



Climate-driven niche dynamics of endangered *Castanopsis argentea* and *C. tungurru* in Indonesia

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Abstract

Predicting suitable habitats and refugia is crucial for species conservation in the face of climate change. This study employed ecological niche modeling (ENM) using maximum entropy principle to assess the impact of projected climate change on two endangered *Castanopsis* species (*C. argentea* and *C. tungurru*) in Indonesia. The objectives were to identify the key climatic drivers, project suitable habitat across the past (Last Glacial Maximum [LGM] and Mid-Holocene [MH]), present, and future (2041–2070 under SSP126 and SSP585), and identify potential refugia of both species. Occurrence data were sourced from GBIF, herbarium records, published articles, and field surveys. Using ten climate variables from CHELSA for initial model construction, we refined models by selecting four key variables for each species. Precipitation in the driest periods emerged as the most significant factor influencing species distributions, highlighting their sensitivity to drought. Historical reconstructions revealed broader suitable ranges during the LGM and MH, except for *C. tungurru* in the MH. Future projections indicated habitat contraction under all scenarios. However, potential stable habitats and refugia, particularly in the Sumatran highlands (Bukit Barisan Mountains), Java's mountain ranges, and scattered parts of Kalimantan, persist despite localized habitat fragmentation. Identification of highly suitable but unrecorded areas, particularly in Aceh, eastern Java, and central Kalimantan, underscores the need for further field surveys to locate potential populations. To manage potential refugia, this study recommends improving management effectiveness inside conservation areas while enhancing community-based forest conservation and promoting sustainable land-use practices outside conservation areas, as well as replanting programs.

Keywords Climate change · *Castanopsis argentea* · *Castanopsis tungurru* · Ecological niche modeling · Maxnet · Potential refugia

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Introduction

The ongoing climate change has significantly been impacting forest ecosystems, biodiversity management, and conservation efforts (Bellard et al. 2012; IPBES 2019). Rising temperatures and shifting precipitation patterns disrupt forest ecosystems on a large scale (Seidl et al. 2017), and this trend is projected to continue in the coming decades (Abrahms et al. 2017; IPCC 2023). These disruptions are expected to affect species diversity and distribution, potentially leading to shifts in abundance, composition, and distribution ranges (Matsui et al. 2018; Tomiolo and Ward 2018). This is highly concerning, as it could result in increased tree mortality, declines in diversity and population, and even extinctions (Allen et al. 2010; Bauman et al. 2022), especially for the endangered species (Kusumadewi et al. 2020; Zhu et al. 2023).

Indonesia harbors the second-highest number of threatened plant species in Southeast Asia (IUCN 2022). Among these are two *Castanopsis* species listed as endangered, i.e., *C. argentea* and *C. tungurru* (Barstow and Kartawinata 2018a, 2018b). Notably, the former is also protected under national law (MoEF 2018) and has been prioritized for conservation over the next decade (Hamidi et al. 2019) reflecting global and national concerns for these species. Both species also hold significant ecological and socioeconomic value. While specific studies on *C. tungurru* are limited, *C. argentea* has been identified as a potential species for watershed rehabilitation and reforestation (Wibowo 2006; Ahmad et al. 2013), a food source of wildlife (Handayani and Hidayati 2020), edible fruits and medicinal properties usage (Harada 2003; Suwardi et al. 2023), and timber utilization (Priyadi et al. 2010; Mark et al. 2014). However, anthropogenic disturbances and projected climate change are expected to further stress these species and alter their suitable habitats (Barstow and Kartawinata 2018a; 2018b). This combination of conservation status, multifaceted value, and current threats underscores the critical importance of safeguarding these species and their habitats.

Given these challenges, identifying potentially suitable habitats and refugia is crucial for their conservation in a changing environment (Tang et al. 2018; 2022). While the concept of refugia has various definitions (Gavin et al. 2014; Morelli et al. 2020), this study adopts the combined perspective of Tzedakis et al. (2013) and Tang et al. (2017; 2018), defining refugia as climatically suitable areas that allow populations to persist through long periods of climate change, from the LGM to the future. Species distribution modeling (SDM), referred to here as ecological niche modeling (ENM), provides a valuable tool for identifying these areas (Phillips et al. 2006; Guisan et al. 2013). Despite its limitation in capturing complex factors such as biotic

interaction, dispersal ability, and physical barrier (Peterson and Soberón 2012), ENM can predict current potential distribution areas and project them under novel conditions, such as past or future climate scenarios (Tang et al. 2018; Shitara et al. 2021). This knowledge is vital for developing effective conservation and adaptation measures (Guisan et al. 2013; Keenan 2015; Pecchi et al. 2019).

Previous studies on *Castanopsis* in relation to past and future climate change have primarily concentrated on East Asian *Castanopsis*-dominated forests (Nakao et al. 2014; Cheuk and Fischer 2021; Tang et al. 2022). In contrast, this study examines the southernmost endangered *Castanopsis* species in Indonesia, a region that has received relatively little attention for their historical, current, and future distribution in the context of climate change. Fossil records indicate that *Castanopsis* occupied highland areas in western Java and western Sumatra both before and after the Last Glacial Maximum (LGM) (Morley 1981; Newsome and Flanlay 1988; Stuijts et al. 1988), which aligns with their present-day distribution in these regions (Soepadmo and van Steenis 1972). Furthermore, fossil evidence suggests that during the LGM, *Castanopsis* had a broader range extending to the exposed Sunda Shelf, as evidenced by findings from the South China Sea near the present-day Natuna Islands (Wang et al. 2009).

Previous studies have also identified that temperature, particularly during the coldest month and the temperature sum of 85 °C-months (Kira's Warmth Index), is a key factor in *Castanopsis* distribution in subtropical and warm-temperate regions, such as southern China (Ouyang et al. 2023; Shen et al. 2023) and Japan (Nakao et al. 2014). In mid-latitude regions, these variables emphasize the species' tolerance to winter freezing (Sakai 1979) and dependence on summer heat energy (Kira 1977; Ohsawa 1993). However, in equatorial regions, heat energy limits coincide with a mean annual temperature (MAT) of approximately 112 °C at the upper limit of the lower montane zone (Ohsawa et al. 1985; Ohsawa 1991), thereby restricting the species to cooler, higher-elevation zones. While *Castanopsis* historically occupied larger suitable habitats, particularly in East Asia (Tang et al. 2022), projections indicate a decline in the near future due to warmer climates and dispersal limitations (Cheuk and Fischer 2021; Tang et al. 2022). This pattern supports the notion that *Castanopsis* species have historically tracked their cool-wet niches rather than adapting to new climate environments (Wilf et al. 2019). Despite this contraction projection, refugia have been identified, such as parts of southwestern and a small patch of southern Yunnan in China and Ryukyu Islands in Japan, where suitable habitats for this species have persisted since the LGM (Aoki et al. 2019; Tang et al. 2022).

However, no empirical studies have yet examined the impact of climate change on these southernmost endangered *Castanopsis* species in Indonesia. Recent studies on these species' distribution in Indonesia have been limited to contemporary and local-scale assessments on Sumatra Island (Harapan et al. 2022) and future projections of *C. argentea* as part of the Indonesian medicinal plant group (Cahyaningsih et al. 2021). This paper aims to address this gap by providing critical insight into these species' conservation in a tropical climate context. Given the distinct tropical environment of Indonesia compared to those in the Asian mainland where *Castanopsis* is predominantly found, we hypothesize that different environmental variables may influence its distribution. We also anticipate that suitable habitats expanded during the cooler climates of the LGM and may contract under future warming scenarios, considering that species track cool-wet niches. Nonetheless, the persistence of potentially stable habitats and refugia since the LGM cannot be ruled out. This study will test these hypotheses by identifying key climatic drivers, reconstructing past, present, and future suitable habitats, and identifying potential stable habitats and refugia for these two endangered *Castanopsis* species.

Materials and methods

Target species and study area

C. argentea (*saninten* or *sarangan*) and *C. tungurrut* (*tunggereut*) are two of twenty-four *Castanopsis* species in Indonesia. They are recognizable by their spiny fruit cupules and can reach up to 40 m in height, inhabiting lowland to montane forests. They can adapt to various soil types, except calcareous (Soepadmo and van Steenis 1972). Although *C. argentea* has a broader natural distribution range extending from eastern Himalayas (Bhutan and Arunachal Pradesh) to Indonesia and *C. tungurrut* occurs in both Indonesia and Malaysia (POWO 2024a; 2024b), this study focuses on their distribution in Indonesia, encompassing Sumatra, Java, Kalimantan, and nearby islands as their native distribution range (Fig. 1). This geographic scope was considered based on Indonesia's most current occurrences and population concentration, the southernmost limit of a species' range representing biogeographic boundaries, and the only one recognizing their endangered status at the country level. This direct alignment of research with national conservation priorities is crucial given the absence of similar acknowledgment status in other countries, such as in Malaysia and Thailand. Indonesia's tropical climate, characterized by relatively constant temperatures and varying precipitation patterns (SI Table 1; Karmalkar et al. 2012), has a diverse range

of climates across the study site. Tropical rainforest climates predominate, while tropical monsoon, savanna, and temperate conditions are also found in specific regions such as in central–eastern Java and the northern part of western Java for the former and at higher elevations around 1,500–3,500 asl for the latter (Beck et al. 2018).

