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## RESEARCH ARTICLE

# Harnessing nature-based solutions in modified tropical peatland to benefit biodiversity

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## Abstract

1. Tropical peat-swamp forests are globally significant for both climate mitigation and biodiversity conservation, yet they are among the most threatened ecosystems due to rapid land-use change and weak protection. As global commitments to net-zero and ecosystem restoration expand, nature-based solutions (NbS)—defined as actions that protect, restore and sustainably manage ecosystems to address societal challenges—are increasingly proposed for tropical peatlands. Many peatland NbS schemes integrate conservation and production within multifunctional landscapes to safeguard carbon stocks while supporting biodiversity. However, the biodiversity outcomes of such schemes remain poorly documented.
2. We assessed mammal communities in a large (723,637 ha) proposed NbS landscape in Sumatra that encompasses intact peat-swamp forest, linear forest remnants and *Acacia* plantations. Using an extensive camera-trap survey (184 locations; 17,132 trap days) and hierarchical multi-species occupancy models, we quantified community occupancy, species richness and functional and phylogenetic diversity. We further evaluated how alternative land-use configurations, representing protection- versus production-focused management, shape biodiversity outcomes relevant to NbS implementation.
3. Intact core forest and linear forest remnants supported high mammal occupancy and richness, while functional and phylogenetic diversity varied little among land-cover types. Species were more strongly associated with environmental features, such as high-biomass forest, interior areas and proximity to water than with direct human pressures.
4. The core forest area targeted for NbS designation emerged as especially important for biodiversity, and its protection delivered the greatest gains in projected mammal occupancy and diversity. In contrast, scenarios of reduced protection and increased development resulted in sharp declines, particularly among disturbance-sensitive threatened species.
5. *Synthesis and applications.* Our findings demonstrate that well-designed protection-production NbS schemes in tropical peat swamps can deliver joint climate and

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biodiversity benefits, provided that governance safeguards core forests while improving habitat quality in production zones. Maintaining landscape configurations that promote connectivity and ecological function will be key to sustaining biodiversity alongside carbon storage. Conservation priorities should therefore emphasise strict protection of core forests, complemented by wildlife-friendly practices within and around plantations. These insights strengthen the evidence base for NbS implementation in working landscapes, highlighting the need for long-term biodiversity monitoring to guide adaptive management in tropical peatlands.

#### KEYWORDS

acacia plantation, camera-trapping, ecosystem restoration concession, land-use planning, mammals, nature-based climate solutions, Southeast Asia, tropical forest

## 1 | INTRODUCTION

Tropical landscapes face complex demands for forest and agricultural production as well as biodiversity conservation and ecosystem services (Girkin et al., 2022; Struebig et al., 2025). These demands are especially prominent for tropical peat swamps, which are unique and ecologically critical ecosystems (Mishra et al., 2021). Tropical peat swamps support high biodiversity and local livelihoods and also play a vital role in global carbon storage, making them essential for climate regulation (Girkin et al., 2022; Harrison, Ottay, et al., 2020). These wetlands are characterised by thick deposits of organic peat soil, typically formed in low-altitude river valleys, floodplains and coastal areas across tropical regions (Page & Rieley, 2018). Although many tropical peat swamps are forested, only about a third of their historical extent remains (up to 500,000 km<sup>2</sup>), of which a mere 8% is strictly protected (Austin et al., 2025). This situation is exemplified in Southeast Asia, which supports roughly half of the World's tropical peatlands (Mishra et al., 2021; Posa et al., 2011).

Historically, the inaccessibility of tropical peat swamps limited both scientific exploration and major development. However, following infrastructural improvements and shifts in land-use policies, these landscapes now face significant developmental pressures, leading to widespread drainage and land clearance (Murdiyarso et al., 2019). Between 1990 and 2015, Southeast Asia lost more than 12.1 Mha of peatlands, with deforestation rates more than double those of other tropical forest types (Sasmitho et al., 2025). Primary drivers of this deforestation include timber extraction and the expansion of plantation estates, especially for palm oil and paper-pulp production (Murdiyarso et al., 2019; Page & Rieley, 2018). Fires further exacerbate the problem, adding greenhouse gas emissions and delaying ecological recovery (Harrison et al., 2024; Mishra et al., 2021). Improved management of tropical peat swamps, therefore, presents a vital opportunity to advance climate mitigation goals and biodiversity conservation simultaneously (Austin et al., 2025).

Peat-swamp forests in Indonesia, particularly in Sumatra, are among the most affected by land-use changes and are critical for implementing nature-based solutions for climate mitigation (Griscom

et al., 2020; Sarira et al., 2022). Large areas have been converted into monoculture plantations of fast-growing softwoods, such as *Acacia* species, especially in Riau province. These plantations covered nearly 2 Mha in 2023 (Nusantara Atlas, 2023) and significantly contribute to Indonesia's economy, generating US\$7.5 billion of revenue in 2021 (Conservation Economics Lab et al., 2023). Yet, this transformation is associated with intensive land-use practices, including short felling rotations and extensive peat drainage, which have profound ecological impacts (Mishra et al., 2021). Despite a growing body of research on tropical biodiversity and land-use change, studies specifically addressing the unique challenges faced by peat-swamp forest landscapes are limited (Harrison, Ottay, et al., 2020; Posa et al., 2011).

Nature-based solutions (NbS) have emerged as a prominent policy framework for addressing these challenges, particularly in countries with large peatland estates. NbS are broadly defined as actions that protect, restore or sustainably manage ecosystems to address societal challenges—such as climate change mitigation, climate adaptation, biodiversity loss and sustainable development—while providing human well-being and biodiversity benefits (Cohen-Shacham et al., 2016). To be considered credible, global standards emphasise that NbS must generate genuine ecological benefits, especially biodiversity gains (IUCN, 2025). In peat-dominated regions, NbS may include protecting remaining intact peat-swamp forests, restoring degraded peatlands to reduce fire risk and emissions and adopting sustainable production models that reduce ecological impacts in plantation landscapes (Griscom et al., 2020). However, despite growing interest, the biodiversity outcomes of tropical NbS remain poorly understood (Key et al., 2022), constraining evidence-based implementation.

The shift from biodiverse peat-swamp forests to simplified monoculture plantations is expected to result in marked changes to species composition and ecosystem function. Studies in oil palm landscapes show that plantations support far fewer forest species and exhibit reduced ecological functioning, such as carbon storage, hydrological regulation and nutrient cycling (Malhi et al., 2022; Meijaard et al., 2018). Remnant forests, especially those along

riparian margins, can serve as essential wildlife habitat and have the potential to facilitate dispersal across the modified landscape (Deere et al., 2022). The presence of some species within plantations may be attributed to spillover from neighbouring habitats, highlighting the value of managing adjacent forests or maintaining forest remnants within plantation estates (Chapman et al., 2019; Lucey & Hill, 2012; Oakley & Bicknell, 2022). For example, research in a mixed landscape of logged forests and *Acacia* plantations in Malaysian Borneo showed relatively high levels of species occupancy across the landscape (Wong et al., 2022). Plantation management practices can also influence biodiversity. In Chile, generalist species were found to move through older plantations, while forest specialists avoided younger plantations and clear-cuts (Plischoff et al., 2020). The concept of matrix contrast, the degree of difference between natural habitats and adjacent managed landscapes, might be particularly important for biodiversity outcomes in forest-plantation landscapes. Contrast between native forests and monoculture plantations, particularly newly planted ones, often intensifies edge effects, where microclimatic changes and increased vulnerability to invasive species impact forest-adapted organisms (Ewers & Didham, 2005; Ramirez-Delgado et al., 2022; Stamps et al., 1987). These edge effects might be particularly pronounced in tropical peat-swamp forests, where species used to moist, shaded conditions are negatively affected by the drier, hotter microclimate at plantation edges (Hardwick et al., 2015). Managing matrix contrast through modified felling regimes, wider buffer zones or preserving forest fragments within plantations might help maintain ecological function and biodiversity within production landscapes - approaches that are increasingly promoted under NbS frameworks. Yet, despite the policy momentum behind NbS, there remains limited empirical evidence guiding how production and protection areas can maximise biodiversity and climate outcomes in tropical countries. This evidence gap is especially salient given that governments, certification bodies and private-sector actors are developing NbS investment standards and peatland management guidelines. In this context, understanding how alternative land-use configurations perform is highly relevant to real-world decision-making.

