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ORIGINAL RESEARCH

Persistence of medium- and large-sized mammals in an oil palm-dominated landscape of Sarawak, Malaysian Borneo

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Abstract
Forest mammals in Sarawak are at risk of local extinction from habitat fragmentation. Remnant forests on oil palm estates are important refugia for mammal metapopulations. Metapopulation persistence depends on species' ability to traverse the oil palm matrix. Using camera traps, we examined the occupancy of medium- to large-mammals in six forest fragments (range = 29–990 ha) and the oil palm matrix in northern Sarawak. The forest fragments collectively contained 22 of 24 mammal species occurring in the nearby Lambir Hills National Park, including three megafauna species (Sun bear *Helarctos malayanus*; Sambar deer *Rusa unicolor*, Bearded pig *Sus barbatus*). Species occupancy and richness increased with forest area and declined with distance from forest into oil palm, except for the mesopredators, the Sunda leopard cat (*Prionailurus javanensis*) and common palm civet (*Paradoxurus hermaphroditus*), whose occupancy remained constant. Mostly larger species displayed a transient presence up to 1 km into oil palm, including the pig-tailed macaque (*Macaca nemestrina*), sambar deer (*Rusa unicolor*), and bearded pig (*Sus barbatus*). Forest-dependent species, including mouse deer (*Tragulus* spp.) and banded civet (*Hemigalus derbyanus*), were rarely observed in oil palm. Source-sink population dynamics appear to determine metapopulation persistence of dietary generalists and mesopredators in oil palm plantations. Retention of forest habitat on oil palm estates improves habitat heterogeneity, enhancing connectivity (forests < 1 km apart), securing forest biodiversity and ecological functions that benefit plantations.

Keywords Oil palm · Mammals · Forest fragments · Occupancy · Distance gradient · Species persistence · Connectivity · Metapopulations

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Original research article Targets conservation biologists interested in the management and conservation ecology of medium- and large-size forest mammals on oil palm estates.

Extended author information available on the last page of the article

Introduction

Unprecedented habitat loss and fragmentation caused by urban and agricultural expansion are the main current threats to biodiversity, especially endemic lowland tropical rainforest species (Rautner 2005; Ocampo-Peñuela et al. 2020; Zou et al. 2025). In general, large-scale agricultural monocultures, such as timber plantations, tea and coffee plantations, sugarcane and oil palm, are a leading cause of a decline in biodiversity (Laurance et al. 2014; Gonçalves-Souza et al. 2020; Kong et al. 2021; Suarez and Gwozdz 2023). Land clearing for agriculture, especially the increasing demand for palm oil (Abram et al. 2016), has resulted in devastating levels of deforestation (Koh and Wilcove 2008). Large-scale total clearance of native vegetation for oil palm plantations, prevents recovery of natural ecosystems and their biodiversity (Sala et al. 2000; Sodhi et al. 2004; Koh et al. 2023; Zou et al. 2025). The persistence of at least some mammal species depends on the retention and management of small forest refugia in oil palm dominated landscapes. Borneo is home to 247 species of terrestrial mammals, of which 26% are considered endemic (Phillipps and Phillipps 2018). Here we examine what medium- and large-size mammal species are most likely to persist in oil palm dominated landscapes.

Malaysia, the second largest palm oil producer worldwide (Statista 2025), has saturated its productive arable areas with oil palm. Sarawak contains the largest planted area (1.6 million ha) of oil palm in Malaysia, contributing approximately 21% to total production (MOPB 2025). Palm oil is an economically important crop that has rapidly expanded in tropical regions, often replacing traditional agricultural systems (Tan et al. 2009; Roberts 2013; Kim 2023). This expansion, driven by sustained global demand, has altered landscapes and affected local communities, including wildlife that depend on forest resources for their livelihoods (Koh and Wilcove 2008; Laurance et al. 2014). In addition to the loss of forest habitat, large-scale plantations intensify edge effects (Murcia 1995; Willmer et al. 2022) in the remaining forest patches, which may further reduce biodiversity (Slater et al. 2024) by preventing movement into the oil palm matrix. These effects of oil palm expansion have fueled a growing awareness for environmentally friendly and sustainable management practices on existing oil palm estates (Naidu and Moorthy 2021), and the optimization of production on land already converted to oil palm to minimize further expansion (Fitzherbert et al. 2008; Koh and Wilcove 2009). Conserving terrestrial mammals in forest fragments, and the challenges of implementing effective conservation strategies in oil palm dominated landscapes, are becoming increasingly urgent with oil palm expansion (Numata et al. 2005; Azhar et al. 2014; Pardo et al. 2018, 2019; Kasper et al. 2024).

Improving the connectivity of forest patches while maintaining oil palm yield (Oon et al. 2023), as well as retaining patches of native vegetation on existing oil palm estates (Zemp et al. 2023), have proven effective ways of managing biodiversity in oil palm landscapes. Understanding how biodiversity can be retained, as well as the movement ecology of wildlife on large-scale oil palm plantations, enables sensible direct conservation management (Fitzherbert et al. 2008; Puttick et al. 2024). Studies show a steep decline in mammal species occupancy and richness from forest to oil palm (Fitzherbert et al. 2008). Nevertheless, several 'forest' species can survive within oil palm plantations, for example the Sunda Leopard Cat (*Prionailurus javanensis*), Malay Stink Badger (*Mydaus javanensis*) (Kwatrina et al. 2018), Long-tailed Macaque (*Macaca fascicularis*) (Kurniawan et al. 2023), Smooth Coated Otter (*Lutrogale perspicillata*), and Asian Small-clawed Otter (*Aonyx cinereus*)

(Pianzin et al. 2019). These dietary generalists use the oil palm alongside forest fragments because suitable foods and/or prey are available there (Prugh et al. 2009; Pardo et al. 2018). Accordingly, mesopredators and generalist species are predicted to use oil palm and have better persistence than forest specialist species, for whom oil palm is inhospitable habitat and their occupancy is expected to decline significantly with distance into the oil palm.

In general, mammals are good indicators of forest ecosystem function and integrity (Caro 2010; Ahumada et al. 2011; Luzar et al. 2011) as they are directly affected by habitat fragmentation to agricultural expansion and urban development (Dirzo et al. 2014). Medium to large mammals are good indicators of habitat quality because of their resource requirements, mobility, and relatively large home ranges (Barlow et al. 2007; O'Brien et al. 2010). Although oil palm plantations support some medium-sized mammals, most species are extirpated from especially large plantations that retain little native vegetation (Cardillo et al. 2005; Danielsen et al. 2009). In Sarawak, most oil palm plantations aim to restore remnant habitat and retain high conservation value forest fragments to the mutual benefit of the plantation and native wildlife. For example, the Sunda leopard cat, commonly found in oil palm plantations, benefits oil palm production by feeding on rodents, which are regarded as pests in oil palm nurseries (Pinnamaneni and Potineni 2023; Narayana et al. 2024). Conversely, small mammal diversity on plantations is important for maintaining predators in the landscape (Jennings et al. 2015; Mohd-Azlan et al. 2019). Consequently, determining what medium- and large-size mammal species persist in oil palm dominated landscapes is important for developing appropriate conservation management strategies (Dotta and Verdade 2011). Here we address the following: (1) what medium to large-size (0.5–35 kg) mammals occupy oil-palm plantations and their associated forest patches; and (2) we examine the forest-oil palm boundary dynamics of these species. Our aim is to determine the extent to which the persistence of these medium- to large-size mammals is dependent on the remaining small forest patches on oil palm estates. As oil palm provides a structurally and compositionally simpler habitat than the adjacent forest, we expected that common generalist species would persist in the plantations while specialist species would not. In addition, because oil palm estates cover very large areas (1000's ha) and forest patches are few and far between, we expected to find larger, or more mobile, generalist forest mammals in the oil palm plantations.

