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Original Research Article

Population status of Sumatran and Tapanuli orangutans: A comprehensive assessment 2021–2023

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ABSTRACT

Both the Sumatran orangutan (*Pongo abelii*) and Tapanuli orangutan (*Pongo tapanuliensis*) are Critically Endangered, yet no range-wide population assessment has been conducted since 2011. We present results from 208 systematic line-transect nest surveys across the full ranges of both species in northern Sumatra, Indonesia (2021–2023), analysed using distance sampling, Negative Binomial Generalised Linear Models with spatial autocorrelation and a matched-distribution framework enabling direct temporal comparison with the 2011 baseline. We estimate 11,694 (95% CI: 10,949–12,518) Sumatran orangutans across eight meta-populations and 716 (95% CI: 645–792) Tapanuli orangutans across three meta-populations (12,410 combined). For the Tapanuli orangutan, this constitutes the first systematic range-wide baseline; at 716 individuals, the species has no demographic buffer against additional mortality. The matched-distribution comparison indicates a 19.5% decline in Sumatran orangutans, equivalent to ~1.8% per year. Forest structure and human population density were the strongest predictors of orangutan density across both species. Forest loss explained 76% of variation in population change across all meta-populations ($R^2 = 0.76$), but several meta-populations, notably Batu Ardan and Siranggas, declined substantially more than habitat loss predicted, suggesting non-habitat mortality

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contributes to losses in these areas. Highest densities were recorded in the Trumon–Singkil peat swamp. Across both species, 82% of orangutans occur within formally protected areas, 2204 individuals (18%) remain in landscapes with no formal conservation status, including the entire Tripa population. Gazettement alone is insufficient: enforcing existing legal protections, restoring connectivity between fragmented meta-populations and targeted intervention in unprotected landscapes are immediate priorities to avert further decline.

1. Introduction

Great apes face unprecedented threats globally, with all species classified as Endangered or Critically Endangered (IUCN, 2023). Among these, the two orangutan species endemic to Sumatra, Indonesia, the Sumatran orangutan (*Pongo abelii*) and Tapanuli orangutan (*Pongo tapanuliensis*) are among the most imperilled, with both listed as Critically Endangered (Nowak et al., 2017; Singleton et al., 2024). As the only great apes in Asia, orangutans serve as flagship taxa for broader biodiversity conservation while providing crucial ecosystem services through seed dispersal and habitat modification (Marshall et al., 2009). The severity of decline is not unique to Sumatra; the Bornean orangutan (*Pongo pygmaeus*) lost more than 100,000 individuals between 1999 and 2015, reflecting a genus-wide crisis driven by habitat destruction and killing (Voigt et al., 2018). On Sumatra, both species face multiple threats, including habitat loss, killing, and human-wildlife conflict (Meijaard et al., 2011; Wich et al., 2016; Kuswanda et al., 2021). In addition, their slow life history and complex social structures mean that even modest additional mortality can drive populations towards extinction (Marshall et al., 2009; van Noordwijk et al., 2018). While conservation investments including protected area management, patrolling and law enforcement, habitat restoration and community engagement programmes have measurably decelerated decline in some regions, they have not been sufficient to halt population loss (Santika et al., 2022; Sherman et al., 2022; Sitompul et al., 2024).

Accurate and precise population estimates are essential for conservation management and policy, yet obtaining them is methodologically demanding. Nest counts have become the standard proxy for orangutan density (van Schaik et al., 1995; Kühl, 2008), requiring careful consideration of nest production rates, nest decay times, and detection probabilities (Mathewson et al., 2008; Husson et al., 2009). Recent advances integrating environmental covariates and improved statistical models have allowed for density-distribution models that predict densities to areas not sampled to obtain abundance estimates (Spehar et al., 2010; Wich et al., 2016; Voigt et al., 2022). The most recent range-wide assessment of orangutans on Sumatra, conducted by Wich et al. (2016), applied systematic and non-systematic line-transect nest surveys with covariate-based spatial modelling to estimate 14,613 orangutans on Sumatra. Wich et al. (2016) represented a major advance over previous estimates by documenting orangutans at higher elevations, in logged forests and in areas west of Lake Toba not previously surveyed. Formalised through the 2016 Orangutan Population and Habitat Viability Assessment (PHVA; Utami-Atmoko et al., 2017), this assessment established the baseline against which population trends are measured.

Since that baseline, the conservation landscape for Sumatran orangutans has changed in several important and compounding respects. First, the formal taxonomic recognition of the Tapanuli orangutan in 2017 (Nater et al., 2017) created a second Critically Endangered species where previously only one had been described, with estimates of fewer than 800 individuals (Wich et al., 2016, 2019) and a corresponding downward revision of Sumatran orangutan numbers. Second, continuing forest loss, driven by agricultural expansion, infrastructure development, extractive industries, and illegal encroachment, has negatively impacted orangutan populations across both species' ranges, including within key strongholds such as the Leuser Ecosystem (Lubis et al., 2019; Gunung Leuser National Park, 2021; Sloan et al., 2018). Third, direct killing of orangutans associated with the illegal pet trade, bushmeat consumption, or human–orangutan conflict, exacerbated by habitat fragmentation and settlement expansion, remains a significant and underestimated cause of mortality even in forested habitats (Kuswanda et al., 2021; Sherman et al., 2022; Withaningsih et al., 2023; Sitompul et al., 2024). Sherman et al. (2022) documented 517 orangutan-related crimes on Sumatra between 2007 and 2019, approximately half involving killings; at expected detection rates below 10%, estimated species mortality from killing alone was 14.3% for both Sumatran species combined, substantially exceeding what habitat-based surveys alone would predict. Government rescue databases maintained by the Natural Resource Conservation Agencies for Aceh (BKSDA Aceh) and North Sumatra (BBKSDA Sumatera Utara), the two provinces where wild orangutans occur on Sumatra, corroborate this pattern: between 2012 and 2024, 319 individual orangutans were recorded in rescue and conflict response operations across both provinces, averaging 24.5 events per year (BBKSDA Sumatera Utara, unpublished data; BKSDA Aceh, unpublished data). Of these, 57 individuals were confiscated from private ownership, 60% aged four years or younger, an age profile implying substantial unreported adult female mortality, as obtaining infant orangutans almost invariably requires killing the mother (Russon, 2009; Sherman et al., 2022).

Wild-to-wild translocation, the direct release of conflict-affected individuals into forest without quarantine, represents a further source of unmonitored mortality risk (Sherman et al., 2025). The same government databases record 169 such direct wild releases in Aceh and North Sumatra between 2012 and 2024, including four confirmed Tapanuli orangutan individuals translocated without quarantine or post-release monitoring between 2019 and 2022. Of the remaining 150 individuals, 13 were driven back to adjacent forest without translocation, 115 were transferred to rehabilitation or reintroduction facilities; a further 22 died prior, during or recently following rescue operations as a result of their injuries or condition at the time of intervention.

These conservation measures have not been sufficient to halt ongoing declines even within the Leuser Ecosystem. For Tapanuli orangutans, the situation is more acute still, with major infrastructure projects including a hydroelectric dam and associated road construction threatening to fragment the Tapanuli orangutan's already limited range (Laurance et al., 2020; Wich and Meijaard, 2021). The cumulative effect of these pressures raises serious questions about whether current populations are tracking predicted deforestation scenarios or declining more rapidly than anticipated.

A decade after the landmark range-wide assessment of Wich et al. (2016), updated empirical data are urgently needed. To address these developments, we conducted a comprehensive survey of Sumatran and Tapanuli orangutan populations between 2021 and 2023 using methods directly comparable to Wich et al. (2016) to enable robust trend detection. This study aims to: 1) determine the current population density and distribution of both species; and, 2) assess the conservation status of populations in relation to protected area coverage and recent habitat change.

2. Methods

2.1. Study area

Our study encompassed the entire recognised ranges of Sumatran and Tapanuli orangutans in northern Sumatra, Indonesia, covering approximately 18,670 km^2 (derived from the IUCN, 2023 range assessment, excluding the Jantho and Bukit Tigapuluh reintroduction sites) across 11 meta-populations (Fig. 1). Habitats ranged from coastal peat swamps to montane forests, at elevations of 0–1500 m above sea level (asl).