Species occurrences and environmental variables

Occurrence data within species known range of *C. argentea* and *C. tungurrut* were used to construct robust model and to avoid model bias towards the study site distribution in Indonesia. It was sourced from GBIF (<https://www.gbif.org/>), herbarium records, published articles, and field surveys. Data quality was ensured through duplicates and outliers' removal and spatial thinning using the *spThin* package (Aiello-Lammens et al. 2015) to retain a single occurrence per 1 km² pixel which is the same resolution as the climate data. This resulted in 160 and 143 occurrence points for *C. argentea* and *C. tungurrut*, respectively.

Focusing on climatic variables due to their well-established role in plant distribution (Woodward and Williams 1987), this study utilized bioclimatic variables (present, past, and future) at 30 arc-sec resolution from CHELSA (<https://chelsa-climate.org/>) due to its suitability for complex terrain and rainfall-influenced regions (Karger et al. 2017), such as Indonesia. While non-climatic factors such as topographic and edaphic can also be important (Dubuis et al. 2013; Maharjan et al. 2022), limitations in past data for these variables hindered their inclusion. Current and future climatic data was retrieved from CHELSA v. 2.1 while past data of downscaled PMIP3 from CHELSA v. 1.2 for the Last Glacial Maximum (LGM, 21-kya) and from TraCE-21 k for the Mid-Holocene (MH, 6-kya) (Karger et al. 2017, 2023). Based on data availability, three past models were used in LGM (CCSM4, MPI-ESM-P, MIROC-ESM) and only a single in MH (CCSM3). Future projections in 2041–2070 employed CMIP6's model availability under the SSP126 and SSP585 scenarios and showing good performance in the region (Desmet and Ngo-Duc 2022), i.e., GFDL-ESM4, MPI-ESM1-2-HR, and MRI-ESM2-0.

The default values of raster climate datasets were processed according to the technical specifications. However, the bioclimatic values within these raster files were maintained in their original form without any other modifications in the individual model using single General Circulation Models (GCM). For analyses involving multiple GCM, i.e., three GCMS, we averaged the habitat suitability values obtained from the final modeling results rather than averaging the bioclimatic variable values. This approach allowed us to generate consensus predictions that reflect the collective output of multiple models, while still preserving

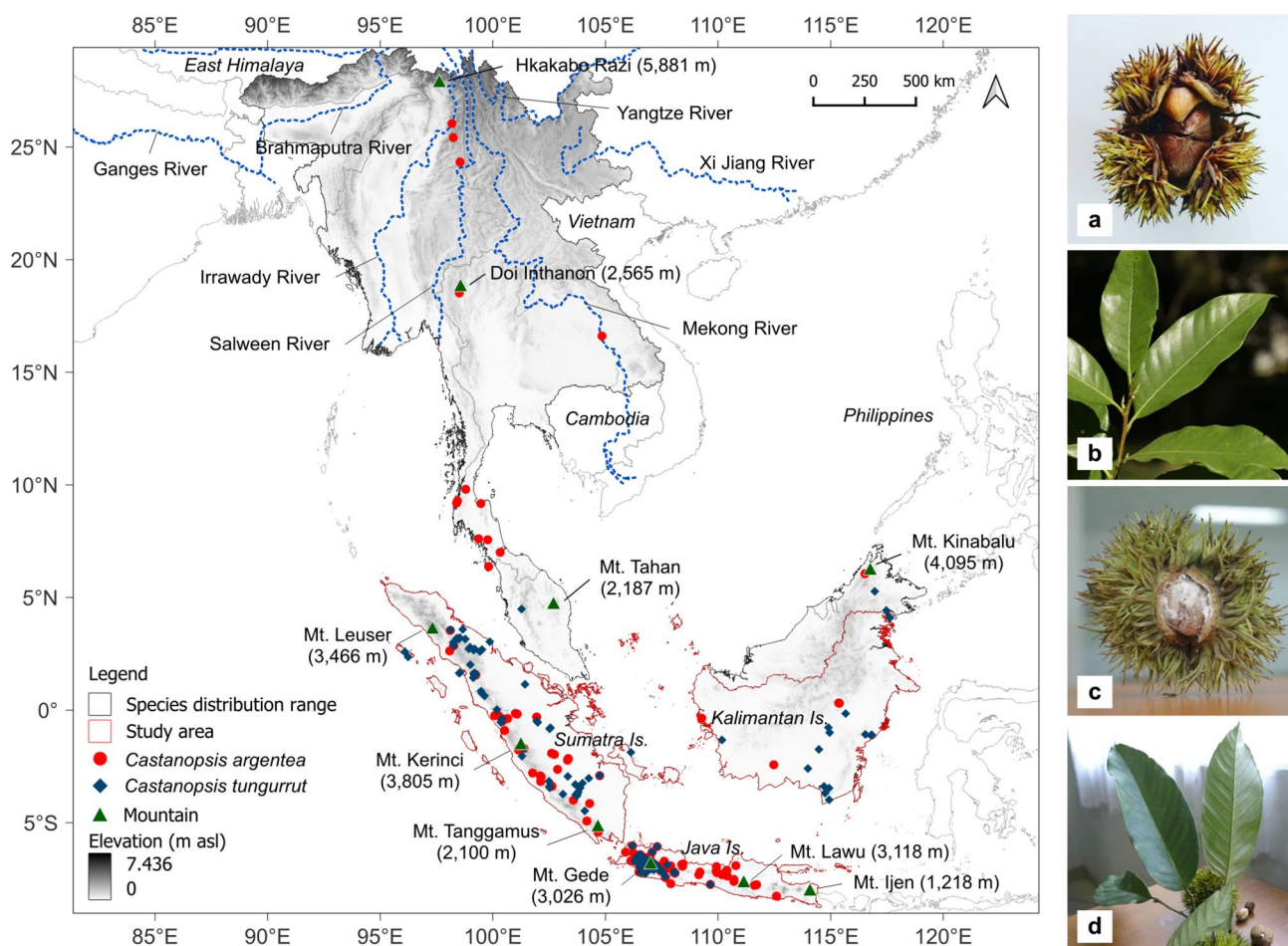


Fig. 1 Current species distribution and occurrences within the global ranges and study site (only selected countries are shown for the purpose of estimating adjacent administrative areas). Fruit and leaf pho-

tos of *Castanopsis argentea* (a – b) and *C. tungurru* (c – d). Photograph by Mount Ciremai National Park (2020) and Cibodas Botanical Garden (2019; 2020)

Table 1 Bioclimatic variables used in the study

No	Variables	Code	Unit
1	Mean annual temperature (MAT) ^{a,b}	bio1	°C/year
2	Maximum temperature in the warmest month	bio5	°C
3	Minimum temperature in the coldest month	bio6	°C
4	Mean annual precipitation ^{a,b}	bio12	mm/year
5	Precipitation in the wettest month	bio13	mm/month
6	Precipitation in the driest month ^b	bio14	mm/month
7	Precipitation in the wettest quarter	bio16	mm/quarter
8	Precipitation in the driest quarter ^a	bio17	mm/quarter
9	Precipitation in the warmest quarter ^{a,b}	bio18	mm/quarter
10	Precipitation in the coldest quarter	bio19	mm/quarter

Variables used in final model construction: ^a*C. argentea*, ^b*C. tungurru*

the original spatial resolution and variability of the environmental datasets.

From our preliminary analysis by putting all 19 bioclimatic variables, it revealed that temperature variability,

i.e., temperature seasonality (bio4) and isothermality (bio3) could be important (SI Fig. 1; SI Fig. 4). However, their ecological interpretation in tropical Indonesia is less straightforward. In higher latitudes, variables such as these variables may play a key role in shaping plant phenology, growth, and reproductive success, as well as defining growing season length (Bykova et al. 2012; Slot and Winter 2016; Zurell et al. 2024). However, in our study area, characterized by relatively constant annual temperatures, they have less ecological relevance.

Furthermore, it also excluded of mean annual temperature (bio1) and annual precipitation (bio12) although these variables are consistently featured as the most frequently used bioclimatic variables in SDM and plant physiology studies (Gardner et al. 2019), indicating that these two variables are easy to understand to interpret for capturing the environmental conditions that influence plant physiology and distribution (Amisshah et al. 2014; Lambers and Oliveira 2019; Martes et al. 2024). Our present model emphasizes the inclusion of bio1 and bio12 to better reflect the climate

factors most critical to the performance and distribution of *Castanopsis* in tropical Indonesia. This selection approach eliminates other highly correlated variables, such as mean seasonal temperatures (bio8 – bio11) (SI Fig. 2: SI Fig. 6).

Consequently, ten bioclimatic variables of global ranges (Table 1), out of 19 available (SI Table 1), were selected for initial modeling in consideration of their influence on the species' ecological preferences, which consisted of three temperature and seven precipitation variables. The mean annual temperature (MAT) relates to plant traits (Moles et al. 2014) and nutrient availability (Litton et al. 2020), which in turn influence plant development and growth. In contrast, the temperature extremes, i.e., the minimum temperature of the coldest month and the maximum temperature of the warmest month, influence their distribution limits (Woodwards and William 1987). For precipitation, we selected annual (bio12), monthly (bio13 and bio14), and seasonal measures (bio16 – bio19) rather than seasonality (bio15). This choice was made because these variables more related to water availability, an essential factor for plant growth (Lambers and Oliveira 2019), rather than focusing on the variability of precipitation.