Methods

Study site

This study was conducted on five oil palm estates (Saremas 1, Saremas 2, Segarmas, Kaminsky and Suai estates) of Wilmar Plantations Sdn Bhd (WPSB) in Miri, Sarawak (1.5533°N, 110.3592°E) (Fig. 1). WPSB is MSPO (Malaysian Sustainable Palm Oil), ISCC (International Sustainability and Carbon Certification), and RSPO (Roundtable of Sustainable Palm Oil) certified. Within the plantations are local villages, staff housing, offices, and plantation mills. The plantation is closely guarded from oil palm theft and hunting on the estate is strictly controlled by WPSB. All entry points are monitored 24 h a day. Patrolling is done near the living quarters. Thus, the plantation estate is better protected than some national parks and hunting pressure on mammals is low. The five oil palm estates comprise

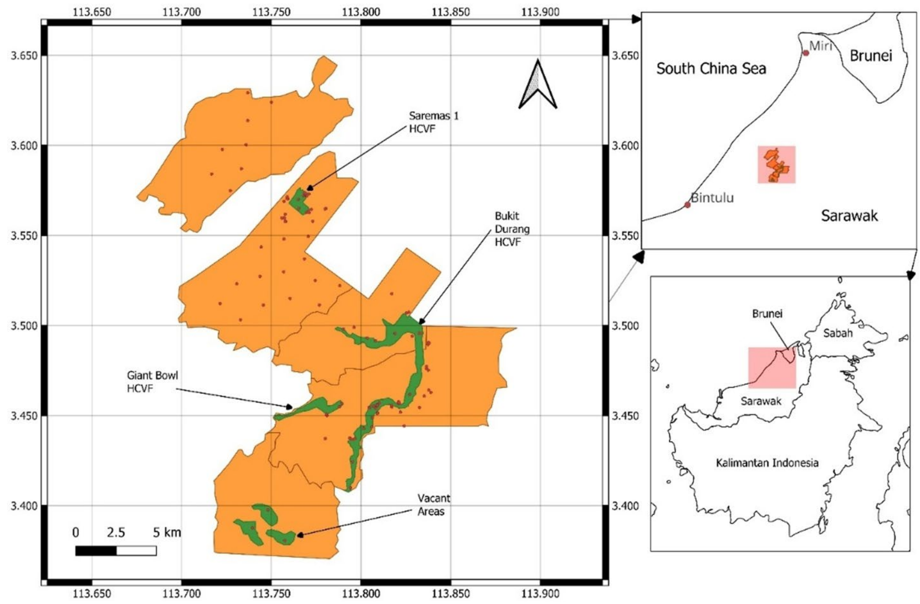

Fig. 1 Location of study sites in the Wilmar Plantations Sdn Bhd in Miri, northern Sarawak. The red points represent the cameras, the green shaded areas are the forest fragments, and the orange shaded areas display the oil palm plantations. Vacant areas are forested areas not declared as HCV

26,512 ha of established oil palm. The estates are surrounded by agricultural land, such as small-holder oil palm plantations, durian orchards, and agroforestry. High conservation value forests (HCVF) cover 9.7% of the WPSB oil palm concession area. HCVF are defined by the Forest Stewardship Council (FSC) (Jennings et al. 2003) and incorporated into the Roundtable for Sustainable Palm Oil (RSPO) guidelines, which mandate the maintenance of HCVF areas within oil palm concessions. HCVFs are typically categorized based on their provision of essential ecosystem services, high biodiversity values, or the presence of habitats supporting endangered or endemic species (Senior et al. 2015), and require management and protection to maintain or enhance these critical values.

The WPSB Miri plantation includes three registered HCVFs. Bukit Durang is the largest of these forest fragment at 990 ha and has been logged over in the past (Mohd-Azlan and Shafreena 2023). Giant Bowl HCVF is 148 ha, and Saremas 1 is 116 ha. Bukit Durang forest cover is continuous along a ridge in the shape of a horseshoe and is long and narrow with little core forest. Forest fragments are secondary forest comprising tree species from the *Euphorbiaceae*, *Leguminosae*, *Moraceae*, but mostly the *Dipterocarpaceae*. Both Bukit Durang HCVF and Saremas 2 HCVF are on steep slopes, while Saremas 1 HCVF is relatively flat. Three smaller clustered forest fragments named 'vacant areas' (28.7 ha, 51.8 ha and 89.7 ha) were also surveyed. These are categorized by the oil palm estate managers as "vacant areas" (Fig. 1). Mean annual rainfall is approximately 3000 mm. Twelve rivers flow through WPSB, all draining into the Suai River. The nearest protected area is the recently designated World Heritage site, Niah National Park, 13.5 km away, and the long established Lambir Hills National Park, ~60 km away. Niah National Park is a 3139 ha protected area established in 1974. Lambir Hills National Park covers 6949 ha and was gazetted in 1975. Both national parks represent long-established, relatively intact forest refugia.

Forest fragments within oil palm estates tend to be on steep slopes, alongside rivers, or around human settlements. Road edges within the plantation are typically colonized by herbaceous plants, such as crepe ginger (*Cheilocostus speciosus*), nettleleaf velvetberry (*Stachytarpheta urticifolia*), African coromandel (*Asystasia intrusa*), Praxelis (*Praxelis clematidea*), false ironwart (*Hyptis capitata*), Sida (*Sida spp*.), and an abundance of Koster's curse (*Miconia crenata*). After trimming old palm fronds, these are laid alongside roads and terraces where insects and rodents use them for food and shelter. The extent and composition of native understory vegetation within oil palm plantations depends on the location and age of the oil palm, and the application of herbicide. However, the understory within the oil palm plantation is usually cleared of native vegetation and there is very little ground cover.

Data collection

We sampled medium- to large-size (≥500 g) terrestrial (as opposed to arboreal) mammals using camera traps, including four domestic species, to determine species occupancy trends with distance into oil palm from the forest edge. Bushnell Trophy HD and Reconyx Hyperfire HC500, passive infra-red cameras were used. Camera traps were placed 25–30 cm above the ground, operated continuously through the day and night and rotated among forests every four months following Mohd-Azlan et al. (2018). Sampling was initially conducted over fifteen months from September 2013 through January 2015 using sixty camera traps over 5,199 trapping nights. A second sampling campaign was conducted at the same locations over 14 months from November 2018 to February 2020. A total of seventy camera traps were placed in WPSB during the second sampling campaign (Fig. 1). Camera traps were rotated among the six fragments with the number traps proportional to forest area (although this was affected by site accessibility). Cameras were placed at the following distances: 50 m, 100 m, 200 m, 300 m, 500 m, 1000 m, 2000 m, 3000 m, 4000 m, and 5000 m into oil palm and 100 m, 200 m, 300 m, and 400 m into the forest; along transects spaced 1 km apart to retain spatial independence (Mohd-Azlan et al. 2018; Kays et al. 2020). Only mature oil palm plantations (> 10 y) were surveyed because areas undergoing active replanting are recently cleared, heavily disturbed by machinery, and largely devoid of understory vegetation, while mature oil palm represents the dominant plantation age class across the study landscape. Cameras were placed in oil palm along functional movement routes (e.g., harvesting paths, drainage lines and frond piles), rather than indiscriminately between rows, to mirror trail-based camera placement used in the forest habitat. We restricted sampling to mature oil palm (> 10 years old). Photograph organization, storage and preliminary analyses were supported by software developed by Sanderson and Harris (2013).

