museu de ciències naturals de Barcelona

Animal Biodiversity and Conservation 47.2 (2024)
DOI: 10.32800/abc.2024.47.0123

Research paper

# Conservation among oil palm plantations? Mammalian diversity in protected forest areas of a mixed-use landscape in Indonesian Borneo

K. Kasper[1,2], N. Devriance[3], K. Aran[3], B. Martin[4,5]

**Author affiliations:**
[1] Mammal Research Institute, Polish Academy of Sciences, Poland
[2] Institute of Ecology, Evolution and Diversity, Goethe University, Frankfurt am Main, Germany
[3] Conservation Department, PT.REA Kaltim Plantations and Group, Indonesia
[4] Yayasan Uiln, Indonesia
[5] Yayasan Jejak Pulang, Indonesia

**Corresponding author:**
K Kasper
k.kasper@ibs.bialowieza.pl

**Handling Editor:**
Beatriz Arroyo

Received: 04/07/2022
Cond. acceptance: 01/08/2022
Final acceptance: 08/07/2024
**Published:** 18/07/2024

**Cite:**
Kasper K, Devriance N, Aran K, Martin B, 2024. Conservation among oil palm plantations? Mammalian diversity in protected forests areas of a mixed-use landscape in Indonesian Borneo. *Animal Biodiversity and Conservation* 47.2, 123-134. DOI: https://doi.org/10.32800/abc.2024.47.0123



**ISSN:** 1578-665 X
**eISSN:** 2014-928 X

## Abstract

*Conservation among oil palm plantations? Mammalian diversity in protected forest areas of a mixed-use landscape in Indonesian Borneo.* Deforestation for land-use change in Borneo has global impacts on biodiversity. Mixed-use landscapes are spatially integrative countermeasures to conserve critical forest habitats for wildlife along with economic development. We used camera-traps to inventory remnant mammalian diversity, species richness, detection counts, and diel activity functions in protected forest areas in a large oil palm plantation landscape in East Kalimantan, Bornean Indonesia. From among 2,286 independent detections of species, our results provide evidence of the presence of at least 33 mammals in these forest areas, including species of high conservation value such as the critically endangered Bornean orangutan *Pongo pygmaeus* and the Sunda pangolin *Manis javanica*. Additionally, we provide diel activity patterns for 14 of the detected species and reflect on their meaning in the context of their habitat. Due to plantation activities, the protected areas may underlie characteristic ecological dynamics with an impoverished large carnivore guild and a majority of small mammals and small carnivores interacting as predator and prey. Abundant oil palm crops likely benefit large populations of small mammals (highest detection counts) while simultaneously supplying resources for a diverse carnivore community (highest species-richness) preying on small mammals. We highlight the potential of the forested protected areas as wildlife refugia in mixed-use landscapes for conservation and production efforts. We recommend further monitoring to ensure fulfilling this potential in the continuous management.

**Key words:** Borneo, Biodiversity, Diel activities, Protected areas, Ecosystem services, Camera-trapping

## Resumen

*¿Medidas de conservación en las plantaciones de palma aceitera? La diversidad de mamíferos en zonas forestales protegidas de un paisaje de uso mixto en la parte de Borneo perteneciente a Indonesia.* La deforestación para cambiar el uso del suelo en Borneo tiene repercusiones mundiales en la biodiversidad. Los paisajes de uso mixto son contramedidas espacialmente integradoras dirigidas a conservar hábitats forestales críticos para la vida silvestre junto con el desarrollo económico. Usamos cámaras trampa para hacer un inventario de la diversidad de mamíferos remanente que incluye la riqueza de especies, recuentos de detección y las funciones de actividad diurna en las zonas forestales protegidas de un extenso territorio de plantaciones de palma aceitera en Kalimantan Oriental, en Borneo (Indonesia). De las 2.286 detecciones independientes de especies, nuestros resultados indican la presencia de un mínimo de 33 mamíferos en las zonas forestales, incluidas especies de alto valor de conservación, como el orangután de Borneo, *Pongo pygmaeus*, en peligro crítico de extinción, y el pangolín de Sunda, *Manis javanica*. Además, proporcionamos los patrones de actividad diurna de 14 de las especies detectadas y reflexionamos sobre su significado en el contexto de su hábitat. Debido a las actividades de plantación, en las zonas protegidas puede subyacer una dinámica ecológica característica con un gremio de grandes carnívoros empobrecido y una mayoría de pequeños mamíferos y pequeños carnívoros que interactúan como depredadores y presas. Los abundantes cultivos de palma aceitera como recurso probablemente

beneficien a grandes poblaciones de pequeños mamíferos (los conteos de detección más elevados) y, a su vez, abastezcan a una comunidad diversa de carnívoros (la mayor riqueza de especies) que se alimentan de pequeños mamíferos. Destacamos la posibilidad de utilizar las zonas forestales protegidas como refugios de vida silvestre en paisajes de uso mixto en las iniciativas de conservación y producción. Recomendamos hacer un mayor seguimiento para que esta posibilidad se pueda materializar en la gestión continua.

**Palabras clave:** Borneo, Biodiversidad, Actividades diurnas, Zonas protegidas, Servicios ecosistémicos, Cámaras trampa

## Introduction

Tropical forests host an estimated half to two-thirds of the Earth's species (Dirzo and Raven 2003, Barlow et al 2016) but are also the most threatened forest biomes, accounting for over half the deforestation on Earth (Potapov et al 2017). The island of Borneo in Southeast Asia is a hotspot for both tropical forest biodiversity and severe deforestation (Myers et al 2000, de Bruyn et al 2014). Thanks to its evolutionary old age and isolated geography at the barrier of Wallace's Line, Borneo has an extraordinary richness of species and functions (de Bruyn et al 2014). However, since the 1930s, over half of the island's forest habitat has disappeared (van Steenis 1935, Langner et al 2007, Cushman et al 2017), largely due to land-use change for commercial palm oil *Elaeis guineensis* cultivation (Gaveau et al 2018, Meijaard et al 2018). The increasing national and international demands for palm oil produced in Indonesia, with its leading production area in Borneo (Abood et al 2015), have grown to dominate the country's economy (Varkkey, 2012), and are expected to be met with plantation expansions or sharp yield improvements by 2025 (Khatiwada et al 2021). Mitigation strategies are thus needed to trade off economic demands and an intensifying biodiversity crisis (Strang and Rusli 2021).

Because oil palm plantations fail to substitute habitats for many forest species (Yue et al 2015, Harich and Treydte, 2016), forest persistence and integrity form the most important basis to mitigate biodiversity loss (Dirzo and Raven, 2003, Lee and Jetz, 2008). Given that potentially productive land is seldom assigned for sparing on large scales (e.g., by establishing national parks; Fischer et al 2013), alternative strategies for forest conservation are spatially integrative countermeasures (Hutton and Leader-Williams 2003, Meijaard et al 2018). Such measures integrate protected area networks into 'mixed-use' landscapes, resulting in a fragmented mosaic of land used for economical purposes, typically used for cultivation of commercial crops, and compensational areas aiming to conserving the ecological values of the overall landscape, such as biodiversity forest habitats (Stuebing 2007). Although mixed land use for oil palm plantations along with protected forests has been widely introduced across Borneo, few data on the conservation potential for biodiversity is collected and shared, and establishment and report remains voluntary (Nurhidayah and Alam 2020).

Previous studies from Borneo suggest that several mammal species in protected forest patches within oil palm plantations withstand human disturbance and habitat fragmentation (Wahyudi and Stuebing 2013, Love et al 2018, Milne et al 2021). Their remnant diversity is what mediates the functionality of the protected areas within the mixed-use landscape as ecosystems (Flynn et al 2009). A diverse mammal community can drive ecological dynamics for the integrity of their habitats, but it can also provide ecosystem services benefitting economic activities, such as, for example, via key roles in bioturbation, nutrient cycling, seed and spore dispersal, and pollination (Lacher et al 2019). Moreover, predation pressures have regulatory effects on ecosystem dynamics by limiting populations (Sinclair et al 2003), which can also include crop pests (Williams et al 2018). For preying on rodent pests in South African rural farming crops, Williams et al (2018) ascribed small carnivores great potential to replace the use of environmentally problematic poisons. Inventories of mammalian diversity thus provide a crucial baseline for planning and managing mixed-use landscapes in the interest of both conservationists and economists.