Here we evaluate the biodiversity implications of plantation development on an extensive area of peat swamp in Sumatra. We focus on terrestrial medium-large mammals that are highly threatened by land-use change, are frequently prioritised by conservation and underpin important ecological functions (Kuipers et al., 2021). To understand the ecological value of peat-swamp forest compared to competing land uses, we first characterise the levels of occupancy, richness, phylogenetic and functional diversity of mammals in young and mature *Acacia* plantations, linear forest remnants and a core area of peat-swamp forest, under the a priori assumption that intact peat-swamp forest would support higher mammal diversity than modified land uses. We examine species responses to landscape covariates, specifically those relating to habitat suitability, disturbance, matrix contrast and configuration. We then evaluate a set of realistic landscape scenarios designed to reflect plausible management

pathways for the region, including enhanced protection of core forest, business-as-usual expansion of production and intermediate 'protection-production' strategies aligned with NbS principles. Such scenario analysis, where various spatial arrangements of natural forest, remnant patches and plantations are simulated, provides a way to test changes to landscape design and explore how different policies might influence environmental outcomes (Lacher et al., 2023). By linking ecological outcomes to spatial planning decisions, our study provides evidence for land managers, companies and policymakers tasked with implementing NbS in tropical peatlands. Our findings have implications for the future management of human-modified tropical peat swamps, which are under increased scrutiny as cost-effective nature-based solutions to the climate and biodiversity crises.

## 2 | MATERIALS AND METHODS

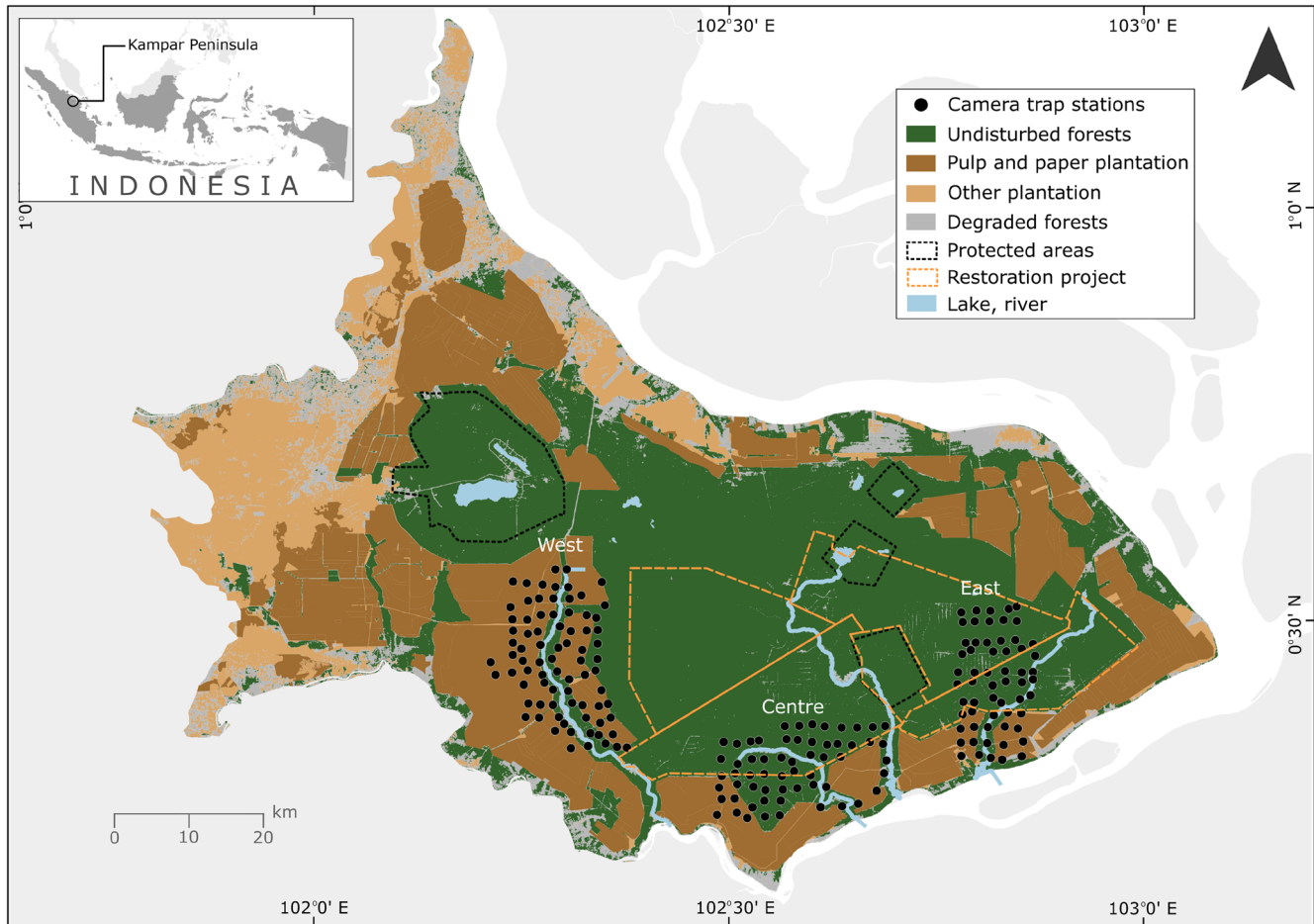
### 2.1 | Study area

Research was conducted under permits and endorsements from Indonesia's National Research and Innovation Agency (formerly RISTEK; 867/KE.01/AMD/11/2024) and the Directorate of Wildlife Conservation (Direktorat Konservasi Keanekaragaman Hayati; S.792/KKH/SDG/KSA.2/10/2021). Ethical approval was obtained from the University of Kent (project ref.: 20231678179524268).

We conducted our study over a 723,637 ha production landscape in the Kampar Peninsula of Riau province, Sumatra (0.46N, 102.62 E; Figure 1). Kampar Peninsula supports one of the largest tracts of peat-swamp forest remaining in what was once an extensive wetland ecosystem along the coastal lowlands of Riau and South Sumatra. The landscape comprises a mosaic of peat swamp and industrial-scale plantations, managed under a plantation-protection forest scheme. At the heart of the landscape, a 344,573 ha core area of old growth and lightly degraded peat-swamp forest is protected for conservation and restoration purposes, with restricted public access. The immediate surrounding matrix comprises ca. 215,500 ha of commercial softwood plantations (primarily *Acacia crassicarpa*), managed on a 4-year harvesting and replanting cycle. A network of linear forest remnants (5–42 km long; 0.1–4.8 km wide) functions as firebreaks and riparian buffers, providing 65,618 ha of additional forest cover. Beyond these management zones lies a broader mosaic of softwood and oil palm plantations.

### 2.2 | Camera-trap sampling

We surveyed medium- to large-bodied terrestrial mammals (>1 kg body mass) using remotely operated camera-traps (Reconyx Hyperfire Covert 2) installed between October 2021 and January 2023. A total of 202 cameras were deployed at single locations on a rotational basis across three sampling grids (East:  $N=60$ ; Centre:  $N=60$ ; West:  $N=82$ ; Figure 1). The grids encompassed a gradient of



**FIGURE 1** The study landscape in the Kampar Peninsula, Sumatra, Indonesia, showcasing the dominant landcovers and camera-trap locations (black points). A core area of old growth peat-swamp forest remains in the centre of the landscape, encompassing both government-managed protected areas (black line), as well as privately managed restoration concessions (orange line). A total of 202 camera-traps were installed on a rotational basis across three sampling blocks: East, Central and West. Data sources used to map the study area are provided in [Table 1](#).

habitat modification from recently planted ‘young *Acacia*’ (<2 years old;  $N = 12$ ), ‘mature *Acacia*’ (>2 years old;  $N = 41$ ), ‘linear forest remnants’ ( $N = 38$ ), and the ‘core area’ ( $N = 93$ ). Within each grid, cameras were separated by a mean inter-trap distance of 1.5 km (range: 0.9–73 km) and placed on trails or areas with notable animal signs to maximise species detections. Cameras were positioned at approximately 30 cm height and operated for up to 90 days. After accounting for losses and malfunctions, we retrieved data from 184 sampling locations, where cameras were active for an average of 90 trap days (range: 35–187).

Prior to analyses, photographs were identified to species-level, with images of non-focal or unidentified taxa discarded. The remaining mammal encounters were summarised into binary, multi-species detection histories using camtrapR (Niedballa et al., 2016). Each 90-day deployment period was collapsed into 7-day sampling occasions, yielding up to 13 occasions per site (range: 4–13; Deere et al., 2018). This temporal aggregation reduced zero inflation in the dataset, while increasing temporal independence among detections (Emmet et al., 2021).

