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.
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. Landscape connectivity emerged as the strongest environmental driver of mammal occurrence. High connectivity buffered biodiversity losses in 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. 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.

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 reserves 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 (Sze et al. 2022, Benzeev et al. 2025), 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 maintain or enhance habitat connectivity - an explicit objective of the Kunming-Montreal Global Biodiversity Framework (KM-GBF; 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 socioeconomic benefits for rural communities (Cook 2024, Struebig et al. 2025). 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, and enables it at scale, 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 geneflow, 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 (Sze et al. 2023, Gerstner and Zarnetske 2025), 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, 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 (Burivalova et al. 2019), 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 (Velho et al. 2016, Neupane et al. 2022). These studies show that community forests can support important wildlife populations, although typically with changes to community composition compared to adjacent protected areas (Velho et al. 2016, Neupane et al. 2022). 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. 2020; 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 focused 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 and Pandit 2020). Schemes can be allocated within government-designated watershed protection or production forest, which further shape permissible activities (Rakatama and Pandit 2020). Community-managed forests are often established on degraded land, with management efforts focused on restoring vegetation cover and improving landscape connectivity through agroforestry and tree planting (Santika et al. 2017, Putraditama et al. 2019).

Impact evaluations of some of the earliest social forestry areas in Sumatra and Kalimantan indicate that, on average, the programme reduced deforestation (Santika et al. 2017, 2019, Putraditama et al. 2019), though with considerable spatial and temporal variability influenced by anthropogenic, biophysical and legal factors (Santika et al. 2017, 2019, Putraditama et al. 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 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 anthropogenic pressures and landscape factors shape species occurrence patterns across these multiple-use landscapes, addressing a key mechanism through which social forestry may support biodiversity.

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; Supporting Information S1) designated on watershed 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 (Fig. 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 (16.2km^2). Land use practices were broadly consistent across these two social forestry areas, 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 sites illustrate contrasting social forestry settings in Indonesia: one focused on forest protection, and the other on sustainable production and restoration (Supporting Information S1).