Mammalian diversity of relevance to assess the utility of mixed-use landscapes for conservation and ecosystem services includes taxonomic diversity, commonly measured as species richness and evenness, and functional diversity as traits in ecological niches (Mason and De Bello 2013). Species diel activity niches, for example, reflect adaptations to temporal regimes, largely of predation or competition, resource availability, and human disturbance (Hut et al 2012, Gaynor et al 2018). Despite a long coevolution of temporal partitioning between predator and prey (Wu et al 2018), interactions with human disturbance can create complex activity patterns in mammals. A study from the US found that an overarching drive to temporally avoid human activities led rodents and lagomorphs to avoid their coyote predator less in human-disturbed areas (Caldwell and Klip, 2022). Red foxes in Spain, on the other hand, avoided human diel activity patterns more than matching those of their lagomorph prey (Díaz-Ruiz et al 2016). Although in Bornean mixed-use landscapes, we can expect humans to disturb the mammals' habitat (Yasuda and Tsuyuki, 2012), the landscape is also characterized by habitat heterogeneity and high resource abundance starting with cultivated oil palm crops, which may be able to nourish a high level of mammalian diversity (Williams et al 2018).

Here, we provide rare insight into the mammalian diversity of fragmented forest conservation patches, protected by a large-scale palm oil production company in Bornean Indonesia. Using camera-traps as effective tools to sample a large set of ground-dwelling mammals, we report our species detections with special emphasis on their conservation value (i.e., rare and threatened species; Butchart et al 2006). Furthermore, from detection counts and extrapolated diel activity patterns, we estimated potential functions within the forest ecosystem (e.g., interaction dynamics) and their services to the plantation activities (e.g., crop pest control). Our findings provide insight into using mixed-use landscapes as an approach to biodiversity conservation and may guide decision-makers in the future.

## Material and methods

### Study area

Our study area is situated on the island of Borneo, in the Indonesian province East Kalimantan, within the Upper Belayan River Basin. It covers a network of protected forest areas that constitute an integrated part of a mixed-use landscape that constitute an integrated part of a mixed-use landscape, serving the production of palm oil for the global market. This land is currently under the management of UK-based company PT.REA Kaltim Plantations and Group (hereafter, REA) that has been granted rights to cultivate ('Hak Guna Usaha'). During their initial operations from 1996 to 2019, REA constituted c. 2.5 % of the province's palm oil cultivation (Directorate General of Estate Crops 2019). Since 2007, the company has been pursuing sustainable management using the mixed-use landscape approach. At the time of our data collection, REA's concession of c. 800 km², covered c. 360 km² of land converted for oil palm cultivation and c. 200 km² fragmented protected areas. Under the local lowland tropical climate, these areas comprise mainly humid and dipterocarp secondary forest remnants, regenerated from wildfires or logging (Goldammer and Seibert 1990, Hoffmann et al 2000), or old swidden cultivation for at least 12 to 20 years. These protected areas also include a few remnant primary forest patches, peat swamps, wetlands, steep areas, riparian buffers, and other land types considered unsuitable economic land. Habitats surrounding REA's concession have been extensively logged for timber by the company and local communities, leaving it in a highly degraded state.

### Camera-trapping protocol

From June 8$^{th}$ 2018 to December 16$^{th}$ 2019, we surveyed REA's protected areas over a total area of 140,12 km², using camera-traps (Bushnell Trophy Cam HD, USA; fig. 1). We attached the camera-traps to tree trunks 30 cm above ground and cleared the vegetation in front of the camera to 2-4 m. Sampling locations were chosen to maximize detection probabilities of ground-dwelling mammals, that is, at water sources, natural salt licks, fruiting trees, and animal trails as signs of recent activity (Gordon and Stewart 2007). To further enhance trapping success, we placed lure-coated sticks (O'Gorman's Powder River Paste Bait, USA) in front of our cameras. This lure was initially designed for carnivorous mammals, yet has attracted the attention of numerous wildlife species in previously collected data from the study area. Monthly relocations of our camera-traps to further sampling locations helped us to expand the spatial coverage and resulted in 357 deployments and 10,714 (mean: 29.46, range: 20-35) trap nights per deployment). Collected image data were identified to species level when possible. To ensure independence of species detection events, we kept only one species record per hour per sampling location and disregarded the number of individuals. Due to often insufficient image quality resulting in especially high numbers of misidentifications in smaller, barely distinctive species (REF) (Clevenger et al 2013), we grouped small mammals into three major families, Tupaiidae, Sciuridae, and Muridae, and only used their detection counts for our analysis. It is of note, however, that Muridae detections are predominantly represented by relatively large rat species, while smaller mice are particularly difficult to detect. Similarly, due to rather fine-scale distinguishing characteristics in local muntjac and chevrotain species, we report them on genus level, i.e., *Muntiacus* and *Tragulus* spp., respectively. Therefore, when we refer to 'species' detections, each of these groups (Tupaiidae, Sciuridae, Muridae, *Muntiacus* spp. and *Tragulus* spp.) is considered to represent at least one.

### Diel activity analysis

With little seasonal variation in the tropical climate and constant activities within the oil palm plantation sites, we did not account for seasonality in our data analyses. Furthermore, the diel photoperiod remained largely stable throughout the study and refers to the marked sunrise at c. 5:30 h and sunset at c. 18.30 h ± < 0.5 h in East Kalimantan's capital, Samarinda (BMKG 2020). Time-stamped camera-trap samples during this period show the proportion of detections of species at a given time of day. Following Niedballa et al (2019), we extrapolated diel activity patterns of species with > 20 independent detections and broadly classified them as diurnal, nocturnal, crepuscular, or cathemeral (van Schaik and Griffiths 1996). We did this by plotting the density distributions of their diel detections non-parametrically, using kernel density functions (Ridout and Linkie 2009) with a von Mises kernel and density curves fitted by nonnegative trigonometric functions (Meredith and Ridout 2016). All statistics were performed in R 4.0.2 (R Core Team 2020).

## Results

### Species detections

Our camera-trap survey yielded significant insight into the mammalian diversity of the protected forest areas of REA's mixed-use landscape. We documented detection of 2,286 independent species of which we identified at least 33 mammal species (table 1). Among these, we report species of particularly high conservation value, including vulnerable carnivores

