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Original research article

Contributions of High Conservation Value Forests (HCVFs) on mammal diversity in heterogeneous oil palm landscapes

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ABSTRACT

Oil palm expansion has transformed lowland tropical forests across Southeast Asia, yet the landscape and accessibility features that sustain mammal diversity within plantation mosaics remain unclear. We quantified how topography and human access shape mammalian species richness and abundance in Peninsular Malaysia across three landscape types: monoculture oil palm (OPP), oil palm with forest patches (OPFP), and oil palm adjacent to contiguous forest (OPCF). We used Generalized Linear Mixed Models (GLMMs) to identify predictors of species richness and relative abundance (based on detection rates). Species richness increased with elevation and with distance from paved roads and showed a modest decline with increasing distance from unpaved service tracks. Abundance was highest in OPP and was strongly influenced by landscape type, increased with distance from paved roads, with a weaker positive association with elevation. Topography and road context jointly structure mammal communities in oil palm landscapes. Species richness was higher in elevated, less-accessible terrain, whereas high detection counts in monoculture plantations likely reflect the dominance of generalist species. State-scale actions such as buffering high-elevation forest, limiting new paved-road encroachment, and maintaining vegetated corridors along low-use service tracks may offer practical pathways to reconcile production with biodiversity goals.

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1. Introduction

Malaysia harbours an exceptional biodiversity, encompassing ecosystems such as tropical rainforests, peat swamps, and mangroves. These habitats sustain over 200 mammal species and thousands of plant species, many of which are endemic to the region (de Bruyn et al., 2014; Sodhi et al., 2010). Despite this richness, Malaysia's wildlife is increasingly under threat, with more than 70 mammal species classified as threatened on the IUCN Red List (IUCN, 2023). Iconic species, including the Malayan tiger (*Panthera tigris jacksoni*), Bornean elephant (*Elephas maximus borneensis*), and Sunda pangolin (*Manis javanica*), face risks primarily from habitat loss, human-wildlife conflicts, poaching, and fragmentation (Shevade et al., 2017; Suba, 2017; Kodoh et al., 2024). Expansion and intensification of agriculture is the greatest current threat to biodiversity. Vegetable oils represent one of the fastest-growing agricultural sectors, with palm oil being the most widely produced and consumed vegetable oil globally (Lieke et al., 2023).

The rapid expansion of oil palm plantations in Malaysia, increasing from 54,000 ha in 1960 to over 5.8 million hectares by 2020, has significantly transformed the country's landscapes (MPOB, 2021). The conversion of diverse forests into monoculture plantations has reduced species richness, affecting flora and fauna (Vijay et al., 2016). Deforestation has also disrupted ecosystem processes, such as carbon storage, soil stability, and water cycles, and worsened climate change (Tang et al., 2020). While sustainability initiatives such as Roundtable on Sustainable Palm Oil (RSPO) aimed to reduce ecological damage, their effectiveness is uncertain as habitat fragmentation continues (Vijay et al., 2016). Addressing these challenges requires strong land-use policies, conservation efforts, and sustainable agriculture to balance economic growth with environmental protection.

Native mammals perform essential functions in ecosystems through their role as seed dispersers, predators, and ecosystem engineers. For instance, frugivorous mammals such as civets and primates contribute to forest regeneration through seed dispersal, while carnivores regulate herbivore populations to maintain ecological balance (Corlett, 2017; Gilbert et al., 2022). Mammals also serve as bioindicators of environmental health, which we define here as the capacity of an ecosystem to support a balanced and resilient community of organisms in the face of anthropogenic pressures (Gaynor et al., 2018). Their ability, or inability, to adapt to modified environments such as oil palm plantations provides insight into the effects of land-use changes (Meijaard et al., 2010).

The ecological functions and services provided by mammals are context-dependent, often declining in simplified habitats such as monoculture plantations where mammalian diversity is reduced (Estrada et al., 2012). As forests are converted into monoculture plantations, critical wildlife habitats are diminished, leading to species displacement and population declines. While the impact of habitat loss on biodiversity has been extensively documented, research on the role of physical landscape factors, including elevation, proximity to human settlements, roads, and water sources, in shaping mammalian diversity in oil palm landscapes remains limited (Fitzherbert et al., 2008; Wearn et al., 2017; Azhar et al., 2012; Jamhuri et al., 2020). Additionally, most existing studies focus on single-site assessments, leading to limited understanding of how mammals respond to oil palm expansion. The current practice of retaining forest fragments or patches within plantation landscapes, particularly those adjoining contiguous forests—is expected to enhance biodiversity outcomes by mitigating habitat loss and supporting species persistence, especially for mammals (Senior et al., 2014; Zanuari et al., 2024). Comparative studies of mammal diversity across different oil palm plantation landscapes remain limited, despite evidence that large-scale monoculture negatively impacts forest-dependent mammals due to habitat homogenization (Azhar et al., 2014). This gap limits our understanding of how landscape heterogeneity influences species diversity and restricts the development of effective conservation strategies.

High Conservation Value Forests (HCVFs), including forest patches and contiguous forest reserves, serve as critical refugia for native species and maintain ecological connectivity within agricultural matrices. This study aims to examine the influence of HCVFs on mammalian diversity within the oil palm landscape of Peninsular Malaysia. We systematically selected three distinct landscape types: Oil Palm Plantation (OPP) monocultures, Oil Palm with Forest Patches (OPFP), and Oil Palm with Contiguous Forest (OPCF). Specifically, we aim to answer: (1) How does mammalian species richness vary across these three landscape types? and (2) Which landscape-scale factors best predict mammal species richness and abundance in these landscapes? Understanding these relationships will provide evidence on the value of HCVFs including both forest patches (OPFP) and contiguous forest reserves (OPCF) for biodiversity conservation in agroecosystems. Furthermore, the study offers practical recommendations for making oil palm plantations more wildlife-friendly, such as maintaining corridors and buffer zones to connect fragmented habitats. Finally, the findings support better conservation planning by providing insights into how agricultural expansion can coexist with biodiversity protection in Malaysia.