The survey area included the Leuser Ecosystem, which harbours the largest remaining Sumatran orangutan populations, as well as smaller fragmented habitats in Batu Ardan, Siranggas, and Sikulaping. Tapanuli orangutan surveys focused on the Batang Toru Ecosystem, comprising three meta-populations: West Batang Toru, East Batang Toru, and Sitandiang–Sibualbuali, separated by roads, agricultural areas and other barriers. A meta-population, as used here, consists of spatially distinct subpopulations connected by only limited dispersal or gene flow, whereas “population” refers to more continuously distributed groups within which orangutans can more readily interact. Meta-population and population boundaries were delineated using recent distribution models, landscape connectivity analysis and genetic data (e.g., Nowak et al., 2017; Singleton et al., 2024; Utami-Atmoko et al., 2017; Ancrenaz et al., 2021; Fig. 1).

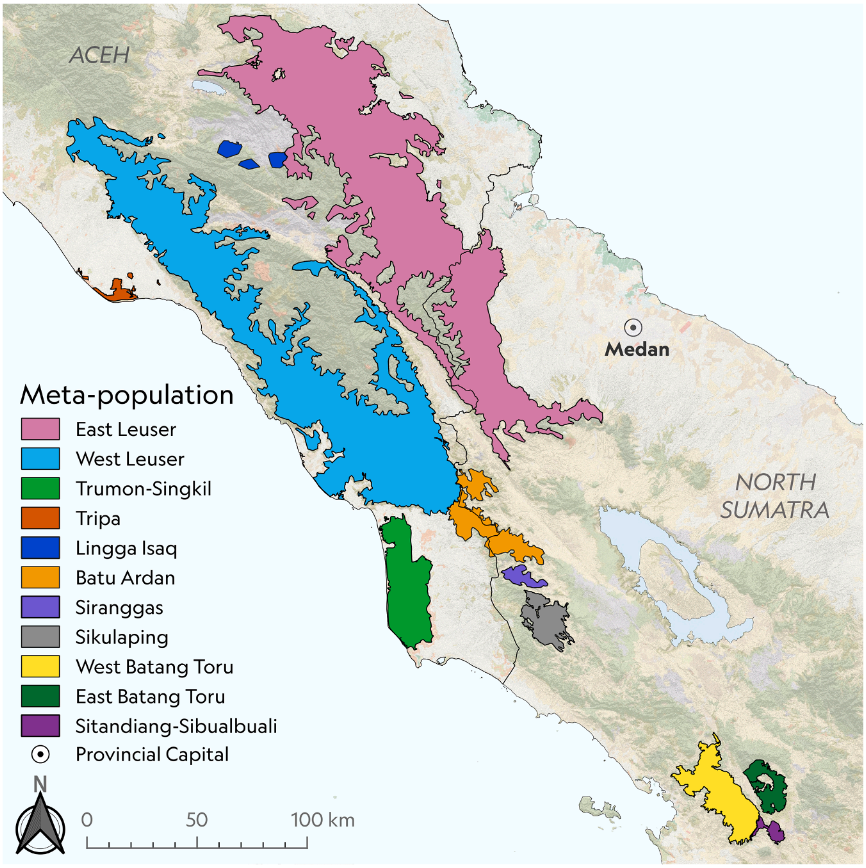

Fig. 1. Meta-population boundaries for Sumatran and Tapanuli orangutans used in this study, northern Sumatra, Indonesia. Eleven meta-populations are delineated across the Leuser Ecosystem (East Leuser, West Leuser, Trumon-Singkil, Tripa, and Linga Isaq), BSS Forest Cluster (Batu Ardan, Siranggas, and Sikulaping), and Batang Toru Ecosystem (West Batang Toru, East Batang Toru, and Sitandiang-Sibualbuali). Map lines do not necessarily depict accepted national boundaries.

2.2. Survey design

Transects were placed using systematic random sampling (Buckland et al., 2001) following Wich et al. (2016) and the IUCN Best Practice Guidelines for Great Ape Surveys (Kühl et al., 2008). A total of 208 line transects were established across the study area, each planned at 1 km in length; some were shortened due to impassable terrain, yielding a total survey effort of 198 km. Transect intervals were approximately 12 km in the Leuser Ecosystem, 7 km in Trumon-Singkil, 8 km in the BSS Forest Cluster and 5 km in the Batang Toru Ecosystem (Fig. 2). All transects were oriented east-west to ensure standardised coverage.

Transects were allocated to each meta-population approximately in proportion to area, with additional consideration for habitat heterogeneity: East Leuser (60 transects), West Leuser (43), Trumon-Singkil (22), Sikulaping (12), Batu Ardan (10), Siranggas (3), West Batang Toru (37), East Batang Toru (15) and Sitandiang–Sibualbuali (6) transects. Within the Leuser Ecosystem, transect locations from Wich et al. (2016) were replicated to enable direct temporal comparison. For the Batu Ardan/Sikulaping/Siranggas cluster and the Batang Toru Ecosystem, which were not systematically surveyed by Wich et al. (2016), new transect locations were established. A small number of transects were positioned outside the IUCN, (2023) range boundary in the BSS Forest Cluster and Batang Toru Ecosystem, targeting areas of potential orangutan habitat not previously surveyed systematically; any nests detected in these locations were included in the analysis. Due to permit restrictions, the Tripa meta-population could not be surveyed (density is therefore model-derived; see Section 3.5).

2.3. Data collection

Field surveys were conducted between 2021 and 2023 by trained teams led by conservation organisations in collaboration with the Indonesian Ministry of Forestry and local partners. All field teams underwent standardised training by experienced nest survey staff, some of whom had been involved in the previous (Wich et al., 2016) surveys to ensure consistent data collection. Surveys were conducted only during favourable weather conditions to maximize visibility and detection probability.

Each transect was walked in one direction, at approximately 1 km/hour, recording all orangutan nests visible from the transect

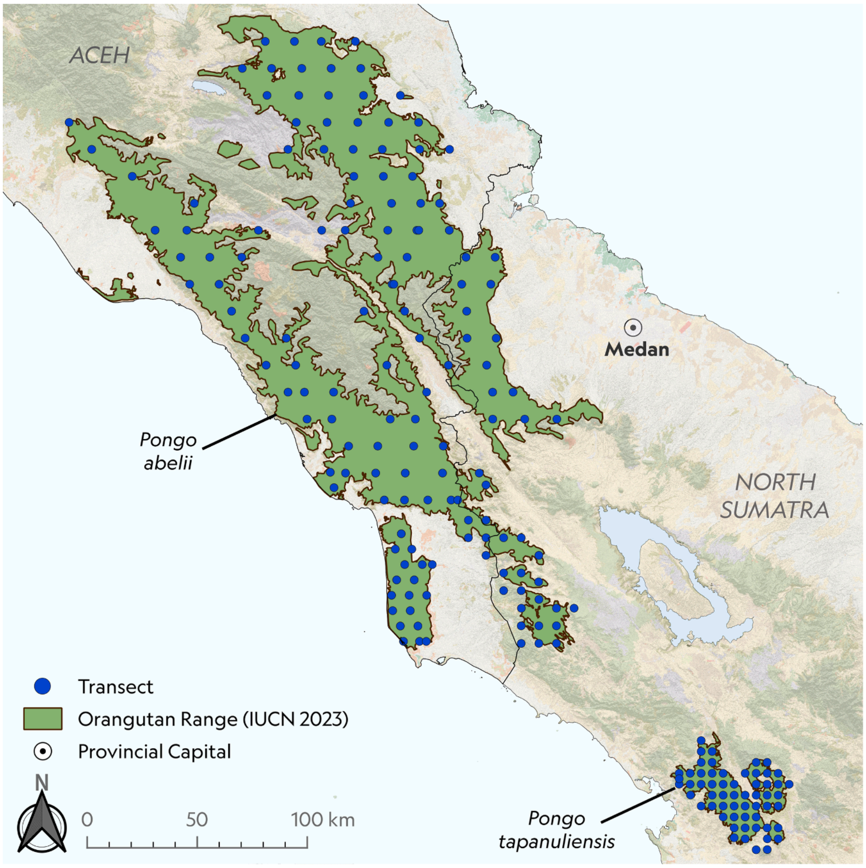

Fig. 2. Locations of the 208 nest-survey transects (~1 km each) used to estimate Sumatran and Tapanuli orangutan population densities across northern Sumatra, Indonesia, 2021–2023. Transects were systematically distributed across 11 meta-populations using stratified random placement. (Note: differences between the Wich et al. 2016 and IUCN 2023 range boundaries reflect a subsequent IUCN range update rather than differences in survey coverage.).

line. For each nest, the perpendicular distance from the transect was measured to the nearest metre for distance sampling analysis. Nest height, tree species, and nest position and decay stage (four classes; Ancrenaz et al., 2004) were also recorded as ancillary data for quality-control measures; missing or inconsistent decay classifications can indicate observer error, but these variables were not used in the density modelling.