Ecological niche modeling (ENM)

ENM was conducted using the maximum entropy principle in R (v4.3.4) (Phillips et al. 2006; R Core Team 2024) within the SDMtune package by the “maxnet” method (Phillips et al. 2017; Vignali et al. 2020). Well-suited for presence-only data, this approach is widely used for ENM (Merow et al.

2013; Phillips et al. 2017). Bioclimatic layers were clipped to the study area and species occurrence data were split for training (80%) and testing (20%). Pearson's correlation analysis was conducted using 10,000 random background points within the species known ranges (SI Fig. 6) with variables having a high correlation coefficient ($|r| \geq 0.70$) were excluded to avoid multicollinearity (Dormann et al. 2013; Tang et al. 2022). Although the algorithm initially removed MAT due to its correlation with temperature extremes (SI Fig. 7), we opted to retain it based on its tropical ecological context with less extreme temperature variations across seasons. The distribution of species occurrences and background points within geographical and environmental space is shown in SI Fig. 8 and SI Fig. 9, respectively.

Following variable selection, four remaining bioclimatic variables were used for the final model (Table 1). A tenfold cross-validation approach was implemented with hyperparameter tuning using seven feature classes (FC) combination, i.e., L, H, LQ, LQH, LQP, LQPH, and LQPHT, and wide regularization multiplier (RM) to avoid overfitting (Merow et al. 2013; Li et al. 2020) from 1 to 5.5 with a step of 0.5 by the “gridSearch” function. The best-performing tuned model was retrained using the full dataset and evaluated on the unseen testing data (Vignali et al. 2020). Model performance was assessed using AUC and True Skill Statistic (TSS). Permutation importance and a jackknife test of variable importance identified key environmental drivers, and response curves visualized the relationship between variables and habitat suitability. The clog-log transformation was applied to improve presence probability estimation. A

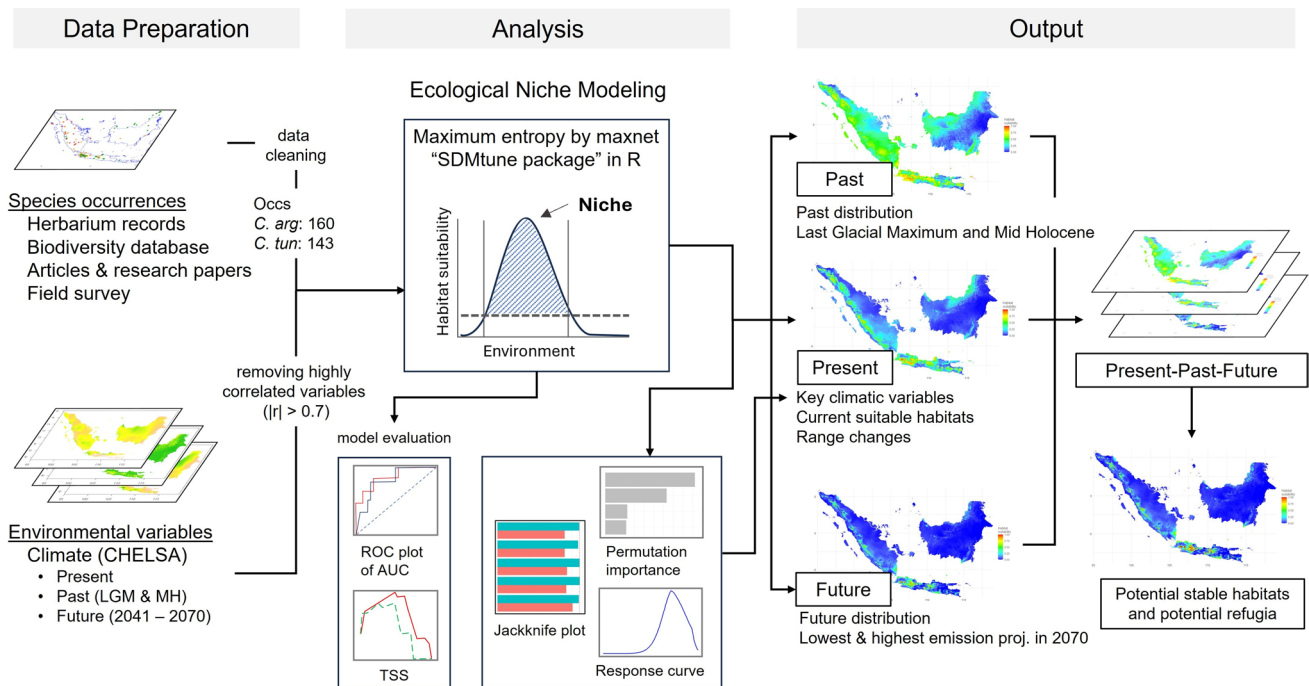


Fig. 2 The methodology flowchart of the study

presence-absence map was generated using the “classify” function in the terra package (Hijmans et al. 2022) with a suitable threshold based on maximum test sensitivity and specificity (MSS) for presence-only data (Liu et al. 2016). Species range changes were mapped using the “BIOMOD_RangeSize” function in the biomod2 package (Thuiller et al. 2024). To obtain a single raster environmental layer, multiple GCMs in the LGM, Future SSP126, and SSP585 were averaged in each one-time slice. Modifying the method of Tang et al. (2017; 2018), overlap between present, past, and future distributions determined by average values above the MSS threshold to identify potential refugia was generated using the “intersect” function and total area was calculated using “expand” function in the terra package. The maps were drawn in QGIS v.3.36.3 (QGIS Development Team 2024). The overall workflow is presented in Fig. 2.

Administrative boundaries, DEM, and conservation areas

The country's land administration boundary and Indonesia's territorial sea boundary were taken from GADM v. 4.1 (<https://gadm.org/data.html>) and Marine Regions (<http://marineregions.org/>), respectively. The LGM landmass shapefile and digital elevation model (DEM) were taken from Assis et al. (2018) and CHELSA (<https://chelsa-climate.org/>) with the elevation profile modified based on the present-day land, so that the value of area below sea level was negative. The topographic map was obtained from the base map used for the DEM of LGM in CHELSA (Karger et al. 2023), i.e. the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) of 30-arcsec resolution (Danielson and Gesch 2011) and the General Bathymetric Chart of the Oceans (GEBCO) 2014 as bathymetry (Weatherall et al. 2015). The polygon shapefile of conservation areas

and protected forests of Indonesia were obtained from the Ministry of Environment and Forestry of Indonesia (2023).

Results

Model performances and variables importance

The final models showed excellent performance, with the test AUC exceeding 0.9 (Swets 1988) and TSS exceeding 0.5 (Allouche et al. 2006) (SI Fig. 10) indicating strong discrimination between suitable and unsuitable habitats for the global habitat suitability maps (SI Fig. 11). In general, precipitation was more important than temperature for these *Castanopsis* species. For *C. argentea*, precipitation during the driest quarter (bio17) contributed 46.10% to the final model, while precipitation during the driest month (bio14) contributed 70.00% for *C. tungurru*. In contrast, MAT (bio1) only accounted for 11.40% and 6.30% of the contribution for *C. argentea* and *C. tungurru*, respectively (Table 2). Other variables, i.e., mean annual precipitation (bio12) and precipitation of the warmest quarter (bio18), showed varying degrees of influence, with bio12 having a more pronounced effect for both species. These patterns were further supported by the jackknife test of variable importance (Fig. 3), which shows that removing bio17 for *C. argentea* and bio14 for *C. tungurru* led to the largest declines in test AUC (highlighted in blue), thereby corroborating the permutation importance results.

Regarding species response curves, the optimum value represents the most favorable climatic conditions for the species to thrive. For curves that exhibit a classic bell shape, the optimum is identified as the single highest peak value. However, when the curve features a flat or plateau-like peak, no single value stands out. In such cases, we determined an optimal range by identifying the two points that mark the lower and upper limits of the plateau where habitat suitability remains consistently high above 0.5 (Shitara et al. 2021; Tang et al. 2022; Shen et al. 2023). For instance, in the case of bio17 for *C. argentea*, the curve did not present a sharp, singular peak but rather a flat plateau. Consequently, we defined the optimum as the range between the two points that bound this plateau. Similarly, the optimum was determined as the interval between the two points at which the response remains consistently high for bio14 in *C. tungurru*.

