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RESEARCH ARTICLE

Habitat connectivity shapes biodiversity outcomes in Indonesia's community-managed forests

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Abstract

1. Social forestry is increasingly promoted as a means to achieve equitable resource governance while contributing to biodiversity conservation. Yet, empirical evidence on how effectively community-managed forests support biodiversity remains limited, particularly in tropical regions.
2. We assessed mammal communities in two contrasting social forestry contexts in Sumatra, Indonesia: (1) a forest-dominated landscape where management emphasised forest retention, and (2) an agroforestry-mosaic characterised by mixed production systems and forest remnants. Using camera-trap data and hierarchical multi-species occupancy models, we compared species richness, community occupancy and the occurrence of forest specialists and globally threatened species between social forestry areas and adjacent watershed protection forests. We also assessed the influence of five environmental (structural connectivity, biomass, forest cover and terrain ruggedness) and anthropogenic (quantified using remoteness) factors in shaping species' occurrence patterns across these multiple-use landscapes.
3. Overall species richness and community occupancy in community-managed forests were comparable to protection forests in both landscapes. However, community composition diverged depending on the landscape context. In the forest-dominated landscape, occupancy of forest specialists and threatened taxa was maintained, while generalist species showed higher occupancy in social forestry areas. Conversely, in the agroforestry-mosaic, forest specialists and threatened taxa had reduced occupancy within social forestry areas, largely driven by lower forest quality and diminished structural connectivity in some areas.

4. Forest structural connectivity emerged as the strongest environmental driver of mammal occurrence. High connectivity buffered biodiversity losses in the forest-dominated community forests, whereas reduced connectivity in the agroforestry-mosaic landscape amplified declines among species with greater forest dependencies. Remoteness further influenced occurrence patterns, particularly favouring forest specialists in the forest-dominated landscape.
5. *Synthesis and applications*. Our findings suggest that community-managed forests established within predominantly forested areas can make a meaningful contribution to area-based conservation, including recognition as Other Effective Area-based Conservation Measures (OECMs). In community-managed forests established in more modified production landscapes, targeted restoration and actions that enhance habitat connectivity are likely required to sustain populations of priority species. Ensuring that social forestry policies explicitly incorporate biodiversity incentives and connectivity-led management can help align community development objectives with global conservation goals.

KEYWORDS
agroforestry, community forest management, community forestry, conservation policy, other effective area-based conservation measures (OECMs), restoration, Southeast Asia, sustainable land management

1 | INTRODUCTION

Tropical forests are among the world's most biodiverse ecosystems (Pillay et al., 2022), providing vital ecosystem services and supporting the livelihoods of at least 1.2 billion people (Fedele et al., 2021). However, rising demand for natural resources is placing mounting pressure on these forests, threatening both biodiversity and human well-being (Edwards et al., 2019; Struebig et al., 2025). Effectively managed protected areas are among the most successful conservation tools for halting biodiversity loss (Cazalis et al., 2020). Yet despite these achievements, many threatened species remain underrepresented within protected area networks (Maxwell et al., 2020), and some protected areas have had negative impacts on local communities, including evictions, restricted access to traditional resources and uncompensated livelihood losses (Tauli-Corpuz et al., 2020).

Most tropical forests are not formally protected, but lie under governance arrangements that do not align neatly with conventional protected area categories, yet still deliver substantial conservation value (O'Bryan et al., 2021). There is growing recognition of the positive contributions that Indigenous Peoples and local communities have made to conservation as forest and land stewards (Benzeev et al., 2025; Sze et al., 2022), including the establishment of the Convention for Biological Diversity's Subsidiary Body for Indigenous Peoples and local communities under Article 8(j) in 2024. This has prompted increased interest in recognising governance models that contribute to biodiversity conservation outside formal protected areas, including those that may qualify as Other Effective Area-based Conservation Measures (OECMs; Cook et al., 2024, Jonas et al., 2024). Such areas are increasingly viewed as important components of larger landscape networks, especially where they help to maintain or enhance habitat connectivity—an explicit objective of the Kunming–Montreal Global Biodiversity Framework (KM-GBF; Convention on Biological Diversity [CBD], 2022).

Social forestry (also referred to as community forestry) is one such governance model and has been highlighted as a potential mechanism to support biodiversity conservation while generating socio-economic benefits for rural communities. Social forestry encompasses a suite of tenure arrangements that devolve certain forest management rights from the state to local communities (Gilmour, 2016). Since the 1980s, many countries have adopted social forestry as part of sustainable development programmes, and local communities now manage at least 28% of tropical and subtropical forests worldwide (Rights and Resources Initiative, 2018). A central tenet of social forestry is that strengthening tenure security and community participation incentivises sustainable forest use, thereby generating both environmental and social gains (Gilmour, 2016).

Community-managed forests often occur within multifunctional landscapes (Gilmour, 2016) and may therefore serve important roles in maintaining structural and ecological connectivity. Where these areas are small and embedded within mosaics of agriculture, secondary forests and human settlements, their biodiversity value is likely to be influenced by how well they connect larger habitat blocks and facilitate species movements across otherwise fragmented terrain. High connectivity can enable dispersal, recolonisation and gene flow, helping to sustain populations of forest specialists that may

not persist based on local habitat quality alone (Naidoo et al., 2025). Conversely, where community-managed forests are more isolated, their contribution may be limited to disturbance-tolerant or generalist taxa (Haddad et al., 2015; Siegel et al., 2024). As such, while social forestry has the potential to deliver significant biodiversity co-benefits, particularly as community-managed lands often overlap with areas of high biodiversity (Gerstner & Zarnetske, 2025; Sze et al., 2023), the magnitude of these outcomes is expected to depend on landscape configuration and management practices adopted by people.

While environmental outcomes of social forestry across the world are generally positive (Hajjar et al., 2021), evidence of simultaneous environmental and livelihood benefits is mixed (Burivalova et al., 2019; Hajjar et al., 2021). This variability reflects the diversity of tenure arrangements, resource-use regulations and management objectives encompassed by social forestry (Gilmour, 2016). In many countries, schemes are implemented in degraded areas, where management often includes restoration activities along with sustainable use or livelihood diversification (Gilmour, 2016). These differences mean that biodiversity outcomes are unlikely to be uniform across social forestry schemes, landscapes or taxa. Some contexts may be effective in meeting area-based biodiversity conservation targets, while others may be more aligned to restoration or sustainable use objectives.

A further complication is that biodiversity outcomes of social forestry are seldom evaluated directly (Burivalova et al., 2019; Meijaard et al., 2021). Most assessments use deforestation avoidance as a proxy for effective biodiversity protection, even though disturbances such as logging, agroforestry and hunting can strongly affect biodiversity without necessarily reducing canopy cover (Burivalova et al., 2019). Empirical studies on faunal communities within community-managed forests remain limited and are concentrated largely in India and Nepal (e.g. Neupane et al., 2022; Velho et al., 2016). These studies show that community forests can support important wildlife populations, although typically with changes to community composition compared to adjacent protected areas (Neupane et al., 2022; Velho et al., 2016). For example, in Nepal, avian diversity, abundance and turnover were higher in community forests than in a neighbouring protected area, but forest specialists and threatened species were less diverse (Neupane et al., 2022). Whether such findings extend to other biodiverse regions—particularly in Southeast Asia where over 138,000km^2 of forest is now managed by communities (RECOFTC, 2024; Struebig et al., 2025)—is poorly understood.

This evidence gap is particularly important in Indonesia, a megadiverse country implementing one of the world's largest social forestry programmes (Struebig et al., 2025). Although first adopted in the early 2000s (Fisher et al., 2018), the programme expanded dramatically in 2014 when the government set a target to allocate 12.7 million ha (~10% of national forest cover) under social forestry. The programme's central goals include reducing deforestation and improving livelihoods, and evaluations to date have therefore focussed predominantly on these outcomes (Meijaard et al., 2021). Indonesia's five principal social forestry schemes differ in their objectives, the types of community groups granted management rights and the livelihood activities permitted (Rakatama & Pandit, 2020). Schemes can be allocated within government-designated watershed protection or production forest, which further shape permissible activities (Rakatama & Pandit, 2020). Community-managed forests are often established on degraded land, with management efforts focussed on restoring vegetation cover and improving landscape connectivity through agroforestry and tree planting (Putraditama et al., 2019; Santika et al., 2017).

Impact evaluations of some of the earliest social forestry areas in Sumatra and Kalimantan indicate that, on average, the programme reduced deforestation, though with considerable spatial and temporal variability influenced by anthropogenic, biophysical and legal factors (Putraditama et al., 2019; Santika et al., 2017, 2019). Given this variability, understanding biodiversity outcomes and the landscape features that shape them remains a critical research need (Meijaard et al., 2021). Yet, despite over a decade of programme expansion, empirical assessments of faunal communities within Indonesia's community-managed forests are almost entirely lacking (Struebig et al., 2025).

Here, we address this gap by presenting one of the first evaluations of biodiversity within Indonesia's social forestry systems, focusing on mammal communities in two contrasting case-study landscapes in Sumatra: (1) community-managed forests where management strongly emphasises maintaining forest cover, and (2) a social forestry context where ecological and livelihood objectives are more balanced, resulting in a mosaic of forest, agroforest and farmland. At each landscape, we also surveyed adjacent watershed protection forests under state-, not community-, management, which served as control areas for comparison. We examined how social forestry influences the occupancy and diversity of mammals—a taxonomic group particularly sensitive to anthropogenic disturbance (Andermann et al., 2020). To evaluate whether community-managed forests can contribute to global conservation priorities, we focus particularly on species that are globally threatened or sensitive to ecological degradation (i.e. forest specialists). Finally, we examined how environmental factors (structural connectivity, above-ground biomass, forest cover and terrain ruggedness) and anthropogenic pressures (quantified using remoteness), which have previously been found to influence biodiversity patterns in socioecological systems (e.g. Deere, Guillera-Arroita, Platts, et al., 2020; Korejs et al., 2025), shape species occurrence patterns across these multiple-use landscapes, addressing a key mechanism through which social forestry may support biodiversity. We predicted that social forestry within the forest-dominated landscape would support greater biodiversity than the agroforestry-mosaic, given the greater availability of intact and connected forest habitat. As a result, we would expect anthropogenic pressure to be a greater limiting factor on species occurrence patterns relative to environmental factors within this landscape, while alterations to forest extent, quality and connectivity would have a greater influence within the agroforestry-mosaic.

