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Distribution and conservation status of four endemic long-tailed macaque subspecies in Indonesia

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Abstract. *Huda R, Moore R, Prameswari W, Itang, Hutabarat ERRB, Yusidarta I, Baratha UW, Mardiono D, Sanchez KL. 2026. Distribution and conservation status of four endemic long-tailed macaque subspecies in Indonesia. Biodiversitas 27 (1): d270147. https://doi.org/10.13057/biodiv/d270147.* Population data for island-endemic subspecies of the long-tailed macaque (*Macaca fascicularis*) remain scarce despite their Critically Endangered status. We conducted rapid grid-based surveys and community interviews (May-July 2023) on four Indonesian islands—Simeulue, Lasia, Maratua, and Karimunjawa—to estimate density, abundance, distribution, and anthropogenic pressures on *Macaca fascicularis fusca*, *Macaca fascicularis lasiae*, *Macaca fascicularis tua*, and *Macaca fascicularis karimondjawae*. Across all sites, we recorded 597 individuals in 51 groups, with mean density indices ranging from 0.79 individuals km^{-2} on Simeulue (95% CI: 0.44-1.16) to 9.43 individuals km^{-2} on Maratua (95% CI: 4.17-15.84). Macaques were strongly associated with forest-settlement and plantation edges, where interview data indicated frequent negative interactions and reliance on anthropogenic food sources. These results reaffirm the Critically Endangered status of three subspecies under IUCN Criterion D and indicate a possible Criterion A2 decline for *M. f. fusca*, underscoring the need for targeted coexistence measures, habitat protection, and structured monitoring.

Keywords: Anthropogenic pressure, human-wildlife interface, island conservation, population assessment, synanthropic primates

INTRODUCTION

Southeast Asia is one of the world's most biologically diverse regions, home to a vast number of endemic species and unique ecosystems (Myers et al. 2000). However, the region is also a global hotspot for biodiversity loss, driven by rapid deforestation, habitat fragmentation, land-use change, and unsustainable wildlife exploitation (Sodhi et al. 2004; Estoque et al. 2019). Conservation efforts have understandably prioritized flagship species such as orangutans, elephants, and tigers—species that are ecologically significant, well-known to the public, and emblematic of broader environmental challenges (Guénard et al. 2025). Yet smaller, more adaptable species often receive less attention, even when they experience comparable or greater levels of decline (Joseph et al. 2009). This neglect overlooks the fact that common or widespread species can also play vital ecological roles and contribute significantly to ecosystem functioning and resilience (Gaston and Fuller 2008; Gaston 2010). Their decline may have cascading effects on ecological processes, such as seed dispersal, nutrient cycling, and food web stability, particularly in ecosystems already under pressure.

The long-tailed macaque (*Macaca fascicularis* (Raffles, 1821)) exemplifies this conservation blind spot. Widely distributed across South and Southeast Asia, the species has long been perceived as abundant and resilient—regularly seen near roadsides, temples, and plantations (Gumert et al. 2011). This reputation for adaptability has contributed to a general underestimation of its conservation needs (Eudey 2008; Fuentes 2011; Lee 2011). However, recent assessments reveal a different picture. Mounting pressures from habitat loss, negative interactions with humans, biomedical and pet trade exploitation, and direct culling have contributed to marked population declines in multiple parts of its range (Hansen et al. 2019; Gamalo et al. 2023). Reflecting this trend, *M. fascicularis* was uplisted to Endangered on the International Union for Conservation of Nature (IUCN) Red List in 2022 (Hansen et al. 2022).

Within the broader species complex, *M. fascicularis* comprises at least ten recognized subspecies (Fooden 1995), several of which are endemic to small islands within the Indonesian archipelago. These insular subspecies are of particular conservation concern due to their restricted ranges, small and isolated populations, and elevated vulnerability to anthropogenic disturbance. Four subspecies, *Macaca fascicularis fusca* (Miller, 1903, Simeulue), *Macaca fascicularis lasiae* (Lyon, 1916; Lasia), *Macaca fascicularis tua* (Kellogg, 1944; Maratua), and *Macaca fascicularis karimondjawae* (Sody, 1949; Karimunjawa), have been classified as Critically Endangered by the IUCN (2024), yet remain underrepresented in both academic literature and national conservation strategies.

Available data suggest these subspecies face a combination of ecological and anthropogenic threats. Habitat conversion for agriculture and tourism development continues to reduce and fragment available forest cover (Afendi et al. 2011; Kristiawan et al. 2022). Meanwhile, negative human-macaque interactions, including crop raiding, retaliatory killings, and the capture of infants for the pet trade, are frequently reported on these islands (Amey et al. 2022a; Nuryati et al. 2022). In Simeulue, for instance, the population of *M. f. fusca* is believed to have declined by more than 90% over a three-generation period—from an estimated 50,000 individuals in 1989 (Sugardjito et al. 1989) to fewer than 1,000 in 2017 (Amey et al. 2022a). Similarly, the most recent assessments suggest that populations of *M. f. lasiae*, *M. f. tua*, and *M. f. karimondjawae* each number fewer than 250 mature individuals, with shrinking areas of occupancy further exacerbating their vulnerability (Nuryati 2015; Taman Nasional Karimunjawa 2017; Kristiawan et al. 2022). Despite these alarming trends, there has been no comprehensive or standardized population assessment of these subspecies in recent years. As a result, conservation planning is severely constrained by the lack of robust data on distribution, population structure, and threats.

Although long-tailed macaques remain widespread in Southeast Asia, many mainland populations are declining sharply due to habitat loss, culling, and exploitation for trade and research (Hansen et al. 2021, 2022; Gamalo et al. 2023). These regional declines highlight the need to assess and safeguard remaining strongholds, particularly on small islands where isolation and limited habitat heighten extinction risk. By focusing on Indonesia's four island-endemic subspecies, this study contributes critical evidence for macaque conservation across the region—providing a baseline for comparative monitoring, Red List assessment, and coordinated Southeast Asian management efforts.

This study aims to fill critical knowledge gaps concerning the population status, distribution, and conservation threats of four Critically Endangered, island-endemic subspecies of long-tailed macaques in Indonesia: *M. f. fusca*, *M. f. lasiae*, *M. f. tua*, and *M. f. karimondjawae*. Specifically, we sought to: (i) assess the current population densities and estimated abundances of each subspecies using rapid field surveys, (ii) map their spatial distribution and key habitat associations, and, (iii) identify anthropogenic pressures, including negative interactions and dependence on human-altered landscapes, through community interviews.