2. Materials and methods

2.1. Study area and sampling design

The study was conducted in oil palm–dominated landscapes across four states in Peninsular Malaysia, all of which experience a humid tropical climate characterized by consistently high temperatures (mean annual ~26–27 °C) and high annual rainfall, generally exceeding 2000 mm. These landscapes were historically covered by lowland dipterocarp forest but have undergone extensive land-use change over recent decades, primarily driven by the expansion of industrial oil palm plantations. As a result, the current study areas comprise mosaics of monoculture oil palm estates interspersed with remnant forest patches and plantations adjoining contiguous forest reserves designated as High Conservation Value Forests (HCVFs). We conducted this study in four states of Peninsular Malaysia: Pahang (Lepar Utara), Terengganu (Setiu), Kelantan (Aring), and Johor (Tenggaroh). These states were selected due to their regional importance in oil palm cultivation and their variation in landscape structure and ecological context. Each state contains oil palm plantations embedded in distinct landscape types, which we classified into three categories. The first, oil palm plantation (OPP), refers

to large-scale monoculture plantations with no adjacent natural forest. The second, oil palm with forest patch (OPFP), includes plantations that contain small, isolated forest fragments or riparian strips retained within the plantation matrix. The third, oil palm with contiguous forest (OPCF), comprises plantations that directly border large tracts of natural or protected forest reserves. Forest elements in both OPFP and OPCF landscapes were designated as High Conservation Value Forests (HCVFs) by plantation management under national sustainability certification schemes and are managed accordingly to maintain biodiversity and ecosystem function (ZSL, 2011). This landscape classification captures a gradient of structural connectivity and habitat complexity. We focused our sampling in mature plantations aged between 10 and 15 years to control for variation in stand age and its potential influence on mammal communities. The sampling area at each landscape type was standardized to a circular area of 78.54 ha (0.79 km^2), defined by a 500-meter radius centred on the forest edge or patch centroid, depending on forest presence. This scale was selected to ensure adequate coverage for terrestrial mammal communities while minimizing edge overlap with adjacent habitats (Bernard et al., 2014; Azhar et al., 2014). We ensured that sampling blocks within each state and between landscape types were spaced at least 2 km apart to maintain spatial independence. Although some large mammals have extensive home ranges, such separation is commonly used in landscape-level biodiversity studies and is effective in minimizing sampling autocorrelation (Wearn et al., 2017; Luskin et al., 2017). The ecological characteristics of each study area, including forest patch size and adjacent reserve identity, are summarized in Table 1 and illustrated in Figs. 1 and 2.

2.2. *Wildlife sampling*

We assessed terrestrial mammal diversity through a combination of camera trapping and live cage trapping across all three landscape types in each of the four study states. Camera traps were deployed to record a broad spectrum of terrestrial species, including small-, medium-, and large-bodied mammals, while live cage traps complemented this method by targeting small and medium-sized taxa that are less frequently detected by camera traps. This integrated approach maximized detection probability across different mammal size classes and diel activity patterns. At each state-level plantation, we deployed 60 camera traps (HC-802A, OEM), with 20 traps allocated per landscape type. Across the four states, this resulted in a total of 240 camera-trap sampling units. The same 60 camera-trap units were rotated among states to ensure standardized sampling effort across all sites. Camera traps were mounted approximately 50 cm above ground and placed along pre-established transects, spaced 200 m apart to minimize detection overlap and ensure adequate coverage of the 0.79 km^2 sampling block. This spacing was selected to improve detectability of small- and medium-bodied species and to maintain spatial independence, as sampling blocks were separated by more than 2 km. Sites were selected based on indicators of animal activity, including trails, vegetation cover, forest margins, and water sources. Each trap was set to operate continuously for at least 30 days per landscape type and programmed to capture three consecutive images per trigger with no delay, optimizing temporal resolution of detections.

We conducted live trapping using a total of 60 wire-mesh cage traps per landscape, resulting in 180 traps per state across the three landscape types. Trap pairs consisted of one medium and two small cages, spaced approximately 200 m apart along independent transects to complement camera trapping (Fig. 2). Due to logistical constraints, including limited equipment and personnel, cage traps were deployed sequentially by landscape type within each state, approximately 10 days per landscape (ranging between 10–12 days depending on weather and accessibility) for a total of about 30–36 trapping days per state. All traps were baited with combinations suited to attract a variety of mammal taxa (e.g., banana, peanut butter, salted fish, jackfruit, and papaya) and positioned near signs of mammal activity such as burrows, fallen logs, and dense vegetation. Traps were checked twice daily, in the morning (7:00–9:00 am) and evening (5:00–7:00 pm), to ensure animal welfare and to detect both diurnal and nocturnal species. Captured individuals were identified to species level using field guides and expert consultation, and standard morphometric data (sex, age class, weight, and body measurements) were recorded before releasing the animals at their point of capture.

All field procedures were conducted in accordance with ethical guidelines approved by the Universiti Kebangsaan Malaysia Animal Ethics Committee (reference: UKM.PPI.AEC.800–4/3/1). Research permits were obtained from relevant authorities, including plantation management, the Department of Wildlife and National Parks (PERHILITAN; reference: JPHLTN.600–6/1/4 JLD2 (119)), and the Forestry Department of Peninsular Malaysia (reference: JH/100 Jld. 35(14)).