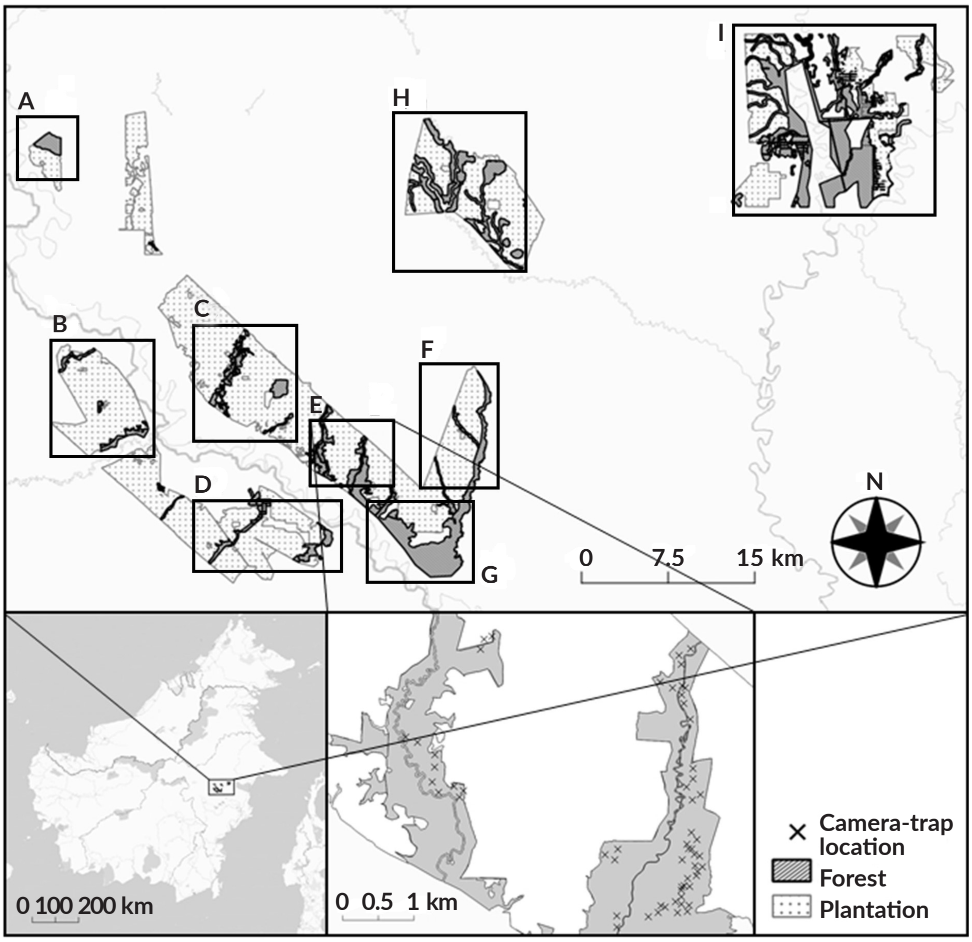


**Fig. 1.** Map of the mixed-used landscape on PT.REA Kaltim Plantations concession (0° 15' N, 116° 11' E) in East Kalimantan, Bornean Indonesia. Oil palm plantations (dotted areas) are traversed by conservation reserves of predominantly secondary forest (striped areas). Camera-traps were relocated monthly across the protected forest areas, resulting in 26 deployments in block A, 28 deployments in block B, 68 deployments in block C, 37 deployments in block D, 60 deployments in block E (camera-trap locations depicted by crosses), 49 deployments in block F, 27 deployments in block G, 57 deployments in block H, and 5 deployments in block I.

***Fig. 1.*** *Mapa del paisaje de uso mixto en la concesión de plantaciones PT.REA Kaltim (0° 15' N, 116° 11' E) en Kalimantan Oriental, en Borneo (Indonesia). Las plantaciones de palma aceitera (áreas punteadas) están atravesadas por reservas ocupadas predominantemente por bosques secundarios dedicadas a la conservación (áreas rayadas). Las cámaras trampa se cambiaron de sitio una vez al mes dentro de las zonas forestales protegidas, lo que dio lugar a 26 instalaciones en el bloque A, 28 instalaciones en el bloque B, 68 instalaciones en el bloque C, 37 instalaciones en el bloque D, 60 instalaciones en el bloque E (las ubicaciones de las cámaras trampa se indican con cruces), 49 instalaciones en el bloque F, 27 instalaciones en el bloque G, 57 instalaciones en el bloque H y 5 instalaciones en el bloque I.*

such as the Sunda clouded leopard *Neofelis diardi* and the binturong *Arctictis binturong*, as well as, instead and critically endangered species such as the Bornean orangutan *Pongo pygmaeus*, and the Sunda pangolin *Manis javanica* (IUCN 2021). Almost half of our species inventory (45.46 %) is based on rare detections with an independent detection count of < 10. Across all species detected, carnivores were most diverse regarding species richness (16 species, comprising mainly small carnivores), although their overall detection count was relatively low (fig. 2). The most frequently detected species were rodents (984 independent detections), with 87.7 % being rats (Muridae) and squirrels (Sciuridae). Together with the similarly-classified family of treeshrews (Tupaiidae) as the only representative of the order Scandentia, they constitute a large part of all small mammal detections (43.18 %). We also frequently camera-trapped Primates and Artiodactyla (499 and 295 independent detections, respectively), while we could identify a minimum species richness of 5 and 4, respectively, at the same time. Eulipotyphla and Pholidota were both only represented by one species (the moonrat *Echinosorex gymnura* and Sunda pangolin *Manis javanica*), yet moonrats were also relatively frequently detected (225 independent detections) while the pangolin appeared only 8 times.

### Diel activity patterns

Based on detection frequencies across the diel cycle, we were able to extrapolate activity patterns for 14 of our recorded mammal species (fig. 3). We found distinct variations in detection frequencies according to the presence

**Table 1.** Camera-trapping inventory of mammals observed in the protected forest areas of PT.REA Kaltim Plantations, East Kalimantan, Indonesian Borneo, in 2018/19. Species counts and independent detection counts are given for order and family levels. Muridae can be biased towards larger rat species due to camera-trapping limitations. Species are presented by their individual independent detection counts and conservation status category according to the IUCN Red List of Threatened Species™ (LC least concern, NT near threatened, VU vulnerable, EN endangered, CR critically endangered, DD data deficient; IUCN, 2021).

***Tabla 1.*** *Inventarios de los mamíferos captados por las cámaras obtenidos de las zonas forestales protegidas de PT.REA Kaltim Plantations, en Kalimantan Oriental, en Borneo (Indonesia), en 2018/19. Los conteos de las especies y los conteos de detección independientes se indican a nivel de orden y de familia. Debido a las limitaciones de las cámaras, es posible que los múridos estén sobrerrepresentados por incluir a especies de roedores más grandes. Las especies están representadas por sus conteos individuales de detección independiente y su estado de conservación según la Lista Roja de la UICN de Especies AmenazadasTM (LC preocupación menor, NT casi amenazado, VU vulnerable, EN en peligro, CR en peligro crítico, DD datos insuficientes; UICN, 2021).*

| Order / Family / Species | Common name | IUCN | Species count | Detection count |
|---|---|---|---|---|
| Artiodactyla | | | 4 | 295 |
| Cervidae | | | 2 | 27 |
| *Rusa unicolor* | Sambar deer | VU | | 12 |
| *Muntiacus* spp. | Muntjac | - | | 15 |
| Suidae | | | 1 | 52 |
| *Sus barbatus* | Bearded pig | VU | | 52 |
| Tragulidae | | | 1 | 216 |
| *Tragulus* spp. | Chevrotain | LC | | 216 |
| Carnivora | | | 16 | 151 |
| Felidae | | | 3 | 22 |
| *Neofelis diardi* | Sunda clouded leopard | VU | | 1 |
| *Pardofelis marmorata* | Marbled cat | NT | | 4 |
| *Prionailurus bengalensis* | Leopard cat | LC | | 17 |
| Herpestidae | | | 1 | 7 |
| *Herpestes brachyurus* | Short-tailed mongoose | NT | | 7 |
| Mustelidae | | | 4 | 11 |
| *Aonyx cinereus* | Asian small-clawed otter | VU | | 6 |
| *Lutrogale perspicillata* | Smooth-coated otter | VU | | 2 |
| *Martes flavigula* | Yellow-throated marten | LC | | 2 |
| *Mustela nudipes* | Malay weasel | LC | | 1 |
| Prionodontidae | | | 1 | 2 |
| *Prionodon linsang* | Banded linsang | LC | | 2 |
| Ursidae | | | 1 | 35 |
| *Helarctos malayanus* | Sun bear | VU | | 35 |
| Viverridae | | | 5 | 74 |
| *Arctictis binturong* | Binturong | VU | | 1 |
| *Arctogalidia trivirgata* | Small-toothed palm civet | LC | | 3 |
| *Hemigalus derbyanus* | Banded palm civet | NT | | 11 |
| *Paradoxurus hermaphroditus* | Common palm civet | LC | | 24 |
| *Paguma larvata* | Masked palm civet | LC | | 2 |
| *Viverra tangalunga* | Malay civet | LC | | 33 |
| Eulipotyphla | | | 1 | 225 |
| Erinaceidae | | | 1 | 225 |
| *Echinosorex gymnura* | Moonrat | LC | | 225 |
| Pholidota | | | 1 | 8 |
| Manidae | | | 1 | 8 |
| *Manis javanica* | Sunda pangolin | CR | | 8 |