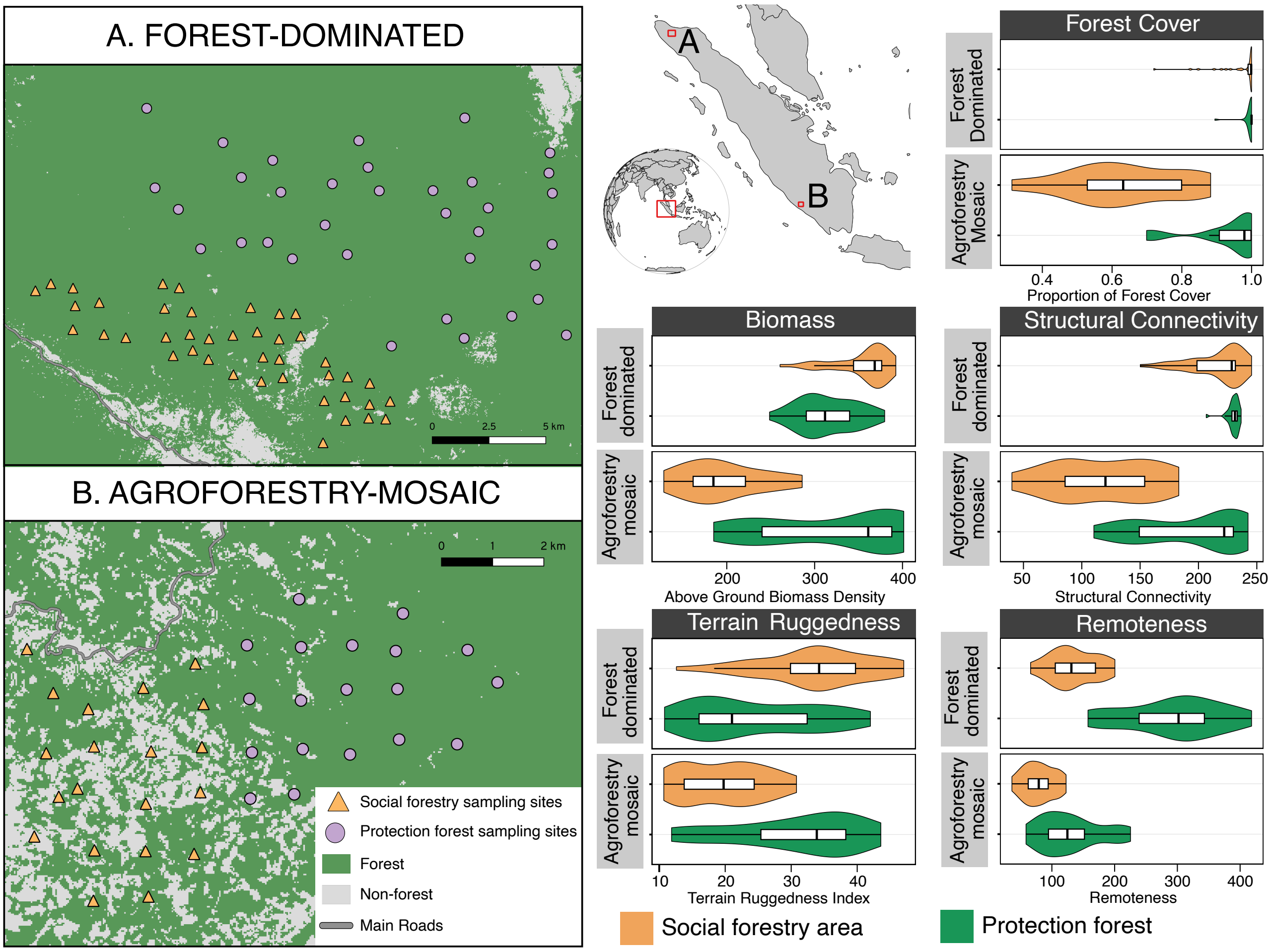

Figure 1 - Maps of study sites and sampling design alongside the broader landscape context in Sumatra. Violin plots depict the kernel distribution of the five environmental and anthropogenic covariates at each sampling location, grouped by landscape and social forestry (orange) and protection forest controls (green). Box plots contained therein describe the median (central vertical line) and interquartile range (outer vertical lines of the box).

2.2 Data collection and processing

2.2.1 Camera trap surveys

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

Across both landscapes, we used a systematic grid design, deploying cameras approximately 1km apart (mean distance 1.04km). 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 20-40cm 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 6,709 camera-trap nights.

All images were identified to species level by an experienced observer. 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 photos of people deleted. Species conservation status was obtained from the IUCN's Red List of Threatened Species (IUCN 2025a), 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 anthropogenic and environmental covariates expected to influence mammalian habitat use across landscapes (Table S1). To capture topographic variation, we calculated terrain ruggedness index (TRI) at 30m 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).

To quantify the availability, quality, and structural continuity of forest habitat, we used 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). Forest cover was quantified as the proportion of forest within the vicinity of each camera-trap station (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 (Supporting Information S2).

We used the canopy height layer to generate a continuous forest structural connectivity metric using the Omniscape algorithm (Landau et al. 2021). This model estimates the relative “flow” through the landscape, representing potential mammal movement pathways based on forest structure, analogous to the flow of 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; Supporting Information S3).

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 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 (Supporting Information S4).

All covariates were extracted as mean values derived from scale-optimized buffers around each camera trap location (Supporting Information S5). Covariates were standardized (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 and 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 and 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 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 these 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).

$$logit(\Psi_{i,j}) = \beta_{0i,l} + \beta_i Management\_type_{jl}$$

(equation 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.

$$logit(p_{i,j,k}) = \alpha_0 + \alpha_{1i}Survey\_effort_{j,k} + \alpha_{2i}Date_{j,k}$$

(equation 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.

$$logit(\Psi_{i,j}) = \beta_{0i,l} + \beta_{1i}Management_{type_{j,l}} + \beta_{2il} * continuous\_covariate_j$$

(equation 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 S3). 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 the Watanabe–Akaike Information Criterion (WAIC; Table 1). 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. 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*), Sumatran tiger (*Panthera tigris sumatrae*), 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 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 mammalian biodiversity, with no significant difference in overall mammal occupancy or richness compared with adjacent protection forest sites (Figs 1a and 1b). 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 management types (Fig. 1a). 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 (Fig. 1a). Consequently, the diversity of forest specialists within this social forestry area was lower relative to the adjacent protection forest (Fig. 1b).

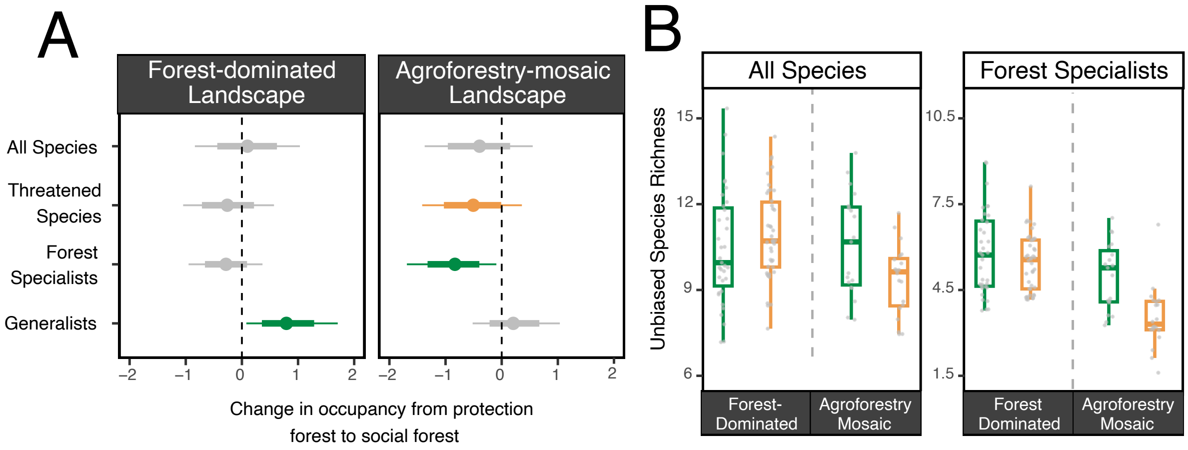

Figure 2 – Mammal community occurrence and diversity in social forestry and protection forest sites in two landscape contexts in Sumatra. A) Effect size of community response to social forestry relative to the protection forest (dashed vertical line). Effect sizes are presented as posterior means (points)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

3.2 Drivers of species occupancy

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 (Fig. 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 (Fig. 3b). Here, 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 (Fig. 3). Species richness at social forestry sampling locations with high structural connectivity and biomass were often similar to those of the protection forest (Fig. 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 (Fig. 3).