### 2.3 | Landscape predictors of mammal presence

We assembled spatial covariates from remotely sensed data, capturing key habitat attributes and human pressures known to influence mammal occurrence in modified tropical landscapes ([Table 1](#)). To represent forest condition, we extracted undisturbed and degraded tropical forest cover from the Tropical Moist Forest (TMF) dataset (<https://forobs.jrc.ec.europa.eu/TMF>). We calculated Euclidean distance to the nearest forest boundary to account for edge effects, which generate gradients in microclimate, habitat structure and resource availability that can disproportionately affect disturbance-sensitive species (Pfeifer et al., 2017). To approximate prominent processes and constraints operating in the landscape, peat depth, road network and hydrological data were provided by the softwood companies operating in the region. Peat characteristics shape hydrology and vegetation structure (Girkin et al., 2022), water is a fundamental resource that dictates biodiversity patterns (Hawkins et al., 2003), and roads alter animal movement, permit human access and increase mortality risk (Laurance et al., 2015). Road and

**TABLE 1** Details of covariates used in occupancy modelling, spatial prediction and landscape configuration scenarios, including the name of the covariate, the data source and a concise description of the environmental or anthropogenic attribute represented. Relevant spatial covariates (Global Ecosystem Dynamics Investigation, GEDI, metrics; Tropical Moist Forest Cover data) were temporally calibrated to the period of observation (2022), and all layers were harmonised to a common resolution of 30m. Values used to simulate changes in forest structure (gap fraction, canopy cover, biomass) in the scenario assessment are summarised, assuming that peat depth, road and water sources remain the same.

Covariate name (unit); and source	Description	Values (median, SD)
Canopy cover (%) GEDI (Dubayah et al., 2024)	The proportion of the ground area that is covered by the vertical projection of tree canopies. Estimated from the proportion of waveform energy intercepted by vegetation >5m in height.	<ul style="list-style-type: none"> <li>Core forest (0.82, 0.07)</li> <li>Modified forests (0.74, 0.13)</li> <li>Mature <i>Acacia</i> (0.82, 0.06)</li> <li>Young <i>Acacia</i> (0.77, 0.09)</li> <li>Other plantations (0.77, 0.11)</li> </ul>
Gap fraction (%) GEDI (Dubayah et al., 2024)	The amount of open area within canopy that is not blocked by wood or foliage. Estimated from the proportion of waveform energy transmitted through canopy openings.	<ul style="list-style-type: none"> <li>Core forest (0.16, 0.05)</li> <li>Modified forests (0.25, 0.08)</li> <li>Mature <i>Acacia</i> (0.19, 0.06)</li> <li>Young <i>Acacia</i> (0.22, 0.07)</li> <li>Other plantations (0.24, 0.07)</li> </ul>
Biomass (Mgha <sup>-1</sup> ) GEDI (Dubayah et al., 2024)	Total mass of all living plant components above the soil layer, including stems, bark, branches, foliage, seeds and fruit.	<ul style="list-style-type: none"> <li>Core forest (139, 26)</li> <li>Modified forests (88, 29)</li> <li>Mature <i>Acacia</i> (128, 29)</li> <li>Young <i>Acacia</i> (106, 31)</li> <li>Other plantations (89, 24)</li> </ul>
Peat depth (m) RER (Hutabarat et al., 2017)	Depth of accumulated peat from the surface to the underlying mineral soil. Estimated from spatial predictions based on 294 sampling plots.	
Forest edge (km) Derived from TMF data (Vancutsem et al., 2021)	Distance of camera stations to the nearest natural forest edge. Includes core forest and linear remnants but excludes commercial plantations. Negative values indicate distance from forest edges to interiors, while positive values express distances beyond edges into non-forest habitats.	
Matrix contrast (range 0–100) Habitat classes non- <i>Acacia</i> age (Vancutsem et al., 2021); <i>Acacia</i> age prediction (RER, <i>unpublished</i> )	An index that quantifies structural differences between adjacent habitats, scaled between 0 and 100. 0 represents structurally similar habitats; 100 reflects habitats with strong differences in structural features. See Supporting Information <a href="#">Appendix S1</a> for more information.	
Distance to road (km) RER ( <i>unpublished</i> )	Euclidean distance to the nearest dirt road, which serves as the primary access route to transport logs from plantations.	
Distance to water (km) RER ( <i>unpublished</i> )	Euclidean distance to permanent water sources, including rivers, lakes, artificial canals.	

hydrological data were represented as proximity measures based on Euclidean distance to the nearest road or permanent water source. To quantify structural differences between adjacent habitat classes, we calculated matrix contrast using Fragstats 4.2 (<https://www.fragstats.org/>). A detailed description of this procedure is provided in Supporting Information [Appendix S1](#). Here, structural differences refer to contrasts in vegetation height, canopy cover, ground-layer openness and overall vegetation complexity between neighbouring habitat types. Matrix contrast was defined based on differences in habitat structure and parameterised based on the expert opinion of the authors, who collectively have over 50 years of research experience in multi-use landscapes. Expert-informed metrics are especially valuable in peatland systems, where detailed, field-based measurements of habitat configuration are difficult to obtain.

Forest structure is a key influence on forest biodiversity (Simonson et al., 2014), and so we utilised high-resolution structural metrics derived from spaceborne LiDAR from NASA's Global

Ecosystem Dynamics Investigation (GEDI) mission (Dubayah et al., 2020). GEDI provides detailed vertical canopy information with an approximate footprint of 25m, spaced ~60m along orbital tracks, with 600m between tracks. We retained only high-quality GEDI observations, filtering by data quality (`l2b_quality_flag=1`), sensitivity (sensitivity  $\geq 0.98$ ) and waveform degradation (`degrade_flag=0`) and masked the dataset to forest cover, as defined by the ESA WorldCover 10m 2020 dataset (Zanaga et al., 2021). From these data, we derived three ecologically relevant variables: gap fraction, canopy cover (both from the GEDI Level 2B product) and above-ground biomass density (AGBD; Level 4A product)—attributes known to influence resource availability, microclimate and habitat suitability for terrestrial mammals (Deere et al., 2020; Joshi et al., 2025).

To generate continuous landscape surfaces, each GEDI metric was modelled using a Random Forest regression in Google Earth Engine. Predictor variables included Landsat 8 optical reflectance,

ALOS PALSAR-2L-band radar backscatter and topographic metrics (elevation and slope) from the Shuttle Radar Topography Mission. All spatial predictors were harmonised to a 30m resolution and common projection. The resulting models produced high-fidelity, spatially continuous maps of forest canopy structure and biomass, with strong correspondence between observed and predicted GEDI values (Table S2).

All covariates were extracted to camera-trap locations as median values aggregated across 500m buffers (ca. 78.5ha) to associate them with the mammal detection data. Scale optimisation assessments from elsewhere in the region indicate that medium- to large-bodied mammals are most responsive to covariates extracted at this spatial extent (Deere et al., 2020). This procedure explicitly accounts for the fact that mammals interact with the environment at broader spatial scales than the point of observation (McGarigal et al., 2016). We assessed collinearity among covariates using Pearson's correlation ( $|r| > 0.7$  threshold; McCarthy et al., 2015) and found no evidence of serious intercorrelation ( $|r| = 0.01-0.61$ ; Supporting Information Figure S1). Prior to modelling, all continuous covariates were mean-centred and scaled to one-unit standard deviation to facilitate quantitative comparison and improve model convergence.

## 2.4 | Modelling framework

We developed two Bayesian hierarchical multi-species occupancy models to evaluate the status of mammal communities. Occupancy models allow the separation of the ecological and observation processes to explicitly account for imperfect detection (Dorazio & Royle, 2005). This allows the joint estimation of occupancy and detection probabilities, denoting whether a species is truly present at a site and the likelihood of observing it during a survey when it is present, respectively. Moreover, multi-species frameworks draw species-specific parameters as random effects from a community-level distribution, which permits inference at multiple taxonomic scales (communities and taxa) and improves estimation precision for rare or infrequently observed species (Guillera-Arroita, 2016). We provide a detailed description of the underlying model in Supporting Information Appendix S2.