2 | MATERIALS AND METHODS

2.1 | Study sites and social forestry context

The study was conducted in two social forestry landscapes in the foothills of the Bukit Barisan mountain range, Sumatra. In Aceh Province, the landscape comprised three neighbouring *Hutan Desa* (village forests; 43.3 km^2; Appendix S1) designated on watershed protection forest (hereafter protection forest), where logging is prohibited. The area is dominated by contiguous tropical moist forest (98.6% forest cover; Vancutsem et al., 2021), with small patches of agroforestry and open grazing areas at the boundary of the social forestry area (Figure 1), where local communities were actively engaged in forest restoration through the planting of multi-purpose native tree species.

In Bengkulu Province, the landscape encompassed adjacent *Hutan Kemasyarakatan* (community forest) and *Hutan Tanaman Rakyat* (community plantation forest) designated on production forest (16.2 km^2). Land use practices were broadly consistent across the two social forestry areas within this landscape, with the site comprising a mosaic of structurally intact and degraded forest, agroforestry of varying intensities (primarily for coffee, durian and petai), and shrubland (60.6% forest cover; Vancutsem et al., 2021). Community members were implementing restoration activities and sustainable land management practices to enhance forest connectivity through tree planting and designation of protection zones, although the construction of a new road had accelerated forest disturbance in some areas. Together, these two landscapes illustrate contrasting social forestry settings in Indonesia: one focused on forest protection, and the other on sustainable production and restoration (Appendix S1).

Research was conducted under a permit from Indonesia's National Research and Innovation Agency (BRIN; 32/SIP/IV/FR/1/2024). Ethics approval was also obtained from BRIN (006/KE.02/SK/01/2024) and the University of Kent (reference number: 20231703767393581).

2.2 | Data collection and processing

2.2.1 | Camera trap surveys

To sample medium- to large-bodied mammals (>1 kg body mass), we implemented camera-trap surveys. Those in the

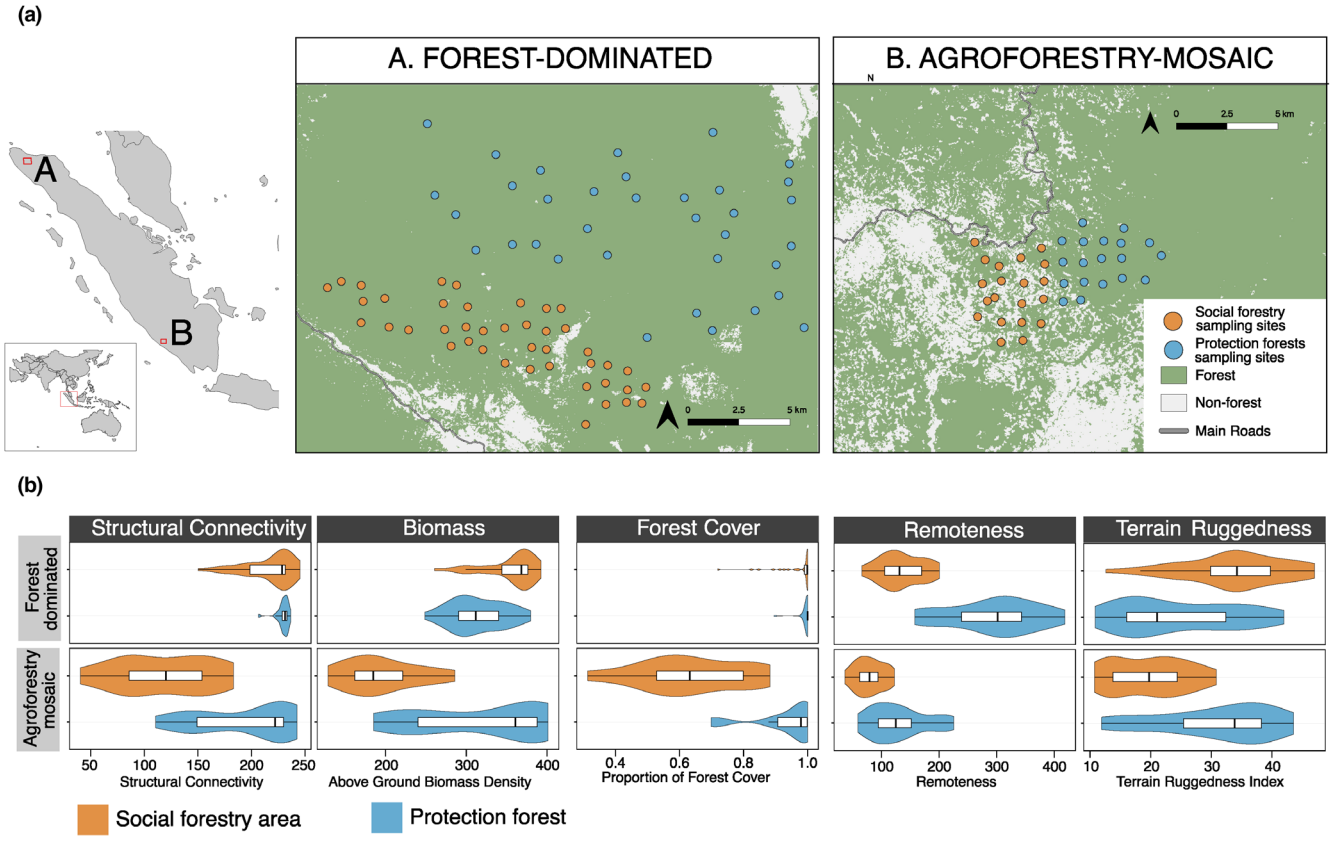

FIGURE 1 Sampling design and context of study landscapes (a) Maps of study sites and sampling design alongside the broader landscape context in Sumatra. (b) Violin plots depicting the kernel distribution of the five environmental and anthropogenic covariates at each sampling location, grouped by landscape and social forestry (orange) and protection forest controls (blue). Boxplots contained therein describe the median (central vertical line) and interquartile range (outer vertical lines of the box).

forest-dominated landscape (Aceh) were conducted from December 2022 to February 2023, and March to June 2024. In the agroforestry-mosaic landscape (Bengkulu), surveys were implemented from July to November 2024. In total, 121 camera-trap stations were installed across both landscapes (81 in the forest-dominated landscape; 40 in the agroforestry-mosaic) and stratified between social forestry and adjacent protection forest areas (Figure 1).

Across both landscapes, we used a systematic grid design, deploying cameras approximately 1 km apart (mean distance 1.04 km). Cameras were preferentially positioned on flat surfaces and along low-resistance travel routes (e.g. game trails and ridge lines) to maximise detections. Each camera was attached to a tree 20–40 cm above-ground and deployed for at least 60 days—an interval sufficient to effectively sample tropical mammal communities whilst ensuring demographic closure (Kays et al., 2020). Only camera stations with >7 days of data were retained for analysis (mean operational camera trap nights: 58; range: 9–90). In Bengkulu, Bushnell Core DS trail cameras were deployed at all locations, whereas in Aceh, a combination of Bushnell Core and Reconyx PC800 Hyperfire cameras were used due to logistical constraints. All cameras were unbaited, set to record continuously at maximum sensitivity, taking five images per trigger with no interval between detections to aid species identification. After accounting for malfunctions, loss and animal damage, data from 116 camera-trap stations were available, representing 6709 camera-trap nights.

All images were identified to species level by an experienced observer (LH). Due to morphological similarity, lesser and greater oriental chevrotains (*Tragulus kanchil*, *T. napu*), and Malayan and Sumatran porcupines (*Hystrix brachyura*, *H. sumatrae*) were identified to genus level. Detections of non-target species (domestic animals, rodents) were excluded from analyses, and photographs of people deleted. Species conservation status was obtained from the IUCN's Red List of Threatened Species (IUCN, 2025), with those listed as Vulnerable, Endangered or Critically Endangered categorised as 'threatened'. Species were further categorised as forest specialists or generalists following Wilson et al. (2010) and Ardiantiono et al. (2024) (Table S1).

2.3 | Environmental and anthropogenic covariates

We modelled a suite of environmental and anthropogenic covariates expected to influence mammalian habitat use across landscapes (Table 1). Changes to the extent, integrity and spatial configuration of forest habitat often shape biodiversity in human-dominated systems (e.g. Deere, Guillera-Arroita, Swinfield, et al., 2020). We therefore quantified the availability, quality and structural continuity of forest habitat using metrics derived from the Joint Research Centre's Tropical Moist Forest dataset (JRC-TMF; Vancutsem et al., 2021) and NASA's Global Ecosystem Dynamics Investigation (GEDI) LiDAR data (Dubayah et al., 2020) at 30-m resolution. Forest cover was quantified as the proportion of forest within the vicinity of each camera-trap station (see Table 1 for specific buffer sizes for each covariate; Vancutsem et al., 2021). Habitat quality and structure were represented by above-ground biomass density (hereafter biomass) and canopy height layers from GEDI data using random-forest models trained on coincident optical and radar remote-sensing variables in Google Earth Engine (Appendix S2; Table S2).

We used the canopy height layer to generate a continuous forest structural connectivity metric using the Omniscape algorithm (Landau et al., 2021). Omniscape estimates the relative 'flow' through the landscape, representing potential mammal movement pathways based on forest structure, analogous to the flow of electrical current through a circuit. We parameterised 'conductance' using canopy height (assuming taller canopies reflect more intact forest), set a moving window equivalent to the median home-range size of study species (2.9 km^2), and weighted current sources by forest condition from JRC-TMF annual change data (Vancutsem et al., 2021; Appendix S3).