Table 1 – Environmental and anthropogenic predictors of mammal occurrence across the two study regions. Optimal scale represents the buffer around camera traps upon which covariates were extracted at 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.

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
Access	Quadratic	250	10188.19	0.444
Forest Cover	Linear	500	10206.98	0.451

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 (Fig. 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 (Fig. 3).

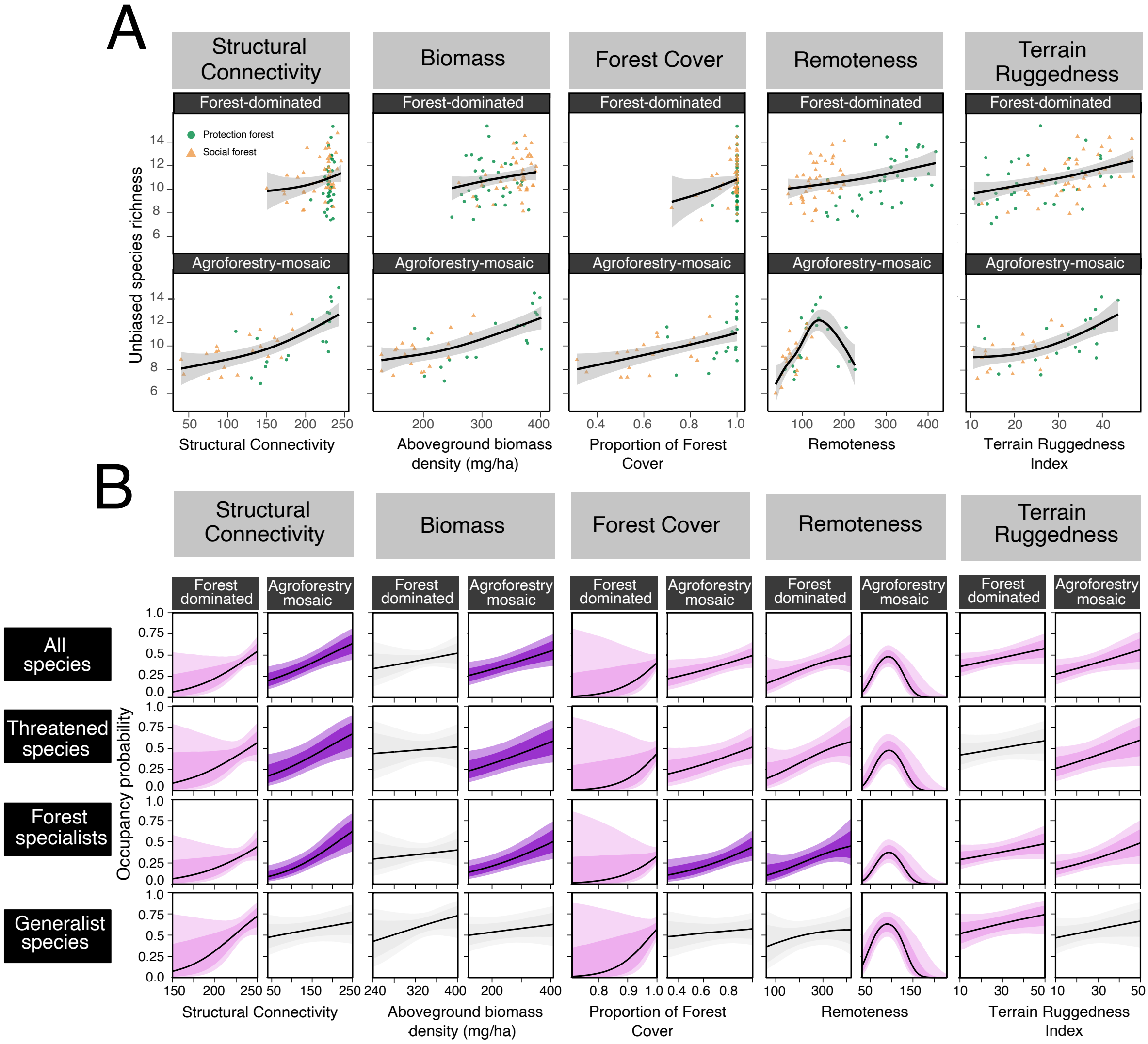

Figure 3 – Effect of environmental and anthropogenic factors in shaping mammal species richness and community occupancy. A) Relationship between unbiased species richness estimates and the five modelled covariates. Points represent individual sampling locations in the social forestry areas (orange) and protection forest controls (green). Smoothed lines represent Generalized 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.

3.3 Social forestry influence on threatened and forest specialist species

Community-level patterns masked several species-specific responses to management type, and environmental and anthropogenic predictors. In both landscapes, most species showed no significant difference in occupancy between social forestry and protection forest controls (Fig. 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 (Fig. 4a). These declines were largely driven by positive associations with remoteness, and in the case of sun bear (*Helarctos malayanus*), also structural connectivity (Fig. 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*) (Fig. 4a).

