Socioeconomic policy and large mature trees are vital for moor macaque (*Macaca maura*) conservation in anthropogenically-modified landscapes

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Abstract

Despite conservation efforts, intensifying anthropogenic pressure is transforming tropical forests into anthropogenically-dominated landscapes. We investigated how current anthropogenic pressure and socioeconomic-climate policies influence tropical forest ecology, using the Endangered moor macaque (*Macaca maura*) in southwestern Sulawesi, Indonesia, as an example species. Deploying camera traps and acoustic recording units across 226 locations, we applied single-season occupancy models to assess the joint impacts of natural and anthropogenic factors on macaque occurrence. We then projected occupancy under three socioeconomic-climate scenarios (SSP-RCP) for 2050, 2075, and 2100. Although deforestation and Human Footprint Index reduced occupancy, the interaction between large mature trees (>30m tall) and forest edge density was the strongest predictor of species occupancy. This highlights that tall canopy structures can mitigate the negative impacts of forest fragmentation. Across all scenarios, the species' distribution declined by at least 34% by 2050 due to agricultural expansion. Declines were most severe under high social inequality scenarios, emphasizing the critical role of socioeconomic equity for species conservation under high anthropogenic pressure. Our findings demonstrate that conserving and restoring high-quality forests is essential for moor macaque conservation, but an urgent reevaluation of their IUCN Red List assessment is needed due to the current and projected population isolation. Ultimately, long-term conservation success requires governance frameworks that integrate climate mitigation with socioeconomic equity to address deforestation drivers. This approach offers a replicable pathway for identifying conservation strategies for other species facing severe anthropogenic pressures.

Keywords:
Conservation policy; forest structure; land-use change; monitoring; socioeconomic pathways; tropical forests

Introduction

Anthropogenic activities have modified at least 75% of Earth's terrestrial ecosystems (IPBES et al., 2019), leading to the sixth mass extinction (Ceballos et al., 2020). In response, COP15 adopted the Kunming-Montreal Global Biodiversity Framework (GBF), a set of 23 targets to be achieved by 2030 and four long-term goals by 2050 (CBD, 2022). The GBF emphasizes the need for the restoration of 30% of degraded ecosystems (Target 2) and the protection of at least 30% of natural areas (Target 3), as critical steps toward halting the extinction crisis. However, the COP17 report identified the lack of standardized monitoring protocols and insufficient financial resources as primary obstacles to meeting the GBF targets (Affinito et al., 2025). These challenges are especially acute in Africa and Asia, where over 83% of tropical forests remain unprotected (UNEP-WCMC & IUCN, 2026). As human populations and infrastructure expand, anthropogenic factors have become the dominant drivers of wildlife ecology in tropical regions, often overriding the influence of natural ecological factors (Finn et al., 2023; Lewis & Maslin, 2015; Vanthomme et al., 2013). There is thus an urgent need to understand how anthropogenic pressures shape the population dynamics of key tropical species and to apply this knowledge to predict future population trends. Such insights are essential for designing science-based conservation strategies that directly inform and track progress toward GBF goals.

The interplay of natural factors and anthropogenic pressure

Deforestation remains the primary driver of anthropogenic tropical forest modification (Potapov et al., 2017), driven predominantly by agricultural expansion, urbanization, and industrial forestry (Hoang & Kanemoto, 2021; Pendrill et al., 2019; Torres-Romero et al., 2023). These activities fundamentally compromise forest availability, structural quality, and connectivity (Almeida-Rocha et al., 2017; Wiebe & Wilcove, 2025). In densely populated tropical regions, however, anthropogenic impact extends far beyond direct deforestation. Persistent human activity within forests increases the level of anthropogenic disturbance (i.e., the cumulative ecological pressure on forests resulting from human activities), degrading habitat quality and altering ecosystem functions (Albuquerque et al., 2018). This degradation is derived primarily from two processes: increased mortality risk due to human presence (Gaynor et al., 2019), and decreased availability of resources (Feurer et al., 2025). If sustained, such disturbance can drive species to relocate and potentially contract their geographic distribution to less disturbed areas (Farris et al., 2014; Hu et al., 2025). Climate change, driven primarily by industrialization (Hansen et al., 2006), can further amplify these anthropogenic pressures, for instance, by increasing wildfire frequency in degraded forests (Bowman et al., 2020; Brodie et al., 2012).

Crucially, the ultimate impact of these combined anthropogenic pressures on wildlife is not uniform, as it is mediated by the interplay between species ecology and environmental factors (Keck et al., 2025; Newbold et al., 2015). In fragmented landscapes, for example, terrestrial and arboreal species can become isolated due to limited dispersal patterns. This restricts gene flow while increasing vulnerability to local extinctions due to disease outbreaks (Possamai et al., 2022) or intensified human-wildlife conflict (Tucker et al., 2018). Conversely, the presence of key natural resources can facilitate wildlife persistence in disturbed areas (Ausprey et al., 2023; Lindenmayer & Laurance, 2017). Frugivorous birds (Xie et al., 2026) and

primates (Bersacola et al., 2022; Johnson et al., 2023), for instance, are significantly more likely to persist in degraded tropical forests when large mature trees are retained. Despite their interconnected effects, large-scale population analyses rarely evaluate anthropogenic factors in combination with natural factors. This fundamentally limits our understanding of contemporary tropical forest ecology and restricts our capacity to accurately assess the drivers of wildlife population changes (Moraga et al., 2019).

The role of socioeconomic-climate policies in tropical forest land-use

Current development trends generally project economic growth concentrated in urban areas, leading to more densely populated cities and declining rural populations (Estrada et al., 2020; van Vuuren et al., 2011). In the absence of equitable social policies, this rapid urbanization expands impoverished urban areas, intensifying the demand for affordable, locally sourced commodities (Balboni et al., 2023). To meet this demand, low-productivity, extensive agricultural systems expand to supply sufficient food at minimal production cost, driving high deforestation rates in rural areas. This trend is exacerbated by global warming, as rising thermal stress can constrain tropical crop yields and trigger a feedback loop of further deforestation to maintain food security (Yang et al., 2024). Therefore, socioeconomic inequality can be considered the main driver of anthropogenic pressure in tropical forests.

To forecast the synergetic effects of different socioeconomic and climate policy scenarios on terrestrial ecosystems, the Intergovernmental Panel on Climate Change (IPCC) proposes the use of a matrix of integrated Shared Socioeconomic Pathway (SSP) and Representative Concentration Pathway (RCP) frameworks (IPCC, 2019; Riahi et al., 2017). This matrix provides a useful tool for predicting population dynamics of species vulnerable to anthropogenic land-use change under a range of plausible policy futures, spanning from low-emission, equitable societies to high-emission, inequitable ones. Combined with up-to-date and targeted monitoring protocols, such predictive capacity allows conservation practitioners to identify spatial hotspots of intervention, directly contributing to the restoration (Target 2) and protection (Target 3) targets of the GBF.

The moor macaque (*Macaca maura*) as example species

Here, we use the Endangered moor macaque (*Macaca maura*) as an example species to test how contemporary anthropogenic pressures can shape the current and future occurrence of threatened species in anthropogenically-modified tropical forests. We investigate how natural and anthropogenic factors interact to drive current occupancy patterns of the moor macaque across the species' entire geographic distribution (Figure 1), and project how shifting socioeconomic-climate policies may alter their occupancy over the next 75 years. By linking present-day ecological drivers to policy-dependent future trajectories, this approach aims to identify science-based conservation strategies for protecting and restoring tropical forests under intense anthropogenic pressure over both the short and long term.

The moor macaque is endemic to southwestern Sulawesi (Indonesia), a global priority region for both conservation (Myers et al., 2000) and ecosystem restoration (Strassburg et al., 2020) due to high levels of endemism and intense deforestation pressure (Supriatna et al., 2020). The species serves as an ideal ecological indicator, as they are frugivorous primates that live in large

groups and act as primary seed dispersers, making them vital to forest regeneration and an effective umbrella species for conservation planning (Supriatna et al., 1992). Despite their ecological importance and endangered status, intensive deforestation driven by agricultural expansion and direct human encroachment continue across the region, reflecting mounting pressure from a growing human population (Supriatna et al., 2020). This pressure is projected to intensify, especially under most plausible socioeconomic scenarios, due to agricultural expansion in mountainous areas (Struebig et al., 2025). Moreover, the relatively restricted geographic distribution of the moor macaque (Riley et al., 2020; Figure 2), allowed us to survey a significant proportion of their entire distribution, enhancing the reliability of the spatial predictions (Solà et al., 2025). We first identified the key environmental factors driving current moor macaque occupancy: land-use type, forest fragmentation, Human Footprint Index and forest quality . We then projected moor macaque occupancy across a range of SSP-RCP scenarios and compared current and future occupancy, identifying spatiotemporal occupancy dynamics and areas with greater occupancy decrease at a spatial resolution of 2 km^2. Collectively, these analyses address two central questions: (1) Which natural factors and anthropogenic pressures drive current moor macaque occupancy? and (2) How will divergent socioeconomic-climate policy pathways shift these occupancy patterns over the next century? Answering these questions will directly guide targeted conservation strategies for this Endangered primate, while providing vital insights into how interacting natural and anthropogenic drivers dictate species persistence in highly modified landscapes. Ultimately, this approach offers a scalable framework to help meet GBF targets across increasingly anthropogenically-dominated tropical forests.

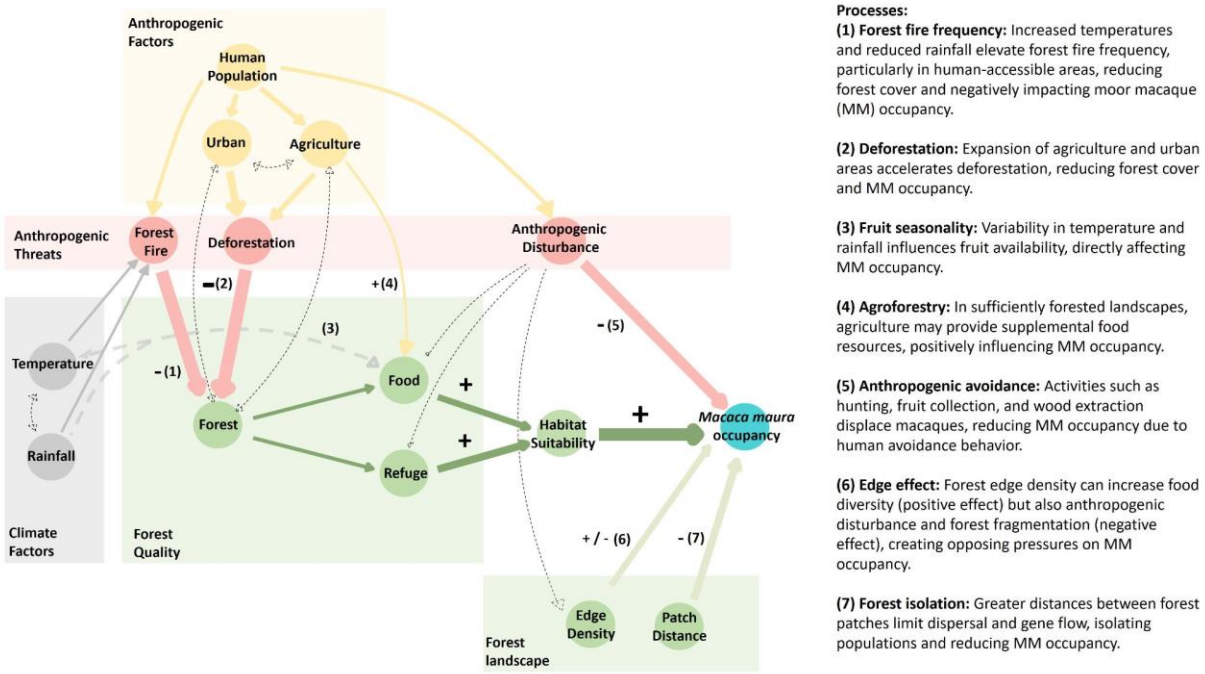

Figure 1. Directed Acyclic Graph of the effect of anthropogenic (red) and natural factors (green) on moor macaque (MM) occupancy. Numbers indicate the different processes that may affect moor macaque occupancy in southwestern Sulawesi forests, Indonesia. Symbols indicate if the processes positively (+) and/or negatively (-) affect moor macaque occupancy.

