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Life in the Canopy:

Revealing the hidden diversity and ecology of Borneo's arboreal mammals

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Life in the canopy: Revealing the hidden diversity and ecology of Borneo's arboreal mammals

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"Kadangkala, masa depan melawatkan kita dan memberitahu apa yang kita sepatutnya jadi

Sometimes the future visits us and tells us what we should be."

[Random Acts of Heroic Love, Danny Scheinmann]

~ ~ ~

Author declaration

J.K. Haysom wrote all of the chapters, with editorial suggestions made by PhD supervisors M.J. Struebig, and J. Groombridge, and mentor N.J. Deere. Chapters 2-4 originated from discussions between J.K. Haysom, M.J. Struebig, and N.J. Deere. Data underpinning Chapters 2-4 derive from fieldwork undertaken in Borneo between 2017 and 2019, assisted with in-country logistics by A. Mahyudin, J. Jami, G. Reynolds, and R. Gray. Sampling protocols were developed by J.K. Haysom, with input from M.J. Struebig and N.J. Deere. Fieldwork was completed by J.K. Haysom, who led on the design for the canopy camera-trapping campaign, and was assisted by the Stability of Altered Forest Ecosystems Project research team: M.S. Bationg, A. Jupri, F. John, A. James, M.-L. Asri, M.-D. Asri, S.M. Rizan, A.-A. Siliwong, and D. Paul. Additional collaborations with other researchers are outlined below.

Chapter 2. Data analysis was performed by J.K. Haysom, with assistance from O.R. Wearn, N.J. Deere, and M.J. Struebig. J.K. Haysom, M.J. Struebig, N.J. Deere, O.R. Wearn, A. Mahyudin, J. Jami, and G. Reynolds wrote the chapter for publication, with J.K. Haysom as the first author.

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Abstract

Tropical rainforest canopies are structurally complex, floristically diverse, and three-dimensionally vast. They play key roles in ecological processes such as nutrient cycling, carbon storage, and plant primary productivity. An ability to utilise the canopy provides wildlife with access to resources and environmental niches not available at ground level, thereby facilitating the co-existence of a very high number of species, and tropical canopies support a substantial proportion of a forest's vertebrate and invertebrate life. Mammals are a biodiverse and functionally important group and within rainforests, more than half of species are arboreal or semi-arboreal, i.e. exclusively or habitually ese the canopy space. However, due to the practical difficulties of sampling at height, tropical forest canopies remain relatively unexplored, and most arboreal taxa, with the exception of some primates, are little known to science.

Arboreal mammal communities consist mainly of species that are small-bodied, cryptically coloured, elusive, and/or nocturnal; yet, traditional ground-based sampling techniques are biased towards larger-bodied, diurnal mammals that do not flee in the presence of people. Camera-trapping, widely used in terrestrial research, has started to be implemented at canopy level with promising initial results, particularly for single-species studies or those focussing on animal use of habitat features such as canopy bridges. However, the implementation of canopy camera-trapping to inventory and study arboreal communities has to date been limited to eight sites, all in the Neotropics or Africa, and with three focussing only on medium- and large-bodied mammals. Furthermore, around half of all arboreal mammal studies utilising camera-traps deployed units at heights of ten metres or less which, in rainforests where canopies reach between 30-60 metres high, misses an extensive portion of the vertical habitat. These factors point to a clear gap in the application of the methodology, and the understanding of arboreal mammal communities, in the extremely tall and hyper-diverse rainforests of Southeast Asia.

The unique height and structure of rainforests on the island of Borneo have given rise to an exceptionally high diversity of canopy-dwelling wildlife; more than half of all mammals are arboreal or semi-arboreal, and the island represents the world epicentre of gliding vertebrate diversity, including 15 gliding mammal species (14 flying squirrels and the colugo, or 'flying lemur'). Meanwhile, logging is a pervasive threat to forests globally, with some of the highest timber extraction rates in Borneo due to the dominance of commercially valuable dipterocarp trees. Many terrestrial taxa are able to persist in recovering-logged forest, but the changes in habitat structure associated with logging activities are likely to have a greater impact on species that directly depend on the complexity and connectivity of the canopy architecture. However, studies explicitly investigating arboreal mammal responses to logging are lacking, and in general, our understanding of rainforest communities is skewed towards terrestrial species and processes. We therefore risk underestimating both the diversity and potential vulnerability of arboreal wildlife, with implications for conservation, and habitat management and restoration.

At our current state of knowledge, it is not clear (i) whether camera-traps set in the forest canopy are an effective sampling method for arboreal mammals in Borneo's immensely tall and biodiverse rainforests; (ii) what the outcome of this sampling would be in terms of community richness and distinctness from terrestrial mammals; and (iii) whether, and to what extent, arboreal mammals are affected by logging.

In this thesis, I document the first community-wide investigation of Borneo's arboreal mammal community using camera-traps. I deployed a network of cameras in the rainforest canopy, paired with units at ground level in both unlogged and recovering-logged forest areas, to test the efficacy and cost-effectiveness of this method in Borneo. Sampling was conducted across fifty locations, divided equally between unlogged forest (*N*=25) and recovering-logged forest (*N*=25), with cameras (Reconyx Hyperfire HC500) deployed in a grid formation and spaced on average 1.26 km apart (range = 0.5-4 km). Every sampling location comprised one terrestrial camera-trap and one canopy camera-trap and, to evaluate the utility of placing more than one canopy camera per tree to maximise species detections, experimental second-canopy units were deployed at a subset of twenty locations, selected at random and divided equally between unlogged (*N*=10) and recovering-logged (*N*=10) forest areas. Total sampling thus comprised fifty terrestrial cameras and seventy canopy cameras. Terrestrial camera-traps were set approximately 0.3 m above the ground, while canopy units were set between heights of 9.8-52.3 m (mean = 25.9 m). Cameras at each location were deployed for 7-8 months except the experimental second-canopy units, which were in place for a subset of 3 months. After accounting for malfunctions, mammal detection data were obtained from 17,226 camera-trap nights (CTN): 6,661 CTN from terrestrial cameras; 9,156 CTN from canopy cameras; and an additional 1,409 CTN from experimental second-canopy units. Using these data, I quantify species diversity, community composition, and diel activity patterns, and document responses to logging, of both arboreal and terrestrial mammals, finding that differences across strata are much greater than differences between unlogged and recovering-logged forest. I further quantify relationships between mammal occurrence and a suite of remotely-sensed, high-resolution vegetation covariates, including a novel measure of canopy connectivity, and show that this is by far the most important predictor of occupancy for arboreal species among many potential covariates.

My results illustrate the applicability of canopy camera-trapping to study arboreal communities in Borneo, and extend those of terrestrial studies by demonstrating that recovering-logged forests can maintain mammal diversity across strata, underscoring their value for species conservation. However, I also highlight that the arboreal community as a whole, and particular taxa within it, are more vulnerable to the effects of habitat degradation than their terrestrial counterparts.

Keywords: arboreal mammal | community inventory | canopy sampling | camera-trap | diel activity | occupancy | forest structure | LiDAR | connectivity | logging impact study | terrestrial comparison | whole community conservation | vertical stratification

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Chapter 1 Introduction

1.1 Tropical rainforests and tropical rainforest canopies

A forest is not a forest without a canopy: the interlinking architecture of trunks, branches, stems, and vines that comprise the vegetation layers from a few metres above ground level to the uppermost tree crowns (Moffett 2000). And yet, forest canopies, especially in tropical regions, remain one of the last ecological frontiers (Lowman 2020). Their height and complexity – the very characteristics that define them – present significant challenges to access, exploration, and sampling. Consequently, our knowledge and understanding of canopy habitats and their fauna lags far behind that of terrestrial (i.e. ground-based) systems (Zhu *et al.* 2021).

Tropical forests are crucial to life on earth, covering less than 12% of the ice-free land surface, but storing a quarter of all the carbon in land-based ecosystems, while producing a third of the planet's net primary productivity (Bonan 2008). They are key components in global biogeochemical and hydrological cycles (Edwards *et al.* 2014), and at the regional scale, their daily pattern of transpiration creates localised weather systems (Makarieva *et al.* 2014). What is perhaps less often considered is that a major part of these processes occurs within the canopy itself (Cannon *et al.* 2021). Old growth tropical rainforests are characterised by their immense height (Dudley and DeVries 1990), structural complexity (Lowman and Moffett 1993), and density of canopy-level vegetation, resulting in dark, shaded conditions on the forest floor and a relatively open habitat at ground level (Milodowski *et al.* 2021). The majority of biomass, foliage, photosynthetic and reproductive structures (i.e. young leaves, flowers, and fruit) in an undisturbed tropical forest is thus contained in the aboveground strata (Lowman and Moffett 1993), with canopies providing a key physical link in ground-to-atmosphere cycles (Lowman and Wittman 1996; Roisin *et al.* 2013).

Equally, the biodiversity for which rainforests are renowned is not confined to the forest floor. Tropical forest ecosystems support at least two-thirds of all land-based biodiversity (Gardner *et al.* 2009). Extremely high levels of plant species richness are linked to year-round climatic stability and availability of resources (Oliveira and Scheffers 2018), and tropical canopies are the most structurally complex of any forest ecosystem, with far more varied tree architecture than temperate regions (Lowman and Moffett 1993). This complexity and floristic diversity gives rise to a high variation in localised substrate characteristics (e.g.

branch strength, texture, and surface chemistry) within the canopy space (Lowman and Rinker 2004), and steep microclimatic gradients across the vertical column (Nakamura *et al.* 2017).