Data analysis

The number of detections of each species at each site formed the basis of the data. We compare species richness because it is a simple and effective measure of community and regional diversity (Magurran 1988; Purvis and Hector 2000; Yoccoz et al. 2001). The species accumulation curves (SAC) were constructed to examine the relationship between sampling effort and the observed species richness. SACs for each habitat (oil palm, forest and edge) and overall were generated using the *specaccum()* function in the R "vegan" package (Oksanen et al. 2018). Rarefaction analysis using the function *rarecurve()*, with random permutations (without replacement), demonstrated that adequate sampling saturation was reached for each habitat (forest, edge, oil palm). Chao2, Jackknife 1, Jackknife 2, and bootstrapping were used to estimate the completeness of our species richness estimates. Chao2 is based on multiple sampling units (camera traps) from several surveys and is better suited than Chao1 to our data. The Chao2 estimator of species richness uses rare observations to predict how many species might have been missed during sampling, by comparing the number of species found in only one sample (uniques), with species found in only two samples (duplicates). For Jackknife 1 and 2, resampling is used to estimate bias and variance, along with bootstrapping, which uses the observed frequency of all species to estimate missing species. These indices were calculated using the *specpool()* function in R package "vegan" (Fisher et al. 1943; Heltshe and Forrester 1983; Smith and Van Belle 1984).

To ensure a unified robust assessment of diversity and evenness for comparison among assemblages, we used species richness estimates derived from Hill's family of diversity numbers (Broms et al. 2015; Maturo and Di Battista 2018). Hill's N0 is the total number of species recorded at sample saturation or the species accumulation asymptote (S). Hill's N1 is $e^{H'}$, where H' is the Shannon Weiner diversity index, and provides the effective number of equally common species. Hill's N2 is $1/\lambda$, where λ is Simpsons evenness index and represents the effective number of dominant or very abundant species (Hill 1973; Jost 2007; Chao et al. 2020). Species richness was estimated for each distance along the sampling transect, from 400 m into the forest to 5000 m into the oil palm and species richness -distance gradient trends were modelled using linear regression (Lucey et al. 2014) and visualized using ridge plots in the ggridges package (Wilke and Wilke 2022).

Naïve occupancy (ψ) was calculated as the ratio of sites where a species was detected to the total number of sites surveyed, without accounting for imperfect detection probabilities (Kéry and Royle 2020). This metric is commonly used to determine simple species occurrence from presence/absence data and is frequently used alongside other more powerful occupancy models (Rovero et al. 2014; Neilson et al. 2018). Occupancy-based Hill's numbers were calculated following (Broms et al. 2015) to account for imperfect detection. (Curveira-Santos et al. 2021) used occupancy-based site-specific diversity indices to compare effective richness with posterior values from different sites. In our case, Multi-Species Occupancy Models (MSOM) were used to estimate the likelihood of species occupancy ($\widehat{\psi}$) *f*rom binary presence/absence data, while accounting for imperfect detection through sampling replication (Kéry and Royle 2016; Tingley et al. 2020; Mourguiart et al. 2021). Species level occupancy probabilities $\left(\widehat{\psi}\right)$ in each habitat, and the occupation probability $\left(\widehat{\psi}\right)$ of N1 and N2 were compared across habitats. The "jagsUI" package was used for Bayesian analyses (Kéry and Royle 2016) of species-specific models, with random effects, organized into a 3-D array for each species based on the total number of sampling days in the study.

The MSOMs used here represent hierarchal models. The ecological process was modeled as the true presence/absence of species (k) at site (i) as a Bernoulli trial probability (ψ_k). The observation process modelled the true occupancy state of species (k) following a Bernoulli distribution. In the MSOMs, the community-level hyperpriors were fixed with a uniform distribution $\mu \sim Uniform\ (0, 1)$ for mean occupancy and detection probabilities, and $\sigma \sim Uniform\ (0, 0.2)$ or the standard deviations. The priors are non-informative, allowing the data to dictate the outcome of the posterior estimates. The species level parameters were modeled on a binomial distribution using a logit scale. The data and selected parameters were subjected to Markov Chain Monte Carlo (MCMC) simulations until convergence was reached for the posterior summaries.

Results

The data comprised 32,876 images, 5,267 of which were independent detections (n) based on 60-minute intervals following Azlan (2006) (forest = 3154; oil palm = 1184; edge = 929), from 13,098 camera trap nights (forest = 5,099; oil palm = 5,826; edge = 2,173). Species accumulation curves show that in this study, at least 8,000 camera trap nights were required for species accumulation to asymptote (Fig. 2). Nevertheless, sampling saturation was satisfactory in all habitats with an overall completeness estimate of 0.673 (Table 1). The edge was less completely sampled (completeness = 0.565) than forest (0.949) and the oil palm (0.601). Based on rarefacted species accumulation curves, fewer mammal species were found in oil palm compared with the edge and forest (Fig. 2). Overall, twenty-five species of medium- to large-mammals (excluding four domestic species) were detected from thirteen families, with observed richness lower in oil palm than in edge and forest (Table 2; forest = 22 species; oil palm = 20; edge = 22). Three species were detected only in the oil palm (masked palm civet *Paguma larvata*, collared mongoose *Urva semitorquata*, Malay weasel *Mustela nudipes*), leaving 22 species detected in forest. The four domestic species that were observed in all habitats were (IUCN 2026): domestic dog (*Canis lupus familiaris*), domestic cat (*Felis catus*), pig (*Sus scrofa domestica*), and domestic water buffalo (*Bubalus bubalis*). One unidentified otter species was included in the total species observed (Table 2). Three species are listed as near threatened (NT) (IUCN 2026): marbled cat (*Pardofelis marmorata*), collared mongoose (*Urva semitorquata*), and banded palm civet (*Hemigalus der-*

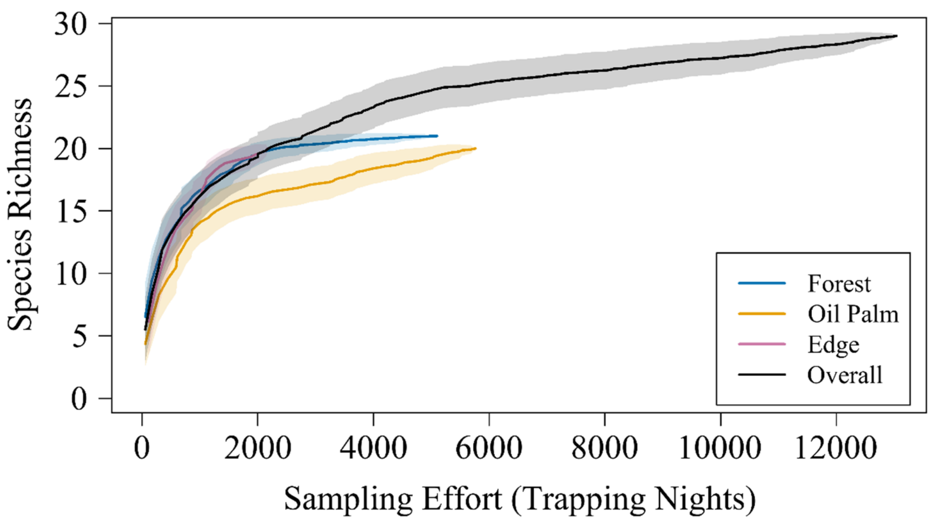

Fig. 2 Species accumulation curves for the different ecotypes or habitats surveyed in the Perlis Plantations Berhad Oil Palm Plantation in Miri. Shaded areas represent the 95% confidence interval

Table 1 Summary of species richness estimators for each habitat and overall, and naïve and occupancy-adjusted Hill's numbers (excluding domestic species)

Habitat	Obs	Richness estimators					Hills (Naïve)		Hills (Occupancy)	
		Chao2	Jack1	Jack2	Boot	Prop. Compl.	N_1	N_2	$\widehat{N_1^{\psi}}$	$\widehat{N_2^{\psi}}$
Overall	25	37.16	31.94	36.88	27.88	0.673	12.67	10.04	22.41	20.00
Forest	18	18.97	19.96	20	19.01	0.949	12.18	10.03	12.72	10.11
Edge	18	29.93	22.77	26.45	20.09	0.601	12.17	9.81	14.00	11.26
Oil Palm	16	28.3	20.92	24.8	17.96	0.565	9.53	7.22	10.84	7.59

Obs = observed number of species in the habitat. Prop. Compl. = proportional completeness of richness estimate

byanus); and four species as vulnerable (VU): the sun bear (*Helarctos malayanus*), bearded pig (*Sun barbatus*), maroon langur (*Presbytis rubicunda*), and sambar deer (*Rusa unicolor*). We observed two endangered primate species (EN): long-tailed macaque (*Macaca fascicularis*), pig-tailed macaque (*Macaca nemestrina*); and one critically endangered (CR) species, Sunda pangolin (*Manis javanica*) (Table 2).