MATERIALS AND METHODS

Study area

The study was conducted on four Indonesian islands—Simeulue, Lasia, Maratua, and Karimunjawa—which are inhabited exclusively by four Critically Endangered, island-endemic subspecies of long-tailed macaques: *M. f. fusca, M. f. lasiae, M. f. tua*, and *M. f. karimondjawae*, respectively (Figure 1). Simeulue (1,844 km²), located approximately 150 km southwest of mainland Aceh, is part of a chain of oceanic islands along Sumatra's western coast. The island's topography includes low-lying coastal areas and inland hills reaching elevations of up to 600 m above sea level. Vegetation is dominated by mangrove forests, coastal beach forest, and mixed agroforestry areas interspersed with smallholder plantations and rice paddies (Whitten et al. 2000). Forest cover is increasingly fragmented, with extensive agricultural encroachment and logging pressure, particularly in lowland zones (Amey et al. 2022a). As of 2020, Simeulue retained approximately 63% natural forest cover, equivalent to 115,000 ha (Global Forest Watch 2020). *M. f. fusca* is typically observed near mangroves, forest edges, and plantation interfaces.

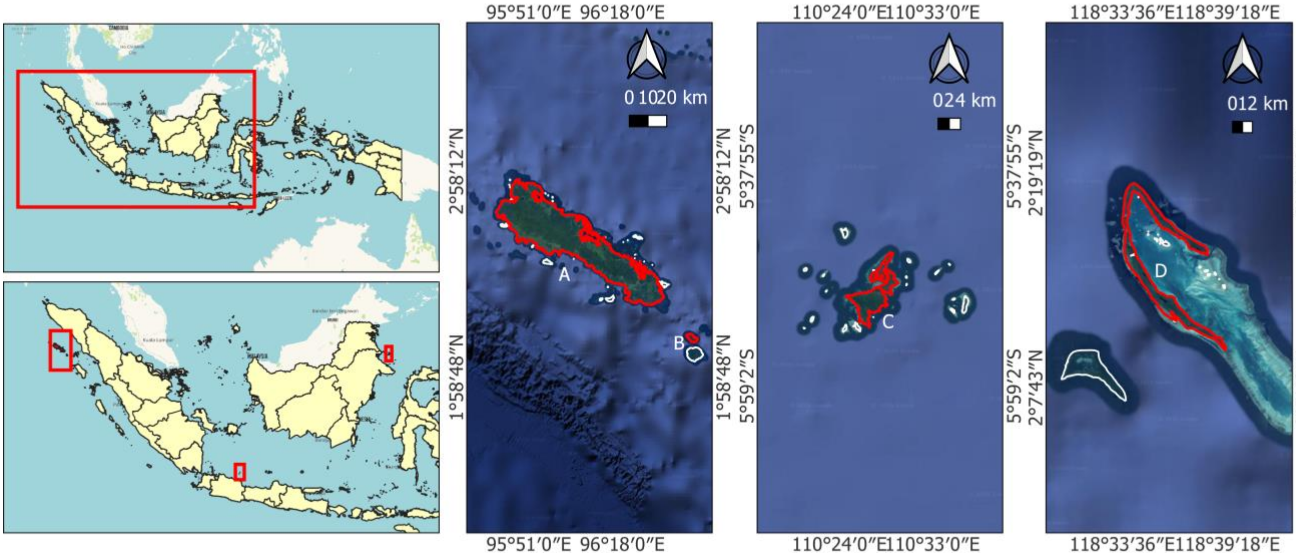

Figure 1. Location of the four surveyed islands in Indonesia—Simeulue, Lasia, Maratua, and Karimunjawa—and the endemic long-tailed macaque subspecies present on each island (*Macaca fascicularis*)

Lasia (15 km²), a small and relatively flat island situated just southeast of Simeulue, is covered by remnants of lowland tropical rainforest and coconut (*Cocos nucifera*) plantations. The island's elevation does not exceed 50 m above sea level. Natural forest cover is limited, and anthropogenic land use dominates much of the island, including small-scale agriculture and coconut harvesting activities. *M. f. lasiae* is presumed to inhabit the remaining forest patches and cultivated areas, although sightings have been rare (Amey et al. 2022b).

Maratua (23 km²) lies 50 km east of Berau District, East Kalimantan, within the Derawan Archipelago. The island is characterized by a ring-shaped limestone and coral structure with low elevation (<30 m), and its vegetation includes coastal forest, lowland tropical rainforest, and extensive mangrove stands. Maratua has remained isolated from the mainland, even during glacial periods, which has led to a unique biotic composition with lower species richness but relatively high abundance of synanthropic species (Voris 2000; Burner et al. 2018). Anthropogenic pressures include expanding tourism infrastructure, village expansion, and coastal development. *M. f. tua* occurs throughout forest edges, coconut groves, roadsides, and near human settlements.

Karimunjawa, an archipelago of 27 islands in the Java Sea, lies approximately 80 km off the northern coast of Central Java. The two largest islands, Karimun (27 km²) and Kemujan (14 km²), support the full known range of *M. f. karimondjawae*. The islands consist of lowland tropical rainforest, coastal forest, and mangrove ecosystems (Afendi et al. 2011; Kristiawan et al. 2022). Elevations range up to 506 m (Mount Gajah). Karimunjawa experiences high anthropogenic pressure due to expanding tourism, land conversion, and plantation agriculture. Forest cover has declined over the past two decades, with macaques often observed in degraded patches, plantation borders, and coastal villages (Kristiawan et al. 2022).

Survey methods

This study was carried out between May and July 2023, spanning three to nine observation days on each of the four islands. Survey duration varied depending on island size, logistical constraints, weather conditions, and habitat accessibility. Larger and more topographically complex islands such as Simeulue and Karimunjawa required longer field time, while smaller islands like Lasia and Maratua were surveyed over shorter periods due to their limited land area and habitat extent. Data were collected non-invasively through a combination of rapid population surveys and community interviews. To assess the presence and density of long-tailed macaques, we established a 1 × 1 km grid and visited a subset of cells on each island. Each visited 1-km cell was then intersected ("clipped") with the island land polygon to remove any ocean portion, and we summed the on-land area to obtain the effective surveyed land area $A_{s,eff}$ (km²) (Figure 2). This step was essential for narrow or convoluted shorelines (e.g., Maratua), where nominal 1-km cells extend substantially over water. Effective surveyed land areas were: Simeulue = 329.38 km², Lasia 10.10 km², Karimunjawa 27.94 km² and Maratua 18.66 km². We report $A_{s,eff}$ rather than nominal grid extents to avoid overestimating survey effort.

The use of 1 × 1 km grid cells (~100 ha) was intended to facilitate systematic data collection across large island landscapes and corresponds well with the estimated home range size of long-tailed macaques. Reported home ranges vary widely depending on habitat type, provisioning, and landscape complexity—from approximately 10 ha in provisioned groups to 250 ha in non-provisioned populations (Sha et al. 2009; Zinner et al. 2013; Hansen et al. 2020). Given this variation, the chosen grid resolution is appropriate for capturing at least one troop's home range in most cases, allowing for localized assessments of group presence and abundance. A similar grid-based approach has been applied in other Indonesian primate surveys, such as Sodik et al. (2019) for Javan slow lorises (*Nycticebus javanicus* É.Geoffroy Saint-Hilaire, 1812).