Consequently, tropical canopies contain a great variety of environmental niches, and the ability to partition these niches across both horizontal and vertical space facilitates the co-existence of a great number of animal species (Oliveira and Scheffers 2018). Indeed, a review of ten years of research from across tropical locations found that more than three-quarters of rainforest vertebrates are arboreal or semi-arboreal (i.e. dwell exclusively in, or habitually use, the canopy), with a high degree of consistency across sites despite differences in their geologic and evolutionary history, and the taxonomic composition of their faunal communities (Kays and Allison 2001). Because of the variation in physical and environmental conditions in the canopy, arboreality – the ability to climb into and utilise the canopy space – can be seen as a form of ecological plasticity, which benefits wildlife by providing access to structural and foraging resources unavailable on the forest floor (Shanahan and Compton 2001; Scheffers *et al.* 2017). For example, cavities in tree trunks are important nest sites for a variety of species (Cockle *et al.* 2011; Honey *et al.* 2021), while being able to reach canopy-level flowers, fruits, and seeds provides a foraging advantage over terrestrial (i.e. ground-dwelling) species, which must wait for them to fall to ground level (Oliveira and Scheffers 2018). An arboreal lifestyle may also confer reduced mortality risk. Evidence suggests that canopy-dwelling species have increased longevity compared to closely-related terrestrial counterparts (e.g. tree- vs. ground-dwelling squirrels), perhaps because of reduced exposure to ground-based predators, disease and environmental hazards (Shattuck and Williams 2010).

Despite these many reasons to study canopy ecosystems, the stature and structure of tropical rainforests present significant barriers to canopy access, which have led to an historic under-sampling of these habitats and their resident wildlife (Lowman and Moffett 1993; Cannon *et al.* 2021). The resultant ground-level bias almost certainly means that the diversity, abundance, and functional roles of arboreal species, and their interactions within community dynamics, have been consistently underestimated (Lowman and Moffett 1993; Zhu *et al.* 2021).

1.2 The Borneo context

The island of Borneo in Southeast Asia is divided between the Malaysian states of Sabah and Sarawak, the Indonesian province of Kalimantan, and the independent sultanate of Brunei Darussalam. It is the world's third largest island and supports 37 million hectares of tropical rainforest (Gaveau *et al.* 2016). Borneo's rainforests are among the most structurally complex

(Ehbrecht *et al.* 2021) and floristically diverse (Barthlott *et al.* 2005; Corlett 2016) on Earth, and recent analyses of rarely-preserved fossilised leaves indicate that these forests have remained largely unchanged for at least the last four million years (Wilf *et al.* 2022).

Bornean lowland rainforests are distinguished from those of other regions by a predominance of dipterocarp trees (family *Dipterocarpaceae*). Whereas in the American and African tropics, average canopy height is 30-45 metres, with occasional emergent trees rising up to 60 metres, in Borneo the canopy reaches 40-60 metres and has a greater abundance of emergents, which commonly exceed 70 metres (Dudley and DeVries 1990). Recent airborne LiDAR (Light Detection And Ranging) surveys over Sabah have documented the presence of several giant trees over 90 metres in height, and led to the identification of the world's tallest tropical tree to date, at 100.8 metres (Shenkin *et al.* 2019). Bornean forests are also characterised by a lower density of lianas (Emmons and Gentry 1983) – woody climbing plants that provide movement pathways in the canopy by linking tree crowns (e.g. one individual vine in Panama was recorded to connect 64 trees (Putz 1988)). Rainforest canopies in Borneo therefore tend to be taller, more uneven, and relatively less connected compared to those in the Neotropics or Africa.

These structural differences present different selection pressures for tree-dwelling wildlife, and are thought to have been the driving forces behind the prevalence of gliding vertebrates in Southeast Asia, versus prehensile-tailed vertebrates in the Neotropics (Emmons and Gentry 1983). The ability to glide between distant, unconnected treetops confers energetic advantages in tall, non-uniform canopies over descending to canopy level, travelling along branches, and re-ascending the next tree (Emmons and Gentry 1983). For all gliding mammals and particularly larger-bodied species, the energetic cost of a glide reduces as glide length increases (Scheibe and Robins 1998; Dial 2003). Taller trees provide higher launch sites, facilitating longer glides; and the ability to make one continuous rather than several shorter glides may also reduce the risk of injury or predation upon landing (Dudley and DeVries 1990). Thus, a forest with an abundance of very tall emergent trees likely presents conditions that make gliding much more advantageous than a forest with a lower and less variable canopy. On the other hand, while lianas provide movement pathways, as vines they may have less physical stability than large branches, giving advantages to prehensile-tailed mammals travelling at canopy level in liana-dense habitats. Thus, the immense height and age of Borneo's rainforests have provided the physical space and evolutionary time for a great number of faunal species to evolve, and with traits uniquely adapted to this tall, floristically diverse habitat. Indeed, Borneo represents the global epicentre of gliding vertebrate diversity, with 33 known species (15 mammals, 15 reptiles, and three amphibians), in stark contrast to three gliding species in Africa and only one in the Neotropics (Emmons and Gentry 1983). In total, Borneo's diverse mammal fauna comprises at least 135 non-volant species, over half of which are arboreal or semi-arboreal, including the world's smallest flying squirrel, the lesser pygmy flying squirrel *Petuarillus emiliae*, and one of the largest, the red giant flying squirrel *Petuarista petaurista* (Payne and Francis 2007; Thorington *et al.* 2012).

Despite their prevalence, many arboreal and semi-arboreal mammals remain poorly known, with even basic information about geographic distributions and habitat preferences lacking. Behavioural and ecological data for Bornean species, where these exist, often originate from studies in other parts of a species' range, such as information on canopy sleeping site selection of binturong *Arctictis binturong* and masked palm civet *Paguma larvata* in Thailand (Chutipong *et al.* 2015), and nesting behaviour of red giant flying squirrel *Petaurista petaurista* in India (Krishna *et al.* 2019). Occurrence data are often patchy, with some species known only from single records (e.g. the Bornean subspecies of Hagen's flying squirrel *Petinomys hageni*, known only from one specimen collected in Kalimantan and since lost, Payne and Francis 2007), or derived from incidental observations. For example in 2018, during bat surveys in Sabah's Crocker Range National Park, a likely individual of Vordermann's flying squirrel *Petinomys vordermanni* was captured – a species not previously recorded throughout the state (N. Yoh, pers.comm., Payne and Francis 2007). There is then much potential to update and expand our knowledge of this understudied community.

1.3 Tropical rainforest mammals and arboreal mammals

Tropical rainforest mammals are diverse and functionally important, and play key roles within ecosystem dynamics as predators, prey, and pollinators, as well as in the regulation of trophic cycles via herbivory, control of invertebrate populations, and seed predation and dispersal (Kays and Allison 2001; Lacher *et al.* 2019). Predators regulate top-down processes by keeping populations of prey under control (Turner 1996). This indirectly aids plant persistence (Laurance 1994) as many prey species are seed and/or seedling predators with rapid reproduction rates and the potential, if left unchecked, to seriously impact floristic abundance and diversity via resource overexploitation (Asquith 1997; Wells *et al.* 2007). When occurring at sustainable levels however, seed consumption and dispersal are equally crucial to rainforest dynamics (De La Sancha *et al.* 2014; Loveridge *et al.* 2016), both for regulating competition within plant communities, and dispersing the seeds of many species greater distances than they would be able to travel themselves (Dittel *et al.* 2015). Indeed, estimates suggest that up to 90% of tropical plant species depend on mutualistic interactions with animals to complete their reproductive cycle (Malhi *et al.* 2014), with some only able to be pollinated or dispersed by one species (Corlett 2017; Gardner *et al.* 2019). Many rainforest trees produce hard-shelled seeds and rely on large-bodied animals, or those with specialised dentition (e.g. tufted ground squirrel *Rheithrosciurus macrotis*, Marshall, Meijaard and Leighton 2020) for dispersal (Lacher *et al.* 2019), and dietary preferences between taxa suggest that, for example, seeds dispersed by mammals are often not dispersed by birds and *vice versa* (McConkey 2018), underscoring the functional importance of specific groups. Forest vertebrates – in particular primates, rodents, and large birds – therefore play vital roles in the maintenance of tree diversity and floristic composition (Gardner et al. 2019), and their loss could have cascading effects at the ecosystem level, potentially destabilising symbiotic relationships (Brodie *et al.* 2014a), inhibiting forest regeneration (Chazdon *et al.* 2009), and reducing the ability of tropical forests to provide crucial services such as carbon storage (Gardner *et al.* 2019).

It is clear that mammals represent an important and informative group to study in tropical forests, and arboreal mammals form a distinct and diverse group in their own right, comprised mainly of species rarely or never detected at ground level (Malcolm 1991; Wells *et al.* 2004a; Gregory *et al.* 2014; Whitworth *et al.* 2019a). In tropical forests, arboreal mammals span a wide range of body sizes and life history strategies, fulfilling similar ecological roles to terrestrial species (Corlett 1998; 2017; Kays and Allison 2001). Smaller mammals such as tree-dwelling squirrels form part of the diet of aerial birds of prey as well as of semi-arboreal carnivores (Becker, Leighton, and Payne 1985). As with terrestrial species, arboreal herbivores regulate plant primary productivity, either inhibiting tree growth via excessive feeding or stimulating growth by consuming terminal buds, which promotes branching (Chapman *et al.* 2013). Primates and civets are important seed dispersers and, given their larger body size and home ranges, may be critical to the wider-scale distribution of resources (Corlett 1998; 2017). In Borneo, over 90% of seeds consumed by gibbons were dispersed more than 100 metres from the source tree, and many at potentially much greater distances throughout their 16-60 hectare territories (McConkey and Chivers 2007). Arboreal rodents are key seed predators, and likely also seed dispersers (Zhu *et al.* 2021). Tropical squirrels have been observed carrying seeds away from source tree crowns, perhaps to reduce predation risk while feeding, and in the process likely facilitating dispersal if seeds are dropped, excreted intact, or cached and not retrieved (Becker, Leighton, and Payne 1985; Becker and Wong 1985). In addition, studies in India and Malaysia have suggested that arboreal mammals may play a role in pollination. Primates, squirrels, flying squirrels, and civets were all observed to consume canopy flowers, with pollen remaining attached to fur on the limbs and around the mouth. While pollen transfer from tree to tree has yet to be confirmed, these observations provide a plausible mechanism for the pollination process (Ganesh and Devy 2000; Yumoto *et al.* 2000).