To capture topographic variation, we calculated terrain ruggedness index (TRI) at 30-m resolution from the Shuttle Radar Topography Mission data (Rabus et al., 2003), as elevation and slope are known to influence species movement and foraging behaviour in tropical forests (e.g. Nguyen et al., 2024). TRI was derived from the digital elevation model using a 3×3 cell moving window (90×90 m neighbourhood) in QGIS.

In addition to environmental factors, anthropogenic activities such as hunting can also influence mammal occurrence patterns in socioecological systems (e.g. Deere, Guillera-Arroita, Platts, et al., 2020). To characterise human pressures, we developed a remoteness metric, representing the travel cost from the nearest settlement, accounting for roads, topography and landcover. Accessibility/remoteness metrics have been used to predict hunting pressure elsewhere in Southeast Asia and are based on the assumptions that hunters are typically central place foragers and will travel to a given cell using the most efficient mode of transport available (Deere, Guillera-Arroita, Platts, et al., 2020). The index was calculated using the distance accumulation tool in ArcGIS, integrating travel speeds derived from land-cover type, slope (Tobler's hiking function), and road class (Appendix S4).

Covariates were extracted as mean values derived from buffers at five spatial scales around each camera trap location (50, 100, 150, 250 and 500 m). To ensure we assessed the effect of covariates at spatial scales most relevant to the mammal community (Niedballa et al., 2015), we followed the scale optimisation procedure used by Deere, Guillera-Arroita, Swinfield, et al. (2020) whereby for each variable, single-covariate models were fit for each spatial scale and compared using the Watanabe–Akaike Information Criterion (WAIC). WAIC is a model selection metric suitable for evaluating models that include latent variables (Broms et al., 2016), in this case the true occupancy status of species at each sampling location (for full information on the scale optimisation procedure, see Appendix S5;

Table S3). Covariates were standardised (mean-centred and scaled to one-unit standard deviation) to place them on a comparable scale and improve computational efficiency.

2.4 | Analytical approach

2.4.1 | Data processing

We employed Bayesian hierarchical multi-species occupancy models (Dorazio & Royle, 2005) to quantify community-level occupancy, species-specific occupancy and unbiased (i.e. detection-corrected) species richness estimates. Hierarchical occupancy models distinguish between the ecological process governing species occurrence and the observation process determining species detection, thereby explicitly accounting for biases arising from imperfect detection (Dorazio & Royle, 2005). Prior to analysis, we combined species detection data from both our study sites and constructed species-specific detection histories by pooling data from each camera trap into 7-day sampling occasions. This resulted in a maximum of 13 sampling occasions per camera trap location (range: 2–13). Due to challenges of disentangling the ecological and observational processes when detection data are sparse, species with ≤4 detections were excluded from analyses. Species-specific responses were drawn as random effects from a common community-level distribution in both occupancy and detection models, with estimable hyperparameters that represent community-level patterns. This approach improves the precision of estimates for species infrequently detected during surveys (Devarajan et al., 2020) and allows for inference at multiple taxonomic scales, including specific species, species groups (e.g. forest specialists or threatened species) and entire communities (e.g. Deere, Guillera-Arroita, Platts, et al., 2020; Haidir et al., 2024).

2.4.2 | Estimating the effect of social forestry

To overcome inherent associations between management status and environmental and anthropogenic characteristics, we constructed separate models to (1) assess the effect of management type on occurrence, and (2) the influence of the environmental and anthropogenic factors shaping species' occurrence patterns. This was to avoid decomposing the effect of social forestry onto covariates that are directly influenced by this form of management (Ferreira et al., 2023).

To estimate the effect of social forestry on mammal occurrence, we modelled the occupancy of species i at sampling site j ($\Psi_{i,j}$) as a function of management type (i.e. social forestry or protection forest) as the sole covariate in the ecological component of the model. To obtain separate estimates of the effect of social forestry at each landscape l (i.e. forest-dominated landscape or agroforestry-mosaic), and to ensure these were compared to the protection forest at the same study landscape, we fit landscape-specific intercepts and set the protection forest within each landscape as the reference level. The beta-coefficient for management type was indexed by landscape, allowing for landscape-specific estimates of the effect of social forestry (Equation 1).

$$\text{logit}(\Psi_{i,j}) = \beta_{0i,l} + \beta_{1i}\text{Management\_type}_{j,l} \quad (1)$$

The probability of detecting species i at site j across temporal replicates k (p_{ijk}), was modelled as a linear function of date and within-replicate survey effort (i.e. number of days within the 7-day detection window that a camera was operational for; Equation 2). Date was included to account for temporal changes in environmental conditions or movement patterns that may impact detection probabilities, and to capture differences in the detection probabilities of the two surveys in the forest-dominated landscape. Survey effort was included to account for the increased likelihood a species would be detected if the camera was operational for more days within a survey window.

$$\text{logit}(p_{i,j,k}) = \alpha_0 + \alpha_{1i}\text{Survey\_effort}_{j,k} + \alpha_{2i}\text{Date}_{j,k} \quad (2)$$

2.4.3 | Estimating the effect of environmental and anthropogenic covariates

After determining the overall impact of management status, we constructed a second set of models to assess the effect of the five environmental and anthropogenic covariates on species' occurrence. Due to high levels of multi-collinearity ($R^2 > 0.7$; Variance Inflation Factor >3.5), we ran single covariate models while retaining management type in all models. Within these models, occupancy was modelled as a function of the covariate and management type. Models were fit with landscape-specific intercepts and slopes, allowing for inference of the relative importance of covariates between the two landscapes (Equation 3). For remoteness, we included a quadratic term to model non-linear responses. As with the management effects model, detection probability was modelled as a function of date and within-replicate survey effort.

$$\text{logit}(\Psi_{i,j}) = \beta_{0i,l} + \beta_{1i}\text{Management}_{\text{type}_{j,l}} + \beta_{2il} * \text{continuous\_covariate}_j \quad (3)$$

Occupancy models were specified within a Bayesian framework using JAGS (Just Another Gibbs Sampler) via the R package jagsUI (Kellner, 2019). In both sets of models, occupancy and detection probability were modelled on the logit scale with species-specific random intercepts and slopes. We used uninformative priors and ran three parallel Markov chains with 200,000 iterations, discarding 50,000 iterations as burn-in, and thinning the remaining iterations by 50. We ensured Markov chains had appropriately mixed by visually inspecting trace-plots and statistically through R-hat values (ensuring all parameters had an R-hat <1.1). Model performance was assessed using Bayesian p-values (Gelman et al., 1995) and showed good fit (i.e. values for all

species were between 0.1 and 0.9; Table S4). Throughout, we consider statistical associations to be substantial if the 95% Bayesian Credible Intervals (BCI, 2.5th and 97.5th percentile of the posterior distribution) did not overlap zero and moderate if the 75% BCI (12.5th and 87.5th percentile of the posterior distribution) did not overlap zero. To assess the relative strength of covariate effects on mammal occurrence, we compared alternative models using WAIC (Table 1). The environmental and anthropogenic covariates included in the model with the lowest WAIC value were interpreted as the most influential factors.

3 | RESULTS

Thirty medium- to large-bodied mammal species were recorded across the two landscapes (Table S1). Most ($n = 22$) were recorded in both social forestry and protection forest sites. Four (small-toothed palm civet *Arctogalidia trivirgata*, collared mongoose *Urva semitorquata*, thomas's langur *Presbytis thomasi* and sunda leopard cat *Prionailurus javanensis*) were only recorded within the social forestry areas. Meanwhile, dhole (*Cuon alpinus*), tiger (*Panthera tigris*), Sumatran hog badger (*Arctonyx hoevenii*) and Sumatran striped rabbit (*Nesolagus netscheri*) were only recorded within the protection forest (Table S1). After removing five species with fewer than four independent detections, 25 species were included in the statistical analyses (Table S1).

3.1 | Mammal community responses to social forestry

Community-managed forests in both landscapes supported high levels of biodiversity, with no significant difference in overall mammal occupancy or richness compared with adjacent protection forest sites (Figure 2a,b). However, in both landscapes, social forestry was associated with shifts in mammal community composition. In the forest-dominated landscape, social forestry areas showed increased occupancy of generalist species, while occupancy of forest specialists and globally threatened species did not differ between this type of social forestry and the protection forest (Figure 2a). In contrast, within the agroforestry-mosaic landscape, social forestry was strongly associated (i.e. at the 95% BCI level) with reduced occurrence of forest specialists and, to a lesser extent (at the 75% BCI level), with threatened species, but showed no effect on generalist species (Figure 2a). Consequently, the diversity of forest specialists within this social forestry area was lower relative to the adjacent protection forest (Figure 2b).

3.2 | Drivers of occurrence patterns

Mammal occupancy was driven by several factors that varied among landscapes and species groups. Among all covariates, structural connectivity had the strongest effect on mammal occurrence (Table 1), showing a positive association with both richness and community occupancy at both landscapes (Figure 3). In the agroforestry-mosaic landscape, this effect was especially pronounced for threatened and forest specialist species, whereas in the forest-dominated landscape, it was consistent across species groups (Figure 3b). In the agroforestry-mosaic, richness and community occupancy were also strongly associated with biomass, and moderately with forest cover and TRI, with these associations being driven by the responses of forest specialist and threatened taxa (Figure 3). Species richness at social forestry sampling locations with high structural connectivity and biomass was often similar to those of the protection forest (Figure 3a). In the forest-dominated landscape, while there was also a moderate positive association of community occupancy with TRI and forest cover, there was no evidence of mammal communities responding to biomass (Figure 3).

In both landscapes, anthropogenic pressure (represented by remoteness) also influenced mammal richness and occupancy. At the forest-dominated landscape, species richness and community occupancy increased with the remoteness of sampling locations—an effect particularly strong for forest specialists (Figure 3b). In the agroforestry-mosaic, remoteness initially had a moderately positive relationship with species richness and occupancy. However, the relationship was non-linear, and species richness and occupancy declined at the most remote locations (Figure 3).

TABLE 1 Environmental and anthropogenic predictors of mammal occurrence across the two study regions.