Considering the shape of these species response curves, the optimum habitat conditions for both species require relatively high rainfall during dry periods: approximately 140–745 mm in the driest quarter (bio17) for *C. argentea* and 68–200 mm in the driest month (bio14) for *C. tungurru* (Fig. 4; Table 3). Other variables also contributed to shaping

Table 2 Permutation importance of climate variables

Variables	Code	Permutation importance (%)	SD
<i>C. argentea</i>			
Precipitation during the driest quarter	bio17	46.1	0.04
Mean annual precipitation	bio12	31.6	0.007
Mean annual temperature	bio1/MAT	11.4	0.004
Precipitation during the warmest quarter	bio18	10.8	0.01
<i>C. tungurru</i>			
Precipitation during the driest month	bio14	70.0	0.029
Mean annual precipitation	bio12	21.3	0.007
Mean annual temperature	bio1/MAT	6.3	0.008
Precipitation during the warmest quarter	bio18	2.5	0.007

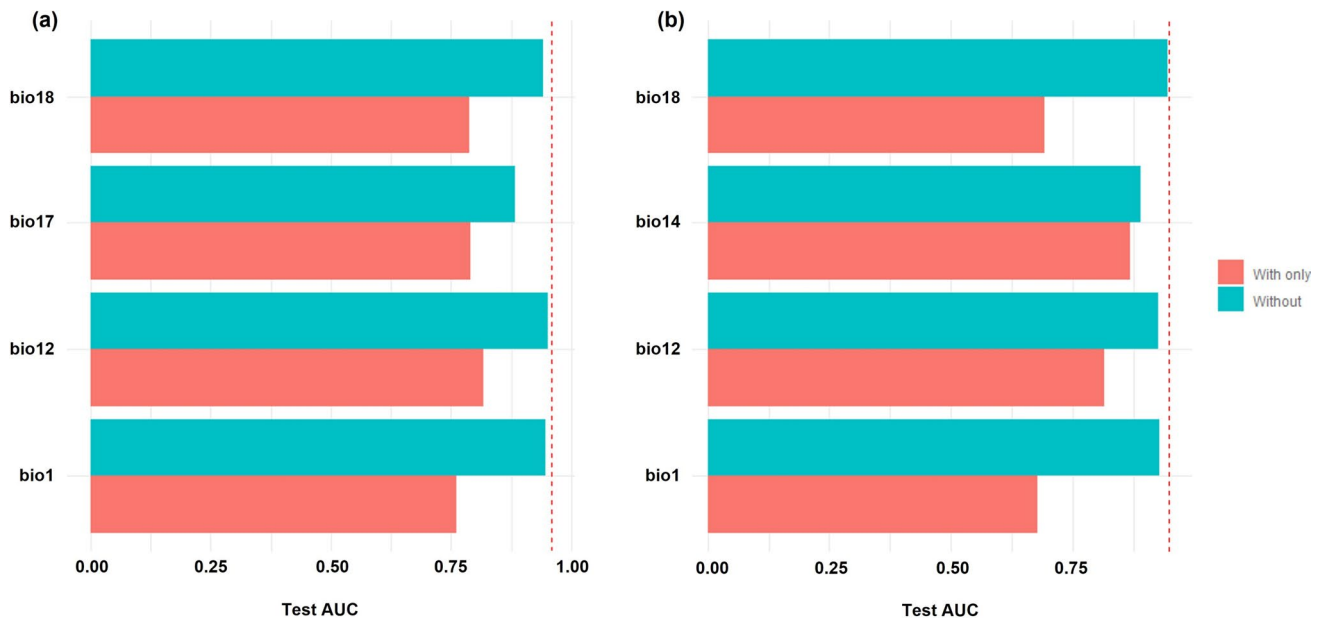


Fig. 3 Jackknife test of variable importance plot for *Castanopsis argentea*(a) and *C. tungurrut*(b). The red bars show the area under the curve (AUC) value when using single variable only; blue bars indicate the AUC value when each one of the four variables is omitted and the rest of the three is used for the model construction. A considerable

decrease in AUC when a variable is omitted (blue bar) or a high AUC when used alone (red bar close to the dashed line) indicates that the variable substantially contributes to model performance. The dashed line marks the full-model AUC

this optimum habitat profile. In relation to the MAT (bio1), which varies with elevation, these suitable conditions are concentrated in regions with cool temperatures between 18–20 °C, typically found in hills and mountainous areas of tropical region (Ohsawa 1993; Beck et al. 2018). However, considering the full extent of the curves above the MSS threshold, the suitable climatic niche for both species may be broader than the areas of peak suitability. Table 3 provides a comparison of the range of suitable conditions based on each species' response curve.

Predicted current suitable habitats

The predicted current suitable habitat distributions for both species shared a similar distribution pattern in Kalimantan but differed considerably in Sumatra and Java (Fig. 5). In Kalimantan, suitable areas were primarily concentrated in the central region. However, *C. argentea* had more extensive potential habitats in Java, while *C. tungurrut* had broader distributions in Sumatra. For *C. argentea* in Java, unsuitable areas were found in the northeast (Madura, Surabaya, and surroundings) and along the western-central border. In Sumatra, unsuitable gaps were observed along the eastern side (Aceh to Jambi) and the west coast (Aceh to West Sumatra). *C. tungurrut*'s predicted distribution covered most of Sumatra, with fragmented unsuitable areas in the central and northern parts. In Java, unsuitable areas were more extensive, particularly in eastern and central regions.

Figure 5 also shows that high-potential habitats of both species were identified in upland areas. In Sumatra, this includes the western Bukit Barisan Mountains, stretching from the north in Aceh to the south in Lampung (including Mt. Leuser and Mt. Tanggamus). In Java, suitable habitats stretched from west to east, including from Mt. Gede Pangrango to Mt. Ijen, with *C. tungurrut* showing a disjunction in the central-east regions. As in Kalimantan, suitable areas were mainly found in the central region, with smaller patches in the south, west, and north near the Malaysian border. However, some of these identified areas currently lack recorded occurrences of the species.

Past and future suitable habitats

Comparing to the present, the predicted suitable habitats for both species changed moderately during the Mid-Holocene (MH) period and future scenarios but differed considerably when compared to the Last Glacial Maximum (LGM) period (Fig. 6). During the LGM, the entire study area was considered suitable, including the exposed Sunda Shelf between the main islands. In contrast, during the MH and future projections, suitable areas began to align more closely with the present distribution patterns, though with some notable losses. For instance, the eastern sides of Sumatra and Kalimantan became less suitable for *C. argentea*, while the eastern side of Java and Kalimantan saw reductions in suitability for *C. tungurrut*. Both species were expected to face

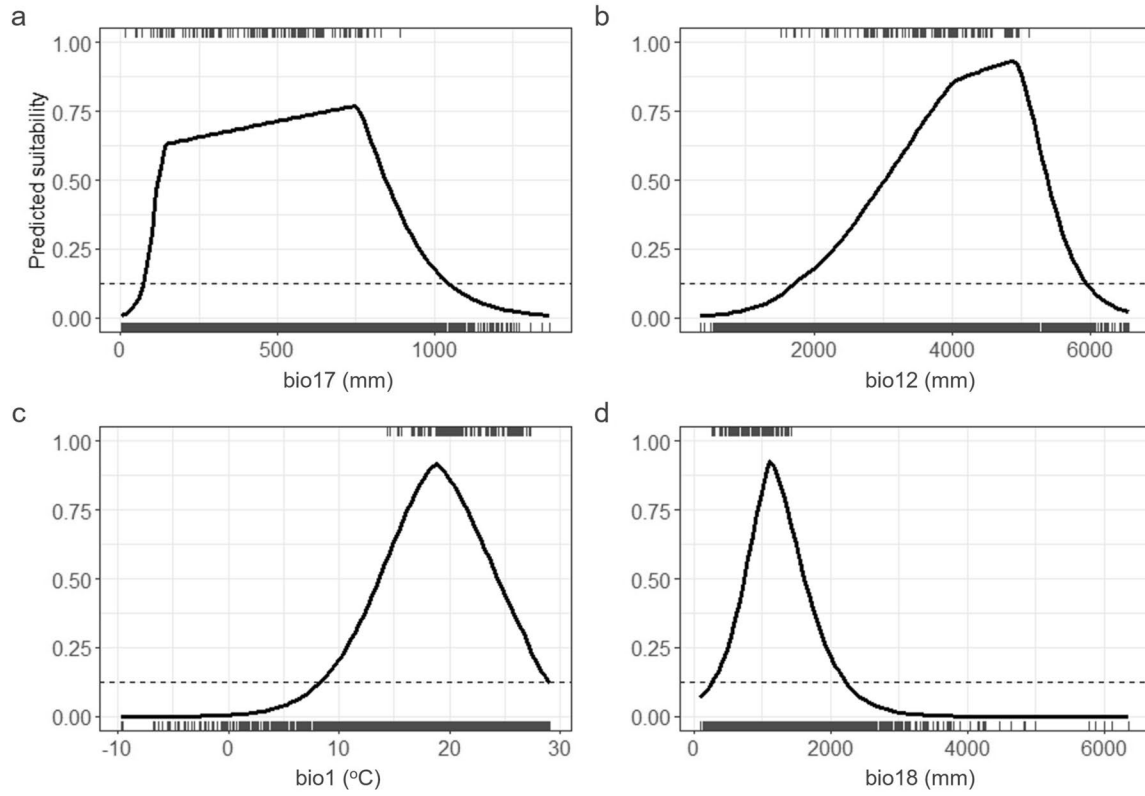
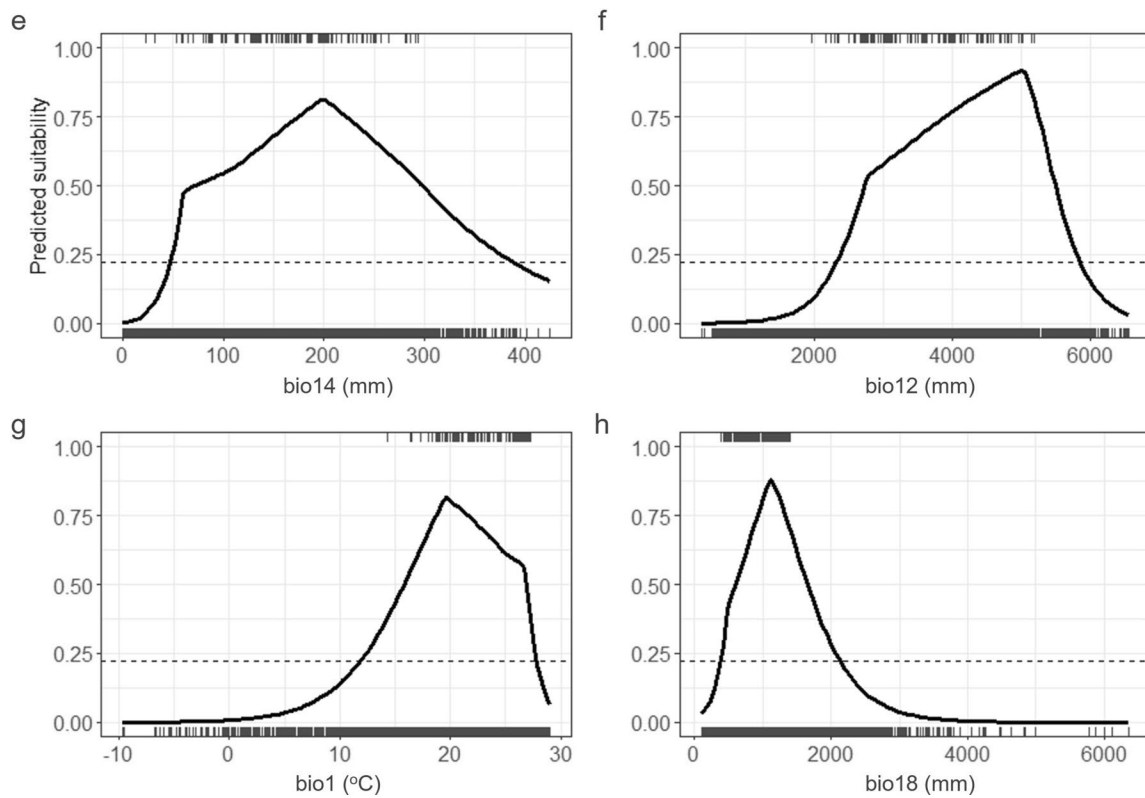
Castanopsis argentea*Castanopsis tungurrut*