To understand the potential for production landscapes to retain biodiversity, we modelled occupancy and detection on the logit scale as a function of species  $i$  and habitat-specific intercepts ( $\alpha$ ,  $\beta$ ):

$$\text{logit}(\psi_{ih}) = \alpha_{(i)habitat\ class(h)}$$

$$\text{logit}(p_{ih}) = \beta_{(i)habitat\ class(h)}$$

where 'habitat class'  $h$  is a categorical covariate representing the dominant habitat classes in the study landscape (core area, linear forest remnants, mature *Acacia* and young *Acacia*). Using this model structure, we estimated four complementary biodiversity metrics corrected to account for observation error: community occupancy, species richness, functional diversity and phylogenetic diversity. Community occupancy was derived from model hyperparameters, while species richness was

calculated as the posterior mean of the estimated true-occurrence matrix (z-matrix). We further applied the z-matrix to estimate functional and phylogenetic diversity (Gorczyński et al., 2021), to explicitly account for unique traits and evolutionary distinctiveness contributed by individual species (Ardiantiono et al., 2024). Functional diversity was measured using the functional diversity metric, which reflects the distribution of species in multidimensional trait space, weighted by true site-level occurrence (Gorczyński et al., 2021). Our measure accounted for five traits: diet type, activity pattern, body mass, social structure and habitat preference. Phylogenetic diversity was calculated as the summed branch lengths of the phylogenetic tree linking species, which represents the evolutionary history of the sampled community at each site (Kembel et al., 2010). Positive values indicate that the community has greater dispersion of diversity than expected by random chance, thus implying that the community is functionally or phylogenetically more diverse. Negative values indicate functional homogeneity or close relations between species. Trait and phylogenetic data used to parameterise these measures were obtained from the PanTHERIA database and mammalian phylogenetic super tree, respectively (Jones et al., 2009). For species not represented in the data (i.e. recently described or taxonomically revised species), we extracted information from the closest extant taxonomic relative. Full details of functional and phylogenetic diversity calculation are provided in Supporting Information Appendix S3 and Tables S3/S4.

To investigate the mechanisms driving spatial heterogeneity in mammal persistence, we developed a second model where occupancy and detection were described as a function of environmental characteristics, human pressures and sampling constraints:

$$\begin{aligned} \text{logit}(\psi_{ij}) = & \alpha_{0i} + \alpha_{1i} * \text{Canopy cover}_j + \alpha_{2i} * \text{Forest edge}_j + \alpha_{3i} * \text{Forest edge}_j^2 \\ & + \alpha_{4i} * \text{Gap fraction}_j + \alpha_{5i} * \text{Peat depth}_j \\ & + \alpha_{6i} * \text{Biomass}_j + \alpha_{7i} * \text{Road}_j + \alpha_{8i} * \text{Matrix contrast}_j \\ & + \alpha_{9i} * \text{Water}_j \end{aligned}$$

$$\text{logit}(p_{ij}) = \beta_{0i} + \beta_{1i} * \text{trap\_effort}_j$$

where  $\alpha_{0i}/\beta_{0i}$  represent species-specific intercepts on occupancy and detection probability, respectively,  $\alpha_{1i}-\beta_{1i}$  are slope parameters describing the direction and magnitude of covariate effects on the occurrence and detection states and at sampling location  $j$ . To account for non-linear responses, we model distance to forest edge using a second order polynomial term. To address uneven sampling arising from camera malfunction and animal damage, we incorporated a survey effort (*trap\_effort*) covariate on the detection component of the model, denoting the number of operational camera days at each station.

We implemented all occupancy models within a Bayesian framework using JAGS via the 'jagsUI' package in R (Kellner & Meredith, 2021). Throughout, we specified vague normal and uniform priors for slope and intercept parameters, respectively. For each parameter, we designated three Markov chains of 100,000 iterations, a burn-in period of 50,000, and a thin rate of 50, resulting in 3000 posterior samples for inference. Convergence was assessed quantitatively using the Gelman-Rubin statistic, where values  $< 1.1$

indicate adequate convergence (Gelman & Rubin, 1992) and verified through visual inspection of trace plots. Model fit was evaluated using Bayesian  $p$ -values, where values of 0.5 indicate perfect model fit and values  $<0.05$  or  $>0.95$  reflect over or underfitting models, respectively. Throughout, we base our inferences on models with strong fit (Bayesian  $p$ -value: 0.38–0.4) and sufficiently converged parameters (Gelman-Rubin statistic = 0.99–1). We gauge the magnitude and direction of covariate effects on mammal occupancy using the posterior mean of the standardised beta coefficients. The statistical strength of covariate associations was based on whether the Bayesian Credible Interval (BCI) overlapped zero. Covariates effects were deemed substantial if the 95% BCI of the associated beta coefficient did not overlap zero and moderate if the 75% BCI did not contain zero.

## 2.5 | Landscape configuration and priority habitats

We implemented a scenario-based assessment to model the impact of alternative landscape management strategies on the provision of priority habitat for mammals. We quantified proportional change in priority habitat by comparing the current landscape configuration as the baseline to four plausible future scenarios that reflect management actions or policy shifts that could be reasonably expected within a NbS landscape in Indonesia (Table 2). These scenarios captured both conservation gains, such as bolstering movement corridors ('Enhanced Connectivity'), and potential degradation pathways following weakened environmental protections ('Diminished Connectivity' and 'Reduced Protection'). We also included a counterfactual scenario ('Reverted Plantation') to explore how mammals might respond if plantation production were scaled back.

To map priority mammal habitat, we first generated 3000 species-specific spatial predictions of occurrence under the baseline scenario by linking model-derived beta coefficients to the environmental and anthropogenic covariates. For each species, occupancy and associated uncertainty were expressed as the posterior mean and standard deviation, respectively, across all spatial predictions. Maps of mean occupancy were subsequently reclassified into tertiles, where the upper third of the occupancy distribution was designated as priority mammal habitat of highest conservation significance. Species-specific priority habitat maps were stacked to produce a multi-species consensus surface, where high values indicate greater agreement among taxa. Uncertainty in the consensus was expressed as the mean of the species-specific standard deviation maps. We considered eight species of conservation concern listed as threatened on the IUCN Red List, which have also been shown to best reflect the broader habitat needs of forest mammals in Sumatra (Ardiantiono et al., 2024): binturong (*Arctictis binturong*), sun bear (*Helarctos malayanus*), Sunda pangolin (*Manis javanica*), Sunda clouded leopard (*Neofelis nebulosa*), Sumatran tiger (*Panthera tigris*), East Sumatran banded langur (*Presbytis percura*), flat-headed cat (*Prionailurus planiceps*) and Sambar deer (*Rusa unicorn*).

To assess changes in priority habitat emerging from scenarios, we replicated the mapping procedure for each alternative scenario

after modifying the corresponding environmental covariates to reflect landscape configuration and forest integrity (Table 2). Initially, the underlying habitat class was modified according to the management or policy change associated with the scenario. Forest structural attributes (above-ground biomass, canopy cover and gap fraction) were then simulated for newly established or modified habitat classes using the observed median and standard deviation for each class under the baseline scenario. Matrix contrast and distance to forest edge were recalculated based on updated habitat boundaries. Throughout, we assume that peat depth, road networks and water sources remain static across scenarios.

## 3 | RESULTS

We recorded 23 medium-large mammal species over 17,132 camera-trap days across the landscape. Species richness varied strongly among habitat classes, with six species detected in young *Acacia*, 11 in mature *Acacia*, 19 in linear forest remnants and 19 in core forest (Figure 3e). One species, the hairy-nosed otter (*Lutra sumatrana*), was detected only once and was therefore excluded from further analyses.

### 3.1 | Variation in diversity among land-cover classes

Mammal diversity varied markedly among the four land-cover classes (Figure 2a–d). Community occupancy was lowest in young *Acacia* (mean 0.21; BCI 0.19–0.26), increased marginally in mature *Acacia*, albeit with greater variability (0.21; 0.11–0.44) and was highest in areas of natural forest (linear forest remnants: 0.33; 0.24–0.48; core forest area: 0.37; 0.23–0.54). Richness was generally lower in *Acacia* plantation (young: mean 4, range 3–5; mature: 5, 2–7) compared to the forest sites, where it was higher (linear forest remnant: 7, 5–9; core forest: 8, 6–11). Functional diversity estimates implied overdispersion of traits in young *Acacia* (median 0.17; range –1.1–1.1), but clustering in mature *Acacia* (–0.9; –2.2–1.0), linear forest remnants (–0.5; –1.5–1.6) and core area (–0.2; –1.6–1.5). Phylogenetic diversity exhibited little variation across land-cover classes.

### 3.2 | Environmental and anthropogenic determinants of mammal occurrence

Mammals were typically more sensitive to environmental attributes of the landscape than human pressures. Species tended to exhibit higher occupancy in high-biomass forest, in the immediate vicinity of water sources and closer to the forest interior—exemplified by the responses of the pig-tailed macaque *Macaca nemestrina*, sun bear and Sumatran tiger (Figure 3). However, species' habitat associations were often nuanced. For example, tiger occupancy was greater near water in the forest interior irrespective of vegetation

**TABLE 2** Description of the four landscape scenarios used to assess how alternative management strategies may influence priority habitat for mammals. For each scenario, the maps show how the baseline spatial layers were modified according to the management or policy change described in the text.