Grid locations were selected non-randomly using three inputs. These were (i) availability of suitable macaque habitat (Fooden 1995); (ii) prior sightings reported in technical implementation unit (UPT) documents (e.g., Karimunjawa National Park, the Natural Resources Conservation Agencies (BKSDA) of Aceh and East Kalimantan, and the Environment and Forestry Service (DLHK) in Aceh; and (iii) personal communication with UPT officers, local communities, and partner organizations. These sources were used solely to guide survey design and grid placement, ensuring that areas with a higher likelihood of macaque presence were covered efficiently given field constraints. Importantly, these prior reports were not included in the dataset or analyses; all results presented in this study derive exclusively from our own standardized field observations. All surveys were conducted along existing roads, tracks and coastlines due to the limited time available for rapid island assessments. Some of these linear features traverse interior forest, but we did not establish any off-road transects away from them. Thus, all detections are associated with accessible linear features, and the design is purposive rather than random, yielding upper-bound density indices that reflect detectability along access routes rather than unbiased population estimates.

Observations were conducted from 05:00 to 12:00 and from 14:00 to 18:00 using the concentrated count method (Santosa et al. 2012; Santosa et al. 2020), which involves 30-minute point counts at locations where macaques are known to gather—such as feeding trees, water sources, and trails. For each encounter, we recorded Global Positioning System (GPS) coordinates, group size, and age-sex class (adult male, adult female, pre-adult male, juvenile, or infant; Table 1), along with environmental descriptors such as habitat type, primary food sources, and visible threats. Threats were documented opportunistically when directly observed during surveys and included signs such as traps, snares, macaques kept as pets, evidence of poisoning, or crop-raiding damage in fields adjacent to observation sites. On each island, surveys were led by a single author (Itang), assisted by YIARI staff and local guides. The lead observer has worked with long-tailed macaques for over eight years and is highly experienced in applying standard classification criteria with confidence. All group size and age-sex classifications were recorded consistently by the same observer to ensure standardisation across sites. As only one primary observer was responsible for each survey, formal interobserver reliability testing was not applicable.

Survey effort was quantified using the total length of survey tracks walked (km), as observer-hours were not recorded during rapid island surveys. GPS tracks were intersected with the 1 × 1 km grid in QGIS (version 3.28.12), and the length of track within each grid cell was calculated using projected coordinates. Track lengths were summed to obtain kilometres walked per grid and per island.

To account for variation in survey effort, grid-level encounter rates were standardised as the number of individuals observed per kilometre walked by dividing summed individual counts per grid by the corresponding track length. These effort-standardised encounter rates are presented as descriptive indices to illustrate heterogeneity in encounters among grids and were not used to derive density estimates or to correct for imperfect detection.

Habitats were classified in situ at the moment of each encounter using field cues (dominant vegetation/land use, canopy structure, proximity to shoreline/settlements). For reporting, we used six categories: (i) Plantations (including agroforestry/mixed gardens), (ii) secondary forest, (iii) coastal/beach forest, (iv) mangrove, (v) rice fields, and (vi) settlements. For each encounter, the lead observer assigned a single habitat label indicating where the group was located when detected; this was a qualitative, point-of-encounter assignment. All assignments were made by the same observer for cross-island consistency.

To complement ecological data, we conducted 46 semi-structured interviews with UPT officers, farmers, village leaders, and tourism stakeholders across the four islands (Karimunjawa n = 11; Maratua n = 18; Simeulue/Lasia n = 17). Participants were selected using random-intercept sampling during field surveys, with a simple quota to ensure a mix of local residents and local authorities. Interviews are conducted in Indonesian and typically lasting 5-15 minutes. Prior to each interview, participants were informed of the study purpose, assured that participation was voluntary and anonymous, and provided verbal informed consent. No personal identifiers or sensitive information were collected, and responses were recorded as field notes only; therefore, formal human-subjects ethics approval was not required under institutional guidelines.

Interviews followed an eight-prompt guide in fixed order: (i) awareness that the island is macaque habitat, (ii) personal sightings and typical locations, (iii) experience of interactions and types, (iv) actions taken in response, (v) feeding of macaques, (vi) awareness that feeding is prohibited, (vii) feasible coexistence measures, and (viii) preferred outreach/education media. Items on perceptions/responses and proposed solutions were open-ended and unprompted (free-list); interviewers did not provide options, and multiple responses were allowed. For the outreach/education media question only, interviewers offered non-exhaustive examples (e.g., signage, videos) to clarify the prompt. Responses were coded into standard categories (negative interactions, perceptions/responses, proposed solutions, educational needs) and converted to binary variables (yes/no). Frequencies were compared among islands using χ^2 tests, with statistical significance set at $\alpha = 0.05$.

Wildlife survey activities were conducted under research permission issued by the Directorate of Biodiversity Conservation, Ministry of Environment and Forestry, Indonesia (Number: S.286/KKHSG/PSG2/ KSA.2/05/2022, issued 24 May 2022), which authorised the rapid survey of long-tailed macaques and associated field activities.

Data analysis

We used the kernel density estimation tool in QGIS to create heatmaps illustrating macaque distribution across the four islands. Individual sightings were weighted by group size, with zero counts included to represent absence. The smoothing radius was set to 630 m for Lasia, Maratua, and Karimunjawa. For Simeulue, a broader 4,000 m radius was used to enhance visual clarity across the island's larger landscape.

Table 1. Age-sex class criteria for *Macaca fascicularis*. Adapted from Brotcorne (2014) and van Schaik et al. (1983). The table summarizes the age-sex classes of long-tailed macaques, incorporating distinguishing features related to age, sex, morphology, sexual traits, and behavioral characteristics

Criteria	Adult male	Adult female	Pre-adult male	Juvenile	Infant
Age	>6 years	>3.5 years	4-6 years	1-4 years	0-1 year
Sex	Male	Female	Male	Unidentified	Unidentified
Morphology	Largest body size; moustache and whiskers	Smaller than subadult males; beard and elongated nipples	80% of adult male size, bigger than adult females	Smaller than (sub)adults; adult coat color	Black infant (0-5 months): black natal coat; old infant (5-12 months): gray/brown coat
Sexual characteristics	Full scrotum development and canine eruption	Red coloration of anogenital region (non-permanent)	Not full scrotum development and canine eruption	-	-
Behavior	-	-	-	Weaned and independently mobile	Not weaned, often carried by the mother

We calculated population densities (D) as:

$D = \sum n / A_{s,eff}$

Where $\sum$n is the total number of macaques observed and $A_{s,eff}$ is the effective surveyed land area (in km²). Densities were calculated as raw counts divided by the effective surveyed land area and were not corrected for imperfect detection; therefore, values should be interpreted as unadjusted indices rather than true densities. Abundance (A) was then extrapolated to the total land area (A_t) of each island using:

$A = D \times A_t$

To account for spatial variation, individual grid cells (1 × 1 km) were also treated as sampling units. For each grid i, density (d_i) was calculated as:

$d_i = count_i / area_i$

Where $count_i$ is the total number of macaques observed and $area_i$ is the on-land portion of that grid (km²), with zeros assigned for non-detections. These grid-level densities were used to assess among-island differences using a Kruskal-Wallis test. Where significant, pairwise comparisons were performed with Mann-Whitney U tests and Holm-adjusted *p*-values ($\alpha = 0.05$). Statistical analyses were conducted in IBM SPSS Statistics v22 and R v4.x.