Predictor	Relationship	Optimal scale (m)	WAIC value	Bayesian *p*-value
Connectivity	Linear	100	10127.14	0.452
Terrain ruggedness index (TRI)	Linear	250	10147.97	0.447
Biomass	Linear	250	10154.81	0.474
Remoteness	Quadratic	250	10188.19	0.444
Forest cover	Linear	500	10206.98	0.451

Note: Optimal scale represents the buffer around camera traps upon which covariates were extracted following a scale optimization process. Predictors are ordered based upon the model's WAIC, with lower values indicating the covariate was the greatest fit to mammal occurrence data.

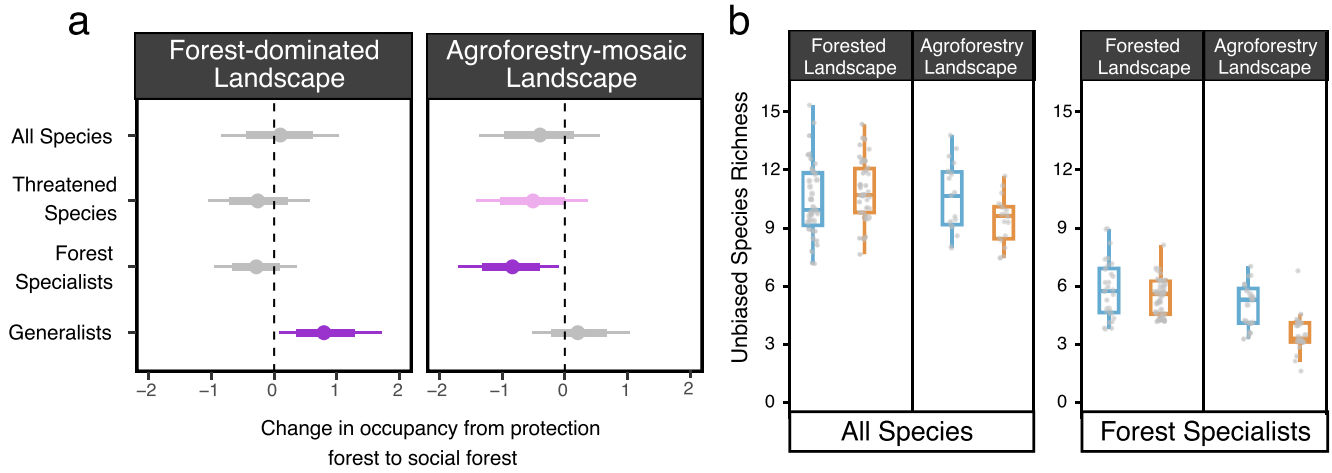

FIGURE 2 Mammal community occupancy and diversity in social forestry and protection forest sites in two landscape contexts in Sumatra. (a) Effect size of community response to social forestry relative to the protection forest (dashed vertical line). Effect sizes are presented as posterior medians (points) and Bayesian Credible Intervals (thick horizontal line denotes 75% BCI and thin line denotes 95% BCI). Purple points and lines represent substantial community responses, pink moderate responses, and grey no response. (b) Unbiased (i.e. detection-corrected) species richness patterns within social forestry (orange) and protection forest (blue) camera trap locations. Boxplots show the interquartile range across camera trap locations, and grey points show estimates of individual sampling locations.

3.3 | Social forestry influence on threatened and forest specialist species

Community-level patterns masked several species-specific responses to management type, and the environmental and anthropogenic predictors. In both landscapes, most species showed no significant difference in occupancy between social forestry and protection forest controls (Figure 4). Within the forest-dominated landscape, although community-level patterns suggested no overall effect of management regime for species of conservation concern, four species exhibited substantially reduced occupancy in social forestry areas (Figure 4a). These declines were largely driven by positive associations with remoteness, and in the case of sun bear (*Helarctos malayanus*), also structural connectivity (Figure 4a). Conversely, six species showed increased occupancy within social forestry areas, including the globally threatened Sunda pangolin (*Manis javanica*) and pig-tailed macaque (*Macaca nemestrina*) (Figure 4a).

In the agroforestry-mosaic, five species had reduced occupancy within the social forestry area, including strong declines in the occurrence of banded linsang (*Prionodon linsang*) and marbled cat (*Pardofelis marmorata*) (Figure 4b). Unlike in the forest-dominated landscape, these reductions were primarily linked to habitat-related factors, with species with reduced occupancy in the social forestry area tending to be those that were positively associated with areas of higher structural connectivity and biomass, and to a lesser extent forest cover and topographic ruggedness (Figure 4b). An exception was marbled cat, which showed no response to any of the habitat covariates. Three species showed higher occupancy within the social forestry area in this landscape (Figure 4b), including a strong increase in the occupancy of chevrotain (*Tragulus* spp.) and a moderate increase of the globally threatened sun bear. Across both landscapes, declines in occupancy in response to social forestry were concentrated among forest specialist species (Figure 4), whereas those with increased occupancy in this management type varied across species groups.

4 | DISCUSSION

Community-managed forests are often highlighted for their potential to contribute to biodiversity conservation (Cook, 2024), yet their effectiveness in supporting biodiversity in tropical regions remains poorly quantified (Burivalova et al., 2019; Meijaard et al., 2021). Here, we provide one of the first evaluations of biodiversity within Indonesia's community-managed forests and show that social forestry can support substantial mammal diversity across contrasting management contexts. In both landscapes, overall mammal community occupancy and species richness within community-managed forests were comparable to adjacent protection forest, although community composition shifted towards species less sensitive to disturbance, as has been observed in Nepal and India (Neupane et al., 2022; Velho et al., 2016). These findings reinforce that while social forestry cannot replace effectively managed protected areas, it can complement them as part of national conservation strategies.

Nevertheless, biodiversity patterns varied between the two social forestry contexts, which differed markedly in land cover and anthropogenic use. In the forest-dominated landscape, social forestry was associated with higher occupancy of generalists but no overall decline in specialist or threatened species, likely reflecting the dominance of intact forest with some areas of forest edge and disturbed habitat at the site. Conversely, in the agroforestry-mosaic, occupancy of specialists and threatened taxa was diminished in the social forestry area, driven by reduced forest cover, forest quality (represented by biomass) and weaker structural connectivity.

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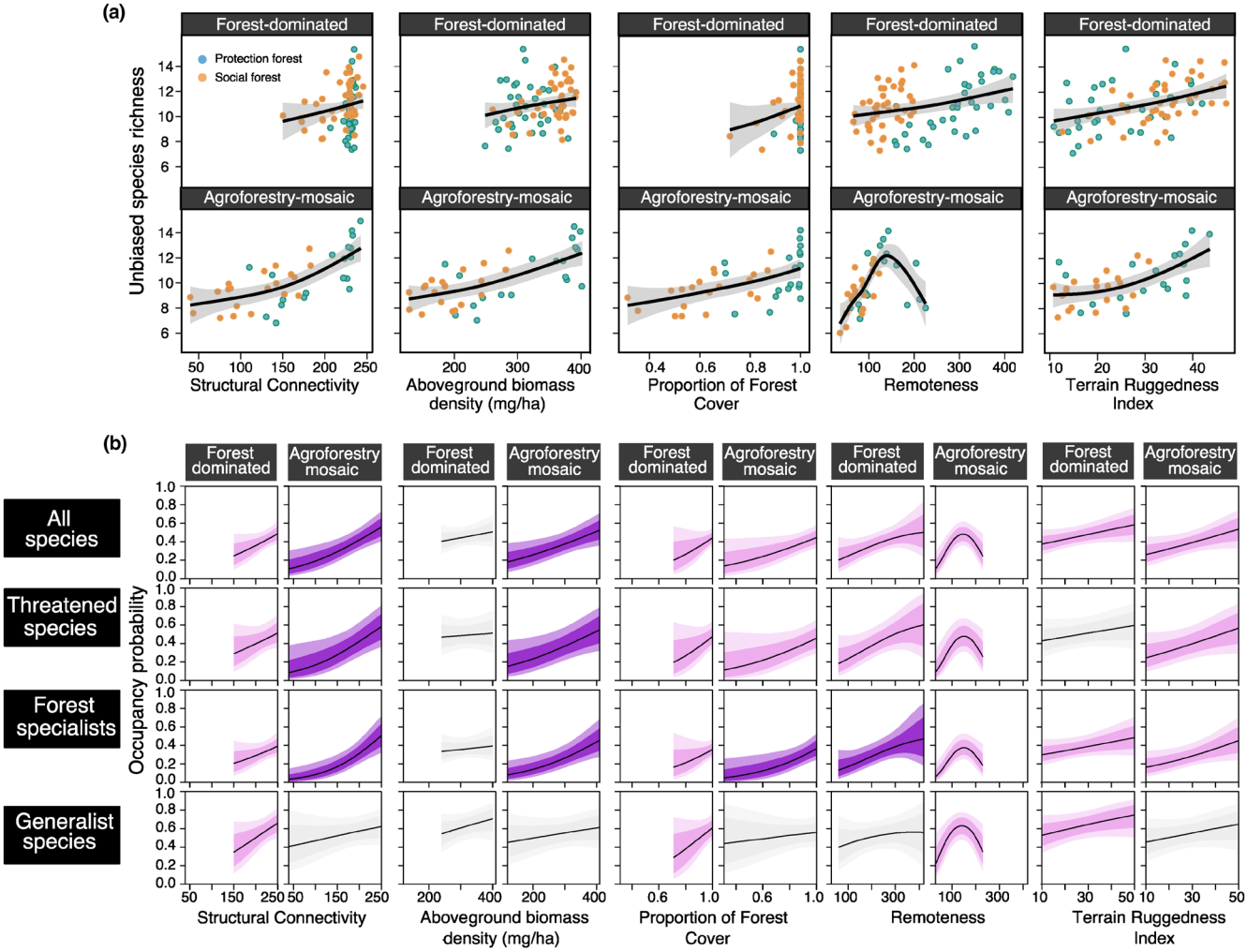

FIGURE 3 Effect of environmental and anthropogenic factors in shaping mammal species richness and community occupancy. (a) Relationship between unbiased species richness estimates and the five modelled covariates. Points represent individual sampling locations in the social forestry areas (orange) and protection forest controls (blue). Smoothed lines represent Generalised Additive Model (GAM) fits and shaded areas represent 95% confidence intervals. (b) Community occupancy predictions across the range of covariate values within each landscape for all species and each species group. Community responses are presented as predicted responses derived from posterior means (solid black lines) and BCIs (shaded areas). Lighter shaded areas represent the 95% BCI and darker shaded areas the 75% BCI. Purple plots indicate a substantial effect of the covariate on community occurrence (95% BCI did not overlap 0), pink plots indicate a moderate effect (75% BCI did not overlap 0) and grey plots indicate no effect.

