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Deforestation, forest fragmentation and malaria risk in critically endangered Bornean Orangutans (Pongo pygmaeus)

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ABSTRACT

Malaria poses a significant threat to non-human primates, yet little is known about how environmental change and habitat configuration influence infection risk in orangutans. Here, we developed the first spatially explicit model of *Plasmodium* infection risk in Bornean orangutans, using data from 106 rescued individuals sampled between 2011 and 2023 in West Kalimantan, Indonesia. We used a binomial generalised additive model to investigate associations between infection probability and environmental covariates, including land cover, forest loss, fragmentation, vegetation greenness and meteorological conditions.

Infection risk was highest in humid, water-rich landscapes characterised by recent deforestation and greater fine-scale fragmentation. At broader spatial scales, infection probability decreased with increasing mean forest patch size and patch number, highlighting the scale-dependent complexity of landscape effects. Vegetation greenness and relative humidity were also positively associated with infection risk, whereas rainfall and temperature showed no clear associations. Predicted risk maps revealed marked spatial heterogeneity but modest intra-annual variation.

Our findings provide new evidence linking land-use change and habitat fragmentation to malaria risk in this critically endangered great ape, highlighting the importance of integrating disease surveillance with forest conservation and sustainable land-use planning.

KEYWORDS: Orangutan conservation, Wildlife disease, forest fragmentation, malaria, Non-human primates, *Pongo pygmaeus*, Spatiotemporal modelling, *Plasmodium pitheci*.

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INTRODUCTION

The Bornean orangutan (*Pongo pygmaeus*), a global conservation icon, is classified as critically endangered due to declining population numbers (Ancrenaz, 2016). Their populations have been decimated by forest conversion and fragmentation, particularly the expansion of oil palm monoculture (Voigt et al., 2018; Wich et al., 2012). Currently, over 70% of orangutan populations live outside protected areas, with many surviving in highly fragmented and vulnerable habitats (Ancrenaz et al., 2021; Wich et al., 2012). These vulnerable populations are forced to live in anthropogenic landscapes, where their long-term survival remains at risk from habitat loss and fragmentation, land and forest fires, hunting, the wildlife pet trade, and negative interactions with humans (Campbell-Smith et al., 2011; Ancrenaz et al., 2015). In addition to these threats, infectious diseases—while often receiving insufficient attention—can pose another risk to these already vulnerable populations. Diseases can impact the health of wild populations by affecting mortality, morbidity, and fecundity (Kilbourn et al., 2003; Wolfe et al., 2002), thus increasing the risk of extinction (Leendertz et al., 2006; Wolfe et al., 1998).

While some research suggests that orangutans can survive and even thrive in oil palm plantations combined with fragmented forest (Ancrenaz et al., 2015, 2021; Oram et al., 2022), there is a lack of long-term, systematic longitudinal studies evaluating the health and wellbeing of these populations. Furthermore, diseases affecting *in situ* orangutan populations are not well documented, with only a few studies identifying pathogens in wild individuals (Grützmacher et al., 2018; Sánchez, 2025). Although the semi-solitary nature of orangutans may reduce opportunities for disease transmission compared with more gregarious great apes (Carne et al., 2014), infectious diseases may still negatively affect their health and population viability.

Plasmodium spp., the parasites responsible for malaria in humans, belong to a highly diverse genus that naturally infects not only primates but also numerous other species of mammals, birds, and reptiles (Duval & Ariey, 2012; Faust & Dobson, 2015; Rayner et al., 2011; Sturrock & Tompkins, 2007). More than 60 different non-human primate (NHP) species, including all extant ape species, are naturally infected with a high diversity of *Plasmodium* species (Faust & Dobson, 2015). To date, two malaria parasites are known to naturally infect orangutans: *Plasmodium pitheci*, first described in 1907, and *Plasmodium silvaticum,* discovered in the 1970s (Peters, 1976; Peters et al., 1976).

Plasmodium spp. infections have been documented in wild populations of Bornean orangutans, with evidence suggesting higher prevalence among individuals housed in rescue and rehabilitation centres or in captivity (Kilbourn et al., 2003; Reid et al., 2006; Wolfe et al., 2002). Research on malaria in free-ranging (*in situ*) orangutans is currently constrained by the need for invasive blood sampling, which is both ethically challenging and logistically impractical in wild settings. Consequently, most malaria studies to date have relied on

medical data from Rescue and Rehabilitation Centres (RRCs), where biological sample collection is feasible (Dharmayanthi et al., 2025; Sánchez et al., 2022; Sánchez et al., 2024; Wolfe et al., 2002).

Recent longitudinal studies of Bornean orangutans in RRCs have challenged the long-standing assumption that malaria is largely benign in its natural primate hosts (Sánchez et al., 2022). Sánchez et al. (2022, 2024) confirmed the endemic presence of *Plasmodium pitheci* at a RRC, infecting orangutans primarily asymptomatically but, in some instances, causing severe life-threatening syndromes.

Malaria has also been associated with decreased immune function, concurrent severe infections, higher infant mortality rates, miscarriages, repetitive linear enamel hypoplasia, biased birth-sex ratios, and chronic subclinical anaemia (Kilbourn et al., 2003; Kuze et al., 2008, 2012; Peters, 1976; Reid et al., 2006; Sánchez et al., 2022; Sánchez et al., 2024; Skinner & Hopwood, 2004). To date, only one report of a potential malaria fatality in an infant orangutan in the wild–possibly the first malaria-related death documented in a wild orangutan–has been published (Sánchez, 2025). Collectively, these findings suggest that malaria may represent an underappreciated health threat to endangered ape populations, particularly in contexts where ecological or anthropogenic factors – such as those at RRCs or in alternative landscapes- alter transmission dynamics.

In most NHP species, the distribution and prevalence of malaria are highly heterogeneous across populations, with some exhibiting high infection levels while others show no infections (De Nys et al., 2017; Liu et al., 2017; Wu et al., 2018). However, the factors influencing malaria infection remain largely unexplained (De Nys et al., 2017; Liu et al., 2017). To date, no studies have conclusively established correlations between risk factors and malaria prevalence in great apes or other NHPs, with the exception of a recent investigation of macaques by Johnson et al. (2024). This study focused on zoonotic *P. knowlesi* parasites in macaques across Southeast Asia and found significantly higher prevalence in Malaysian Borneo, a region historically affected by extensive deforestation and land conversion for plantation agriculture (such as oil palm). These land-use changes have made Malaysian Borneo a hotspot for *P. knowlesi* spill-over into humans (Fornace et al., 2016, 2019; Grigg et al., 2018). Analysis of the environmental factors driving observed spatial differences in prevalence found that malaria infection in macaques was associated with both dense tree canopy cover and higher degrees of habitat fragmentation within a 5 km radius (Brock et al., 2019; Johnson et al., 2024).