Effects of area and sampling effort on species richness

The number of mammal species detected in the forest fragments was affected by fragment area and sampling effort (Table 3). Although sampling effort was roughly proportional to the area of the forest fragment, Saremas1 (116 ha) was sampled more intensively than others in relation to its size, and more species were observed there than in Giant Bowl (148 ha), which was of roughly the same area (Table 3). Nevertheless, these sampling discrepancies are ecologically instructive. They show that even with much greater sampling effort a clear area-effect on species richness persists, with only a few common forest generalist species added with more effort. The clear area effect followed an expected trend with most species detected in the largest forest fragment—Bukit Durang (990 ha)—and the least species detected in the small "vacant area" forests (29–90 ha) (Table 3).

Species richness in the habitats

Richness estimates exceeded the observed richness, indicating some species likely went undetected during sampling (Table 1). Several relatively common species went undetected because of their cryptic nature or distribution limitations, for example the two muntjac species (*Muntiacus spp.*) and Sunda stink badger (*Mydaus javanensis*), short-tailed mongoose (*Urva brachyura*), and the Sunda clouded leopard (*Neofelis diardi*). Overall $\widehat{N_1^{\psi}}$ and $\widehat{N_2^{\psi}}$ were much larger than the naïve estimates, emphasizing the effect of imperfect detection on estimating species richness. Both oil palm N_2 and $\widehat{N_2^{\psi}}$ estimates were substantially less than all other habitats, indicating that a subset of dominant species consistently enter the oil palm. Similarly, much lower estimates of the common species, derived from N_1 and $\widehat{N_1^{\psi}}$, were observed in the oil palm, showing a peak at the edge (Table 1). This reflects that edges are transitional zones.

Table 2 List of species found in each habitat, ordered by most to least detections overall (Naïve occupancy). The overall likelihood of occupancy derived from Multi-Species Occupancy Models (MSOM) are provided for comparison. IUCN status is indicated by "*" for protected and "**" for fully protected species under the wildlife protection ordinance (WPO) in Sarawak

Scientific name	Common name	Naïve Occup.	MSOM occup.	Forest/Edge/Oil palm	Forest/Edge only	Edge only	Oil palm only	>2 km into Oil palm
Macaca nemestrina (EN)	Sunda Pig-tailed Macaque*	0.649	0.404 ± 0.032	X				
Prionailurus javanensis (LC)	Sunda Leopard Cat*	0.595	0.382 ± 0.032	X				X
Hystrix crassispinis (LC)	Borneo Thick-spined Porcupine*	0.405	0.275 ± 0.028	X				X
Viverra tangalunga (LC)	Malay Civet*	0.389	0.283 ± 0.030	X				
Rusa unicolor (VU)	Sambar Deer	0.366	0.270 ± 0.029	X				
Macaca fascicularis (EN)	Long-tailed Macaque*	0.344	0.256 ± 0.029	X				
Sus barbatus (VU)	Bearded Pig	0.305	0.234 ± 0.027	X				X
Manis javanica (CR)	Sunda Pangolin*	0.137	0.169 ± 0.024	X				X
Paradoxurus hermaphroditus (LC)	Common Palm Civet*	0.13	0.160 ± 0.022	X				
Tragulus napu (LC)	Greater Mousedeer	0.122	0.146 ± 0.020		X			
Hystrix brachyura (LC)	Malayan Porcupine*	0.122	0.149 ± 0.020	X				
Hemigalus derbyanus (NT)	Banded Palm Civet*	0.076	0.130 ± 0.018		X			
Trichys fasciculata (LC)	Long-tailed Porcupine*	0.076	0.133 ± 0.019	X				
Helarctos malayanus (VU)	Sun Bear*	0.046	0.125 ± 0.019	X				
Tragulus kanchil (LC)	Lesser Mousedeer	0.038	0.121 ± 0.018		X			
Prionodon linsang (LC)	Banded Linsang*	0.023	0.116 ± 0.018		X			
Pardofelis marmorata (NT)	Marbled Cat**	0.015	0.112 ± 0.017		X			
Paguma larvata (LC)	Masked Palm Civet*	0.015	0.113 ± 0.017				X	X
Urva semitorquata (NT)	Collared Mongoose*	0.008	0.109 ± 0.017				X	
Otter spp.	Otter spp.	0.008	0.109 ± 0.017			X		
Mustela nudipes (LC)	Malay Weasel	0.008	0.108 ± 0.017				X	
Martes flavigula (LC)	Yellow-throated Marten	0.008	0.109 ± 0.017			X		
Arctogalidia trivirgata (LC)	Small-toothed Palm Civet*	0.008	0.109 ± 0.017			X		
Presbytis rubicunda (VU)	Maroon Langur**	0.008	0.109 ± 0.017		X			
Echinosorex gymnurus (LC)	Moonrat	0.008	0.108 ± 0.017			X		

Table 3 Species detected in the surveyed forest fragments, showing the relative effects of area and sampling effort

Forest patch	Bukit Durang	Giant Bowl	Saremas1	Vacant1	Vacant2	Vacant3
Forest area (ha)	990	148	116	29	90	51
Camera hours	3579	216	1042	134	135	135
Sampling effort (h/ha)	3.62	1.46	8.98	4.62	1.5	2.65
Species	*Helarctos malayanus*					*Helarctos malayanus*
	Hemigalus derbyanus					
	Hystrix brachyura	*Hystrix brachyura*	*Hystrix brachyura*			
	Hystrix crassispinis		*Hystrix crassispinis*			*Hystrix crassispinis*
	Macaca fascicularis	*Macaca fascicularis*	*Macaca fascicularis*			
	Macaca nemestrina	*Macaca nemestrina*	*Macaca nemestrina*			*Macaca nemestrina*
	Manis javanica		*Manis javanica*			
	Pardofelis marmorata					
	Presbytis rubicunda					
	Prionailurus javanensis	*Prionailurus javanensis*	*Prionailurus javanensis*		*Prionailurus javanensis*	
	Prionodon linsang					
	Rusa unicolor		*Rusa unicolor*		*Rusa unicolor*	
	Sus barbatus		*Sus barbatus*		*Sus barbatus*	
	Tragulus napu		*Tragulus napu*			
	Trichys fasciculata		*Trichys fasciculata*			
	Viverra tangalunga	*Viverra tangalunga*	*Viverra tangalunga*		*Viverra tangalunga*	
			Tragulus kanchil			
			Paradoxurus hermaphroditus			
		Urva semitorquata				
	Martes flavigula					
	Otter sp.					
	Echinosorex gymnura					

Table 3 (continued)

Forest patch	Bukit Durang	Giant Bowl	Saremas1	Vacant1	Vacant2	Vacant3
	Arctogalidia trivirgata					
	Paguma larvata					