4.1 | The role of connectivity in shaping biodiversity outcomes

Among the covariates we included in our models, structural connectivity emerged as the strongest predictor of species occurrence, exceeding the influence of forest cover. This underscores the need to move beyond forest cover as the only primary proxy for biodiversity in social forestry evaluations, particularly in multifunctional landscapes where tree cover can mask important variation in spatial configuration. Connectivity is rarely quantified in site-level biodiversity studies (Beger et al., 2022), yet our findings show that it can shape species occurrence even at fine spatial scales, not only across broad landscape gradients. In the agroforestry-mosaic landscape, sampling locations within better-connected forest had occupancy levels approaching those in contiguous forest, whereas those embedded in areas dominated by intensive agroforestry plots had particularly low occupancy, consistent with findings from intensive agroforestry elsewhere (De Beenhouwer et al., 2013). Together, this demonstrates the ecological value of even modest improvements to connectivity across social forestry landscapes.

Remoteness (as a proxy for anthropogenic pressure) also shaped occupancy patterns, particularly in the forest-dominated site, where specialist species such as sun bear, sambar, and tiger occurred disproportionately in more remote areas. These species are known to have experienced localised declines elsewhere in Sumatra due to over-exploitation and persecution (e.g. Haidir et al., 2024), highlighting that human pressures can suppress populations even where habitat remains intact.

Occupancy was also moderately associated with remoteness within the agroforestry-mosaic landscape, though the relationship

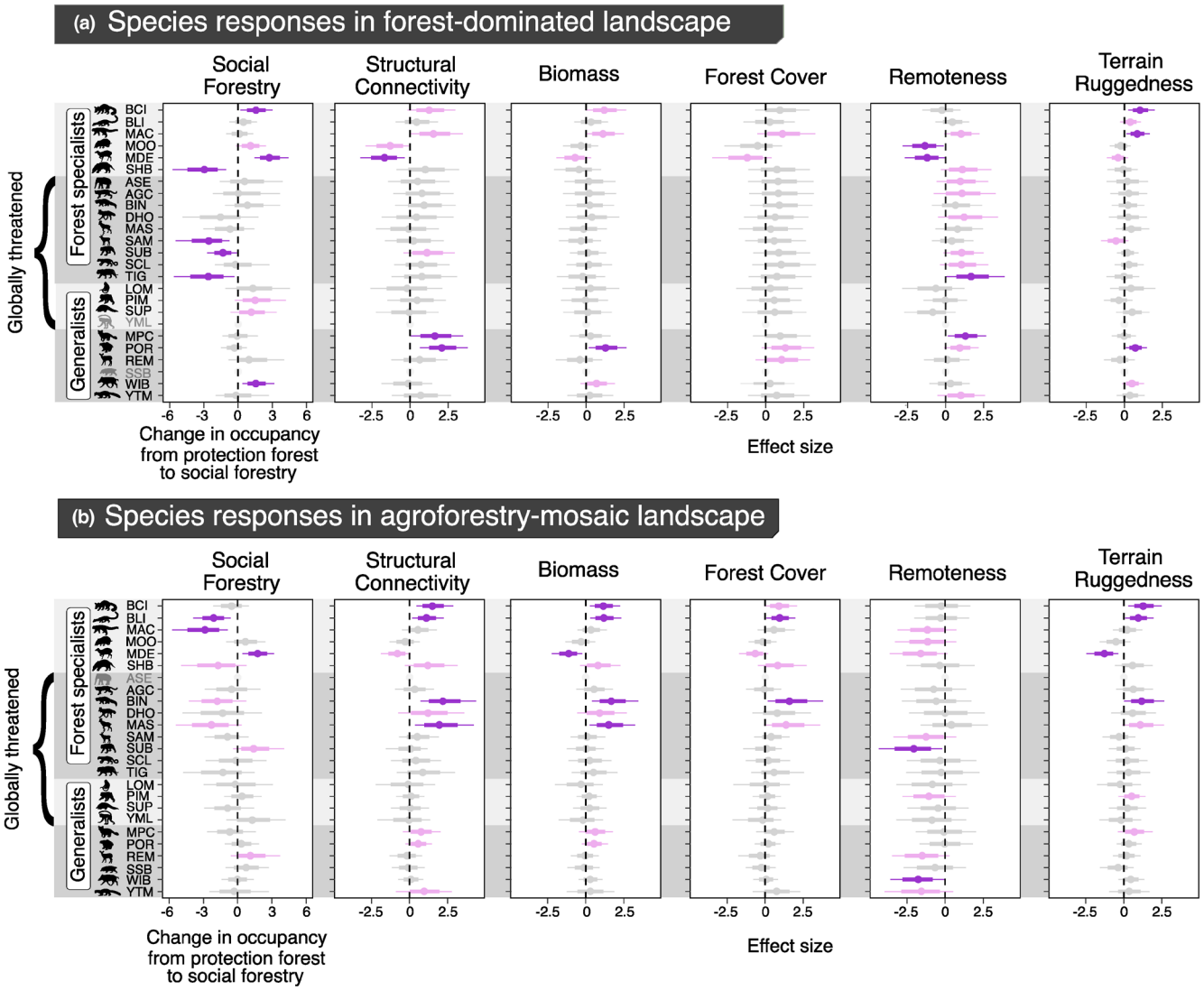

FIGURE 4 Species-specific responses to management type and the environmental and anthropogenic predictors for (a) the forest-dominated landscape and (b) the agroforestry-mosaic landscape. We present effect sizes as the posterior medians (points) and BCIs (thick horizontal line denotes 75% BCI and thin line denotes 95% BCI). Dark purple points and lines represent substantial species responses, pink moderate responses, and grey no response. Species with greyed out silhouettes and labels were not present in the given landscape based upon their IUCN range maps.

plateaued and declined at the most remote sites. The non-linear relationship between remoteness and occupancy should be interpreted with caution, however, as anthropogenic disturbance was observed near two of the more remote sampling locations (personal observations). This highlights the challenges of using remote-sensing products to quantify human pressure in rapidly changing landscapes, given inherent time lags in such data.

4.2 | Implications for biodiversity-compatible social forestry

Our findings suggest that community-managed forests in Indonesia can be compatible with biodiversity conservation, but their contribution will align with different aspects of the conservation agenda depending on landscape context. Schemes emphasising forest retention can achieve biodiversity outcomes similar to protection forests, and may therefore warrant OECM recognition (supporting KM-GBF Target 3 to protect 30% of land and sea by 2030), while community-managed forests in production-oriented systems with more degraded forest are better suited to restoration and sustainable-use and management targets (KM-GBF Target 2 and 10).

As restoration activities and sustainable land management practices are often incorporated into social forestry management plans (Gilmour, 2016), our findings suggest that these efforts should explicitly consider their influence on connectivity, not merely on forest extent, and to retain patches of mature forest where possible. Additional biodiversity gains are likely to arise from increasing the permeability of agroforestry plots (e.g. planting and retaining

additional shade trees; Manson et al., 2024) and the targeted planting of species' food sources (Blakesley et al., 2002). Preventing further fragmentation could substantially benefit forest specialists and threatened taxa by enhancing species movement (Haddad et al., 2015; Siegel et al., 2024). In turn, accelerated forest regeneration through the restoration of animal-mediated ecological functions such as seed dispersal (Estrada-Villegas et al., 2022) could provide ecosystem service benefits to smallholders, such as pest control (Hernandez-Aguilera et al., 2019).

Increasing the emphasis on the biodiversity outcomes of social forestry does, however, require careful consideration of potential trade-offs with well-being objectives. Retaining and restoring forests can constrain access to natural resources (Hajjar et al., 2021), and interventions aimed at improving ecological connectivity (e.g. shade-grown crops) may reduce, or be perceived to reduce, yields (Hernandez-Aguilera et al., 2019). Indeed, in the agroforestry-mosaic landscape, this concern has contributed to low uptake of shade-grown coffee. Human–wildlife conflict, already evident in both landscapes, also requires integrated mitigation strategies (Wong et al., 2015). For example, simulation studies in Tanzania showed that restoring landscapes to improve connectivity can increase the risk of elephant crop raiding (Pfeifer et al., 2022). Human–wildlife conflicts have received little research attention within the social forestry literature (Bista & Song, 2022), yet they affect livelihoods and human safety and can foster negative attitudes towards conservation (Abdullah et al., 2019; Struebig et al., 2018). Measures to improve biodiversity outcomes within social forestry should therefore be coupled with appropriate mitigation strategies.

4.3 | Social forestry as potential OECMs

The potential for social forestry areas to contribute to area-based conservation targets has been widely discussed, particularly through recognition as OECMs (Cook, 2024; Jonas et al., 2017). The forest-dominated social forestry areas showed biodiversity outcomes largely consistent with OECM criteria in achieving positive outcomes for the in situ conservation of biodiversity (Jonas et al., 2024). Conversely, the overall reduction in species of conservation concern observed within the social forestry area of the more modified agroforestry-mosaic suggests that such sites are unlikely to meet the requirements for OECM recognition. Nevertheless, the site still supported multiple threatened species, and therefore if restoration activities successfully enhance forest cover and connectivity, such sites may eventually fulfil OECM criteria. However, the threshold at which restoration constitutes the required in situ conservation of biodiversity remains unclear (Cook, 2024). Given that community-managed forests tend to be in close proximity to settlements and embedded within multifunctional landscapes (Gilmour, 2016), they may play an important role in enhancing connectivity across such landscapes, which is often highlighted as an important contribution of integrating OECMs into area-based conservation policy (Alves-Pinto et al., 2021).