Methods

Predictors of macaque occupancy

Sampling design

To survey moor macaque occurrence across their entire range, we superimposed a grid of 2-km^2 cells over the most recent geographic distribution published by the IUCN (Riley et al., 2020). To avoid oversampling unsuitable habitats, we restricted our site selection to cells containing at least 10% forest cover, a threshold corresponding to the species' minimum estimated home range size of 0.2 km^2 (Riley et al., 2020). We quantified baseline forest cover using the Global Forest Canopy Height 2019 (GFCH2019) database (Potapov et al., 2021) processed in ArcGIS Pro (ESRI, 2022). For this classification, we defined forest as grid cells with a canopy height of 10 m or taller, which aligns with standard thresholds for tropical forest classification (Adrah et al., 2022). A total of 5799 grid cells contained at least 10% forest cover, of which we randomly selected 250 cells (hereafter, "sampling locations") to survey (Figure 2). We excluded the northern region of the IUCN geographic distribution (Riley et al., 2020) because it is also occupied by Tonkean macaques (*Macaca tonkeana*), whose presence could confound species identification.

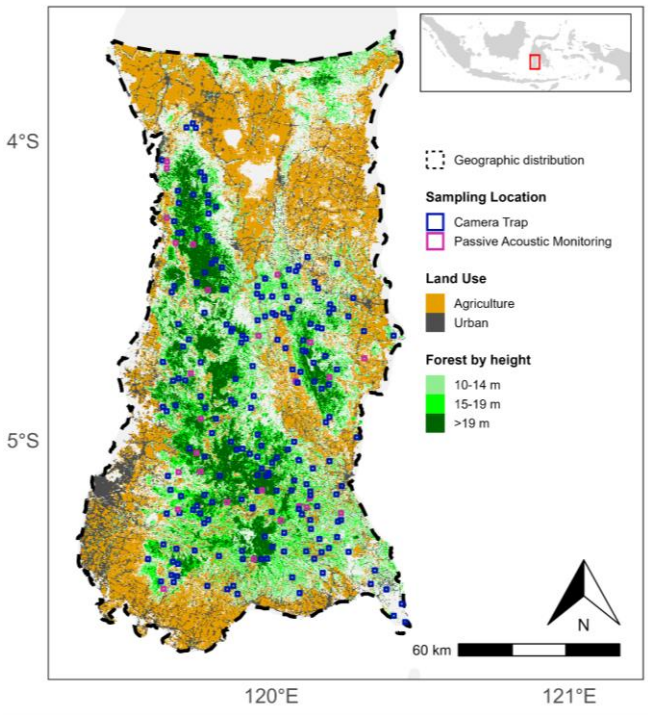

Figure 2. Geographic distribution and sampling locations of the moor macaque (*Macaca maura*) in southwestern Sulawesi, Indonesia. Blue (CTs) and pink (ARUs) squares represent individual sampling locations (n = 226) within the species' geographic distribution based on the latest IUCN Red List assessment (Riley et al., 2020). Land-use data was obtained from the DynamicWorld database (2019-2023; Brown et al., 2022) and forest height from the Global Forest Canopy Height database (2019; Potapov et al., 2021). The top-right inset map displays the location of the study area (red bounding box) within Indonesia.

Field data collection

We collected moor macaque presence data between March and October 2023 using 45 camera traps (CTs) and 5 acoustic recording units (ARUs; Audiomoths v.1.9.0). We deployed each device for 30 consecutive days at the center of a given sampling location (Rovero & Zimmermann, 2016). After collecting the devices from each location, we relocated devices to a new one until all 250 locations were surveyed (Johnson et al., 2020). Each sampling location was surveyed using either a CT or an ARU. To ensure that the devices collected data for 30 days, we installed the devices one day prior to, and removed them at least one day after the designated 30-day data collection window. Where rugged terrain (e.g., steep slopes, rivers) prevented central placement, we located the device at least 50 m from the border of the sampling location (Johnson et al., 2020). We set CTs at 30 cm off the ground, to take 3 consecutive pictures every time that the sensor triggered the CT, with 3 seconds interval between triggerings, and with high sensitivity following recommendations to maximize macaque detection (Beltrán Francés et al., 2026). We installed ARUs at a height of 2 m above the ground (Enari et al., 2019) and programmed them to record daily during peak macaque vocal activity periods from 04:00 - 07:00 and 16:00 - 21:00 (Beltrán Francés et al., 2026). To optimize data storage, we configured ARUs to record 50 seconds of audio per minute, maintaining individual file sizes below 100 MB.

Data codification

Following methods established for the closely related *Macaca nigra* (Johnson et al., 2020), we defined a sampling occasion as 5 consecutive days, resulting in a detection history of six occasions per 30-day survey at each sampling location. We codified a survey as "moor macaque detected" if the CT or ARU detected at least one macaque during the 5-consecutive day survey. We codified surveys without detections as "moor macaque not detected". For the data codification process we used Agouti software (www.agouti.eu) and the Megadetector model (v.5.0; Beery et al., 2019) for CT footage and the DeepAudioSegmenter software (Steinfath et al., 2021) with a self-developed model to detect the moor macaque "loud call" from audio recordings (see Supplementary Material for expanded data codification methods).

Natural and anthropogenic predictors

To analyze the effects of natural and anthropogenic factors on moor macaque occupancy, we collected data on forest quality, forest landscape structure, and anthropogenic activity for each sampling location, and included them as covariates of occupancy in the analyses (Table 1; Figure 1). Except for forest edge density and mean euclidean inter-patch distance (see below), we calculated all the covariates using the "zonal_stats" function in the *geemap* Python package (Wu, 2020) with Google Earth Engine (Gorelick et al., 2017). For each sampling location polygon, this function computed the selected statistic value (e.g., mean, max, min) of all raster pixels falling within its boundaries at the original resolution of each input dataset.

Table 1. Covariates used to analyze the effect of natural and anthropogenic factors on moor macaque (*Macaca maura*) occupancy (see Table S1 for a complete description including detectability covariates).

Covariate group	Covariate[1]	Definition	Source[2]	Resolution[3]	Prediction[4]
Forest quality	Forest cover	Percentage of pixels in the sampling location with forest cover (i.e., tree height > 9 m)	Global Forest Canopy Height (Potapov et al., 2021)	30 m	Occupancy is positively related to suitable forest cover, as more habitat is available.
	NDVI	Mean Normalized Difference Vegetation Index	Landsat 8 (U.S.Geological Survey)	30 m	Occupancy is positively related to NDVI, as forest is more productive.
	Tree height	Maximum tree height pixel value (m) within the sampling location	Global Forest Canopy Height (Potapov et al., 2021)	30 m	Occupancy is positively related to tree height, as a greater number of refuges and feeding trees are available in forests with taller trees.
Forest landscape structure	Forest edge density	Sum of the lengths (m) of all forest edges divided by the sampling area of each sampling location (ha)	Global Forest Canopy Height (Potapov et al., 2021)	30 m	Occupancy may be positively related to edge density because edges can provide a greater variety of food resources than forest interiors, but may also be negatively related where edges experience elevated human disturbance.
	Inter-patch distance	Mean Euclidean distance between forest patches in the sampling location	Global Forest Canopy Height (Potapov et al., 2021)	30 m	Occupancy is negatively related to inter-patch distance, as forest patches are less connected, hindering mobility between habitat patches.
Anthropogenic activity	Agriculture land cover	Percentage of agriculture land pixels	Dynamic World (Brown et al., 2022)	10 m	Occupancy is positively related to agriculture when it is present at a low percentage (i.e., forest cover > 50%), as macaques benefit from crop foraging, and is negatively related to agriculture when it is present at a high

				percentage (forest cover < 50%), as less habitat is available.
Urban land cover	Percentage of urban land pixels	Dynamic World (Brown et al., 2022)	10 m	Occupancy is negatively related to urban land cover, as less habitat is available.
Human population	Human population density (humans/2km^2)	GHS-POP R2023A (Carioli et al., 2023)	100 m	Occupancy is negatively related to human population, as anthropogenic pressure is higher.
HFI	Mean Human Footprint Index	HFI 2022 (Gassert et al., 2023)	100 m	Occupancy is negatively related to HFI, as human pressure is higher.
Forest fire	Frequency of yearly presence of forest fires from 2012 to 2022	FIRMS (NASA, 2024)	375 m	Occupancy is negatively related to forest fire frequency, as less habitat is available and anthropogenic pressure is higher.

[1] Name of the covariate used in the occupancy models.

[2] Source used to access and download the covariate dataset.

[3] Original spatial resolution for each covariate.

[4] Expected effect of each covariate.

Forest quality

To measure forest availability (forest cover), we crop the forest raster obtained from GFCH2019 to karst and lowland forest areas in Sulawesi (0 - 1500 m above sea level [a.s.l.]; estimated by Cannon et al., 2007), as moor macaques preferentially use karst and lowland forest (Supriatna et al., 1992) and they are not found in montane forest exceeding 2000 m a.s.l. (Riley et al., 2020).

We used the Normalized Difference Vegetation Index (NDVI) and maximum tree height as proxies for forest quality (Table 1). NDVI is an index that estimates forest productivity and greenness, serving as a proxy of food availability in macaque species (Johnson et al., 2020; Nurda et al., 2020). Higher NDVI values are related to greener and thus more productive forests. Moreover, we used tree height in forest as a measure of both food availability and structural refuge (Gazagne et al., 2020). As semi-arboreal species, moor macaques depend on the presence of trees high enough to provide refuge from predators and as a place to rest at night (Rodríguez Del Castillo et al., 2025). Recent research on closely related macaques (*M. leonina*; *M. assamensis*) underscores that canopy height is a critical positive predictor of occupancy (Alexiou et al., 2024).

Forest landscape structure

To assess the effect of forest landscape structure on moor macaque occupancy (Table 1), we measured the forest edge density (forest fragmentation and anthropogenic pressure) and mean Euclidean inter-patch distance (forest isolation; McGarigal et al., 2002). We calculated both metrics from the forest cover raster (GFCH2019) using the functions "lsm_c_ed" and "lsm_c_enn_mn", respectively, of the *Landscapemetrics* package (Rempel et al., 2012) in R (v4.1.1; R Core Team, 2024). Although edge density is a forest landscape metric, in highly anthropogenically-modified tropical forests it is expected to correlate with increased anthropogenic pressure due to edge effects, and a concentration of anthropogenic activities such as hunting, crop-foraging conflicts, and agricultural encroachment along forest edges (Murcia, 1995).