Predation, herbivory, seed dispersal and pollination in the canopy all form part of wider nutrient cycling and plant reproduction at the ecosystem level. Canopy-derived resources are transferred via mishandling, defecation, or movement between strata, to the ground, where they may be consumed or further transported by secondary dispersers. For example, excrement of Neotropical arboreal primates that falls to ground level has been shown to present a resource itself, attracting an array of species including terrestrial dung beetle communities, whose burying activity can aid germination of the seeds contained within (Whitworth *et al.* 2019b). Thus, arboreal mammal-mediated processes are likely integral to the distribution and regeneration of many rainforest tree species, so helping to maintain plant heterogeneity across the landscape. However, aside from a handful of primates, arboreal mammals as a group are under-sampled and poorly known, especially in comparison to their terrestrial counterparts (Kays and Allison 2001; Whitworth *et al.* 2019a). In most areas, canopy-based, community-wide surveys are lacking (Gregory *et al.* 2014), and arboreal species are often missed from inventories altogether (Bowler *et al.* 2017). Thus, their true diversity and contributions to ecosystem processes are likely to have been significantly underestimated.

1.4 The effects of logging on forest structure and species' persistence

Globally, the extent of human-disturbed forests exceeds that of intact habitat (Watson *et al.* 2018), and one of the most pervasive causes of disturbance is selective logging, with most tropical forests having already undergone at least one round of timber extraction (Malhi *et al.* 2014). Selective logging involves the disproportionate removal of large timber species while leaving sufficient younger trees to allow repeated future harvests (Johns 1985). This method has less impact than complete forest clearance, where all vegetation is removed in a single felling cycle, but nonetheless even selective removal can cause substantial damage to the forest ecosystem (Pinard and Putz 1996; Gibson *et al.* 2011). Southeast Asian forests are particularly vulnerable to degradation via logging because the dominance of commercially valuable dipterocarps allows timber to be extracted at ten times the rate of forests in other tropical regions (Malhi *et al.* 2014). On Borneo for example, 45% of all lowland rainforest – and 59% in the state of Sabah – had undergone at least one round of logging by 2015 (calculated from figures reported in Gaveau *et al.* 2016).

This removal of large trees and collateral damage to surrounding vegetation leads to considerable changes in forest structure. Overall canopy height and the density of canopy vegetation are reduced, and the number of canopy gaps increased (Laurance and Laurance 1996; Milodowski *et al.* 2021), with the effect of reducing connectivity between trees and allowing more light to penetrate below the canopy, raising temperatures and lowering humidity (Johns 1985; Fauset *et al.* 2017). On the forest floor, brighter light conditions enable fast-growing pioneer plant species to out-compete the slower growing, shade tolerant seedlings of canopy trees, resulting in a higher density of herbs, shrubs, and saplings, and altering plant community composition (Johns 1985; Villela *et al.* 2006). The effects are long lasting: dipterocarp seeds for example require a closed canopy to germinate (Johns 1985), and a return to these conditions can take decades (Fauset *et al.* 2017; Milodowski *et al.* 2021).

Although old growth rainforests are irreplaceable for protecting tropical biodiversity, it has become clear in recent years that recovering selectively-logged forests – i.e. those in which logging activities have now ceased, and which were previously considered too degraded to be of use for conservation (Johns 1985) – represent a valuable refuge for biodiversity, as well as retaining important carbon and timber stocks (Gibson *et al.* 2011; Putz *et al.* 2012; Edwards *et al.* 2014). This is equally true in Borneo, where multiple studies have shown that recovering-logged forests support a large variety of species (e.g. Berry *et al.* 2010; Granados *et al.* 2016; Maiwald *et al.* 2021), with some mammal groups potentially benefitting from the increased concealment or foraging opportunities provided by more dense ground-level vegetation (Meijaard and Sheil 2007). However, the ability of recovering-logged forests to retain biodiversity depends on the extent of disturbance to the physical environment. Conventional selective logging techniques result in an overall structural simplification of forest architecture, and the occurrence and abundance of terrestrial mammal communities has been shown to decrease as degradation increases (Wearn *et al.* 2017; Deere *et al.* 2020a).

Arboreal mammals are thought to be more vulnerable to the effects of logging because they are directly reliant on the structural features impacted – i.e. tree height, tree size, and canopy complexity and connectivity (Cassano, Barlow, and Pardini 2012; Whitworth *et al.* 2019a). Connectivity between trees is a key driver of habitat selection for a number of arboreal taxa (e.g. small rodents, Wells *et al.* 2004b, Fedyn *et al.* 2021; civets, Mudappa 2006; lemurs, Chen *et al.* 2021; gibbons, Hankinson *et al.* 2021), and the loss of large, interconnected branches disrupts movement pathways at canopy level (Johns 1986; McLean *et al.* 2016). Lower canopy heights compact the vertical space, while fewer mature trees reduces the number of critical habitat features such as cavities (which can take hundreds of years to form, Cockle *et al.* 2011). Together, these impacts diminish the available niche space and may increase competitive interactions and/or lead to the extirpation of less competitive species (Scheffers *et al.* 2017).

To date only one study, in Peru, has directly investigated community-wide responses of arboreal mammals to logging, finding that many taxa were more susceptible to declines in occupancy post-disturbance than their terrestrial counterparts (Whitworth *et al.* 2019a). Other studies of canopy environments, while not explicitly testing the effects of logging, have revealed links between arboreal mammal occurrence and forest structural integrity. In Mexico, arboreal assemblages responded positively to increased size and quality of forest patches (measured by tree density, basal area, and connectivity; canopy closure; and liana and epiphyte cover) (Cudney-Valenzuela *et al.* 2021). In Borneo, small arboreal rodents were less common in logged than unlogged forest, a finding attributed to reduced habitat space and altered tree composition (Wells *et al.* 2007). In single-species studies, tree size and canopy connectivity were positively associated with the presence of Japanese flying squirrels *Pteromys momonga* (Suzuki and Ando 2019) and maned sloths *Bradypus torquatus* (Santos *et al.* 2016); bald-headed saki monkeys *Pithecia irrorata* were reliant on the availability of tall trees (Palminteri *et al.* 2012); and occurrence of yellow-bellied gliders *Petaurus australis* increased with structural and floristic diversity at canopy level, but decreased with tree basal area (a proxy for logging) (Eyre 2007).

Thus, many arboreal mammals appear to respond to changes in forest structure, but studies directly investigating responses to logging are lacking, especially those that take a community approach. As the extent of forest subjected to logging increases globally, understanding the responses of tropical species to these disturbances is essential for effective conservation (Gibson *et al.* 2011). Failing to account for arboreal mammals, which comprise a sizeable proportion of rainforest communities and play important functional roles (Kays and Allison 2001), risks underestimating the true impacts of logging. Losing key vertebrates affects the capability of rainforests to recover from disturbance (Chazdon *et al.* 2009), with far-reaching implications for long-term ecosystem stability and resilience (Gardner *et al.* 2019). An incomplete understanding of species' responses may lead to misdirected conservation actions, either by overlooking highly vulnerable species that remain poorly known due to arboreal habits, or channelling precious funds towards species thought rare due to a lack of terrestrial records, but which are in fact abundant at canopy-level (Gerber *et al.* 2014). In addition, some authors have suggested that findings of high terrestrial biodiversity in recovering-logged forests may be partially due to greater detections of semi-arboreal species using the ground more frequently in these environments (Malcolm and Ray 2000, Berry *et al.* 2010). However, the lack of comparative studies sampling communities in both strata across both unlogged and logged forests means that this hypothesis remains untested. In the context of rapid rates of global forest degradation, there is a pressing need to better understand whole-community (i.e. ground-to-canopy) wildlife responses to logging, as this underpins effective management, conservation, and restoration strategies.

1.5 Challenges of sampling arboreal species in canopy environments

The paucity of information on arboreal mammals is largely due to the practical difficulties of accessing the canopy and sampling at height (Lowman and Rinker 2004). While some arboreal species may descend to the forest floor under specific circumstances, e.g. ground-level travel and foraging observed in maroon langurs *Presbytis rubicunda* (Cheyne *et al.* 2018), most do not do so reliably or frequently enough to enable robust data collection by ground-based remote-monitoring techniques such as camera-traps. This is evidenced in numerous terrestrial camera-trapping studies, where arboreal species are not present on the inventory list due to negligible detections (e.g. Cove *et al.* 2013; Wearn *et al.* 2017; Deere *et al.* 2020a; 2020b). As a result, arboreal mammals have traditionally been surveyed using ground-based techniques that require an observer to be present, such as transects. However, most rainforest mammals are wary of humans, and many are rare, cryptic in appearance or behaviour, and/or nocturnal, (Kays and Allison 2001; Gregory *et al.* 2014; Whitworth *et al.* 2016) presenting challenges to obtaining comprehensive community data via this method. Arboreal species have the added sampling difficulty of living at height, often obscured above several layers of vegetation. Consequently, while effective for some species, transect surveys tend to be biased towards detections of those which are larger-bodied, active during the day, and show a degree tolerance to human presence (Whitworth *et al.* 2016).

Since the 1980s, canopy access (initially using modified rock climbing equipment) and canopy sampling techniques have evolved (Lowman 2020; Cannon *et al.* 2021). Some researchers have set small mammal live-traps in the rainforest canopy, with results demonstrating that arboreal assemblages are distinct from those at ground level (Malcolm 1991; Wells *et al.* 2004a; Nakagawa *et al.* 2007; De Camargo, Sano, and Vieira 2018). In Brazil, live trapping at heights of zero, two, and 15 metres revealed significant differences in species composition and abundance in the higher-canopy traps, but not between the two lower levels (Malcolm 1991), while in Sabah, live-trapping detected a greater proportion of rarely-captured species in the canopy than on the ground (Wells *et al.* 2004a). Similarly in Sarawak, trapping over nine years found that a fifth of small mammals were only ever recorded above 20 metres height. Records included three captures of Vordermann's flying squirrel *Petinomys vordermanni*, a species previously known only from Brunei and Kalimantan (Payne and Francis 2007), with the authors noting that its small body size and exclusive use of the canopy layers likely made it easy to overlook (Nakagawa *et al.* 2007). More reliable estimates of species diversity and abundance can thus be obtained when both canopy- and ground-level sampling are undertaken (De Camargo, Sano, and Vieira 2018), and failing to sample across an appropriate height range can lead to false conclusions about the presence or commonness of arboreal species (Malcolm 1991), in turn affecting our understanding of community diversity and dynamics.

