

Karst-specific distribution of endangered *Hopea celebica* in Bantimurung Bulusaraung National Park, South Sulawesi, Indonesia

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Abstract. Nasri, Kamiya K, Shimamura T, Ichie T. 2025. Karst-specific distribution of endangered *Hopea celebica* in Bantimurung Bulusaraung National Park, Sulawesi. *Biodiversitas* 26: 5395-5404. *Hopea celebica* is an endangered tree species endemic to Sulawesi, Indonesia, with limited ecological information available on its habitat preferences. This study aimed to investigate its distribution and habitat association in karst and non-karst areas of Bantimurung Bulusaraung (Babul) National Park, South Sulawesi, Indonesia. Seedlings, saplings, and adult trees were counted in 36 plots (50×20 m) selected using purposive sampling (18 plots in karst and 18 in non-karst areas). Elevation, slope, and canopy cover, were measured in each plot, and soil samples were analyzed for nutrient content and texture. *Hopea celebica* occurred exclusively in karst areas (12 of 18 plots), particularly in porous and massive karst types, showing a clumped distribution (χ^2 : 36, $p < 0.001$; Morisita's $I_s > 3$, $p < 0.001$). Generalized Linear Model (GLM) and Principal Component Analysis (PCA) showed that *H. celebica* was positively associated with steeper slope, higher soil pH, and denser canopy, but negatively with elevation. These findings highlighted porous and massive karst areas as key habitats, characterized by well-drained conditions at lower elevation, with healthy regeneration (inverted J-shaped diameter class distribution). This study suggests the need to protect porous and massive karst zones to ensure the long-term survival of *H. celebica* populations.

Keywords: Bantimurung Bulusaraung National Park, habitat preference, *Hopea celebica*, karst distribution, Sulawesi

INTRODUCTION

Dipterocarpaceae is among the most dominant tree families in the tropical regions of Southeast Asia, with notable species richness recorded in Malaya (155 species, 26 endemic), Borneo (267 species, 158 endemic), Sumatra (106 species, 10 endemic), and the Philippines (50 species, 21 endemic) (Ashton 1982; Maury-Lechon and Curtet 1998; Ng et al. 2022). In East Malesia, the number of dipterocarp species is markedly lower, with only 7 species recorded on Sulawesi (Ashton 1982), including widespread species, such as *Shorea assamica* and *Anisoptera costata*, and several endemics, such as *Hopea celebica* and *Vatica flavovirens* (Sirimorok and Rusdianto 2020; Arsyad et al. 2022).

Hopea celebica is one of the most endangered tree species in Sulawesi (Celebes), Indonesia, primarily due to intensive logging and overexploitation. Furthermore, *H. celebica* is confined to ecologically unique habitats in limited areas across the island. The IUCN Red List (2023) categorizes *H. celebica* as endangered (Hamidi et al. 2023). While most *Hopea* species produce resin, *H. celebica* is predominantly harvested in Sulawesi for its durable timber, underscoring its economic value in Southeast Asia (Quy et al. 2022; Ariati et al. 2024). Within Sulawesi, dominant populations of *H. celebica* are in only a few regions, including the karst areas of Bantimurung Bulusaraung (Babul) National Park and the ultrabasic soils of Malili

(Ashton 1982). Its ecological specialization and restricted distribution have made it a conservation priority within the park. The dissolution of soluble rocks such as limestone, dolomite, marble, and gypsum forms karst areas (Goldscheider et al. 2020; Veress 2020; Masilela and Beckedahl 2022), which often support unique ecosystems (Wang et al. 2019). Karst areas, characterized by limestone formations, sinkholes, and underground drainage systems (Lewis et al. 2020; Zhou et al. 2022), are significant for regulating hydrological systems, storing water, and harboring endemic species. In tropical Asia, karst areas have been recognized as centers of endemism and refugia for rare plant species, including dipterocarps (Tolentino et al. 2020; Tan et al. 2024). However, species-specific studies on their ecological adaptations remain limited.

Karst areas in Indonesia are protected under the Ministry of Environment and Forestry Regulation No. 8 (2018) on ecoregion designation, and the Ministry of Energy and Mineral Resources Regulation No. 17 (2012) on karst area protection. Babul National Park covers 43,750 ha, of which 22,800 ha are karst (Duli and Mulyadi 2019; Mas'ud et al. 2023), representing the largest karst area in the country (Nasri et al. 2021; Yelastri et al. 2023). Within this karst area, *H. celebica* exhibits a limited distribution, particularly along karst cliffs. Karst areas in Babul National Park create unique environmental conditions that support *H. celebica* and act as natural barriers against deforestation and land conversion due to their steep, rocky terrain, which

limits human access. Particularly, agricultural expansion is the primary driver of habitat loss in Sulawesi, mainly occurring in non-karst plains (Rijal et al. 2019). Public awareness and community involvement further enhance conservation outcomes by curbing illegal logging and other forms of habitat degradation (Samal and Dash 2023). Nonetheless, *H. celebica* remains threatened by agricultural expansion in karst valleys, encroachment, and mining activities, contributing to habitat degradation and fragmentation.

Despite these threats, habitat-based ecological studies on *H. celebica* remain limited, especially on habitat drivers and suitability. A better understanding of its spatial distribution and habitat preferences is urgently needed to inform conservation strategies. This study aimed to investigate the distribution and habitat associations of *H. celebica* in karst and non-karst areas of Babul National Park. Specifically addressed two questions: (i) Does *H. celebica* preferentially occur in karst areas compared to non-karst habitats? and (ii) Which environmental variables predict the presence or abundance of *H. celebica*? It also underscores the ecological role of karst areas and provides conservation insights for this endangered species.

MATERIALS AND METHODS

Study area

This research was conducted from August to October 2023 in Babul National Park, located in Maros and Pangkep Districts, South Sulawesi, Indonesia (Figure 1).