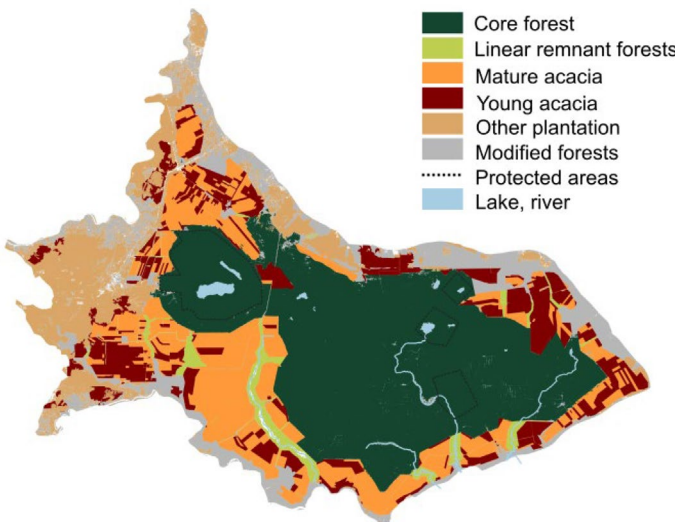

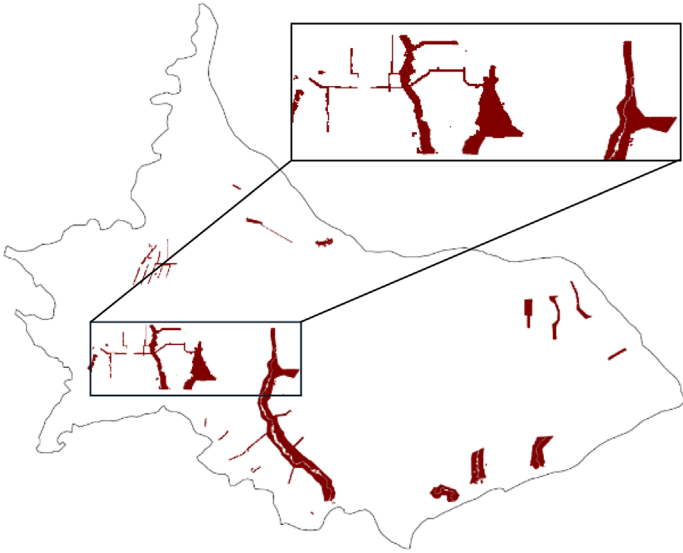


Scenario	Description
<p>Current conditions</p>  <p>Legend:</p> <ul style="list-style-type: none"> <li><span style="display: inline-block; width: 10px; height: 10px; background-color: #004d00; margin-right: 5px;"></span> Core forest</li> <li><span style="display: inline-block; width: 10px; height: 10px; background-color: #90ee90; margin-right: 5px;"></span> Linear remnant forests</li> <li><span style="display: inline-block; width: 10px; height: 10px; background-color: #ffa500; margin-right: 5px;"></span> Mature acacia</li> <li><span style="display: inline-block; width: 10px; height: 10px; background-color: #8b0000; margin-right: 5px;"></span> Young acacia</li> <li><span style="display: inline-block; width: 10px; height: 10px; background-color: #d2b48c; margin-right: 5px;"></span> Other plantation</li> <li><span style="display: inline-block; width: 10px; height: 10px; background-color: #a9a9a9; margin-right: 5px;"></span> Modified forests</li> <li><span style="display: inline-block; border-bottom: 1px dotted black; width: 10px; margin-right: 5px;"></span> Protected areas</li> <li><span style="display: inline-block; width: 10px; height: 10px; background-color: #add8e6; margin-right: 5px;"></span> Lake, river</li> </ul>	<p>Landscape composition:</p> <ul style="list-style-type: none"> <li>• 43% core forest,</li> <li>• 3% linear forest remnants,</li> <li>• 15% mature <i>Acacia</i>,</li> <li>• 9% young <i>Acacia</i>,</li> <li>• 15% other plantations,</li> <li>• 13% modified forests.</li> </ul>
<p>Enhanced connectivity</p> 	<ul style="list-style-type: none"> <li>• Forest cover extended alongside linear forest remnants to improve connectivity from the core forest area to other parts of the landscape.</li> <li>• Minimum width of all linear forest remnants increased to 1 km at the expense of plantation.</li> <li>• New linear remnants created to connect riparian or core forest to the remnants, following Euclidean routes from the core area to the nearest riparian forest.</li> <li>• Total area of linear forest remnants doubled to ~31,000 from 17,925 ha.</li> </ul> <p>Landscape composition:</p> <ul style="list-style-type: none"> <li>• 43% core forest,</li> <li>• 5% linear forest remnants,</li> <li>• 15% mature <i>Acacia</i>,</li> <li>• 10% young <i>Acacia</i>,</li> <li>• 14% other plantations,</li> <li>• 13% modified forests.</li> </ul>

TABLE 2 (Continued)

Scenario	Description
<p data-bbox="135 216 359 237">Diminished connectivity</p> 	<ul data-bbox="869 216 1452 378" style="list-style-type: none"> <li>• Plantation production maximised in the matrix by clearing all fire breaks, and reducing riparian buffer width to the legal minimum (100m, each side of riverbank (PPRI, 2011)).</li> <li>• Resulted in 16,800 ha of remnant forest reclassified as young Acacia, leaving only 1125 ha of forest linear forest remnants, thus increasing fragmentation effects.</li> </ul> <p data-bbox="869 388 1093 409">Landscape composition:</p> <ul data-bbox="869 415 1157 577" style="list-style-type: none"> <li>• 43% core forest,</li> <li>• 0.2% linear forest remnants,</li> <li>• 16.2% mature Acacia,</li> <li>• 12.1% young Acacia,</li> <li>• 14.8% other plantations,</li> <li>• 13% modified forests.</li> </ul>
<p data-bbox="135 825 319 846">Reverted plantation</p> 	<ul data-bbox="869 825 1444 877" style="list-style-type: none"> <li>• Production in the landscape is discontinued and plantations revert back to modified forest.</li> </ul> <p data-bbox="869 882 1093 903">Landscape composition:</p> <ul data-bbox="869 909 1141 1071" style="list-style-type: none"> <li>• 43% core forest,</li> <li>• 3% linear forest remnants,</li> <li>• 3.3% mature Acacia,</li> <li>• 3.2% young Acacia,</li> <li>• 15.7% other plantations,</li> <li>• 32% modified forests.</li> </ul>

(Continues)

TABLE 2 (Continued)

Scenario	Description
<p data-bbox="135 216 319 237">Reduced protection</p> 	<ul data-bbox="874 216 1444 352" style="list-style-type: none"> <li>• Environmentally destructive scenario where restoration areas become vulnerable to human-induced modifications.</li> <li>• Core forest is safeguarded by formal government protected areas and privately managed restoration ecosystem concessions.</li> </ul> <p data-bbox="874 359 1093 380">Landscape composition:</p> <ul data-bbox="874 386 1209 548" style="list-style-type: none"> <li>• Core forest 6% in protected areas,</li> <li>• 3% linear forest remnants,</li> <li>• 15.5% mature <i>Acacia</i>,</li> <li>• 10.4% young <i>Acacia</i>,</li> <li>• 14.5% other plantations,</li> <li>• 50% modified forests.</li> </ul>

biomass, whereas wild boar *Sus scrofa* were more prevalent within edge habitats close to water. To a lesser degree, species exhibited higher occupancy in deep peat forested areas and open habitats with low canopy cover. These trends towards more open vegetation were predominantly driven by disturbance tolerant generalists, such as the Malayan civet *Viverra zangalunga* and yellow-throated marten *Martes flavigula*. In contrast, we found no clear responses of mammals to matrix contrast or distance to roads, indicating a degree of resilience to human pressures.