To quantify the uncertainty of these density estimates, we also derived 95% confidence intervals (CIs) using a nonparametric, grid-level bootstrap that captures spatial heterogeneity. For each island, we assembled a vector of counts for all surveyed grids, including zeros for non-detections, and resampled grids with replacement (10,000 iterations), recomputing density at each draw by dividing the resampled total count ($\sum$n) by the fixed $A_{s,eff}$. The 2.5th and 97.5th percentiles of the bootstrap distribution defined the 95% CI for density. Bootstrap and CI calculations were implemented in R (v4.x; percentile method, 10,000 iterations). Abundance CIs were obtained by multiplying the density bounds by A_t. These bootstrap confidence intervals reflect variability among surveyed grid cells and do not account for imperfect detection or other sources of observation error. Given the generalist ecology of long-tailed macaques and low human density on all four islands, we assumed all 1-km² land grids were potentially suitable; no habitat mask was applied. Spatial dependence in grid-level density indices was assessed within islands using Moran's I. No significant spatial autocorrelation was detected for islands with sufficient grid numbers to support testing (e.g., Karimunjawa: Moran's I = 0.016, p = 0.32; Simeulue: Moran's I = −0.005, p = 0.54).

This approach provides rapid island-wide estimates while explicitly reflecting between-grid variation. Nevertheless, because grid placement was habitat-informed (non-random) and detectability may vary with habitat, access, or time of day, extrapolations may be biased upward and the CIs reflect sampling variability within surveyed grids rather than imperfect detection. Results should therefore be interpreted cautiously as upper-bound indices (e.g., in Simeulue, only ~21% of the land area was surveyed; see Table 3) and used to guide prioritization and the design of future, more rigorous monitoring, ideally using randomized or stratified sampling frameworks and detection-based methods (e.g., distance sampling or occupancy modelling) to reduce potential bias and improve precision.

RESULTS AND DISCUSSION

Island occurrence and group composition

The population surveys confirmed the presence of *M. f. fusca, M. f. lasiae, M. f. tua*, and *M. f. karimondjawae* on the islands of Simeulue, Lasia, Maratua, and Karimunjawa, respectively (Figure 2). Adult male photographs illustrate distinguishing field-visible traits among islands (Figure 3). In total, we recorded 51 groups comprising 597 individuals across all age-sex classes (Table 2). Group encounters were predominantly concentrated in edge habitats, areas where natural forest borders beaches, plantations, community gardens, and settlements. Across islands, mean group size ranged from 8.6 on Lasia to 13.5 on Maratua. Adult males per group averaged 1.6 (Simeulue), 1.2 (Lasia), 1.0 (Karimunjawa), and 2.2 (Maratua), while adult females averaged 4.3, 2.0, 2.0, and 3.2, respectively. Juveniles were consistently numerous (4-5 per group) and infants were few (0.5-0.7 per group). Maratua (*M. f. tua*) groups were the largest and male-heavier; Lasia (*M. f. lasiae*) groups were the smallest.

Survey effort, population density, and spatial heterogeneity

Survey effort, encounter rates, and density estimates varied markedly among islands (Table 3). On Simeulue, surveys covered 416 grid cells (21% of land area; A_s,eff = 329.38 km²) with 354.1 km walked, yielding 259 individuals and the lowest island-level encounter rate (0.81 individuals km^{-1}). Encounter rates were substantially higher on the smaller islands, reaching 2.43 individuals km^{-1} on Lasia (17.7 km walked; 43 individuals), 3.27 individuals km^{-1} on Karimunjawa (36.4 km; 119 individuals), and 4.58 individuals km^{-1} on Maratua (28.4 km; 176 individuals). Corresponding density indices ranged from 0.79 individuals km^{-2} on Simeulue to 9.43 individuals km^{-2} on Maratua, with intermediate values on Lasia and Karimunjawa (Figure 4). Collectively, these estimates yielded an extrapolated abundance of 1,906 individuals across all islands. However, because survey coverage differed among islands and was concentrated in accessible, high-suitability areas, these density and abundance values should be interpreted as upper-bound approximations rather than precise population estimates.