In orangutans, several factors–including population density, exposure to humans and human settlements, arboreality, diet, moisture cycles, stress, standing water, and forest fragmentation–have been hypothesized to influence malarial prevalence (Wolfe et al., 2002). However, we still lack spatially explicit, *in situ* evidence testing how environmental

conditions and landscape change shape variation in *Plasmodium* spp. prevalence across orangutan populations and through time.

Since malaria is primarily transmitted by mosquitoes of the *Anopheles* genus, which exhibit specific host and habitat preferences (Beier et al., 1999; Brown et al., 2018), its distribution and prevalence are influenced by environmental factors that affect the presence of these vectors (De Nys et al., 2017; Liu et al., 2017; Yasuoka & Levins, 2007). Mosquito vectors are highly sensitive to environmental conditions such as temperature, humidity, sun exposure, rainfall patterns, and air movement (Yasuoka & Levins, 2007). Consequently, ecological or climatic drivers—whether natural or anthropogenic—affect vector abundance, distribution, species diversity, and behaviour of mosquito vectors (including how they breed, develop or transmit disease), thereby shaping the geographical and temporal variations of malaria infection (Afrane et al., 2008; Brock et al., 2019; Brown et al., 2018; Chang et al., 1997; Fornace et al., 2016; Hawkes et al., 2019; Reisen, 2010; van de Straat et al., 2022; Yasuoka & Levins, 2007). For example, one study in the western Kenyan highlands estimated that vectorial capacity was 77.7% higher at a deforested site than at a forested site (Afrane et al., 2008). Climatic variation can shape temporal fluctuations and seasonal patterns in malaria transmission. (Grillet et al., 2021; Reiner et al., 2015; Wu et al., 2018). Understanding the ecological and climatic factors that influence vector ecology and behaviour could help explain the spatiotemporal heterogeneity in malaria infection in great apes (Liu et al., 2017; Scully et al., 2022), as well as predict malaria distribution in wild populations.

By developing a spatiotemporal model of malaria risk in orangutans and overcoming the difficulties to study malaria in wild populations, this study aims to bridge a significant knowledge gap concerning malaria transmission in orangutan populations, specifically in relation to environmental and temporal factors. The specific objectives of this research were: i) to assess the geographical and temporal variation in *Plasmodium* spp. prevalence among Bornean orangutans; ii) to evaluate the environmental risk factors associated with *Plasmodium* spp. infection; and iii) to understand the potential impacts of deforestation and land-use change on malaria transmission.

METHODS

Study Site and Subjects

The *Inisiasi Alam Rehabilitasi Indonesia* Foundation (YIARI) operates under the Directorate of Biodiversity Conservation of the Ministry of Forestry (MoF) of the Republic of Indonesia to run a rescue and rehabilitation centre (RRC) for Bornean orangutans in Ketapang, West Kalimantan, Indonesia (YIARI RRC). This centre began operations in 2009 and has since rescued over 260 orangutans.

At the YIARI RRC, the endemic presence of *Plasmodium pitheci* has been confirmed by morphological description first, and followed by molecular analysis (whole mitochondrial

sequencing) that confirmed *P. pitheci* infections in all samples analysed (Dharmayanthi et al., 2025; Sánchez et al., 2022). Although the presence of other *Plasmodium* spp. cannot be ruled out, *P. pitheci* was the only species detected molecularly.

This study included malaria infectivity results from blood samples collected from 106 orangutans (49 females and 57 males) rescued between 2011 and 2023. Individuals were classified as infants (n=14), juveniles (n=32), subadults (n=11) and adults (n=49). All orangutans were rescued by YIARI and MoF from various locations within West Kalimantan province. The sample included both wild, free-ranging (*in-situ*) orangutans rescued from forest edge or anthropogenic landscapes such as plantations or deforested areas (n=64); as well as wild orangutans kept in captivity as pets and transferred to the RRC for medical care and rehabilitation (n=42). All those ex-pet orangutans were considered to have originated from nearby/local sites where they had been poached illegally.

Sample collection and analysis for *Plasmodium* spp. detection

Blood samples were obtained by venepuncture from each individual, either at the time of rescue or shortly after arrival at the RRC (within a timeframe that would indicate transmission prior arriving at the rehabilitation facility). *Plasmodium* spp. infection status was assessed by microscopy and/or real-time PCR. For analysis, samples were classified as *Plasmodium* spp. positive if infection was detected by either method, following Sánchez et al. (2022, 2024). All parasites were morphologically consistent with *P. pitheci* and in a subset of samples, *P. pitheci* was confirmed by molecular analysis (whole mitochondrial sequencing) (Dharmayanti et al. 2025); no other *Plasmodium* species was detected either morphologically or molecularly. However, because not all positive samples were sequenced, species-level assignment cannot be made with absolute certainty, and we therefore report outcomes at the genus level (*Plasmodium* spp.). Of the samples tested, 85 were diagnosed by PCR (or PCR plus microscopy) while the rest only by microscopy. 21 samples were assessed by microscopy only, of which ten were microscopically negative. Sánchez et al. (2024) estimated microscopy sensitivity relative to real-time PCR as 79.33% (95% CI 73.40–85.26%) in this study.

Environmental data

We extracted covariates within buffer radii of 200 m, 500 m, 1 km, 2 km, and 5 km for each georeferenced rescue point. These radii were selected to represent nested spatial contexts ranging from the immediate surroundings of the rescue location to the broader landscape, because the spatial scale at which environmental conditions may influence malaria infection in orangutans is unknown. The 200-m buffer was included to characterise highly local conditions, particularly for ex-captive individuals that were likely to have had restricted movements around houses or private gardens. The larger buffers were included to capture broader environmental conditions potentially relevant to free-ranging orangutans, which

may travel substantial daily distances and use home ranges extending well beyond the immediate rescue location. The buffers should therefore be interpreted as exploratory spatial scales rather than as direct estimates of individual home ranges, movement areas or the precise location at which infection was acquired (Figure 1).

Land-use covariates were derived from Esri's 10 m global land use/land cover product based on Sentinel-2 imagery and deep learning (Karra et al., 2021). For each individual, we extracted land-cover information from the map corresponding to the year of sample collection. The land use was grouped into seven classes: surface water, grass, flooded vegetation, crops, shrubs, built-up areas, and bare ground. These variables were measured as proportions within circular buffers around each rescue point.