Table 1
Description of each study area showing plantation area (ha), forest patch area, adjacent forest reserve, and sampling period. Coordinates indicate the central location of each study site.

	Study Site/ Plantation (Coordinates)	Plantation area (ha)	Forest patch area (ha)	Adjacent forest reserve	Period of sampling
1	Pahang (Lepar) (3.898858, 102.836178)	619.48	37.13	Hutan Lipur Berkelah (1575 ha)	19 May - 22 June 2023
2	Terangganu (Setiu) (5.541451, 102.710733)	718.62	124.25	Hutan Simpan Gunung Tebu (25,259 ha)	12 Aug - 8 Oct 2023
3	Johor (Tenggaroh) (2.016331, 104.060802)	653.05	105.81	Hutan Simpan Tenggaroh (2023.72 ha)	27 Dec 2023–18 Feb 2024
4	Kelantan (Aring) (4.970705, 102.453080)	567.88	40.86	Taman Negara Kuala Koh (80,250 ha)	7 May - 14 July 2024

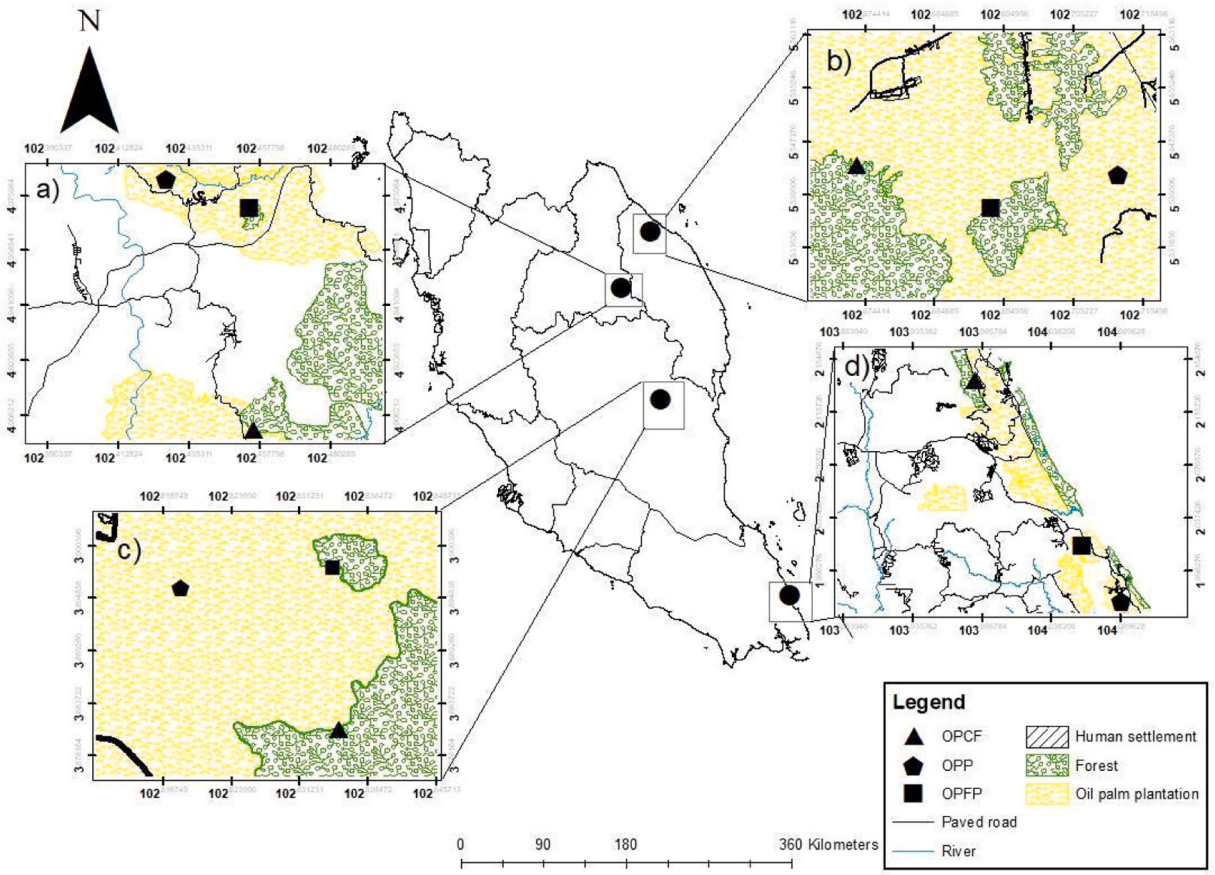

Fig. 1. Study locations of different landscapes (OPP, OPFP, OPCF) at four states in Peninsular Malaysia; a) Kelantan (Aring), b) Terengganu (Setiu), c) Pahang (Lepar) and d) Johor (Tenggaroh).