Bold text refers to species observed only in the oil palm

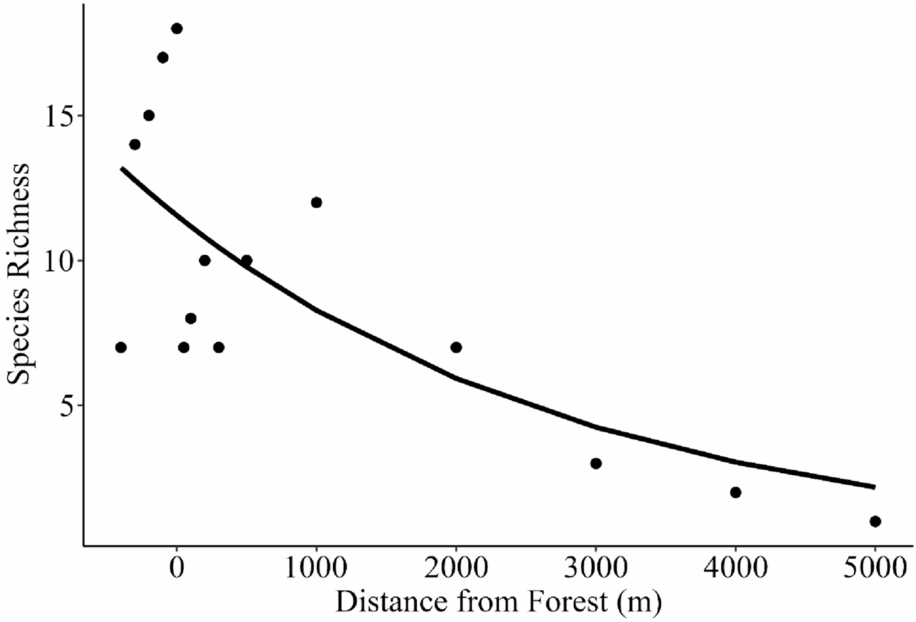

Fig. 3 The exponential decay model provided the best fit for species richness and distance from forest (R^2 = 0.53, AIC = 40.8). This plot shows the decline in species richness (excluding domestic species) with distance from the forest (negative values) forest-oil palm edge (0) into the oil palm plantation (positive values) (r = -0.747, P < 0.032)

Species occupancy with distance into the oil palm

There was a significant decline in species richness with increasing distance from the forest into the oil palm (r = −0.747, P = 0.032; Fig. 3). Most of the species detected in the oil palm were observed within 1 km (85% of detections) of the forest edge, however, many did not penetrate beyond 300 m into the oil palm plantation, and four forest species (lesser mousedeer *Tragulus kanchil*, maroon leaf monkey *Presbytis rubicunda*, banded palm civet *Hemigalus derbyanus* and marbled cat *Pardofelis marmorata*) were not observed in oil palm plantations (Fig. 4). While 10 species were regularly observed beyond 1 km into the oil palm (Fig. 4), only seven species were found beyond 2 km into the oil palm (Table 2), including Sunda leopard cat, domestic dog, Malay civet (*Viverra tangalunga*), domestic cat, common palm civet (*Paradoxurus hermaphroditus*), and Sunda pangolin (*Manis javanica*) (Figs. 4 and 5; Table 2). The three species with the most detections deep (> 1 km) in oil palm

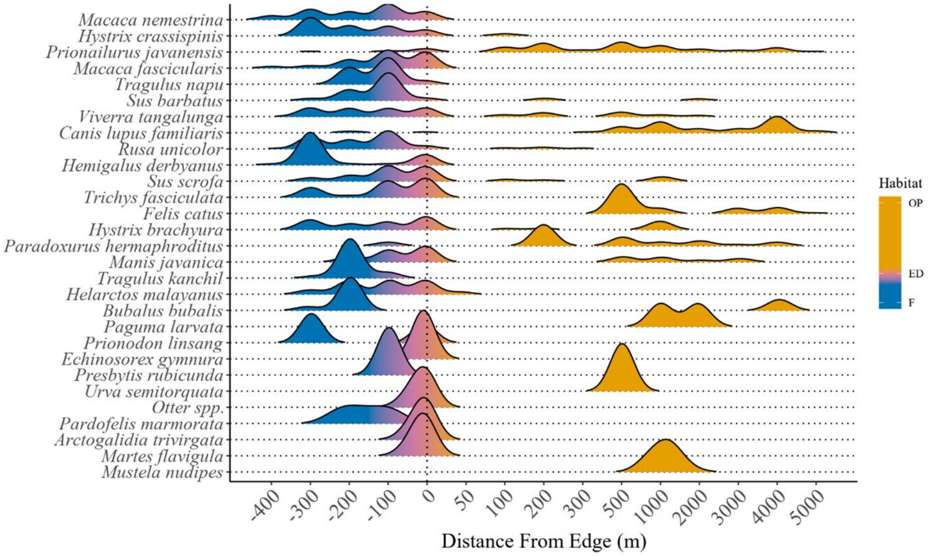

Fig. 4 Detection frequencies per species (y-axis) along the distance gradient from the edge into forest (F) or oil palm (OP). "0" denotes the edge between forest and oil palm plantations. Positive values on the x-axis represent distance into oil palm, and negative values represent distance into the forest. The ridges display the counts (proportional number of observations of each species) of species and are arranged in descending order of frequency of detection

were mesopredators: (Malay civet *Viverra tangalunga*, masked palm civet *Paguma larvata*, and Sunda leopard cat *Prioinailurus javanesis*). The Sunda leopard cat accounted for 87% of all detections at distances > 1 km into the oil palm plantation. Surprisingly, although very abundant in forest (Fig. 4), both primate species (*Macaca nemestrina; M. fascicularis*) were seldom detected in oil palm (7% likelihood of detection) and no further than 1 km into oil palm, showing a preference for the forest and edge habitat. Domestic dogs (*Canis lupus familiaris*) were most often observed deep in the oil palm (Fig. 4).

Species habitat occupancy

Forest was most likely to be occupied by mammal species ($\widehat{\psi}$ = 0.160), followed by the edge ($\widehat{\psi}$ = 0.097) and oil palm ($\widehat{\psi}$ = 0.097) (Table 4). The species with the greatest likelihood of occupancy of the oil palm was the Sunda leopard cat *Prionailurus javenensis* ($\widehat{\psi}$ = 0.513), and *Macaca nemestrina* had the greatest likelihood of occupancy of the forest ($\widehat{\psi}$ = 0.583) and second greatest likelihood of occupancy of the oil palm ($\widehat{\psi}$ = 0.203). The Malay civet *Viverra tangalunga* had the third highest likelihood of occupancy of oil palm ($\widehat{\psi}$ = 0.195), conversely, the predicted probability indicated no significant difference between oil palm and forest (Fig. 5). The semi-arboreal common palm civet *Paradoxurus hermaphroditus*, preferred oil palm ($\widehat{\psi}$ = 0.154) compared with forest ($\widehat{\psi} = 0.047$). *Macaca nemestrina/ fascicularis* were most likely to occupy the edge habitat, followed by *Hystrix crassispinis*, suggesting that these dietary generalist species are capable of using both forest and the oil palm. Four of the five species with the highest detections had predicted higher probability in the forest compared to the oil palm three of which being significant (Fig. 5).