Forest cover data was obtained from a 30-meter resolution map provided by Hansen's Global Forest Watch (Hansen et al., 2013), following the approach of Johnson et al. (2024). Tree cover was calculated as the proportion of forested area (≥50% crown density) within the circular buffers and matched to the samples by the year of collection. Forest fragmentation and complexity measurements were derived from the same layer using the R package *landscapemetrics* (Hesselbarth et al., 2019), including number of forest patches, mean patch size, edge density, mean shape index (the ratio between the perimeter of the patch and the hypothetical minimum perimeter of the patch), and forest fragmentation index (the ratio between number of patches and mean patch size). Additionally, forest loss was calculated as the cumulative surface area of forest loss within the circular buffer for the rescue year and the previous year (Figure 1).

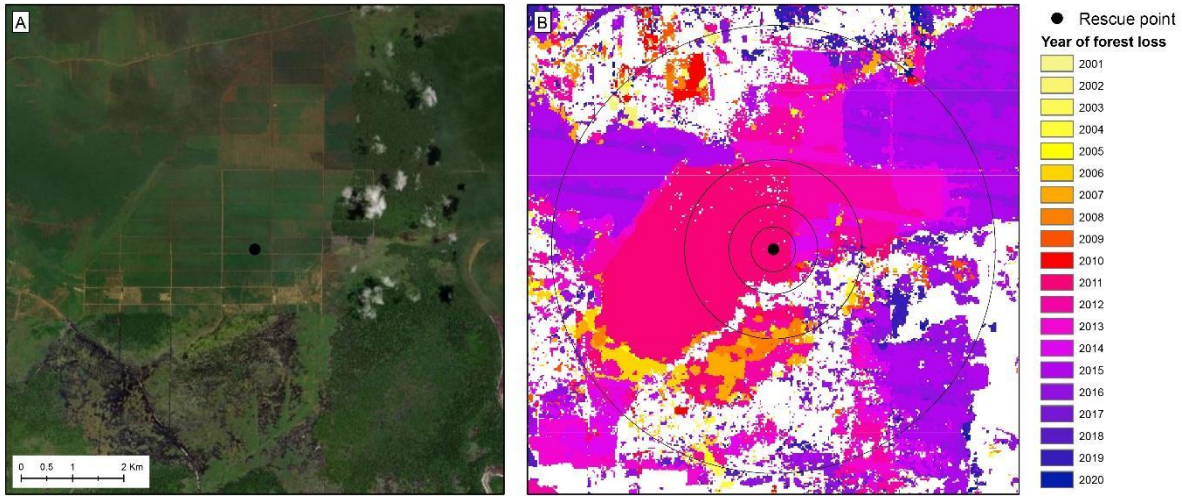


Figure 1 – Examples of data extraction for multiple buffer zones around rescue sites, shown for forest loss between 2001 and 2020.

Data on oil palm plantations were obtained from Danylo et al. (2021) and was calculated as the proportion of land dedicated to oil palm plantations in the circular buffers, and by the year of blood collection.

Human footprint was measured using eight variables, including built-up environments, population density, electric power infrastructure, crop lands, pasture lands, roads, railways, and navigable waterways. It was assessed on a continuous scale from 0 (low human pressure) to 50 (high human pressure) (Venter et al., 2016). Human population density was obtained from Gridded UN-adjusted human population estimates from WorldPop (Lloyd et al., 2017). Mean human population density and human footprint within the circular buffers were used for the analysis.

Monthly climate covariates (rainfall, air temperature, and relative humidity) were obtained from the NASA Prediction Of Worldwide Energy Resources (POWER) Project using the *nasapower* package for R (Sparks, 2018). For each rescue location, monthly values were extracted and then summarised over the month of rescue, over a two-month window including the rescue month and the preceding month, and over a six-month window including the rescue month and the preceding five months. Because the native spatial resolution of these products is coarse (~0.5°), climate variables were extracted at the rescue point location rather than averaged within buffers.

Normalized Difference Vegetation Index (NDVI) was obtained from the MODIS/Terra Vegetation Indices 16-Day L3 product (MOD13Q1, Version 6.1) via NASA's AppEEARS (Didan, 2021). NDVI was temporally matched to each rescue by using the MOD13Q1 composite corresponding to the month and year of rescue, and summarised as the mean within circular buffers around each rescue location.

A digital elevation model at 30 arc-second resolution (Danielson & Gesch, 2011) was used to calculate the Terrain Roughness Index (TRI) (Riley et al., 1999). TRI represents terrain complexity and is defined as the mean of the absolute elevation differences between a focal (central) pixel and its eight surrounding neighbouring cells.

Statistical analyses

We developed a spatially explicit regression framework to quantify how environmental conditions and habitat configuration were associated with *Plasmodium* spp. infection status, likely dominated by *P. pitheci*, in individual orangutans. The response variable was a binary indicator of infection status for each animal (Pos = 1 for positive by microscopy or PCR; Pos = 0 otherwise), and we modelled the infection probability using binomial generalized additive models (GAMs) with a logit link (Guisan et al., 2002).

Because most environmental covariates were available at several spatial scales, we first carried out a targeted scale-selection step. For each thematic group of predictors (land-cover classes, forest cover and loss, oil palm plantation, NDVI, patch metrics and fragmentation indices, and climatic variables), we considered the same variable measured at different buffer radii around each rescue location or over different temporal windows. Within each group we fitted a set of simple logistic regression models with infection status

as the response and a single candidate covariate as the predictor, and compared models using Akaike's Information Criterion (AIC). The spatial or temporal scale that yielded the lowest AIC was retained as the representative covariate for that group (Burnham & Anderson, 2002). This procedure selected, among others, the proportion of surface water, forest loss, NDVI, local fragmentation, the number and mean size of forest patches and relative humidity as the most informative descriptors for subsequent multivariable modelling. Rainfall and temperature, although evaluated at multiple temporal windows, did not appreciably improve model fit and were not carried forward.

We then constructed a multivariable spatial GAM including all covariates retained from the scale-selection step together with a smooth spatial term to account for residual spatial dependence. For observation i, let X_{ij} denote the value of the j-th selected environmental covariate and $(\mathrm{LON}_i, \mathrm{LAT}_i)$the projected rescue coordinates. Continuous predictors were centred and scaled to zero mean and unit variance prior to fitting, to aid numerical stability and allow direct comparison of effect sizes. The final model took the form

$$\mathrm{logit}\{\Pr(\mathrm{Pos}_i = 1)\} = \beta_0 + \sum_{j=1}^{7} \beta_j \tilde{X}_{ij} + f(\mathrm{LON}_i, \mathrm{LAT}_i),$$

where $\tilde{X}_{ij}$ denotes the standardised covariate value and $f(\cdot)$is a smooth bivariate function of longitude and latitude. The seven retained predictors were the proportion of surface water within 2 km, forest loss within 500 m, NDVI within 500 m, relative humidity in the month of sampling, a fine-scale fragmentation index within 200 m, and the number and mean size of forest patches within 2 km. The spatial smooth $f(\cdot)$was represented using a thin-plate regression spline with an upper basis dimension of 20. Smoothing parameters were estimated by restricted maximum likelihood (REML), which provides stable and approximately unbiased smoothing-parameter estimates in GAMs (Wood, 2011, 2017).