Therefore, while both ground-based surveys and canopy-based live-trapping can provide useful data on arboreal mammals, both have inherent and important limitations. Transects are labour intensive, requiring repeated sampling across tens or hundreds of kilometres during both day and night, and are more likely to miss small and elusive species (Whitworth *et al.* 2016). Live-trapping is disruptive to captured animals, also labour intensive – with traps requiring daily checking, and the use of bait introduces capture bias depending on dietary preferences (Caravaggi *et al.* 2020). In addition to these approaches, certain arboreal species can be sampled without the need for direct observations, e.g. acoustic surveys for gibbons *Hylobates sp.* (Gilhooly, Rayadin and Cheyne 2015), or nest surveys for orangutans *Pongo sp.* (Seaman *et al.* 2019). However, neither indirect monitoring for individual species, nor direct sampling via transects or live-trapping, are able to comprehensively sample the entire arboreal mammal community in a way that is comparable to standard inventory methods for terrestrial communities.

1.6 The advent of canopy camera-trapping

Camera-trapping – the deployment of remotely-operated camera units that use inbuilt heat and motion sensors to capture images of passing wildlife – is well-established as a sampling method for terrestrial mammals (Tobler *et al.* 2015). Camera-traps can be cost-effective, minimally invasive, and, after initial setup, require relatively low labour inputs, as well as allowing continuous monitoring across the 24-hour cycle of multiple species simultaneously (Bridges and Noss 2011; Whitworth *et al.* 2016). In recent years, with the improvement of canopy access techniques and development of more durable camera-traps, the method has begun to be tested at height. Early applications included quantifying foraging behaviour of Yakushima macaques *Macaca fuscata yakui* in Japan (Otani 2001), surveying the population of the elusive and Endangered buff-headed capuchin *Cebus xanthosternos* in Brazil (Kierulff *et al.* 2004), and evaluating arboreal species' use of rope connections over a road in Australia (Goosem *et al.* 2005).

In early 2015, at the time that I initially developed the proposal for this thesis, there was no published research testing the utility of canopy camera-traps to inventory arboreal mammal communities. Tremaine Gregory and colleagues had identified the potential of the technique to provide robust community data in a study monitoring wildlife crossing points over a pipeline clearing in Peru (Gregory *et al.* 2014), but this had yet to be fully tested. The majority of canopy camera-trapping research for mammal studies was, and remains, limited to documenting the presence or activity of one or a small group of species, or determining responses to a specific habitat feature such as canopy bridges or fruiting trees (Moore *et al.* 2021, and see Supplementary Table S2.1).

Nevertheless, in the intervening years, eight community inventory studies have been published, all from sites in tropical America or Africa (Whitworth *et al.* 2016; 2019a; Bowler *et al.* 2017; Hongo *et al.* 2020; Moore *et al.* 2020; Kaizer *et al.* 2021; Scabin and Peres 2021; Agostini *et al.* 2022). All highlighted the efficacy of canopy camera-traps to survey arboreal mammal assemblages in their respective study regions, although three excluded small-bodied species from analyses (Whitworth *et al.* 2016; 2019a; Bowler *et al.* 2017), and three did not set paired units at ground level (Whitworth *et al.* 2016; Bowler *et al.* 2017; Kaizer *et al.* 2021), limiting the inferences that could be made regarding the distinctness of arboreal and terrestrial communities. Studies that did deploy cameras in both strata (Whitworth *et al.* 2019a; Hongo *et al.* 2020; Moore *et al.* 2020; Scabin and Peres 2021; Agostini *et al.* 2022) revealed arboreal and terrestrial communities to be comprised mainly of different species (reflecting results of the live-trapping research discussed previously). Furthermore, comparisons between sampling methods consistently found that canopy camera-traps detect greater numbers of arboreal species than diurnal and nocturnal transect surveys or incidental observations, and determined that for whole-community inventories, a combination of terrestrial and canopy camera-trapping would be most effective (Whitworth *et al.* 2016; Bowler *et al.* 2017; Moore *et al.* 2020), with authors noting the utility of canopy cameras to record a high number of otherwise undetected taxa (Scabin and Peres 2021). Several studies additionally detected the presence of species previously undocumented in the study areas, in some cases despite decades of terrestrial research, enhancing knowledge of species' distributions and community dynamics (Whitworth *et al.* 2016; Moore and Niyigaba 2018; Hongo *et al.* 2020; Kaizer *et al.* 2021; Agostini *et al.* 2022). Beyond contributions to species diversity assessments, their results have contributed to a wider understanding of arboreal communities, for example highlighting the vulnerability of arboreal mammals to habitat disturbance (Whitworth *et al.* 2019a) and hunting (Scabin and Peres 2021). Others have afforded new insights into previously unknown behaviour, such as the role of northern olingos *Bassaricyon gabbii* in Panama for dispersing the seeds of an endemic plant (Monteza-Moreno *et al.* 2022), or revealing frequent nighttime activity of the Guizhou snub-nosed monkey *Rhinopithecus brelichi* – a species thought to be exclusively diurnal, but which may in fact display behavioural plasticity in response to seasonal fluctuations in day length and resources (Tan, Yang, and Niu 2013).

Canopy camera-trapping clearly has great potential for studies of canopy-dwelling wildlife. However, it has yet to be commonly implemented as a standard sampling technique for tropical arboreal communities in the way that terrestrial cameras are routinely used to monitor mammals at ground level. A further point to consider is that almost half of all canopy studies placed cameras ≤10 metres above the ground, missing a large portion of the available vertical space and thus potentially discounting high canopy species, which are often the least known (Gregory *et al.* 2014). Substantial differences in community identity and species abundance have been detected between the ground and heights of 15-30 metres in both live- and camera-trapping studies (e.g. Malcolm 1991; Wells *et al.* 2004a; Nakagawa *et al.* 2007; Whitworth *et al.* 2019a; Hongo *et al.* 2020; Moore *et al.* 2020). Given that Borneo's rainforests reach up to 60 metres, with emergent trees taller still, there is great scope for further advances in arboreal mammal research. However, there have previously been no studies testing the application of canopy camera-traps in Borneo. Indeed, with higher reported incidents of false triggers from non-target stimuli in the canopy – attributed to increased wind and light exposure in tree crowns (Gregory *et al.* 2014) – questions arise as to whether this method would be feasible in Borneo's extremely tall and non-uniform canopies.

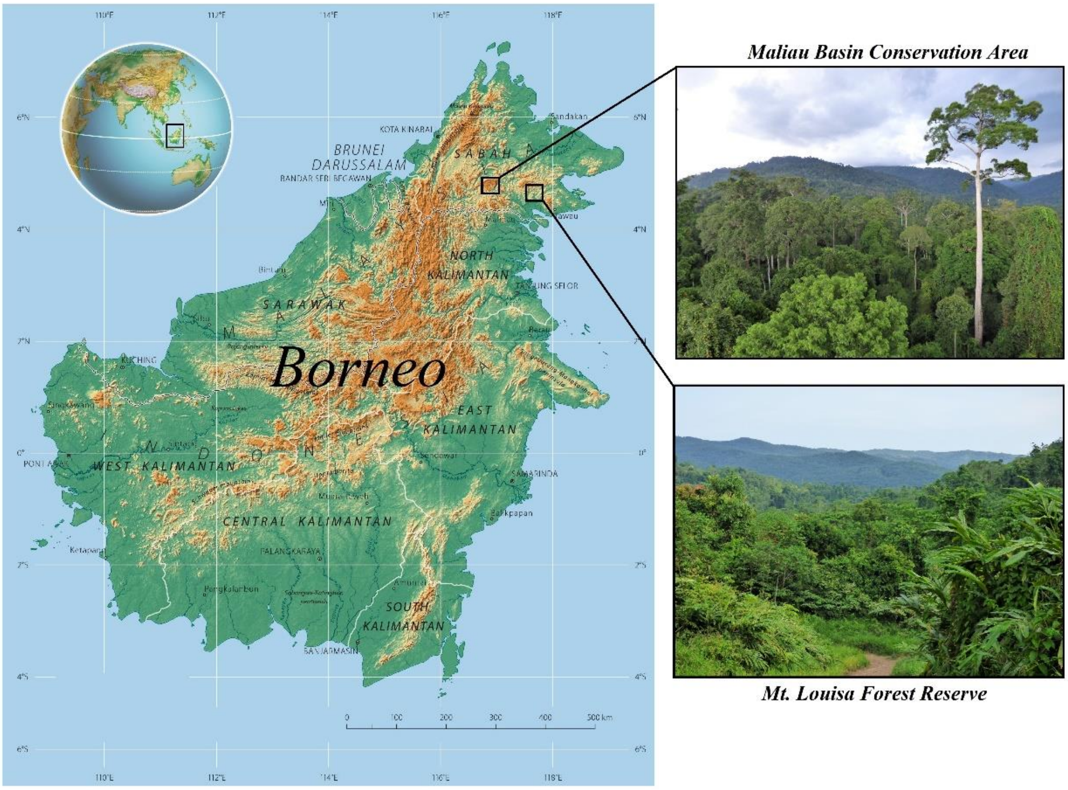

Figure 1.1 Location of sampling sites in Sabah, Malaysian Borneo (left): unlogged forest at Maliau Basin Conservation Area (top right), and recovering-logged forest at Mt. Louisa Forest Reserve (bottom right). Map reproduced with kind permission from Wich *et al.* 2015, and edited to show sites in this study. Photographs taken by J.K.Haysom during fieldwork.

1.7 Aims and objectives

Tropical canopies remain largely unexplored, particularly in Southeast Asia. The height and complexity of Bornean rainforests have given rise to a great diversity of arboreal mammal species, many of which are endemic, and the island further represents the global epicentre of gliding mammal diversity. However, due to the historic difficulties of canopy access resulting in a ground-based research bias, most arboreal mammals, as well as the canopy aspect of semi-arboreal mammal ecology, are little known. Borneo's rainforests are threatened by selective logging, and while many terrestrial species can persist in recovering-logged habitats, the tolerance of arboreal mammals to degradation remains poorly understood. My aim in this thesis is to explore, for the first time, the application of canopy camera-trapping to study the Bornean arboreal mammal community.