**Table 1.** (Cont.)

| Order / Family / Species | Common name | IUCN | Species count | Detection count |
|---|---|---|---|---|
| Primates | | | 5 | 499 |
| Cercopithecidae | | | 3 | 444 |
| *Macaca fascicularis* | Crab-eating macaque | VU | | 153 |
| *Macaca nemestrina* | Southern pig-tailed macaque | EN | | 290 |
| *Nasalis larvatus* | Probiscis monkey | EN | | 1 |
| Hominidae | | | 1 | 54 |
| *Pongo pygmaeus* | Bornean orangutan | CR | | 54 |
| Tarsiidae | | | 1 | 1 |
| *Cephalopachus bancanus* | Horsfield's tarsier | VU | | 1 |
| Rodentia | | | 5 | 984 |
| Muridae | | | | |
| | Rat | - | | 88 |
| Sciuridae | | | | |
| | Squirrel | LC | | 775 |
| Hystricidae | | | 3 | 121 |
| *Hystrix brachyura* | Malayan porcupine | LC | | 45 |
| *Hystrix crassispinis* | Thick-spined porcupine | LC | | 71 |
| *Trichys fasciculata* | Long-tailed porcupine | LC | | 5 |
| Scandentia | | | 1 | 124 |
| Tupaiidae | | | | |
| *Tupaia* spp. | Treeshrew | LC | | 124 |

of daylight in over half of them (64.29 %): Squirrel species (Sciuridae), the bearded pig *Sus barbatus*, recorded primates (Bornean orangutan *Pongo pygmaeus*, crab-eating macaque *Macaca fascicularis*, and Southern pig-tailed macaque *M. nemestrina*) showed clear diurnal activity patterns, contrasting to the moonrat *Echinosorex gymnura*, rat species (Muridae), treeshrew species (Tupaiidae), and the thick-spined porcupine *Hystrix crassispinis* that were predominantly detected at night. We found the activity peak of the thick-spined porcupine just before sunrise, while the close-related Malayan porcupine *H. brachyura* was most active shortly after sunset. Cathemeral activity patterns of multiple activity peaks without clear preference for phases of daylight were exhibited by the Malayan porcupine as well as the presented small carnivore species (common palm civet *Paradoxurus hermaphroditus* and Malay civet *Viverra tangalunga*).

## Discussion

Our findings provide comprehensive indications about the conservation status and potential functional roles of mammalian diversity in the protected forest areas of REA's mixed-use landscape in Borneo. Despite the pressure of human disturbances in form of plantation activities adjacent to the habitat fragments, we inventoried a rich species community, including even several species of high conservation value that were rarely detected and internationally classified to be threatened by extinction. It remains unclear whether the protected habitat patches buffer the disappearance of a formerly intact community or whether they may sustain the mammals in a long-term manner. However, we identified a landscape-specific ecological dynamic in the area: Bottom-up from abundant oil palm crops, this dynamic seems to be largely driven by small mammal and small carnivore predator-prey interactions. Small mammals, that may likely benefit from the oil palm fruits as well as their insect pests, were detected extremely frequently and showed distinct diurnal or nocturnal activity. We found their cathemeral small carnivore predators to be the species-richest group. Moreover, herbivorous or partly herbivorous primates, Artiodactyla, and also insectivorous moonrats, were strongly represented in our data. Large predators, such as the Sunda clouded leopard, were rarely detected. In view of these dynamics, the sustainability of wildlife refugia within these mixed-use landscapes with plant cultivation focus requires careful consideration.

When grouping taxa according to our identification method (Muridae, Sciuridae, and Scandidae families, and *Muntiacus* and *Tragulus* genera), camera-trap sur-

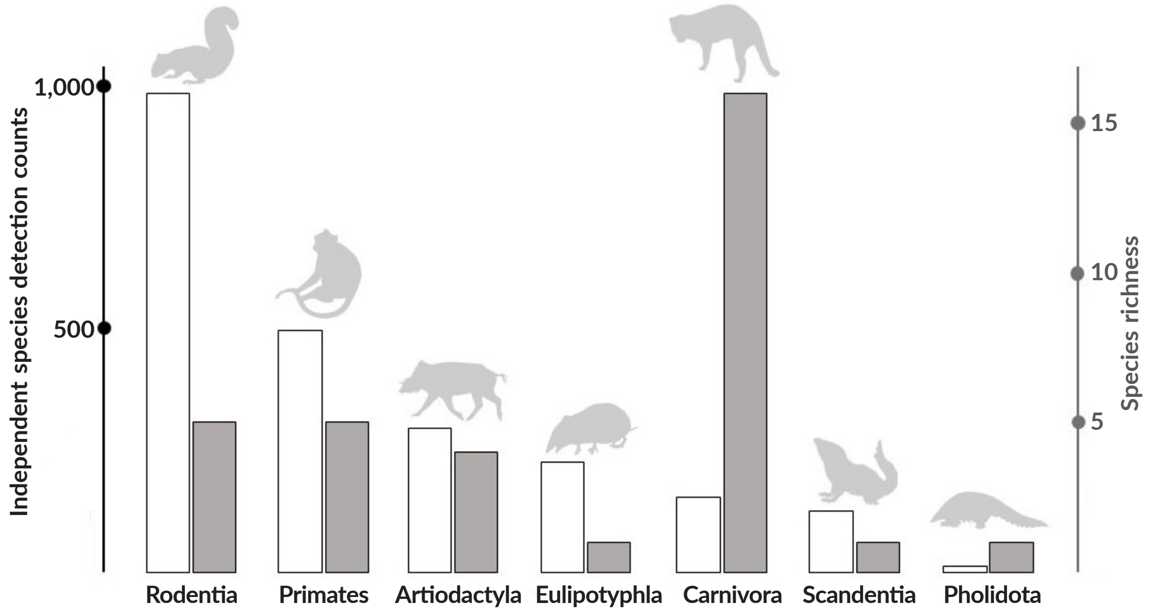


**Fig. 2.** Independent species detection counts (white bars) and minimum species richness (grey bars) for camera-trapped mammal orders in protected forest areas within oil palm plantations in East Kalimantan, Indonesian Borneo. Rodentia are represented by Hystricidae and grouped detections for the families Muridae and Sciuridae, and Scandentia are grouped by Tupaiidae. Artiodactyla include grouped detections for *Muntiacus* and *Tragulus* spp.

***Fig. 2.*** *Conteos independientes de detección de especies (barras blancas) y riqueza de especies mínima (barras grises) de los órdenes de mamíferos captados con las cámaras en zonas forestales protegidas situadas entre plantaciones de palmas aceiteras en Kalimantan Oriental, en Borneo (Indonesia). Los roedores están representados por la familia Hystricidae, las detecciones agrupadas de las familias Muridae y Sciuridae y las detecciones agrupadas de Tupaiidae. Artiodactyla incluye las detecciones agrupadas de* Muntiacus *y* Tragulus *spp.*

vey results from other Bornean forest habitats yielded a similarly high species richness of 33, such as 36 mammals in Malaysian Sabah (Wearn et al 2016) and 35 mammals in Indonesian East Kalimantan (Wall et al 2021). In mixed-use landscapes, only a small share of species occupies both forest and plantation areas, as McShea et al (2009) showed in Malaysian Borneo. There, 18 out of 24 mammals used *Acacia* plantations for transiting or foraging activities, while maintaining a close distance to the next forest (McShea et al 2009). Similar forest associations have been observed in orangutans and in Amazonian mammals in oil palm plantations (Ancrenaz et al 2015, Mendes-Oliveira et al 2017), suggesting the indispensability of forest refugia for wild mammals in mixed-use landscapes.

Regulatory regimes within the protected areas, e.g., originating from mammalian predators or humans, may act as diversely as is the mammal community. Responses to human disturbances, such as those from activities in adjacent plantation areas, can be expressed in temporal avoidance (Caldwell and Klip, 2022). Commonly, this results in increased nocturnality activity due to mainly diurnal human activity (Gaynor et al 2018), yet plantation and protected areas differ. For example, capybaras in Colombia were more nocturnal in oil palm plantations than in adjacent riparian forests (Pardo et al 2021), suggesting that habitat reserves can release wildlife from temporal partitioning against their preferred niche. We found activity patterns in the protected forest areas to be widely within the species' biological norm (Bernard et al 2013, Mohd-Azlan et al 2018, Ruppert et al 2018). Even those known to show high adaptability in their diel activity, e.g., bearded pigs, corresponded to their undisturbed diurnal activity pattern (Mohd-Azlan, 2004). Under human disturbances from visitors or hunters, they have been found to exhibit cathemeral or nocturnal patterns, respectively (Mohd-Azlan and Engkamat 2013, Mohd-Azlan et al 2018). Moreover, our results indicate that predation pressure plays a minor role for medium- to large-sized mammals, such as bearded pigs, macaques, or chevrotains, as we found an impoverished equivalent large carnivore community. We detected a Sunda clouded leopard only once. As opposed to small mammals, large carnivores in particular are prone to be highly disturbed by the presence of humans (Suraci et al 2019). This could be observed in black bears that avoided areas of high human presence, where a predator-prey community of rodents, lagomorphs, and coyotes thrived (Caldwell and Klip 2022).