Inspection of detection distance histograms (fig. S1; table S2) revealed a lower frequency of nests detected on and immediately adjacent to the transect line compared to the second distance interval, suggesting some on-line detection failure in the new survey; this is reflected in the lower estimated detection probability (44%) relative to Wich et al. (2016) (52%) and is discussed further in Section 4.4.

2.4. *Data analysis*

2.4.1. *Detection functions and truncation*

Total survey effort was 198 km of line transects, comprising 141 km within Sumatran orangutan habitat and 57 km within Tapanuli orangutan habitat. Detection functions and effective strip widths (ESW) were estimated using conventional distance sampling in Distance 7.3 Release 2 (Thomas et al., 2010).

Species-specific hazard-rate detection functions were selected following AIC criteria, with truncation distances of 32.5 m for Sumatran orangutans (retaining 99% of observations) and 35 m for Tapanuli orangutans (94%). Full model selection details are provided in table S1.

2.4.2. *Nest-to-orangutan density conversion*

orangutan density was derived from nest density following standard protocols (Buckland et al., 2001; Kühl et al., 2008; van Schaik et al., 1995) and the methodology of Wich et al. (2016):

$$\widehat{D}_{OU} = \frac{\widehat{D}_N}{\widehat{p} \times \widehat{r} \times \widehat{t}}$$

Where $\widehat{D}_{OU}$ represents orangutan density, $\widehat{D}_N$ is nest density, $\hat{p}$ is the proportion of nest-builders in the population (set at 0.89), $\hat{r}$ is the daily nest production rate (1.8 nests /individual per day), and $\hat{t}$ is the nest decay time (days). Values for $\hat{p}$ and $\hat{r}$ were taken from published literature (Buij et al., 2003; van Schaik et al., 1995; Husson et al., 2009) and are the same as those used in Wich et al. (2016), enabling direct comparison.

Nest decay times ($\hat{t}$) were assigned to each transect and prediction grid cell using elevation- and habitat-based rules consistent with Wich et al. (2016), ensuring direct comparability (table S6). Four categories were applied: Ketambe highland (244.8 days; >1000 m asl), Ketambe lowland (142.9 days; 300–1000 m), Suaq peat swamp (284.8 days; <300 m in peat), and Marike/Sikundur (194.4 days; <300 m in non-peat). A longer site-specific estimate from Batang Toru (501.5 days; Wich et al., 2012a) exists but was not broadly applied, consistent with Wich et al. (2016). Because variation in nest decay time can substantially influence population estimates (Mathewson et al., 2008), maintaining consistent assignment rules was essential for valid temporal comparison.

These conversion parameters ($\hat{p}$, $\hat{r}$, $\hat{t}$) were incorporated into the GLM offset term so that model predictions directly yielded orangutan density rather than raw nest counts (Section 2.4.4). Confidence intervals were derived through parametric bootstrapping (1000 iterations) following the percentile method described in Wich et al. (2016).

2.4.3. *Environmental predictors and factor analysis*

Twelve environmental predictors were selected following Wich et al. (2016), each extracted at 1 km^2 resolution for transect midpoints and grid cells. Topographic variation was represented by elevation (SRTM 1 Arc-Second; NASA JPL, 2013). Ecological conditions were characterised by binary forest cover and categorical forest type (peat-swamp, lowland, lower montane), derived from the MoEF land-cover maps with elevation-based delineation (Margono et al., 2012), and above-ground biomass (ESA CCI Biomass; Santoro et al., 2021). Human disturbance was captured through gridded population density (WorldPop 2020) and Euclidean distance

Table 1
Varimax-rotated factor loadings for 10 environmental predictors used in the density model for Sumatran and Tapanuli orangutan, northern Sumatra. Four factors were retained (eigenvalue ≥ 1), explaining 78% of total variance. **Bold** values indicate loadings ≥ 0.5.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Elevation	0.121	**0.696**	**0.510**	0.231
Carbon	**−0.467**	0.248	0.152	**0.570**
Forest Cover	0.060	−0.040	0.021	**0.735**
Type 1 - Peatland	0.058	−0.017	**−0.845**	−0.057
Type 2 - Lowland	0.282	**−0.834**	0.401	0.243
Type 3 - Upland	**−0.176**	0.847	0.190	0.092
Total Rainfall	**0.921**	−0.088	−0.017	0.043
Rainfall Variation	**0.964**	−0.098	−0.077	−0.069
Temperature Range	**−0.507**	0.185	**0.561**	0.006
Temperature Mean	**0.989**	−0.104	−0.073	−0.043
% Variance explained	32%	22%	16%	8%

to the nearest road (BIG road dataset; Geospatial Agency of Indonesia, 2017). Climate was represented by four CHELSA v2.1 variables (Karger et al., 2017): mean annual precipitation, precipitation seasonality, mean annual temperature and temperature annual range. All layers were resampled to 1 km (30 arc-second) resolution (see table S4 and S5).

Factor Analysis (FA) with varimax rotation was applied to the 10 ecological and climatic predictors to reduce multicollinearity following Wich et al. (2016), using the psych package (Revelle, 2024) in R Studio 2023.06.1.524 (R Core Team, 2024). To maximise the geographic and ecological coverage of the factor structure across the northern Sumatran orangutan landscape, FA was conducted on the combined dataset of 208 current survey transects and the 259 Wich et al. (2016) baseline transects ($n = 467$); the negative binomial GLM for current abundance estimation was subsequently fitted to the 2021–2023 transects only. Human population density and distance to roads were retained as separate predictors, as these did not load on factors with eigenvalues ≥ 1. Four interpretable ecological gradients were extracted: climate, elevation, peat-swamp habitat, and forest structure, explaining 78% of total variance (Table 2). These four factors and the two human impact variables served as predictors in subsequent modelling. The Kaiser-Meyer-Olkin measure of sampling adequacy was 0.67, and Bartlett's Test of Sphericity was highly significant ($\chi^2 = 4372.63$, df = 45, $P < 0.001$), confirming the data were suitable for FA.

2.4.4. *Generalized linear modelling*

Orangutan density was modelled using Negative Binomial Generalized Linear Models (GLMs) (Venables and Ripley, 2013) with spatial autocorrelation terms, following Wich et al., (2016). An offset term incorporating nest decay time, proportion of nest-builders, and nest production rate was included so that model predictions yielded orangutan density directly, while also accounting for variation in transect length (Hedley and Buckland, 2004; Wich et al., 2016). The spatial autocorrelation term was calculated as the distance-weighted average of neighbouring residuals (Dormann et al., 2007). The full model was specified as:

$$\log(\lambda_i) = \beta_0 + \beta_1(\text{Factor1}_i) + \beta_2(\text{Factor2}_i) + \beta_3(\text{Factor3}_i) + \beta_4(\text{Factor4}_i) + \beta_5(\text{HumanPop}_i) + \beta_6(\text{Roads}_i) + \text{ac.term} + \text{offset}$$

Where λ_i represents the expected nest count at location i, the β parameters are regression coefficients, and ac.term is the spatial autocorrelation term. This full model was compared against a null model containing only the intercept and autocorrelation term using likelihood ratio tests. The full model significantly outperformed the null model ($\chi^2 = 28.15$; df = 6; $P < 0.001$). Model diagnostics, including residual plots, Q-Q plots, and observed versus predicted values, showed no evidence of model misspecification or failure to meet assumptions (figure S2).

2.4.5. *Spatial predictions*

Orangutan density was estimated across the entire study area at 1 km^2 resolution. All 64 possible combinations of the six predictor variables were evaluated, each retaining the autocorrelation term and offset, with predictions AIC-weighted across models. For each of 1000 bootstrap iterations, new coefficients were drawn from normal distributions centred on each model's estimates with standard errors and predictions were generated from a negative binomial distribution. Confidence intervals (95%) were computed for overall species populations and for each meta-population separately by summing the bootstrapped cell-level predictions within each boundary.