Specifically, I aim to test this method in both unlogged and recovering-logged rainforest, and from the results compare the species richness and composition of arboreal and terrestrial mammal communities (**Chapter 2**); examine the activity strategies of species in both strata to discover what they might reveal about the constraints and opportunities present at ground- and canopy-level (**Chapter 3**); and quantify and compare the responses of arboreal and terrestrial communities to logging, investigating how these are related to changes in vegetation structure (**Chapter 4**). Due to the collaborative nature of these chapters I adopt a shift in passive voice, replacing singular with plural pronouns.

Although rainforest bat assemblages are also diverse and functionally important, the differences in life-history traits and sampling techniques arising from their ability to fly meant that it was beyond the scope of my PhD research to include this group, and no images of bats were obtained during sampling. All references to mammals therefore refer to the non-volant community (but see Hirakawa 2005 and Aziz *et al.* 2017 for potential applications of camera-traps in the study of some bat species, detailing use of a lure to capture images, and confirming the role of flying foxes *Pteropus hypomelanus* in durian pollination, respectively).

1.8 Thesis structure

In **Chapter 2**, I examine the efficiency and cost-effectiveness of canopy- versus ground-level sampling using camera traps. I generate species accumulation curves for arboreal and terrestrial communities in unlogged and recovering-logged rainforest, encompassing species of all body sizes across strata, and demonstrate that the inclusion of canopy-level sampling significantly increases species inventories. I also compile a detailed cost comparison, and provide recommendations on how to minimise the additional expense that canopy sampling incurs. This work was published in *Frontiers in Forests and Global Change*, and serves as the first community-wide inventory of Bornean mammals in the canopy.

In **Chapter 3**, I quantify activity metrics (proportion of the daily cycle spent active, and the time or times of this activity) for 37 arboreal and terrestrial species, and show clear dissimilarities in diel patterns between strata, while patterns between unlogged and recovering-logged forest remained largely consistent. I discuss how these differences help to shed light on the varying environmental conditions and selective pressures faced by ground-dwelling and tree-dwelling mammals.

In **Chapter 4**, I use multi-species occupancy models to investigate both species-level and community-level responses to logging for arboreal and terrestrial mammals, and highlight the increased vulnerability of arboreal species. I test how the occupancy of each community responds to a suite of high-resolution vegetation covariates derived from LiDAR surveys, including a novel measure of canopy connectivity, and reveal the importance of both local- and landscape-level canopy connectivity for arboreal mammals.

Chapter 5 discusses the contribution of these findings in the context of global arboreal mammal research, noting the limitations and remaining knowledge gaps, and highlighting potential avenues for future studies.

Chapter 2 Life in the canopy: Using camera-traps to inventory arboreal rainforest mammals in Borneo

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*****_References relating to other canopy camera-trap research for arboreal mammals have been updated to include studies published after the publication of this manuscript in 2021 (N = 11). Citations in Section 2.1 and Supplementary Materials Table S2.1 reflect this._

Keywords: camera-trap | biodiversity monitoring | tropical rainforest | disturbance | logging | Southeast Asia | mammal survey

Abstract

Arboreal mammals form a diverse group providing ecologically important functions such as predation, pollination and seed dispersal. However, their cryptic and elusive nature, and the heights at which they live, makes studying these species challenging. Consequently, our knowledge of rainforest mammals is heavily biased towards terrestrial species, limiting our understanding of overall community structure and the possible impacts of human-induced disturbance. We undertook the first in-depth appraisal of an arboreal mammal community in Southeast Asia, using camera-traps set in unlogged and recovering-logged tropical rainforest in Sabah, Borneo. Using paired canopy and terrestrial camera-traps at 50 locations (25 in unlogged forest, 25 in recovering-logged), we assessed the effectiveness of camera-trapping at characterising the arboreal versus terrestrial community, and tested the influence of strata and logging on community structure and composition. The paired design detected 55 mammal species across 15,817 camera-trap nights, and additional canopy sampling in a subset of trees added a further two arboreal species to the inventory. In total, 30 species were detected exclusively by terrestrial camera-traps, 18 exclusively by canopy camera-traps, and nine by units set at both heights, demonstrating significant differences between arboreal and terrestrial communities. This pattern was strongest in unlogged forest, reflecting greater structural diversity of this habitat, but held in recovering-logged forest as well. Species accumulation curves revealed that canopy camera-trapping significantly boosted species inventories compared to terrestrial-only sampling, and was particularly effective at detecting gliding mammals, rodents and primates. Canopy inventories took longer to reach an asymptote, suggesting that a greater sampling effort is required when deploying canopy camera-traps compared to those set on the ground. We demonstrate that arboreal mammals in Borneo's rainforest form a diverse and distinct community, and can be sampled effectively using canopy camera-traps. However, the additional costs incurred by sampling in the canopy can be substantial. We provide recommendations to maximise sampling effectiveness, while bringing down costs, to help encourage further study into one of the last frontiers of tropical forest research.

2.1 Introduction

Tropical rainforests support exceptional levels of biodiversity, but are highly threatened by anthropogenic activities such as logging (Barlow *et al.* 2018). Rainforests are structurally complex environments, comprising not only ground-level (i.e. terrestrial) vegetation, but also several interlinked above-ground strata (hereafter the canopy (Moffett 2000)), and culminating in tree crowns that can reach 30-45 m in height (Dudley and DeVries 1990). However, due mainly to the difficulties of canopy access (Lowman, Devy, and Ganesh 2013), most rainforest research is heavily biased towards terrestrial communities and processes (Whitworth *et al.* 2019a). Consequently, the canopy remains a largely unexplored ecological frontier (Godoy-Guinao, Diaz, and Celis-Diez 2018). With only a limited understanding of canopies and the wildlife they support, we are missing key insights into the composition, dynamics and functioning of rainforest ecosystems as a whole.

The wildlife utilising the forest canopy plays essential roles in ecosystem functioning, for example by regulating biogeochemical and nutrient cycles, and facilitating forest regeneration via animal-mediated seed dispersal (Nakamura *et al.* 2017). An estimated 75% of rainforest vertebrates are arboreal or semi-arboreal, spending all or part of their lives in the canopy (Kays and Allison 2001). Among them, mammals are one of the most diverse and numerous taxonomic groups, filling a wide variety of ecological roles including seed dispersal, pollination, herbivory and predation (Kays and Allison 2001; Nakabayashi *et al.* 2019; Whitworth *et al.* 2019a). Removal of these key vertebrates may affect the capability of rainforests to recover from disturbance, with potentially cascading consequences for ecosystem stability and resilience (Gardner *et al.* 2019).

In addition, arboreal mammals may be more vulnerable to the effects of logging than their terrestrial counterparts because the large, tall trees that constitute the main structure of their canopy habitat are often also those lost through logging. At present, most tropical research into the effects of logging on wildlife does not include targeted sampling for arboreal mammals, and it is not clear to what extent this group is affected, or whether populations can recover after the cessation of logging activities (Bowler *et al.* 2017). For many terrestrial taxa, species diversity in recovering-logged forest can return to approximately pre-logging levels within a few decades of the cessation of logging (Berry *et al.* 2010; Brodie *et al.* 2014b). However, it has also been suggested that terrestrial mammal inventories in recovering-logged forest may be artificially inflated by increased detections of semi-arboreal species spending more time on the ground (Berry *et al.* 2010). While this has been demonstrated for some small-bodied arboreal mammals in some areas (Malcolm 1997; Malcolm and Ray 2000), other studies have shown post-logging reductions in the abundance of small arboreal rodents (Wells *et al.* 2007) and occupancy of medium- and large-bodied arboreal mammals (Whitworth *et al.* 2019a) without an apparent influx effect at ground-level. The current lack of monitoring of the canopy strata is a barrier to our understanding of whether this phenomenon occurs, and highlights the risk that we may be missing declines in arboreal species, and underestimating the true impact of logging.

Traditionally, arboreal mammals have been sampled using ground-based visual surveys, but these tend to be biased towards larger-bodied, diurnal species that can be readily observed and identified from below, and show some degree of tolerance to people (Whitworth *et al.* 2016; Bowler *et al.* 2017; Moore *et al.* 2020). Moreover, the heights at which arboreal species are detected present significant challenges for accurate identification from the ground (Jayasekara *et al.* 2007; Gregory *et al.* 2014; Whitworth *et al.* 2016). Canopy-based live-trapping has also been tested, but is labour-intensive, tends to exclude larger-bodied species, and can result in biased sampling, particularly as bait is used (Caravaggi *et al.* 2020).

Advances in camera-trapping technology have led to the widespread use of this survey method in the study of terrestrial mammals (Wearn and Glover-Kapfer 2019), but it is yet to be commonly implemented at canopy-level. To date, applications of camera-trapping in the canopy have focused mainly on documenting animal presence (e.g. Suzuki and Ando 2019), behaviour (e.g. Godoy-Guinao, Diaz, and Celis-Diez 2018), or activity in relation to particular habitat features such as fruiting trees (e.g. Jayasekara *et al.* 2007) or canopy bridges (e.g. Gregory *et al.* 2017) (see also Supplementary Materials Table S2.1). Published inventories of arboreal mammal communities based on camera-trap data are limited to eight sites (Whitworth *et al.* 2016; 2019a; Bowler *et al.* 2017; Hongo *et al.* 2020; Moore *et al.* 2020; Kaizer *et al.* 2021; Scabin and Peres 2021; Agostini *et al.* 2022), all in the Neotropics or Africa, and with three focusing on medium- and large-bodied mammals. Three of these studies did not compare canopy inventories to those generated from camera-traps on the ground (Whitworth *et al.* 2016; Bowler *et al*. 2017; Kaizer *et al*. 2021), limiting the inferences that can be made when describing arboreal versus terrestrial communities. Further, almost half of all published canopy-based camera-trap studies that recorded camera height (28 of 64, Supplementary Materials Table S2.1) placed camera-traps ≤10 m above the ground, missing a large portion of the vertical space from their sampling. While canopy camera-trapping has shown great potential as a sampling technique, it has yet to be employed as a standard tool for monitoring arboreal mammal communities. Understanding the advantages and limitations of this method is therefore essential if it is to be more widely adopted.