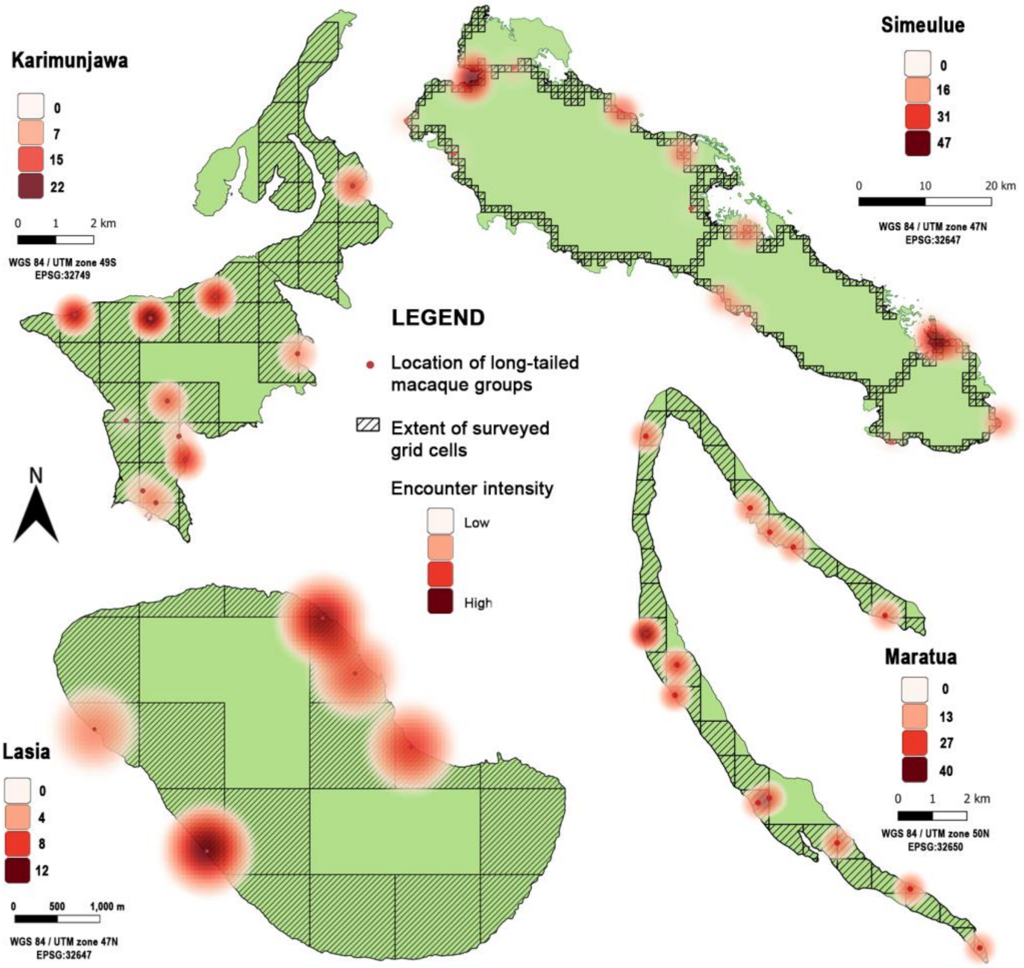

Figure 2. Surveyed areas and macaque encounter density across four Indonesian islands. Outlines show island boundaries and surveyed 1-km² grid extents; points indicate macaque encounter locations, and heatmaps depict relative encounter intensity from high to low numbers of individuals. Kernel density surfaces were generated using Gaussian kernels with a smoothing radius of 630 m for Lasia, Maratua, and Karimunjawa, and 4,000 m for Simeulue, with a 50-m pixel resolution

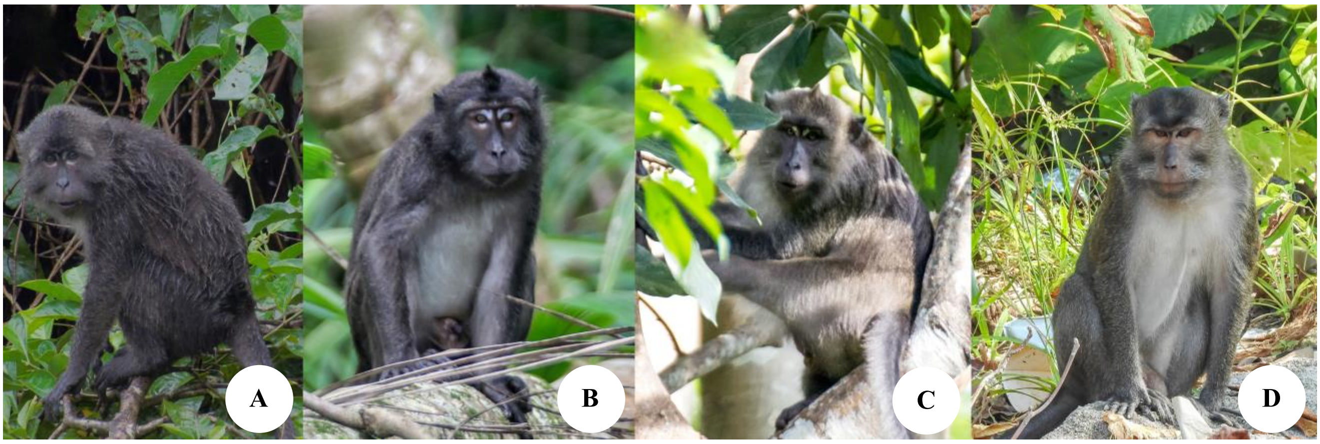

Figure 3. Morphology of adult male long-tailed macaque subspecies. A. Simeulue (*Macaca fascicularis fusca*) — very dark pelage, thick cheek/brow hair, no visible crest, B. Lasia (*Macaca fascicularis lasiae*) — dark pelage with faint whitish periocular markings, short dark crown crest, C. Maratua (*Macaca fascicularis tua*) — dark-gray pelage with paler inner hair, short crown crest and relatively elongated ears, D. Karimunjawa (*Macaca fascicularis karimondjawae*) — brown-gray pelage with lighter "moustache" cheek hair and a blackish crown "cap". These characteristics are field-based, provisional observations by the survey team, and some features may not be clearly visible in the photographs due to lighting, angle, or posture

Across islands, detections were unevenly distributed among surveyed grid cells, indicating strong spatial heterogeneity. Macaques were detected in only 5% of surveyed grids on Simeulue, compared with approximately 21-26% on Lasia, Karimunjawa, and Maratua. Grid-level encounter rates standardised by distance were strongly zero-inflated, particularly on Simeulue, where most grids recorded no detections despite survey effort. Among grids with detections, group sizes were highly variable, ranging from 4-25 individuals on Simeulue, 5-12 on Lasia, 1-22 on Karimunjawa, and 4-40 on Maratua. This patchy distribution, combined with higher encounter rates on smaller islands, indicates that macaques were concentrated in a limited number of accessible, high-suitability locations rather than being evenly distributed across the landscape. Grid-level encounter rates are therefore presented as descriptive indices to illustrate heterogeneity and were not used to derive density estimates.

Per-grid densities differed significantly among islands (Kruskal-Wallis H = 36.52, $p = 5.8 \times 10^{-8}$). Pairwise comparisons showed that Simeulue had significantly lower densities than Maratua (Holm-adjusted p = 0.000002), Karimunjawa (p = 0.000077), and Lasia (p = 0.0099). Densities did not differ significantly among Maratua, Karimunjawa, and Lasia (all Holm-adjusted $p \geq 0.87$).

Habitat distribution and use of anthropogenic food resources

Across sites, detections were concentrated in human-modified habitats (Table 4). Simeulue was dominated by plantations (including agroforestry) with additional encounters in secondary and coastal forest. Lasia detections were overwhelmingly coastal, with some in plantations (e.g., coconut groves), consistent with boat-based coastal coverage. Karimunjawa showed a mixed edge pattern spanning coastal forest, plantations, settlements, and mangroves. Maratua detections were split mainly between plantations and secondary forest, with fewer in coastal forest. These summaries reflect where encounters occurred along our routes, not unbiased habitat use.