While most mammals seem to be resilient habitation in REA's protected areas, the community appears to follow dynamics characteristic to mixed-use landscapes.

Plantations provide resources that may be a prevailing factor for ecological dynamics in mammal communities and their ecosystems. For instance, abundantly cultivated fruits of oil palms may form a basis for correspondingly abundant animal populations feeding

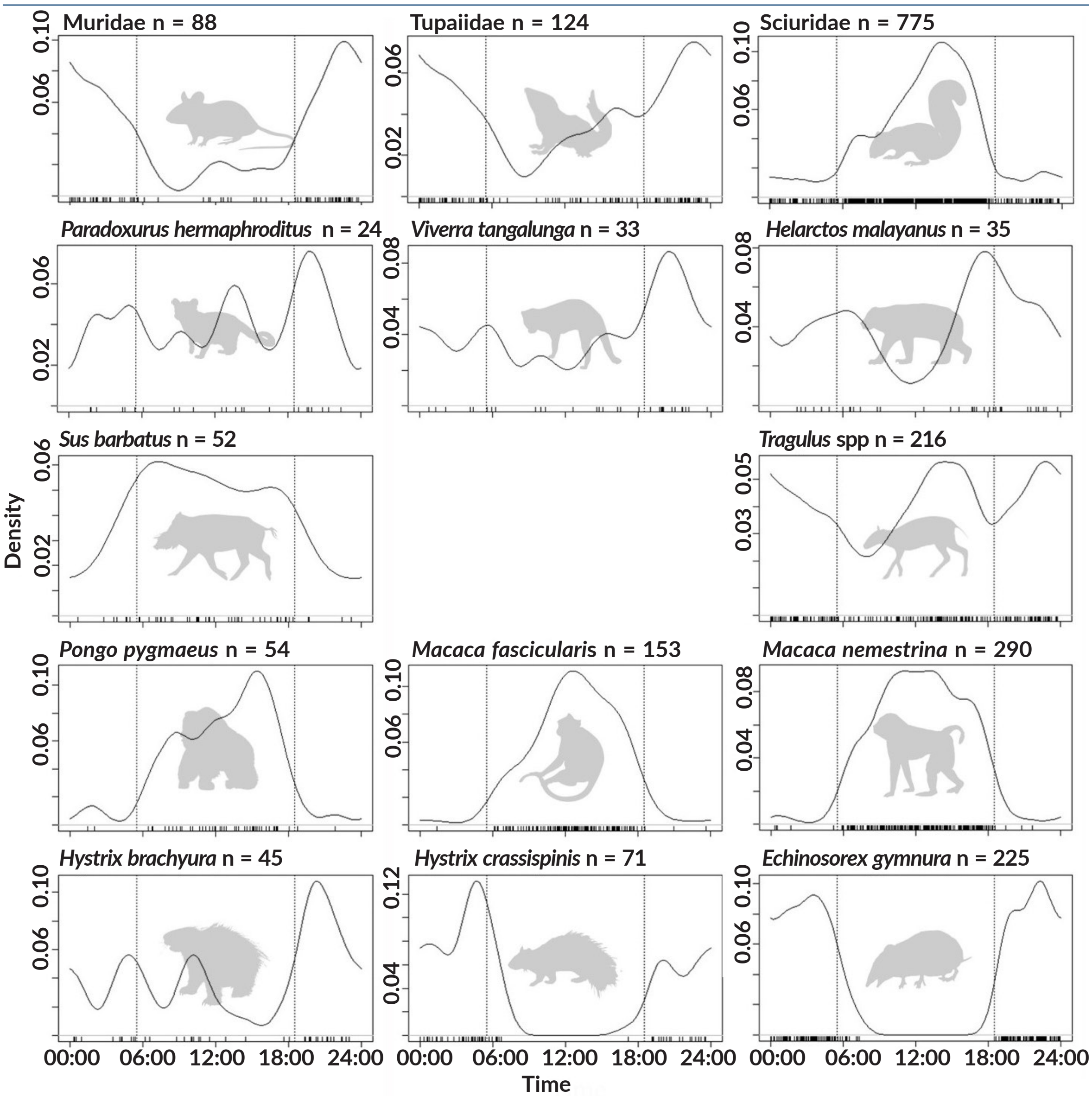


**Fig. 3.** Diel activity plots showing kernel density curves of proportional species detection counts over 24 hours. Sunrise and sunset are marked by dotted lines. Each plot is based on more than 20 independent detections (the exact count is represented by the sample size n for each species). The data were collected using camera-traps in protected forest areas in a mixed-use landscape among oil palm cultivation activities by PT.REA Kaltim Plantations, East Kalimantan, Bornean Indonesia. Muridae can be biased towards larger rat species due to camera-trapping limitations.

*Fig. 3. Gráficos de la actividad diurna en los que se muestran las curvas de la densidad del kernel de los conteos proporcionales de la detección de especies durante 24 horas. La salida y la puesta de Sol se marcan con líneas discontinuas. Cada gráfico se basa en más de 20 detecciones independientes (el número exacto está representado por el tamaño de la muestra n de cada especie). Los datos se recopilaron utilizando cámaras trampa en zonas forestales protegidas en un paisaje de usos mixtos en el que PT.REA Kaltim Plantations llevan a cabo actividades de cultivo de palma aceitera en Kalimantan Oriental, en Borneo (Indonesia). Debido a las limitaciones de las cámaras, es posible que los múridos estén sobrerrepresentados por incluir a especies de roedores más grandes.*

on them (Narayana et al 2024). These populations include semi-arboreal primates such as macaques and orangutan (fig. 4), civets, and, foremost, small mammals such as rats, squirrels, and treeshrews (Meijaard et al 2018). In high numbers, small mammals can become pests to the economic efforts of the plantations, yet in their role as prey, they can also supply carnivore communities of, for example, felids, civets, and mustelids (Moreno-Rueda and Pizarro 2010). We emphasize that small mammal species can provide diverse temporal niches (e.g., competing nocturnal rats and diurnal squirrels) that may promote a diversity of sympatric predators overlapping with their diel activities. In line with previous studies that have pointed to the


**Fig. 4.** Bornean orangutan *Pongo pygmaeus* camera-trapped in a subsequent 2020/21 survey, while feeding on the red fruits of an oil palm *Elaeis guineensis* in a protected forest area among oil palm plantations in East Kalimantan, Indonesian Borneo.

***Fig. 4.*** *El orangután de Borneo* Pongo pygmaeus *captado por una cámara en un estudio posterior de 2020/21, mientras se alimenta de los frutos rojos de una palma aceitera* Elaeis guineensis *en una zona forestal protegida entre plantaciones de palmas aceiteras en Kalimantan Oriental, en Borneo (Indonesia).*

predator-prey relationship between small mammals and small carnivores of oil palm plantations (Jennings et al 2015, Verwilghen 2015, Nurdiansyah et al 2016), we recorded the highest detection counts in small mammals and the highest species richness in small carnivores, which may be additionally released from predation pressure in absence of large carnivores. Williams et al (2018) reported comparable findings of crop areas supporting most small carnivore species. Thus, in the context of resource-rich ecosystems such as mixed-use landscapes with fruit-bearing plants at the base, bottom-up forces may be the prime driver of their dynamics.

Although we can expect Bornean mixed-use landscapes (*sensu* Stuebing 2007) to be severely impacted by humans, these landscapes are also characterized by habitat heterogeneity and high resource abundance, shaping a special ecological dynamic (Narayana et al 2024). After roughly 40 years of extensive oil palm cultivation in REA, our findings reaffirm the potential of spatially integrative countermeasures to conserve a valuable mammalian diversity within protected forest areas, functioning to support the stability and services of their ecosystems (Emmerson et al 2016, Lacher et al 2019). Mitigating threats posed by deforestation in this stronghold for global biodiversity (de Bruyn et al 2014) is of major importance, as the mammals of Borneo's lowland forests have already lost roughly one third of functionally connected habitat over the last four decades (Ocampo-Peñuela et al 2020), which has led to rapid population declines (FAO and UNEP, 2020). The amount of forest among plantations was previously estimated to be the best measure of conservation potential (Naranjo and Bodmer 2007). Facilitating conservation and production support through forest areas in mixed-use landscapes relies on ecological guidance for decision-makers based on assessments from the field that document the status and developments. Despite valuable insights gained from this study, methodlogical differences allow only limited links to past states of the area, such as during the first species inventory in 2008-2012 (Wahyudi and Stuebing 2013), only one year after REA has implemented first conservation actions.