Fig. 4 Species response curves for *Castanopsis argentea* (a – d) and *C. tungurru* (e – h). The y-axis reflects predicted suitability and the top and bottom rugs on x-axis represent species occurrences and background points, respectively. The dotted lines indicate the maximum test sensitivity plus specificity (MSS) threshold which was 0.1224 and 0.2210 for *C. argentea* and *C. tungurru*, respectively. The variable names also correspond to Table 2 and Table 3

future habitat loss, with the most severe reductions occurring under the highest emission scenario (SSP585). Specifically, *C. argentea* potential areas were predicted to see a substantial reduction in Sumatra and Kalimantan, while for *C. tungurru* was projected to remain only in the western parts, some central regions, and fragmented patches in the eastern part of Java (Fig. 6).

The extent of current potential habitats for *C. argentea* and *C. tungurru*, using MSS threshold, was 713,186 km² and 946,498 km², respectively (Table 4). The potential habitats during the LGM were remarkably large, about two-fold larger than present, with very high overlap (>98%) compared to present suitable areas. However, when considering current topography and excluding the landmass submerged in the ocean today, the suitable areas gained during the LGM were approximately 58% of the current suitable habitat for *C. argentea* and about 21% for *C. tungurru*. In the MH period, suitable habitats of *C. argentea* were approximately 12% larger compared to the present, while *C. tungurru*'s loss was around 7%. However, both species were expected to face future habitat shrinkage, with *C. argentea* predicted to suffer a greater reduction, with an estimated loss of about 14% to 28% under the SSP126 and SSP585 emission scenarios, respectively.

Climate potential stable habitats and refugia

Despite the predicted overall suitable habitats' shrinkage for both species, this analysis identified some areas of persisted suitable habitats, that may have been served since LGM and could continue to function as potential stable habitats and climate refugia in the future (Table 5; Fig. 7). These areas demonstrate consistent suitability across past, present, and future climate scenarios. The extent of these potential stable habitats varied geographically and between species. In Sumatra and Java, these areas remained relatively constant compared to current suitable habitats. However, in Kalimantan, there were considerable changes, particularly for *C. argentea*, with new fragmentation emerging in the central and southern regions. Similarly, *C. tungurru*'s potential stable habitats became fragmented in southern Sumatra and more restricted in Java (Fig. 7).

Although the total area of potential stable habitats remained relatively extensive under the highest emission scenario (SSP585) – about 469,856 km² for *C. argentea* and 711,301 km² for *C. tungurru* – the areas with truly high

suitability (>0.5) and considered as potential refugia within these areas were considerably smaller (Table 5). Notably, the extent of *C. argentea*'s potential refugia was less than one-third (about 25%) than its total areas. Importantly, the highlands of Sumatra, Java and Kalimantan remained as potential stable habitats potential refugia for the species (Fig. 7).

Discussion

Climate influence on species response

Precipitation in the driest quarter (bio17) and driest month (bio14), contributing 46.10% and 70.00% for *C. argentea* and *C. tungurru*, respectively, emerged as the most critical factors influencing their distribution. This emphasis on precipitation rather than temperature aligns with the climate profile in the equatorial zone, where temperatures remain relatively constant throughout the year, but rainfall intensity varies, including in Indonesia (SI Fig. 8). Consequently, precipitation becomes the key driver of plant water availability, especially during dry seasons. This significance on water availability is also reported by Comita and Engelbrecht (2014) highlighting the importance of precipitation and water availability as a major influence on tree distribution in the tropics. Soepadmo and van Steenis (1972) also noted that *Castanopsis* species in Malesia regions prefer climates with minimal dry season stress, further emphasizing the importance of consistent water access for these species.

A clear contrast emerges when comparing our preliminary analysis and final model's findings for this southernmost species to those from other areas, such as in East Asia (SI Table 2). Studies in that regions primarily highlight temperature, particularly minimum temperature of the coldest month (bio6), as a key climatic control, such as on *C. eyrei*, and *C. hystrix* in China (Ouyang et al. 2023; Shen et al. 2023). Additionally, summer heat availability (bio10) also highly influences on limiting *C. sieboldii* and *C. cuspidata* distribution in Japan (Nakao et al. 2014; Aoki et al. 2019). Tang et al. (2022) further shows various climate important variables, e.g., precipitation seasonality (bio15) and temperature seasonality (bio4) among ten others for each of 32 dominant *Castanopsis* species in the region. However, our study in the equatorial tropics reveals a different pattern, with temperature variability (bio4 and bio3) in the preliminary analysis and precipitation in the driest periods (bio 17 and bio14) in the final analysis emerging as the dominant climatic factor (SI Fig. 4; SI Fig. 5). While this discrepancy may be driven by the differences in variables selection methodologies, such as in Tang et al. (2022) who adopted a broader approach of climate variable choice and sampling

Table 3 Comparison of above threshold and optimum environmental conditions^a

Variables	<i>C. argentea</i>		<i>C. tungurru</i>		Unit
	Above threshold	Optimum	Above threshold	Optimum	
bio1/MAT	8.2–28.7	18.8	11.7–27.8	19.6	°C
bio12	1660–5960	4020–4860	2300–5860	2780–5000	mm/year
bio14	–	–	47–392	68–200	mm/month
bio17	70–1050	140–745	–	–	mm/quarter
bio18	260–2230	1,110	380–2150	1120	mm/quarter

^a The Above threshold ranges indicate the values where habitat suitability exceeds the defined threshold, while the Optimum values represent the peak conditions. For bell-shaped curves, the optimum corresponds to the peak value. For non-bell-shaped curves, the optimum is defined as the range between the two peaks on the flat or plateau-like peak, reflecting the most favorable environmental conditions. This table corresponds to Fig. 3

background points for multiple species across East Asia regions, it also likely reflects the distinct climatic conditions between equatorial and mid-latitude regions, where precipitation plays a more critical role in influencing species distribution in tropical climate such as Indonesia. We also acknowledge that while our variable selection approach contributes to differences in variables importances between preliminary and final model, we recognize this as a limitation to be further explored in future studies.

Furthermore, our results also unsurprisingly contrast with a study of these same species in Sumatra by Harapan et al. (2022) emphasizing elevation, soil quality, and temperature seasonality as key drivers. We attribute this difference to our exclusion of topographic and edaphic as variables and scale-related factors. The Massenerhebung effect (mass elevation effect) and regional climate can influence elevational tree line variations of vegetation zones across mountains of different sizes and locations (Grubb 1971; Pouteau et al. 2018). Additionally, incorporating elevation as a predictor can be challenging due to its indirect link to temperature (Mod et al. 2016; Bradie and Leung 2017). Similarly, soil properties might influence distribution patterns but more within a local scale (John et al. 2007; Baldeck et al. 2013). Therefore, our study suggests that climatic variables, particularly the influence of precipitation, may provide a more robust explanation for these species' broad distribution across tropical regions in Indonesia.