Here, we provide the first in-depth appraisal of the arboreal mammal community in Southeast Asia, using camera-traps set in unlogged and recovering-logged tropical rainforest of Sabah, Malaysian Borneo. The rainforests of Borneo are among the tallest in the world (Dudley and DeVries 1990), and are renowned for their arboreal and semi-arboreal mammal fauna, comprising over 70 species and including 14 flying squirrel taxa, representing the global epicentre of gliding mammal diversity (Payne and Francis 2007; Thorington *et al.* 2012). We compare the ability of camera-traps to define the arboreal and terrestrial mammal community, and extend our assessment from the medium- and large-sized mammals typically investigated in camera-trap studies to include the numerous smaller-bodied arboreal species, most of which can also be identified by this method (De Bondi *et al.* 2010). We evaluate the comparative costs of terrestrial versus canopy camera-trapping, and quantify the diversity missed or gained by each technique, revealing how studies of rainforest mammals that focus only on terrestrial species may be overlooking a key component of ecosystem dynamics.

2.2 Methods

2.2.1 Study System

Research was undertaken in and around the Stability of Altered Forest Ecosystems Project (Ewers *et al.* 2011; Figure 2.1) in Sabah, Malaysian Borneo. We sampled mammals in unlogged forest at Maliau Basin Conservation Area, and in recovering-logged forest in the Mt. Louisa Forest Reserve. These areas form part of an extensive contiguous block of dipterocarp forest covering approximately one million hectares in south-central Sabah (Reynolds *et al.* 2011). Mt. Louisa experienced multiple rounds of logging between 1978 and 2008, but has since been formally protected, whereas the unlogged forest at Maliau Basin has experienced very little disturbance. Our recovering-logged forest sampling area was characterised by lower canopy height and reduced canopy cover, with fewer canopy pathways and more canopy gaps than our unlogged forest sampling area (Deere *et al.* 2020a). Camera-trap locations in both unlogged and recovering-logged forest covered similar elevations (mean 482 m, range 225-933 m).

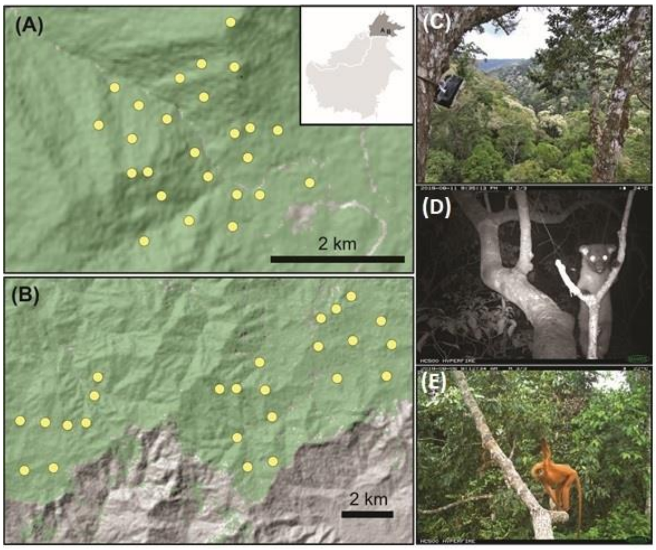

Figure 2.1 Camera-trap locations in unlogged (A) and recovering-logged (B) forest of Sabah, Borneo, with the location of the sampling in relation to Borneo shown on the inset map. Canopy camera-traps were set on the trunk of trees, facing focal branches (C). Example arboreal species detected included small-toothed palm civet *Arctogalidia trivirgata* (D) and maroon langur *Presbytis rubicunda* (E).

2.2.2 Camera-trapping

Camera-traps (Hyperfire HC500, Reconyx, WI, USA) were deployed across 50 locations between October 2017 and September 2019. Locations were divided equally between unlogged and recovering-logged forest and identified in advance using a 1.5 km^2 grid, whereby every corner of each grid cell comprised a sampling location. Upon navigating to a location either via pre-existing trails or by creating new trails, the nearest tree to the marked point that could be safely climbed (hereafter the focal tree) was rigged with climbing ropes. We did not target a particular species, height or branch architecture type.

Accounting for accessibility and safety constraints, the mean distance between sampling locations was 1.26 km (range: 0.5-4 km). Each location comprised one terrestrial camera-trap set approximately 0.3 m above the ground, paired with a canopy camera-trap in the mid- or upper-canopy of the focal tree, which was situated within a 10 m horizontal distance of the terrestrial placement. Canopy camera-traps were set at an average of 25.9 m above ground (range: 9.8-52.3 m), with the average height of cameras in unlogged forest (36.0 m) and recovering-logged forest (19.3 m) reflecting the differences in canopy height between unlogged and previously-logged habitats. To reduce false triggers, camera-traps were attached to trunks or large, stable branches (Figure 2.1) and any leaves within the detection zone were removed (Gregory *et al.* 2014). Where possible, canopy camera-traps faced north or south to reduce the likelihood of overexposed images, which is a particular risk in the upper canopy (Otani 2001). Most camera-traps faced branches of the focal tree, were set approximately 0.2-0.3 m above the branch and were angled where necessary using a wooden wedge to account for slope of the focal branch. Three units faced trunks of adjacent trees (two in unlogged forest, one in recovering-logged) where these were judged to be within trigger distance (5-10 m away). Terrestrial camera-traps were also attached to medium-large, stable trunks and any vegetation within the detection zone deemed likely to result in false triggers (e.g. thin herb stems) was cleared. Vegetation disturbance was kept to a minimum in both strata, and canopy orchids and epiphytes in particular were left undisturbed. In order to reduce detection bias for terrestrial species that may either preferentially use or avoid trails (Wearn and Glover-Kapfer 2017), and in line with our canopy protocol, terrestrial camera-traps did not target any particular habitat feature.

Camera-traps at each location were deployed for a total of 7-8 months. In unlogged forest this occurred continuously with one check mid-deployment to replenish batteries and SD cards, while due to scheduling practicalities, the recovering-logged forest deployment occurred in two separate phases. Each camera-trap was set to take three consecutive images per detection with no delay between triggers and no sleep delay before retriggering. The camera-traps we used were equipped with infrared flash for low light conditions to minimise disturbance. This is particularly important for nocturnal species, some of which suffer temporary blindness or may exhibit 'trap shyness' when using white flashes (Schipper 2007).

Sampling comprised a total of 100 camera-trap deployments and, after accounting for malfunction, we obtained data from 99, comprising 49 terrestrial camera-traps (24 in unlogged forest, 25 in recovering-logged) and 50 in the canopy (25 in unlogged forest, 25 in recovering-logged). Three functioning units did not obtain any mammal captures during deployment (all canopy, two in unlogged forest, one in recovering-logged). Thus in total, camera-traps were deployed for 15,817 camera-trap nights (CTN): 6,661 terrestrial CTN (3,995 in unlogged forest, 2,666 in recovering-logged) and 9,156 canopy CTN (6,041 in unlogged forest, 3,115 in recovering-logged).

To evaluate whether placing more than one camera-trap in a tree simultaneously could maximise species detection, we set a second canopy camera-trap in 20 of our original focal trees over a period of approximately 3 months. Trees were randomly selected and additional camera-traps were deployed concurrently with the main canopy camera-trap, but positioned at different heights and facing different branches. These second camera-traps (10 in unlogged forest and 9 in recovering-logged after excluding one malfunctioning unit) resulted in an additional 1,409 CTN (903 in unlogged forest, 506 in recovering-logged).

2.2.3 Data analysis

Mammal detections were summarised by camera-trap location (per camera-trap night) and species using the R package gtools (R version 4.0.2). Capture events were considered independent if they were separated by a minimum period of 30 minutes, or if subsequent detections within this threshold contained different species (Laughlin *et al.* 2020).

To compare species accumulation between canopy and terrestrial strata, we generated sample-based rarefaction curves based on camera-trap nights using the R package iNEXT (Hsieh, Ma and Chao 2016). This approach accounts for differences in sampling effort between camera-trap locations (i.e. variation in deployment duration due to units being set and collected, or failing, at different times), without needing to discard data. Rather than reducing all locations to the lowest sampling effort, we interpolated species detections up to the maximum observed sample size and then extrapolated detections to a common sample size above this (S_{max}). Extrapolations were made to approximately double the maximum obtained sample size, as recommended by Hsieh, Ma and Chao (2016). Where rarefaction results are referred to as statistically significant, this indicates non-overlapping confidence intervals of the relevant species accumulation curves.

Inventory comparisons were made between (a) arboreal and terrestrial communities and (b) unlogged and recovering-logged forest, and rarefactions were repeated with subsets of the community data, with species assigned to groupings according to: arboreality, IUCN threat status, body size, and taxonomic group (Supplementary Materials Table S2.2). Arboreality was defined according to the strata in which the species was detected (arboreal = exclusively detected on canopy camera-traps, terrestrial = exclusively on terrestrial camera-traps, semi-arboreal = on camera-traps in both strata); IUCN threat status was categorised as threatened = categories Vulnerable, Endangered, or Critically Endangered; not threatened = Near Threatened, Least Concern, or Data Deficient; body size was defined as small = <1 kg, medium = 1-5 kg, large = >5 kg; and taxonomic group was divided into Carnivora (viverrids: *Arctictis binturong, Arctogalidia trivirgata, Hemigalus derbyanus, Paguma larvata, Paradoxurus hermaphroditus, Viverra tangalunga*; mustelids: *Herpestes brachyurus, H. semitorquatus, Martes flavigula, Mydaus javanensis*; felids: *Neofelis diardi, Pardofelis marmorata, Prionailurus bengalensis*; bear *Helarctos malayanus*), gliding mammals (flying squirrels: *Aeromys tephromelas, A. thomasi, Iomys horsfieldi, Petaurista petaurista, Petinomys setosus, Pteromyscus pulverulentus*; and Sunda colugo *Galeopterus variegatus*), non-gliding rodents (murid rodents: *Leopoldamys sabanus, Maxomys rajah, M. surifer, M. whiteheadi*; non-flying squirrels: *Callosciurus adamsi, C. prevostii, C. sp., Exilisciurus exilis, Ratufa affinis, Rheithrosciurus macrotis, Sundasciurus brookei, S. lowii, S. hippurus*; porcupines: *Hystrix brachyura, H. crassispinis, Trichys fasciculata*), Insectivora (treeshrews: *Ptilocercus lowii, Tupaia longipes, T. minor, T. tana*; moonrat *Echinosorex gymnura*; Sunda pangolin *Manis javanica*), Primates (macaques: *Macaca fascicularis, M. nemestrina*; langurs: *Presbytis rubicunda, P. sabana*; gibbon *Hylobates funereus*; orangutan *Pongo pygmaeus*) and Ungulates (deer: *Muntiacus atherodes, M. muntjak, Rusa unicolor*; mousedeer: *Tragulus kanchil, T. napu*; pig *Sus barbatus*; and banteng *Bos javanicus*; plus elephant *Elephas maximus*). Information on body size and taxonomic classifications was obtained from Payne and Francis 2007 and the IUCN Red List, accessed February 2021.