2.4.6. *Meta-population delineation*

Meta-population boundaries were refined from the 2016 PHVA (Utami-Atmoko et al., 2017) on the basis of habitat connectivity, natural barriers and observed population structure, resulting in eight meta-populations for Sumatran orangutan and three for Tapanuli orangutans (11 total). Two reintroduced populations (Jantho and Bukit Tigapuluh) were excluded from the analysis as they originate from rehabilitant and translocated individuals rather than wild populations. Key refinements included: (1) establishing Lingga Isaq as a distinct Sumatran orangutan meta-population, separated from northern East Leuser by non-forest habitat; (2) reassigning the northern portion of Batu Ardan, east of the Alas River, from West Leuser to join southern Batu Ardan, reflecting the river's role as a dispersal barrier; (3) retaining Siranggas as distinct from Batu Ardan, given its geographic isolation; and (4) recognising Sitandiang–Sibualbuali as a separate Tapanuli orangutan meta-population, now isolated south-east of the Batang Toru River.

Table 2

Negative Binomial Generalised Linear Model (GLM) results for combined Sumatran and Tapanuli orangutan nest density, northern Sumatra. Full model (AIC = 1138) compared to spatial null model (AIC = 1154); likelihood ratio test $\chi^2 = 28.15$, df = 6, $P < 0.001$. Predictors include four factor scores, human population density, distance to roads, and a spatial autocorrelation term (ac.term).

Model		Estimate	SE	z value	Pr(> [z])
Full model	**AIC = 1138**				
(Intercept)		−0.263	0.082		*
Factor 1		−0.048	0.092	−0.525	0.600
Factor 2		−0.130	0.09	−1.440	0.150
Factor 3		−0.401	0.104	−3.864	< 0.001
Factor 4		0.422	0.114	3.707	< 0.001
z.human.pop		−0.266	0.102	−2.613	0.009
z.roads		0.034	0.081	0.418	0.676
ac.term		0.641	0.109	5.868	< 0.001
Null model	**AIC = 1154**				
(Intercept)		−0.163	0.087		*
ac.term		0.670	0.116	5.751	< 0.001

2.4.7. *Habitat Status Analysis*

To assess the level of formal protection afforded to orangutan populations, the estimated population and range area within each Indonesian forest management category were calculated per meta-population. The analysis was conducted within the IUCN, (2023) range polygons for each species. To exclude areas that no longer constitute orangutan habitat, the range was restricted to forested areas below 1500 m asl (based on Hansen et al., 2013 forest cover data for 2023), consistent with the known elevational limit of the species (Wich et al., 2016). The resulting area (1,673,003 ha) was overlaid with the Indonesian Ministry of Environment and Forestry (MoEF) forest management zone classifications, which were grouped into five categories for analysis: (1) strict protection forest (*Kawasan Konservasi*), comprising nature reserves (*Cagar Alam*, CA), wildlife reserves (*Suaka Margasatwa*, SM), national parks (*Taman Nasional*, TN), hunting parks (*Taman Buru*, TB), and nature recreation parks (*Taman Wisata Alam/Hutan Suaka Alam*, HSA/W/SA); (2) protection forest (*Hutan Lindung*, HL); (3) limited production forest (*Hutan Produksi Terbatas*, HPT); (4) production forest, including permanent production forest (*Hutan Produksi Tetap*, HP) and convertible production forest (*Hutan Produksi Konversi*, HPK); and (5) other use areas (*Area Penggunaan Lain*, APL), which lie outside the designated forest estate and have no formal forest protection. Both the percentage of range area and the estimated population within each category were calculated for each meta-population (Table 4; Table S4).

2.4.8. *Forest Cover Loss Analysis*

Forest cover loss within orangutan range areas was quantified using the Hansen et al. (2013) Global Forest Change dataset (version 1.11), which provides annual tree cover loss at 30 m resolution derived from Landsat imagery; forest gain was not assessed as it falls outside the scope of this study. Analyses were conducted within the Wich et al. (2016) range rather than the IUCN (2023) range, as the latter partially reflects current forest extent and would therefore underestimate historical habitat loss. Baseline forest cover (2011) was defined using the Hansen treecover2000 layer with a $\geq$ 30% canopy cover threshold, intersected with the IUCN 2016 range; 2011 was selected as the start of the post-baseline period, immediately following the Wich et al. (2016) current-status reference year of 2010 and coinciding with the close of their systematic surveys (2009–2011). Annual tree cover loss for 2011–2023 was extracted from the Hansen lossyear layer, restricted to pixels classified as forest in 2011. Cumulative loss was calculated per meta-population as absolute area (ha) and as a proportion of baseline 2011 forest area. To assess whether habitat loss was associated with population change, proportional forest loss was regressed against proportional abundance change at the meta-population scale using ordinary least

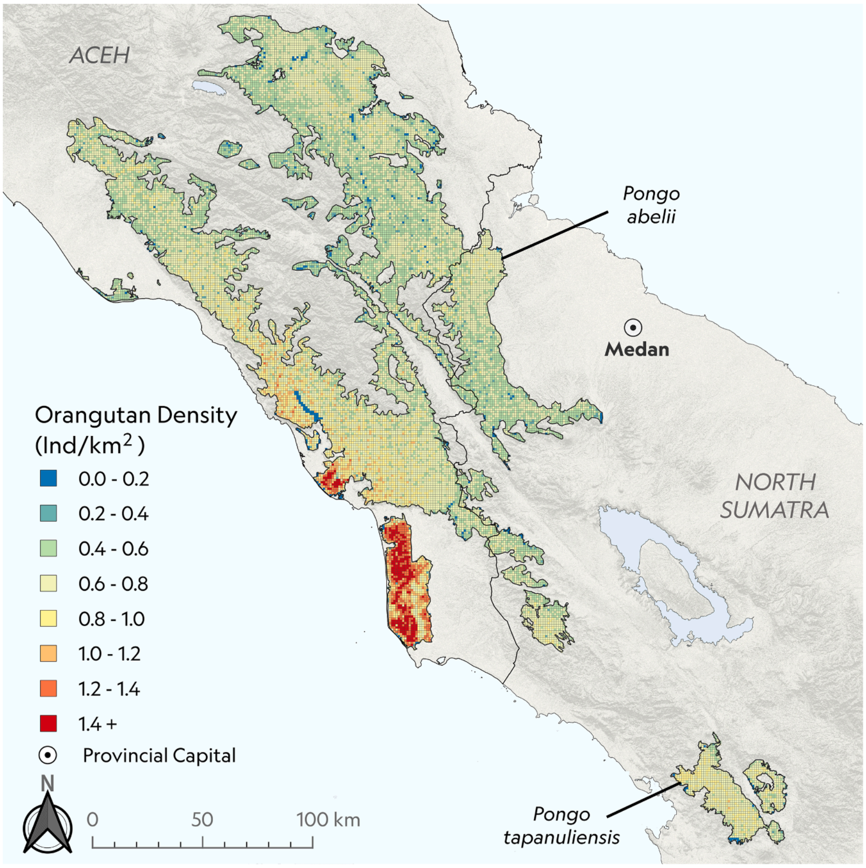

Fig. 3. Predicted orangutan density (individuals/km^2) across the ranges of Sumatran (upper) and Tapanuli orangutan (lower), northern Sumatra, 2021–2023, derived from Negative Binomial GLM spatial predictions at 1 km^2 resolution. Predictions are AIC-weighted across all 64 predictor combinations.

squares regression.

To enable direct temporal comparison of population estimates (hereafter "matched-distribution comparison"), both models were applied to the same 2016 spatial grid (17,796 cells). The 2016 baseline replicates Wich et al. (2016) using their 259 survey transects, detection function, and factor structure. The 2023 estimate uses an independently fitted model based on the 208 transects from the present study, with factor analysis conducted on both transect sets combined and a detection function estimated from the 2023 surveys. All nest-to-density conversion parameters ($\hat{p}$, $\hat{r}$, $\hat{t}$) were held constant between runs. This holds the spatial boundary constant, so that differences in estimated abundance reflect changes in environmental conditions rather than boundary definitions. These estimates are reported alongside, but are distinct from, the current population estimates derived from the IUCN, (2023) range (Section 3.3).

3. Results

3.1. *Nest survey findings*

A total of 1238 orangutan nests were documented across 208 transects, with an average encounter rate of 6.25 nests/km (range: 0–88 nests/km). Of these, 908 nests were recorded along 141 km of Sumatran orangutan transects and 330 along 57 km of Tapanuli orangutan transects. The ESW for Sumatran orangutans was 14.301 m (95% CI: 13.15–15.55), corresponding to a detection probability of 0.440 (95% CI: 0.404–0.478). For Tapanuli orangutans, ESW was 15.014 m (95% CI: 13.19–17.09) with a detection probability of 0.429 (95% CI: 0.377–0.488) (figure S1, tables S2 and S3).