The predicted optimal environmental conditions for the species align with previous observations. Both species thrive in areas which receive annual rainfall around 4,000–4,500 mm/year such as in Mt. Gede Pangrango and

Mt. Halimun-Salak, and where temperature range between 20–24 °C such as in remnant forests of Cibodas and Talaga Warna Nature Reserves, West Java (Nurdiana and Buot 2021; Putri et al. 2022). Additionally, Kooyman et al. (2022) suggest this species historically inhabited lowland areas, and Soepadmo and van Steenis (1972) recorded their occurrences near the Banten coast in West Java. This may indicate a broader ecological niche for these species, although they are likely restricted by susceptibility to drought.

Predictive suitable habitats shaped by climate change over time

Changes in temperature and precipitation have significantly influenced the historical expansion and contraction of the distribution of *C. argentea* and *C. tungurru*. During the Last Glacial Maximum (LGM), conditions were relatively drier with cooler temperatures (Kershaw et al. 2001; Hamilton et al. 2024) but probably remained within the MSS threshold identified in this study, allowing suitable habitat to expand beyond current ranges. This expansion includes the Sunda Shelf which supported by fossil records around South China Sea (Wang et al. 2009). A recent study also suggests that those areas supported a forest mosaic suitable for forest vegetation (Hamilton et al. 2024), rather than being limited to savanna corridors as previously thought (Bird et al. 2005; Wurster et al. 2010).

Following the LGM, most suitable habitats are predicted to have shrunk continuously from the mid-Holocene into the future (Fig. 6; SI Fig. 12; SI Fig. 13). This aligns with studies showing a decline in potential areas in future for *Castanopsis*, such as in China and East Asia (Cheuk and Fischer 2021; Tang et al. 2022). Interestingly, Kooyman et al. (2022) predict future habitat expansion for *Castanopsis* in Southeast Asia, likely due to modeling the entire genus rather than specific species. However, despite these dynamic changes, high-potential habitats remain geographically consistent, particularly in highland areas, suggesting some potential refugia for these species during harsh environmental conditions (Cannon 2012; Hamilton et al. 2024).

Nonetheless, some highland areas are currently unsuitable for these species, such as Mt. Lawu in Java, west slope of Barisan Mountain areas in West Sumatra, and around the summit of Mt. Kerinci (indicated by grey areas in the elevation map in Fig. 5). This unsuitability may be attributed to unfavorable climate conditions in such areas. Mt. Lawu and several mountains in east Java are among the areas experiencing minimal rainfall due to eastern monsoon winds carrying less water vapor from Australia during the dry season and the ENSO phenomena (Whitten et al. 1996; Arjasakusuma et al. 2018). In West Sumatra, while areas such Mt. Gadut and Mt. Sipisang receive high rainfall up

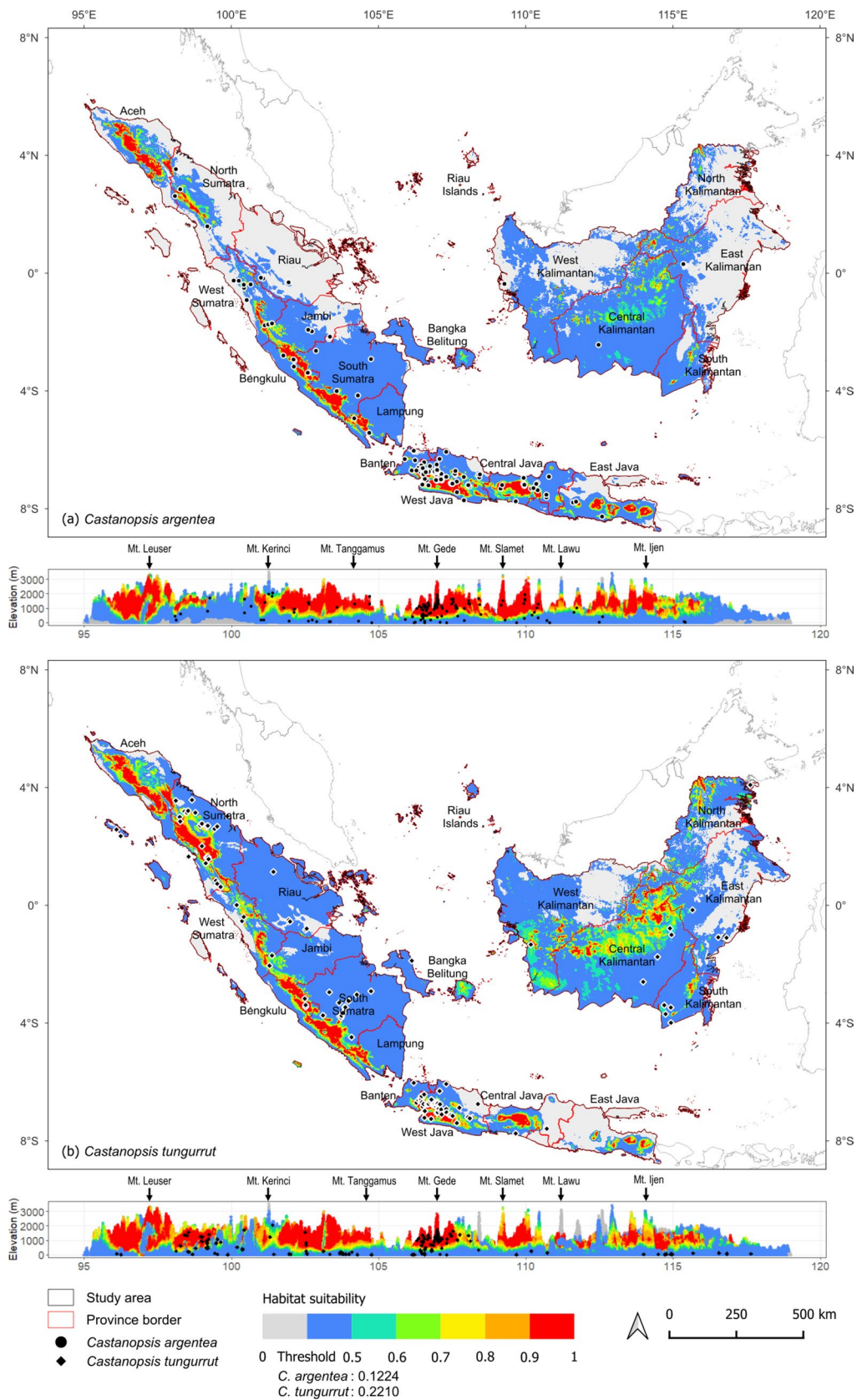
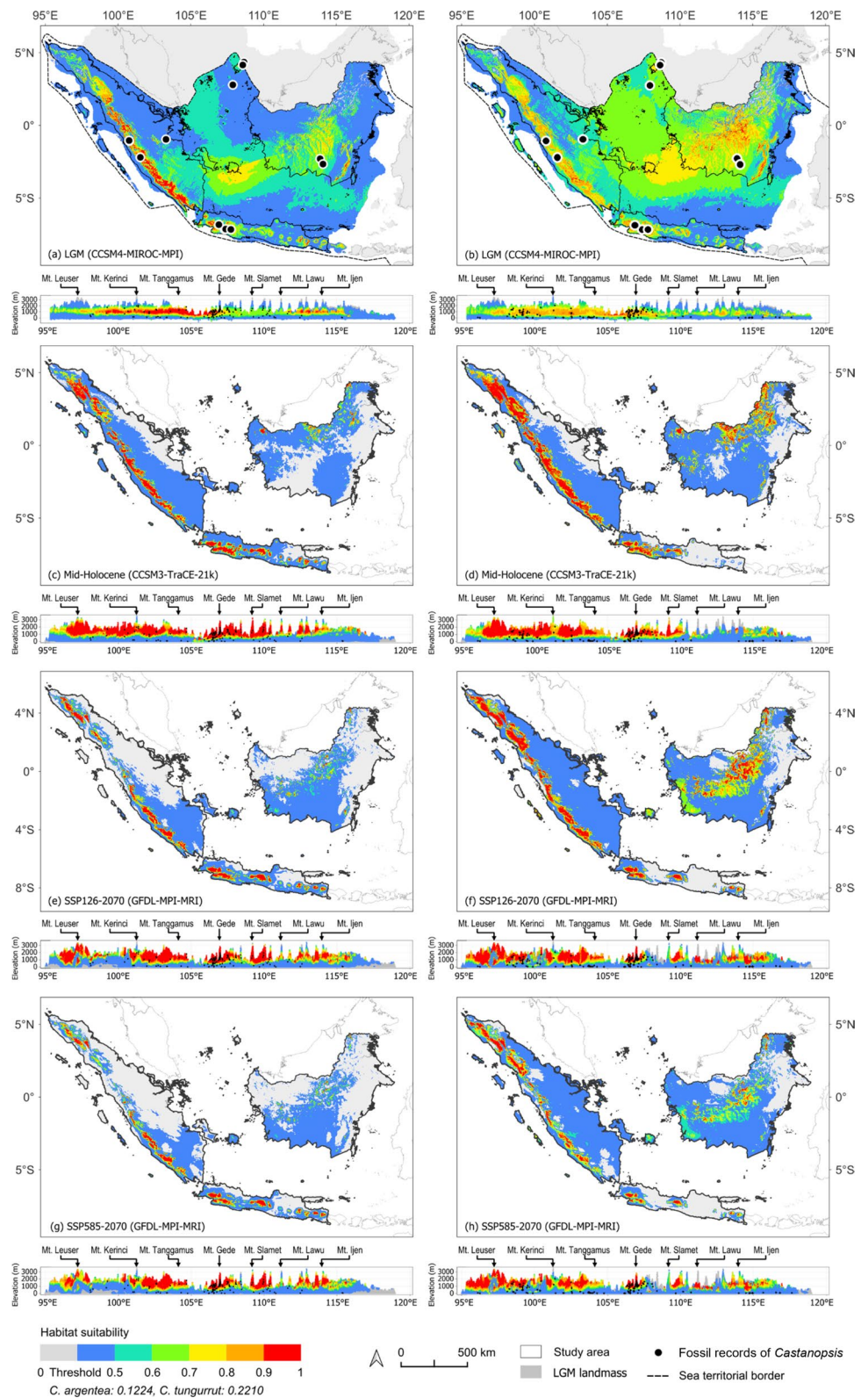