We propose further monitoring is needed to provide key momentum for timely adaptations in conservation management (DeFries et al 2010, Rovero and Ahumada et al 2017), based on further continuity and an improved survey standard. Temporal effort as a main factor for inventorying species (Tobler et al 2008) has been surpassed when comparing our over 10,000 trap nights with a species accumulation curve plateau of 4,600 trap nights in Malaysian Borneo (Azlan 2006). However, taking into account the different habitat types in mixed-use landscapes as well as the vertical habitat stratification of tropical forests from forest floors into canopies might further advance the completeness of survey results. For example, ground-based camera-traps can represent a significant portion of the mammal community, but arboreal camera-traps can improve species detections by a further 12%, as shown for strictly arboreal species (Moore et al 2020). Also, tracking species across habitat types, including the plantations they use (Harich and Treydte 2016) and the forest strata, may help capture a more complete spectrum of activities in order to interpret their lives in the mixed-use landscape (Haysom et al 2023). Sun bears, for example, might not be as nocturnal as their detections on our camera-traps indicate. While a similar nocturnality was found in several camera-trapping studies (Guharajan et al 2018, Nakabayashi et al 2021), radiotelemetry previously provided insight into a rather diurnal pattern (Te Wong et al 2004), suggesting foraging activities in the trees. Future surveys could act as reliable early-warning systems regarding land-use impacts, saving temporal efforts by half while extending spatial efforts by combining ground-based and arboreal camera-traps.

## References


Abood SA, Lee JSH, Burivalova Z, Garcia-Ulloa J, Koh LP, 2015. Relative contributions of the logging, fiber, oil palm, and mining industries to forest loss in Indonesia. *Conservation Letters* 8(1), 58-67. DOI: 10.1111/conl.12103

Ancrenaz M, Oram F, Ambu L, Lackman I, Ahmad E, Elahan H, Kler H, Abram NK, Meijaard E, 2015. Of Pongo, palms and perceptions: a multidisciplinary assessment of Bornean orang-utans Pongo pygmaeus in an oil palm context. *Oryx* 49(3), 465-472. DOI: 10.1017/S0030605313001270

Azlan JM, 2006. Mammal diversity and conservation in a secondary forest in peninsular Malaysia. *Biodiversity Conservation* 15, 1013-1025. DOI: 10.1007/s10531-004-3953-0

Barlow J, Lennox GD, Ferreira J, Berenguer E, Lees AC, Mac Nally R, Thomson JR, de Barros Ferraz SF, Louzada J, Fonseca Oliveira VH, Parry L, Ribeiro de Castro Solar R, Vieira ICG, Aragão LEOC, Anzolin Begotti R, Braga RF, Moreira Cardoso T, de Oliveira Jr RC, Souza Jr CM, Moura NG, Serra Nunes S, Siqueira JV, Pardini R, Silveira JM, Vaz-de-Mello FZ, Stulpen Veiga RC, Venturieri A, Gardner TA, 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535(7610), 144-147. DOI: 10.1038/nature18326

Bernard H, Ahmad AH, Brodie J, Giordano AJ, Lakim M, Amat R, Hue SKP, Khee LS, Tuuga A, Malim PT, Lim-Hasegawa D, Wai YS, Sinun W, 2013. Camera-trapping survey of mammals in and around Imbak Canyon Conservation Area in Sabah, Malaysian Borneo. The *Raffles Bulletin of Zoology* 61(2), 861-870.

BMKG (Meteorological Climatological and Geophysical Agency), 2020. *Time Mark*. Available online at: https://www.bmkg.go.id/tanda-waktu/terbit-terbenam-matahari.bmkg?Tgl=17&Bln=12&Thn=2020&Cari=True [Accessed 22 May 2022].

Butchart SH, Akcakaya HR, Kennedy E, Hilton-Taylor C, 2006. Biodiversity indicators based on trends in conservation status: strengths of the IUCN Red List Index. *Conservation Biology* 20(2), 579-581. DOI: 10.1111/j.1523-1739.2006.00410.x

Caldwell MR, Klip JMK, 2022. Patterns of wildlife activity and predator-prey dynamics in a highly touristed area. *The Southwestern Naturalist* 66(1), 35-47. DOI: 10.1894/0038-4909-66.1.35

Clevenger AP, Dorsey B, Barrueto M, Ford AT, 2013. Activity patterns of wildlife at crossing structures as measure of adaptability and performance. *Proceedings of the 2013 International Conference on Ecology and Transportation (ICOET 2013).* North Carolina State University, Raleigh. Available online at: http://www. icoet. net/icoet_2013 [Accessed 22 May 2022].

Cushman SA, Macdonald EA, Landguth EL, Malhi Y, Macdonald DW, 2017. Multiple-scale prediction of forest loss risk across Borneo. *Landscape Ecology* 32(8), 1581-1598. DOI: 10.1007/s10980-017-0520-0

de Bruyn M, Stelbrink B, Morley RJ, Hall R, Carvalho GR, Cannon CH, van den Bergh G, Meijaard E, Metcalfe I, Boitani L, Maiorano L, Shoup R, von Rintelen T, 2014. Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Systematic Biology* 63(6), 879-901. DOI: 10.1093/sysbio/syu047

DeFries R, Rovero F, Wright P, Ahumada J, Andelmann S, Brandon K, Dempewolf J, Hansen A, Hewson J, Jianguo L, 2010. From plot to landscape scale: linking tropical biodiversity measurements across spatial scales. *Frontiers in Ecology and the Environment* 8(3), 153-160. DOI: 10.1890/080104

Díaz-Ruiz F, Caro J, Delibes-Mateos M, Arroyo B, Ferreras P, 2016. Drivers of red fox (*Vulpes vulpes*) daily activity: prey availability, human disturbance or habitat structure? *Journal of Zoology* 298(2), 128-138. DOI: 10.1111/jzo.12294

Directorate General of Estate Crops, 2019. Tree Crop Estate Statistics of Indonesia 2018-2020: Palm Oil. Ministry of Agriculture, Jakarta, December 2019, https://repository.pertanian.go.id/server/api/core/bitstreams/a700c5b4-5ef1-4ee6-bb0d-d6c6e1179e63/content [Accessed on 23 May 2022].

Dirzo R, Raven PH, 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* 28, 137-167. DOI: 10.1146/annurev.energy.28.050302.105532

Emmerson M, Morales MB, Oñate JJ, Batary P, Berendse F, Liira J, Aavik T, Guerrero I, Bommarco R, Eggers S, Part T, Tscharntke T, Weisser W, Clement L, Bengtsson J, 2016. How agricultural intensification affects biodiversity and ecosystem services. In: *Advances in Ecological Research* 55, 43-97. DOI: 10.1016/bs.aecr.2016.08.005

FAO, UNEP, 2020. The State of the World's Forests 2020. Forests, biodiversity and people, Rome. DOI: 10.4060/ca8642en

Fischer J, Abson DJ, Butsic V, Chappell MJ, Ekroos J, Hanspach J, Kuemmerle T, Smith HG, von Wehren H, 2013. Land sparing versus land sharing: moving forward. *Conservation Letters* 7(3), 149-157. DOI: 10.1111/conl.12084

Flynn DF, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F, 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* 12(1), 22-33. DOI: 10.1111/j.1461-0248.2008.01255.x

Gaveau DLA, Locatelli B, Salim MA, Yaen H, Pacheco P, Sheil D, 2018. Rise and fall of forest loss and industrial plantations in Borneo (2000–2017). *Conservation Letters* 12(3), e12622. DOI: 10.1111/conl.12622

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS, 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360(6394), 1232-1235. DOI: 10.1126/science.aar7121

Goldammer JG, Seibert B, 1990. The impact of droughts and forest fires on tropical lowland rain forest of East Kalimantan. In: *Fire in the Tropical Biota. Ecological Studies* 84 (JG Goldammer, Ed). Springer, Berlin, Heidelberg. DOI: 10.1007/978-3-642-75395-4_2

Gordon CH, Stewart AME, 2007. The use of logging roads by clouded leopards. *Cat News* 47, 12-13. Available online at: https://typeset.io/pdf/the-use-of-logging-roads-by-clouded-leopards-188vpflkdd.pdf [Accessed 20 July 2021].