As wildlife-forest landscape structure relationships are highly scale-dependent, we assessed the multi-scale effects of forest availability (forest cover) and forest isolation (inter-patch distance) across three concentric buffers centered on each sampling location: 0.25 km^2, 2 km^2, and 6.25 km^2 (Arasa-Gisbert et al., 2021). This multi-scale framework mirrors the species´ known variations in home range size , which typically span from 0.25 km^2 to 2 km^2 (Okamoto et al., 2000; Riley et al., 2020; Rodríguez Del Castillo et al., 2025). The maximum buffer size of 6.25 km^2 represents a broader landscape matrix capable of encompassing the movements of multiple interacting social groups.

Anthropogenic activity

To assess the effect of deforestation from land-use conversion, we measured the percentage of agricultural and urban land covers in each sampling location using the Dynamic World dataset (Table 1; Brown et al., 2022). It includes a global near real-time and fine-scale

raster classification of the two main anthropogenic activities within the moor macaque landscape: agriculture and urban development (Riley et al., 2020). To generate the raster, Dynamic World uses an algorithm that automatically classifies the land-use of every new Sentinel-2 image updated. We used data from the most recent cloud-free Sentinel-2 satellite imagery (January 2020 until October 2023), to ensure that the database included all the pixels within the geographic distribution of the moor macaque without clouds and avoided cloud interference with land-use classification.

We derived human population density from the Global Human Settlement Global Population Layer (Table 1; GHS-POP R2023A; Carioli et al., 2023). The GHS-POP dataset provides grid-cell estimates of human population by disaggregating census data from the Global Population of the World dataset (CIESIN, 2018) for the year 2020. This disaggregation process utilizes the distribution, classification, and volume of built-up areas mapped in the Global Human Settlement Built-up Layers for the year 2020 (for a detailed overview of the methodology, see Carneiro Freire et al., 2016). As population counts are provided at a spatial resolution of 0.01 km^2, we calculated the total human population for each sampling location by summing the values of all grid cells nested within its boundaries.

To analyze the effect of anthropogenic disturbance on moor macaque occupancy, we used the Human Footprint Index (HFI; Table 1; Gassert et al., 2023). The HFI is a gridded global dataset that maps the cumulative anthropogenic disturbance on terrestrial ecosystems by integrating eight variables: built-up areas, crop and pasture lands, human population density, electric power infrastructure (nighttime lights), roads, railways and navigable waterways (Venter et al., 2016). Index values range from 0 to 50 per grid cell, where values greater than 10 represent areas under high anthropogenic disturbance that are usually associated with reduced species richness and biodiversity loss (Williams et al., 2020). Accordingly, the HFI serves as a comprehensive composite proxy for anthropogenic disturbance, capturing the synergistic effects of infrastructure and landscape modification rather than assessing population density or agricultural and urban expansion in isolation.

We further assessed the effect of the frequency of forest fires on the occupancy of moor macaques across their geographic distribution (Table 1). In the tropics, forest fires are commonly caused by human-induced fires in agricultural areas next to forest patches (Bowman et al., 2020). Climate change can affect fire frequency, as higher temperature and less rainfall increase the likelihood of forest fires (Abatzoglou, et al., 2018b). We used the dataset Fire Information for Resource Management System (FIRMS; NASA, 2024) to calculate the frequency of forest fires between the years 2012 and 2022 (Table 1). For each sampling location and year, we recorded a binary presence/absence of forest fires. We then summed the annual values to calculate the total fire frequency per sampling location. We did not include fires for the year 2023 to avoid confounding with survey timing (i.e., fires could have happened after the survey).

Data analysis

Occupancy modelling

To estimate the effect of natural and anthropogenic factors on moor macaque occupancy along its geographic distribution, we used single-season, single-species occupancy models

(MacKenzie et al., 2017). We assumed demographic closure (no births, deaths, or range shifts) across our target sampling locations throughout the survey period. Prior to modelling, we standardized all numerical covariates into z-scores (MacKenzie et al., 2017), assessed multicollinearity using Variance Inflation Factors (VIFs) and did not include in the same model covariates with VIF > 3 (Burnham et al., 2011). To analyze the effect of each covariate on moor macaque occupancy, we included forest quality (forest cover; NDVI; maximum tree height), forest landscape structure (forest edge density; mean inter-patch distance) and anthropogenic activity (agriculture and urban cover; human population density; HFI; fire frequency over the last 10 years) as occupancy covariates (Table 1; Morrissey & Ruxton, 2018; Ruffell et al., 2016). For detection probability, we used maximum surface temperature (ºC) and mean rainfall (mm) for the 30-day survey period, mean slope (degrees) and device model (Table S1).

We estimated moor macaque occupancy using the function "occu" in the package *unmarked* in R (Kellner et al., 2023). Model selection followed a two-stage, stacked approach (MacKenzie et al., 2017). First, we modelled the detectability of moor macaques while keeping occupancy model structure constant to identify the optimal detection structure. We ranked all candidate detection models according to their AIC and selected the top ranked model(s) (ΔAIC < 2) structure as the fixed detectability model for subsequent steps (Burnham et al., 2011). Second, while retaining the selected detection structure, we modelled occupancy using all univariate models, full multivariate models for each covariate group (forest quality, forest landscape structure, and anthropogenic activity), and a final model that included the significant covariates from the group models together with all biologically meaningful interactions. To determine the spatial scales for forest cover and forest inter-patch distance that most strongly influence macaque occurrence, we fitted univariate occupancy models for each of these covariates at each buffer size (Cudney-Valenzuela et al., 2022). We then selected the best-performing scale for each variable to carry forward into our multivariate occupancy models, ensuring that multiple spatial scales of the same variable were never included in a single model (Mandujano et al., 2023). We ranked the resulting occupancy models by AIC, and selected the most parsimonious model(s) (ΔAIC < 2). We evaluated the goodness-of-fit for the final model(s) using the MacKenzie and Bailey test (MacKenzie & Bailey, 2004), which compares observed and simulated model fits using chi-square tests. Finally, we predicted moor macaque occupancy along their complete geographic distribution at a 2 km^2 resolution (pixel = 1414 m) using the "predict" function and the most parsimonious model in R.

Future occupancy projections under SSP–RCP scenarios

To evaluate global socioeconomic-climate policy effects on moor macaque occupancy patterns, we projected future species' occupancy under plausible socioeconomic and climatic scenarios. Our analysis relied on the latest global land-use and land-cover change (LUCC) dataset projected until 2100 (Chen et al., 2022). This dataset integrates the IPCC framework by pairing SSPs and RCPs to simulate rasters of future land-use changes at fine spatial resolutions (1 km^2). SSPs represent future societal trajectories, accounting for demographic, economic, policy, and technological developments (Riahi et al., 2017), while RCPs provide different climate potential outcomes based on greenhouse gas emissions and radiative forcing (van Vuuren et al., 2011). Of the seven scenarios endorsed by the IPCC Sixth Assessment Report and the Coupled Model Intercomparison Project Phase 6 included in the LUCC dataset, we selected the

three more plausible scenarios (Sarofim et al., 2024) that span a spectrum of scenarios ranging from equitable socioeconomic development with low emissions to high inequality paired with high-moderate emissions (Table 2). We therefore excluded scenarios with very low emissions (SSP1-1.9) and very high emissions (SSP3-7.0, SSP4-6.0, and SSP5-8.5), as they are considered too optimistic and pessimistic, respectively, according to recent climate trends and projections (Sarofim et al., 2024).

Table 2. Description of selected Shared Socioeconomic Pathway and Representative Concentration Pathway (SSP-RCP) scenarios used for future moor macaque occupancy projections, including their expected global warming ranges by 2100 relative to pre-industrial levels (IPCC, 2023).

Scenario	SSP-RCP	Global warming[1]	Characteristics[2]
Low-emission sustainability	SSP1-2.6	1.8°C (1.3 - 2.4)	Low emissions, high equity, reliance on renewable energy
Current development trends	SSP2-4.5	2.7°C (2.1 - 3.5)	High-moderate emissions, continuation of historical socioeconomic trends
Moderate-emissions inequality	SSP4-3.4	2.2°C (1.7 - 2.8)	Moderate emissions, high inequality, uneven development

[1]Mean (min-max) expected global warming by 2100 relative to pre-industrial levels.
[2]Key expected socioeconomic, political and emissivity characteristics.

For each selected scenario, we extracted future LUCC raster projections for three time periods (2050, 2075, and 2100) at 1 km resolution, across the current moor macaque range. From these 18 rasters, we derived projected covariates for forest quality (forest cover, maximum tree height), landscape structure (edge density, mean inter-patch distance), and anthropogenic activity (expansion of urban and agricultural land). We followed a conservative approach to modifying baseline rasters to reflect future projections. First, for forest cover, we cropped the forest cover raster used in occupancy modelling (GFCH2019) to include only those pixels that remained classified as forest in each future scenario. This method intentionally excluded potential reforestation processes, as systematic large-scale reforestation has not been documented in the region for the past 30 years (Supriatna et al., 2020). Second, for agricultural and urban cover, we updated the 2023 rasters by adding all pixels projected for conversion to these anthropogenic classes in each future scenario. This process generated a 30 m resolution forest cover raster and 10 m resolution agricultural/urban rasters for each scenario and time period.

Using the scenario-specific forest cover rasters, we recalculated the percentage of forest cover, maximum tree height, forest edge density, and mean inter-patch distance for each projection, following the same methodology described for the 2023 occupancy model. Similarly, we recalculated the percentage of agriculture and urban land cover from their respective scenario-specific rasters. Only covariates retained in the final, most parsimonious occupancy model were incorporated into future projections. We generated occupancy predictions using the "predict" function in R, incorporating the projected forest cover covariates while holding non-forest covariates constant at their 2023 (NDVI, human population density), 2022 (HFI), or 2012-2022 (fire frequency) baseline values.

To compare current and projected occupancy, we calculated three metrics for each scenario and time period relative to the 2023 baseline: (1) the mean occupancy probability across the moor macaque distribution, (2) the intensity of occupancy change per pixel, and (3) the macaque occupied area lost. We defined the intensity of occupancy change as the difference in occupancy values for each specific pixel between 2023 and the corresponding climate change scenario and year (i.e., intensity of occupancy change for $pixel_i$ = occupancy value climate change scenario $pixel_i$ – occupancy value 2023 $pixel_i$), with a negative value indicating a decrease and a positive value an increase in the occupancy value in the future scenario, as compared to 2023. We defined macaque occupied areas as pixels with an occupancy probability > 0.4, a threshold commonly used to distinguish regularly occupied from sporadically used areas (MacKenzie et al., 2017). We calculated the macaque occupied area lost as the number of baseline pixels (occupied in 2023) that fell below this occupancy threshold in each future projection, multiplied by the pixel area (2 km^2). Prior to all analyses, we ensured spatial consistency across all raster datasets by verifying their extent, resolution, and coordinate reference system using the "compareGeom" function from the *terra* package in R (Hijmans et al., 2026).

Results

Naive detectability

Between 13 March and 24 October 2023, we surveyed 226 sampling locations across the geographic distribution of the moor macaque, representing a total sampled area of 452 km^2. We deployed CTs at 199 locations (88%) and ARUs at 27 locations (12%; Figure 2). Over 155 days of fieldwork, we accumulated an effort of 5970 CT-days (25,817 pictures) and 810 ARU-days (6480 hours of audio recordings). Of the 250 planned sampling locations originally selected, we excluded 23 locations situated outside of conservation areas because they were completely deforested by the time of the survey. Additionally, one location within the Bantimurung-Bulusaraung National Park was canceled due to inaccessibility, and two others were relocated to the nearest accessible locations. Data from 19 surveyed locations were lost due to device malfunction (CTs: n = 11; ARUs: n = 3) or theft of CTs (n = 5). After these exclusions, 207 locations (183 CT, 24 ARU) yielded usable detection histories. We detected moor macaques in 117 of the 207 locations, corresponding to an overall naïve occupancy of 56.5% (55.4% for CTs: 102 of 184 locations; 66.7% for ARUs: 16 of 24 locations).