Fig. 5 Current suitable habitats for *Castanopsis argentea*(a) and *C. tungurru*(b)

Fig. 6 Predicted suitable habitats in the past (LGM and Mid Holocene) and future in 2041–2070 (SSP126 and SSP585) for *Castanopsis argentea*(left: a, c, e, g) and *C. tungurrut*(right: b, d, f, h). The dots (6a and 6b) indicate fossil records of the genus *Castanopsis* from approximately 39,000 B.P. to 3,800 B.P. (see also Fig. 7a, 7b; SI Table 3)



to 5,900 mm/year (Fujii et al. 2006), they likely represent the upper limits of the climatic range where the species can persist (Table 3; Fig. 4; Fig. 5). Conversely, the excessively high annual rainfall observed on the west slope of the

Barisan Mountains, which sometimes exceed 8,000 mm/year (Hotta et al. 1992), even in the dry season in the surrounding Padang regions, including in the southern and northern part of West Sumatra and a small portion of North

Table 4 Suitable habitats in the present and its comparison with past and future projections

Species/ time slice model	Suitable habitats (km ²)	Range change (%)	Over- lap areas (%)	Lost areas (%)	Gained areas (%)
<i>C. argentea</i>					
Present	713,186	–	–	–	–
LGM ^a	2,229,016.5	+58.01 (+212.54)	98.50	1.50	59.51 (214.05)
Mid Holocene	800,311	+12.22	81.88	18.12	30.33
Future SSP126	612,309	–14.14	84.66	15.34	1.20
Future SSP585	510,665	–28.40	70.63	29.37	0.98
<i>C. tungurru</i>					
Present	946,498	–	–	–	–
LGM ^a	2,221,927.1	+20.86 (+134.75)	98.67	1.33	22.19 (136.08)
Mid Holocene	875,961	–7.45	83.47	16.53	9.08
Future SSP126	933,175	–1.41	94.10	5.90	4.49
Future SSP585	895,034	–5.44	89.89	10.11	4.67

^a The landmass in study area during LGM is much larger than present time. Values represent % range change in suitable habitat: top– compared to the same study extent as today’s, bottom (parentheses)– total LGM areas within Indonesia’s landmass and ocean area extent in present. Lost areas: present minus overlap areas, gained areas: projected (past or future) minus overlap areas

Table 5 Potential stable habitats and refugia with three different suitability classes obtained from the overlap areas between present, past (LGM and MH), and future (two scenarios)

Potential stable habitats and refugia	Predicted area			
	Total area (km ²)	Very high > 0.9 (%)	High 0.5–0.9 (%)	Low < 0.5 (%)
<i>C. argentea</i>				
Present–Past–Future eSSP126	535,810	24,201 (4.52)	104,972 (19.59)	406,636 (75.89)
Present–Past–Future eSSP585	469,856	20,611 (4.39)	100,609 (21.41)	348,636 (74.20)
<i>C. tungurru</i>				
Present–Past–Future eSSP126	744,766	25,254 (4.71)	221,6189 (29.76)	497,894 (66.85)
Present–Past–Future eSSP585	711,301	19,615 (2.76)	216,346 (30.42)	475,340 (66.83)

Sumatra (SI Fig. 8; Whitten et al. 1997; Senior et al. 2023), results in conditions that surpass the species’ thresholds, rendering these areas unsuitable.

Moreover, while these species are often abundant at lower mountain elevations (Soepadmo and van Steenis 1972), their distribution is limited by low temperatures at higher elevations (Ohsawa et al. 1985). On higher mountains, the tree line for these species that belong to Fagaceae family is at around 2,500 m, where MAT reaches approximately 12 °C

(Ohsawa 1991). Since temperatures drop below 5 °C at the summits of high mountains such as Mt. Kerinci (3,805 m) (Ohsawa 1991; Whitten et al. 1997), these areas fall outside the suitable habitat range.

Aside from environmental variables, animal dispersers also play a crucial role in shaping these species distributions. In East Asia, for example, small rodents such as squirrels and mice are well documented as effective seed dispersers (Xiao et al. 2005; Chou et al. 2011; Yang et al. 2015; Wang et al. 2019), and similar dispersal agents have been observed in our study region (Hamidi et al. 2019). While some studies suggest that these animals can expand their ranges and even invade new areas (Di Febbraro et al. 2019; Yang et al. 2023), other report indicates that they are vulnerable to the effects of climate change (Gur 2022; Nie et al. 2023; Steiner and Huettmann 2023; Nash and McCain 2024). Considering that *Castanopsis* species has inherently weak dispersal capabilities and are expected to face habitat contraction in the future, these combined factors may further restrict their distribution.

Potential stable habitats and refugia under climate change

Our study identifies extensive suitable habitats that persist from the LGM era to future projections in 2041–2070 under the most extreme climate scenario (SSP585), that may serve as potential stable habitats for *C. argentea* and *C. tungurru*, covering approximately 469,000 km² and 711,000 km², respectively. This suggests that these areas have a long history of withstanding environmental changes, particularly climatic fluctuations (Morelli et al. 2020; Rossetto and Kooyman 2021) and have served as persistent population habitats over long-time (Tzedakis et al. 2013). Building upon the concept of climate-stable refugia introduced by Tang et al. (2017; 2018), which identifies long-term refugia using the overlap of suitable areas of “refined” model across time scales which reduce a large portion of suitable areas with low probability (<0.5) (Tang et al. 2017), about one-third of the high probability of potential stable habitats (>0.5) located in mountainous regions, such as Bukit Barisan in Sumatra and montane regions in Java and Kalimantan may also be considered as potential long-term climate refugia for *C. argentea* and *C. tungurru*.

While specific fossil records for *C. argentea* and *C. tungurru* are lacking, palynological studies reveal the presence of *Castanopsis* (genus-level) within projected suitable habitats during both the MH and LGM periods, and possibly even earlier. The genus-level climate requirements are assumed to have remained stable since the Eocene (Mosbrugger and Utescher 1997), and study suggests that using of taxonomic ranks, i.e., species, genus, and family to infer

