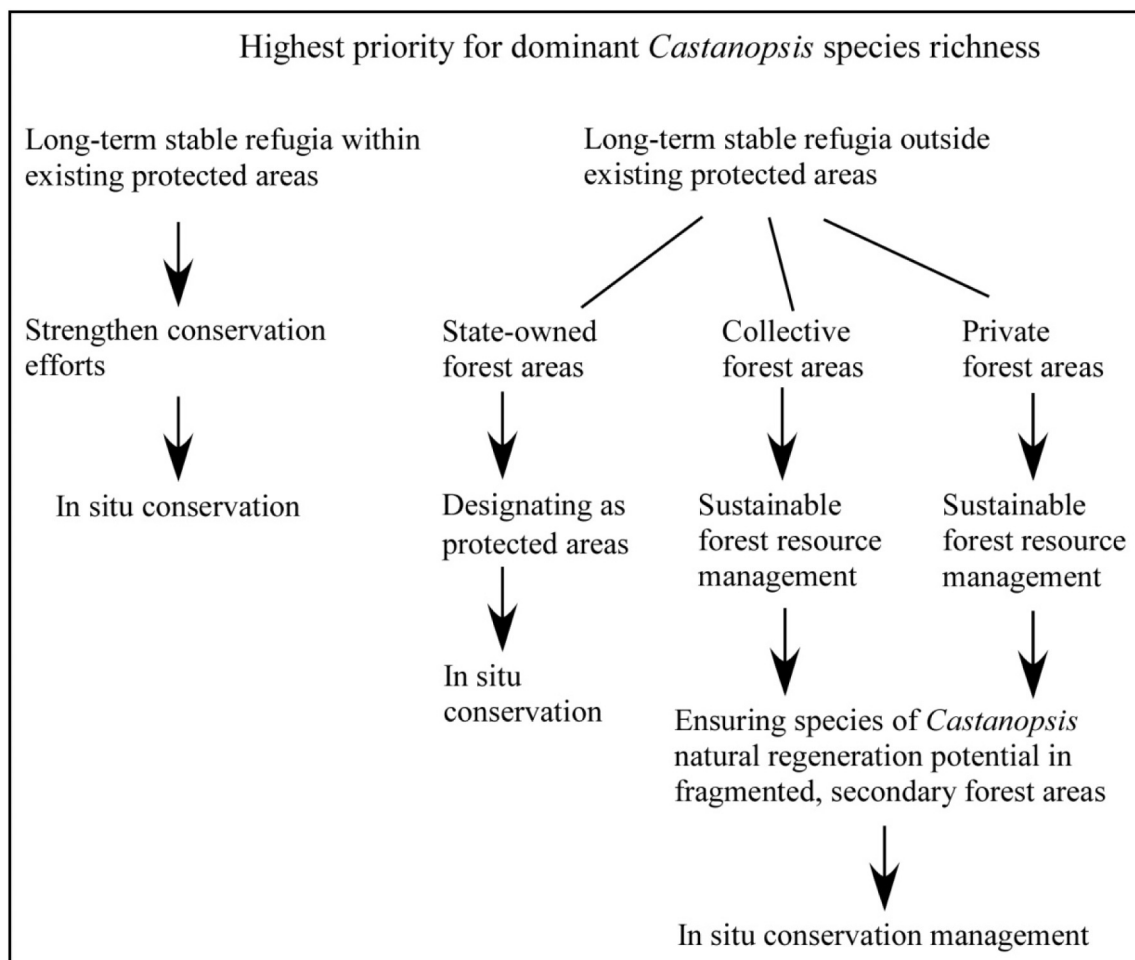


Fig. 7. A framework of conservation strategies suggested for dominant *Castanopsis* species of evergreen broad-leaved forests.



et al., 2002; Yang et al., 2019). Secondly, according to various land uses in the long-term stable refuge areas outside the PAs, state-owned forests should be designated in order to expand the network of PAs to cover a larger fraction of *Castanopsis* refugia. We have detected some threats that may put dominant *Castanopsis* species at risk outside the protected areas within the refugia, such as firewood cutting, domestic animal grazing, and human planted medicinal herbs for economic gain in the understory of *Castanopsis* forests (Tang, 2023). Finally, our framework of conservation strategies (Fig. 7) also includes the recommendation of implementing sustainable forest resource management in fragmented and natural secondary forests of collective forestland (areas where local villagers are allowed to use the forests through a paid-use system in the condition of constant usage of the land) and private forest areas to secure natural regeneration potential of *Castanopsis* species. In southwestern and southern Yunnan, rural landscapes are a mosaic of disturbed and less disturbed patches of forest, ranging from fragmented natural, semi-natural, secondary forests to severely degraded forests or woodland (Guo et al., 2002; Shi and Zhu, 2002; Tang, 2023). Species of *Castanopsis* as dominants are found in natural, semi-natural and secondary forests (Tang, 2023). In private and collective forest areas, local people have exploited their forests such as cutting trees for firewood and planting medicinal herbs as cash crops (e.g., *Amomum villosum*) in the forest understory at an unsustainable rate (Zhu et al., 2015; Tang, 2023), and the remaining forests are under constant pressure to meet various human needs. Sustainable management of forests should be a process of managing permanent forest land to achieve multiple objectives to produce desired forest products and services without undue reduction of future productivity, and without undue undesirable effects on the physical and social environment (ITTO, 1992).