Model simplification was guided by AIC, inspection of coefficient estimates and their uncertainty, and ecological interpretability. Starting from a richer model that included additional land-cover and fragmentation metrics and alternative meteorological summaries, we iteratively removed covariates that had small and imprecise estimated effects and whose exclusion produced only minor changes in AIC or deviance explained, while retaining variables that corresponded to our key ecological hypotheses regarding water availability, recent forest loss, fragmentation and local meteorological conditions. Competing models with and without the spatial smooth were also compared using AIC and visual inspection of spatial patterns in the residuals; the spatial term was retained in the final model because it modestly improved overall fit and reduced residual spatial structure.

Model performance and diagnostics were evaluated using the proportion of deviance explained, adjusted R^2, inspection of deviance and Pearson residuals, and standard GAM

diagnostics, including checks of basis dimension adequacy for the spatial smooth (Wood, 2017). For interpretation and plotting of partial effects we used the standardised model above, extracting fitted effects on the probability scale with associated confidence intervals. To generate spatial prediction maps, we refitted the same model structure using covariates on their original scales and predicted infection probabilities on a regular grid, with 500 m resolution, covering the study area. Month-specific risk surfaces were obtained by combining the static landscape covariates with monthly NDVI and humidity corresponding to a given calendar month and then averaging across months to produce an annual mean risk surface.

All analyses were conducted in R (R Development Core Team, 2024), using the *mgcv* package for GAM fitting (Wood, 2001, 2017), *sf* for handling vector spatial data (Pebesma & Bivand, 2023), and *terra* (Hijmans, 2022) and *tidyterra* (Hernangómez, 2023) for raster processing and visualisation.

RESULTS

Malaria prevalence and overall model fit

Of the 106 orangutans with complete infection and location data, 30 tested positive for *Plasmodium* infection. The final spatial logistic model, which included surface water, recent forest loss, vegetation greenness, humidity, fine-scale fragmentation, forest patch number and mean patch size together with a smooth spatial term, explained 61.7% of the deviance (adjusted $R^2 = 0.60$) (Table 1). The bivariate smooth of longitude and latitude had moderate effective degrees of freedom but was not statistically significant at conventional levels, suggesting limited evidence for additional residual spatial structure beyond measured covariates, noting that the spatial resolution of inference is constrained by the sample size and clustering of rescue locations.

Table 1 - Fixed effects from the final spatial logistic regression model of malaria infection risk in Bornean orangutans in West Kalimantan, Indonesia. Continuous covariates were standardised (mean 0, SD 1) before fitting; coefficients (β), z-scores and odds ratios (OR) therefore describe the change in log-odds and odds of infection associated with a one–standard deviation increase in each covariate. SE: standard error; z: Wald z-statistic; p: p-value from Wald tests.

Predictor	β	SE	z	OR	p-value
Intercept	−2.359	0.683	−3.454	–	<0.001
Water_2000	1.662	0.563	2.952	5.27	0.003
FORL_500	1.360	0.693	1.962	3.90	0.050
NDVI_500	1.262	0.559	2.258	3.53	0.024
HUM	2.059	0.806	2.555	7.84	0.011
FRAG_200	1.200	0.528	2.273	3.32	0.023
n_patches_2000	−1.906	0.755	−2.525	0.15	0.012
mean_patch_size_2000	−4.266	0.265	−16.098	0.014	<0.001

Environmental drivers of infection risk

The final model retained seven standardised environmental predictors (Table 1; Figure 2): the proportion of surface water within 2 km, forest loss within 500 m, NDVI within 500 m, relative humidity in the month of sampling, a fine-scale fragmentation index within 200 m, the number of forest patches within 2 km, and mean forest patch size within 2 km. Continuous covariates were centred and scaled to zero mean and unit variance, so their coefficients represent the change in log-odds of infection associated with a one–standard deviation increase in each predictor.

Five variables showed clear positive associations with infection risk (Table 1). The proportion of surface water within 2 km was strongly associated with higher malaria risk (Figure 2A), corresponding to an approximate five-fold increase in the odds of infection per standard deviation increase in water cover. Recent forest loss within 500 m had a positive effect (Figure 2B), implying that orangutans rescued from landscapes that had undergone recent deforestation experienced substantially higher malaria risk. NDVI within 500 m was also positively associated with infection, indicating that greener, more vegetated local environments were linked to elevated infection probabilities (Figure 2C). Relative humidity in the month of sampling was a further strong predictor, with the odds of infection increasing steeply along the humidity gradient (Figure 2D). At very local scales, the fragmentation index within 200 m had a positive and significant effect, suggesting that more fragmented immediate surroundings are associated with higher malaria risk (Figure 2E).

In contrast, both patch-based metrics at the 2 km scale were negatively associated with infection. The number of forest patches within 2 km had a negative standardised coefficient, indicating that, after controlling for other covariates, infection odds decreased as the number of patches increased (Figure 2F). Mean forest patch size within 2 km showed an even stronger negative effect, suggesting that larger average patch sizes are associated with substantially lower infection probabilities (Figure 2G), whereas landscapes dominated by small patches are associated with much higher odds of infection. These metrics capture aspects of habitat configuration across scales. The fragmentation index reflects local forest dissection and edge-dominated conditions around the rescue site, whereas patch number and mean patch size describe broader landscape subdivision and forest continuity within 2 km. Taken together, these results indicate that malaria risk was associated with recent forest loss and landscape configuration at multiple spatial scales. Infection risk increased with fine-scale fragmentation within 200 m, whereas at the broader 2 km scale it decreased with both the number of forest patches and mean patch size. These scale-dependent effects suggest a more complex relationship between forest amount and configuration than a simple increase in risk with increasing fragmentation.