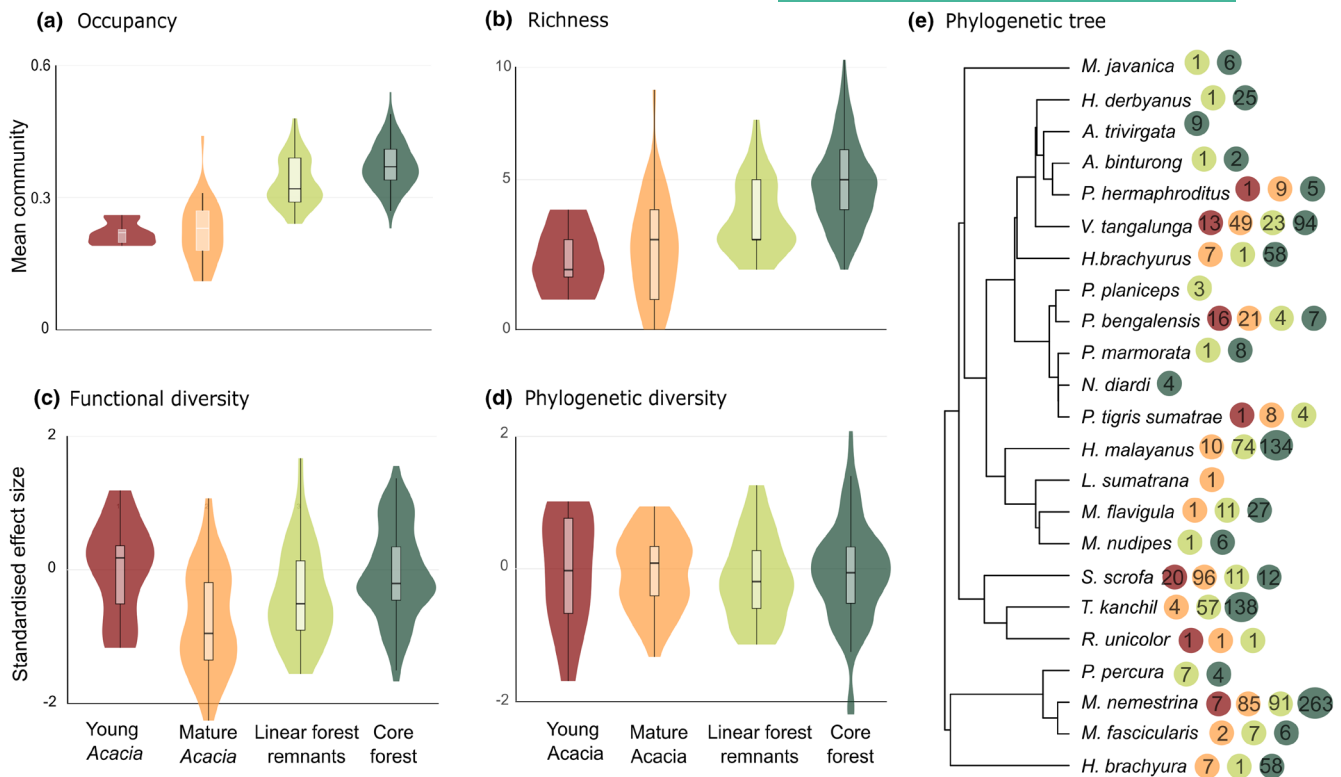
### 3.3 | Landscape configuration scenarios

The distribution of priority mammal habitat among the forest classes differed among the development scenarios (Figure 4 and Supporting Information Table S5). Under the 'Current Conditions' baseline, 240,643 ha of core forest was predicted as a priority habitat, together with 13,379 ha of linear forest remnants, 91,188 ha of mature *Acacia*, 57,417 ha of young *Acacia*, 74,010 ha in other plantations and 55,293 ha in modified forest. Under the 'Enhanced Corridor' scenario, the amount of priority habitat in linear forest remnants increased by 70% (9416 ha), 38.6% of which demonstrated high levels of agreement between the focal taxa (5–8 species). However, in the 'Diminished Corridor' scenario, remnants lost most of their priority habitat (96.4%; 12,903 ha), predominantly due to displacement by *Acacia* plantations, with consistent losses across all levels of consensus (95.8%–97.8%). Abandoning plantations (the 'Reverted Plantation' scenario) led to 3.3% more priority habitat in the core forest and 8.5% in linear forest remnants at the expense of the small amounts originally in plantations. The most notable gains were for areas of highest consensus (7–8 species), which increased by 24.6% (3707 ha) in

the core forest and 124.1% (1125 ha) in linear remnants. Last, the relaxation of environmental protection across much of the core forest area ('Reduced Protection' scenario), led to 82.7% reduction of priority habitat in that area, decimating areas of importance for all consensus classes (71.44%–99.8% losses in priority habitat). For comparative purposes, we provide consensus maps for all 22 observed species with sufficient data in Supporting Information Table S6 and Figure S2 and species-specific responses to landscape scenarios in Supporting Information Figure S3.

## 4 | DISCUSSION

There is growing concern over the intertwined crises of climate change and biodiversity loss (IPBES, 2022; IPCC, 2022). In response, nature-based solutions (NbS) have emerged as a broad framework of interventions designed to address societal challenges while simultaneously protecting, restoring and managing ecosystems for the benefit of climate, people and biodiversity (Cohen-Shacham et al., 2016). While the evidence base to achieve these outcomes is growing, evaluations typically prioritise climate, societal and ecosystem benefits, giving comparatively less attention to biodiversity outcomes despite their integral connection to ecosystem health (Key et al., 2022). This imbalance is increasingly recognised as a barrier to credible NbS implementation, with international standards now requiring robust evidence for biodiversity gains (IUCN, 2025). Our study helps address this gap by evaluating the status of biodiversity in a candidate NbS: a tropical peatland comprising extensive forest and *Acacia* plantations. By assessing the relative contribution of various landscape designs to biodiversity outcomes, we show that the current landscape configuration that safeguards core forest area and linear forest remnants across



**FIGURE 2** (a–d) Biodiversity characteristics of four dominant habitat classes in a multi-use landscape. Violin plots depict the kernel density distribution of the data (coloured shapes), where wider sections illustrate greater probability that the habitat class will represent a corresponding biodiversity value. Boxplots describe the median (central horizontal lines), interquartile range (outer horizontal lines) and 95% Bayesian Credible Intervals (thin vertical lines); (e) a phylogenetic tree of the observed species, including colour-coded summaries of total detections within each habitat class.

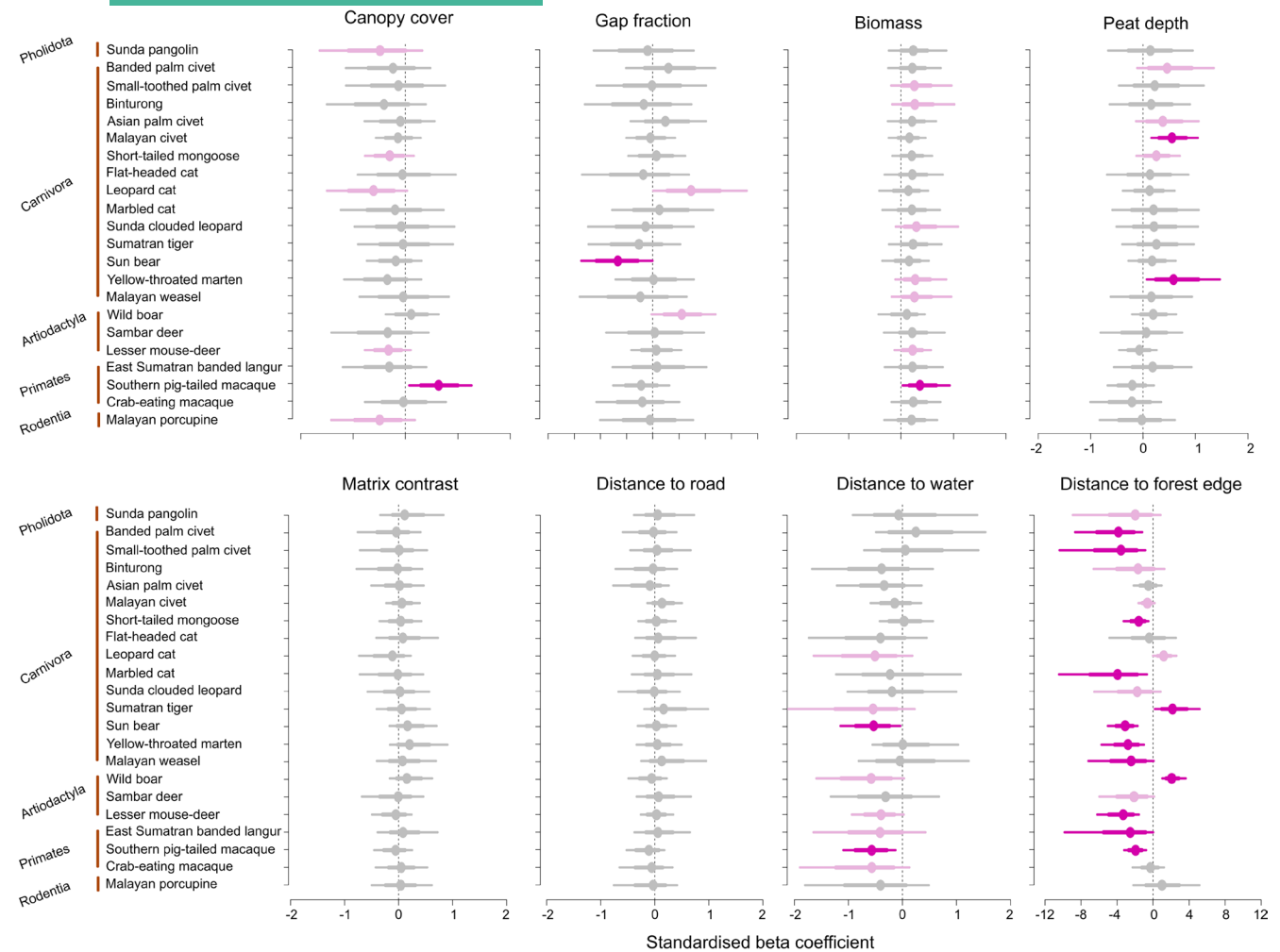
the plantation mosaic supports high mammal diversity compared to other feasible configurations.