3.2. *Environmental predictors of orangutan density*

Factor loadings revealed clear ecological gradients (Table 1), with the full model significantly outperforming the null model ($\chi^2 = 28.15$; df = 6; $P < 0.001$). Forest structure (Factor 4: $\beta = 0.422$, $P < 0.001$) and human population density ($\beta = -0.266$, $P = 0.009$) were the strongest predictors, with peat-swamp habitat (Factor 3: $\beta = -0.401$, $P < 0.001$) also significant, indicating higher densities in peat-swamp than highland habitats. Climate (Factor 1), elevation (Factor 2) and distance to roads were non-significant. Spatial autocorrelation was highly significant ($\beta = 0.641$, $P < 0.001$).

3.3. *Population density and distribution*

The Sumatran orangutan population is estimated at 11,694 individuals (95% CI: 10,949–12,518), with a mean density of 0.67 individuals/ km^2 across eight meta-populations (Fig. 3, Table 3). Densities varied markedly, from 1.18 individuals/ km^2 in Trumon-Singkil to 0.47 individuals/ km^2 in Lingga Isaq. East Leuser (4926 individuals) and West Leuser (4934 individuals) together account for 84% of the total Sumatran orangutan population; within Gunung Leuser National Park specifically, an estimated 3281 individuals occur at a mean density of 0.40 individuals/ km^2.

The Tapanuli orangutan population is estimated at 716 individuals (95% CI: 645–792), with a mean density of 0.70 individuals/ km^2 across three meta-populations (Fig. 3, Table 3). The largest meta-population is in West Batang Toru (514 individuals), followed by East Batang Toru (159) and Sitandiang–Sibualbuali (43).

Table 3

Population estimates (individuals) and mean density (individuals/km^2) for Sumatran and Tapanuli orangutan meta-populations, northern Sumatra, 2021–2023, derived from Negative Binomial GLM spatial predictions (1000 bootstrap iterations; 95% CI). Range areas derived from the IUCN, (2023) range polygon.

Meta-population	Area (Ha)	Individuals	CI			Density (Ind/Km^2)	CI		
			2.5%		97.5%		2.5%		97.5%
Leuser Ecosystem	**1,655,916**	**11,049**	**10,091**	**-**	**12,162**	**0.67**	**0.58**	**-**	**0.83**
West Leuser	706,219	4935	4605	-	5317	0.70	0.65	-	0.75
East Leuser	836,162	4926	4555	-	5333	0.59	0.54	-	0.64
Trumon - Singkil	91,392	1079	844	-	1377	1.18	0.93	-	1.51
Lingga Isaq	13,048	63	53	-	73	0.47	0.40	-	0.55
Tripa	9095	46	33	-	62	0.51	0.37	-	0.69
BSS Forest Cluster	**104,941**	**644**	**582**	**-**	**710**	**0.61**	**0.55**	**-**	**0.69**
Batu Ardan	59,720	350	319	-	382	0.58	0.53	-	0.63
Sikulaping	34,944	232	209	-	256	0.67	0.60	-	0.73
Siranggas	10,278	62	54	-	72	0.60	0.52	-	0.70
Batang Toru Ecosystem	**102,185**	**716**	**637**	**-**	**804**	**0.70**	**0.58**	**-**	**0.77**
West BT	71,046	514	462	-	573	0.72	0.65	-	0.81
East BT	24,196	159	140	-	179	0.66	0.58	-	0.75
Sitandiang - Sibualbuali	6943	43	35	-	52	0.61	0.50	-	0.74

Note: Area totals derived from IUCN (2023) population range polygon. Grid-based totals differ slightly (~0.2%) due to the inclusion of partial boundary cells.

3.4. Habitat protection status

Across both species, strict protection forest and protection forest together support 82% of all orangutans (10,206 individuals), while 18% (2204 individuals) occur in production forests, limited production forests, or other use areas (Table 4; figure S3). The species differ notably: Sumatran orangutans are relatively evenly split between strict protection and protection forest, whereas Tapanuli orangutans depend overwhelmingly on protection forest with minimal strict protection coverage (table S8).

Protection status also varies markedly among meta-populations (Table 4; table S8). Most orangutans occur in strict protection or protection forest, but notable gaps exist: Tripa has no formal habitat protection, Batu Ardan and Sikulaping lack strict protection coverage and East Leuser has the largest number of individuals in production forest. For Tapanuli orangutans, West Batang Toru is almost entirely protection forest with no strict protection and the small Sitandiang-Sibualbuali population has a substantial proportion in unprotected other use areas.

3.5. Forest cover change and population trends

Between 2011 and 2023, a total of 94,399 ha of forest were lost within the IUCN 2016 range, representing 4.6% of baseline (Table 5). Annual loss rates declined from an average of 8761 ha/yr during 2011–2016, the period corresponding to the Wich et al. (2016) survey window, to 5976 ha/yr during 2017–2023, a 32% reduction (figure S4, S5 and table S9). However, loss increased again in 2023 (7218 ha), with Trumon–Singkil (1989 ha) and East Batang Toru (290 ha) both recording their highest annual losses during the study period. Cumulative loss was highest in Tripa, where 50.9% of 2011 forest cover was cleared, predominantly through peat-swamp conversion to oil palm, followed by Trumon–Singkil (10.5%) and Batu Ardan (8.8%). Forest loss was lowest in Sikulaping (0.8%) and Siranggas (1.0%).

The matched-distribution comparison between 2011 and 2023 shows Sumatran orangutans declining from 13,846 to 11,146 individuals (−19.5%; Table 5), with losses ranging from −75.4% in Tripa to −14.0% in West Leuser. Batu Ardan (−40.2%), Siranggas (−28.2%) and Sikulaping (−14.5%) experienced disproportionately large declines relative to their forest loss, though Wich et al. (2016) did not systematically survey the BSS forest cluster and differences may partly reflect improved coverage. For Tapanuli orangutans, the apparent change from 767 to 716 individuals (−6.6%) should similarly be interpreted with caution, as Wich et al. (2016) did not systematically survey Batang Toru. The current population estimate based on the IUCN, (2023) range (11,694 Sumatran orangutans; 716 Tapanuli orangutans) is reported in Section 3.3; the higher Sumatran orangutan population figure reflects the slightly larger extent of the IUCN, (2023) range.

Regression analysis across all meta-populations revealed a significant relationship between proportional forest loss and proportional population decline ($R^2 = 0.76$, $P < 0.001$; Fig. 4), though the relationship is partly driven by Tripa, which experienced both the highest forest loss (50.9%) and population decline (−75.4%; no direct surveys were conducted in Tripa and this estimate is derived entirely from model extrapolation). Forest loss thus explained 76% of variation in population change across meta-populations, with 24% of variation attributable to other factors.

Disaggregating forest loss by land management category reveals that Other Use areas (APL) account for the largest share of loss in most meta-populations, including all loss in Tripa, 64% in Trumon–Singkil and 48% in East Leuser (table S7). Substantial loss also occurred within strict protection areas, notably 4768 ha in West Leuser, 4328 ha in East Leuser and 4145 ha in Trumon–Singkil. In the Batang Toru Ecosystem, Other Use areas accounted for 65% of loss in West Batang Toru and 48% in East Batang Toru.

Table 4

Distribution of estimated Sumatran and Tapanuli orangutan populations (individuals and % of total) across Indonesian forest management categories, by meta-population. Analysis restricted to forested areas below 1500 m asl within the IUCN (2023) range (total area: 1,673,003 ha).