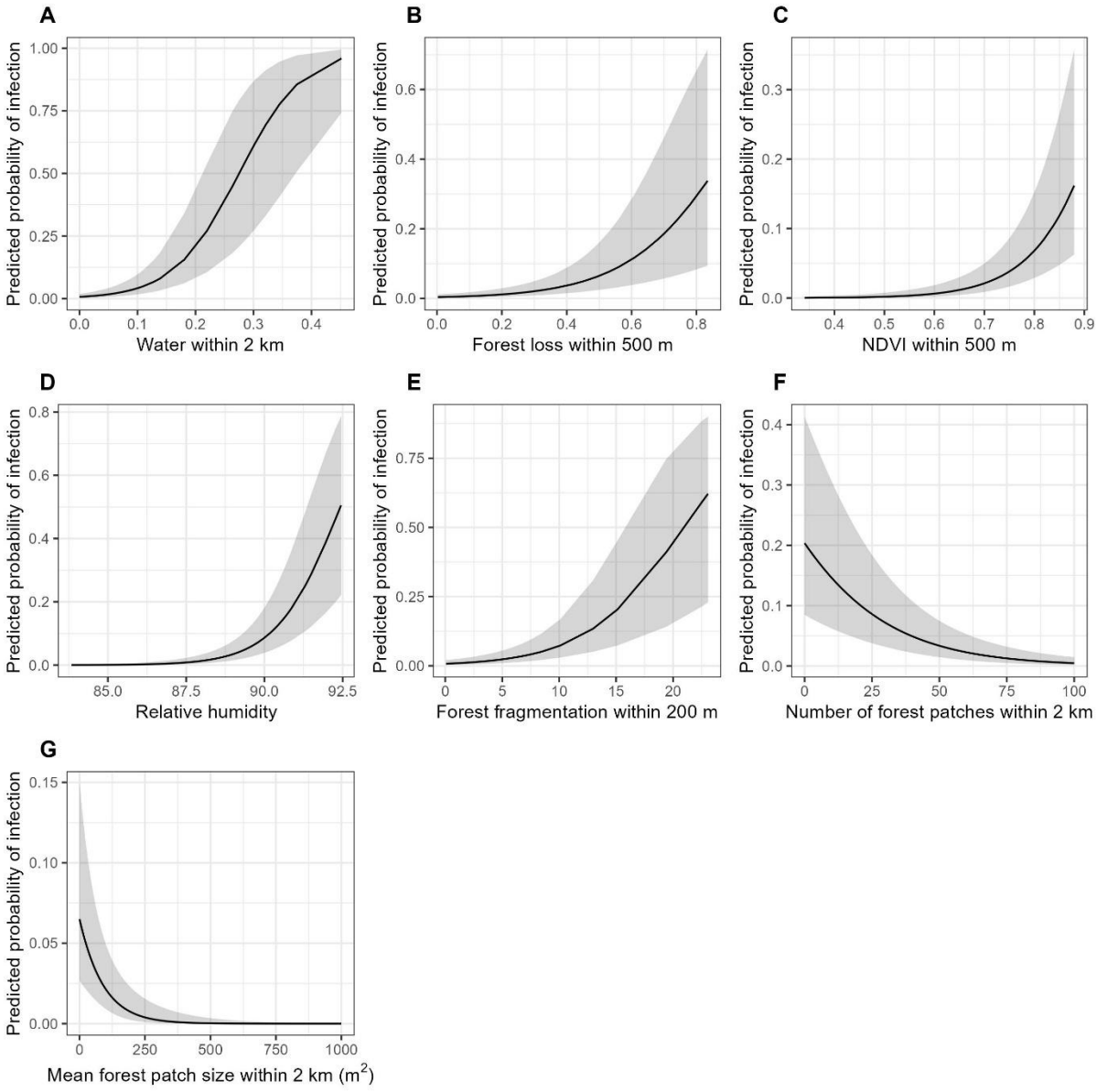


Figure 2. Partial effects of environmental covariates on the predicted probability of malaria infection in Bornean orangutans, obtained from the final spatial logistic regression model. Panels show marginal effects (solid lines) with 95% confidence intervals (shaded bands) for: A) proportion of surface water within 2 km, B) forest loss within 500 m, C) NDVI within 500 m, D) relative humidity, E) forest fragmentation within 200 m, F) number of forest patches within 2 km, and G) mean forest patch size within 2 km. All covariates are plotted on their original scales, but the effects correspond to the model fitted with standardised predictors; other covariates are held at their mean values.

Predicted spatial and seasonal patterns

Applying the final model to a regular prediction grid covering the study area revealed clear spatial gradients in predicted infection probability (Figure 3A). Areas where high water cover, recent forest loss, high NDVI, strong fine-scale fragmentation and humid conditions co-occurred showed the highest predicted risk, whereas predicted probabilities were lowest in drier landscapes with limited surface water, little recent forest loss and larger, more

continuous forest patches. The annual mean risk surface summarises these patterns, highlighting clusters of elevated risk within the broader landscape. When predictions were restricted to the confirmed and potential distribution of wild orangutans (Atmoko et al., 2017) (Figure 3B; 14,992 km²), the mean predicted infection probability was 0.61; 10,180 km² (67.9%) of the area had predicted risk >0.50, 5,966 km² (39.8%) >0.75, and 2,676 km² (17.8%) >0.90.