Ordinations were used to explore variation in mammal community composition between terrestrial and canopy camera-trap locations, as well as unlogged versus recovering-logged forest. We standardised the species-camera data matrix by maximum values (a Wisconsin double standardisation) to improve detection of community patterns, and calculated pairwise Bray–Curtis dissimilarity coefficients using species detections pooled from the first 91 days of sampling at each camera-trap location (the maximum sampling effort common to a majority of locations, since units functioned for varying time periods). Using the vegan package in R, we generated a non-metric multidimensional scaling (NMDS) ordination to organise camera locations by similarity in species composition. To examine compositional differences between strata and unlogged/recovering-logged forest, we applied a permutational multivariate analysis of variance (permanova) using the ADONIS function in vegan. Last, we applied the envfit function with 999 permutations, and the Pearson's coefficient function (akin to an indicator species analysis) to the species detections and ordination axis scores to identify species that contributed the most to variation in community structure between locations.

2.2.4 Costs of canopy versus terrestrial camera-trapping

Since we deployed camera-traps at both terrestrial and canopy levels, we calculated the additional costs incurred by our canopy deployments. Calculations assumed a fixed number of camera-traps available for use and compared the cost of setting all units on the ground versus half on the ground and half in the canopy. We assumed cost per unit did not vary between strata (damage and repair bills during our study were similar between strata), but this will differ depending on the camera model and battery type. For our study, cost per unit was USD $464, including one Reconyx Hyperfire HC500 ($450), one 16 GB memory card ($7) and 12 x AA batteries ($7 per camera-trap per deployment) – prices valid for January 2021.

2.3 Results

2.3.1 Species detections and richness

We recorded 55 mammal species during 8,008 capture events across 15,817 camera-trap nights (CTN) (Table 2.1). Of these species, 30 were only detected on terrestrial camera-traps, 16 were restricted to canopy camera-traps, and nine were detected by camera-traps in both strata (hereafter referred to as semi-arboreal species) (Supplementary Materials Table S2.2). The 19 experimental second canopy camera-traps added a further 1,409 CTN, with 253 capture events of 18 species. These additional records included two arboreal species otherwise undetected (Bornean pygmy squirrel *Exilisciurus exilis*, and Temminck's flying squirrel *Petinomys setosus*, both in unlogged forest), bringing the total number of species recorded exclusively on canopy camera-traps to 18. Second canopy cameras also obtained an unusual canopy record of banded civet *Hemigalus derbyanus*, in recovering-logged forest, otherwise recorded only on terrestrial cameras (see Supplementary Materials Table S2.2).

There was substantial overlap of species recorded in unlogged and recovering-logged forest areas, although each included records of a limited number of species not detected in the other (Supplementary Materials Table S2.2). The number of camera-trap nights and capture events varied between unlogged and recovering-logged forest and between terrestrial and canopy strata (Table 2.1). Mammal detections on unlogged forest camera-traps totalled 47 species (29 terrestrial, 12 arboreal, six semi-arboreal), while those in recovering-logged forest totalled 44 (24 terrestrial, 15 arboreal, five semi-arboreal), including one arboreal squirrel (referred to as *Callosciurus sp.*) whose appearance does not fit the description of any known Bornean species (Supplementary Materials Figure S2.4). Twenty-one species potentially present within the landscape and likely detectable using camera-traps were not detected at all (Supplementary Materials Table S2.2). Of these, nine are presumed terrestrial, six arboreal, and six semi-arboreal (Payne and Francis 2007). Assumption of presence was based on known body size, geographic distribution, elevation range and habitat preferences (Payne and Francis 2007; IUCN Red List, accessed February 2021). Any mammals that could not be identified to species level were excluded from analyses. Of a total of 8,276 capture events of mammal species across all camera-traps, 15 capture events were excluded on this basis, leaving 8,261 for analysis (8,008 from terrestrial and main canopy camera-traps, and 253 from second canopy camera-traps) (Table 2.1). The 15 exclusions comprised: one arboreal squirrel, one arboreal murid rodent, and two terrestrial squirrels where only a small portion of the body was visible; and one arboreal squirrel, and 10 terrestrial murid rodents (likely of two species) where identification to species level could be proposed with some confidence, but not with enough certainty to include in analyses.

Table 2.1 Sampling effort, mammal species recorded and number of independent capture events for camera-traps set in terrestrial and canopy strata of unlogged and recovering-logged forest in Borneo. Rarefaction indicated that sample completeness exceeded 0.98 in all cases. Parentheses denote number of arboreal species added to records from experimental second canopy camera-traps. The sum of species from terrestrial and canopy camera-traps is greater than the total number of mammal species detected (marked with an asterisk*), because some species (nine overall: six in unlogged forest and five in recovering-logged) were detected by both terrestrial and canopy camera-traps and so are included in the figures for both strata.

Dataset	No. Camera-traps	Camera-trap Nights (CTN)	No. Mammal Species	Independent Capture Events	Capture Events per 100 CTN
Main Dataset					
All canopy & terrestrial cameras	118	15,817	55*	8008	50.6
Terrestrial camera-traps					
All terrestrial cameras	49	6,661	39	6885	103.4
Unlogged forest	24	3,995	35	3880	97.2
Recovering-logged forest	25	2,666	29	3005	112.7
Canopy camera-traps					
All single canopy cameras	50	9,156	25	1123	12.3
Unlogged forest	25	6,041	18	705	11.7
Recovering-logged forest	25	3,115	20	418	13.4
Additional Dataset: second canopy camera-traps					
All additional canopy cameras	19	1,409	18 (2)	253	17.9
Unlogged forest	10	903	15 (2)	169	18.7
Recovering-logged forest	9	506	10	84	16.6

2.3.2 Effectiveness of sampling across strata and unlogged and recovering-logged forests

Rarefaction curves for terrestrial communities combined across both unlogged and recovering-logged forest reached an asymptote after 3000-5000 CTN, suggesting that terrestrial inventories were near complete for this method (Figure 2.2). In contrast, while canopy inventories also approached an asymptote at 3000-5000 CTN, curves still increased gradually (Figure 2.2), indicating that further sampling effort in the canopy would likely result in further detections of unique species. This was corroborated by extrapolated accumulation curves, which predicted arboreal communities may require more than double the sampling effort of terrestrial communities to generate complete or near-complete inventories (Supplementary Materials Figure S2.2).

Arboreal mammal species diversity in both unlogged and recovering-logged forest was significantly lower than that characterised at the terrestrial level (Figure 2.2). The signal was stronger in unlogged forest (35 species across terrestrial camera-trap locations versus 18 species across canopy camera-trap locations) than recovering-logged forest (29 species across terrestrial camera-trap locations versus 20 species across canopy locations) and this was driven by lower detections of terrestrial species in recovering-logged forest. Arboreal communities in both unlogged and recovering-logged forest largely comprised different species than those found at ground level, with a majority of species (46 of 55; 84%) detected exclusively by camera-traps in one strata, and only nine species (16%) captured on camera-traps at both heights (Supplementary Materials Table S2.2).

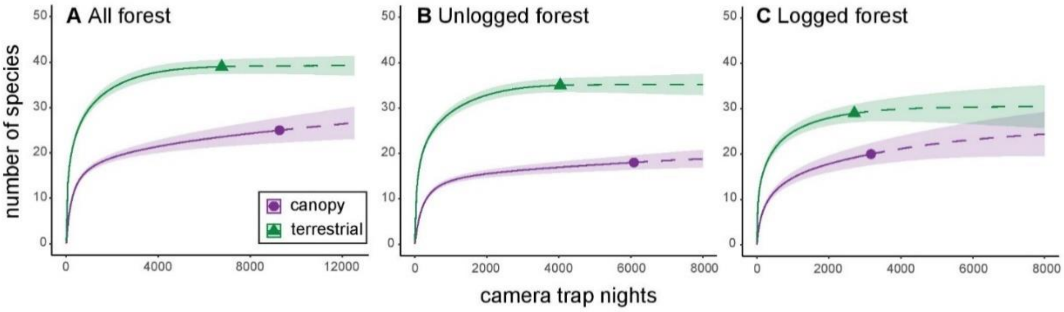

Figure 2.2 Rarefied species accumulation curves for arboreal and terrestrial mammal communities in (A) both unlogged and recovering-logged forest combined, (B) unlogged forest only, and (C) recovering-logged forest only. Curves were extrapolated (dashed line) to approximately double the minimum observed sample size in each comparison. Confidence intervals (CIs) were set at 84%, which has been demonstrated equivalent to a p-value of 0.05 significant difference (MacGregor-Fors and Payton 2013). CIs are represented by shaded areas around the curves. Additional analyses with CIs at 95% are presented in Supplementary Materials (Figure S2.1) for comparison.

Canopy camera-traps were particularly effective at detecting gliding mammals, primates, and non-gliding rodents (Figure 2.3), reflecting the main taxa present in the canopy. Canopy camera-traps matched terrestrial units in their ability to detect semi-arboreal species (Figure 2.3). On the other hand, terrestrial cameras detected more viverrids, mustelids, and felids. Terrestrial camera-traps were also effective at sampling non-gliding rodents, although examination of species' identity (Supplementary Materials Table S2.2) reveals little overlap with the non-gliding rodent species detected in the canopy, reflecting the high diversity within this group. Significantly more threatened arboreal mammals were detected in unlogged forest than in recovering-logged forest, although there was no significant difference in detection of threatened terrestrial mammals between unlogged and recovering-logged forest (Figure 2.3).