The park lies between 4°42'49"-5°06'42"S and 119°34'17"-119°55'13"E on the island of Sulawesi, and covers a total area of 43,750 hectares, with karst areas comprising approximately 22,800 hectares (52%). Karst areas are mainly distributed in the western part of the National Park (Figure 1).

Based on the physical appearance of the rocks in the Maros Pangkep Karst, Achmad (2011) identified four types of carbonate rocks in the Maros Pangkep Karst based on their physical characteristics: massive, porous, layered, and metagamping. Massive karst (MaK) consists of dense and homogeneous carbonate layers with minimal porosity. Porous karst (PK) has abundant pores that facilitate greater water and fluid movement. Layered karst (LK) is characterized by stratified carbonate deposits formed by gradual sedimentation. Metamorphosed karst (MeK), locally known as rock metagamping, develops under high pressure and temperature, resulting in a denser, crystalline structure.

Hopea celebica (Dipterocarpaceae) is a monoecious, emergent tree reaching 15-25 m in height. Its leaves are alternate, ovate-lanceolate with revolute leaf margins, measuring about 8-22×2.5-8 cm, with 1-1.6 cm petioles, and distinctive axillary domatia on the lower abaxial surface (Ashton 1982, Figure 2.A). The fruit is dark green with two long and three short wings (Figure 2.B). Resin exudation is visible on the trunk (Figure 2.C) a common trait in dipterocarps. Figure 2.D shows a seedling on karst rock substrates in Babul National Park. Locally, the species is known as "kerih" or ironwood, reflecting both its cultural value and the strength of its timber.

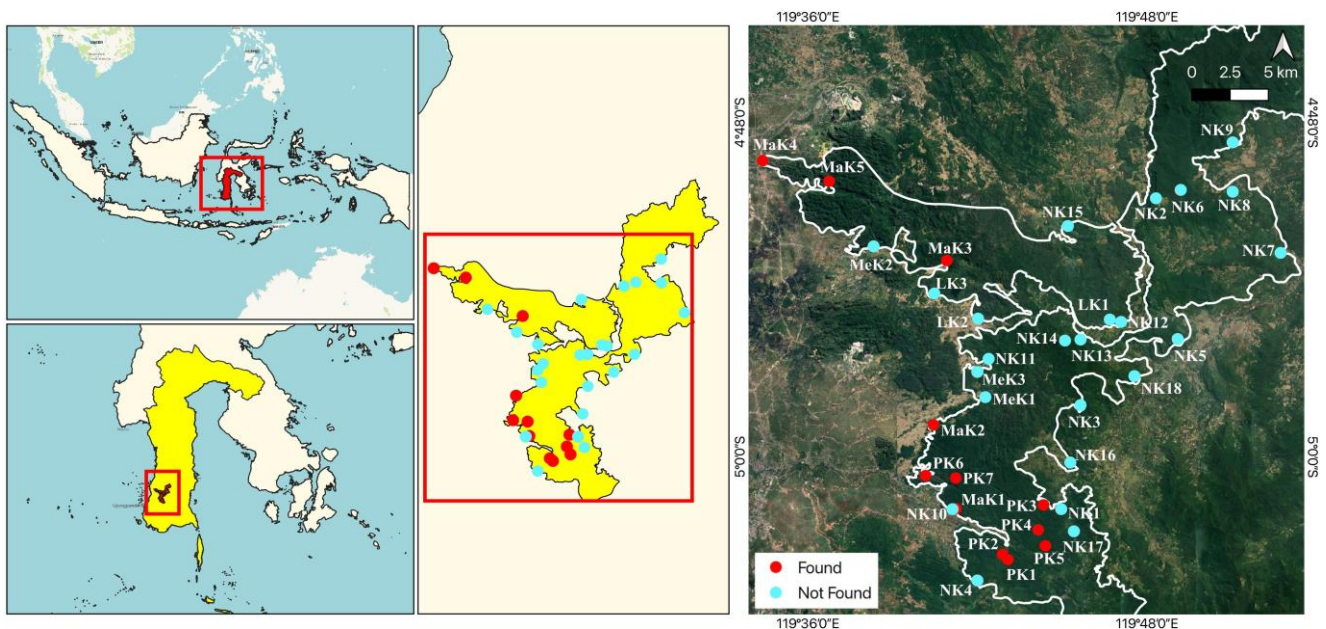


Figure 1. Distribution of research plots in Babul National Park, South Sulawesi, Indonesia. The ecosystem type is based on the landform map of the Directorate General of Forestry Planning and Environmental Governance, Ministry of Environment and Forestry of Indonesia (Decree No. SK.1272/MENLHK/SETJEN/PLA.3/12/2021; scale 1:250,000)