Direct observations revealed that macaques from all four subspecies frequently exploited anthropogenic food sources. On Simeulue and Lasia, individuals were seen consuming kedondong fruit (*Spondias dulcis*), areca nut (*Areca catechu*), banana (*Musa* spp.), and coconut. A group on Simeulue was observed feeding on waste products from a coconut oil factory. Coconut plantations also served as key foraging areas on Maratua and Karimunjawa. In several instances, macaques were observed scavenging at garbage collection points and along roads. On Karimunjawa, *M. f. karimondjawae* was seen feeding on cashew (*Anacardium occidentale*), tamarind (*Tamarindus indica*), sea pandanus (*Pandanus odorifer*), Chinese pete (*Leucaena leucocephala*), and guava (*Syzygium aqueum*).

Table 2. Long-tailed macaque group and individual counts on four Indonesian Islands. This table presents the subspecies recorded on each island, along with the number of observed groups and individuals in Simeulue, Lasia, Maratua, and Karimunjawa. Individual counts are categorized by five age-sex classes: adult males (AM), adult females (AF), pre-adult males (pre-AM), juveniles, and infants

Site	Subspecies	Number of groups	Number of individuals					
			Total	AM	AF	Pre-AM	Juvenile	Infant
Simeulue	*Macaca fascicularis fusca*	22	259	36	95	25	88	15
Lasia	*Macaca fascicularis lasiae*	5	43	6	10	1	24	2
Karimunjawa	*Macaca fascicularis karimondjawae*	11	119	11	22	21	57	8
Maratua	*Macaca fascicularis tua*	13	176*	29	41	19	65	9

Note: *: The age-sex class of 11 individuals could not be determined

Table 3. Survey effort, detections, and population estimates for four endemic long-tailed macaque subspecies

Subspecies	Total grids (N^{tot})	Grids surveyed N (%)	$A_{s,eff}$ (km^2)*	Grids with macaques N (%)	Density (individuals km^{-22}), mean (95% CI)	Abundance (individuals), mean (95% CI)
Macaca fascicularis fusca	2,012	416 (21%)	329.38	22 (5%)	0.79 (0.44-1.16)	1,450 (811-2,139)
Macaca fascicularis lasiae	23	18 (78 %)	10.10	4 (22%)	4.26 (0.79-8.81)	64 (12-132)
Macaca fascicularis karimondjawae	69	42 (61%)	27.94	11 (26%)	4.26 (1.79-7.08)	175 (73-290)
Macaca fascicularis tua	59	42 (71%)	18.66	10 (24%)	9.43 (4.17-15.84)	217 (96-364)

Note: Total grids (N^{tot}) = total 1-km^2 grid cells per island; Surveyed grids (N) = number of visited cells; % grids surveyed = 100 × N /N^{tot}; $A_{s,eff}$ (km^2) = effective surveyed land area; Grids with macaques (n, %) = number (and percent) of surveyed grids with detections; Density = individuals per km^2 of land; Abundance = density × total terrestrial island area (A_t). 95% CIs are 10,000-sample percentile bootstrap. Confidence intervals reflect within-surveyed-grid variability derived from grid-level bootstrap resampling and do not incorporate detection uncertainty. *$A_{s,eff}$ is the sum of on-land area within visited 1-km cells (island polygon-clipped) to prevent inflation from ocean area on narrow islands

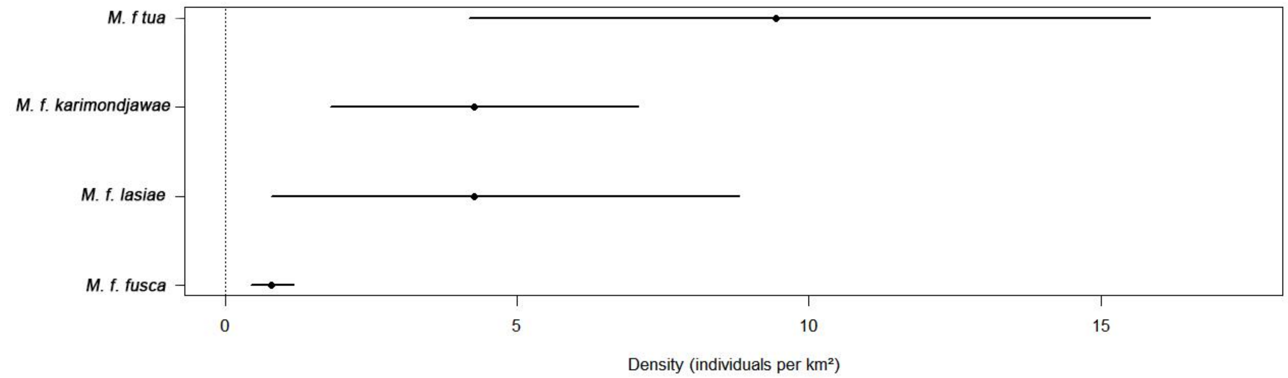

Figure 4. Comparison of island-level density estimates (individuals per km²) for four endemic long-tailed macaque subspecies. Points indicate mean density estimates; horizontal bars show 95% confidence intervals derived from grid-level nonparametric bootstrap resampling (10,000 iterations). Confidence intervals reflect within-surveyed-grid variability and do not incorporate detection uncertainty

Table 4. Encounter-based habitat associations by island and subspecies—percentage of individuals detected in each habitat category (counts in brackets). Zeros indicate no detections in that habitat during surveys. Habitats present but with no detections are noted in the text

Site	Plantations % (n)	Secondary forest % (n)	Coastal forest % (n)	Mangrove % (n)	Rice fields % (n)	Settlements % (n)	Total (n)
Simeulue	70% (182)	12% (31)	15% (39)	0% (0)	3% (7)	0% (0)	259
Lasia	16% (7)	0% (0)	84% (36)	0% (0)	0% (0)	0% (0)	43
Karimunjawa	37% (44)	1% (1)	38% (45)	10% (12)	0% (0)	14% (17)	119
Maratua	55% (96)	27% (48)	18% (32)	0% (0)	0% (0)	0% (0)	176

Table 5. Summary of semi-structured interview findings (n = 46) grouped into three themes—negative interactions, perceptions and responses, and proposed solutions and educational needs. Values show counts and percent of respondents; multiple responses allowed

Theme	Item	n	%	Notes
Negative interactions	Crop raiding	21	46	Plantations and rice fields
	Entering homes/shops	4	9	
Perceptions and responses	Actively drove animals away	17	37	Chasing/scaring tactics (e.g., noise, dogs, stones)
	Ignored / no action	4	9	Tolerated or did nothing
	Traps / capture	3	7	Some reports of infants later kept as pets
Proposed solutions and educational needs	Leave as is / passive stance	16	35	Preference to maintain status quo
	Protect natural habitat	9	20	Reduce conflict via habitat protection
	Direct education / awareness materials	18	39	Posters/briefings; island breakdown: Simeulue+Lasia 17, Maratua 1
	Install signage to discourage feeding	11	24	Karimunjawa 4; Maratua 7
	Ecotourism initiatives	2	4	Reported from Maratua
	School-based outreach	1	2	Reported from Maratua

Community perceptions and human-macaque interactions

We conducted 46 semi-structured interviews with community members, farmers, village leaders, entrepreneurs, and UPT officers across four islands. All respondents were aware of macaque presence and reported personal or community-level experiences. Key coded results are summarized in Table 5. In brief, crop raiding was the most frequently reported problem, active deterrence the most common response, and education/signage the most requested interventions.