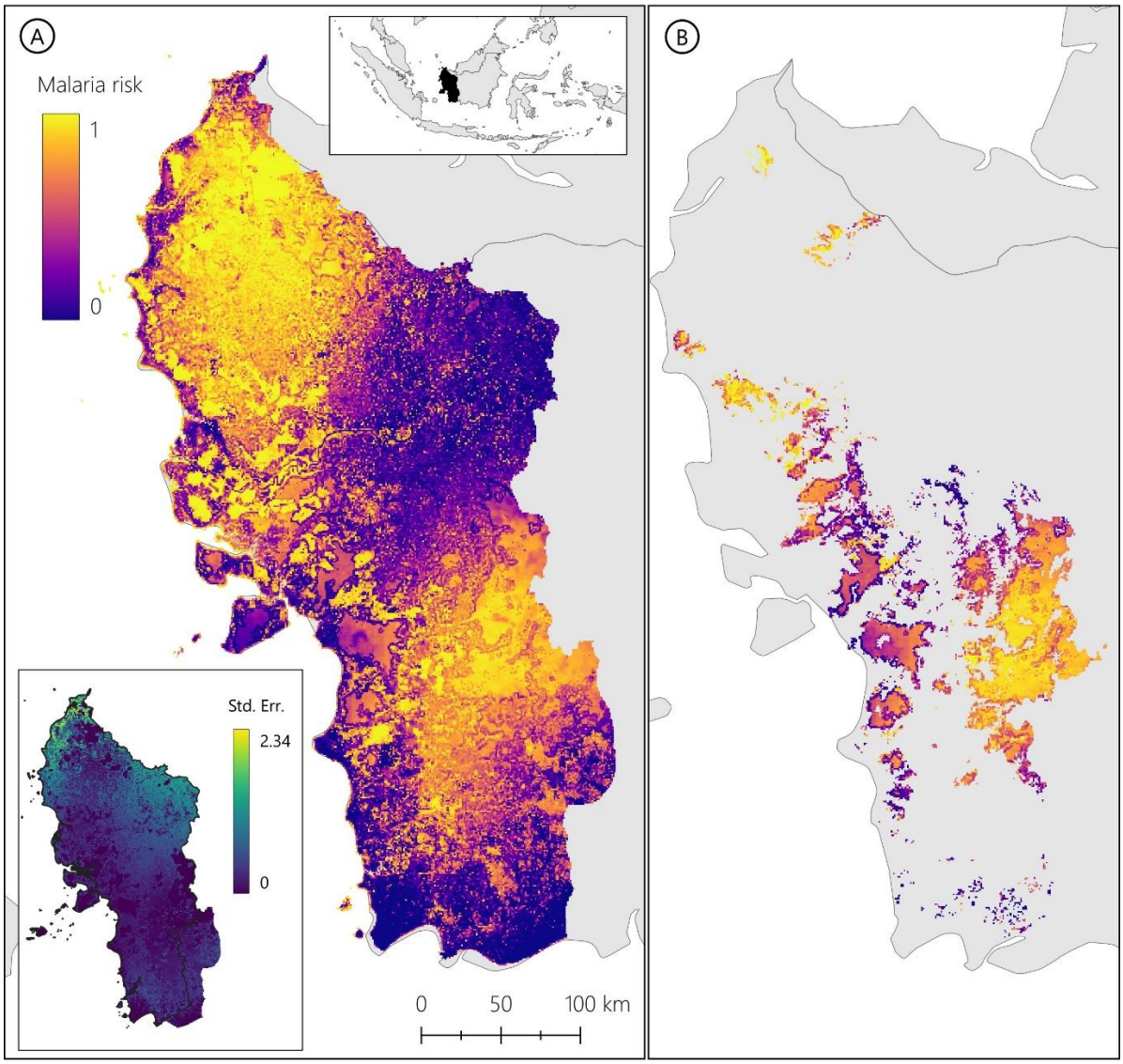


Figure 3. A) Annual mean predicted malaria risk in Bornean orangutans across the study area in West Kalimantan, Indonesia. Colours indicate the predicted probability of *Plasmodium* infection from the final spatial model, averaged over the 12 monthly risk surfaces (0 = low risk, 1 = high risk). The inset maps show the uncertainty of the prediction, and the location of the study area (black polygon) within Indonesia. B) The same annual mean risk surface masked to the confirmed and potential distribution of wild orangutans in West Kalimantan.

To explore temporal variation, we generated a series of monthly risk surfaces by combining the fitted model with calendar-month averages of NDVI and relative humidity, computed over the 2011–2023 sampling period, while holding landscape and fragmentation covariates

fixed using 2024 layers (Figure 4). Predicted malaria risk was broadly similar across months, with only modest fluctuations superimposed on the strong spatial gradients seen in the annual mean surface. Overall, the maps indicate that, within the observed range of conditions, spatial heterogeneity linked to land use and forest configuration is more pronounced than the recurrent intra-annual variation attributable to NDVI and humidity.

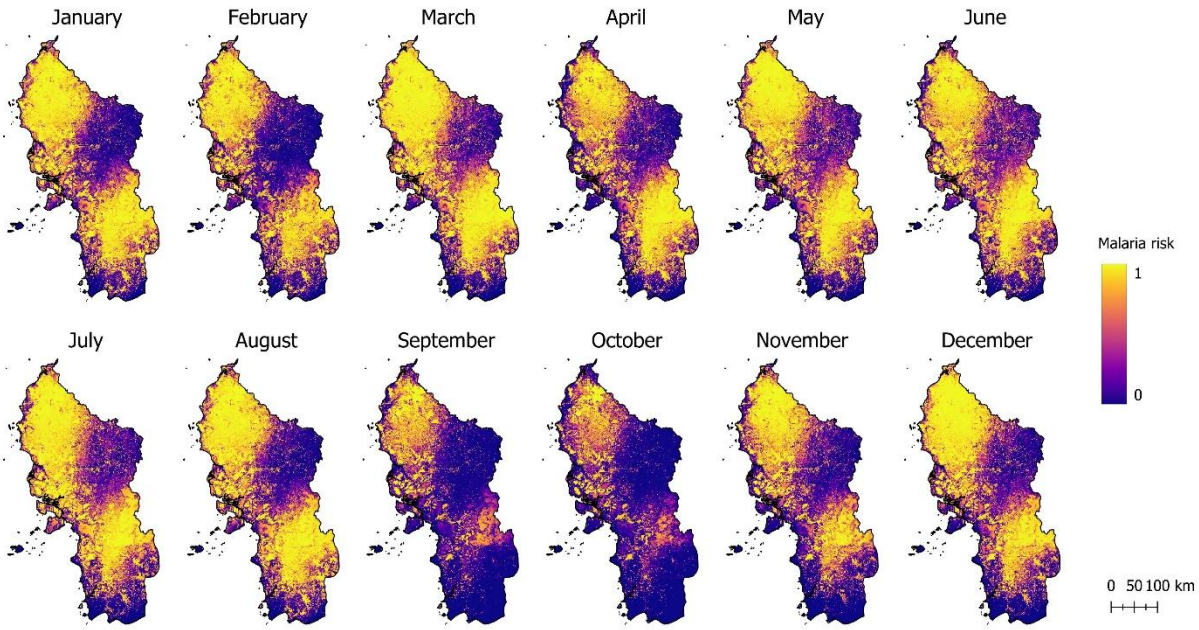


Figure 4. Monthly predicted malaria risk across West Kalimantan, Indonesia. Panels show predicted infection probability for each calendar month (January–December) on a common colour scale (0–1). Landscape and fragmentation covariates (land use, forest cover, forest loss and fragmentation metrics) are held constant using 2024 layers, while NDVI and relative humidity vary by month based on calendar-month averages computed across 2011–2023 (the sampling period).

DISCUSSION

Malaria in great apes has received far less attention than human malaria, and Bornean orangutans remain particularly understudied with respect to malaria despite mounting evidence of substantial health impacts. To our knowledge, this is the first study to develop a spatially explicit model of environmental correlates of *Plasmodia* infection, likely dominated by *Plasmodium pitheci* in rescued orangutans, and one of very few to link orangutan malaria to quantified environmental and landscape metrics. By combining individual-level infection data with information on land cover, forest loss, habitat configuration and local meteorological conditions, we show that infection risk is associated with recent deforestation, fine-scale forest fragmentation, surface water availability and humidity, with landscape configuration showing scale-dependent effects.

Long-term studies of malaria in African great apes have shown that most free-living populations harbour malaria parasites, although some populations appear to be free of infection (De Nys et al., 2017; Liu et al., 2017; Scully et al., 2022; Wu et al., 2018). While host

genetic factors such as protective polymorphisms may contribute to this heterogeneity (Wroblewski et al., 2023), the absence or low abundance of competent mosquito vectors in particular habitats is a plausible explanation. Environmental change, forest degradation, deforestation and forest fragmentation can strongly affect vector communities and biting rates, thereby influencing malaria transmission in great apes (Brant et al., 2016; Hawkes et al., 2019; Johnson et al., 2024; Reiner et al., 2015). In this study, predicted orangutan malaria risk was highest in humid, water-rich and recently deforested landscapes, while associations with forest configuration differed across spatial scales. However, the mosquito vector(s) responsible for transmitting orangutan *Plasmodium* remain poorly characterised, so these associations should be interpreted as ecological correlates rather than direct evidence of a specific transmission pathway.