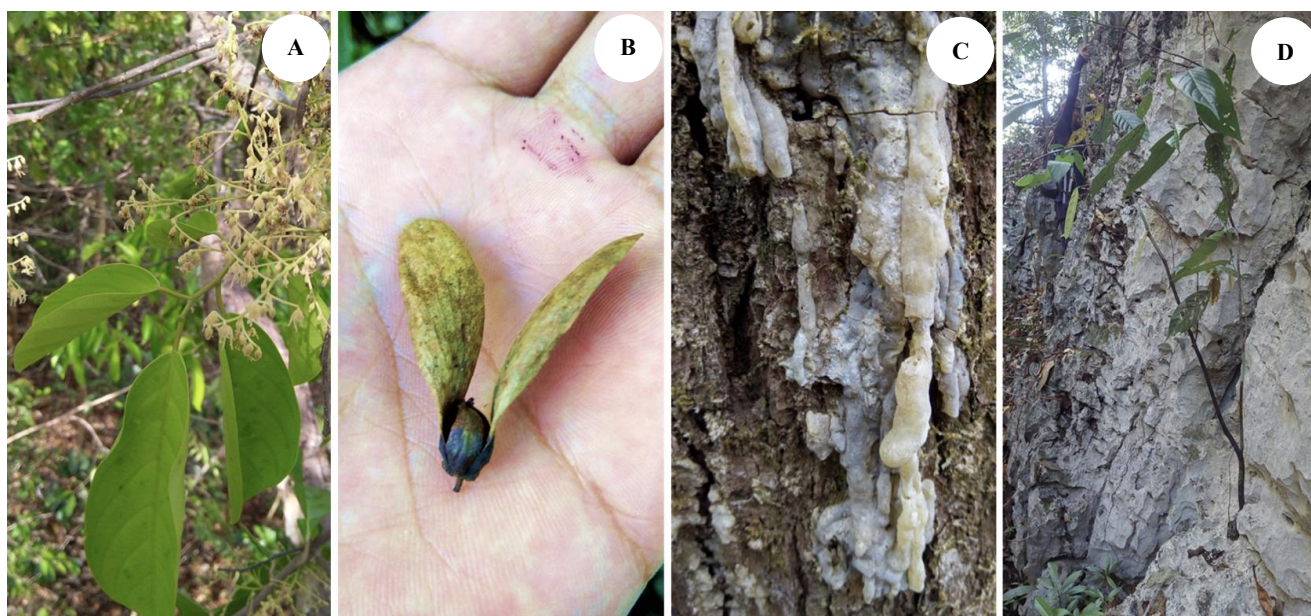


Figure 2. Morphological and ecological features of *Hopea celebica*: A: Leaf and flower, B: Fruit, C: Resin exudation, D: Seedling emerging from karst rock substrate

Procedures

Individuals with a diameter of ≥ 10 cm of *H. celebica* were counted in thirty-six 20×50 m plots (18 in karst and 18 in non-karst areas) established by purposive sampling within Babul National Park (Figure 1). Saplings (height >150 cm; diameter <10 cm) were counted in 5×5 m subplots, with three replicates per plot. Seedlings (height ≤ 150 cm) were recorded in 2×2 m subplots, using the same replication. In karst areas dominated by cliffs, plot coordinates were determined using the GPS AlpineQuest map application. To account for topographic variation, 20×10 m subplots were positioned along slopes in karst areas with distinct microtopographic features, representing valleys, cliffs, and hills (Figure 3).

Each plot was characterized by elevation, slope, canopy cover, soil pH, and soil moisture. Elevation was recorded using GPS AlpineQuest; slope with a Nikon Forestry Pro II range finder; canopy cover at 130 cm above ground using a Densimeter Model-C; and soil pH and moisture with a 3-in-1 Soil Meter (MS02). Canopy cover, soil pH, and moisture levels were measured in triplicate per plot. Soil moisture was rated on a scale of 1-10 (1-3: dry, 4-7: moderate, 8-10: wet). Land cover and karst geological distribution were also documented.

Soil samples were collected from six locations for analysis of texture and nutrient content: two cliff plots (PK1-Pattunuang and PK3-Karaenta), two valley plots (PK1-Pattunuang and PK3-Karaenta), and two non-karst plots (NK8-Samaenre and NK13-Bulusaraung). The samples were processed in the Laboratory of Silviculture and Tree Physiology, Faculty of Forestry, Universitas Hasanuddin. Soil texture was determined using the hydrometer method, which measures the weight of soil particles to obtain the percentages of sand, silt, and clay, and then classified using the USDA textural triangle (Hunduma and Kebede 2020). Permeability was

determined by soaking soil samples in water for 24 hours, followed by infiltration measurements at three 15-minute intervals. Bulk and particle densities were measured using the oven-dried method, with soil samples weighed before and after drying at 105°C, and porosity was calculated from these values (Whittington et al. 2021). Soil pH (H₂O and KCl) was measured potentiometrically with a 1:2.5 soil-to-water ratio. Organic carbon was quantified using the Walkley-Black wet oxidation method (Shamrikova et al. 2024), and total nitrogen via Kjeldahl digestion (Aguirre 2023); the C/N ratio was calculated accordingly. Available phosphorus (P₂O₅) was extracted using the Olsen method (Recena et al. 2022).

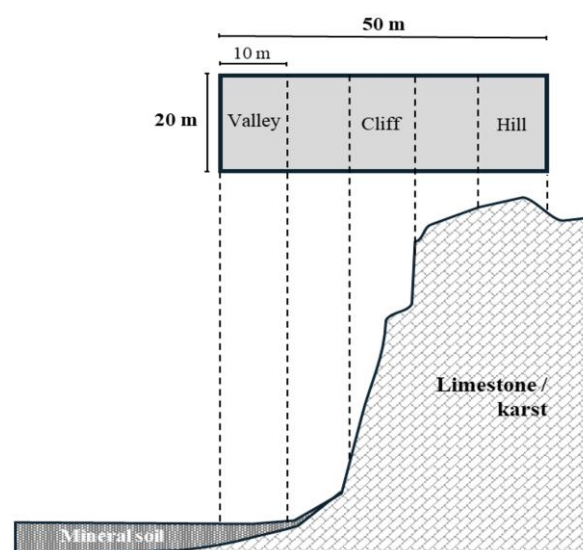


Figure 3. Plot design in the karst area. Large plots (20×50 m) were used for general distribution and population sampling, while small plots (20×10 m) were established separately in valley, hill, and cliff areas for detailed environmental and population analysis

Data analysis

Descriptive analysis was conducted to examine the distribution, population structure, and habitat characteristics of *H. celebica*, using Microsoft Excel for data tabulation and visualization. Species distribution patterns reflect the spatial arrangement of individuals within a community. To ascertain the distribution pattern of *H. celebica* in Babul National Park, Morisita's index (I_{δ}) was applied (Morisita 1959) using the following formula:

$$I_{\delta} = \frac{q \sum n(n-1)}{N(N-1)}$$

where q : number of plots, n : number of individuals per plot, and N : total number of individuals.