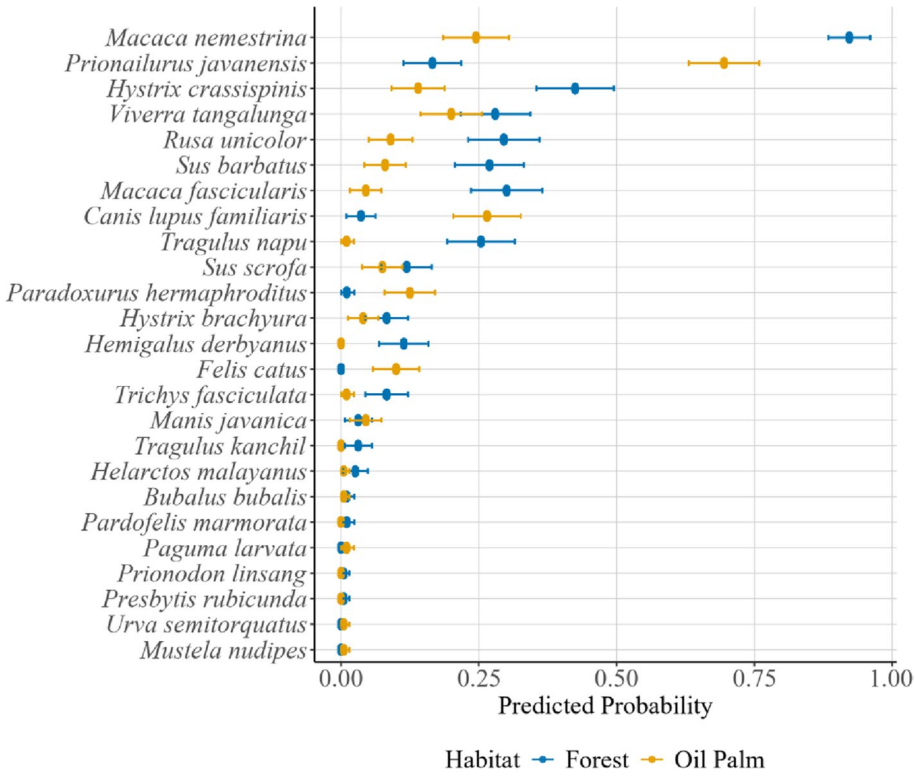

Fig. 5 Predicted probabilities of species occurrence in oil palm and forest habitats derived from logistic regression. Whiskers indicate the 95% confidence intervals

Discussion

Forest patches are important for mammal persistence in oil palm-dominated landscapes. The barrier to movement that the oil-palm edge poses is largely species-specific in its effect, but there are some generalizable trends regarding dietary guild, body size and vagility, which are discussed below. Thirteen of the 22 native species found in the forest patches entered and/or moved through the adjacent oil palm plantation. Nine species were not detected in the oil palm and three species were detected exclusively in the oil palm (Table 2). Species persistence in forest fragments appears to rely on source-sink metapopulation dynamics (Gilroy and Edwards 2017) among forest fragments. Previous studies have shown that the area of secondary forest preserved within agricultural plantations is the best measure of the conservation potential of landscape-dominating plantations (McShea et al. 2009; Zemp et al. 2023). Forests patches are a population source for mammal species that spill over into the oil palm (Azhar et al. 2014; Mendes-Oliveira et al. 2017). In contrast, oil palm is a much lower quality habitat than forest and a potential population sink for most species, where net mortality is higher than net natality for many species (Holt 1985). Large forest patches (~900 ha), such as Bukit Durang, act as sources (Table 3) while nearby small patches (~100 ha) are potential sinks (Gundersen et al. 2001), and oil palm may be a "black-hole sink" for many species, drawing them in but not sustaining them (Holt 2011). More

Table 4 Naïve occupancy (ψ) and MSOM occupancy ($\widehat{\psi}$) ($\pm$1SE) for each habitat category (overall O, oil palm OP, forest F and edge ED)

	Scientific name	Common name	Naïve occupancy ψ				MSOM occupancy $\widehat{\psi}$			
Order Atriodactlya			O	OP	F	ED	O	OP	F	ED
Cervidae	*Rusa unicolor*	Sambar Deer	0.366	0.213	0.532	0.455	0.270 ± 0.029	0.126 ± 0.036	0.306 ± 0.058	0.156 ± 0.053
Tragulidae	*Tragulus napu*	Greater Mousedeer	0.122	0.016	0.255	0.136	0.146 ± 0.020	0.036 ± 0.015	0.132 ± 0.040	0.063 ± 0.028
	Tragulus kanchil	Lesser Mousedeer	0.038	0	0.106	0	0.121 ± 0.018	0.034 ± 0.015	0.071 ± 0.029	0.040 ± 0.020
Suidae	*Sus barbatus*	Bearded Pig	0.305	0.148	0.468	0.409	0.234 ± 0.027	0.089 ± 0.029	0.260 ± 0.055	0.139 ± 0.049
Order Carnivora										
Felidae	*Prionailurus javanensis*	Sunda Leopard Cat*	0.595	0.77	0.426	0.5	0.382 ± 0.032	0.513 ± 0.055	0.231 ± 0.052	0.171 ± 0.055
	Pardofelis marmorata	Marbled Cat**	0.015	0	0.043	0	0.112 ± 0.017	0.039 ± 0.019	0.055 ± 0.026	0.043 ± 0.022
Ursidae	*Helarctos malayanus*	Sun Bear*	0.046	0.016	0.085	0.045	0.125 ± 0.019	0.041 ± 0.018	0.067 ± 0.028	0.049 ± 0.023
Herpestidae	*Urva semitorquata*	Collared Mongoose*	0.008	0.016	0	0	0.109 ± 0.017	0.047 ± 0.023	0.041 ± 0.020	0.044 ± 0.022
Mustelidae	*Otter spp.*	Otter spp.	0.008	0	0	0.045	0.109 ± 0.017	0.039 ± 0.020	0.041 ± 0.020	0.052 ± 0.026
	Mustela nudipes	Malay Weasel	0.008	0.016	0	0	0.108 ± 0.017	0.047 ± 0.023	0.041 ± 0.020	0.044 ± 0.022
	Martes flavigula	Yellow-throated Marten	0.008	0	0	0.045	0.109 ± 0.017	0.040 ± 0.020	0.041 ± 0.020	0.052 ± 0.026
Viverridae	*Arctogalidia trivirgata*	Small-toothed Palm Civet*	0.008	0	0	0.045	0.109 ± 0.017	0.039 ± 0.020	0.041 ± 0.020	0.052 ± 0.026
	Viverra tangalunga	Malay Civet*	0.389	0.328	0.489	0.364	0.283 ± 0.030	0.195 ± 0.044	0.275 ± 0.056	0.124 ± 0.045
	Paradoxurus hermaphroditus	Common Palm Civet*	0.130	0.246	0.043	0	0.160 ± 0.022	0.154 ± 0.043	0.047 ± 0.020	0.041 ± 0.019
	Paguma larvata	Masked Palm Civet*	0.015	0.033	0	0	0.113 ± 0.017	0.053 ± 0.025	0.040 ± 0.020	0.043 ± 0.022
	Hemigalus derbyanus	Banded Palm Civet*	0.076	0	0.149	0.136	0.130 ± 0.018	0.032 ± 0.014	0.082 ± 0.030	0.063 ± 0.028
Prionodontidae	*Prionodon linsang*	Banded Linsang*	0.023	0	0.021	0.091	0.116 ± 0.018	0.039 ± 0.018	0.047 ± 0.022	0.060 ± 0.029
Order Primates										
Cercopithecidae	*Macaca nemestrina*	Sunda Pig-tailed Macaque*	0.649	0.344	0.936	0.909	0.404 ± 0.032	0.203 ± 0.045	0.583 ± 0.059	0.357 ± 0.076
	Macaca fascicularis	Long-tailed Macaque*	0.344	0.115	0.511	0.636	0.256 ± 0.029	0.074 ± 0.026	0.291 ± 0.058	0.230 ± 0.065
	Presbytis rubicunda	Maroon Langur**	0.008	0	0.021	0	0.109 ± 0.017	0.040 ± 0.020	0.049 ± 0.024	0.044 ± 0.023
Order Pholidota										
Manidae	*Manis javanica*	Sunda Pangolin*	0.137	0.148	0.106	0.182	0.169 ± 0.024	0.104 ± 0.036	0.074 ± 0.030	0.078 ± 0.034
Order Eulipotphyla										
Echinosorex	*Echinosorex gymnurus*	Moonrat	0.008	0	0	0.045	0.108 ± 0.017	0.033 ± 0.015	0.036 ± 0.017	0.048 ± 0.022

Table 4 (continued)