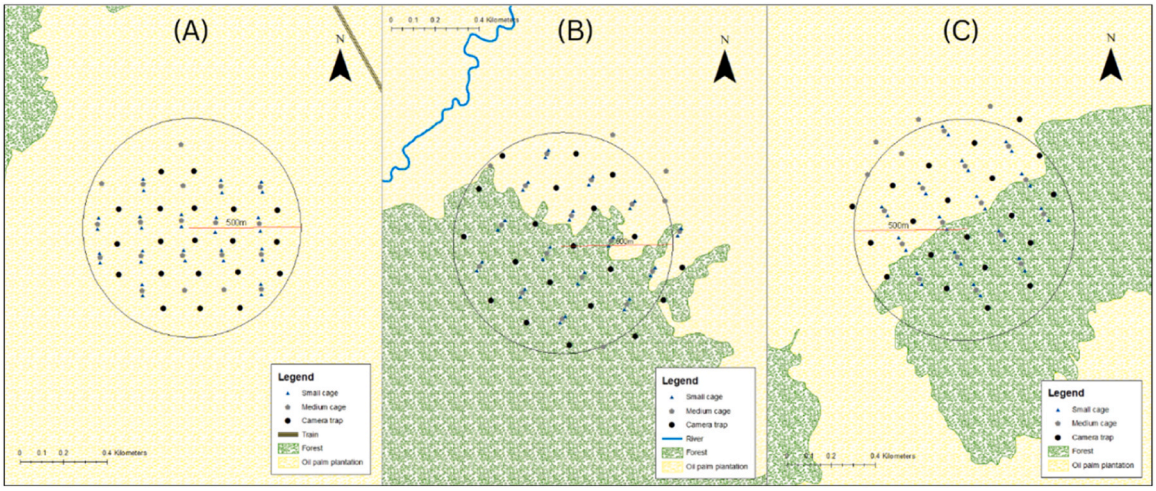

Fig. 2. Sampling design of study area: (A) Oil Palm plantation (OPP), (B) Oil Palm-Contiguous Forest (OPCF), and (C) Oil Palm-Forest Patch (OPFP). The map indicates the locations of camera traps, small and medium cage traps (20:40:20) used for mammals' diversity assessment.

2.3. Species identification and detection rates

We identified terrestrial mammals to the species level using field guides (Francis, 2008) and further categorized mammals into three body size classes based on adult average body mass following Meijaard et al. (2005): small (<1 kg), medium (1–15 kg), and large (>15 kg). We omitted photographs of animals that could not be confidently identified due to poor image quality or incomplete visibility from the analysis. We included all non-volant mammals, such as small mammals like rats and squirrels. However, we grouped rats that could not be reliably identified to the species level as *Rattus* sp.

Detection rates were calculated as the number of independent detections per 100 trap-nights, where total trap-night effort combined both camera and cage traps, as both contributed to detections across the small-to-large mammal spectrum. Independent detections were defined as occurrences of the same species at the same site separated by at least 60 min, to reduce temporal autocorrelation and overrepresentation of highly active species (Smith, 2025). Because individual mammals could not be uniquely identified using either camera trapping or live cage trapping, detection rates were used as a relative index of abundance rather than a direct measure of population size. Accordingly, all references to "abundance" in this study reflect variation in detection frequency across landscapes and environmental gradients and should be interpreted as relative differences in activity or occurrence rather than true demographic abundance. To enhance interpretability, detection rates were summarized by landscape type and species, with species richness and detection metrics reported in Supplementary Table S1. These summaries provide insight into species-specific detectability patterns, particularly for rare and conservation-priority species such as *Panthera tigris* and *Tapirus indicus*.

2.4. Habitat variables

At each landscape, we recorded several habitat variables, including distance to paved roads, distance to unpaved roads, distance to human settlements, distance to water sources, and elevation. We selected these variables not as direct measures of spatial configuration (e.g., fragmentation metrics), but as indicators of human accessibility and environmental gradients that influence mammal presence and behaviour. We calculated Euclidean (straight-line) distances from each camera trap centroid to the nearest paved road, unpaved road, water source, and human settlement using the measurement tool in Google Earth Pro v7.3.4, with all measurements exported and verified in ArcGIS 10.8. All landscape features were derived from pre-existing base layers available in Google Earth (2022–2024 imagery), which corresponds closely with the mammal sampling periods (May 2023 to July 2024). We manually verified and cross-referenced mapped features with ground-truth observations at each site (e.g., visible roads and streams). Elevation data were obtained in situ using a Garmin eTrex 22x handheld GPS. All GPS coordinates were georeferenced in WGS 84 datum. We then incorporated these habitat variables into the analysis to assess their influence on mammalian diversity across different landscapes.

2.5. Statistical analysis

We assessed sampling completeness and species richness across the three landscape types which are the Oil Palm Plantation (OPP), Oil Palm with Forest Patches (OPFP), and Oil Palm with Contiguous Forest (OPCF) using rarefaction and extrapolation curves implemented in the iNEXT package (R version 4.4.2) and Paleontological Statistics (PAST v4.17). Sample coverage, calculated as the proportion of observed to estimated species richness, was used to evaluate sampling completeness and standardize comparisons among landscapes. In addition, we quantified classical diversity metrics (Shannon's H′, Simpson's D, Evenness E, and Chao1) to describe variation in diversity across landscapes. To provide ecological context, we computed detection rates (independent detections per 100 trap-nights) for all species and highlighted the distribution of conservation-priority taxa (e.g., *Panthera tigris*, *Tapirus indicus*, *Elephas maximus*) listed as Endangered, Vulnerable, or Near Threatened on the IUCN Red List.

We formulated clear, hypothesis-driven predictions for each covariate based on previous research on mammalian responses to disturbance and habitat heterogeneity. Specifically, we expected species richness and abundance to increase with elevation, as higher-elevation sites are typically less disturbed and maintain cooler microclimates. We predicted negative effects of proximity to paved roads due to noise, traffic, and human disturbance, whereas moderate proximity to unpaved roads could have weak or positive effects by facilitating movement of adaptable species. Distance to human settlements was expected to show a positive relationship with both richness and abundance, reflecting reduced disturbance and hunting pressure in remote areas. Conversely, distance to water bodies was predicted to have a negative relationship, as many mammals depend on nearby water sources. Finally, we hypothesized that landscape type would influence diversity, with OPFP sites supporting higher richness and abundance than monoculture (OPP) or continuous-forest (OPCF) sites, reflecting intermediate habitat heterogeneity.