An I_{δ} value of 1.0 indicates a random distribution, $I_{\delta} < 1$ indicates a uniform distribution, whereas $I_{\delta} > 1$ indicates a clumped distribution. To test the significance of I_{δ} , a chi-square (χ^2) test was applied, with χ^2 approximated for $N-1$ degrees of freedom (Ludwig and Reynolds 1988). A clumped distribution pattern is inferred when the calculated χ^2 exceeds the critical value of the chi-square distribution, indicating a significant difference in the distribution. Conversely, a random distribution is indicated when χ^2 is below the critical value, suggesting no discernible difference in the distribution.

To examine environmental factors influencing the distribution of *H. celebica*, we used a Generalized Linear Model (GLM) with negative binomial regression to predict distribution patterns across habitat types (karst and non-karst). The dependent variable was the number of *H. celebica* individuals per plot, while the independent variables included environmental factors such as elevation, slope, canopy cover, soil moisture, soil pH, and habitat type (as a categorical variable, Figure 7). Model selection was conducted using the dredge function from the "MuMIn" package in R (Barton 2022). Predicted distribution of *H. celebica* was constructed using the GLM, with environmental variables as predictor inputs. These variables were analyzed in raster format with a spatial resolution of 10 meters, including elevation and slope data derived from a Digital Elevation Model (DEM), and tree canopy cover percentage from Sentinel-2 satellite imagery following Eskandari et al. (2020). Soil pH and moisture were interpolated from field-collected data. Principal Component Analysis (PCA) was also performed using the "factoextra" package (Kassambara 2017) to explore relationships among environmental variables in karst areas. The variables included in the PCA, elevation, slope, canopy cover, soil pH, and soil moisture, represent key environmental gradients across the study area. All statistical analyses were conducted using R version 4.4.1. Statistical analysis included tests for normality and homogeneity prior to conducting ANOVA with Tukey's

HSD ($p < 0.05$) for parametric data and Kruskal-Wallis with Dunn's test ($p < 0.05$) for non-parametric data. Spatial analysis was generated using QGIS 3.40.1.

RESULTS AND DISCUSSION

Distribution and population

Populations of *H. celebica* were predominantly found in karst areas within Babul National Park, occurring in 12 of the 18 karst plots (Figure 1), while they were absent in all 18 non-karst plots. Morisita's (I_{δ}) was 4.4, 4.6, and 3.3 for seedlings, saplings, and adult trees, respectively, showing a clumped distribution across all size classes ($p < 0.001$, chi-square test). Distribution was concentrated in cliff and hill regions typical of karst terrain (Figure 4). In contrast, a single seedling and a single sapling were recorded in one valley plot.

The plots were classified into four karst types: porous (7 plots, Figure 5.A), massive (5 plots, Figure 5.B), layered (3 plots, Figure 5.C), and metamorphosed (3 plots, Figure 5.D) karst. Individuals of *H. celebica* were found exclusively in porous and massive karst types (Figure 5.E), a pattern that was statistically confirmed by a chi-square test (χ^2 : 36, df: 4, $p < 0.001$). In layered and metamorphosed karst, *Dracaena multiflora* (Asparagaceae) was dominated (Figure 5.F).

Populations of *H. celebica* with diameters ≥ 5 cm were more frequently observed in porous karst, with 268 individuals per ha, compared with 130 individuals per ha in massive karst (Figure 6). In porous karst, individuals were predominantly in the 5-10 cm diameter class (146 individuals), followed by the 10-15 cm class (71 individuals). The number of individuals decreased steadily with increasing diameter, with only 4 individuals recorded in the >40 cm class (Figure 6.A). In massive karst, the population was similarly dominated by individuals in the 5-10 cm diameter class (80 individuals), with a sharp decline in larger diameter classes and no individuals recorded beyond the 25 cm class (Figure 6.B). This size class distribution in both habitats formed an inverted J-shaped growth curve.

Characteristics of habitat

Research plots in the karst areas were located at elevations ranging from 34 to 654 m asl, while those in the non-karst areas ranged from 52 to 1205 m asl (Figure 7). Individuals of *H. celebica* were distributed primarily within karst regions at elevations between 34 and 331 meters. *Hopea celebica* was absent in the layered karst area situated above 400 m asl, specifically in the Bulusaraung Resort area (LK1, Figure 1). Additionally, slopes in the karst areas were significantly steeper (74-87°, average 82.7°) than in non-karst areas (10-66°, average 30.6°).

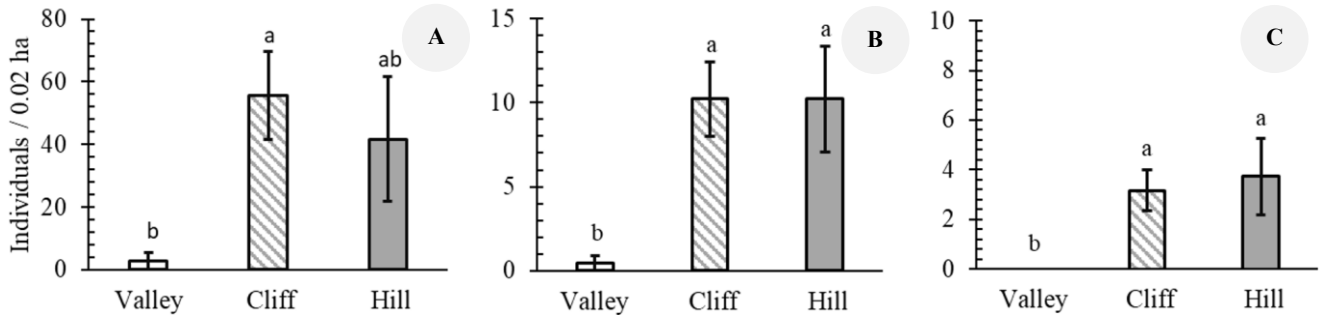


Figure 4. Distribution of *Hopea celebica* in the karst areas in Babul National Park, South Sulawesi, Indonesia. Different letters show significantly different means based on a Kruskal-Wallis test followed by Dunn’s post-hoc test ($p < 0.05$). A: Seedling, B: Sapling, C: Adult tree