	Scientific name	Common name	Naïve occupancy ψ				MSOM occupancy $\widehat{\psi}$			
Order Atriodactlya			O	OP	F	ED	O	OP	F	ED
Order Rodentia										
Hystricidae	*Hystrix crassispinis*	Borneo Thick-spined Porcupine*	0.405	0.23	0.574	0.545	0.275 ± 0.028	0.132 ± 0.037	0.329 ± 0.059	0.189 ± 0.059
	Hystrix brachyura	Malayan Porcupine*	0.122	0.082	0.17	0.136	0.149 ± 0.020	0.059 ± 0.022	0.092 ± 0.032	0.063 ± 0.028
	Trichys fasciculata	Long-tailed Porcupine*	0.076	0.016	0.128	0.136	0.133 ± 0.019	0.036 ± 0.016	0.074 ± 0.028	0.063 ± 0.028
Domestic Species										
Felis catus	*Felis catus*	Domestic Cat	0.084	0.18	0	0	0.136 ± 0.019	0.107 ± 0.033	0.034 ± 0.016	0.040 ± 0.019
Canis lupus familiaris	*Canis lupus familiaris*	Domestic Dog	0.275	0.443	0.128	0.136	0.215 ± 0.025	0.107 ± 0.33	0.034 ± 0.016	0.040 ± 0.019
Bubalis bubalis	*Bubalus bubalis*	Domestic Water Buffalo	0.023	0.016	0.043	0	0.114 ± 0.017	0.043 ± 0.020	0.052 ± 0.024	0.043 ± 0.021
Sus scrofa	*Sus scrofa*	Domestic Pig	0.191	0.098	0.298	0.227	0.183 ± 0.024	0.068 ± 0.025	0.160 ± 0.045	0.085 ± 0.035

IUCN status is indicated by "*" for protected and "**" for fully protected species under the wildlife protection ordinance (WPO) in Sarawak intensive area-dependent sampling of one small forest patch (116 ha; Saremas1) revealed two medium-sized mammals (lesser mousedeer *Tragulus kanchil*, common palm civet *Paradoxurus hermaphroditus*) that were not detected in the larger patch (990 ha; Bukit Durang) (Table 3). Less intensive sampling of a small patch (148 ha; Giant Bowl) revealed one medium-size species (collared mongoose *Urva semitorquata*) not detected in Bukit Durang. For the most part the latter species are either common in the oil palm or found deep in the oil palm (Table 2). Furthermore, the species found in the small patches were all larger-sized dietary generalists or mesopredators (Supplementary information, Table S2). While species richness of patches is area-dependent, the somewhat unpredictable patterns of species occupancy described above suggest persistence of many species as source-sink metapopulations in oil palm dominated landscapes.

Remarkably, despite being surrounded by a vast oil palm estate, the small forest patches surveyed in this study collectively included all the medium- to large-size mammal species (22 species) that could reasonably be expected to occur there when compared with the composition of the mammal community in a nearby potential species pool (Lambir Hill National Park). Thirty-seven medium- to large-sized forest mammal species are recorded from the nearby Lambir Hills National Park (LHNP; Shahanan and Debski 2002; Mohd-Azlan and Lading 2006), of which 14 species are squirrels (Shahanan and Debski 2002). Squirrel species were excluded in our study because the camera traps did not consistently monitor strictly arboreal species, and squirrel species could not be identified to species or even genus level. Thus, the 22 medium- to large-sized mammal species recorded in the three fragments is consistent with the 24 species recorded from LHNP, even though our forest fragments are an order of magnitude smaller than Lambir Hills National Park (116–990 ha versus 6523 ha, respectively). While sampling methods undoubtedly influence what mammal species were detected, this comparison between sites does indicate that metapopulations comprising small forest fragments have the potential to protect most, if not all, medium-to large-size mammal species, even if they are surrounded by oil palm. There may of course be a delay in local extinction of species (Kuussaari et al. 2009) from smaller forest fragments. Certainly, where sampling effort was similar, fewer species were observed in the smaller (< 100 ha) forest patches (e.g., Saremas 1, 116 ha) than in the large Bukit Durang (990 ha), although some of these (e.g., were not observed in the large patch (Table 3). The latter indicates that while an extinction debt undoubtably affects species richness in these fragmented forests, quite which species are affected varies from forest to forest. That species richness of smaller fragments is not a nested subset of larger fragments suggests that all forests at a locality should be managed collectively to optimize their metapopulation potential.

Missing from our fragments were at least two megafauna species that we expected to occur in our fragments (Amir et al. 2022), a large carnivore—the clouded leopard (*Neofelis* spp.) and a megaherbivore—domestic wild boar (*Sus scrofa vittatus*). Clouded leopards have been widely extirpated from Borneo in the Anthropocene, while introduced domestic wild boar occur at low density in LHNP (Amir et al. 2022) and are possibly excluded by the more social and nomadic bearded pig (*Sus barbatus*; Luskin and Ke 2017). Domesticated wild boar were not detected in the small forest fragments surveyed in this study because they are a free-ranging domesticated species, which live near human settlements that were not surveyed using camera traps. The three megafauna species (sun bear (*Helarctos malayanus*), Sambar deer (*Rusa unicolor*), bearded pig (*S. barbatus*) observed in our study all used the oil palm, although only the bearded pig (*S. barbatus*) was observed deep in the oil palm plantation, as were three mesopredator species (Table 2; Sunda leopard cat (*Prionailurus javanensis*), common palm civet (*Paradoxurus hermaphroditus*), masked palm civet (*Paguma larvata*).

Oil palm plantations provide sufficient cover and resources for movement between forest fragments by some species. Some species that entered oil palm exhibited back-emigration behavior, such as the pig-tailed macaque (*Macaca nemestrina*), while some species were found deep into (>2 km), and appeared to be living in, the oil palm plantations (Table 2). The species observed deep in the oil palm plantation were mainly dietary generalists (civets, porcupines), mesopredators (cats and mongooses) or megafauna (deer and pigs). Pangolins, which are dietary specialists (mainly ants and termites that are abundant in the plantations) were also observed deep in the oil palm plantation (Table 1). For these species the oil palm is a ‘soft’ or permeable habitat allowing movement. However, for all other species, detections declined with distance into oil palm (Yue et al. 2015) with most detections in oil palm (97%) within 1 km of the forest edge. The forest patches within our study area are within 2 km of each other (Fig. 1) and are within movement range of each other for many species and are potentially mutually reinforcing. Our findings demonstrate that larger mammals, but particularly mesopredators and dietary generalists, can persist as metapopulations in an oil-palm dominated landscape, if the forest patches are within movement range or connected by native vegetation and are relatively undisturbed.

Mesopredators

The mesopredators, Sunda leopard cat (*Prionailurus javanensis*), common palm civet (*Paradoxurus hermaphroditus*), masked palm civet (*Paguma larvata*), Malay civet (*Viverra tangalunga*), and collared mongoose (*Urva semitorquata*) were often encountered in oil palm in this and other studies (Jennings et al. 2015; Yue et al. 2015; Chua et al. 2016; Wearn et al. 2017; Solina et al. 2018; Hood et al. 2019; Luskin et al. 2023). Excluding domestic species, the Sunda leopard cat and common palm civet were the only species more frequently detected in the oil palm ($\Psi = 0.77$ and 0.25, respectively) than in the forest ($\Psi = 0.43$ and 0.04, respectively; Table 3), with the Sunda leopard cat accounting for 55% of all detections in oil palm. The other four mesopredators were detected less frequently overall (Table 4). The yellow-throated marten (*Martes flavigula*), another arboreal mesopredator, was not detected by low-set camera traps in the oil palm (Table 1), although it has been recorded by other studies in oil palm areas near forests (Bernard et al. 2014). The frequent use of oil palm by mesopredators is not only associated with resource availability (Mohd-Azlan et al. 2019) but also with mesopredator release in the oil palm and at the forest edge (Prugh et al. 2009; Luskin et al. 2023). Our data confirms that mesopredator species can disperse through the oil palm over greater distances (>3 km) than many dietary generalists and most forest specialist species, and oil palm does not present a significant barrier to movement for mesopredators.