Vector-borne pathogens such as malaria are notoriously sensitive to rapid deforestation and land-use change (McFarlane et al., 2013). In our study, malaria infection in orangutans was strongly associated with recent forest loss and fine-scale forest fragmentation, highlighting the important role of habitat disturbance in shaping infection risk. This pattern is consistent with studies on *P. knowlesi* in non-human primates, which have demonstrated links between landscape change, including forest fragmentation, and parasite distribution (Johnson et al., 2024). Wild orangutan populations in Borneo face increasing pressure from the conversion of natural forests for agriculture (particularly oil palm plantations), mining and infrastructure development, and human encroachment into forest edges (Voigt et al., 2018). The fragmentation resulting from these activities creates mosaics of edge-dominated forest patches that can facilitate the spread of vector-borne parasites between habitats, potentially increasing malaria prevalence in orangutans living in fragmented landscapes (Borremans et al., 2019; Johnson et al., 2024; McFarlane et al., 2013). However, our results indicate that the relationship between forest configuration and infection risk differs across spatial scales.

At the local scale, infection probability increased in landscapes characterised by higher fragmentation within 200 m, suggesting that the breakdown of contiguous forest may favour transmission. At the broader 2 km scale, however, both patch number and mean patch size were negatively associated with infection risk, indicating that the relationship is more complex than a simple increase in risk with increasing numbers of forest fragments. A plausible mechanism for the positive fine-scale fragmentation effect is that fragmentation increases forest–nonforest edge and the availability of suitable mosquito habitats at the forest fringe, which could elevate local vector abundance as well as species diversity, augmenting opportunities for host–vector contact (Byrne et al., 2021; Fornace et al., 2019; Grillet et al., 2021), which in turn could lead to higher transmission intensity. Mosquito species transmitting *Plasmodium* in other great apes are typically forest-dwelling and associated with shaded, humid habitats (Scully et al., 2022), so the creation of fragmented, humid mosaics with abundant edge could be particularly favourable to these vectors. At the same time, it has been hypothesised that orangutan immunity to malaria, which resembles

naturally acquired immunity in humans, could be impaired if exposure to the parasite is strongly reduced or interrupted (Sánchez et al., 2022; Sánchez et al., 2024). In such settings, altered patterns of exposure might increase the likelihood that infections, when they do occur, progress to clinically significant disease.

The presence of freshwater, high humidity and greener vegetation were also positively associated with malaria risk in orangutans. In our final model, infection probability increased with the proportion of surface water within 2 km, with NDVI within 500 m, and with contemporaneous relative humidity, underscoring the importance of moist, productive, water-rich environments for parasite transmission. Orangutans commonly inhabit peat-swamp and other wet forest ecosystems, which have distinctive hydrological and microclimatic conditions, but it remains unclear whether these habitats consistently favour or inhibit the presence of competent mosquito vectors (Wolfe et al., 2002). The positive association with surface water should be interpreted cautiously as an empirical correlate, because the vector(s) and transmission ecology of orangutan *Plasmodium* spp. remain poorly characterised. Surface water may be acting as a proxy for riparian habitat, local moisture regimes, or correlated landscape features that were not explicitly measured, rather than indicating a direct mechanistic pathway. Targeted entomological work across hydrological settings will be needed to resolve these alternatives. Our results highlight the potential importance of such humid, vegetated environments for transmission, and point to the need for targeted studies comparing malaria infection rates and vector communities across different orangutan habitat types.

While ambient temperature and rainfall are known to affect *Plasmodium* spp. transmission dynamics in humans and to influence the geographic and seasonal variation of infection (Eckhoff, 2012; Scully et al., 2022), we did not detect clear associations between these variables and malaria infection in orangutans. Temperature and rainfall, evaluated at several temporal windows, did not appreciably improve model fit once water, humidity, NDVI and fragmentation metrics were included, and were therefore not retained in the final model. This absence of a detectable effect may reflect the relatively coarse spatial resolution of the climate products used, the limited range of climatic conditions within our study area, or the modest sample size, rather than a lack of underlying climatic influence on transmission.

Although we did not detect strong seasonal structure overall, the monthly prediction maps suggest modest temporal fluctuations, with relatively higher predicted risk in parts of the study area during December–January and June–July, and lower predicted risk during September–October. These prediction maps represent landscape receptivity or relative risk conditional on orangutan presence and exposure, rather than a model of orangutan occupancy. Hence, the model maps relative environmental receptivity within the sampled rescue-based framework, not the distribution of wild orangutans. Because some sampled individuals were rescued from captive situations, infections in these animals may reflect exposures occurring before or during captivity, potentially outside typical orangutan habitat

or at different times from those represented by the environmental data. Seasonal and interannual variation in malaria infectivity rates has been described in other great apes as well as in humans (Grillet et al., 2021; Reiner et al., 2015; Wu et al., 2018). For example, a study in endemic human malaria areas in Venezuela detected multi-annual epidemics correlated with El Niño–Southern Oscillation (ENSO) patterns, suggesting that climate change, by increasing the intensity and periodicity of ENSO events, could drive higher malaria prevalence (Grillet et al., 2021). Wu et al. (2018) also observed stochastic increases in malaria detection rates in a longitudinal study of chimpanzees, potentially linked to ENSO-driven climatic anomalies. While our data and study design do not allow us to directly test such mechanisms, the broader malaria–climate relationship and the potential influence of climate change on orangutan malaria risk remain concerning and warrant targeted long-term surveillance and further research.

Our data span the period 2011–2023, but the limited sample size and non-uniform sampling across years mean that we cannot reliably infer long-term trends in orangutan malaria prevalence from this dataset. Nevertheless, any sustained increase in infection risk would be cause for concern considering wider patterns observed in Southeast Asia. Increasing reports of zoonotic *P. knowlesi* infection across human populations in the region highlight the re-emergence of malaria in areas where it was previously considered under control or eliminated (Barber et al., 2017), and various ecological disruptions caused by land-use change have been implicated in this process (Fornace et al., 2019). By analogy, ongoing forest fragmentation and alteration of orangutan ecosystems could plausibly lead to increased frequency or magnitude of malaria outbreaks in orangutan populations. This possibility, although not directly demonstrated here, deserves careful attention, as sustained or increasing malaria pressure could have serious implications for the long-term viability of wild orangutan populations, especially for those in anthropogenic landscapes where a large proportion of the remaining populations are found.