Across the three islands, the frequency of reported negative interactions differed significantly ($\chi^2 = 6.74$, $p = 0.034$). Negative encounters—such as crop raiding, property damage, and intrusion into settlements—were most frequently reported on Karimunjawa (82% of respondents), followed by Maratua (72%) and Simeulue-Lasia (53%). Active deterrence or control behaviours (e.g., chasing, noise use, or trapping) were also common and varied among islands ($\chi^2 = 8.29$, $p = 0.016$), highest on Karimunjawa (82%) and lowest on Simeulue-Lasia (41%). These patterns suggest differing intensities of human-macaque conflict and response across sites, reflecting variation in both macaque abundance and human land-use context.

Discussion

This study provides the first field-based baseline collected with the same rapid protocol across four previously under-surveyed subspecies of long-tailed macaques—*M. f. fusca*, *M. f. lasiae*, *M. f. tua*, and *M. f. karimondjawae*—from Simeulue, Lasia, Maratua, and Karimunjawa islands, respectively. We confirmed the continued presence of all four subspecies and recorded 597 individuals in 51 groups. Estimated population densities ranged from 0.79 to 9.43 individuals km^{-2}. However, given that survey coverage was limited and targeted toward suitable habitats (e.g., ~21% of Simeulue), these extrapolated densities likely represent upper-limit estimates and should be interpreted with caution, with island-level encounter rates used only as descriptive indices of relative detectability and clustering. Our density estimates are uncorrected for detection probability, as the rapid survey design precluded the use of distance sampling or other detection-based methods. Imperfect detection is likely, particularly in dense vegetation where macaques may be missed at greater distances. As a result, our values should be viewed as upper-bound indices rather than true densities. Future surveys could incorporate distance sampling, double-observer methods, or occupancy modelling to account for detection probability and provide more robust population estimates.

All transects followed existing roads, tracks, or coastal paths, restricting detections to accessible areas rather than randomly sampled habitat. This may inflate density estimates if macaques preferentially use these linear features or if detectability is higher along them. Accordingly, the density values presented here are best viewed as relative, upper-limit indices for comparing islands, underscoring the need for repeated surveys using randomized or stratified sampling designs to produce more accurate population baselines.

In context, these densities are low relative to published figures for long-tailed macaques and comparable insular macaques. For example, a nationwide census in Singapore reported a mean of 6.86 individuals km^{-2} across areas with macaques (range 0.89-33.63), already above three of our four island means (Riley et al. 2015). By contrast, the semi-natural breeding population on Tinjil Island reaches about 111 individuals km^{-2}, illustrating the potential for very high densities under atypical conditions (Perwitasari-Farajallah et al. 2023). Recent studies on Deli Island off Java (Fitriana et al. 2024) and on small islands off southern Sumatra, including Enggano and Legundi (Hasibuan et al. 2025), have reported relatively low densities of *M. fascicularis*—ranging from approximately 2-8 individuals km^{-2}—consistent with our findings for the four study islands. For other small-island macaques, *Macaca siberu* on Siberut has been estimated at ~16.2 individuals km^{-2} in primary forest, while *Macaca pagensis* on the Pagai Islands has ~7-12 individuals km^{-2} in suitable habitat, both above most of our values (Whittaker 2006; Waltert et al. 2008).

Densities also differed significantly among our four islands. Simeulue supported consistently lower grid-level densities than the other sites ($H = 36.52$, $p<0.001$), whereas Maratua, Karimunjawa, and Lasia showed broadly comparable values. Even under conservative sampling conditions, the contrast for Simeulue was pronounced, indicating substantial depletion relative to the others and matching the historical context of decline discussed below.

These density estimates, though variable across islands, align with a broader pattern of decline observed in long-tailed macaque populations throughout Southeast Asia. Across the region, formerly abundant populations are diminishing due to habitat conversion, human-wildlife conflict, culling, and commercial exploitation for research and trade (Gumert et al. 2011; Hansen et al. 2022). Comparable declines have been reported across the species' range, including an estimated 70% reduction in Lao PDR over the past decade (Gamalo et al. 2023), a 50% decline in parts of Cambodia between 2010 and 2020 (Nuttall et al. 2022), and local extirpations documented in Vietnam (Hoàng et al. 2019) and Bangladesh (Hasan and Feeroz 2010).

Simeulue provides the only clear temporal reference within our study area. Line-transect surveys in 1982-1984 recorded habitat-specific densities (about 1-1.5 monkeys/ha in alluvial/limestone forest and 0.5-0.7 in hills) and, using standard methods, extrapolated—based on coarse habitat-area assumptions—to a conservative island total of ~50,000 monkeys (Sugardjito et al. 1989). Our current abundance estimate (~1,450; 95% CI 811-2,139) and low island-wide density (0.79 individuals km^{-2}) are substantially lower than those historical indications. Because the 1989 island total depended on approximate habitat extents and our own design targeted accessible, high-suitability areas, we do not assert a precise percent decline. Instead, we interpret present densities as low relative to historically reported levels and consistent with concern under IUCN A2, and we prioritize a standardized resurvey using comparable methods to quantify trend.

While this study provides only a single temporal snapshot, it establishes another critical reference point for assessing long-term population change. Historical data from Simeulue (Sugardjito et al. 1989) already suggest a major decline over four decades, but published temporal data for the other islands remain scarce. Sustained and coordinated monitoring is therefore essential to evaluate population health, viability, and management effectiveness. Future efforts should build on this baseline while addressing current methodological limitations through randomized or stratified sampling and detection-aware approaches (e.g. distance sampling or occupancy modelling) to improve precision and comparability. Beyond density, long-term monitoring should incorporate demographic and health indicators (e.g. age-sex ratios, recruitment, and visible disease signs) and quantify human-macaque interaction intensity. Integrating these biological and socio-ecological indicators would enable assessment of both demographic trend and population resilience, providing the longitudinal evidence needed to inform conservation status reassessments and guide management responses proactively rather than reactively.

Macaque encounters were concentrated in human-modified landscapes—forest edges, plantations, and coastal settlements—where anthropogenic food sources were frequently used (Figure 4, Table 4). Comparable patterns of edge reliance and anthropogenic resource use have been documented for long-tailed macaques in other parts of Southeast Asia. In Sumatra, Bali and Thailand, macaques frequently exploit human-provisioned food sources in temples, tourist areas, and agricultural fringes, leading to elevated conflict and disease-transmission risks (Malaivijitnond and Hamada 2008; Fuentes 2011; Ilham et al. 2017; Hasibuan et al. 2025). In Indonesia, spatial analyses of human-macaque conflict reveal similar concentration patterns around settlements and plantation boundaries (Rifaie et al. 2024), reinforcing that edge-associated interactions are a key driver of negative outcomes across the species' range.