Meta-population	Est. Population	Strict Protection (%)	Protection Forest (%)	Limited Production (%)	Production (%)	Other Use (%)
Pongo abelii	**11,693**	**38.5**	**43.4**	**2.8**	**10.1**	**5.2**
East Leuser	4926	32.6	42.9	0.9	19.5	3.9
West Leuser	4934	36.6	53.3	3.1	3.8	3.2
Trumon–Singkil	1079	91.9	0.1	0.0	0.0	8.0
Lingga Isaq	64	79.3	2.0	0.1	18.5	0.1
Tripa	46	0.0	0.0	0.0	0.0	100.0
Batu Ardan	350	0.0	66.0	18.6	8.6	6.8
Sikulaping	232	0.0	83.1	13.9	0.0	3.0
Siranggas	62	55.1	11.3	33.5	0.1	0.1
Pongo tapanuliensis	**716**	**9.5**	**78.6**	**0.1**	**1.9**	**9.9**
West Batang Toru	514	0.0	93.7	0.0	0.0	6.3
East Batang Toru	159	30.1	49.8	0.0	5.5	14.7
Sitandiang–Sibualbuali	43	53.1	0.0	0.0	15.3	31.6
Grand Total	**12,410**	**34.4**	**47.9**	**2.7**	**10.6**	**4.5**

Note: See Box S1 in Supplementary Materials for definitions of Indonesian forest management categories.

Table 5
Matched-distribution comparison of Sumatran and Tapanuli orangutan population estimates and forest cover change by meta-population 2011–2023. *Note: the 2016 baseline estimate replicates* Wich et al. (2016) *using their survey transects and spatial grid. The 2023 estimate applies an independently fitted model to the same spatial boundary. Forest cover loss from* Hansen et al. (2013) *Global Forest Change v1.11.*

Meta-population	Orangutan Population			Forest Loss	
	2011	2023	Change(%)	ha	%
Leuser Ecosystem	**12,931**	**10,519**	**−18.7**	**85,416**	**4.7**
East Leuser	5893	4634	−21.4	40,940	4.4
West Leuser	5499	4729	−14.0	23,245	2.9
Trumon–Singkil	1295	1077	−16.8	11,465	10.5
Tripa	212	52	−75.4	9412	50.9
Lingga Isaq	32	27	−15.5	354	5.4
BSS Forest Cluster	**915**	**627**	**−31.5**	**6410**	**5.3**
Batu Ardan	556	332	−40.2	5953	8.8
Sikulaping	272	232	−14.5	341	0.8
Siranggas	87	63	−28.2	116	1.0
Batang Toru Ecosystem	**767**	**716**	**−6.6**	**2574**	**2.2**
West Batang Toru	561	514	−8.2	1101	1.3
East Batang Toru	162	159	−2.1	1263	4.5
Sitandiang–Sibualbuali	44	43	−3.1	211	2.6
Total - *P. abelii*	**13,846**	**11,146**	**−19.5**	**91,825**	**4.7**
Total - P. tapanuliensis	**767**	**716**	**−6.6**	**2574**	**2.2**
Combined Total	**14,613**	**11,862**	**−18.8**	**94,399**	**4.6**

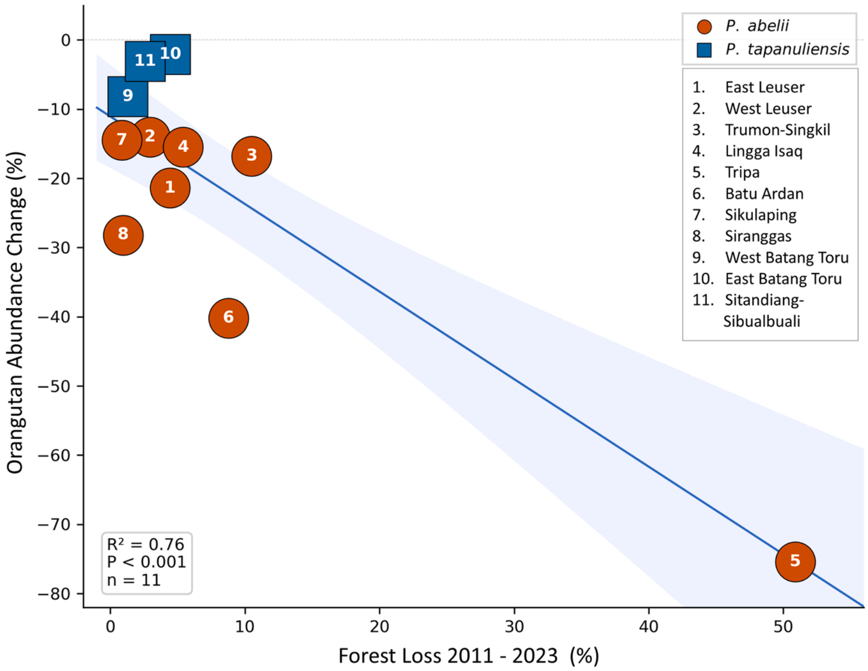

Fig. 4. Relationship between proportional forest loss (2011–2023) and proportional population change across Sumatran and Tapanuli orangutan meta-populations, northern Sumatra. Forest loss explains 76% of variation in population change ($R^2 = 0.76$, $P < 0.001$). Numbers identify meta-populations. Meta-populations falling below the regression line (notably Batu Ardan and Siranggas) experienced declines exceeding those predicted by habitat loss alone, implicating additional non-habitat threats.

4. Discussion

4.1. *Population trends and threats*

The matched-distribution comparison indicates a 19.5% decline in Sumatran orangutan numbers since the Wich et al. (2016) baseline, equating to approximately 1.8% per year. While serious, this is somewhat less severe than the 2–3% annual losses reported for Bornean orangutans over similar periods (Santika et al., 2017; Voigt et al., 2018), possibly reflecting regional differences in threat intensity or conservation investment (Santika et al., 2022). For Tapanuli orangutans, the apparent decline of 6.6% should be interpreted cautiously, as Wich et al. (2016) did not systematically survey Batang Toru, so differences may partly reflect improved survey coverage rather than true population loss. The Tripa decline (−75%) is consistent with documented rates of peat-swamp conversion (Husson et al., 2009; Wich et al., 2011) but similarly represents model-derived extrapolations lacking ground-truth validation.

The 32% reduction in annual forest loss rates between study periods may reflect strengthened enforcement following the 2016 peat moratorium (Santika et al., 2022), though the resurgence in 2023, particularly in Trumon–Singkil and East Batang Toru, suggests this progress is fragile. At the aggregate level, overall decline has broadly tracked Wich et al. (2016) moderate projections; the current estimate of 12,410 from the IUCN, (2023) range sits between their 2020 moderate-deforestation scenario (scenario 2: 12,546) and the 2030 land-use plan scenario (scenario 3: 12,019). However, this aggregate figure masks regional variation. The Leuser Ecosystem populations, where methods are most directly comparable, show losses more consistent with the high-deforestation scenarios.

The close correspondence between current estimates and the moderate-deforestation scenarios projected by Wich et al. (2016) demonstrates the value of combining predictive scenario modelling with periodic empirical surveys. Together, these tools provide not just a snapshot of population status but a framework for evaluating whether conservation interventions are delivering measurable outcomes. Realising this potential requires that future assessments are designed explicitly to test intervention effectiveness, attributing observed trends to specific conservation actions rather than treating surveys as endpoints in themselves.

Habitat loss alone does not explain the full extent of population decline. The 24% of variation in population change not accounted for by forest loss is concentrated in meta-populations falling clearly below the regression line. This is most pronounced across the BSS forest cluster, where all three constituent meta-populations deviate markedly from the regression. That these are small, fragmented, and accessible meta-populations suggests they are disproportionately affected by killing, the pet trade, and human–orangutan conflict (Marshall et al., 2006; Meijaard et al., 2011; Wich et al., 2012a). Regional government records corroborate this directly: 15 individuals recorded across Aceh and North Sumatra between 2012–2024 bore confirmed air rifle pellet wounds, consistent with deliberate persecution rather than incidental injury. The disproportionate declines in the BSS cluster should be interpreted with the caveat that Wich et al. (2016) did not systematically survey these areas, and differences may partly reflect improved survey design. Nonetheless, these residual declines are consistent with direct mortality operating at a scale sufficient to drive population decline independently of habitat change. Critically, excess decline is not confined to small or poorly protected populations; East Leuser, the largest meta-population in the study, also sits below the regression line, indicating that non-habitat mortality operates across the range rather than only in its most vulnerable corners. Sherman et al. (2022) estimated that killing alone accounted for annual mortality substantially exceeding sustainable demographic thresholds for both Sumatran species combined, a rate that, compounded with habitat loss, readily explains the residual declines we observe. This pattern is not confined to the present day; Meijaard et al. (2021) showed that a combination of habitat fragmentation and unsustainable hunting drove the historical range contraction of Tapanuli orangutans prior to the industrial-scale deforestation that began in the 1970s.