Detection probability

The model including all detection covariates was the most parsimonious for detection probability (MD1; Table 3). All detection covariates significantly influenced moor macaque detectability. Detectability increased significantly with steeper slopes ($\beta = 0.838 \pm 0.132$, $p < 0.001$) and higher maximum temperatures ($\beta = 0.363 \pm 0.108$, $p < 0.001$). In contrast, rainfall was associated with a significant decrease in detection probability ($\beta = -0.481 \pm 0.111$, $p < 0.001$), likely due to increased background noise and reduced visibility during precipitation events. Among the survey devices, Wingscapes cameras exhibited significantly lower detectability than AudioMoth recorders ($\beta = -0.566 \pm 0.286$, $p = 0.047$) and Bushnell cameras ($\beta = -1.081 \pm 0.218$, $p < 0.001$), but did not differ significantly from Findn cameras ($\beta = -0.465 \pm 0.373$, $p = 0.212$; Figure S1).

Table 3. List of the three top-ranked models for detectability, scale effects, and occupancy (see Table S2 for the complete list of models analysed).

Model[1]	nPars[2]	AIC[3]	ΔAIC[4]	AICwt[5]	cumWt[6]
Detectability					
MD1: p(Slope+Ta+Rain+Device) ψ(·)	**8**	**1073.886**	**0**	**1**	**1**
MD2: p(Device) ψ(.)	5	1127.327	53.441	0	1
MD3: p(Rain) ψ(.)	3	1132.271	58.385	0	1
Scale effect (Forest cover)					
MF1: p(Slope+Ta+Rain+Device) ψ(Forest_2km²)	**9**	**1058.16**	**0**	**0.515**	**0.515**
MF2: p(Slope+Ta+Rain+Device) ψ(Forest_6.25km²)	**9**	**1058.472**	**0.312**	**0.441**	**0.957**
MF3:p(Slope+Ta+Rain+Device) ψ(Forest_0.25km²)	9	1063.113	4.954	0.043	1
Scale effect (Forest inter-patch distance)					
MID1: p(Slope+Ta+Rain+Device) ψ(PatchDistance_2km²)	**9**	**1062.463**	**0**	**0.518**	**0.518**
MID2: p(Slope+Ta+Rain+Device) ψ(PatchDistance_6.25km²)	**9**	**1062.765**	**0.302**	**0.445**	**0.963**
MID3: p(Slope+Ta+Rain+Device) ψ(PatchDistance_0.25km²)	9	1067.85	5.387	0.035	0.998
Occupancy					
MO1: p(Slope+Ta+Rain+Device) ψ(MaxTreeHeight*EdgeDensity+HFI+Forest_2km²)	**13**	**989.1**	**0**	**0.57**	**0.57**
MO2: p(Slope+Ta+Rain+Device) ψ(MaxTreeHeight+HFI+EdgeDensity+Forest_2km²)	13	989.986	0.886	0.366	0.936

MO3: p(Slope+Ta+Rain+Device) ψ(MaxTreeHeight*EdgeDensity+HFI+Forest_6.25km²)	12	994.565	5.465	0.037	0.974

[1]Specification of the fitted occupancy model, including model ID, covariates for detection (p) and occupancy (ψ). For each model group, we considered models with ΔAIC < 2 as competitive and selected the most parsimonious among them (indicated in bold). For occupancy, with two competitive models, we selected the model containing the interaction term as the most parsimonious due to its statistical significance (MO1).
[2]Number of parameters in the model.
[3]Akaike's Information Criterion value for the model.
[4]Difference in AIC between the model and the model with the lowest AIC.
[5]Akaike weight, representing the relative likelihood of the model given the data.
[6]Cumulative Akaike weight, representing the summed weight of the current and all better-ranked models.

Predictors of macaque occupancy

Scale of effect

The analysis of scale-dependent forest landscape structure effects revealed that forest cover and inter-patch distance significantly influenced moor macaque occupancy, with the strongest support at medium (2 km^2) and large (6.25 km^2) spatial scales. Forest cover was positively related to occupancy at all scales, but models using medium (MF1; $\beta = 0.738 \pm 0.181$, $p < 0.001$) and large (MF2; $\beta = 0.729 \pm 0.179$, $p < 0.001$) scales received the greatest statistical support (Table 3; Figure S2). Greater inter-patch distance reduced occupancy at all scales, but again most strongly at medium (MID1; $\beta = -0.663 \pm 0.200$, $p = 0.001$) and large (MID2; $\beta = -0.805 \pm 0.281$, $p = 0.0040$) scales, as indicated by lower AIC values (Table 3). These results highlight the importance of both forest extent and connectivity at spatial scales relevant to macaque ecology.

Effects of forest quality, landscape structure and anthropogenic activity

Variance inflation factor analysis revealed strong collinearity (VIF > 3) between urban land cover and human population density. To prevent multicollinearity, we did not include these covariates in the same models. Model selection yielded two competitive models with identical covariates (MO1 and MO2; Table 3), but the top-ranked model (MO1) contained a significant interaction term and was therefore selected as the most parsimonious. This model included the Human Footprint Index (HFI), forest cover at the 2 km^2 and the interaction between maximum tree height and edge density (MO1; Table 3). It estimated a mean occupancy probability of 0.709 ± 0.053 and a mean detection probability of 0.583 ± 0.057. Forest cover had a significant positive effect on occupancy (Figure 3; Table 4), whereas higher HFI values reduced occupancy probability. The strongest effect in the model was the interaction between maximum tree height and edge density (Table 4). It suggests that taller trees enable moor macaques to persist even in highly fragmented and disturbed landscapes, particularly where tree height exceeds 30 m (Figure 3). The MacKenzie-Bailey goodness-of-fit test indicated that the model fit the observed data adequately (c-hat = 1.01, $p = 0.412$; Figure S3).

Table 4. Summary of conditional model averaged parameters based on the most parsimonious model (MO1).

Parameter	Estimate ± SE[1]	z value	P(>|z|)
Occupancy model			
Intercept	0.889 ± 0.232	3.47	0.001*
Ψ(MaxTreeHeight)	0.741 ± 0.334	2.22	0.026*
Ψ(HFI)	-0.674 ± 0.283	-2.38	0.017*
Ψ(EdgeDensity)	-0.928 ± 0.299	-3.11	0.002*
Ψ(ForestCover 2km^2)	0.566 ± 0.266	2.13	0.033*
Ψ(MaxTreeHeight*EdgeDensity)	0.821 ± 0.302	2.72	0.007*
Detection model[2]			
Intercept	0.334 ± 0.232	1.44	0.001*
p(Slope)	0.479 ± 0.127	3.78	0.001*
p(MaxT[a])	0.314 ± 0.106	2.96	0.003*
p(Rainfall)	-0.421 ± 0.010	-2.96	0.001*
p(Bushnell)	0.515 ± 0.268	1.92	0.055
p(Findn)	-0.101 ± 0.409	-0.23	0.805
p(Wingscapes)	-0.566 ± 0.286	-1.98	0.047*

[1] Estimates of the β coefficient are reported for standardized covariates (scaled to mean = 0 and unit variance of 1).
[2] For the pairwise comparisons the reference level was AudioMoth.
HFI: Human Footprint Index
*Significant.

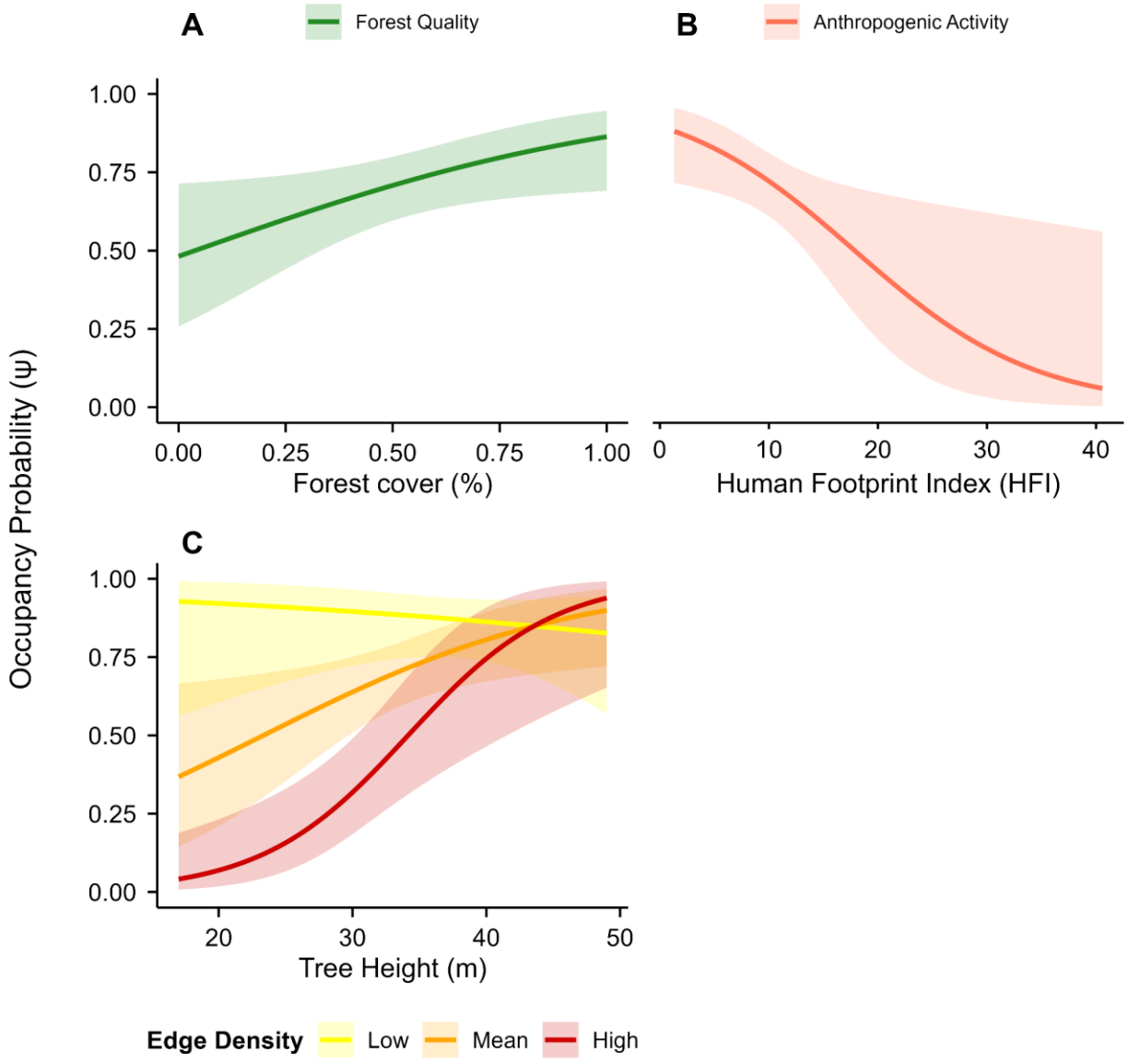

Figure 3. Predicted effects of landscape variables on moor macaque (*Macaca maura*) occupancy probability. (A) effect of forest cover (%) within a 2 km² buffer, (B) effect of the Human Footprint Index (range: 0–50; Gassert et al., 2023) and (C) interactive effect of maximum tree height (m) and forest edge density on occupancy probability. Forest edge density categories represent low (15 m/ha; 10th quantile), medium (76 m/ha; mean), and high (128 m/ha; 90th quantile) values. Predictions and 95% confidence intervals (shaded bands) are derived from the most parsimonious occupancy model (MO1).