We analyzed mammalian species richness and abundance using Generalized Linear Mixed Models (GLMMs) in R (v 4.4.2). Species richness was modeled with a Poisson GLMM using the *lme4* package, and abundance (independent detections per trap-night) with a negative-binomial GLMM using glmmTMB to account for overdispersion. Continuous predictors (elevation, distances to paved roads, unpaved roads, settlements, and water) were z-standardized to improve model convergence and comparability. Landscape type (OPCF, OPFP, OPP) was included as a fixed effect, and State as a random intercept to account for spatial non-independence among sites. We adopted an information-theoretic model-selection framework using *MuMIn*, generating all-subset models with up to four fixed predictors (m.lim = c(1, 4)) to maintain parsimony. Candidate models were ranked by AICc, and those with $\Delta AICc \leq 2$ were considered strongly supported. We performed model averaging across the top model set to obtain averaged coefficients, standard errors, and relative variable importance (ΣAICc weights). Model assumptions were validated using DHARMa (residual uniformity, overdispersion, zero-inflation), and multicollinearity was assessed with generalized variance inflation factors (GVIF), all < 3.0. To aid interpretation, we calculated marginal (R^2m) and conditional (R^2c) coefficients of determination using performance, and visualized partial-effect plots

for the most influential predictors on the response scale using *ggeffects*.

3. Results

3.1. Mammals diversity in a heterogeneous oil palm plantation landscapes

We recorded a total of 3182 independent mammal detections across all camera and cage traps, using a 60-minute threshold to define detection independence. Detection rates per 100 trap-nights were calculated for each species and disaggregated by landscape type to capture fine-scale variation in species-specific activity and detectability. The detection for each species and species richness was summarized per landscape type (see Supplementary Table S1), with Oil Palm with Contiguous Forest (OPCF) showing the highest diversity, followed by Oil Palm near Forest Patches (OPFP) and Oil Palm Plantation without adjacent forest (OPP) are presented in Supplementary Table S1. Rare and conservation-priority species, such as *Elephas maximus, Panthera tigris* and *Tapirus indicus*, were detected at low rates (e.g., 0.27, 0.16 and 1.25 detections per 100 trap-nights, respectively).

Camera traps and cage traps deployed across 12 landscapes in four states of Peninsular Malaysia recorded a total of 30 mammal species, representing a diverse assemblage at the different oil palm landscapes. Among the recorded species, 51 % were classified as Endangered, Vulnerable, or Near Threatened on the IUCN Red List. These included the Malayan Tiger (*Panthera tigris*), Leopard (*Panthera pardus*), Asian Elephant (*Elephas maximus*), Malayan Tapir (*Tapirus indicus*), and Sun Bear (*Helarctos malayanus*), among others. These species were predominantly detected in OPCF and OPFP landscapes, emphasizing the conservation importance of these habitat types (Supplementary Table S2). In contrast, OPP landscapes supported fewer species of conservation concern and were dominated by generalist species classified as Least Concern, such as wild boar (*Sus scrofa*), common palm civet (*Paradoxurus hermaphroditus*) and Malayan civet (*Viverra tangalunga*).

Rarefaction and extrapolation analyses indicated high sampling completeness across all landscapes, suggesting that the majority of species present were likely detected (Supplementary Figure S1). Diversity patterns among landscape types were evaluated using Shannon diversity (H'), Simpson diversity (1-D), observed species richness and Chao-1 estimated richness (Fig. 3). The highest Shannon diversity index (H) was recorded in OPCF (H = 2.69), followed by OPFP (H = 2.35), and was lowest in OPP (H = 1.12). Similarly, Simpson's diversity (1 – D) was highest in OPCF (0.91), followed by OPFP (0.86) and OPP (0.46). Observed species richness was highest in OPCF (26 species), while OPFP and OPP recorded 22 and 13 species, respectively. Chao1 estimated richness showed a similar pattern, with OPCF estimated at 27.5 species, OPFP at 28, and OPP at 14. We then focused on modelling the environmental and landscape predictors of mammalian species richness and abundance using generalized linear mixed models (GLMMs).

3.2. Variation in mammal species richness and abundance with environmental predictor variables

We used generalized linear mixed models (GLMMs) to examine the effects of landscape type and environmental variables on mammalian species richness and abundance. Assessment of multicollinearity using generalized variance inflation factors (GVIF) indicated that all predictors were below the common threshold (GVIF < 3.0), confirming that no problematic collinearity was present among covariates (Supplementary Table S3). For richness, model selection and model averaging revealed that elevation, distance to paved roads, and distance to unpaved roads were the most influential predictors of mammalian species richness across oil palm landscapes (ΣAICc weights = 1.00, 1.00, and 0.95, respectively; Table 2). Model-averaged variable importance values further confirmed that elevation, distance to paved roads, and distance to unpaved roads were the most influential predictors of species richness (ΣAICc weight ≥ 0.95; Supplementary Table S4). The best-supported model (AICc = 765.67, weight = 0.46) included

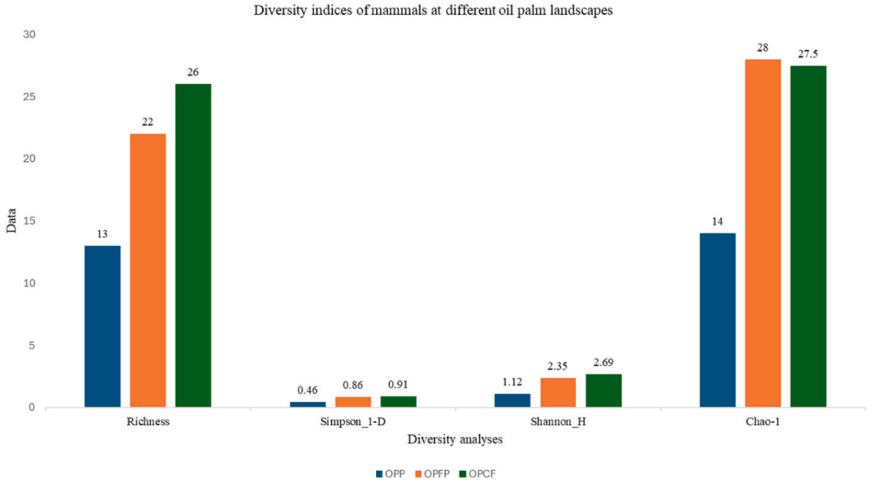

Fig. 3. Observed species diversity recorded in three oil palm landscape: OPP, OPFP, and OPCF.