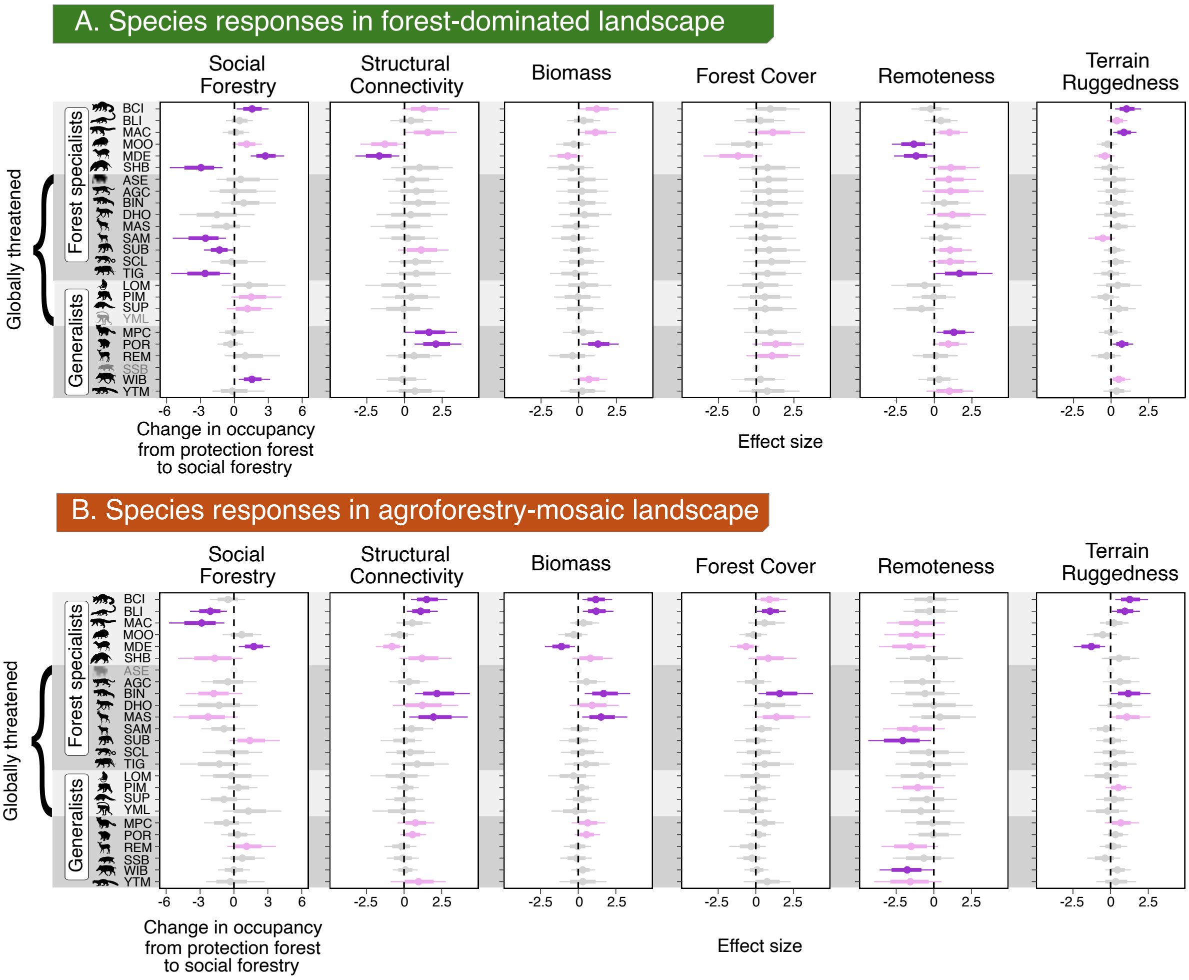

Figure 4 – Species-specific responses to management type and the environmental and anthropogenic predictors for A) the forest-dominated landscape and B) the agroforestry-mosaic landscape. We present effect sizes as the posterior means (points) and BCIs (thick horizontal line denotes 75% BCI and thin 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.

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*) (Fig. 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 (Fig. 4b). An exception was marbled cat, which showed no response to any of the habitat covariates. Three species showed higher occupancy within social forestry areas in this landscape (Fig. 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 (Fig. 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 toward species less sensitive to disturbance, as observed in Nepal and India (Velho et al. 2016, Neupane et al. 2022). These findings reinforce that while social forestry cannot replace effectively managed protected areas, it can complement them as part of national conservation strategies.

Nevertheless, the two social forestry contexts 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 canopy cover, forest quality (represented by biomass) and weaker structural connectivity.

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 alone. 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 experience 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 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 outcomes similar to protection forest, and may therefore warrant

OECM recognition (supporting KM-GBF Target 3 to protect 30% of land and sea by 2030), while production-oriented systems in 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 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 and Song 2022), yet they affect livelihoods and human safety and can foster negative attitudes towards conservation (Struebig et al. 2018, Abdullah et al. 2019). 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 Other Effective Area-based Conservation Measures (OECMs) (Jonas et al. 2017, Cook 2024). 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 et al., 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 and 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 wellbeing (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 support 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 is currently lacking, and therefore we cannot infer population trends, which are important for assessing whether biodiversity outcomes are sustained. Nevertheless, social forestry had been implemented at both landscapes for at least nine years at the time of data collection, indicating that the biodiversity patterns described reflect established management contexts rather than short-term responses.