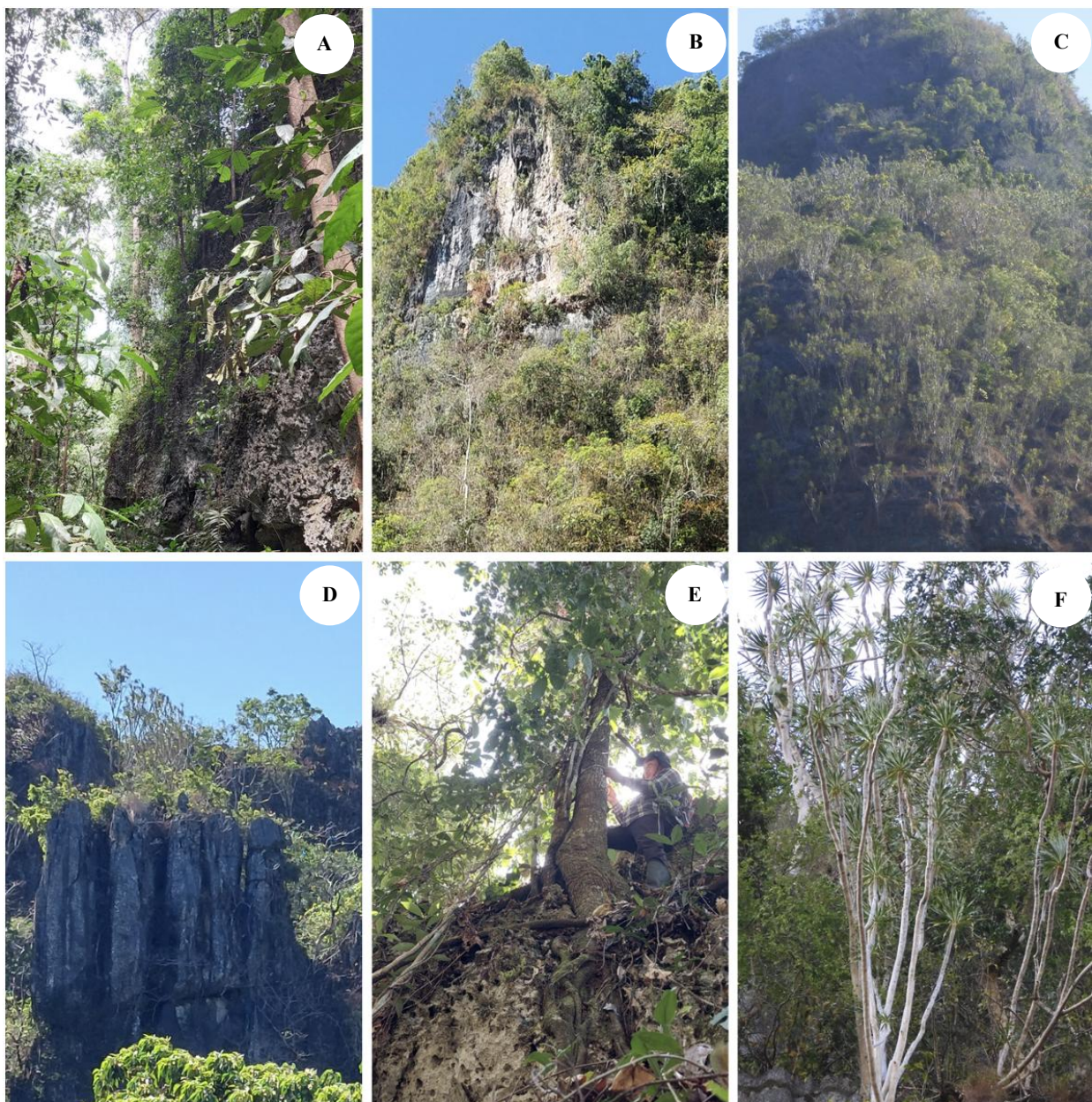


Figure 5. Karst types in Babul National Park, South Sulawesi, Indonesia. A-B: *Hopea celebica* is generally found in (A) Porous and (B) Massive karst cliffs. C-D: *Hopea celebica* is generally not found in (C) layered and (D) metamorphosed karst cliffs. E: *Hopea celebica* grows along the cliffs of porous and massive karst types. F: *Dracaena multiflora* is the dominant species in layered and metamorphosed karst types

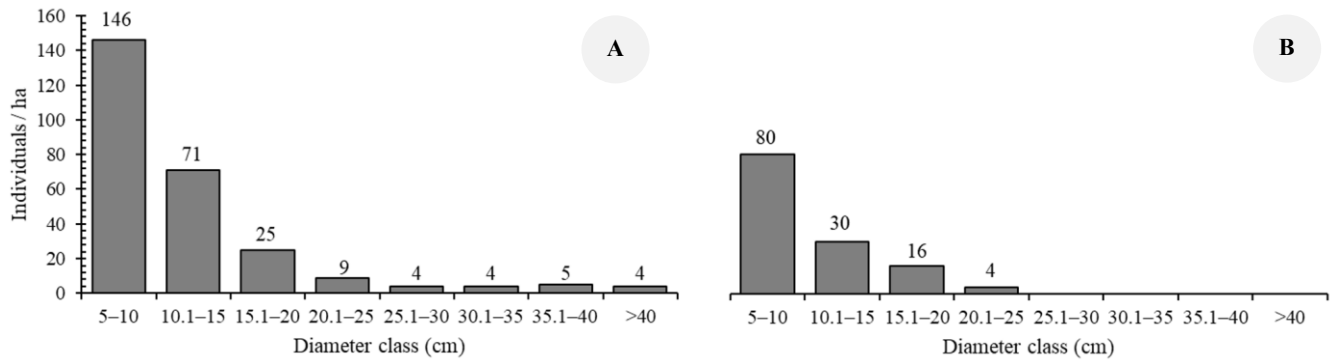


Figure 6. The populations of *Hopea celebica* in Babul National Park, South Sulawesi, Indonesia. A. Porous karst and B. Massive karst