These findings have direct implications for how interventions are designed across both species' ranges. Government records document 169 direct wild releases in Aceh and North Sumatra between 2012 and 2024, none with post-release monitoring. Sherman et al. (2025) demonstrated that wild-to-wild translocation carries significant mortality risks for translocated individuals and can disrupt receiving populations - risks that remain unquantifiable in the absence of such data, and that compound existing demographic pressure in populations where non-habitat mortality is already driving declines that habitat protection alone cannot arrest.

The implications of non-habitat mortality are most severe for Tapanuli orangutans, for which this study provides the first systematic baseline. At 716 individuals, Tapanuli orangutans are acutely vulnerable to stochastic events, genetic bottlenecks, and ongoing fragmentation (Nater et al., 2017). The species faces specific threats from a hydroelectric project fragmenting its range (Laurance et al., 2020), a gold mine, and agricultural conversion (Wich and Meijaard, 2021). Any further losses may be unsustainable and conservation efforts should aim for zero additional mortality (Wich and Meijaard, 2021).

4.2. Environmental drivers of orangutan density

Forest structure was the strongest positive predictor of orangutan density, consistent with the importance of intact, carbon-rich forests with complex canopies and fruit abundance (Husson et al., 2009; Marshall et al., 2009; Wich et al., 2016). Human population density had a significant negative effect, as in Wich et al., (2016), reflecting the compounding threats of conflict and hunting in human-dominated landscapes (Meijaard et al., 2010; Wich et al., 2012a).

A notable contrast to Wich et al. (2016) is the non-significance of climate (Factor 1) and elevation (Factor 2), which were among the strongest predictors in the earlier study. Conversely, forest structure (Factor 4) and peat-swamp habitat (Factor 3) are highly significant here but were not in Wich et al. (2016). These contrasts most likely reflect differences in how variables loaded across factors between studies, driven by changes in the underlying environmental datasets and transect configurations rather than genuine ecological differences. The non-significance of elevation in particular may reflect that its effect on orangutan density operates primarily through its correlates - forest type, temperature, and food availability - which are captured by other factors in the model rather than by elevation directly. It is also possible that the lower nest encounter rates observed in interior areas, which tend to be at higher elevations, reduced the statistical power to detect an elevation effect independently of other correlated predictors.

The significant negative association with Factor 3 (Peat-swamp vs. Highland) indicates that peat-swamps support higher orangutan densities than highland habitats. These high densities likely reflect more stable year-round food availability in peat-swamp forests compared to dryland forests, where fruit production fluctuates with masting events (Wich and van Schaik, 2000; Marshall et al., 2009; Wich et al., 2011). A historical refugium effect from minimal human settlement and hunting relative to dryland forests on mineral soils may also contribute (Marshall et al., 2006; Wich et al., 2012a); the ongoing conversion of peat-swamps for oil palm cultivation is therefore particularly consequential.

Distance to roads was non-significant despite published evidence linking road development to orangutan decline (Gaveau et al., 2009a, 2009b; Sloan et al., 2018). Wich et al. (2016) also found distance to roads non-significant, suggesting this result is consistent rather than anomalous. Road impacts likely operate indirectly through human population density, which is significant, rather than exerting an independent effect once human presence is accounted for. This interpretation is consistent with the broader finding that orangutan distribution responds more strongly to socio-ecological context than to physical landscape features alone (Marshall et al., 2006; Wich et al., 2012a). The highly significant spatial autocorrelation term indicates that orangutan densities are spatially clustered beyond what the measured environmental predictors explain. While the drivers of this residual clustering cannot be determined from the model alone, they likely include fine-scale variation in hunting pressure and social structure, as documented in comparable contexts by Marshall et al. (2006) and Wich et al. (2012a).

4.3. Protection status and policy implications

Under Indonesian law, strict protection forests (*Kawasan Konservasi*) afford the highest level of habitat protection, yet only 38.5% of Sumatran orangutans and 9.5% of Tapanuli orangutans occur within these areas. Protected forests (*Hutan Lindung*) support a further 43.4% and 78.6% *respectively*. The remaining populations occur in production forests and other use areas (*Area Penggunaan Lain,* APL), where habitat protection is minimal. In total, 18% of all orangutans (ca. 2204 individuals) reside in these low protection landscapes.

Orangutans are fully protected under Indonesian law (Government of Indonesia, 1990, 1999; MoEF, 2018), but the effectiveness of that protection depends on the underlying land-use designation. Tripa, where the entire estimated population occurs in APL, represents the most acute vulnerability. Even within larger meta-populations, substantial numbers occur in production forest: nearly 1000 orangutans in East Leuser alone. Studies in Borneo consistently show that orangutan populations in unprotected areas decline more rapidly than those within formally gazetted areas (Wich et al., 2012b; Voigt et al., 2022; Santika et al., 2022), a pattern our data support, though well-managed production forest can maintain viable orangutan populations where logging intensity is low and hunting is controlled (Ancrenaz et al., 2010), indicating that production forests are not inherently without conservation value.

Trumon–Singkil, where 90% of the population falls within a strict protection forest, illustrates the value of formal protection, though declines occur even there, indicating that gazettement alone is insufficient without effective management (Santika et al., 2022). Disaggregating forest loss by land management category further contextualises this: the concentration of loss in Other Use areas across most meta-populations underscores the inadequacy of protected area coverage as the sole conservation instrument, while losses within formally designated strict protection forest reflect encroachment and indicate that on-the-ground conversion continues despite legal prohibition. In the BSS Forest Cluster, losses concentrated in Protection Forest and Other Use areas are consistent with the cluster's lack of strict protection coverage and its vulnerability to agricultural encroachment. In the Batang Toru Ecosystem, the majority of loss in Other Use areas reflects the limited strict protection afforded to *P. tapanuliensis* habitat; 94% of West Batang Toru is *Hutan Lindung* rather than national park, a vulnerability the ongoing hydropower development demonstrates clearly (Laurance et al., 2020; Wich and Meijaard, 2021).

Protection forests, even those with lesser legal status than full conservation areas, support over 80% of Sumatran orangutans and nearly 90% of Tapanuli orangutans, making their continued integrity the single most important conservation priority. Restoring connectivity between fragmented meta-populations, particularly between the three Batang Toru populations where gene flow is essential to long-term viability (Wich and Meijaard, 2021) and strengthening community-based conflict mitigation (Ancrenaz et al., 2021; Sitompul et al., 2024) are equally critical. In unprotected landscapes, including oil palm concessions where orangutans persist outside the formal forest estate, coexistence approaches developed in Borneo, including retention of small forest fragments, high conservation value assessments, and conflict mitigation protocols, provide applicable models for Sumatra (Ancrenaz et al., 2021).

The legal framework to achieve this exists: the National Conservation Strategy and Action Plan (MoEF, 2019), Aceh's Wildlife Management Qanun (Qanun No. 11/2019) and the North Sumatra Regional Spatial Plan (Peraturan Daerah No. 2/2017) together provide the statutory basis for protecting orangutan habitat across both species' ranges; the Qanun additionally mandates species-specific action planning and prohibits killing and trade, providing the foundation for targeted wildlife crime enforcement. Translating this framework into coordinated action across national, provincial, district, and community levels remains the central implementation challenge, and progress on subsidiary instruments such as species-specific action plans will be critical to realising the Qanun's full potential. What is urgently needed is a coordinated conservation action plan for both species that clearly defines roles and responsibilities across land management agencies, NGOs, the research community, and local governments, grounded in the empirical priorities identified here. Santika et al. (2022) demonstrated that well-targeted conservation investment in Sumatra generates measurable returns; the population and protection data presented here provide the empirical foundation for directing that investment to where the need is greatest.

4.4. Methodological considerations and limitations

The analytical approach closely follows Wich et al. (2016), enabling direct temporal comparison for Sumatran orangutan populations within the Leuser Ecosystem, where both studies applied comparable methods, survey designs, and nest-to-density conversion parameters. For Batang Toru, comparison is more limited: Wich et al. (2016) included Batang Toru within a single-species estimate that predated the description of the Tapanuli orangutan, while earlier estimates for Batang Toru were derived from localised surveys using different methods (Wich et al., 2012a; Kuswanda et al., 2021). The present estimate of 716 Tapanuli orangutan individuals can be compared tentatively with earlier figures of 577–760 (Wich et al., 2019; Kuswanda et al., 2021), but differences in coverage, transect placement, and modelling approach preclude definitive conclusions about trends. Establishing a robust temporal baseline for Tapanuli orangutans is a key contribution of this study, against which future surveys can be directly compared. The GLM with spatial autocorrelation confirms the established roles of forest structure and human population density in determining orangutan density (Wich et al., 2016); the primary value of this framework lies in generating spatially explicit density predictions for conservation planning rather than identifying novel ecological relationships.