The spatial distribution of moor macaque occupancy estimates differed from the most recent IUCN range map (Riley et al., 2020; Figure 4). Occupancy probabilities were consistently low (< 0.4) across most remaining lowland forest fragments in southwestern Sulawesi, indicating limited habitat suitability or high anthropogenic pressure in these regions. High-occupancy patches clustered into four distinct subpopulations with potential minimal functional connectivity due to a lack of dispersal corridors and ongoing deforestation. The southernmost population within protected areas (TAHURA Bontobahari Nature Reserve) exhibited critically low occupancy and appeared completely isolated from the larger moor macaque metapopulation.

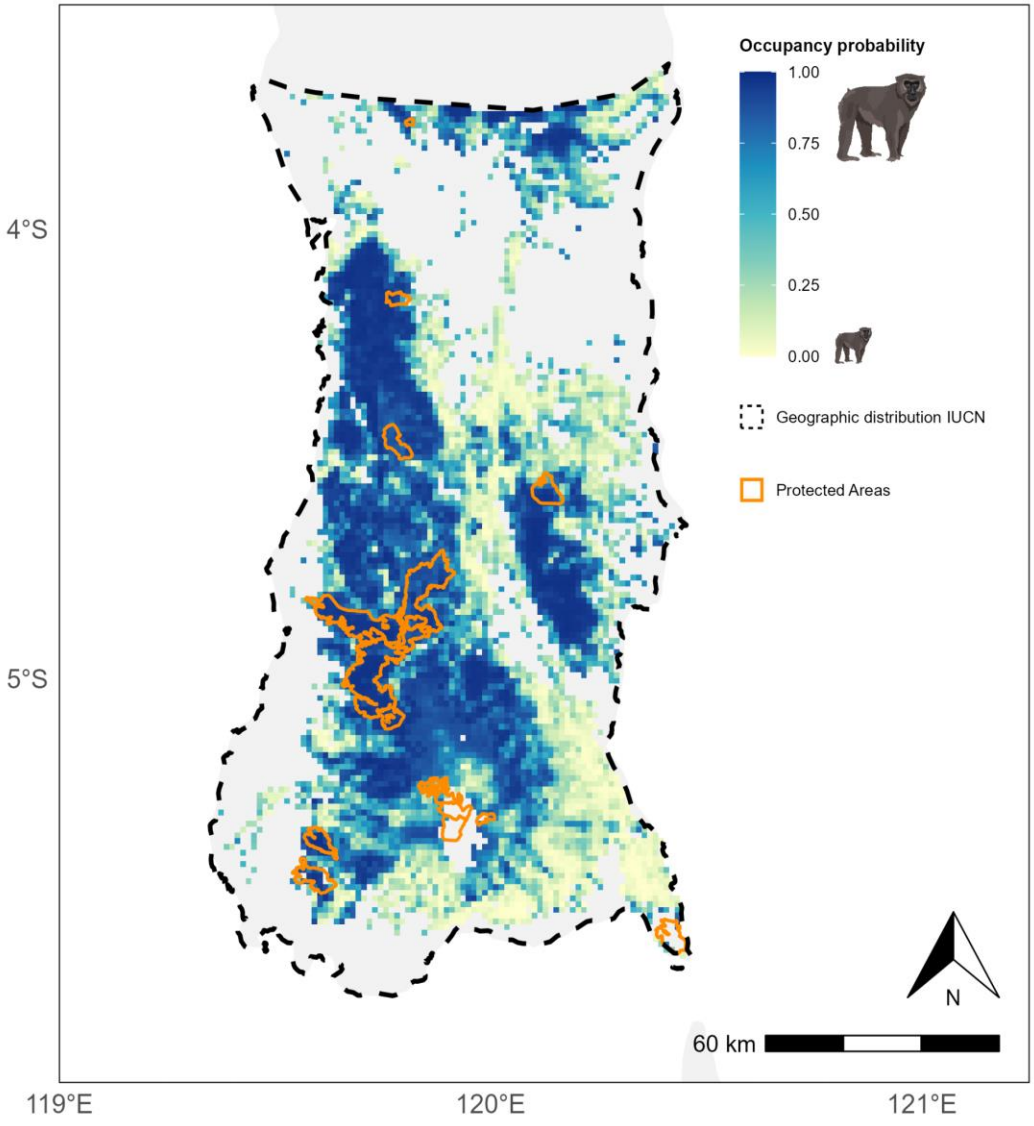

Figure 4. Estimated moor macaque occupancy probability across its complete geographic distribution according to the latest IUCN Red List assessment (Riley et al., 2020; black dashed line). Protected forest areas are delineated in dark orange. Occupancy values were estimated using the most parsimonious occupancy model (MO1).

Future occupancy projections under SSP–RCP scenarios

Model projections predicted a critical decline in moor macaque occupancy area by 2050 under all the SSP-RCP scenarios examined (Figure 5, Table S3). The extent of deforestation varied substantially among socioeconomic-climate policy pathways. Under the current development scenario (SSP2-RCP4.5; ~2.7 °C by 2100), moor macaque occupied area declined by 57%, 71%, and 76% after 25, 50, and 75 years, respectively (Figure S4; Table S3). The high inequality and moderate emissions scenario (SSP4-RCP3.4; ~1.5 °C by 2100) predicted particularly severe long-term losses due to elevated deforestation driven by agricultural expansion. Across all scenarios, per-pixel occupancy change was low while mean occupancy estimates remained high. This pattern indicates that, without proactive restoration, moor macaques are likely to persist only in a few high-quality forest fragments, becoming progressively isolated over time (Figure 5). However, the low magnitude of the per-pixel changes should be interpreted with caution, as it may partly reflect the conservative assumption of holding the HFI constant across future projections.

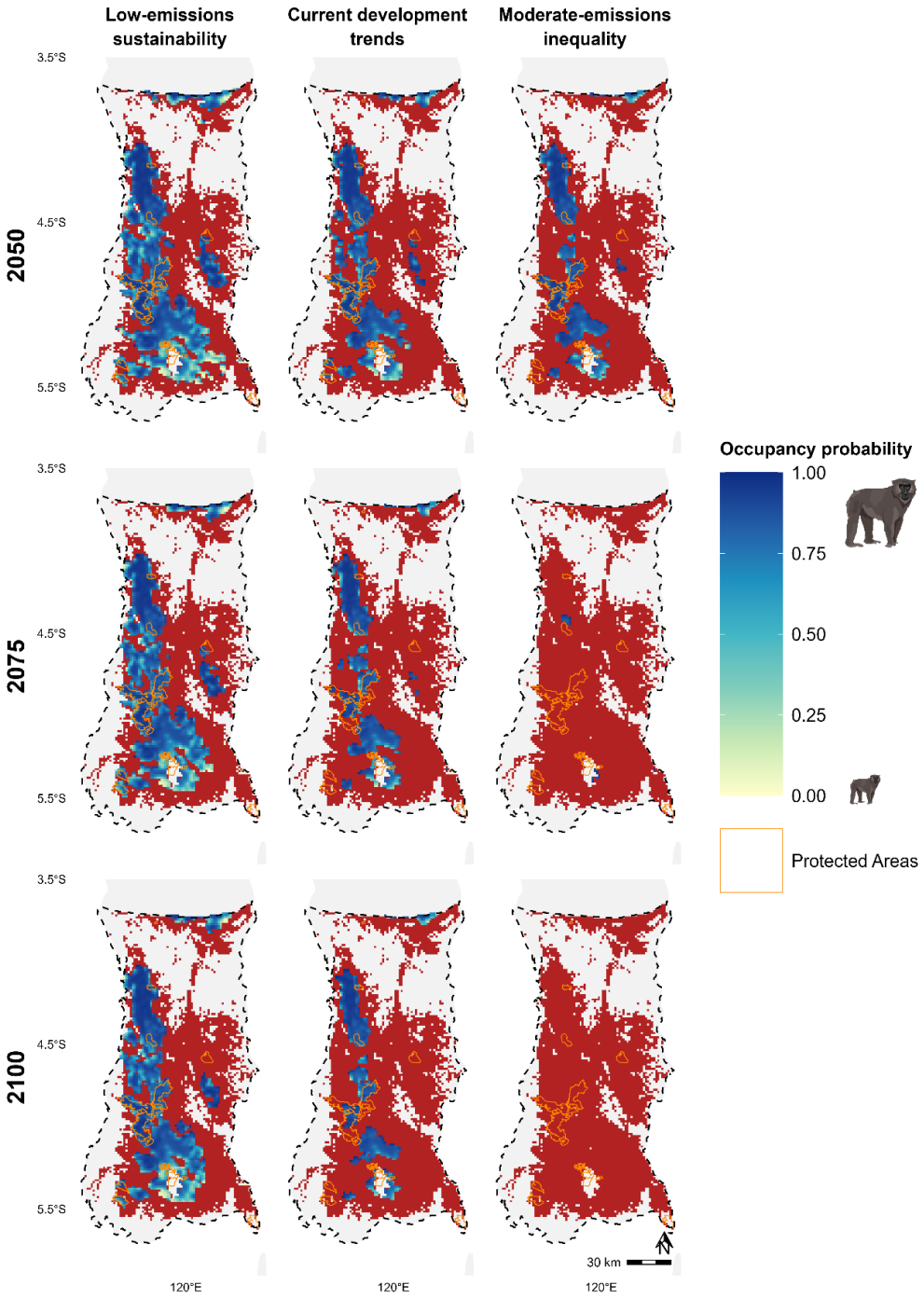

Figure 5. Maps of estimated moor macaque occupancy probability for the years 2050, 2075, and 2100 under various socioeconomic and climate scenarios. The terrain color palette ranges from white (occupancy = 0) to green (occupancy = 1). Blue lines indicate the boundaries of protected forest areas. Red shaded regions represent areas occupied in 2023 that are projected to be unoccupied (occupancy = 0) in the corresponding period and scenario. Black lines denote the species' geographic distribution based on the latest IUCN assessment (Riley et al., 2020).

Discussion

Our findings demonstrate that, despite inhabiting a highly anthropogenically-modified region, moor macaque occupancy is governed by the interplay between key forest structures and anthropogenic pressure, and that this relationship may become predominantly shaped by socioeconomic policies in the future.