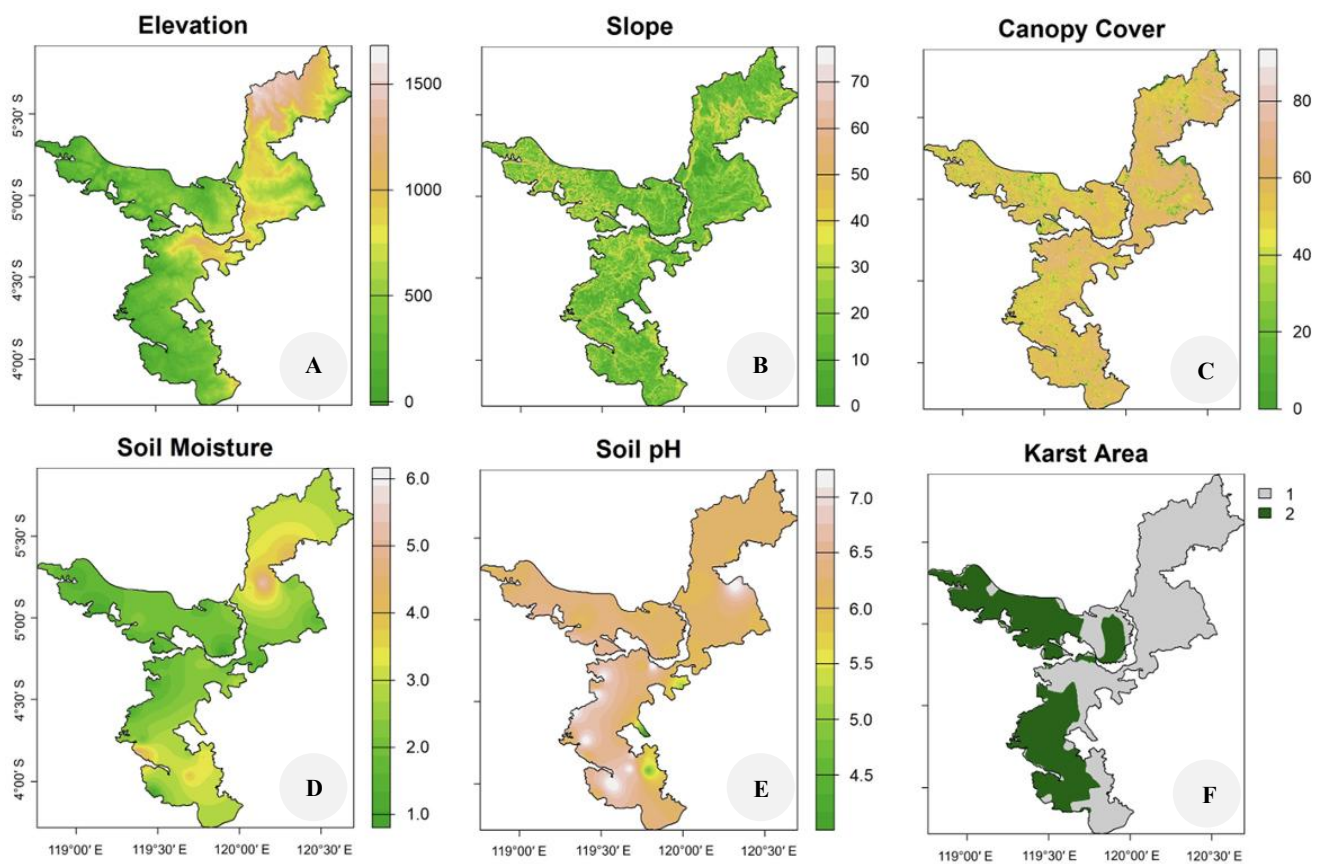


Figure 7. Spatial distribution of environmental predictor variables: A: Elevation (m), B: Slope ($^{\circ}$), C: Canopy cover (%), D: Soil moisture (level; 1-3: Dry, 4-7: Moderate, 8-10: Wet), E: Soil pH, F: Karst area (1: Non-karst, 2: Karst). The horizontal and vertical coordinates represent latitude and longitude, respectively

Hopea celebica is more prevalent in karst areas with relatively open canopy cover, particularly in cliff-hill topographies, compared with karst valleys. Canopy cover is significantly lower in these cliff-hill karst areas (33-87%, average 66.0%) compared with valley karst areas (66-94%, average 81.0%) and non-karst areas (65-92%, average 81.3%; $p < 0.05$, Kruskal-Wallis followed by Dunn's post-hoc). This species was not commonly found in extremely open areas, such as those found in metamorphosed and

layered karst areas, where the canopy cover is sparse and environmental conditions are more extreme.

Cliff-hill karst regions exhibited the driest conditions (Table 1). In contrast, karst valley areas exhibited higher moisture levels, spanning from dry to wet conditions, while non-karst areas had intermediate, categorized as dry to moderate. Soil permeability was considerably higher in cliff-hill karst areas, compared with the valley karst and non-karst areas. Additionally, soils in the karst areas were

generally thinner than in the valley and non-karst areas. Alkaline carbonate bedrock in karst regions likely contributes to a more neutral soil pH, whereas non-karst soils tend to be more acidic. Furthermore, the C/N ratio was higher in the cliff-hill karst soils compared with the valley karst and non-karst areas. The concentration of P₂O₅ (phosphorus) was significantly higher in non-karst soils than in karst valleys, while cliff-hill karst showed intermediate values (Table 1). All differences mentioned above were statistically significant ($p < 0.05$, ANOVA followed by Tukey's HSD), while other soil characteristics varied but were not statistically significant.