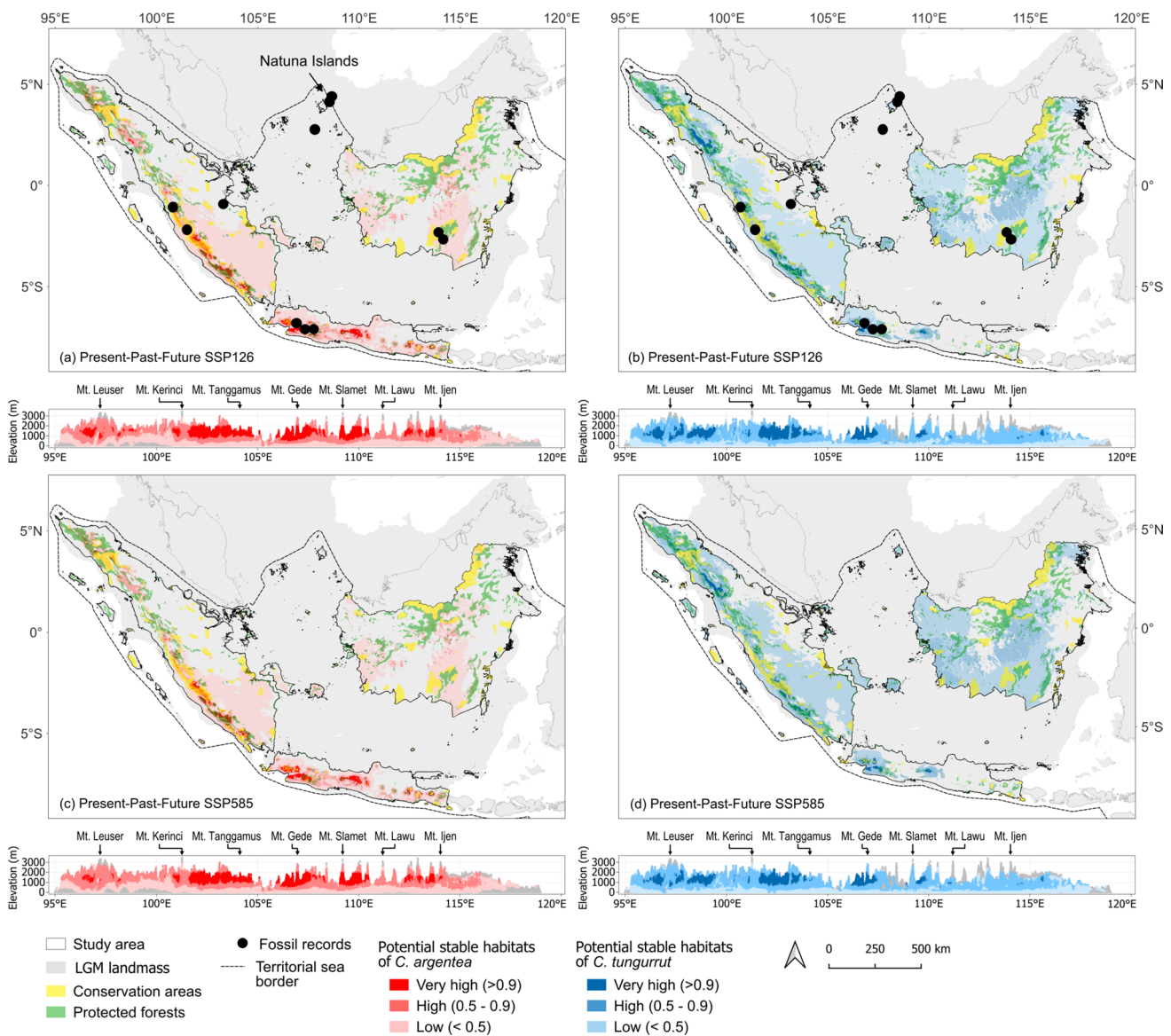


Fig. 7 Potential stable habitats and refugia overlap with the conservation areas and protected forests for *Castanopsis argentea* (a and c) and *C. tungurrut* (b and d). Fossil records of genus *Castanopsis* from approximately 39,000 B.P. to 3,800 B.P. (end of the Mid-Holocene)

paleoclimates show similar precision and accuracy (Harris et al. 2017), hence, genus-level fossil records still provide reliable validation of the predicted past suitable habitats for these species. Pollen fossil records indicate the past presence in several regions (Fig. 6a, 6b; Fig. 7a, 7b; SI Table 3), such as in Java (Stuijts et al. 1988; Stuijts 1993; Van Der Kaars and Dam 1995), Sumatra (Morley 1982; Newsome and Flenley 1988), and Kalimantan (Morley 1981; Kershaw et al. 2001). Moreover, other pollen records found in the areas resemble current lower montane vegetation pattern, with taxa such as *Altingia excelsa*, *Quercus*, and *Engelhardtia* in Java and Myrtaceae in Sumatra (Morley 1982; Stuijts et al. 1988). These findings, along with the presence of

(7a, 7b; SI Table 3). Building on the concept of refugia by Tang et al. (2017), we propose that potential stable habitats with high probability (>0.5) is potential climate refugia

Castanopsis pollen on the exposed Sunda Shelf in the South China Sea around Natuna Islands during the LGM (Wang et al. 2009; Luo et al. 2019), suggest that these mountainous areas served as refugia for *Castanopsis* during past climate changes (Fig. 6a, 6b; Fig. 7a, 7b).

It is also worth noting that the discovery of new *C. argentea* individuals in suitable habitats considered as potential stable habitats and refugia but previously unrecorded occurrences, such as Mt. Leuser in Aceh and Mt. Arjuna in East Java (*Alnus Meinata*, pers. comm. 2024), highlight the value of ongoing field surveys. While the record on Mt. Leuser aligns with nearby occurrences, the finding on Mt. Arjuna is surprising due to the dominant monsoon climate

in surrounding areas. Nevertheless, Soepadmo and van Steenis (1972) also mentioned that *Castanopsis* species may occur in dry climate areas of Java but are typically confined to a few local complexes of ever-wet forests, yet only citing central Java such as Mt. Muria, Mt. Ungaran, and Mt. Telo-mojo. However, their occurrence in eastern Java, characterized by a strong monsoon influence, remains unclear and warrants further investigation.

Recommendations for conservation and management

Under the highest emission scenario, approximately 73,200 km² (60%) and 114,270 km² (48%) of the total potential stable habitats considered as potential refugia for *C. argentea* and *C. tungurrut* are within conservation areas and protected forests (Table 5; Fig. 7). Despite this promising sign, threats such as deforestation, logging, and land-use change persist within these protected areas, albeit at a slower rate (He et al. 2023; Santoro et al. 2023; Nugraha et al. 2024). Moreover, potential refugia beyond conservation areas may lack protection. Consequently, strategies for conserving and managing these potential refugia, both inside and outside conservation areas, are crucial for these species' survival.

To conserve these species, various measures can be implemented both within and outside protected areas. While expanding conservation areas may be necessary (Yang et al. 2020; Zeng et al. 2022), improved management of existing ones is often more effective due to resource constraints and ongoing local pressures (Adams et al. 2019; Coad et al. 2019; Nugraha et al. 2024). This involves strengthening institutional capacity, enforcing laws, and providing adequate funding (Appleton et al. 2022; Sreekar et al. 2024). Outside conservation areas, community-based forest conservation management and sustainable land-use practices are crucial, particularly in countries such as Indonesia with high socioeconomic and population pressures (Sunderlin et al. 2005; Santika et al. 2017; He et al. 2023). Indonesia's social forestry framework offers opportunities for community participation in forest co-management programs, contributing to biodiversity conservation and improving livelihoods (Rakatama and Pandit 2020; MoEF 2016). Additionally, reintroduction programs and establishing ecological corridors can help augment and connect isolated populations and potential refugia across regions, aligning with national conservation action plans for priority tree species (Hamidi et al. 2019; MoEF 2024).

For Sumatra, where potential refugia are well-covered by conservation areas and protected forests forming a corridor along the Bukit Barisan Mountains (Fig. 7), the focus should be on improving forest management and implementing social forestry programs. In Java, although some

potential refugia are protected within conservation areas, many remain unprotected, especially in western and central Java. Given the fragmentation and smaller size of Java's remaining forests and the most populous island, efforts should focus on connecting refugia outside conservation areas through wildlife corridors or reforestation, reintroduction program, and improving social forestry implementation. In Kalimantan, the central and southern regions, where fragmentation of refugia is becoming more pronounced, require immediate attention to prevent further habitat loss such as maintaining the remaining forests and assessing high conservation value areas in forest patches within plantation landscapes for local refugia. These management and conservation efforts can ensure the long-term persistence of *C. argentea* and *C. tungurrut* and potentially have broader biodiversity benefits as well, protecting other species that share similar habitats.

Although our study identifies potential stable habitats and refugia and overlaps them with conservation areas for *C. argentea* and *C. tungurrut*, it is essential to acknowledge ongoing threats to these tropical lowland and montane forests, including those in Indonesia (Harrison et al. 2020). Habitat loss in lowland and montane forests due to deforestation, agricultural expansion, and infrastructure development (Margono et al. 2014; Gaisberger et al. 2022; He et al. 2023; Santoro et al. 2023) are significant threats that could drastically reduce the extent of these potential stable habitats and refugia in the future. These human-induced pressures, alongside climate change, could jeopardize the long-term persistence of these species within these areas. Therefore, conservation efforts focused on protecting these remaining forests and promoting sustainable land-use practices are critical for safeguarding these species, and the biodiversity they represent. Future studies should integrate projections of anthropogenic disturbances, such as forest cover loss, and climate change models to assess the effectiveness of these potential areas.

Conclusions

This study sheds light on the crucial role of precipitation in shaping the distribution of *C. argentea* and *C. tungurrut* in Indonesia. While annual precipitation and temperature also play a contributory role, precipitation during the driest quarter and month emerged as the most influential factor. These variables have likely shaped their suitable habitats over time. Historical climate reconstructions show that suitable habitat areas were much larger during the Last Glacial Maximum, encompassing the Sunda Shelf, but have since contracted and are predicted to continue shrinking into the future. Despite this decline, a network of potential stable

habitats and refugia persists, particularly in the highlands of Sumatra (Bukit Barisan), Java, and Kalimantan, where conditions have remained consistently suitable over extended periods. Furthermore, the discovery of new individuals in areas predicted to be highly suitable but with no current record highlights the value of ongoing field surveys. These findings emphasize the need for continued monitoring and conservation efforts to safeguard these ecologically important species and the potential stable habitats and refugia that will be critical for their long-term survival.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11258-025-01550-w>.

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Author contributions A.H.L., T.M., and T.S. contributed to the study's conceptualization and design, data collection, and analysis. All authors provided contributions to data interpretation. A.H.L. drafted the initial manuscript, which was subsequently reviewed and improved upon by all authors. C.Q.T. proofread the English language editing. All authors agreed on the final version of the manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

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