Forest structure and anthropogenic pressures interact to drive occupancy

Recent research highlights that large trees serve as keystone structures in tropical forests, sustaining critical ecological processes such as seed dispersal and pollination (Ausprey et al., 2023; Xie et al., 2026). For primates, large mature trees provide essential food resources and sleeping refuges (Anderson, 1998; Wich et al., 2002), with macaques preferentially selecting large sleeping trees with closed canopies to avoid predators and optimize energy balance (Albert et al., 2011; Gazagne et al., 2020; Rodríguez Del Castillo et al., 2025; Sulai et al., 2025). In Sulawesi, large trees in anthropogenically-modified forests are frequently figs (*Ficus* spp.), offering year-round fruit productivity and large structures essential for the species' social dynamics (Supriatna et al., 1992). This might explain why macaque presence in highly fragmented landscapes substantially relies more on the presence of forest patches containing large-mature trees than on total forest cover alone. While cumulative anthropogenic disturbance (HFI) and low forest cover emerged as dominant negative predictors, the strongest determinant of moor macaque occupancy was the interaction between tree height and edge density. Tall trees (> 30 m), correlated with large trees characteristics of mature forest patches in the tropics (Banin et al., 2012), significantly mitigated the detrimental effects of fragmentation, enabling macaque persistence even in heavily disturbed landscapes (Figure 3). By contrast, in fragmented forests lacking large trees, occupancy declined sharply. While forest edges occasionally benefit generalist species, they typically amplify anthropogenic pressures (Bolt et al., 2024; He et al., 2024), as they can be high-risk zones for human-macaque conflict. Moor macaques experience direct conflict with humans due to deforestation and crop foraging (Beltrán Francés et al., 2022; Supriatna et al., 1992). The loss of large trees in fragmented forests, which are especially targeted by illegal logging in the tropics (Estrada et al., 2018), may therefore drive greater reliance on anthropogenic resources such as crops, exacerbating conflict and compromising long-term population persistence (Zhang et al., 2025). These findings underscore that effective conservation in anthropogenically modified tropical forests requires managing not only forest extent but also the functional integrity of structural factors that mediate species' responses to anthropogenic pressure. Future research must prioritize identifying and mapping large tree species across Sulawesi, assessing their ecological interactions with macaques, and modeling how selective logging and climate change may alter their distribution. Such knowledge is vital for informing conservation strategies in this globally significant endemism hotspot (Voigt et al., 2021), where the loss of keystone structures could trigger cascading ecological degradation.

Beyond local habitat quality, landscape-scale configuration emerged as a strong predictor of moor macaque occupancy. At medium and large spatial scales, occupancy probability fell below 0.25 in landscapes with less than 25% forest cover or where forest patches were separated

by more than 100 m (Figure S2). These findings align with previous studies identifying 20-30% forest cover as a critical threshold for tropical biodiversity loss (Banks-Leite et al., 2014) and primate occupancy declines (Arroyo-Rodríguez et al., 2008), and likely reflect limits to dispersal capacity, with isolated populations facing elevated extinction risks from demographic stochasticity and reduced genetic flow (Fletcher et al., 2018). Our estimated occupancy map, moreover, reveals a population more fragmented and isolated than reported in recent IUCN assessments (Riley et al., 2020; Supriatna et al., 1992). At the scale of the geographic distribution, moor macaques are becoming isolated across three main mountain regions, while at the local scale, fragmentation is intensifying due to agricultural expansion into montane areas (Supriatna et al., 2020). Collectively, these results underscore an urgent need to reevaluate the species' IUCN Red List status to ensure their extinction risk category accurately reflects this heightened isolation. Under Criterion A3, a projected population reduction of ≥ 80% over three generations qualifies a species for Critically Endangered, while a reduction of ≥ 50% qualifies for Endangered (IUCN, 2012). Given an estimated generation length of 10 years for this species (Okamoto et al., 2000), a three-generation window spans 30 years, aligning closely with our 2050 projections, which forecast distribution declines between 57% and 70%, approaching or exceeding 80% by 2075 (Figure 5; Table S2). These trajectories, coupled with our conservative modeling approach which does not account for future increases in fine-scale fragmentation or intensified anthropogenic disturbance, suggest the species could qualify for uplisting to Critically Endangered. At minimum, they should maintain their Endangered status, subject to immediate reassessment if the projected land-use scenarios are met or exceeded before 2050. Given the increasing isolation of moor macaque populations and the critical role that mature forest patches play in supporting their persistence under intense anthropogenic pressure, conservation policies must prioritize restoring forest corridors to maintain functionally connected habitat networks at large spatial scales. Furthermore, protecting mature forest patches, even at small spatial scales, is essential to facilitate species persistence in highly disturbed areas. Future work should also integrate genetic analyses to assess population connectivity, inbreeding, and vulnerability across the species' remaining range.

Socioeconomic policy implications for long-term conservation

Our future scenario projections reveal that socioeconomic policies may be as influential as climate drivers in shaping the species' future distribution. Under all SSP-RCP scenarios, moor macaque occupied area is projected to decline by at least 34% by 2050 (Figure S4). However, scenarios characterized by social inequality (current development trend: SSP2; high inequality: SSP4) and moderate to high warming (2.2 - 2.7 °C in 2100) produced the most severe losses, exceeding 57% by 2050 and 75% by 2100. This aligns with evidence from Kalimantan (Indonesia), where poverty indices negatively predicted wildlife occupancy (Spencer et al., 2023). Aligning with the GBF's Target 2 and 3, Indonesia has committed to restoring and protecting 30% of its forest by 2045 (FOLU 2030; Ministry of Environment and Forestry, 2022). For the moor macaque, this requires protecting an additional 1237 km² (17.42%) of occupied habitat within two decades. Achieving this necessitates improved forest governance that integrates local communities into conservation strategies (Fajardo et al., 2026; Nurrochmat et al., 2023). We propose maintaining and expanding the existing protected area network through a system of Other Effective Area-Based Conservation Measures (OECMs) with flexible governance. Rather than applying a uniform management model, we advocate for the tailored

implementation of OECMs with variable governance and management intensities, based on local ecological needs and community capacity (Cook, 2024; Kuemmerle, 2024). This flexibility would contribute to determining the degree of anthropogenic activities allowed across OECMs, balancing mature forest conservation and forest restoration with local sustainable development. OECMs have already proven effective in Indonesia as community-managed forests (*Hutan Desa*) and Indigenous-managed forests (*Hutan Adat*), which are associated with reduced deforestation, improved income equality, and forest restoration that benefits traditional resource use (Meijaard et al., 2021; Putraditama et al., 2019; Santika et al., 2019). Implementing this strategy is especially crucial given 1) increasing forest fragmentation between existing protected areas and 2) the region's status as one of the world's highest-priority areas for restoration.

A critical caveat of our analysis is that our projections held the HFI constant, likely yielding conservative estimates of occupancy decline. In particular, small forest patches projected to persist near expanding agricultural areas may experience substantially lower occupancy than predicted, because in reality anthropogenic pressure and edge effects would intensify in such fragments. Incorporating dynamic projections of anthropogenic pressure and forest structural degradation would substantially improve the precision of future forecasts.

Beyond southwestern Sulawesi: global implications

Using the moor macaque as an example species, we demonstrated how targeted occupancy analysis can identify key ecological drivers to inform science-based conservation policies. This study provides both a species-specific assessment and a transferable analytical framework, integrating current occupancy modeling with future socioeconomic-climate scenarios, for identifying proactive strategies for other species facing severe anthropogenic pressures globally. Our findings capture the spatial consequences of unequal development pathways, underscoring that the long-term persistence of threatened species in anthropogenically-modified tropical forests relies fundamentally on advancing equity, governance, and land-use policy at regional and global scales. The key role of forest structure in supporting macaque persistence within highly anthropogenic landscapes, as demonstrated here, reinforces global analyses indicating that restoring 15% of degraded lands in priority hotspots could avert 60% of expected biodiversity loss (Strassburg et al., 2020). Realizing these objectives will ultimately require substantially greater national and international financial investment, equitable fiscal mechanisms that hold overconsuming nations accountable, and locally grounded policies securing communal land tenure and corporate restoration commitments. Furthermore, future monitoring must integrate socioeconomic variables, such as human needs, land-use systems, and governance conditions (Karimi et al., 2017; Stephanson & Mascia, 2014). Developing global and regional open-access socioeconomic datasets will be essential for refining conservation monitoring, spatial prioritization, and predictive land-use modeling under varied policy scenarios (Fajardo et al., 2026). Such data would elucidate how fine-scale anthropogenic disturbances impact biodiversity globally, expanding upon the significant HFI effects observed here (Torres-Romero et al., 2025). Ultimately, translating these global frameworks into regional success requires targeted, collaborative strategies. Because the seven macaque species inhabiting Sulawesi share similar ecology and face common threats, we recommend formalizing the conservation efforts proposed here within a dedicated Sulawesi Macaque Action Plan, developed jointly with IUCN specialist groups, Indonesian conservation authorities, and local NGOs. This is especially urgent given that Sulawesi's macaques are the

island's primary seed dispersers and that deforestation is accelerating due to expanding nickel mining concessions driven by global demand for technology components.

Data availability:
The sampling locations surveyed during this study and the code scripts used for all analyses are available online at https://doi.org/10.5281/zenodo.21450871

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Supporting Information for

Socioeconomic policy and large mature trees are vital for moor macaque (Macaca maura) conservation in anthropogenically-modified landscapes

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Data codification

Camera trap

To codify the presence of moor macaques in CT images we used the online platform Agouti (www.agouti.eu). Agouti is a free platform developed by the Wageningen University (Netherlands) and the Research Institute for Nature and Forest (Belgium) to code CT images using both manual coding and artificial intelligence models. First, the platform groups the images of each CT into sequences (i.e., group of images which were separated from each other by less than 120 seconds), creating a variety of sequences for each sampling location. Second, we used the "Generic human/blank model (MegaDetector) v5a" (Beery et al., 2019) model to process the dataset of every survey location surveyed to automatically separate the blank sequences from the sequences containing animal detections. Depending on the content of the images in the sequence, the model automatically annotated each sequence as "human" or "blank". The model classified the entire sequence as "human" if at least one human was detected in it. The model classified the sequence as "blank" if no animal species were detected in any of the photos belonging to the sequence. Finally, if the sequence contained unknown objects (e.g., falling branches, vehicles) or animal species (other than humans), the model left the sequence unannotated. Once the model finished coding all the CT images from a sampling location, we manually reviewed and coded all the unannotated sequences for the presence of moor macaques. Finally, as the model was not specifically trained for Sulawesi fauna, we reviewed all the sequences to ensure that no moor macaque detection was misclassified as "human" or "blank".

Passive Acoustic Monitoring

We used the software DeepAudioSegmenter to automatically identify the loud call vocalizations of the species from the audios recorded with the ARUs (Steinfath et al., 2021). The DeepAudioSegmenter software autonomously classifies vocalizations from audio recordings based on a deep-learning derived hierarchical classification (Steinfath et al., 2021). To train the model to detect the moor macaque loud call vocalization from ARU recordings, we used a dataset of 100 different loud call vocalizations from ARU recordings from a previous study (Beltrán et al. 2026). The model detected loud calls within the training data with a precision of 0.95 (recall = 0.7199). We then used the DAS model to predict the presence of moor macaque

loud calls within all our sampling locations. To avoid missing moor macaque detections due to deep neural network model false negatives (i.e., loud call present but not detected), we visually reviewed the spectrogram of every survey occasion (i.e., 5 consecutive days) where the deep neural network did not detect any loud call. Moreover, in these locations we codified moor macaque as present if at least one moor macaque vocalization was detected during the survey occasion. If we did not detect moor macaque vocalization, we codified the survey occasion as "moor macaque not detected".

Table S1. Covariates used to analyze the effect of natural and anthropogenic factors on moor macaque (MM) occupancy and detectability. All covariates were continuous, except for the Device model covariate that was categorical.