GLM analysis revealed that environmental variables influenced the distribution of *H. celebica* individuals (Table 2). Among these, slope ($z: 24.30, p < 0.001$) and canopy cover ($z: 28.34, p < 0.001$) emerged as the most significant positive predictors of *H. celebica* abundance. Soil pH ($z: 16.51, p < 0.001$) also showed a significant positive relationship. Although soil moisture exhibited a positive effect ($z: 2.38$), it was not statistically significant ($p: 0.195$). In contrast, elevation ($z: -13.15, p < 0.001$) had a significant negative association with the number of *H. celebica* individuals. Modelled distribution of *H. celebica* based on these predictors showed that areas with higher slope, denser canopy, and moderate soil pH correspond to a higher predicted probability of *H. celebica* presence (Figure 8). The map also highlighted karst ridges and hill slopes within the Babul National Park as core habitats, with probabilities exceeding 0.6 in several zones.

Principal Component Analysis (PCA) revealed clear relationships between karst types and key environmental variables: elevation (EL), canopy cover (CC), slope (SL), and soil moisture (M) (Figure 9). The first (PC1) and second (PC2) principal components together explain 67.5% of the total variation, capturing the majority of the ecological gradient in the study area and thus providing a robust basis for interpretation. The result showed that karst areas were generally associated with higher slope and pH values, and lower elevation, soil moisture, and canopy cover. In contrast, non-karst areas were associated with

higher elevation, soil moisture, and canopy cover, but with lower slope and pH. Among the karst types, porous karst and massive karst, which are the main habitats of *H. celebica*, were situated along the positive axis of PC1. Porous karst areas were associated with negative PC2 scores, while massive karst occurred around neutral PC2 values. These karst types were closely related to high soil pH and steep slopes, as well as low elevation. In contrast, layered and metamorphosed karst were more closely related to high slope, low soil moisture, and sparse canopy cover.

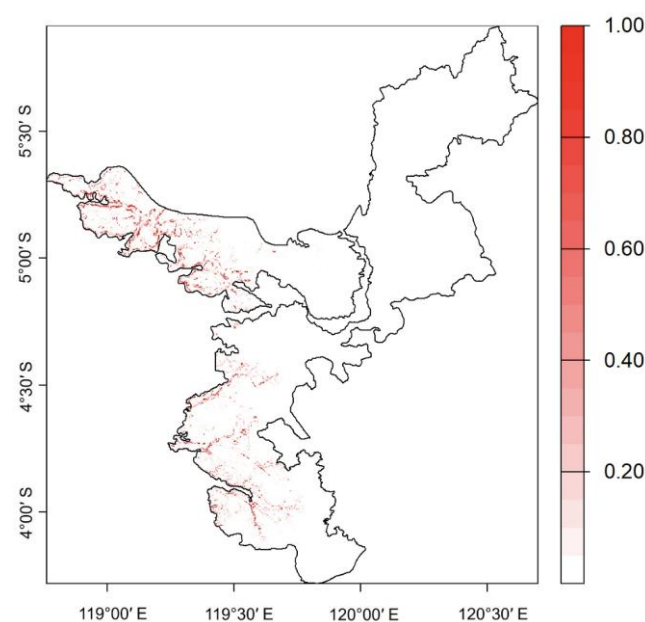


Figure 8. Model distribution of *Hopea celebica* in Babul National Park, South Sulawesi, Indonesia, showing probability of presence. Red shades represent areas with a higher probability of presence. The black polygon shows the national park boundary. Non-karst and areas with elevations exceeding >400 m were masked out

Table 1. Soil characteristics of karst and non-karst areas in Babul National Park, South Sulawesi, Indonesia

Soil characteristics	Karst		Non-karst (Mean±SD)
	Cliff-Hill (Mean±SD)	Valley (Mean±SD)	
Sand (%)	84.3±3.5 ^a	54.4±4.4 ^a	67.1±8.7 ^a
Silt (%)	9.4±3.8 ^a	23.7±1.0 ^a	17.4±5.7 ^a
Clay (%)	6.3±0.3 ^a	21.9±5.3 ^a	15.5±3.0 ^a
Permeability (cm/hour)	1251.7±18.1 ^a	13.4±12.9 ^b	29.6±8.5 ^b
Bulk density (gr/cm ³)	0.3±0.1 ^b	0.8±0.1 ^a	0.7±0.0 ^a
Particle density (gr/cm ³)	1.7±0.1 ^b	2.2±0.0 ^a	1.9±0.0 ^b
Porosity (%)	85.8±3.0 ^a	53.2±13.2 ^a	62.1±1.7 ^a
pH H ₂ O	6.2±0.1 ^a	6.2±0.1 ^a	4.9±0.0 ^b
pH KCL	6.0±0.1 ^a	6.0±0.0 ^a	4.4±0.0 ^b
C-Walkey & Black (%)	5.9±0.1 ^a	2.8±0.1 ^b	2.7±0.1 ^b
N-Kjeldahl (%)	0.2±0.0 ^a	0.2±0.0 ^a	0.2±0.0 ^a
Ratio C/N	27.1±1.5 ^a	12.0±0.2 ^b	13.6±0.0 ^b
P ₂ O ₅ Olsen (ppm)	12.2±0.1 ^{ab}	10.9±0.0 ^b	14.4±0.8 ^a

Note: Different letters denote significantly different means based on ANOVA, followed by Dunn's post-hoc test ($p < 0.05$)

Table 2. Effect of environmental predictors on the number of *Hopea celebica* individuals from the GLM analysis

Parameter	Effect	z-value	p-value
Elevation (m)	-	-13.15	<2e-16
Slope (°)	+	24.30	<2e-16
Canopy cover (%)	+	28.34	<2e-16
pH	+	16.51	<2e-16
Soil moisture (level)	+	2.38	0.195