Encounter rates reflect the combined influence of orangutan density and survey conditions; the 37% decline in encounter rate between studies (9.98–6.25 nests/km) exceeds the modelled population decline of 19.5%, suggesting that variation in field conditions between survey periods, including differences in available survey time and weather constraints, may have contributed to lower nest detection in the present study. Inspection of the detection distance histograms (Fig. S1) supports this interpretation: the lower frequency of nests recorded on and immediately adjacent to the transect line relative to the second distance interval suggests some on-line detection failure, which is also consistent with the lower estimated detection probabilities in the current survey (Sumatran orangutan: 44%; Tapanuli orangutan: 43%) compared to Wich et al. (2016) (52%). This represents an unresolved limitation that future surveys should address through standardised time allocation per transect independent of external scheduling constraints.

Several limitations merit consideration. Survey coverage, while the most extensive to date, represents less than 0.01% of the total range area and model prediction warrants caution (Kühl et al., 2008). Systematic random sampling, transect allocation proportional to habitat area, and the use of spatial autocorrelation in the GLM together reduce, but do not eliminate extrapolation uncertainty. Estimates for meta-populations with lower transect density should be interpreted with additional caution, as model predictions in unsurveyed areas rely entirely on environmental covariates without empirical nest count validation. Variation in nest decay rates across habitat types can substantially influence population estimates (Mathewson et al., 2008); identical decay rates and assignment rules as Wich et al. (2016) were applied to ensure comparability, but dedicated decay rate studies in each meta-population would improve precision. The BIG (Geospatial Agency of Indonesia, 2017) road dataset used here aggregates all road classes; disaggregating by type (e.g., logging roads vs. national highways) may reveal stronger associations with orangutan density, as different road categories facilitate different levels of forest access and encroachment. Future analyses incorporating road classification and density metrics could better capture these effects. The Tripa estimate is derived entirely from model extrapolation and requires validation with ground surveys when access permits. The absence of direct hunting data limits the ability to model non-habitat threats. Finally, while this study provides the first systematic assessment of the Tapanuli orangutan, the lack of a comparable historical baseline limits temporal inference for this species.

Emerging methods offer complementary approaches for future assessments. Thermal infrared drone surveys have demonstrated the ability to detect and directly count individual Tapanuli orangutans in closed-canopy forest, with counts matching ground-based totals and providing broader spatial coverage (Rahman et al., 2025); Koloski et al. (2025) provide a broader review of the strengths, challenges, and opportunities of such approaches for orangutan monitoring. Citizen science-based occupancy monitoring, recently trialled for orangutans in Kalimantan, offers an additional means of generating presence data across large unprotected areas while building local community support for conservation (Omar, 2025). Integrating these approaches with systematic nest surveys could reduce reliance on environmental extrapolation in areas of low transect density.

5. Conclusion

This study provides the most comprehensive range-wide reassessment of Sumatran and Tapanuli orangutans since Wich et al. (2016), estimating 11,694 Sumatran orangutans and 716 Tapanuli orangutans across the IUCN, (2023) range (12,410 combined). On a constant 2016 population footprint, Sumatran orangutans declined by 19.5% between 2011 and 2023, already falling below most 2030 projections made a decade ago. Forest loss explains much, but not all, of this decline, indicating that additional mortality pressures operate alongside habitat conversion.

In several meta-populations, declines substantially exceeded proportional forest loss, implicating killing, conflict, and fragmentation as compounding drivers. Given the exceptionally slow life histories of both species, recovery from non-natural mortality is inherently limited (Marshall et al., 2009; van Noordwijk et al., 2018). Stabilisation therefore requires not only halting habitat conversion but also reducing anthropogenic mortality to the lowest achievable level. The severe contraction of the Tripa meta-population, driven by peat-swamp conversion, illustrates the vulnerability of populations outside effective protection.

For Tapanuli orangutans, this study establishes the first systematic baseline against which future change can be measured. At 716 individuals distributed across three increasingly fragmented meta-populations, the species remains demographically fragile. Hydropower development and associated infrastructure in the Batang Toru landscape pose immediate risks to connectivity; maintaining functional linkage between West and East Batang Toru is therefore essential for long-term viability. Since the surveys presented here were completed, Cyclone Senyar brought extreme rainfall to northern Sumatra in late November 2025, triggering widespread landslides across the Batang Toru landscape. Satellite analysis estimated 8303 ± 1760 ha of intact forest destroyed in the West Block alone, with a projected 11% mortality among the West Block population (~58 individuals). This single-event loss far exceeds the ~1%/year mortality threshold considered sufficient to drive the species toward extinction (Meijaard et al., 2026). The same storm caused extensive flooding and habitat damage across parts of the Sumatran orangutan range in the Leuser Ecosystem; the full impacts on both species remain to be quantified and impact surveys are currently underway. The population baselines established in this study have therefore already been overtaken by events, and the urgency of the conservation actions identified here has only increased.

Although 82% of all orangutans occur within strictly-protected or protected forest, the remaining 18% in production forest and APL landscapes represent a concentrated exposure to continued loss. Within concessions, incorporation of the density data presented here into High Conservation Value (HCV) and High Carbon Stock (HCS) reviews, concession management planning, and licensing evaluation processes provides an evidence-based mechanism to retain high-density habitat within existing regulatory frameworks. In non-concession APL areas, particularly in parts of East Leuser, the BSS cluster and the Batang Toru landscape, these findings can inform prioritisation within social forestry zoning and potential reclassification to protection status where densities remain significant. Targeting enforcement and conflict mitigation in meta-populations where decline exceeds proportional forest loss offers a focused response to the excess declines not explained by habitat loss alone. Improving protocols for human–orangutan conflict response, including the adoption of post-release monitoring standards for wild-to-wild translocations as recommended by Sherman et al. (2025), is a prerequisite for any strategy that aims to reduce anthropogenic mortality to sustainable levels, particularly for Tapanuli orangutans where demographic margins are critically small.

The refined meta-population framework and population baseline established here provide a foundation for future range-wide reassessment under an identical methodological framework. The close correspondence between current estimates and the moderate-deforestation scenarios projected by Wich et al. (2016) demonstrates that combining predictive scenario modelling with periodic empirical surveys is a powerful tool for tracking conservation outcomes. The next decade should not simply be a waiting period until the next assessment. Rather, the scenario framework and the empirical baseline established here together provide the tools to actively evaluate conservation effectiveness, to determine which interventions are working, where gaps remain, and what additional action is needed. This should be treated as an urgent priority.

CRediT authorship contribution statement

Adhi N. Hadi: Conceptualization, Resources, Writing – original draft, Writing – review & editing. **Julius P. Siregar:** Conceptualization, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Nunu Anugrah:** Conceptualization, Supervision, Resources. **Wanda Kuswanda:** Conceptualization, Resources, Validation, Writing – review & editing. **Joy H. Boang Manalu:** Data curation, Formal analysis, Methodology, Software, Validation. **Nursaniah Nasution:** Data curation, Project administration. **Rahmad Fauzan:** Data curation, Formal analysis, Methodology, Visualisation. **Novita K. Wardani:** Project administration, Resources, Supervision. **Subhan:** Project administration, Resources, Supervision. **Ujang W. Barata:** Project administration, Resources, Supervision. **Dede A. Rahman:** Conceptualization, Writing – review & editing. **M. Yakob Ishadamy:** Conceptualization, Funding acquisition, Project administration, Supervision, Resources. **Susandro F. Sitorus:** Data curation, Project administration. **Noviar Andayani:** Resources, Supervision. **Jatna Supriatna:** Conceptualization, Writing – review & editing. **Serge Wich:** Conceptualization, Methodology, Writing – review & editing. **Hjalmar S. Kühl:** Methodology, Software, Writing – review & editing. **Benjamin J.W. Buckley:** Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used ChatGPT to assist with language editing, improving the clarity and readability of the English-language text. All scientific content, data analysis, interpretation of results, and conclusions are entirely the work of the authors. The authors reviewed and edited all AI-assisted output and took full responsibility for the content of the published article.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04302.

Data availability

Data will be made available on request.

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