Covariate[1]		Definition	Source[2]	Res[3]	Years[4]	Mean (min - max)[5]	Prediction[6]
Occupancy							
Covariate group	**Covariate**						
Forest quality	Forest cover	Percentage of pixels in the sampling location with forest cover (i.e., tree height > 9 m)	Global Forest Canopy Height (Potapov et al., 2021)	30 m	2019	0.51 (0 - 1)	MM occupancy is positively related to suitable forest cover, as more habitat is available
	NDVI	Mean Normalized Difference Vegetation Index	Landsat 8 (U.S.Geological Survey)	30 m	2023	0.65 (0.23 - 0.78)	MM occupancy is positively related to NDVI, as forest is more productive
	Tree height	Maximum tree height pixel value (m) within the sampling location	Global Forest Canopy Height (Potapov et al., 2021)	30 m	2019	30.34 (17 - 49)	MM occupancy is positively related to tree height, as a greater number of refuges and feeding trees are available in forests with taller trees.
Forest landscape structure	Forest edge density	Sum of the lengths (m) of all forest edges divided by the sampling area (ha)	Global Forest Canopy Height (Potapov et al., 2021)	30 m	2019	75.89 (0 - 164)	MM occupancy can be positively related to increase in forest edge density, as forest edges provide more variety of food than forest core areas. However, MM occupancy can be also negatively

							related to increases in forest edge density, as forest edges experience greater disturbance by humans than forest core areas
	Inter-patch distance	Mean Euclidean distance between forest patches in the sampling location	Global Forest Canopy Height (Potapov et al., 2021)	30 m	2019	62.83 (0 - 180)	MM occupancy is negatively related to inter-patch distance, as forest patches are less connected, hindering mobility between habitat patches
Anthropogenic factors	Agriculture land cover	Percentage of agriculture land pixels	Dynamic World (Brown et al., 2022)	10 m	2019-2023	0.10 (0 - 0.68)	MM occupancy is positively related to agriculture when it is present at a low percentage (i.e., forest cover > 50%), as macaques benefit from crop foraging, and is negatively related to agriculture when it is present at a high percentage (forest cover < 50%), as less habitat is available
	Urban land cover	Percentage of urban land pixels	Dynamic World (Brown et al., 2022)	10 m	2019 - 2023	0.04 (0 - 0.31)	MM occupancy is negatively related to urban land cover, as less habitat is available
	Human population	Human population density (humans/2km^2)	GHS-POP R2023A (Carioli et al., 2023)	100 m	2023	245.24 (0 - 3513.80)	MM occupancy is negatively related to human population, as anthropogenic pressure is higher
	HFI	Mean Human Footprint Index (i.e., standardized index for built	HFI 2022 (Gassert et al., 2023)	100 m	2022	10.59 (1.32 - 40.59)	MM occupancy is negatively related to HFI, as human pressure is higher

		up, pasture and crop lands, human population density, power electric infrastructures, roads, railways and navigable waterways)					
	Forest fire	Frequency of yearly presence of forest fires from 2012 to 2022	FIRMS (NASA, 2024)	375 m	2012 - 2022	0.07 (0 - 0.45)	MM occupancy is negatively related to forest fire frequency, as less habitat is available and anthropogenic pressure is higher
Detectability							
	Temperature	Maximum daily air temperature (ºC) at 2 m above ground level averaged to the 30 survey days	TerraClimate (Abatzoglou, et al., 2018a)	4638.3 m	2023	28.26 (21.02 - 34.38)	MM detectability is positively related to temperature, as macaques use shaded areas where devices are located
	Rainfall	Total daily rainfall (mm) averaged to the 30 survey days	CHIRPS Pentad (Funk et al., 2015)	5566 m	2023	5.64 (4.38 - 6.70)	MM detectability is negatively related to rainfall, as ambient noise increases and visibility decreases

	Slope	Mean slope angle (degrees)	MERIT DEM (Yamazaki et al., 2017)	92.77 m	2016	12.27 (0.85 - 32.22)	MM detectability is positively related to slope, as understory vegetation decreases, increasing visibility
	Device model	Device model (AudioMoth, Bushnell, Findn, Wingscapes) used to survey macaque presence					MM detectability is positively related to Bushnell devices, as device trigger speed is faster and more precise than the other device models

[1] Name of the covariate used in the occupancy models.

[2] Source used to access and download the covariate dataset.

[3] Original spatial resolution for each covariate.

[4] Temporal resolution (years) for each covariate.

[5] Mean (minimum and maximum) value for each covariate

[6] Expected effect of each covariate.

Table S2. Complete list of all fitted models, including candidate models for detectability, scale effects, and occupancy. For each model group, we considered models with ΔAIC < 2 as competitive and selected the most parsimonious among them (indicated in bold). For occupancy, with two competitive models, we selected the model containing the interaction term as the most parsimonious due to its statistical significance (MO1).

Model[1]	nPars[2]	AIC[3]	ΔAIC[4]	AICwt[5]	cumWt[6]
Detectability					
MD1: p(Slope+Ta+Rain+Device) ψ(·)	**8**	**1073.886**	**0**	**1**	**1**
MD2: p(Device) ψ(.)	5	1127.327	53.441	0	1
MD3: p(Rain) ψ(.)	3	1132.271	58.385	0	1
MD4: p(Ta) ψ(.)	3	1132.84	58.954	0	1
MD5: p(Slope) ψ(.)	3	1137.651	63.765	0	1
MNull: p(.) ψ(.)	2	1139.752	65.866	0	1
Scale effect (Forest cover)					
MF1: p(Slope+Ta+Rain+Device) ψ(Forest_2km²)	**9**	**1058.16**	**0**	**0.515**	**0.515**
MF2: p(Slope+Ta+Rain+Device) ψ(Forest_6.25km²)	**9**	**1058.472**	**0.312**	**0.441**	**0.957**
MF3: p(Slope+Ta+Rain+Device) ψ(Forest_0.25km²)	9	1063.113	4.954	0.043	1
MF4: p(Slope+Ta+Rain+Device) ψ(.)	8	1073.886	15.726	0	1
MNull: p(.) ψ(.)	2	1139.752	81.592	0	1
Scale effect (Forest inter-patch distance)					
MID1: p(Slope+Ta+Rain+Device) ψ(PatchDistance_2km²)	**9**	**1062.463**	**0**	**0.518**	**0.518**

MID2: p(Slope+Ta+Rain+Device) ψ(PatchDistance_6.25km²)	**9**	**1062.765**	**0.302**	**0.445**	**0.963**
MID3: p(Slope+Ta+Rain+Device) ψ(PatchDistance_0.25km²)	9	1067.85	5.387	0.035	0.998
MID4: p(Slope+Ta+Rain+Device) ψ(.)	8	1073.886	11.423	0.002	1
MNull: p(.) ψ(.)	2	1139.752	77.289	0	1
Occupancy					
MO1: p(Slope+Ta+Rain+Device) ψ(MaxTreeHeight*EdgeDensity+HFI+Forest_2km²)	**13**	**989.1**	**0**	**0.57**	**0.57**
MO2: p(Slope+Ta+Rain+Device) ψ(MaxTreeHeight+HFI+EdgeDensity+Forest_2km²)	**13**	**989.986**	**0.886**	**0.366**	**0.936**
MO3: p(Slope+Ta+Rain+Device) ψ(MaxTreeHeight*EdgeDensity+HFI+Forest_6.25km²)	12	994.565	5.465	0.037	0.974
MO4: p(Slope+Ta+Rain+Device) ψ(MaxTreeHeight+HFI+EdgeDensity+Forest_6.25km²)	12	995.257	6.157	0.026	1
MO5: p(Slope+Ta+Rain+Device) ψ(Forest_2km²+MaxTreeHeight+NDVI)	11	1006.849	17.749	0	1
MO6: p(Slope+Ta+Rain+Device) ψ(Forest_6.25km²+MaxTreeHeight+NDVI)	11	1007.538	18.438	0	1
MO7: p(Slope+Ta+Rain+Device) ψ(MaxTreeHeight)	9	1008.994	19.895	0	1
MO8: p(Slope+Ta+Rain+Device) ψ(EdgeDensity+PatchDistance_6.25km²)	10	1022.186	33.086	0	1
MO9: p(Slope+Ta+Rain+Device) ψ(HFI)	9	1027.491	38.392	0	1
MO10: p(Slope+Ta+Rain+Device) ψ(EdgeDensity)	9	1028.741	39.641	0	1

MO11: p(Slope+Ta+Rain+Device) ψ(HFI+Agriculture+HumanDensity+FireFreq)	12	1030.684	41.584	0	1
MO12: p(Slope+Ta+Rain+Device) ψ(NDVI)	9	1038.836	49.736	0	1
MO13: p(Slope+Ta+Rain+Device) ψ(HumanDensity)	9	1054.882	65.782	0	1
MO14: p(Slope+Ta+Rain+Device) ψ(Agriculture)	9	1055.004	65.905	0	1
MO15: p(Slope+Ta+Rain+Device) ψ(Forest_2km²)	9	1058.16	69.06	0	1
MO16: p(Slope+Ta+Rain+Device) ψ(Forest_6.25km²)	9	1058.472	69.372	0	1
MO17: p(Slope+Ta+Rain+Device) ψ(PatchDistance_6.25km²)	9	1062.463	73.363	0	1
MO18: p(Slope+Ta+Rain+Device) ψ(PatchDistance_2km²)	9	1062.765	73.665	0	1
MO19: p(Slope+Ta+Rain+Device) ψ(.)	9	1069.649	80.549	0	1
MO20: p(Slope+Ta+Rain+Device) ψ(FireFreq)	9	1075.499	86.399	0	1
MNull: p(.) ψ(.)	2	1139.752	150.652	0	1

[1]Specification of the fitted occupancy model, including covariates for detection (p) and occupancy (ψ).

[2]Number of parameters in the model.

[3]Akaike's Information Criterion value for the model.

[4]Difference in AIC between the model and the top-ranked model (i.e., the model with the lowest AIC).

[5]Akaike weight, representing the relative likelihood of the model given the data.

[6]Cumulative Akaike weight, representing the summed weight of the current and all better-ranked models.

Table S3. Projected changes in moor macaque occupancy under different climate change scenarios for 2050, 2075, and 2100. For each scenario and period, the table presents the mean occupancy estimate (SD), the mean intensity of occupancy change per pixel (relative to the 2023 baseline, SD), and the percentage (and area in km^2) of the 2023 geographic distribution lost (occupancy probability < 0.4). The 2023 baseline mean occupancy was 0.542 (± 0.339), with an estimated occupied range of 7390 km^2. Empty cells for moderate-emissions inequality scenarios in 2100 indicate no pixels with occupancy above the 0.4 threshold remained in the projection.