Table 2
Model-averaged coefficients and performance statistics for predictors of mammalian species richness across oil palm landscapes (ΔAICc ≤ 2 candidate set). Bold values indicate high relative importance (ΣAICc ≥ 0.90).

Predictor	Estimate (β) ± SE	p	Direction	ΣAICc Importance	95 % CI	Interpretation
Elevation	0.30 ± 0.07	< 0.001	↑	1.00	[0.18,0.42]	Richness increases at higher elevation
Distance to paved roads	0.26 ± 0.08	< 0.01	↑ (farther = richer)	1.00	[0.11,0.40]	Fewer paved-road disturbances favour diversity
Distance to unpaved roads	−0.16 ± 0.08	< 0.05	↓ (closer = richer)	0.95	[-0.28, −0.04]	Light-use tracks promote heterogeneity
Distance to settlement	0.02 ± 0.02	0.41	—	0.18	[-0.07, 0.11]	Weak human-settlement effect
Distance to water	0.02 ± 0.02	0.44	—	0.18	[-0.09, 0.13]	Minimal effect
Landscape type	−0.01 ± 0.10	0.62	—	0.13	[-0.36, 0.15]	Weak landscape-level influence

Model metrics: Best model AICc = 765.67; ΔAICc range (top 3 models) = 0–2.04; cumulative weight = 0.82; Marginal R^2 = 0.17; Conditional R^2 = 0.57; Overdispersion (p) = 1.09 (0.572); Zero-inflation (p) < 0.001.

elevation, distance to paved roads, and distance to unpaved roads, while the next two competing models (ΔAICc ≤ 2) incorporated either distance to settlements or distance to water (Supplementary Table S5). Model-averaged coefficients indicated that species richness increased significantly with elevation (β = 0.30 ± 0.07), decreased near paved roads (β = 0.26 ± 0.08), and increased near unpaved roads (β = −0.16 ± 0.08), consistent with expectations that less-disturbed and more heterogeneous habitats promote higher richness (Fig. 4A-C). Distances to human settlements and water bodies showed weak effects (β ≈ 0.02, p > 0.05), and landscape type exhibited only minor influence (ΣAICc = 0.13). The top three models collectively explained most of the information in the candidate set (cumulative AICc weight = 0.82). R^2 values were computed for the best-supported model only, as R^2 cannot be directly averaged across models with different fixed-effect structures. The best-supported model achieved moderate explanatory power, with marginal $R^2 \approx 0.17$ and conditional $R^2 \approx 0.57$, indicating that both fixed and random effects contributed substantially to variance in species richness (Table 2). Model diagnostics (DHARMa) indicated no overdispersion and evidence of zero-inflation in the richness model (p < 0.001), but residuals were otherwise uniform; overall fit was adequate (Supplementary Figure S2A; Table S7).

For species abundance, model selection identified landscape type and distance to paved roads as the most influential predictors of mammal abundance (ΣAICc weights = 0.57 and 0.57, respectively), with elevation showing moderate support (ΣAICc = 0.37; Table 3). Consistently, variable importance analysis identified landscape type, distance to paved roads, and elevation as the strongest predictors of mammal abundance (ΣAICc weight ≥ 0.37; Supplementary Table S4). The best-supported model (AICc = 1525.99, weight = 0.13) included distance to paved roads and landscape type, while several additional models within ΔAICc ≤ 2 (cumulative weight ≈ 0.36) incorporated elevation or minor spatial covariates (Supplementary Table S6). Model-averaged coefficients (ΔAICc ≤ 2 set) indicated that abundance increased farther from paved roads (β = 0.15 ± 0.05) and varied significantly among landscape types, being highest in OPP, intermediate in OPCF, and lowest in OPFP (OPP vs OPCF: β = 0.30; OPFP vs OPCF: β = −0.11). Elevation had a modest positive effect (β = 0.10 ± 0.05), whereas distances to unpaved roads, settlements, and water showed minimal effects (|β| ≤ 0.03; Table 3). These results suggest that disturbance-tolerant generalists dominate monoculture plantations, while structurally complex habitats near forests sustain fewer but more specialized species (Fig. 4D-E). Model diagnostics from DHARMa indicated no overdispersion (dispersion = 1.17, p = 0.388) and mild zero deflation (p = 0.002). Despite this, simulation-based residual checks (Supplementary Figure S2B) and statistical summaries (Supplementary Table S7) confirmed satisfactory fit and appropriate negative-binomial error structure.

4. Discussion

This study shows that mammalian diversity in oil palm–dominated landscapes is governed primarily by topography and human accessibility. Species richness increased with elevation and with distance from paved roads, whereas richness tended to decline with increasing distance from unpaved roads. In contrast, total abundance was highest in monoculture plantations and was positively associated with distance from paved roads, with landscape type emerging as the most influential factor for abundance. Together, these results indicate that oil palm landscapes can host substantial mammal diversity, but community composition differs markedly among landscape types, with simplified monoculture plantations dominated by a small number of abundant generalist species, while more structurally complex landscapes support higher species richness, including forest-dependent taxa.