However, OECM recognition requires more than biodiversity performance. Free, prior and informed consent from all relevant stakeholders is a prerequisite (Jonas et al., 2024), yet communities are internally diverse, making divergent views likely. Consent and verification processes must therefore acknowledge and address such concerns to avoid reinforcing existing power asymmetries and to secure long-term support. Several authors have also noted the high standard set by the OECM criteria, with many sites not fully meeting requirements despite positive biodiversity outcomes (Alves-Pinto et al., 2021; Cook et al., 2024). The most challenging criteria for social forestry mirror those in many potential OECMs (Cook et al., 2024), including the capacity to address biodiversity threats, the presence of activities partially incompatible with conservation and limited resources for management and monitoring.

4.4 | Financial incentives to promote biodiversity in social forestry

Financial constraints are a common issue in social forestry implementation in Indonesia (Resosudarmo et al., 2019) and may be particularly acute for sites located in protection forests, which although more likely to warrant OECM status, are often remote and characterised by high poverty levels (Santika et al., 2019). Numerous examples from the social forestry literature highlight the importance of economic incentives in improving environmental outcomes in such contexts (Putraditama et al., 2019; Rochmayanto et al., 2023), and identifying appropriate mechanisms is especially important when considering the implementation of biodiversity-friendly practices, given the potential for trade-offs with socioeconomic objectives. While ecotourism is often proposed (Rakatama & Pandit, 2020), many community-managed forests lack the infrastructure necessary for tourism, though there are some successful examples in Sumatra (e.g. Rochmayanto et al., 2023).

Certification and Payment for Ecosystem Service (PES) schemes offer additional pathways to fund social forestry, particularly given the strong potential to demonstrate uplifts in community well-being (Newton et al., 2015). Carbon credit schemes have been successfully integrated with social forestry in several countries (e.g. Tanzania and Nepal; Newton et al., 2015). The emerging biodiversity credit market could eventually provide direct incentives for biodiversity management, though metrics and accreditation protocols remain to be fully tested in this context (Wauchope et al., 2024). For community-managed forests that do fulfil OECM criteria, biodiversity credit schemes could also help to support the long-term biodiversity monitoring necessary for such recognition. Structural connectivity may be particularly suitable as a metric, offering a replicable indicator of biodiversity potential in mosaic landscapes and helping identify priority areas for investment.

4.5 | Caveats and future research directions

While our findings demonstrate the potential of social forestry in Indonesia to support biodiversity, some caveats apply. Although our study sites represent widespread forms of social forestry, case-study work always carries a risk of limited generality (Meijaard et al., 2021). Temporal data are currently lacking, and therefore, we cannot infer population trends, which are important for assessing whether biodiversity outcomes are sustained. However, social forestry had been implemented at both landscapes for at least 9 years at the time of data collection, indicating that the biodiversity patterns described reflect established management contexts rather than short-term responses. Nevertheless, in human-modified systems, there can be substantial time lags in species' responses to habitat degradation and fragmentation, with species often continuing to persist despite poor ecological conditions that are insufficient to support viable long-term populations, before subsequently declining or, in some cases, being extirpated locally (i.e. extinction debt; Figueiredo et al., 2019; Kuussaari et al., 2009). Consequently, there is a risk that the biodiversity patterns we observed within the community-managed forests may not be sustained over the long term, particularly in the agroforestry-mosaic, given the greater proportion of forest modification at this site. Further research could incorporate temporal data into biodiversity assessments of community-managed forests to evaluate whether the patterns we observed can be maintained.

Both social forestry landscapes were adjacent to large tracts of forest experiencing little disturbance, and thus, spillover effects may partly influence the biodiversity patterns observed (Estrada-Villegas et al., 2022). As a result, extinction debts could be slower to manifest and more challenging to detect, as species presence may in part be maintained by more transient immigration from surrounding intact forests (Kuussaari et al., 2009). Future research should assess whether similar patterns hold in more isolated community-managed forests located in lowland areas dominated by cash crop plantations (e.g. oil palm), particularly those on peat soils. Externalities and soil type were found to be key determinants of deforestation trajectories and community well-being outcomes in early evaluations of the village forest scheme in Sumatra and Kalimantan, in part due to exposure to wildfires and competing land uses (Santika et al., 2017, 2019). It is likely that this translates to differing biodiversity outcomes as well.

5 | CONCLUSIONS

We show that community-managed forests in Indonesia can support high biodiversity. However, there was substantial variation between the social forestry contexts, suggesting that different forms of social forestry are more suited to contributing to different aspects of the global conservation agenda. Social forestry schemes emphasising forest retention achieved biodiversity levels comparable to adjacent protection forests, indicating that such systems can deliver sustained conservation benefits consistent with OECM recognition, especially if threats such as unsustainable hunting are addressed. In contrast, production-oriented community forests in degraded landscapes supported reduced occupancy of forest specialists and threatened species, largely due to lower forest quality and reduced structural connectivity. These sites are therefore less likely to qualify as OECMs but can contribute meaningfully to the Kunming–Montreal Global Biodiversity Framework's restoration and sustainable-use targets. Enhancing connectivity should be central to such restoration efforts. Moving forward, embedding conservation within social forestry policy will require mechanisms that enable communities to derive tangible benefits from protecting biodiversity.

AUTHOR CONTRIBUTIONS

Liam J. Hughes, Matthew J. Struebig and Lindsay F. Banin conceived the ideas and designed the methodology, with input from Nicolas J. Deere. Liam J. Hughes, Radinal, Melani Massie, Muhammad Roddini and Nicolas J. Deere collected the data. Liam J. Hughes analysed the data with support from Nicolas J. Deere and Dave J. I. Seaman. Liam J. Hughes wrote the first draft of the manuscript, with input from Matthew J. Struebig, Lindsay F. Banin and Nicolas J. Deere. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. Radinal, Joseph Hutabarat, Ryan Avriandy and Dedi Kiswayadi work for Fauna and Flora—Indonesia Programme and Emmy Primadona, Muhammad Roddini and Melani Massie work for Komunitas Konservasi Indonesia WARSI (KKI WARSI). These organisations are engaged in community-led sustainable land management and governance, and are the NGO facilitators of social forestry at the two study sites. However, these organisations did not inform the analysis or interpretation of the data. Matthew J. Struebig is an Associate Editor of the *Journal of Applied*

Ecology but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data and code are available from Figshare https://doi.org/10.6084/m9.figshare.32287515 (Hughes et al., 2026). Due to Indonesian data sharing regulations, and that several of the species in our analysis are globally threatened, the coordinates of individual sampling locations are not disclosed, and species' identity is anonymised.

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REFERENCES

Abdullah, A., Sayuti, A., Hasanuddin, H., Affan, M., & Wilson, G. (2019). People's perceptions of elephant conservation and the human-elephant conflict in Aceh Jaya, Sumatra, Indonesia. *European Journal of Wildlife Research*, *65*(5), *69*. https://doi.org/10.1007/s10344-019-1307-1

Alves-Pinto, H., Geldmann, J., Jonas, H., Maioli, V., Balmford, A., Ewa Latawiec, A., Crouzeilles, R., & Strassburg, B. (2021). Opportunities and challenges of other effective area-based conservation measures (OECMs) for biodiversity conservation. *Perspectives in Ecology and Conservation*, *19*(2), 115–120. https://doi.org/10.1016/j.pecon.2021.01.004

Andermann, T., Faurby, S., Turvey, S. T., Antonelli, A., & Silvestro, D. (2020). The past and future human impact on mammalian diversity. *Science Advances*, *6*(36), eabb2313. https://doi.org/10.1126/sciadv.abb2313

Ardiantiono, Deere, N. J., Ramadiyanta, E., Sibarani, M. C., Hadi, A. N., Andayani, N., Ginting, Y., Bull, J. W., & Struebig, M. J. (2024). Selecting umbrella species as mammal biodiversity indicators in tropical forest. *Biological Conservation*, *292*, 110511. https://doi.org/10.1016/j.biocon.2024.110511

Beger, M., Metaxas, A., Balbar, A. C., McGowan, J. A., Daigle, R., Kuempel, C. D., Treml, E. A., & Possingham, H. P. (2022). Demystifying ecological connectivity for actionable spatial conservation planning. *Trends in Ecology & Evolution*, *37*(12), 1079–1091. https://doi.org/10.1016/j.tree.2022.09.002

Benzeev, R., Zhang, S., Piffer, P. R., & Mills-Novoa, M. (2025). Land tenure regimes influenced long-term restoration gains and reversals across Brazil's Atlantic forest. *Nature Communications*, *16*(1), 9656. https://doi.org/10.1038/s41467-025-64732-0

Bista, R., & Song, C. (2022). Human-wildlife conflict in the community forestry landscape: A case study from two Middle Hill districts of Nepal. *Human Dimensions of Wildlife*, *27*(6), 554–570. https://doi.org/10.1080/10871209.2021.1980158

Blakesley, D., Hardwick, K., & Elliott, S. (2002). Research needs for restoring tropical forests in Southeast Asia for wildlife conservation: Framework species selection and seed propagation. *New Forests*, *24*(3), 165–174. https://doi.org/10.1023/A:1021311700220

Broms, K. M., Hooten, M. B., & Fitzpatrick, R. M. (2016). Model selection and assessment for multi-species occupancy models. *Ecology*, *97*(7), 1759–1770. https://doi.org/10.1890/15-1471.1

Burivalova, Z., Allnutt, T. F., Rademacher, D., Schlemm, A., Wilcove, D. S., & Butler, R. A. (2019). What works in tropical forest conservation, and what does not: Effectiveness of four strategies in terms of environmental, social, and economic outcomes. *Conservation Science and Practice*, *1*(6), e28. https://doi.org/10.1111/csp2.28

Cazalis, V., Princé, K., Mihoub, J. B., Kelly, J., Butchart, S. H. M., & Rodrigues, A. S. L. (2020). Effectiveness of protected areas in conserving tropical forest birds. *Nature Communications*, *11*(1), 4461. https://doi.org/10.1038/s41467-020-18230-0

Convention on Biological Diversity (CBD). (2022). Kunming-Montreal Global Biodiversity Framework: COP 15 Decision L25.