Scenario	Period	Occupancy	Occupancy Change	% Geographic Range Lost (km^2)
Low-emission sustainability SSP1-RCP2.6	2050	0.742 (0.231)	-0.022 (0.188)	36.103 (2668)
	2075	0.76 (0.216)	-0.031 (0.175)	40.97 (3028)
	2100	0.771 (0.209)	-0.026 (0.167)	46.14 (3410)
Current development trends SSP2-RCP4.5	2050	0.808 (0.179)	-0.017 (0.162)	57.13 (4222)
	2075	0.823 (0.157)	-0.016 (0.14)	70.66 (5222)
	2100	0.837 (0.147)	-0.008 (0.132)	76.37 (5644)
Moderate-emissions inequality SSP4-RCP3.4	2050	0.826 (0.161)	-0.015 (0.138)	70.39 (5202)
	2075	0.912 (0.079)	0.072 (0.094)	99.13 (7326)

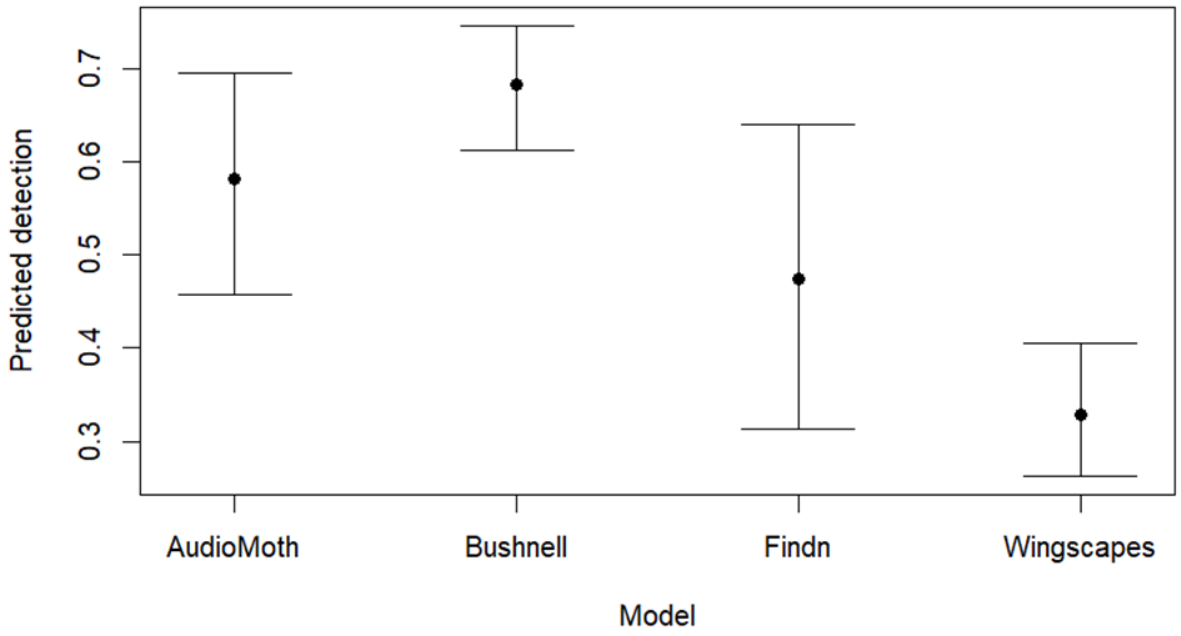

Figure S1. Estimated detection probabilities for the four device models (AudioMoth, Bushnell, Findn and Wingscapes) used to detect moor macaques, derived from the most parsimonious detection model.

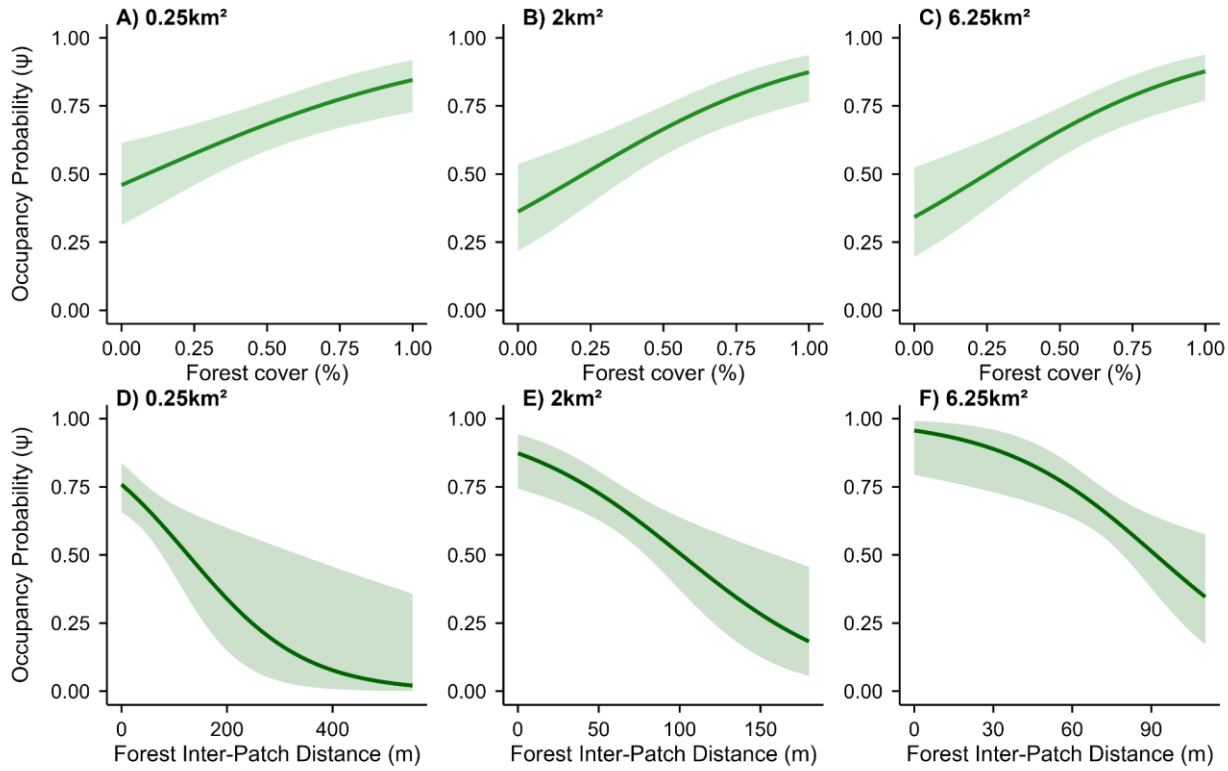

Figure S2. Predicted effects of forest cover percentage (A, B and C) and mean inter-patch distance (D, E and F) on moor macaque occupancy at small (0.25 km^2), medium (2 km^2) and large (6.25 km^2) spatial scales. Estimates are derived from univariate occupancy models fitted for each covariate at each respective spatial scale.

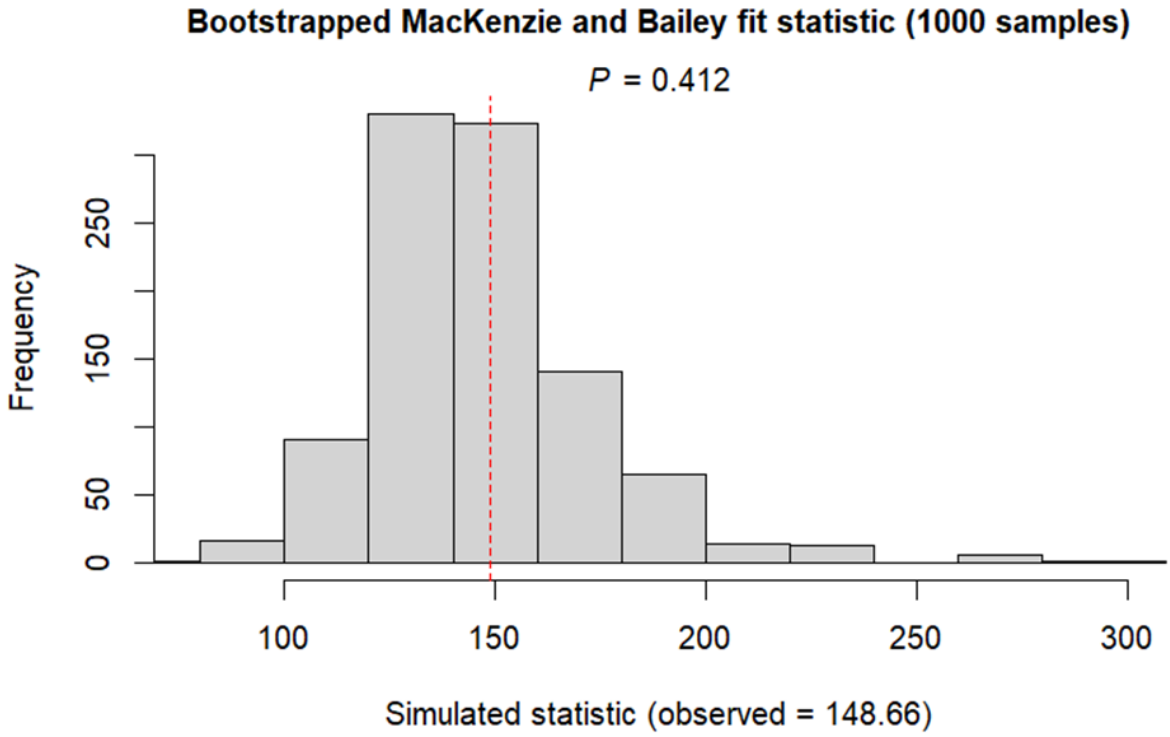

Figure S3. Goodness-of-fit assessment for the occupancy model using the MacKenzie-Bailey test. The histogram shows the distribution of Chi-square values from 1,000 parametric bootstrap simulations under the null hypothesis (model fits the data, $\hat{c}$ = 1.01). The red dashed line indicates the observed Chi-square statistic from the data.

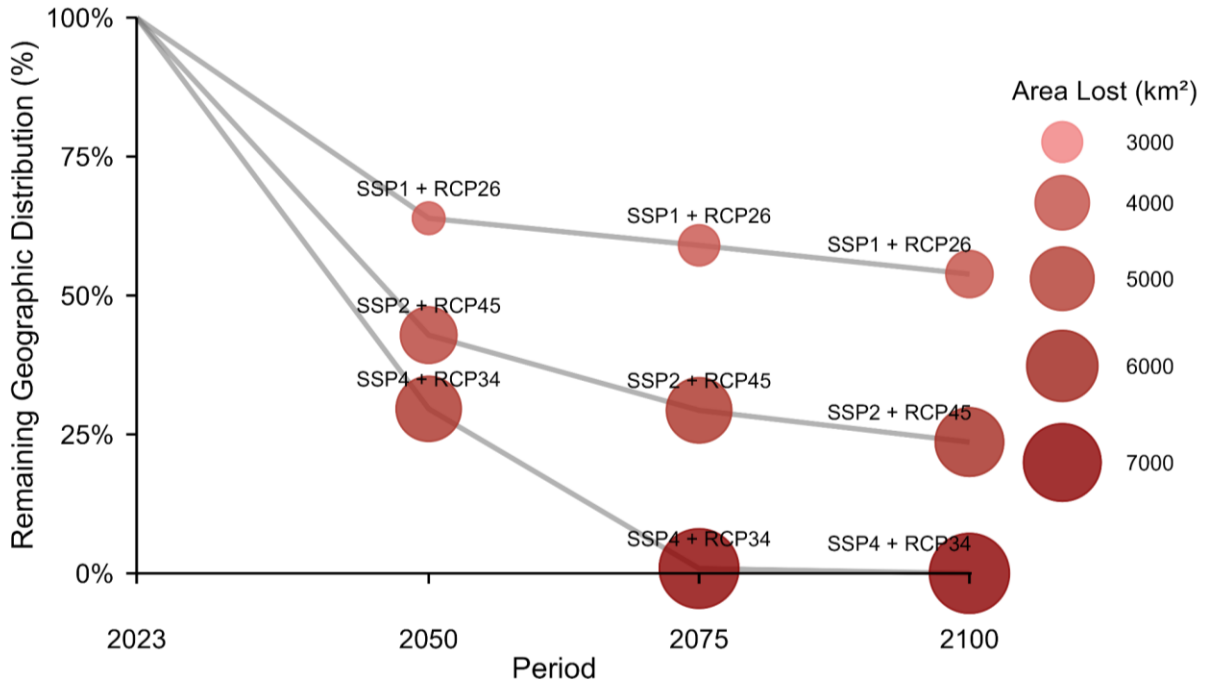

Figure S4. Predicted decline in the moor macaque geographic distribution from 2023 to 2100 under three Shared Socioeconomic Pathway (SSP) and Representative Concentration Pathway (RCP) scenarios. The distribution is defined as areas with occupancy probability > 0.4. Circle size and color intensity represent the magnitude of area lost (km²) relative to the 2023 baseline (7390 km²).