Both social forestry landscapes were adjacent to large tracts of little-disturbed forest, and thus spillover effects may partly influence the biodiversity patterns observed (Estrada-Villegas et al. 2022). 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.

Conclusion

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.

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Author contributions

Liam J. Hughes, Matthew J. Struebig and Lindsay F. Banin conceived the ideas and designed 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.

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 organisation's did not inform the analysis or interpretation of the data.

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Supporting Information

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

Contents

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

The study was conducted across two social forestry landscapes that encompassed the three most prominent social forestry schemes in Indonesia: village forests (*Hutan Desa*, HD), community forests (*Hutan Kemasyarakatan*, HKm) and community plantation forests (*Hutan Tanaman Rakyat*, HTR). Together, these schemes account for more than two-thirds of Indonesia's social forestry area (Santika et al., 2017). In all three schemes, management rights are granted to communities under 35-year licenses, while the state retains ownership.

HD and HKm are similar in purpose but differ in the community groups granted management rights: HD social forestry permits are granted at the village level, whereas HKm permits are granted to local user groups (e.g., farmer associations). Under both schemes, social forestry can be designated on state forest allocated as production or watershed protection forest (hereafter protection forest). Across all designations, communities may engage in activities such as non-timber forest collection and agroforestry (Rakatama and Pandit, 2020). In production forests, low-intensity logging is permitted along and small-scale cultivation on previously cultivated land and degraded areas with limited tree cover, provided this is conducted in ways that support the rehabilitation of forests. For social forestry designated within protection forests, logging and cultivation that exposes soils is prohibited. HTR schemes are established only on production forests, often in degraded areas, where communities or farmers can obtain licenses for timber harvesting or the operation or restoration of timber plantations (Rakatama and Pandit, 2020).

Data were collected in two social forestry landscapes located in the foothills of the Bukit Barisan mountain range in Sumatra, each representing a distinct social forestry context. In Aceh, surveys were conducted across three neighbouring HD areas (total size: 43.3 km^2) designated on protection forest, where logging is prohibited. Most of the area comprised highly connected, contiguous tropical moist forest (98.6% forest cover; Fig. 1). Agricultural production, predominantly rice paddies, occurred mainly adjacent to the forest boundary. Although large parts of the social forestry area are relatively remote from villages, there are pockets of open livestock grazing areas and small-scale agroforestry plots towards the periphery (Fig. 1). The local community was engaged in an active restoration project to recover forest in some of these areas through the planting of multi-purpose tree species.

The second case study was implemented in Bengkulu province, encompassing a neighbouring HKm and HTR (total area: 16.2 km^2) designated on production forest. Although formally different schemes, both are managed similarly, and no timber plantations were operating within the HTR. The primary livelihood source for most community members was agriculture and agroforestry, primarily coffee, durian and petai cultivation. The landscape comprised a mosaic of primary and degraded forest, agroforestry plantations of varying intensity, and overgrown shrubland from abandoned coffee plots (60.6% forest cover). The community was implementing a restoration project to enhance forest cover and connectivity through both tree planting and protected zoning. Six parcels of relatively mature forest were designated for natural regeneration. During the survey period, construction of a new government road through part of the area had accelerated agroforestry expansion and caused some encroachment into the protection forest.

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

We derived layers of above-ground biomass and canopy height from NASA's Global Ecosystem Dynamics Investigation (GEDI) data, a spaceborne LiDAR system that measures the vertical structure of forests (Dubayah et al., 2020). GEDI data is available in the form of point clouds, with forest structural information obtained at 25m resolution LiDar footprints acquired along the satellite's trajectory. The spatial and temporal coverage of GEDI points is thus constrained by the satellite's orbital route and can be especially limited in tropical regions due to high cloud cover, which can interfere with the LiDar measurements (Liu et al., 2021). Most biodiversity analyses require spatially continuous layers of a given covariate. A widespread approach to producing such layers is to combine GEDI waveform data with spectral remote sensing information and use random forest models to predict the given forest structural metric across an area of interest (e.g Burns et al., 2025; Liu et al., 2021).

We used Google Earth Engine (Gorelick et al., 2017) to produce biomass and canopy height layers for our study areas. We first extracted geolocated GEDI waveforms from the GEDI L2A and L4A granules across our study regions (Dubayah et al., 2020). To maximise GEDI training data points, all GEDI waveforms were extracted from the year 2021 in the forested landscape and 2019 in the agroforestry-mosaic landscape. For canopy height, we used the RH98 metric, which represents the height below which 98% of waveform energy is contained, as it provides more stable estimates of canopy height than RH100 (Qi et al., 2025). To ensure only high-quality GEDI footprints were used for analyses, we applied the quality filtering process outlined by (Burns et al., 2025), whereby only points with ‘degrade_flag’ = 0 and ‘quality_flag’ = 1 were retained. As our study sites primarily consist of dense tropical forest, only GEDI footprints with a beam sensitivity of at least 98% were used (Bourgoin et al., 2024). Given the reduced accuracy of GEDI where vegetation is below 3m, we followed Burns et al (2025) in setting points with RH98 <3m to zero. Additionally, points with RH98 >100m or biomass > 900 mg/h were removed as these were deemed to be potential outliers.