Patterns of human interaction mirrored these ecological differences. Interview data revealed frequent negative encounters: 46% of respondents reported crop damage, 37% reported deterrence actions, and 7% reported trapping or capture (Table 5). These rates differed significantly among islands ($\chi^2 = 6.74$, $p<0.05$), as did control behaviors ($\chi^2 = 8.29$, $p<0.05$). The two islands with the highest macaque densities—Maratua and Karimunjawa—also reported the most frequent conflict responses, while Simeulue-Lasia showed both the lowest densities and least conflict. Direct observations of feeding and garbage foraging further confirm regular contact at human-modified edges. Practical measures favored by respondents included education and awareness activities (39%), feeding-prohibition signage (24%), and improved waste management. Similar behavioral plasticity has prompted management programs in Singapore focused on food-waste control, feeding bans, and public education (Riley et al. 2015). Adopting comparable coexistence strategies—tailored to local conditions—would align with proven approaches elsewhere while addressing the compounded vulnerability of these small, isolated island populations.

Taken together with the low densities and small group sizes reported above, these observations suggest potential demographic decline—most clearly for *M. f. fusca*, whose current densities are markedly below historical estimates. This decline likely reflects interacting pressures of habitat loss, direct persecution, and the demographic consequences of small, isolated populations, which may be susceptible to inbreeding and genetic drift. Likewise, the extremely low group counts of *M. f. lasiae*, *M. f. tua*, and *M. f. karimondjawae* affirm their classification under IUCN Criterion D. These findings highlight the continued vulnerability of these taxa and the importance of targeted conservation action.

Although this study did not directly measure ecosystem services, long-tailed macaques are known seed dispersers (Lucas and Corlett 1998; Gumert and Malaivijitnond 2012) and may play a disproportionately important ecological role on islands with reduced frugivore guilds. Their observed presence in mangrove zones and agricultural mosaics may indirectly support coastal stability and forest regeneration. Given that some study sites, such as Karimunjawa, have lost significant portions of primary forest, the persistence of macaque-mediated seed dispersal could be critical for maintaining secondary forest dynamics. However, definitive claims regarding roles in flood mitigation or ecosystem function remain speculative in our context and require further empirical investigation. Future research integrating dietary analysis, seed germination trials, and spatial movement tracking could clarify the extent of their ecological contributions.

Given the low densities (Table 3), edge-associated encounters (Figure 2), and interview evidence of conflict (Table 5), immediate priorities for relevant authorities include (i) reducing anthropogenic attractants at settlement/plantation edges (e.g., waste management, feeding-ban signage) and (ii) safeguarding key edge mosaics through existing land-use planning instruments. Where applicable, these actions can be supported under existing subnational mandates concerning forest rehabilitation and protection (e.g., Law No. 23/2014). These points are offered as implementation context grounded in our findings rather than prescriptive policy.

The conservation implications of our findings are significant. Our results support the current Critically Endangered status of *M. f. lasiae*, *M. f. tua*, and *M. f. karimondjawae* under IUCN Red List Criterion D, due to their extremely small and isolated populations (IUCN 2024). For *M. f. fusca*, our data indicate very low current densities relative to historical reports and are consistent with a Criterion A2 decline, noting that earlier figures were habitat-area extrapolations and are not directly comparable to our density-based estimates. Together with its restricted distribution on Simeulue—an area prone to natural disasters and ongoing habitat degradation—this suggests heightened vulnerability to demographic and environmental stochasticity, underscoring the need for targeted management and structured monitoring. Continued monitoring and updated population assessments remain essential to guide conservation priorities.

Although the species is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)—which regulates cross-border trade via export permits and non-detriment findings—and is assessed as Endangered on the IUCN Red List of Threatened Species, *M. fascicularis* is not currently designated as a protected species under Indonesia's national protected-species regulation (Permen LHK P.106/2018). Of the four study islands, only Karimunjawa benefits from a formal conservation designation as a national park, offering some habitat protection. However, since *M. fascicularis* itself is not legally protected, enforcement remains limited even there—representing a case of partial protection (area protected, species unprotected). In contrast, Simeulue, Lasia, and Maratua lack any conservation area status, leaving both the species and its habitats exposed to exploitation and degradation. Our study did not evaluate policy mechanisms; however, the combination of low densities and reported conflict suggests enforcement capacity and funding priorities merit review by relevant authorities. We note this as a management implication rather than a prescriptive recommendation.

Implications for conservation and management

The results highlight distinct island-specific conservation priorities. On Simeulue, very low densities relative to historical reports indicate a need for urgent population monitoring and protection of remaining forest-plantation mosaics, alongside conflict mitigation in agricultural areas. On Lasia, the extremely small population and limited habitat extent emphasize the importance of preventing further habitat loss and minimizing disturbance in remaining coastal and plantation-edge habitats. On Maratua and Karimunjawa, higher densities combined with frequent human-macaque interactions point to coexistence-focused management, including feeding prohibition, waste management, and community outreach at settlement and tourism interfaces. Across all islands, structured monitoring using detection-aware methods and integration of macaque management into local land-use planning are needed to prevent further population decline.

In conclusion, this study provides the first field-based baseline collected with the same rapid protocol for four island-endemic subspecies in Indonesia, confirming their continued presence while documenting low, spatially clustered density indices and frequent associations with human-modified edge habitats. Despite their synanthropic tendencies, all four subspecies appear vulnerable to ongoing habitat degradation, isolation, and recurrent negative human-macaque interactions, given their small population sizes and restricted ranges. Based on these findings, we suggest that conservation efforts could benefit from prioritising the retention of remaining forest-mangrove-agroforestry mosaics through existing district and provincial spatial-planning frameworks (e.g., Law No. 23/2014), including the use of recognised subnational mechanisms such as *Hutan Desa* and *Areal Preservasi* where locally appropriate. Although long-tailed macaques are not currently protected under Indonesia's national wildlife regulation (Permen LHK P.106/2018), interim safeguards may be considered through provincial *Satwa Dilindungi Daerah* regulations and village-level initiatives such as *Desa Ramah Satwa*, alongside measures to reduce anthropogenic attractants and conflict at forest-settlement interfaces (e.g., waste management, feeding prohibition, and community-based education). Finally, we suggest that structured population monitoring using stratified or randomised designs and detection-aware methods would be valuable for generating more robust population trends and informing future conservation planning for these highly vulnerable island populations.

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