Guharajan R, Arnold TW, Bolongon G, Dibden GH, Abram NK, Teoh S., Magguna MA, Goossens B, Wong ST, Nathan SKSS, Garshelis DL, 2018. Survival strategies of a frugivore, the sun bear, in a forest-oil palm landscape. *Biodiversity and Conservation* 27(14), 3657-3677. DOI: 10.1007/s10531-018-1619-6

Harich FK, Treydte AC, 2016. Mammalian wildlife diversity in rubber and oil palm plantations. *CAB Reviews* 11. DOI: 10.1079/PAVSNNR201611020

Haysom JK, Deere NJ, Mahyudin A, Struebig MJ, 2023. Stratified activity: Vertical partitioning of the diel cycle by rainforest mammals in Borneo. *Biotropica* 55(5), 991-1005. DOI: 10.1111/btp.13248

Hoffmann AA, Hinrichs A, Siegert F, 2000. Fire damages in East Kalimantan in 1997/98: relations to and land use and proposals for future action. *International Forest Fire News* 22, 31–35, https://gfmc.online/iffn/country/id/id_23.html

Hut RA, Kronfeld-Schor N, van der Vinne V, De la Iglesia H, 2012. In search of a temporal niche: environmental factors. *Progress in Brain Research* 199, 281-304. DOI: 10.1016/B978-0-444-59427-3.00017-4

Hutton JM, Leader-Williams N, 2003. Sustainable use and incentive-driven conservation: realigning human and conservation interests. *Oryx* 37(2), 215-226. DOI: 10.1017/S0030605303000395

IUCN, 2021. *IUCN Red List of Threatened Species.* Available online at: https://www.iucnredlist.org/ [Accessed 20 July 2021].

Jennings AP, Naim M, Advento AD, Aryawan AAK, Ps S, Caliman JP, Verwilghen A, Veron G, 2015. Diversity and occupancy of small carnivores within oil palm plantations in central Sumatra, Indonesia. *Mammal Research* 60(2), 181-188. DOI: 10.1007/s13364-015-0217-1

Khatiwada D, Palmén C, Silveira S, 2021. Evaluating the palm oil demand in Indonesia: production trends, yields, and emerging issues. *Biofuels* 12(2), 135-147. DOI: 10.1080/17597269.2018.1461520

Lacher Jr TE, Davidson AD, Fleming TH, Gómez-Ruiz EP, McCracken

GF, Owen-Smith N, Peres CA, Vander Wall SB, 2019. The functional roles of mammals in ecosystems. *Journal of Mammalogy* 100(3), 942-964. DOI: 10.1093/jmammal/gyy183
Langner A, Miettinen J, Siegert F, 2007. Land cover change 2002–2005 in Borneo and the role of fire derived from MODIS imagery. *Global Change Biology* 13(11), 2329-2340. DOI: 10.1111/j.1365-2486.2007.01442.x
Lee, T. M., Jetz, W., 2008. Future battlegrounds for conservation under global change. *Proceedings of the Royal Society B: Biological Sciences* 275(1640), 1261–1270. DOI: 10.1098/rspb.2007.1732
Love K, Kurz DJ, Vaughan IP, Ke A, Evans LJ, Goossens B, 2018. Bearded pig (*Sus barbatus*) utilisation of a fragmented forest–oil palm landscape in Sabah, Malaysian Borneo. *Wildlife Research* 44(8), 603-612. DOI: 10.1071/WR16189
Mason NW, De Bello F, 2013. Functional diversity: a tool for answering challenging ecological questions. *Journal of Vegetation Science* 24(5), 777-780. DOI: 10.1111/jvs.12097
McShea WJ, Stewart C, Peterson L, Erb P, Stuebing R, Giman B, 2009. The importance of secondary forest blocks for terrestrial mammals within an *Acacia*/secondary forest matrix in Sarawak, Malaysia. *Biological Conservation* 142(12), 3108-3119. DOI: 10.1016/j.biocon.2009.08.009
Meijaard E, Garcia-Ulloa J, Sheil D, Wich SA, Carlson KM, Juffe-Bignoli D, Brooks TM, 2018. Oil palm and biodiversity: A situation analysis by the IUCN Oil Palm Task Force. IUCN Oil Palm Task Force Gland, Switzerland. DOI: 10.2305/IUCN.CH.2018.11.en
Mendes-Oliveira AC, Peres CA, Maués PCRA, Oliveira GL, Mineiro IG, de Maria SLS, Lima RC, 2017. Oil palm monoculture induces drastic erosion of an Amazonian forest mammal fauna. *PloS One* 12(11), e0187650. DOI: 10.1371/journal.pone.0187650
Meredith M, Ridout MS, 2016. *Overview of the overlap package. R Project*, 1-9. Available online at: https://cran.microsoft.com/snapshot /2016-08-05/web/packages/overlap/vignettes/overlap.pdf [Accessed 20 June 2020].
Milne S, Martin JGA, Reynolds G, Vairappan CS, Slade EM, Brodie JF, Wich SA, Williamson N, Burslem DFRP, 2021. Drivers of Bornean organutan distribution across a multiple-use tropical landscape. *Remote Sensing* 13(3), 458. DOI: 10.3390/rs13030458
Mohd-Azlan J, 2004. *Camera trapping survey in the Maludam National Park, Betong Division Sarawak*. Forest Department Sarawak, and Sarawak Forestry Corporation, Wageningen, Kuching.
Mohd-Azlan J, Engkamat L, 2013. Camera trapping and conservation in Lanjak Entimau wildlife sanctuary, Sarawak, Borneo. *The Raffles Bulletin of Zoology* 61, 397-405.
Mohd-Azlan J, Nurul-Asna H, Jailan TS, Tuen AA, Engkamat L, Abdillah DN, Zainudin R, Brodie JF, 2018. Camera trapping of terrestrial animals in Tanjung Datu National Park, Sarawak, Borneo. *The Raffles Bulletin of Zoology* 66, 587-594.
Moore JF, Pine WE, Mulindahabi F, Niyigaba P, Gatorano G, Masozera MK, Beaudrot L, 2020. Comparison of species richness and detection between line transects, ground camera traps, and arboreal camera traps. *Animal Conservation* 23(5), 561-572. DOI: 10.1111/acv.12569
Moreno-Rueda G, Pizarro M, 2010. Rodent species richness is correlated with carnivore species richness in Spain. *Revue d'Ecologie, Terre et Vie* 65(3), 265-278. DOI: 10.3406/revec.2010.1531
Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J, 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853-858. DOI: 10.1038/35002501
Nakabayashi M, Kanamori T, Matsukawa A, Tangah J, Tuuga A, Malim PT, Bernard H, Ahmad AH, Matsuda O, Hanya G, 2021. Temporal activity patterns suggesting niche partitioning of sympatric carnivores in Borneo, Malaysia. *Scientific Reports* 11(1), 19819. DOI: 10.1038/s41598-021-99341-6
Naranjo EJ, Bodmer RE, 2007. Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. *Biological Conservation* 138(3-4), 412-420. DOI: 10.1016/j.biocon.2007.05.010
Narayana S, Affandi A, Yahya MS, Tohiran KA, Jambari A, Norhisham AR, Azhar B, 2024. Site occupancy of native terrestrial mammals in oil palm landscapes is driven by the synergy of land sparing and sharing strategies. *Journal for Nature Conservation* 80, 126634. DOI: 10.1016/j.jnc.2024.126634
Niedballa J, Wilting A, Sollmann R, Hofer H, Courtiol A, 2019. Assessing analytical methods for detecting spatiotemporal interactions between species from camera trapping data. *Remote Sensing in Ecology and Conservation* 5(3), 272-285. DOI: 10.1002/rse2.107
Nurdiansyah F, Denmead LH, Clough Y, Wiegand K, Tscharntke T, 2016. Biological control in Indonesian oil palm potentially enhanced by landscape context. *Agriculture, Ecosystems and Environment* 232, 141-149. DOI: 10.1016/j.agee.2016.08.006
Nurhidayah L, Alam S, 2020. The forest and ist biodiversity: Assessing the adequacy of biodiversity protection laws in Indonesia. *Asia Pacific Journal of Environmental Law* 23(2), 178-201. DOI: 10.4337/APJEL.2020.02.04
Ocampo-Peñuela N, Garcia-Ulloa J, Kornecki I, Philipson CD, Ghazoul J, 2020. Impacts of four decades of forest loss on vertebrate functional habitat on Borneo. *Frontiers in Forests and Global Change* 3, 53. DOI: 10.3389/ffgc.2020.00053
Pardo LE, Edwards W, Campbell MJ, Gómez-Valencia B, Clements GR, Laurance WF, 2021. Effects of oil palm and human presence on activity patterns of terrestrial mammals in the Colombian Llanos. *Mammalian Biology* 101(6), 775-789. DOI: 10.1007/s42991-021-00153-y
Potapov P, Hansen MC, Laestadius L, Turubanova S, Yaroshenko A, Thies C, Smith W, Zhuravleva I, Komarova A, Minnemeyer S, Esipova E, 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science Advances* 3(1), e1600821. DOI: 10.1126/sciadv.1600821
R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org [Accessed 14 April 2020].
Ridout MS, Linkie M, 2009. Estimating overlap of daily activity patterns from camera trap data. *JABES: Journal of Agricultural, Biological, and Environmental Statistics* 14(3), 322-337. DOI: 10.1198/jabes.2009.08038
Rovero F, Ahumada J, 2017. The Tropical Ecology, Assessment and Monitoring (TEAM) Network: An early warning system for tropical rain forests. *Science of the Total Environment* 574(1), 914-923. DOI: 10.1016/j.scitotenv.2016.09.146
Ruppert N, Holzner A, See KW, Gisbrecht A, Beck A, 2018. Activity Budgets and Habitat Use of Wild Southern Pig-Tailed Macaques (*Macaca nemestrina*) in Oil Palm Plantation and Forest. *International Journal of Primatology* 39(2), 237-251. DOI: 10.1007/s10764-018-0032-z
Sinclair AR, Mduma S, Brashares JS, 2003. Patterns of predation in a diverse predator–prey system. *Nature* 425(6955), 288-290. DOI: 10.1038/nature01934
Strang K, Rusli N, 2021. The challenges of conserving biodiversity: A spotlight on Southeast Asia. *Wildlife Biodiversity Conservation*: 47-66. DOI: 10.1007/978-3-030-64682-0_3
Stuebing RB (Ed), 2007. Biodiversity in Theory and Practice: Lessons from the Planted Forest Zone, Sarawak. *Proceedings of the Regional Conference of Biodiversity Conservation in Tropical Planted Forests in Southeast Asia, 15-18 January 2007*: 25-38. Forest Dept, Sarawak Forestry Corp., Grand Perfect Sdn Bhd Kuching, Sarawak.
Suraci JP, Clinchy M, Zanette LY, Wilmers CC, 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters* 22(10), 1578-1586. DOI: https://doi.org/10.1111/ele.13344
Te Wong S, Servheen CW, Ambu L, 2004. Home range, movement and activity patterns, and bedding sites of Malayan sun bears Helarctos malayanus in the rainforest of Borneo. *Biological Conservation* 119(2), 169-181.
Tobler MW, Carrillo-Percastegui SE, Leite Pitman R, Mares R, Powell G, 2008. An evaluation of camera traps for inventorying large-and medium-sized terrestrial rainforest mammals. *Animal Conservation* 11(3), 169-178. DOI: 10.1111/j.1469-1795.2008.00169.x
van Schaik CP, Griffiths M, 1996. Activity periods of Indonesian rain forest mammals. *Biotropica* 28(1), 105-112. DOI: 10.2307/2388775
van Steenis CGGJ, 1935. Schets van de flora van het eiland Dapoer (Duizend Eilanden). *De Tropische Natuur* 24(2), 31-34.
Varkkey H, 2012. The growth and prospects for the oil palm plantation industry in Indonesia. *Oil Palm Industry Economic Journal* 12(2), 1-13.
Verwilghen A, 2015. Rodent pest management and predators communities in oil palm plantations in Indonesia: comparison of two contrasted system. Doctoral dissertation, Université de Franche-Comté.
Wahyudi D, Stuebing RB, 2013. Camera trapping as a conservation tool in a mixed-use landscape in East Kalimantan. *Journal of Indonesian Natural History* 1(2), 37-46.
Wall JL, Loken B, Brodie JF, 2021. Reconciling resource extraction and species conservation in a multi-use landscape: Immediate and long-term impacts of logging on rainforest mammal diversity. *Global Ecology and Conservation* 28, e01642. DOI: 10.1016/j.gecco.2021.e01642
Wearn OR, Carbone C, Rowcliffe JM, Bernard H, Ewers RM, 2016. Grain-dependent responses of mammalian diversity to land use and the implications for conservation set-aside. *Ecological Applications* 26(5), 1409-1420. Available online at: http://www.jstor.org/stable/24818125 [Accessed 20 June 2020].
Williams ST, Maree N, Taylor P, Belmain SR, Keith M, Swanepoel LH,