Cook, C. N. (2024). Diverse approaches to protecting biodiversity: The different conservation measures discussed as possible other effective area-based conservation measures. *Conservation Letters*, *17*(4), e13027. https://doi.org/10.1111/conl.13027

Cook, C. N., Rao, M., Clyne, P. J., Rathbone, V., Barrientos, C., Boveda, A., Diment, A., Parra, J., Falabella, V., Linkie, M., Kujirakwinja, D., Ostrowski, S., Olson, K., Patankar, V., Rasolofomanan, L., & Grantham, H. S. (2024). Evaluating the likelihood for areas important for conservation to be recognized as Other Effective area-based Conservation Measures. https://doi.org/10.1101/2024.02.05.579011

De Beenhouwer, M., Aerts, R., & Honnay, O. (2013). A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. *Agriculture, Ecosystems & Environment*, *175*, 1–7. https://doi.org/10.1016/j.agee.2013.05.003

Deere, N. J., Guillera-Arroita, G., Platts, P. J., Mitchell, S. L., Baking, E. L., Bernard, H., Haysom, J. K., Reynolds, G., Seaman, D. J. I., Davies, Z. G., & Struebig, M. J. (2020). Implications of zero-deforestation commitments: Forest quality and hunting pressure limit mammal persistence in fragmented tropical landscapes. *Conservation Letters*, *13*(3), e12701. https://doi.org/10.1111/conl.12701

Deere, N. J., Guillera-Arroita, G., Swinfield, T., Milodowski, D. T., Coomes, D. A., Bernard, H., Reynolds, G., Davies, Z. G., & Struebig, M. J. (2020). Maximizing the value of forest restoration for tropical mammals by detecting three-dimensional habitat associations. *Proceedings of the National Academy of Sciences*, *117*(42), 26254–26262. https://doi.org/10.1073/pnas.2001823117

Devarajan, K., Morelli, T. L., & Tenan, S. (2020). Multi-species occupancy models: Review, roadmap, and recommendations. *Ecography*, *43*(11), 1612–1624. https://doi.org/10.1111/ecog.04957

Dorazio, R. M., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, *100*(470), 389–398. https://doi.org/10.1198/016214505000000015

Dubayah, R., Blair, J. B., Goetz, S., Fatoyinbo, L., Hansen, M., Healey, S., Hofton, M., Hurtt, G., Kellner, J., Luthcke, S., Armston, J., Tang, H., Duncanson, L., Hancock, S., Jantz, P., Marselis, S., Patterson, P. L., Qi, W., & Silva, C. (2020). The global ecosystem dynamics investigation: High-resolution laser ranging of the Earth's forests and topography. *Science of Remote Sensing*, *1*, 100002. https://doi.org/10.1016/j.srs.2020.100002

Edwards, D. P., Socolar, J. B., Mills, S. C., Burivalova, Z., Koh, L. P., & Wilcove, D. S. (2019). Conservation of tropical forests in the anthropocene. *Current Biology*, *29*(19), R1008–R1020. https://doi.org/10.1016/j.cub.2019.08.026

Estrada-Villegas, S., Stevenson, P. R., López, O., DeWalt, S. J., Comita, L. S., & Dent, D. H. (2022). Animal seed dispersal recovery during passive restoration in a forested landscape. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *378*(1867), 20210076. https://doi.org/10.1098/rstb.2021.0076

Fedele, G., Donatti, C. I., Bornacelly, I., & Hole, D. G. (2021). Nature-dependent people: Mapping human direct use of nature for basic needs across the tropics. *Global Environmental Change*, *71*, 102368. https://doi.org/10.1016/j.gloenvcha.2021.102368

Ferreira, G. B., Thomas, L., Ingram, D. J., Bevan, P. A., Madsen, E. K., Thanet, D. R., Rayamajhi, S., & Jones, K. E. (2023). Wildlife response to management regime and habitat loss in the Terai arc landscape of Nepal. *Biological Conservation*, *288*, 110334. https://doi.org/10.1016/j.biocon.2023.110334

Figueiredo, L., Krauss, J., Steffan-Dewenter, I., & Sarmento Cabral, J. (2019). Understanding extinction debts: Spatio–temporal scales, mechanisms and a roadmap for future research. *Ecography*, *42*(12), 1973–1990. https://doi.org/10.1111/ecog.04740

Fisher, M. R., Moeliono, M., Mulyana, A., Yuliani, E. L., Adriadi, D., Kamaluddin, A., Judda, J., Sahide, M. A. K., & Adriadi, A. (2018). Assessing the new social forestry project in Indonesia: Recognition, livelihood and conservation? *International Forestry Review*, *20*(3), 346.

Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (1995). *Bayesian data analysis*. Chapman and Hall/CRC. https://doi.org/10.1201/9780429258411

Gerstner, B. E., & Zarnetske, P. L. (2025). Evaluating the effectiveness of protected areas and community-managed lands in capturing multiple dimensions of frugivorous biodiversity in the Tropical Andes. *Biological Conservation*, *302*, 110904. https://doi.org/10.1016/j.biocon.2024.110904

Gilmour, D. A. (2016). *Forty years of community-based forestry: A review of its extent and effectiveness*. Food and Agriculture Organisation of the United Nations (FAO).

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2), e1500052. https://doi.org/10.1126/sciadv.1500052

Haidir, I. A., Wearn, O. R., Deere, N. J., Struebig, M. J., Dohong, A., Macdonald, D. W., & Linkie, M. (2024). Prioritizing wildlife conservation along habitat gradients in Sumatra. *Biological Conservation*, *299*, 110795. https://doi.org/10.1016/j.biocon.2024.110795

Hajjar, R., Oldekop, J. A., Cronkleton, P., Newton, P., Russell, A. J. M., & Zhou, W. (2021). A global analysis of the social and environmental outcomes of community forests. *Nature Sustainability*, *4*(3), 216–224. https://doi.org/10.1038/s41893-020-00633-y

Hernandez-Aguilera, J. N., Conrad, J. M., Gómez, M. I., & Rodewald, A. D. (2019). The economics and ecology of shade-grown coffee: A model to incentivize shade and bird conservation. *Ecological Economics*, *159*, 110–121. https://doi.org/10.1016/j.ecolecon.2019.01.015

Hughes, L. J., Deere, N., Radinal, R., Primadona, E., Roddini, M., Massie, M., Seaman, D. J., Hutabarat, J., Budiharta, S., Avriandy, R., Kiswayadi, D., Olsen, K., Smith, R. J., Winarni, N. L., Banin, L., & Struebig, M. J. (2026). Data from: Habitat connectivity shapes biodiversity outcomes in Indonesia's community-managed forests. *Figshare*. https://doi.org/10.6084/m9.figshare.32287515

IUCN. (2025). The IUCN Red List of Threatened Species. Version 2025-2. https://www.iucnredlist.org

Jonas, H. D., Lee, E., Jonas, H. C., Matallana-Tobon, C., Wright, K. S., Nelson, F., & Enns, E. (2017). Will "other effective area-based conservation measures" increase recognition and support for ICCAs. *Parks*, *23*(2), 63–78.

Jonas, H. D., Wood, P., & Woodley, S. (Eds.). (2024). *Guidance on other effective area-based conservation measures (OECMs)*. IUCN, International Union for Conservation of Nature. https://doi.org/10.2305/LAAW4624

Kays, R., Arbogast, B. S., Baker-Whatton, M., Beirne, C., Boone, H. M., Bowler, M., Burneo, S. F., Cove, M. V., Ding, P., Espinosa, S., Gonçalves, A. L. S., Hansen, C. P., Jansen, P. A., Kolowski, J. M., Knowles, T. W., Lima, M. G. M., Millspaugh, J., McShea, W. J., Pacifici, K., … Spironello, W. R. (2020). An empirical evaluation of camera trap study design: How many, how long and when? *Methods in Ecology and Evolution*, *11*(6), 700–713. https://doi.org/10.1111/2041-210X.13370

Kellner, K. (2019). *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses*. (Version R package version 1.6.2) [Computer software].

Korejs, K., Koane, B., Jeppy, S., Sam, L., Jorge, L. R., Novotny, V., & Sam, K. (2025). Comparing impacts of fragmentation on bird functional and phylogenetic diversity in primary and secondary rainforests. *Journal of Applied Ecology*, *62*(7), 1674–1684. https://doi.org/10.1111/1365-2664.70083

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology & Evolution*, *24*(10), 564–571. https://doi.org/10.1016/j.tree.2009.04.011

Landau, V. A., Shah, V. B., Anantharaman, R., & Hall, K. R. (2021). Omniscape.jl: Software to compute omnidirectional landscape connectivity. *The Journal of Open Source Software*, *6*(57), 2829. https://doi.org/10.21105/joss.02829

Manson, S., Nekaris, K. A. I., Nijman, V., & Campera, M. (2024). Effect of shade on biodiversity within coffee farms: A meta-analysis. *Science of the Total Environment*, *914*, 169882. https://doi.org/10.1016/j.scitotenv.2024.169882

Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S. L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B. B. N., Wenger, A., Jonas, H. D., Venter, O., & Watson, J. E. M. (2020). Area-based conservation in the twenty-first century. *Nature*, *586*(7828), 217–227. https://doi.org/10.1038/s41586-020-2773-z

Meijaard, E., Santika, T., Wilson, K. A., Budiharta, S., Kusworo, A., Law, E. A., Friedman, R., Hutabarat, J. A., Indrawan, T. P., Sherman, J., St. John, F. A. V., & Struebig, M. J. (2021). Toward improved impact evaluation of community forest management in Indonesia. *Conservation Science and Practice*, *3*(1), e189. https://doi.org/10.1111/csp2.189