We compiled a range of remote sensing data to be used as predictors of biomass and canopy height in the RF classifier. Landsat 8 surface reflectance imagery (Collection 2, Level 2) was pre-processed by applying the quality assurance bands to mask clouds, cloud shadows, cirrus, and saturated pixels. Radiometric scaling factors were applied to the optical and thermal bands, and annual median composites were produced and clipped to the study region. From this Landsat composite, several vegetation indices were derived to capture forest condition: Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI) and Atmospherically Resistant Vegetation Index (ARVI). To assess forest disturbance, we used data from the JRC-TMF annual change product (Vancutsem et al., 2021). To integrate landscape textural information into the classifier, we used radar data from the Copernicus Sentinel-1 mission. For each orbit, median backscatter composites of VV and VH polarisations were used, resulting in four bands: VV ascending, VV descending, VH ascending and VH descending. Finally, as geophysical conditions can influence forest structure, elevation, slope, TRI and aspect were derived from the SRTM (Rabus et al., 2003) and included in the models. Remote sensing information was extracted from the same years as the GEDI waveforms to ensure temporal alignment (i.e 2021 in the forested landscape and 2019 in the agroforestry-mosaic landscape) and resampled to 30m resolution.

To build the RF classifier, approximately 10,000 independent GEDI waveforms were randomly selected for each metric across both study regions and split into training (70%) and validation (30%) datasets. Separate RF models were fit for each metric at each landscape using 500 trees. We fit a range of classifiers with different combinations of predictors and selected the best-performing model based on its R2 and Root Mean Squared Error (RMSE) when applied to the validation dataset (see Table S2 for predictors used for each classifier and model performance metrics). The classifiers were then applied to remote sensing information from 2024 (our study year) to ensure that the canopy height and biomass layers temporally matched the biodiversity data collection period. Biomass was used as a standalone covariate for forest quality, whereas canopy height was used to calculate a forest structural connectivity metric.

Appendix S3 – Generating a circuit theory based forest structural connectivity metric

We quantified forest structural connectivity using the Omniscape algorithm (Landau et al., 2021; Mcrae et al., 2016), which estimates landscape connectivity by treating the landscape as a conductive surface and simulating current flow between all points. Unlike traditional connectivity metrics that focus on discrete core habitats, Omniscape considers connectivity between all points within the landscape continuously. This makes it particularly useful for assessing how mammal species respond to fine-scale alterations in connectivity within sites.

Omniscape requires three inputs: (1) A resistance/conductance layer, representing the cost of moving through a given landscape feature; (2) a moving window radius, which represents the species search distance for suitable habitat; and (3) a source strength raster, which for every pixel defines the relative amount of current to be injected (Landau et al., 2021). To generate the structural connectivity metric, the GEDI-derived canopy height layer was used as the conductance layer, based on the assumption that forests with taller canopies tend to be more intact (Bourgoin et al 2024), thus facilitating more movement pathways for species compared to more disturbed forests with lower canopies. As our metric aimed to capture the spatial continuity of forest habitat, the canopy height layers were processed so that non-tree cover pixels were assigned a conductance value of one based on the Sentinel-2 10-Meter Land Use/Land Cover layer. A moving window of 2.885km2 was used, which is the median home range size of the 16 species included in our analyses for which data is available (Broekman et al., 2023; Soria et al., 2021). Finally, JRC-TMF Annual Change data (Vancutsem et al., 2021) were used for the source weight raster, assigning a value of 10 to undisturbed forest pixels, 5 to degraded forest pixels, and 0 to non-forest pixels.

Appendix S4 – Producing a remoteness index across the study sites

To assess human pressure, we developed a remoteness metric, representing the travel cost from the nearest settlement, accounting for roads, topography and landcover. The remoteness layer was calculated using the distance accumulation tool in ArcGIS . Settlement data were obtained through the Indonesian government's Land cover layer and the Global Human Settlement Layer (Pesaresi et al., 2024). Landcover information was obtained from the Sentinel-2 10-Meter Land Use/Land Cover layer (Karra et al., 2021) for the year 2024. This was resampled to 30m and used to assign walking speeds for each landcover type based upon those calculated by Weiss et al. (Weiss et al., (2018).

Road and footpath data were obtained from OpenStreetMap (OpenStreetMap 2025). We additionally digitized known footpaths from our study areas and the new road under construction within the agroforestry-mosaic landscape. Speed values for different road types were assigned based on Indonesian national speed limits. For unpaved tracks, speed values were assigned based upon previously assessed average speeds for rural roads in tropical forest systems (e.g Yoh et al., 2024), given that many of the roads near our sampling locations were unpaved and of poor quality, thus rendering national speed limits unrealistic. The landcover and road travel time layers were then stacked, with speed values standardized to a walking speed of 5km/hr and inverted to generate a travel cost layer. Terrain slope was derived from SRTM data (Rabus al., 2003), and we applied Tobler's hiking function to reflect the variation in walking speeds of traversing different slopes (Tobler, 1993). Finally, we followed Deere et al., (2020) in setting slopes >30 degrees as barriers to access.