The positive association between elevation and richness suggests that higher, cooler, and less-accessible terrain functions as refugia within plantation mosaics. It is consistent with elevational filtering of mammal communities documented on Bornean mountains, where community composition and richness shift with climate and structure along elevation (Camacho-Sánchez et al., 2019). These regional data support our inference that elevational contexts within plantation matrices can help maintain richness through reduced disturbance and greater niche availability (Camacho-Sánchez et al., 2019). Accordingly, conserving and buffering high-elevation forest tracts within agricultural matrices should be a management priority where the objective is to maintain diverse mammal communities rather than merely high detection rates.

Distance to paved roads was positively related to richness and abundance, consistent with paved roads acting as disturbance corridors that fragment habitat, elevate access, and increase mortality risk (Jamhuri et al., 2020; Pardo et al., 2019). In Peninsular Malaysia, medium-to-large mammals are killed more frequently on plantation roads than on highways, underscoring that internal

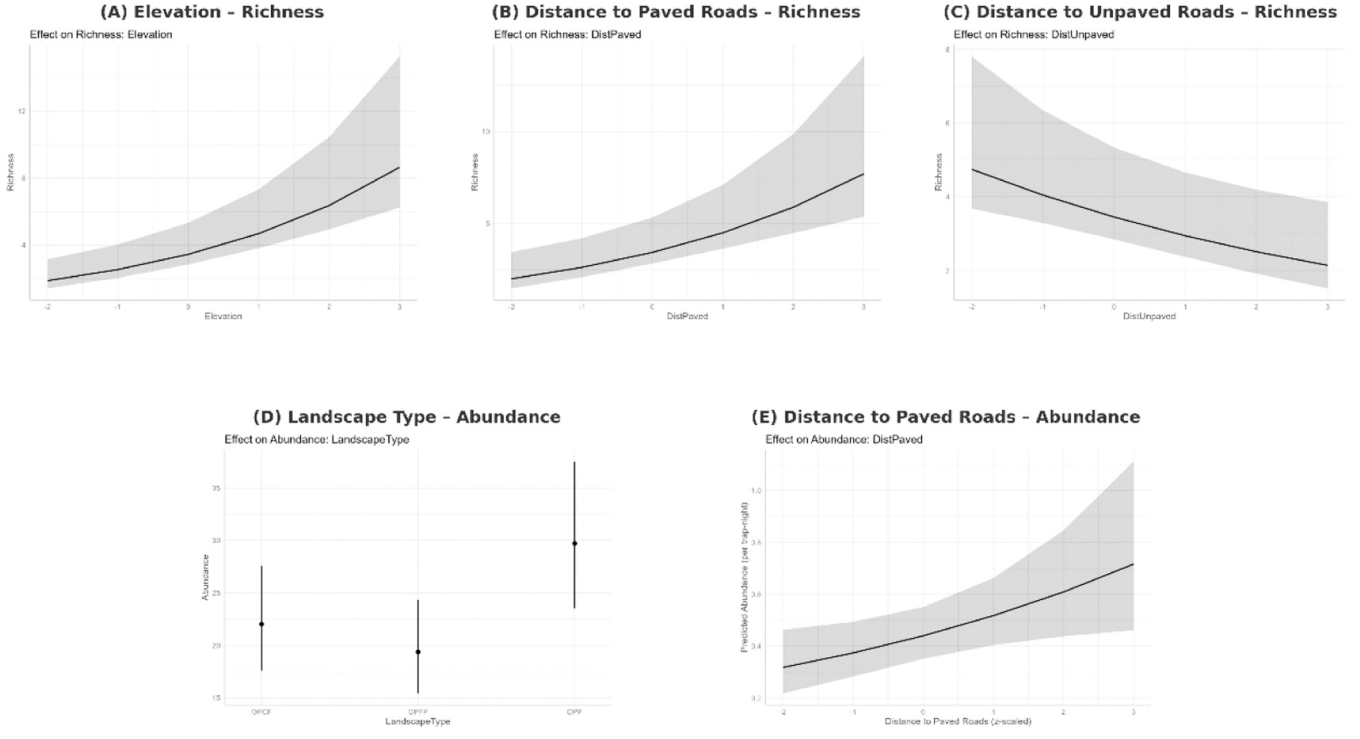

Fig. 4. Partial-effect plots showing relationships between key predictors and mammalian diversity across oil palm landscapes. (A–C) Species richness increased with elevation and distance to paved roads but declined with distance to unpaved roads. (D–E) Total abundance was highest in monoculture plantations and at greater distances from paved roads. Shaded areas represent 95 % confidence intervals.

Table 3
Model-averaged coefficients and performance statistics for predictors of mammalian abundance across oil palm landscapes (ΔAICc ≤ 2 candidate set). Bold values denote relatively strong effects (ΣAICc ≥ 0.50).

Predictor	Estimate (β) ± SE	p	Direction	ΣAICc Importance	95 % CI	Interpretation
Distance to paved roads	0.15 ± 0.05	< 0.05	↑	0.57	[0.01, 0.31]	Abundance rises farther from paved roads
Landscape type – OPP vs OPCF	0.30 ± 0.09	< 0.05	↑	0.57	[-0.02, 0.67]	OPP shows higher total abundance
Landscape type – OPFP vs OPCF	−0.11 ± 0.07	0.18	↓	0.57	[-0.44, 0.22]	Lowest abundance in OPFP
Elevation	0.10 ± 0.05	0.10	↑	0.37	[-0.06, 0.23]	Slight increase at higher elevation
Distance to unpaved roads	−0.02 ± 0.02	0.40	—	0.21	[-0.25, 0.13]	Minor effect
Distance to settlement	−0.03 ± 0.02	0.28	—	0.23	[-0.12, 0.20]	Weak negative trend
Distance to water	0.01 ± 0.01	0.45	—	0.22	[-0.18, 0.21]	Negligible effect