In addition to the *Castanopsis*-oriented conservation strategies above, we urge to reinforce and expand the current network PAs of topographically complex mountainous areas of the whole southwestern China (i.e., southern Hengduan Mountains, Yunnan-Guizhou Plateau, eastern Sichuan/Chongqing, and, ideally, also of neighboring areas of northern Vietnam and Myanmar). These areas, in addition to harboring all *Castanopsis* refugia, are also home of most of the East Asian relict forests (Tang et al., 2018) and, in general, of a large fraction of East Asian biodiversity (Rahbek et al., 2019). These areas link together several ecoregions and mountain ranges, and span a wide elevation range, all vital in a changing climate.

## 5. Conclusions

Our results show that there is a high richness of dominant *Castanopsis* species in East Asia, with highest ecological significance. Richness and potential distribution patterns of dominant *Castanopsis* species in East Asia based on modeling have been shaped by climate change from the Last Glacial Maximum to the present and will be also shaped by climate change in future (2070). No correlation between species niche breadths and distribution ranges is found, which could be due to regional climate stability. Mountains of southwestern (the Lincang and southern Boashan areas) and southern (the Simao and Xishuangbanna areas) Yunnan of China have been identified here as climatically long-term (LGM to the year 2070) stable refugia for dominant *Castanopsis* species.

Conservation of dominant *Castanopsis* species in the long-term stable refugia aims to maintain the evolutionary processes of the species. We provide a framework of conservation; recommend that these areas have the highest priority of conservation to prevent their complete extinction under climate change. We suggest strategies that include strengthening the conservation efforts of currently protected *Castanopsis* species, expanding the network of PAs to cover a larger fraction of *Castanopsis* refugia, implementing sustainable forest management in private and collective forests, and ensuring species of *Castanopsis* natural regeneration potential in the areas.

## CRedit authorship contribution statement

**Cindy Q. Tang:** Conceptualization, Methodology, Writing – original draft, Formal analysis, Writing – review & editing, Investigation, Validation. **Tetsuya Matsui:** Methodology, Formal analysis, Writing – review & editing, Investigation, Validation. **Haruka Ohashi:** Methodology, Formal analysis, Writing – review & editing, Investigation, Validation. **Neus Nualart:** Formal analysis, Writing – review & editing, Validation. **Sonia Herrando-Moraira:** Formal analysis, Writing – review & editing, Validation. **Yi-Fei Dong:** Investigation, Writing – review & editing, Validation. **Paul J. Grote:** Investigation, Writing – review & editing, Validation. **Nguyen Van Ngoc:** Investigation, Writing – review & editing, Validation. **Hoang Van Sam:** Investigation, Writing – review & editing, Validation. **Shuaifeng Li:** Investigation, Writing – review & editing, Validation. **Peng-Bin Han:** Writing – review & editing, Validation. **Li-Qin Shen:** Investigation, Writing – review & editing, Validation. **Diao-Shun Huang:** Investigation, Writing – review & editing, Validation. **Ming-Chun Peng:** Investigation, Writing – review & editing, Validation. **Chong-Yun Wang:** Investigation, Writing – review & editing, Validation. **Xiao-Shuang Li:** Investigation, Writing – review & editing, Validation. **Hai-Zhong Yan:** Investigation, Writing – review & editing, Validation. **Ming-Yuan Zhu:** Investigation, Writing – review & editing, Validation. **Xia Lu:** Investigation, Writing – review & editing, Validation. **Jian-Ran Wen:** Investigation, Writing – review & editing, Validation. **Shi-Qian Yao:** Investigation, Writing – review & editing, Validation. **Min-Rui Du:** Investigation, Writing – review & editing, Validation. **You-Cai Shi:** Investigation, Writing – review & editing, Validation. **Shu-Li Xiao:** Investigation, Writing – review & editing, Validation. **Jia-Le Zeng:** Investigation, Writing – review & editing, Validation. **Huan-Chong Wang:** Investigation, Writing – review & editing, Validation. **Jordi López-Pujol:** Conceptualization, Methodology, Writing – original draft, Formal analysis, Writing – review & editing, Validation.

## Declaration of competing interest

The authors declare no conflict of interest.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109663>.

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