Naidoo, R., Aylward, C., Elliott, W., Keeley, A., Kinnaird, M., Knight, M., Papp, C.-R., Thapa, K., & Antelo, R. (2025). From science to impact: Conserving ecological connectivity in large conservation landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, *122*(31), e2410937122. https://doi.org/10.1073/pnas.2410937122

Neupane, B., Dhami, B., Panthee, S., Stewart, A. B., Silwal, T., & Katuwal, H. B. (2022). Forest management practice influences bird diversity in the Mid-Hills of Nepal. *Animals*, *12*(19), 2681. https://doi.org/10.3390/ani12192681

Newton, P., Schaap, B., Fournier, M., Cornwall, M., Rosenbach, D. W., DeBoer, J., Whittemore, J., Stock, R., Yoders, M., Brodnig, G., & Agrawal, A. (2015). Community forest management and REDD+. *Forest Policy and Economics*, *56*, 27–37. https://doi.org/10.1016/j.forpol.2015.03.008

Nguyen, A., Tilker, A., Le, D., Niedballa, J., Pflumm, L., Pham, X. H., Le, V. S., Luu, H. T., Tran, V. B., Kramer-Schadt, S., Sollmann, R., & Wilting, A. (2024). Ground-dwelling mammal and bird diversity in the southern Annamites: Exploring complex habitat associations and the ghost of past hunting pressure. *Conservation Science and Practice*, *6*(4), e13093. https://doi.org/10.1111/csp2.13093

Niedballa, J., Sollmann, R., Mohamed, A. b., Bender, J., & Wilting, A. (2015). Defining habitat covariates in camera-trap based occupancy studies. *Scientific Reports*, *5*(1), 17041. https://doi.org/10.1038/srep17041

O'Bryan, C. J., Garnett, S. T., Fa, J. E., Leiper, I., Rehbein, J. A., Fernández-Llamazares, Á., Jackson, M. V., Jonas, H. D., Brondizio,

E. S., Burgess, N. D., Robinson, C. J., Zander, K. K., Molnár, Z., Venter, O., & Watson, J. E. M. (2021). The importance of Indigenous Peoples' lands for the conservation of terrestrial mammals. *Conservation Biology*, *35*(3), 1002–1008. https://doi.org/10.1111/cobi.13620

Pfeifer, M., Sallu, S. M., Marshall, A. R., Rushton, S., Moore, E., Shirima, D. D., Smit, J., Kioko, E., Barnes, L., Waite, C., Raes, L., Braunholtz, L., Olivier, P. I., Ishengoma, E., Bowers, S., & Guerreiro-Milheiras, S. (2022). A systems approach framework for evaluating tree restoration interventions for social and ecological outcomes in rural tropical landscapes. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *378*(1867), 20210111. https://doi.org/10.1098/rstb.2021.0111

Pillay, R., Venter, M., Aragon-Osejo, J., González-del-Pliego, P., Hansen, A. J., Watson, J. E. M., & Venter, O. (2022). Tropical forests are home to over half of the world's vertebrate species. *Frontiers in Ecology and the Environment*, *20*(1), 10–15. https://doi.org/10.1002/fee.2420

Putraditama, A., Kim, Y. S., & Sánchez Meador, A. J. (2019). Community forest management and forest cover change in Lampung, Indonesia. *Forest Policy and Economics*, *106*, 101976. https://doi.org/10.1016/j.forpol.2019.101976

Rabus, B., Eineder, M., Roth, A., & Bamler, R. (2003). The shuttle radar topography mission—A new class of digital elevation models acquired by spaceborne radar. *ISPRS Journal of Photogrammetry and Remote Sensing*, *57*(4), 241–262. https://doi.org/10.1016/S0924-2716(02)00124-7

Rakatama, A., & Pandit, R. (2020). Reviewing social forestry schemes in Indonesia: Opportunities and challenges. *Forest Policy and Economics*, *111*, 102052. https://doi.org/10.1016/j.forpol.2019.102052

RECOFTC. (2024). *Community forestry and forest landscape restoration: Attracting sustainable investments for restoring degraded land in Southeast Asia*. RECOFTC. https://www.recoftc.org/id/publications/0000313

Resosudarmo, I. A. P., Tacconi, L., Sloan, S., Hamdani, F. A. U., Subarudi, Alviya, I., & Muttaqin, M. Z. (2019). Indonesia's land reform: Implications for local livelihoods and climate change. *Forest Policy and Economics*, *108*, 101903. https://doi.org/10.1016/j.forpol.2019.04.007

Rights and Resources Initiative. (2018). At a crossroads: Consequential trends in recognition of community-based forest tenure from 2002–2017.

Rochmayanto, Y., Nurrochmat, D. R., Nugroho, B., Darusman, D., Satria, A., Casse, T., Erbaugh, J. T., & Wicaksono, D. (2023). Devolution of forest management to local communities and its impacts on livelihoods and deforestation in Berau, Indonesia. *Heliyon*, *9*(5), e16115. https://doi.org/10.1016/j.heliyon.2023.e16115

Santika, T., Meijaard, E., Budiharta, S., Law, E. A., Kusworo, A., Hutabarat, J. A., Indrawan, T. P., Struebig, M., Raharjo, S., Huda, I., Sulhani, Ekaputri, A. D., Trison, S., Stigner, M., & Wilson, K. A. (2017). Community forest management in Indonesia: Avoided deforestation in the context of anthropogenic and climate complexities. *Global Environmental Change*, *46*, 60–71. https://doi.org/10.1016/j.gloenvcha.2017.08.002

Santika, T., Wilson, K. A., Budiharta, S., Kusworo, A., Meijaard, E., Law, E. A., Friedman, R., Hutabarat, J. A., Indrawan, T. P., St. John, F. A. V., & Struebig, M. J. (2019). Heterogeneous impacts of community forestry on forest conservation and poverty alleviation: Evidence from Indonesia. *People and Nature*, *1*(2), 204–219. https://doi.org/10.1002/pan3.25

Siegel, T., Magrach, A., Laurance, W. F., & Luther, D. (2024). A global meta-analysis of the impacts of forest fragmentation on biotic mutualisms and antagonisms. *Conservation Biology*, *38*(3), e14206. https://doi.org/10.1111/cobi.14206

Struebig, M. J., Lee, J. S. H., Deere, N. J., Gevaña, D. T., Ingram, D. J., Lwin, N., Nguyen, T., Santika, T., Seaman, D. J. I., Supriatna, J., & Davies, Z. G. (2025). Drivers and solutions to Southeast Asia's biodiversity crisis. *Nature Reviews Biodiversity*, *1*, 1–18. https://doi.org/10.1038/s44358-025-00064-7

Struebig, M. J., Linkie, M., Deere, N. J., Martyr, D. J., Millyanawati, B., Faulkner, S. C., Le Comber, S. C., Mangunjaya, F. M., Leader-Williams, N., McKay, J. E., & St. John, F. A. V. (2018). Addressing human-tiger conflict using socio-ecological information on tolerance and risk. *Nature Communications*, *9*(1), 3455. https://doi.org/10.1038/s41467-018-05983-y

Sze, J. S., Carrasco, L. R., Childs, D., & Edwards, D. P. (2022). Reduced deforestation and degradation in Indigenous lands pan-tropically. *Nature Sustainability*, *5*(2), 123–130. https://doi.org/10.1038/s41893-021-00815-2

Sze, J. S., Childs, D. Z., Carrasco, L. R., Fernández-Llamazares, Á., Garnett, S. T., & Edwards, D. P. (2023). Indigenous Peoples' lands are critical for safeguarding vertebrate diversity across the tropics. *Global Change Biology*, *30*, e16981. https://doi.org/10.1111/gcb.16981

Tauli-Corpuz, V., Alcorn, J., Molnar, A., Healy, C., & Barrow, E. (2020). Cornered by PAs: Adopting rights-based approaches to enable cost-effective conservation and climate action. *World Development*, *130*, 104923. https://doi.org/10.1016/j.worlddev.2020.104923

Vancutsem, C., Achard, F., Pekel, J.-F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Aragão, L. E. O. C., & Nasi, R. (2021). Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Science Advances*, *7*(10), eabe1603. https://doi.org/10.1126/sciadv.abe1603

Velho, N., Srinivasan, U., Singh, P., & Laurance, W. F. (2016). Large mammal use of protected and community-managed lands in a biodiversity hotspot. *Animal Conservation*, *19*(2), 199–208. https://doi.org/10.1111/acv.12234

Wauchope, H. S., Zu Ermgassen, S. O. S. E., Jones, J. P. G., Carter, H., Schulte To Bühne, H, & Milner-Gulland, E. J. (2024). What is a unit of nature? Measurement challenges in the emerging biodiversity credit market. *Proceedings of the Royal Society B: Biological Sciences*, *291*(2036), 20242353. https://doi.org/10.1098/rspb.2024.2353

Wilson, K. A., Meijaard, E., Drummond, S., Grantham, H. S., Boitani, L., Catullo, G., Christie, L., Dennis, R., Dutton, I., Falcucci, A., Maiorano, L., Possingham, H. P., Rondinini, C., Turner, W. R., Venter, O., & Watts, M. (2010). Conserving biodiversity in production landscapes. *Ecological Applications*, *20*(6), 1721–1732. https://doi.org/10.1890/09-1051.1

Wong, W.-M., Leader-Williams, N., & Linkie, M. (2015). Managing human-sun bear conflict in Sumatran agroforest systems. *Human Ecology*, *43*(2), 255–266.

SUPPORTING INFORMATION

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

Appendix S1. Details of study sites and social forestry context in Indonesia.

Appendix S2. Processing GEDI data and fitting random forest models to predict above-ground biomass and canopy height.

Appendix S3. Generating a circuit theory-based forest structural connectivity metric.

Appendix S4. Producing a remoteness index across the study sites.
Appendix S5. Scale optimisation protocol.
Table S1. Mammal inventory comprising the 30 medium- to large-bodied species detected during the camera trap campaigns in Aceh and Bengkulu.
Table S2. Predictors and performance of forest structural random forest models.
Table S3. Results of scale optimisation procedure.
Table S4. Bayesian *p*-values used to assess model fit.

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