Appendix S5 Scale optimisation protocol

To ensure important associations are not missed, it’s important that environmental and anthropogenic covariates must be assessed at spatial scales relevant to the focal species. However, as the ecology of many tropical mammals is poorly understood, it is challenging to establish optimal spatial extents a priori (Niedballa et al., 2015). We therefore followed Deere et al (2020) in extracting covariates at five spatial scales around each camera trap location (circular buffer around the camera trap with radii of 50m, 100m, 150m, 250m and 500m) using the R package ‘terra’ (Hijmans et al. 2025. To identify the optimal spatial scale for each covariate, we constructed multi-species occupancy models for each of the unique combinations of covariates and spatial scales. As with the models reported in the main text, models were fit with landscape-specific intercepts and slopes. Model performance was compared using WAIC (Watanabe-Akaike Information Criterion; Watanabe; 2010), a measure of a model’s predictive power, where lower values indicate greater statistical support. For models of similar performance (difference in WAIC<2), we also assessed which scales species were generally most responsive to, based on whether the covariate had substantial community- or species-level associations with occupancy (i.e 95% BCI not overlapping 0), and selected models that had the greatest number of effects. This approach was first undertaken including a quadratic term for each covariate to assess for non-linear responses. If no substantial non-linear response was found, we repeated the process with only linear terms. Results of this scale optimization procedure are available in Supplementary Table 4.

Table S1: Mammal inventory comprising the 30 medium- to large-bodied species detected during the camera trap campaigns in Aceh and Bengkulu. Species excluded from occupancy analyses due to insufficient detections (<4) are shaded in grey (N=4). Species IUCN Red List status was obtained from IUCN (2025), with species listed as Vulnerable, Endangered or Critically Endangered categorised as threatened. Ecological specialisation data was obtained from Wilson et al (2010) and Ardiantiono et al., (2024). No. of detections refers to the number of individual 7 day sampling windows a species was detected in. Species excluded from occupancy analyses due to insufficient detections (<4) are shaded in grey (N=4).

Species	Species code	IUCN Red List status	Threat status	Ecological specialisation	No. of detections
Asian Elephant *Elephas maximus*	ASE	Vulnerable	Threatened	Forest Specialist	18
Asian Golden Cat *Catopuma temminckii*	AGC	Vulnerable	Threatened	Forest Specialist	44
Banded Civet *Hemigalus derbyanus*	BCI	Near Threatened	Non-threatened	Forest Specialist	45
Banded Linsang *Prionodon linsang*	BLI	Least Concern	Non-threatened	Forest Specialist	78
Binturong *Arctictis binturong*	BIN	Vulnerable	Threatened	Forest Specialist	24
Collared Mongoose *Urva semitorquata*	-	Near Threatened	Non-threatened	Generalist	2
Dhole *Cuon alpinus*	DHO	Endangered	Threatened	Forest Specialist	4
Long-tailed Macaque *Macaca fascicularis*	LOM	Endangered	Threatened	Generalist	5
Mainland Serow *Capricornis sumatraensis*	MAS	Vulnerable	Threatened	Forest Specialist	9
Marbled Cat *Pardofelis marmorata*	MAC	Near Threatened	Non-threatened	Forest Specialist	44
Masked Palm Civet *Paguma larvata*	MPC	Least Concern	Non-threatened	Generalist	77
Moonrat *Echinosorex gymnura*	MOO	Least Concern	Non-threatened	Forest Specialist	42
Mouse Deer spp. *Tragulus spp.*	MDE	Least Concern	Non-threatened	Forest Specialist	124
Pig-tailed Macaque *Macaca nemestrina*	PIM	Endangered	Threatened	Generalist	385

Porcupine sp. *Hystrix spp.*	POR	Least Concern	Non-threatened	Generalist	210
Red Muntjac *Muntiacus muntjak*	REM	Least Concern	Non-threatened	Generalist	208
Sambar *Rusa unicolor*	SAM	Vulnerable	Threatened	Forest Specialist	25
Small-toothed Palm Civet *Arctogalidia trivirgata*	-	Least Concern	Non-threatened	Forest Specialist	2
Sumatran Hog Badger* *Arctonyx hoevenii*	SHB	Least Concern	Non-threatened	Forest Specialist	15
Sumatran Striped Rabbit *Nesolagus netscheri*	-	Data Deficient		Forest Specialist	3
Sun Bear *Helarctos malayanus*	SUB	Vulnerable	Threatened	Forest Specialist	72
Sunda Clouded Leopard *Neofelis diardi*	SCL	Vulnerable	Threatened	Forest Specialist	28
Sunda Leopard Cat *Prionailurus javanensis*	-	Not evaluated		Generalist	2
Sunda Pangolin *Manis javanica*	SUP	Critically Endangered	Threatened	Generalist	23
Sunda Stink Badger *Mydaus javanensis*	SSB	Least Concern	Non-threatened	Generalist	11
Thomas's Langur *Presbytis thomasi*		Vulnerable	Threatened	Forest Specialist	1
Tiger *Panthera tigris*	TIG	Critically Endangered	Threatened	Forest Specialist	11
Wild Boar *Sus scrofa*	WIB	Least Concern	Non-threatened	Generalist	222
Yellow-handed Mitered Langur* *Presbytis melalophos*	YML	Endangered	Threatened	Generalist	6
Yellow-throated Marten *Martes flavigula*	YTM	Least Concern	Non-threatened	Generalist	36

*The two species in our analysis not present in either of those studies (Yellow-handed Mitered Langur *Presbytis melalophos and Sunda Stink Badger Mydaus javanensis*) were listed as generalists given that their IUCN Red List accounts state that they can tolerate a degree of habitat conversion and have been found in plantations (IUCN 2025b; IUCN 2025c; see table xx for species' classifications).