#### 4.1 | Mammal diversity across the plantation-forest landscape

Forest conversion to other land uses negatively impacts biodiversity, although the magnitude of these effects varies considerably across taxonomic groups, regions, land-use types (Newbold et al., 2015) and management practices (Oakley & Bicknell, 2022). Terrestrial biodiversity of tropical peat swamps is typically lower than other forest types (Paoli et al., 2010; Posa et al., 2011), yet we found mammal occupancy and diversity to be high, supporting the findings of less-intensive studies in other landscapes (Adila et al., 2017; Harrison et al., 2024). Studies of birds and mammals in Asian forests on mineral soils have shown that tree plantations are frequently used by species for foraging or as transit habitats (Wong et al., 2022), although species richness and abundance remain lower than in natural forests (Adila et al., 2017). Abundance also varies with stand age: older oil palm plantations support higher bird abundance (Azhar et al., 2011), whereas for mammals in *Acacia* plantations, abundance shows the opposite trend (McShea et al., 2009; Wong et al., 2022). These contrasting responses reinforce that landscape context and

configuration can be stronger determinants of community structure than crop type alone. Our results align with previous findings that young *Acacia* plantations support lower mammal occupancy and diversity than more established plantations of greater height. Interestingly, functional and phylogenetic diversity was similar among land-use classes, implying that community composition is changing without disproportionate erosion of particular traits or lineages, at least under current management conditions.

Distance to the forest edge was a prominent predictor of mammal detections across species, indicating edge effects shape forest mammal biodiversity. We expect this pattern reflects variation in water availability and soil properties near forest edges adjacent to plantations. Water availability is intricately linked to greater species presence, and soils at edges were firmer and more stable, facilitating easier access for animals compared to the softer and less stable peat soils within the peat swamp. While edges were exposed to contrasting modified habitats, matrix contrast did not appear to influence detections. Whether this benign influence persists under other plantation types or more intensive management regimes remains unclear. *Acacia* trees are harvested after 4 years in the landscape at ~19 m height (Deshmukh et al., 2023), while oil palms, for example, reach comparable height over a longer cultivation period (Foster et al., 2011). Differences in crop height, rotation schedules and disturbance intensity underscore the need for more research on



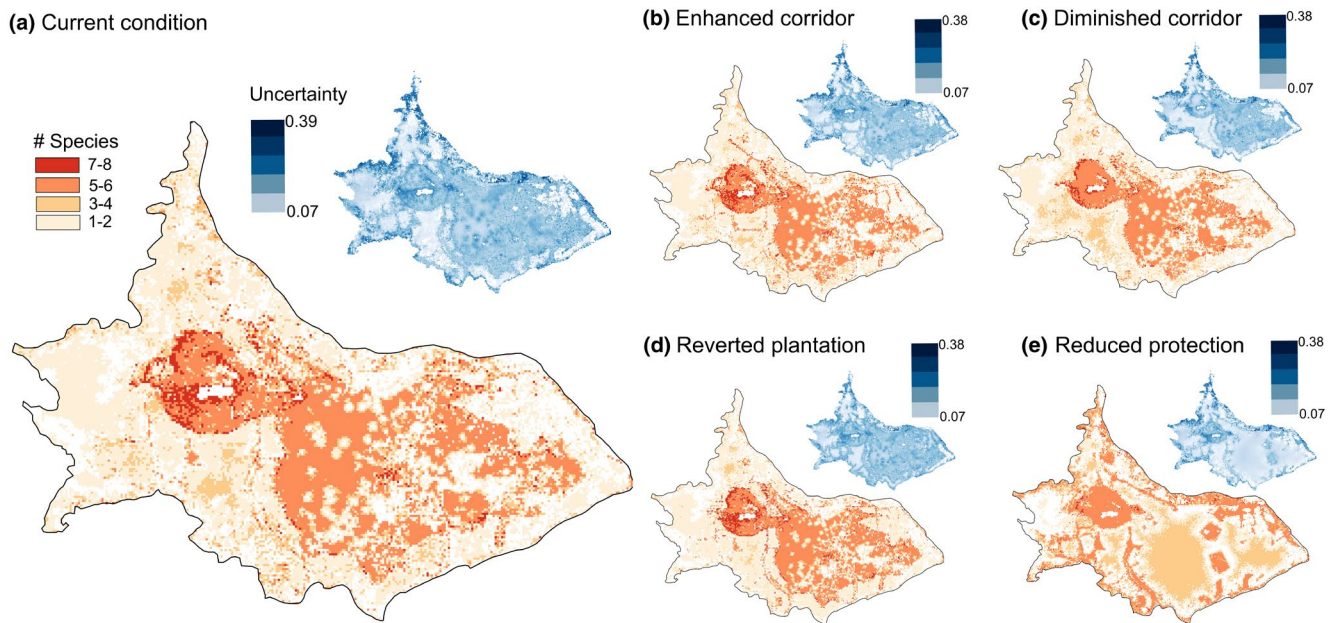
**FIGURE 3** Standardised beta coefficients (95% BCI and 75% BCI) showing species-specific responses to landscape covariates. Points denote posterior means, while horizontal lines communicate uncertainty based on the 75% Bayesian Credible interval (thick lines) and 95% BCI (thin lines). Elements are colour coded to denote the strength of covariate effects: Grey bars indicate no notable association (75% and 95% BCI both overlap zero), light purple bars indicate moderate associations (75% BCI does not overlap zero) and dark purple bars indicate substantial associations (95% BCI does not overlap zero).

how clearing and replanting cycles affect adjacent forests and their fauna (Padfield et al., 2019).

## 4.2 | Implications of landscape configuration

The current landscape configuration of a core forest area alongside substantial linear forest remnants was optimal for biodiversity compared to other feasible land-use options. It should be emphasised that the landscape is managed beyond legal requirements to maximise peat wetting and eliminate fires, which curb emissions and align the site with the principles of an effective NbS (RER, 2024). Some forest remnants set aside as firebreaks are several 100 m wide. Thus, while riparian and linear forest remnants are crucial for wildlife habitat and landscape connectivity (Deere et al., 2022), in this context, further increasing remnant width made little difference to biodiversity value because the existing remnants were already relatively wide.

The most substantial biodiversity gains in our scenarios occurred when plantations were removed, but this is an unrealistic option that would undermine the protection–production model through which this NbS operates. Kampar Peninsula is predominantly managed by private entities that help protect and restore the core peat-swamp forest while using surrounding plantations as a buffer to limit encroachment, fire and hunting pressure (RER, 2024). Crucially, the plantation zone also generates the financial resources needed to sustain long-term forest protection and restoration, an attractive feature of hybrid conservation–production NbS schemes. Tropical peatlands hold vast carbon stocks and become major greenhouse gas sources when degraded (Deshmukh et al., 2023; Murdiyarto et al., 2019). There are signs that restoration activities and protection are reducing fires and emissions (Harrison, Swinfield, et al., 2020; Mishra et al., 2021; RER, 2024). Our findings extend this evidence base by showing that such climate-focused NbS can simultaneously deliver measurable co-benefits for terrestrial biodiversity, provided they are



**FIGURE 4** Consensus maps denoting areas of high priority habitat based on modelled habitat associations of eight threatened forest specialist species. Within each panel, main maps (orange-red gradient), represent the upper tertile of the predicted occupancy distribution stacked across species, high values indicate strong agreement between taxa. Insets (blue gradient) communicate uncertainty, derived as the mean standard deviation across species. We visualise priority mammal habitat for (a) 'Current conditions', representing the current landscape configuration and used as a baseline for comparison against four plausible scenarios: (b) Enhanced corridor, the width of linear forest remnants is extended to a minimum of 1 km; (c) Reduced connectivity, linear forest remnants are converted to young *Acacia* plantations and riparian forests are narrowed to a width of 100 m; (d) Reverted plantation: *Acacia* plantations are abandoned; (e) Reduced protection, only formal protected areas in the core forests are maintained.

underpinned by ecologically informed management of both forest and production components of the landscape.