2018. Predation by small mammalian carnivores in rural agro-ecosystems: an undervalued ecosystem service? *Ecosystem Services* 30(C), 362-371. DOI: 10.1016/j.ecoser.2017.12.006
Wu Y, Wang H, Wang H, Feng J, 2018. Arms race of temporal partitioning between carnivorous and herbivorous mammals. *Scientific Report* 8(1), 1713. DOI: 10.1038/s41598-018-20098-6
Yasuda RM, Tsuyuki S, 2012. Comparison of mammalian communities in a human-disturbed tropical landscape in East Kalimantan, Indonesia. *Mammal Study* 37(4), 299-311. DOI: 10.3106/041.037.0404
Yue S, Brodie JF, Zipkin EF, Bernard H, 2015. Oil palm plantations fail to support mammal diversity. *Ecological Applications* 25(8), 2285-2292. DOI: 10.1890/14-1928.1

**Acknowledgements**
This paper has been possible thanks to the initiative of Thomas Ziegler who brought the authors together and inspires unbounded scientific practice. Our deepest thanks for fostering research and conservation there go to Rob Stuebing. Without his indispensable scientific guidance and support, the implementation of this study would not have been possible. Keystones for data collection, including remarkable field work, were laid by REA KON's team, especially Ingan Njuk, Budi Utomo and Sebastianus Njau. Additional support during activities on site and great contributions to data processing were made by Jonas Schweikhard. We also deeply appreciate the work of James Pasaribu and Suimah Darmansyah who provided invaluable administrative and technical support. Special thanks are extended to Bjorn Mols for his assistance with data interpretation and Eva Sánchez Arribas for Spanish translations. Order indicating illustrations were obtained from https://www.phylopic.org/ under the CC BY 4.0 license https://creativecommons.org/licenses/by/4.0/

**Author contributions**
**K. Kasper**: conceptualization, validation, data curation, formal analysis, visualization, writing original draft; **N. Devriance**: conceptualization, methodology, investigation, validation, writing, review and editing; **K. Aran**: conceptualization, methodology, investigation and validation; **B. Martin**: conceptualization, investigation, writing, review and editing.

**Conflicts of interest**
No conflicts declared.

**Funding**
This study was funded by PT.REA Kaltim Plantations and Group, which intructed and authorised the Conservation Department (REA KON) to undertake the mission to 'conserve or enhance landscape level biodiversity in all plantation sites and adjacent natural habitats', concerning foremost the original biodiversity of the landscape, human impacts, and long-term developments.

**Complete affiliations**
**Katharina Kasper**, Mammal Research Institute (MRI), Polish Academy of Sciences, Stoczek 1, 17-230, Białowieża, Poland; and Institute of Ecology, Evolution and Diversity, Goethe University, Max-von-Laue-Str. 13, 60438, Frankfurt am Main, Germany.
**Nova Devriance, Kahang Aran**, Conservation Department (REA KON), PT.REA Kaltim Plantations and Group, Hulu Belayan, East Kalimantan, Indonesia.
**Brian Martin**, Yayasan Uiln, Jl. Wira Benu RT.2, Muara Ancalong, East Kalimantan, Indonesia; and Yayasan Jejak Pulang, Jl. Soekarno Hatta RT.9, Samboja, East Kalimantan, Indonesia.