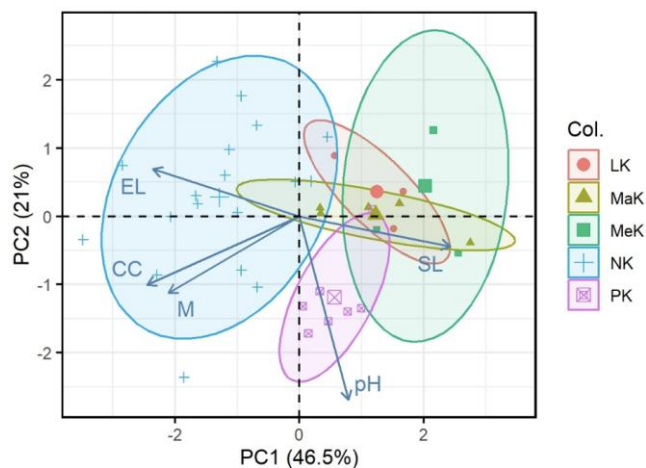


Figure 9. Principal Component Analysis (PCA) of environmental variables in the habitat of *Hopea celebica* in Babul National Park, South Sulawesi, Indonesia. The arrows represent environmental variables: elevation (EL), canopy cover (CC), slope (SL), and soil moisture (M). Different symbols and colors represent the five karst types: porous karst (PK), massive karst (MK), metamorphosed karst (MeK), layered karst (LK), and non-karst (NK)

Discussion

Our study showed that the distribution of *H. celebica* is strictly limited to karst areas in Babul National Park. Similar karst-dependent distributions are also found in other *Hopea* species, such as *H. vietnamensis* from Vietnam (Sam et al. 2013) and *H. bilitonensis* from Malaysia (Ariati et al. 2024). Since this pronounced habitat specificity makes *H. celebica* particularly vulnerable to habitat disturbance and extinction, Babul National Park should serve as the principal refuge for this endangered species. Such findings can directly inform zoning and habitat delineation strategies within protected karst areas, in line with other karst-specific dipterocarps in Southeast Asia, such as *Vatica kanthanensis*, which is confined to the ridges of massive limestone hills (Tan et al. 2024).

This species was predominantly observed on karst cliffs and hills, specifically in porous and massive karst types, which are characterized by relatively thin soil layers due to the rapid decomposition and weathering of organic litter. The abundance and widespread distribution of *H. celebica* in these karst types are likely attributable to the physical structure of the substrates, which facilitates root penetration and development into the karst bedrock. According to Achmad (2011), porous and massive karst areas support a

higher diversity of plant species compared with layered and metamorphosed karst. In contrast, layered and metamorphosed karst consists of denser, less permeable rock with minimal porosity, posing significant limitations to root growth. Consequently, plant species capable of establishing in these karst types are typically restricted to those with shallow root systems, such as *D. multiflora*, which frequently dominates the vegetation in these areas.

Our results suggest that *H. celebica* is hard to grow in karst valley areas with thicker soil layers, high moisture, and high clay content. These valleys and fault corridors, serving as depositional sites receiving leached materials from the upper slopes, have relatively moist conditions and deeper soil solum (Achmad 2011). In contrast, the cliff-hill karst regions are significantly drier, with lower soil moisture and higher permeability, offering better drainage that is more suitable for *H. celebica*. Although seedlings may temporarily emerge in the valley areas, persistently high moisture levels and reduced light availability due to denser canopy cover and greater plant diversity limit their long-term survival and establishment. These contrasts in microclimate may help explain the species' preference for cliff-hill habitats. Topographic factors such as light availability, moisture retention, and drainage influence the distribution of other dipterocarps (Bartholomew et al. 2022; O'Brien and Escudero 2022). Statistical analyses (GLM and PCA) indicated that *H. celebica* is associated with well-drained habitats at lower elevations, steeper slopes, and moderately open canopies. In these environments, favorable soil pH and moisture conditions promote establishment and growth of this species. Therefore, edaphic and topographic variables are the main factors in the presence of *H. celebica*. Our results are consistent with other studies showing that slope, elevation, and soil availability strongly influence tree distribution in karst areas (Suwasono and Matius 2018; Xiao et al. 2023).

These observed habitat conditions clearly support the regeneration of *H. celebica*. Current populations of *H. celebica* showed an inverted J-shaped growth curve, commonly interpreted as a sign of healthy population regeneration, characterized by a high number of seedlings and saplings capable of replacing mature trees as they senesce (Sharma et al. 2020; Temesgen and Warkineh 2020). Although *H. celebica* produces winged fruits adapted for wind dispersal (Song et al. 2020), seed movement is likely limited by the steep and fragmented karst landscape that restricts airflow. In addition to these physical barriers, *H. celebica* shows a strong dependence on specific microhabitat conditions, including well-drained, porous substrates with adequate light and slope, which further restrict its spatial distribution. These factors contribute to the clumped distribution observed in the field, a pattern commonly found in other *Hopea* species that regenerate through localized seedling recruitment rather than long-distance dispersal (Quy et al. 2022; Huang et al. 2025). Habitat heterogeneity within karst environments reinforces this pattern and highlights the species specialization. Despite successful regeneration, surrounding land use pressures, such as agricultural, limestone quarry activities, and tourism trails near karst

cliffs may lead to edge effects that threaten seedling survival (Benitez-Malvido 2023). These risks highlight the need for spatially targeted monitoring and buffer zone enforcement.

In conclusion, this study revealed that *H. celebica* was strictly confined to porous and massive karst areas in Babul National Park, preferring well-drained habitats with steeper slopes, higher soil pH, and moderate canopy cover and soil moisture at lower elevations. Populations of this species were well-regenerated, as indicated by the inverted J-shaped diameter class distribution. This sustainability remains highly dependent on the persistence of these karst-specific conditions. This study suggests that conservation strategies for *H. celebica* in Babul National Park should focus on prioritizing porous and massive karst areas below 400 m elevation with steep slopes for forest zoning, promoting restoration efforts in degraded karst areas, and integrating karst-specific habitat mapping into conservation planning. These site-specific strategies based on ecological data are essential for translating the IUCN Endangered status of *H. celebica* into actionable local policies. Therefore, conservation efforts must continue through regular habitat monitoring, enforcement of protective regulations within Babul National Park, and increased public engagement to ensure the long-term survival of *H. celebica* in its natural habitat.

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