### 4.3 | Harnessing nature-based interventions for biodiversity in tropical peat swamps

There is a growing interest in aligning sustainable development, nature conservation and human actions to both adapt to and mitigate climate change. This has led to the adoption of NbS and REDD+ (Reduced Emissions from Deforestation and Degradation; <https://redd.unfccc.int/>) approaches across tropical countries. These interventions are widely endorsed by governments, non-governmental organisations and businesses (Seddon et al., 2021) and improved peatland management forms a prominent component of Indonesia's and other nations' Nationally Determined Contributions to help climate change mitigation (Austin et al., 2025). Yet the contribution of peatland NbS to biodiversity targets (e.g. Kunming-Montreal Global Biodiversity Framework's 2030 goals) remains insufficiently quantified. Our findings help address this gap by showing that these NbS schemes could qualify as Other Effective Area-based Conservation Measures (OECMs; Cook, 2024) to complement the conservation functions of traditional protected areas.

There are multiple ways that conservation actions can help halt or reverse further biodiversity loss, but success is often site-specific and dependent on progress being reliably measured.

Globally, peatlands are underprotected, and only 8% of tropical peatlands have strict area-based protection (Austin et al., 2025). However, Southeast Asian countries are increasingly adopting landscape management approaches involving private-sector stewardship (Struebig et al., 2025). Indonesia's ecosystem restoration licences offer an important example (Harrison, Ottay, et al., 2020). Such licences enable the private and public sector to manage and restore degraded ecosystems, including through four licences in Kampar Peninsula. Ecosystem restoration licences are likely to play an expanding role in meeting both biodiversity and climate commitments, provided their outcomes are independently monitored and transparently reported.

Additional actions could further enhance conservation outcomes in peatland NbS landscapes. Retaining patches of native trees within plantations (i.e. 'tree islands') has enhanced biodiversity and ecosystem functioning in oil palm landscapes (Zemp et al., 2023). In more rugged landscapes, setting aside unproductive land (e.g. in flood-prone areas or steep slopes) for conservation improves ecological outcomes at landscape scale (Bicknell et al., 2023). Harvest planning that minimises disturbance (e.g. in a directional order from the outer plantation boundary towards forest) and ensures predictable refugia for wildlife remains an overlooked but potentially valuable intervention.

By integrating biodiversity provisions with sustainable practices in production forest landscapes, our findings underscore the importance of balancing ecological and economic objectives to foster long-term environmental sustainability of managed tropical peatlands.

Preserving large core forests and maintaining connectivity are essential for safeguarding critical biodiversity areas. We strongly argue that further conversion of natural old growth peat-swamp forest would have severe consequences for biodiversity and ecological systems across Kampar Peninsula and more broadly in other parts of Sumatra and Southeast Asia. For NbS schemes to deliver on their promises, biodiversity safeguards must be central rather than ancillary, and peatland landscapes such as Kampar Peninsula illustrate how such integration can be operationalised.

### AUTHOR CONTRIBUTIONS

Irene M. R. Pinondang, Matthew J. Struebig, Nicolas J. Deere and Bradford M. Sanders conceived the study. Irene M. R. Pinondang, Matthew J. Struebig and Nicolas J. Deere designed the camera-trapping study. Irene M. R. Pinondang led the camera-trapping fieldwork and conducted data management and modelling with the supervision of Nicolas J. Deere and Dave J. I. Seaman. Irene M. R. Pinondang and Matthew J. Struebig wrote the manuscript with input from Bradford M. Sanders and John Pereira. Irene M. R. Pinondang revised and synthesised the inputs to the manuscript. All authors provide critical inputs to the manuscript and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. Matthew J. Struebig is an Associate Editor of Journal of Applied Ecology but took no part in the peer review and decision-making processes for this paper.

### DATA AVAILABILITY STATEMENT

This study arose from a collaboration between researchers at University of Kent and Riau Ecosystem Restoration, endorsed by the Directorate of Wildlife Conservation of the Indonesian Government in 2021. The collaboration is governed by non-disclosure agreements to protect privacy and sensitive information. Consequently, the camera-trap data on which the study is based cannot be shared publicly, but are available upon reasonable request subject to agreement by all parties. Spatial covariate data owned by Riau Ecosystem Restoration are also available upon request, following the organisation's data-sharing procedures.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Methodology for calculating matrix contrast.

**Appendix S2.** Occupancy model description.

**Appendix S3.** Calculating functional and phylogenetic diversity.

**Figure S1.** Pairwise correlation matrix of covariates used in occupancy modelling based on Pearson's correlation coefficients ( $r$ ). Points are coded by colour and size to reflect the direction (red hues = negative correlation; blue hues = positive correlation) and magnitude (larger points = stronger correlation) of the correlation, respectively.

**Figure S2.** Consensus maps denoting areas of high priority habitat based on modelled habitat associations of 22 species observed during sampling. Within each panel, main maps (orange-red gradient), represent the upper tertile of the predicted occupancy distribution stacked across species, high values indicate strong agreement between taxa. Insets (blue gradient) communicate uncertainty, derived as the mean standard deviation across species. We visualise priority mammal habitat for (a) 'Current conditions', representing the current landscape configuration and used as a baseline for comparison against four plausible scenarios: (b) Enhanced corridor, the width of linear forest remnants is extended to a minimum of 1 km; (c) Reduced connectivity, linear forest remnants are converted to young Acacia plantations and riparian forests are narrowed to a width of 100 m; (d) Reverted plantation: Acacia plantations are abandoned; (e) Reduced protection, only formal protected areas in the core forests are maintained.

**Figure S3.** Predicted occupancy and associated uncertainty for each species across Kampar Peninsula. Within each panel, main maps (dark red), represent the upper tertile of the predicted occupancy distribution. Insets (blue gradient) communicate uncertainty, derived as the standard deviation across the posterior distribution. We visualise priority habitat for (a) 'Current conditions', representing the current landscape configuration and used as a baseline for comparison against four plausible scenarios: (b) Enhanced corridor, the width of linear forest remnants is extended to a minimum of 1 km; (c) Reduced connectivity, linear forest remnants are converted to young Acacia plantations and riparian forests are narrowed to a width of 100 m; (d) Reverted plantation: Acacia plantations are abandoned; (e) Reduced protection,

only formal protected areas in the core forests are maintained.

**Table S1.** Adjacency matrix used to estimate Edge Contrast index, parameterised based on the expert opinion of four co-authors with nearly 50 years of experience working in multi-use tropical landscapes. Values represent pairwise structural differences between habitats on a 0–100 scale (0 = structurally identical; 100 = strong structural differences).

**Table S2.** Model accuracy for GEDI-derived structural metrics. Model performance was assessed using root mean squared error (RMSE), which provides an absolute measure of predictive accuracy in the same units as the observed GEDI metrics. The gap fraction and canopy cover models reproduced GEDI observations with validation RMSE values of 0.206 and 0.207, respectively (0–1 scale), indicating mean deviations of approximately 0.2 from observed values. The biomass model achieved a validation RMSE of  $62.8 \text{ Mg ha}^{-1}$ , consistent with the GEDI L4A product's target relative uncertainty of approximately 20% at the footprint level (Duncanson et al., 2022).

**Table S3.** Summary of conservation status, ecological and behavioural characteristics for the 22 mammal species observed during the study. Species are listed according to their scientific names, with common names provided in parentheses. For each species, we attach information on: IUCN Red List status (LC: Least Concern; NT: Near Threatened; Vu: Vulnerable; En: Endangered; CR: Critically endangered); dietary classification (Omn: omnivorous; Car: carnivore; Her: herbivore); primary activity pattern (Noc: nocturnal; Diu: diurnal); dominant habitat use (Arb: arboreal; Sem: semi-arboreal; Ter: terrestrial); average adult body mass (grams); sociality score (0 = solitary); suitable habitat types based on IUCN habitat classification codes (see Table S2), and; endemism status (0 = not endemic). Information on IUCN status, dietary classification, primary activities, dominant habitat use, average adult body mass and sociality score were used to calculate functional diversity.

**Table S4.** IUCN codes for suitable habitats used in the calculations of functional diversity (see Table S1).

**Table S5.** Predicted total area (ha) for eight threatened species in six forest classes for the current landscape configuration and under four hypothetical landscape configuration scenarios. Changes in the area of each scenario relative to the baseline are displayed as black positive values (indicating an increase) or red negative values (indicating a decrease).

**Table S6.** Predicted total area (ha) for 22 species in six forest classes for the current landscape configuration and under four hypothetical landscape configuration scenarios. Changes in the area of each scenario relative to the baseline are displayed as black positive values (indicating an increase) or red negative values (indicating a decrease).

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