Other ecological factors influencing malaria transmission in great apes, such as fine-scale variation in vector species composition, host behaviour and co-infections, were not captured in our analysis (De Nys et al., 2017; Mapua et al., 2018). A further limitation is that the rescue location may not correspond precisely to the location at which infection was acquired. For free-ranging individuals, the rescue point may represent only one part of a considerably larger home range, whereas the previous movements and locations of confiscated ex-pet orangutans may be uncertain. In addition, if infections persist for extended periods, relevant environmental exposure may have occurred before rescue and outside the surrounding landscape considered here. The environmental covariates should therefore be interpreted as characterising conditions around rescue locations across a range of spatial scales, rather than as reconstructing each individual's complete exposure history. This uncertainty may have resulted in some misclassification of environmental exposure and should be considered when interpreting the estimated associations.

We also acknowledge that the relatively small sample size of 106 orangutans limits the statistical power of our study, both in terms of the total number of individuals and the uneven timing of data collection across years. As discussed above, our data do not allow interannual variation in infection rates to be characterised in detail, and un-modelled temporal fluctuations may therefore contribute to residual uncertainty in our estimates. A further limitation is heterogeneity in diagnostic methods. A small subset of individuals were assessed by microscopy only, which is less sensitive than PCR and may have led to under-ascertainment of infection in those animals, potentially attenuating estimated associations. Future surveillance would benefit from standardised molecular testing across all samples and, where feasible, sequencing to improve comparability and parasite characterisation.

Once the selected environmental covariates were included, the remaining spatial smooth contributed only modestly to model fit and its approximate test was not significant at conventional levels. This suggests that much of the observed spatial pattern was captured by the measured covariates, while additional residual spatial dependence was comparatively weak. However, inference regarding residual spatial structure remains constrained by the sample size and clustering of rescue locations, and broader spatial and temporal coverage will be needed to characterise any remaining spatial heterogeneity robustly.

Despite the above limitations, this work presents the first spatially explicit model of malaria risk in orangutans, combining individual infection data with high-resolution environmental covariates and time-varying vegetation and humidity indices, and provides new insight into how land-use change and habitat configuration shape infection risk in this critically endangered primate. Our study lays essential groundwork for understanding and addressing the impact of environmental change on malaria in orangutans. Moving forward, concerted efforts will be required to expand the dataset and improve temporal coverage, thereby strengthening model robustness. Collaborative initiatives and data-sharing between governmental and non-governmental organisations, as well as across the range states that share responsibility for orangutan conservation, will be key to increasing sample sizes and enhancing the power of future analyses. As the urgency to protect orangutan populations grows, sustained investment in data collection and research collaboration will be instrumental in developing targeted conservation strategies and advancing our understanding of malaria dynamics in orangutans.

The implications of this research extend beyond orangutans and have broader relevance for understanding malaria transmission in other primates and the potential consequences for public health. NHP, including a wide range of monkey and ape species, serve as important reservoirs for a diverse array of *Plasmodium* parasites (De Nys et al., 2017; Rayner et al., 2011). By identifying environmental and landscape features that shape malaria risk in orangutans, our study provides insight into the types of habitat changes that are likely to influence transmission dynamics in other primate–parasite systems. In particular, our

finding that recent deforestation, fine-scale fragmentation and humid, water-rich conditions are associated with variation in infection risk underscores the potential importance of land-use change in structuring disease dynamics. In regions where humans and wildlife co-occur, such habitat disturbance can increase the likelihood of contact between people, primates and vectors, thereby escalating the risk of pathogen spill-over and spill-back (Borremans et al., 2019; Gibb et al., 2020; Gottdenker et al., 2014; McFarlane et al., 2013; Patz & Norris, 2004). Although the *Plasmodium* species infecting orangutans are not currently recognised as zoonotic, similar environmental drivers are likely to govern the distribution of other NHP malaria parasites, including those with known zoonotic potential. Our results therefore reinforce the need for proactive conservation and land-use policies that limit deforestation and fragmentation, both to reduce malaria burden in primates and to help mitigate the emergence and spread of vector-borne zoonoses in human populations.

Finally, this study emphasizes the need to consider the tight coupling between environmental change, disease ecology and wildlife conservation when assessing and mitigating malaria risk in orangutans. This is of particular concern for resident orangutan populations within highly fragmented and degraded habitats. The existing threat to their survival, combined with potential malaria infection risks, significantly elevates the overall extinction risk for these populations. By explicitly linking infection probability to recent deforestation, fine-scale fragmentation, surface water, vegetation greenness and humidity, our spatial modelling framework shows how disease transmission models can be used to identify high-risk landscapes, prioritise surveillance and guide targeted interventions. In a region where climate change is expected to alter rainfall regimes, humidity and vegetation dynamics, the environmental drivers highlighted here are themselves likely to shift, with uncertain but potentially profound consequences for malaria transmission in orangutans and other primates. These findings underscore the value of embedding One Health approaches within orangutan conservation strategies—treating forest protection, climate resilience and disease risk reduction as interdependent objectives rather than separate agendas—so that land-use and climate policies can simultaneously safeguard primate health, biodiversity and human well-being. Our findings also highlight the importance of considering malaria infectivity status in all rescued orangutans either at the time of rescue, during rehabilitation or at reintroduction.

AUTHORS CONTRIBUTIONS

KLS and DZ conceived and designed the study and contributed to manuscript preparation; KLS coordinated sample collection; LN developed the modelling framework, analysed the data, and drafted the manuscript; AB collected, cleaned, and formatted the environmental variables and contributed to manuscript preparation; EJ and KF contributed to the extraction of forest-loss data and fragmentation metrics and to manuscript preparation; RTPN, FF, FA, K, AP, and ABD contributed to sample collection, diagnostic data generation, and interpretation of the biological data, and critically revised the manuscript; GCS and IN reviewed and edited the manuscript. All authors critically reviewed and approved the final manuscript.

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ETHICAL STANDARDS

The Ethics in Research Commission of the National Research and Innovation Agency of the Republic of Indonesia approved this research activity (Experimental Use of Animals, Letter Number 86/CI/2021; 21 November 2021). The Decree by the General Director of the Natural Resources and Ecosystems Conservation Number - SK. 31/KSDAE/SET.3/KSA.2/2/2022 regarding Permission to Access Genetic Resources of Wild Animal Samples for Research Purposes.

DATA AVAILABILITY

The dataset contains precise rescue-location information for a critically endangered species and is therefore not publicly deposited because of conservation and data-sensitivity considerations. Requests for access to the data should be directed to the corresponding author and will be considered for legitimate research purposes, subject to appropriate conservation, ethical and data-governance requirements.

COMPETING INTERESTS

The authors have no competing interests.

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