Model metrics: Best model AICc = 1525.99; ΔAICc range (top 5 models) = 0–2.01; cumulative weight = 0.36; Marginal $R^2 \approx 0.10$–0.12; Conditional $R^2 \approx 0.15$; Overdispersion (p) = 1.17 (0.388); Zero-inflation (p) = 0.002.

estate networks can strongly shape mammal survival and distribution (Jamhuri et al., 2020). More broadly, new road development is repeatedly implicated in facilitating hunting and disorganized human occupation, reinforcing the value of limiting paved-road expansion and buffering existing routes (Pardo et al., 2019). By contrast, richness decreased with distance from unpaved tracks in our models, a pattern plausibly reflecting moderate, fine-scale edge structure and linear cover that some species use for movement or foraging; if managed carefully (low traffic, vegetation retained, no night driving), such service tracks may carry lower ecological costs than major paved roads (Pardo et al., 2019).

Abundance peaked in monoculture plantations, while richness tracked features typical of more complex or less disturbed settings. This divergence implies that generalist species dominate counts in simplified habitats, whereas species-rich assemblages require habitat heterogeneity and reduced disturbance (Guerrero-Sánchez et al., 2021). In Southeast Asia, mammal richness declines steeply with distance from native forest into plantations, and plantation structural tweaks rarely offset this loss. This highlights the irreplaceable role of retaining native forest near or within estates (Yue et al., 2015). Practically, estates should not equate high encounter rates with healthy communities; instead, they should invest in structural complexity by retaining forest patches and edges, widening riparian buffers, and linking patches to contiguous forest to provide shaded, cooler, and quieter movement routes (Yue et al., 2015).

Our results reinforce the biodiversity value of High Conservation Value Forests (HCVFs) embedded within or adjacent to oil palm. Evidence from Peninsular Malaysia shows that large, homogeneous estates tend to be structurally simple and poor for biodiversity, whereas mosaics with remnant forest and diversified elements perform better(Azhar et al., 2015). Recent Malaysian occupancy work also indicates that a synergy of land-sparing (large reserves) and land-sharing (on-farm patches, corridors) strategies best supports native mammals in plantation landscapes (Narayana et al., 2024). Estate-scale design that clusters HCVFs in higher terrain, keeps major paved access on the periphery, and maintains continuous vegetated corridors along low-traffic estate tracks can reconcile production with biodiversity objectives and complement regional connectivity initiatives (Azhar et al., 2015; Narayana et al., 2024).

For estates and regulators, protecting high-elevation forest, minimizing new paved-road encroachment, and engineering vegetated connectivity along low-use service tracks are priority actions (Azhar et al., 2015; Narayana et al., 2024). These actions align with Malaysian certification contexts and are likely to yield disproportionate gains for mammal richness. Future work should integrate behavioral and genetic indicators of connectivity, quantify traffic and hunting pressure, and deploy microclimate and vegetation sensors to disentangle mechanisms behind elevation and road-distance signals, enabling estate-specific thresholds (e.g., buffer widths, traffic limits, corridor shading targets) that balance production with biodiversity conservation (Pardo et al., 2019).

5. Conclusion

This study demonstrates that mammalian diversity in oil palm–dominated landscapes is shaped primarily by topography and human accessibility. Species richness increased with elevation and distance from paved roads, highlighting the importance of highland areas and low-disturbance zones for maintaining diverse mammal communities. In contrast, abundance was highest in monoculture plantations and near low-traffic unpaved roads, reflecting the numerical dominance of adaptable generalist species. These patterns suggest that while oil palm landscapes can still support substantial mammalian activity, true biodiversity persistence depends on reducing disturbance intensity and maintaining structural heterogeneity within plantations.

From a management perspective, conserving and buffering high-elevation forests, restricting new paved road development, and maintaining vegetated corridors along service tracks can significantly enhance the ecological value of plantation mosaics. The retention of forest patches and adjacent contiguous forests provides critical refugia for forest-dependent mammals and sustains ecological connectivity across fragmented landscapes. Collectively, these findings reinforce the role of High Conservation Value Forests (HCVFs) as biodiversity reservoirs within agricultural matrices. Future work should integrate behavioral and genetic monitoring to assess population connectivity and explore the long-term viability of mammal species in modified tropical landscapes. Such approaches will help refine sustainable land-use strategies that balance agricultural productivity with biodiversity conservation.

CRediT authorship contribution statement

Hairulazim Mahmud: Project administration, Funding acquisition. **Ahmad Shahdan Kasim:** Writing – review & editing, Project

administration, Funding acquisition, Conceptualization. **Zalifah Ramli:** Project administration, Investigation, Funding acquisition, Conceptualization. **Sharifah Nur Afni:** Validation, Project administration, Data curation, Conceptualization. **Mohamad Azam Akmal Abu-Bakar:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Naim Mustafa:** Methodology, Investigation, Formal analysis. **Farah Shafawati Mohd-Taib:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Kamaruddin Zainul Abidin :** Writing – review & editing, Formal analysis, Data curation, Conceptualization. **Pazil Abdul-Patah:** Writing – review & editing, Project administration, Investigation, Conceptualization. **Badrul Azhar:** Writing – review & editing, Supervision, Formal analysis, Data curation, Conceptualization. **Zamira Hasanah Zamzuri:** Validation, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Farah Shafawati Mohd-Taib reports financial support and administrative support were provided by Malaysian Palm Oil Green Conservation Foundation. If there are other authors, they 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.2025.e04047.

Data availability

Data will be made available on request.

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