Table S2 – Predictors and performance of forest structural random forest models

Metric	Location	Predictors					R2	Root mean square error (RMSE)	Range normalised RMSE
		Landsat 8 spectral imagery+	**Sentinel Radar imagery**	**Forest condition**	**Terrain**	**Vegetation indices**			
Biomass	Aceh	Band 1 - Band 7*	VV and VH ascending, VV and VH descending	JRC-TMF Annual change 2021	Elevation, aspect, slope, TRI	ARVI	0.29	148.19	23.32%
	Bengkulu	Band 1 - Band 7	VV and VH ascending, VV and VH descending	JRC-TMF Annual change 2019	Elevation, aspect, slope, TRI	ARVI	0.38	135.65	26.79%
Canopy Height	Aceh	Band 1 - Band 7	VV and VH ascending, VV and VH descending	JRC-TMF Annual change 2021	Elevation, aspect, slope, TRI	EVI	0.38	10.9	19.19%
	Bengkulu	Band 1 - Band 7	VV and VH ascending, VV and VH descending	JRC-TMF Annual change 2019	Elevation, aspect, slope, TRI	ARVI	0.47	10.17	17.73%

*Landsat -8 bands represent: Band 1 (Coastal aerosol), Band 2 (Blue), Band 3 (Green), Band 4 (Red), Band 5 - Near Infrared (NIR), Band 6 (Shortwave Infrared (SWIR) 1), Band 7 - (Shortwave Infrared (SWIR) 2)

Table S3 – Bayesian p-values used to assess model fit. P-values of 0.5 indicate perfect agreement between observed and simulated data. P-values between 0.1-0.9 indicate adequate model fit. In bold are mean Bayesian p-values across all species.

Species	Bayesian p-values					
	Management type	Connectivity	TRI	Biomass	Access	Forest Cover
Community Mean	**0.451**	**0.452**	**0.456**	**0.451**	**0.444**	**0.451**
Asian Elephant	0.466	0.466	0.459	0.456	0.451	0.453
Asian Golden Cat	0.468	0.474	0.461	0.466	0.476	0.472
Banded Civet	0.536	0.553	0.543	0.536	0.518	0.550
Banded Linsang	0.511	0.518	0.515	0.521	0.528	0.524
Binturong	0.525	0.507	0.512	0.509	0.529	0.509
Dhole	0.691	0.699	0.694	0.695	0.691	0.692
Long-tailed Macaque	0.575	0.579	0.570	0.570	0.571	0.578
Mainland Serow	0.523	0.510	0.518	0.512	0.530	0.518
Marbled Cat	0.380	0.379	0.385	0.385	0.390	0.385
Masked Palm Civet	0.398	0.400	0.396	0.398	0.412	0.402
Moon Rat	0.525	0.507	0.526	0.526	0.498	0.513
Mouse Deer spp.	0.589	0.588	0.583	0.590	0.586	0.604
Pig-tailed Macaque	0.467	0.478	0.479	0.463	0.460	0.474
Porcupine sp.	0.439	0.444	0.438	0.434	0.465	0.446
Red Muntjac	0.549	0.551	0.564	0.558	0.558	0.556
Sambar	0.428	0.434	0.421	0.424	0.432	0.429
Sumatran Hog Badger	0.443	0.451	0.453	0.462	0.456	0.451
Sun Bear	0.406	0.413	0.416	0.413	0.414	0.404
Sunda Clouded Leopard	0.521	0.523	0.520	0.525	0.504	0.527
Sunda Pangolin	0.502	0.504	0.513	0.523	0.492	0.506
Sunda Stink Badger	0.405	0.399	0.408	0.410	0.398	0.393
Tiger	0.431	0.438	0.421	0.428	0.424	0.427
Wild Boar	0.390	0.385	0.393	0.393	0.383	0.384
Yellow-handed Mitered Langur	0.454	0.467	0.454	0.464	0.447	0.458

Yellow-throated Marten	0.599	0.611	0.612	0.607	0.616	0.601

Table S4 Results of scale optimisation procedure. Highlighted are the models and spatial scales included in the second set of models.

Continuous covariate	***Spatial scale (m)***	***WAIC***	***bpv***
Connectivity	50	10266.563	0.472
	100	**10252.199**	**0.465**
	150	10252.524	0.467
	250	10255.430	0.471
	500	10255.288	0.481
TRI	50	10399.488	0.472
	100	10363.559	0.475
	150	10343.715	0.480
	250	**10339.783**	**0.490**
	500	10355.770	0.488
Biomass	50	10368.271	0.507
	100	10347.175	0.505
	150	10332.567	0.511
	250	**10331.237**	0.505
	500	10338.459	0.496
Remoteness (quadratic)	50	10245.888	0.453
	100	10248.277	0.445
	150	10250.067	0.449
	250	**10238.282**	**0.447**
	500	10244.901	0.446
Forest Cover	50	10474.049	0.493
	100	10458.281	0.498
	150	10447.968	0.487
	250	10404.371	0.485
	500	**10357.594**	**0.494**

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