Dietary generalists

Many dietary generalist species (Supplementary information Table S2) were detected in oil palm within 1 km of the forest edge, suggesting that if forest patches are spaced roughly 1 km apart, these species can maintain connectivity across plantations. The dietary generalists, pig-tailed macaque (*Macaca nemestrina*), long-tailed macaque (*Macaca fascicularis*), *Hystrix* spp. (porcupines), and long-tailed porcupine (*Trichys fasciculata*) were commonly observed within oil palm (Figs. 4 and 5) (Wahyudi and Stuebing 2013; Jennings et al. 2015; Phillipps and Phillipps 2018; Holzner et al. 2019). Consistent with our findings, the terrestrial group living *Macaca nemestrina* was more predisposed to using oil palm than the more arboreal long-tailed macaque (*Macaca fasciculata*) (Mohd-Azlan and Cheok 2017). Both macaque species and *Hystrix* spp. exploit oil palm fruits, making them potential pests of oil palm. Like the *Macaca* spp., their generalist diet enables *Hystrix* spp. to live relatively deep (≤1 km) in oil palm. The Bornean thick-spined porcupine (*Hystrix crassispinis*) was detected on 10% of occasions at distances >2 km in the oil palm. This species rests in burrows during daytime hours (Matsukawa et al. 2018) and is probably resident in the oil palm. The long-tailed porcupine (*Trichys fasciculata*) was detected only twice at 200 m into the oil palm, although burrows have been observed in the oil palm plantations (Matsukawa et al. 2018). Notably, the sun bear (*Helarctos malayanus*), a megafaunal dietary generalist, while most frequently detected in forest (Fig. 5), also used the immediate oil palm edge (<100 m; Fig. 4).

Forest specialists

Forest specialist species seldom penetrated beyond the forest edge into oil palm. Most of the forest specialist species, particularly the arboreal ones, were exclusively found in forest patches or were rarely detected ($n<10$) in the oil palm. Ground-based camera traps may have missed arboreal species, such as the marbled cat (*Pardofelis marmorata*), which has been recorded in oil palm preying on rats (Phillipps and Phillipps 2018), but was detected only twice in the forest camera traps. The forest specialist species observed in the oil palm, such as mousedeer (*Tragulus* spp.), Malay sun bear (*Helarctos malayanus*), Bearded pig (*Sus barbatus*) and Sambar deer (*Rusa unicolor*) cannot sustain their populations in the forest patches without immigration. *Tragulus* spp. were detected in oil palm on only 2% of occasions. For *Tragulus* spp., oil palm poses a hard barrier to dispersal and recruitment. Their frequent use of the forest edge suggests that dispersal corridors may encourage movement among forest patches. At low rates of dispersal by forest specialists, oil palm likely functions as a population sink where most migrants perish or are hunted (Remeš 2000). While the social bearded pig ranges up to 2 km into plantations, it is a culturally important game animals that is hunted legally in Sarawak (Yi and Mohd-Azlan 2020). The bearded pig's movement over relatively long-distances across oil palm is reflected in its susceptibility to African Swine Flu outbreaks (Kurz et al. 2021). The critically endangered Sunda pangolin (*Manis javanica*) was observed far into the oil palm (≤3 km), consistent with the findings of (Azhar et al. 2014). Their penetration deep into the oil palm is surprising given their arboreal nature (Rizali et al. 2021) and may be due to lower hunting pressure in our study. In general, pangolin use of the lower quality oil palm habitat is a potential example of an 'ecological trap' (Battin 2004). Oil palm presents as an ecological trap to pangolins rather than as a population sink, because while food resources (ants and termites) may be abundant in the oil palm plantations, the risk of local population extinction due to hunting pressure in the region is potentially very high (Panjang et al. 2024). Of the species exclusively found in the forest/edge (Table 1), the banded civet (*Hemigalus derbyanus*) is a species for which the oil palm is a hard barrier to dispersal. This species was not detected in oil palm. Conserving forest specialists in oil palm landscapes requires maintaining protected vegetation corridors or wide riparian belts to connect forest patches.

Conclusions

Oil palm plantations on their own have low conservation value, with significantly less diversity than any type of forested landscape (Fitzherbert et al. 2008). However our study shows that significant mammal diversity can persist in forest fragments in the oil palm matrix.

1. Collectively, small forest patches in an oil palm dominated matrix contained 92% (22 of 24 species) of potential forest species compared with nearby intact large forests.
2. Persistence of mammal species in forest fragments within an oil palm dominated landscape is likely regulated by source-sink metapopulation dynamics. These dynamics are in turn dependent on the spatial configuration and size of forest patches and mammal species' ability to use and move through the oil palm matrix. Of the 22 mammal species detected in forest patches, all but two showed declining occupancy with distance into oil palm, yet most dietary generalists, mesopredators and megafauna species still used this moderately permeable habitat.
3. Without management interventions, further extirpation of forest species will occur in these forest fragments because of the interaction between ongoing anthropogenic disturbance and declining population size associated with source-sink metapopulation dynamics of most species (Love et al. 2017; Pardo et al. 2019).
4. Connectivity between forest remnants is a critical management intervention, essential for maintaining biodiversity on oil palm estates (Perfecto and Vandermeer 2008; Ancrenaz et al. 2021; Zemp et al. 2023; Mohd-Azlan et al. 2023). Retaining, restoring and managing native vegetation on oil palm estates is crucial for increasing connectivity between forest remnants. At the very least, these management interventions will enhance migration into and through oil palm by dietary generalists. mesopredators and some megafauna.
5. In general, forest specialists consider oil palm an impermeable barrier, making connected corridors essential for their dispersal. Riparian corridors are an efficient solution to increasing dispersal rates for vulnerable arboreal/non-arboreal forest specialists and reduce the effects of runoff in a cost-effective way (Gillies and St. Clair 2008; Pashkevich et al. 2022).
6. Where habitat corridors are not possible, a practical alternative is to limit the maximum distance between forest remnants in an oil palm matrix to <1 km, as nearly all forest mammal populations in this study penetrated this distance into the oil palm.
7. Plantation design should prioritize a network of spared forest islands that are no more than 1 km apart. As much native vegetation as possible should be retained on oil palm estates (Zemp et al. 2023). Even small patches of indigenous vegetation on oil palm estates retained most of the generalist medium- and large-size mammal species. Small forest patches are stepping stones for their movement (Tews et al. 2004; McShea et al. 2009; Wong et al. 2022; Zemp et al. 2023), mitigate some of the negative effects of source-sink population dynamics (e.g., cross-boundary subsidy cascades - *sensu* Luskin

et al. 2017) and maintain metapopulation persistence (Hansson and Angelstam 1991; Chapman et al. 2019; Zemp et al. 2023).

In summary, small forests (in our case < 1000 ha) in oil palm plantations have the potential to maintain metapopulations of most medium- and large-size mammal species. Management of these metapopulations requires that oil palm estates prioritize the conservation of forest patches within 1 km of each other in the oil palm, as well as protecting existing vegetation corridors, such as riparian zones. Protecting forest habitat on oil palm estates, and the mammals they support, protects vital ecological functions that benefit both nature and agriculture.

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Author contributions JM-A and ML contributed to the study conception and design. Material preparation, data collection and analysis were performed by LL, TW aided by JM-A and ML. The first draft of the manuscript was written by LL, TW, JM-A and ML, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial competing interests to disclose. The authors declare no competing interests.

Ethics approval This study was conducted with permission from Forest Department Sarawak (251, JHS/NCCD/600-7/2/107) and Sarawak Forestry Corporation.

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