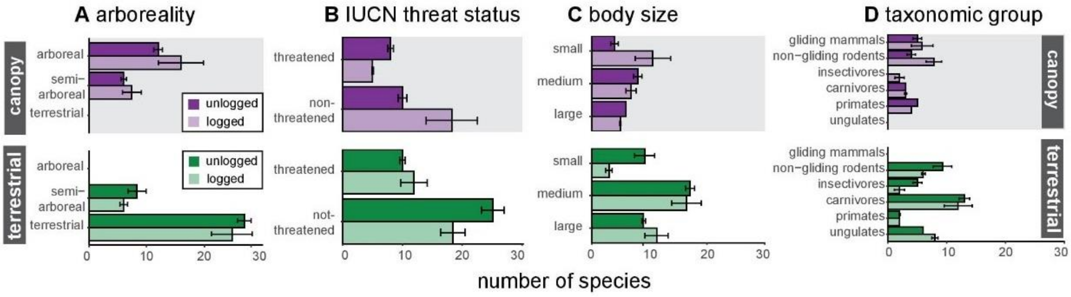

Figure 2.3 Number of species detected by canopy and terrestrial camera-traps in unlogged and recovering-logged forest, split into groups according to (A) arboreality, (B) IUCN threat status, (C) body size, and (D) taxonomic group. Richness data were extracted from rarefied species accumulation curves at a common sample size, with 84% confidence intervals.

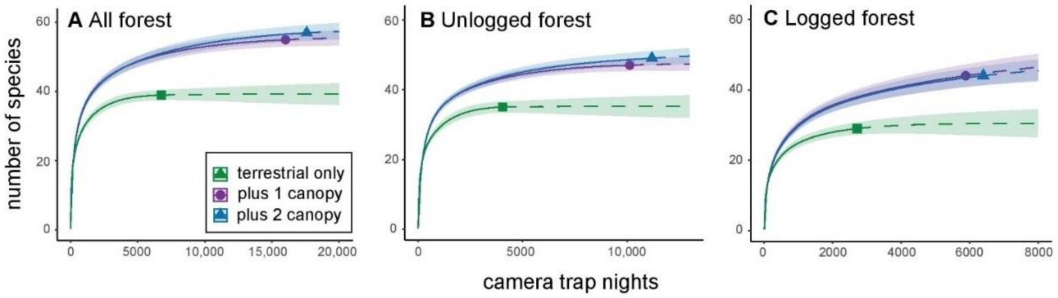

Figure 2.4 Species accumulation curves comparing species numbers obtained from terrestrial-only camera-traps with those obtained by pooling data from terrestrial- plus one canopy camera-trap, and terrestrial- plus two canopy camera-traps. Inventories are shown for (A) all data, (B) unlogged forest only, (C) recovering-logged forest only. Confidence intervals were set at 84% in line with Figure 2.2 and are represented by shading around the curves. Analyses utilised all data (6,661 CTN for terrestrial cameras; 9,156 CTN for single canopy cameras; 1,409 CTN for second canopy cameras). Analyses were repeated using a standardised subset of 1,409 CTN (the minimum trapping effort arising from the second canopy camera-traps), and are presented in Supplementary Materials Figure S2.3 for comparison.

Rarefaction analyses based on comparisons of data from terrestrial-only versus terrestrial-and-canopy camera-traps showed that the inclusion of canopy sampling significantly improved inventories in both unlogged and recovering-logged forest (Figure 2.4). Canopy camera-traps added 12 unique species in unlogged forest, 15 unique species in recovering-logged forest, and 16 species overall, or 18 species if detections from the experimental second canopy camera-traps are included (Figure 2.4, Supplementary Materials Table S2.2). This difference was greatest in recovering-logged forest, driven mainly by the lower number of species detected by terrestrial-only camera-traps. However, the addition of a second camera-trap elsewhere in the canopy did not significantly improve inventories (Figure 2.4, Supplementary Materials Figure S2.3).

2.3.3 Community variation between strata and unlogged/recovering-logged forest

The NMDS ordination utilised information from 79 camera-trap locations that photographed mammals, and was statistically robust (stress = 0.120). Canopy and terrestrial camera-traps formed distinct groupings in ordination space, highlighting significant differences in community structure between the strata (permanova, $R^2 = 0.215$, $p<0.001$) (Figure 2.5). Terrestrial camera-trap locations were more similar to each other than canopy camera-trap locations, irrespective of whether they were in unlogged or recovering-logged forest. Differences between the communities of unlogged and recovering-logged forest were much subtler ($R^2 = 0.027$, $p<0.015$).

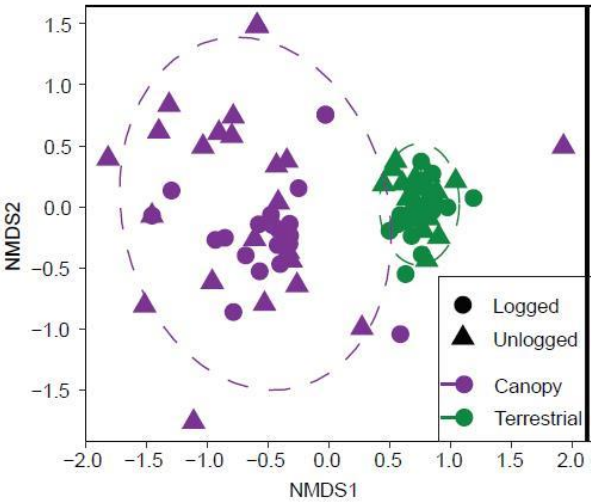

Figure 2.5 Non-metric multidimensional scaling (NMDS) ordination showing variation in mammal community structure detected by camera-traps set in the canopy versus terrestrial strata of unlogged and recovering-logged forest.

Key species identified by both envfit and Pearson's coefficient tests to be driving community differences between strata were small-toothed palm civet *Arctogalidia trivirgata* and Prevost's squirrel *Callosciurus prevostii*, indicative of the canopy, and Malay porcupine *Hystrix brachyura*, tufted ground squirrel *Rheithrosciurus macrotis*, pig-tailed macaque *Macaca nemestrina*, red muntjac *Muntiacus muntjak*, Bornean yellow muntjac *Muntiacus atherodes*, greater mousedeer *Tragulus napu*, bearded pig *Sus barbatus*, sun bear *Helarctos malayanus*, Malay civet *Viverra tangalunga*, banded civet *Hemigalus derbyanus* and leopard cat *Prionailurus bengalensis*, indicative of ground level (Figure 2.5; Supplementary Materials Table S2.3).

2.3.4 Cost

Canopy camera-trapping was more expensive than terrestrial camera-trapping due to the following additional costs that sampling at height brings: (i) hire or purchase of climbing equipment, (ii) canopy-access training; (iii) increased salary costs for trained climbers, (iv) more personnel needed to carry climbing equipment; and (v) increased time needed to rig trees and access the canopy (Table 2.2). For both terrestrial and canopy camera-trap locations, setup took substantially longer than maintenance or collection due to the extra time necessary to cut trails, identify suitable locations and position camera-traps. Total costs will vary depending on study design, field conditions and resources already available. In the context of our study, we estimated the implementation costs of canopy camera-trapping to be double those of terrestrial-only sampling (approximately \$5,000-\$6,000 for terrestrial-and-canopy sampling vs. approximately \$2,500 for terrestrial-only sampling, per site) (Table 2.2). However, we calculated that a terrestrial-only study under our sampling conditions would have taken longer to implement (an estimated 164 days vs. the 119 days for paired canopy-and-terrestrial locations, Table 2.2). This is because terrestrial and canopy camera-traps are targeting different elements of the mammal community (i.e. ground-dwelling vs. canopy-dwelling species), and thus are deliberately deployed very close to each other in order to sample as much of the community as possible at each location. In contrast, terrestrial cameras target only ground-dwelling species, and are widely spaced in order to satisfy independence assumptions. At our field station, two staff members were already trained in canopy access, and climbing equipment was available, with the cost of its hire built into the increased daily salary of the climbing crew. Our additional one-off expenses therefore totalled \$686 for canopy access training for one researcher (JKH, undertaken in Malaysia). For studies where equipment is not already available, we estimate an approximate additional cost of \$4,317 (Table 2.2).

Table 2.2 Costs (US dollars) of terrestrial-only versus terrestrial-and-canopy camera-trapping, based on our experience in Sabah. Items followed by ^ indicate one-off expenses; those followed by * indicate estimates. Costs are calculated for a three-person team (one ground crew, two climbers) in line with safety protocols. In our study, fieldwork implementation was led by JKH, who comprised one half of the two-person climbing team, and received funding separately via a PhD scholarship. Salary costs for research assistants are therefore calculated for 1x ground crew and 1x climbing crew per day. For studies that will be implemented entirely by on-site field staff, salary estimates can be adjusted accordingly as we have given a per-day per-person estimate for ground and climbing crew. For studies where climbing equipment is not available, we provide prices from recognised online retailers, current as of January 2021, based on two climbers ascending trees up to 70 m height using one main climbing rope and one safety rope. The 'Implementation' comparison assumes a fixed number of camera traps (here, based on our experience, a 50-camera-trap survey implemented at two sampling sites) and so costs reflect the actual number of days we required to deploy all terrestrial-and-canopy camera-traps at our sampling locations, vs. the estimated number of days that would have been required to deploy the same number of cameras at double the number of locations, if terrestrial-only sampling had been conducted. In our study, locations were widely spaced across difficult terrain, largely without trails or roads, and one-third required multi-night camping trips for access. We therefore estimated an average setup rate of two locations per day under a terrestrial-only design. Likewise, for maintenance checks and collection under a terrestrial-only design, we allowed double the time necessary than for our terrestrial-and-canopy design due to the wide spacing of locations and the fact that a terrestrial-only study would have double the number of locations. Studies in other regions with less challenging terrain, or where sampling locations are less widely spaced, may adjust budget projections accordingly in line with the per-person, per-day estimates provided below.

Item	Terrestrial & Canopy Sampling	Terrestrial-only Sampling
Training Expenses		
Canopy access course^	$686 per person (in Malaysia)	n/a
Climbing Equipment		
Climbing rope 150 m x 2^	$1,457 *($728.50 per unit)*	n/a
Rope 50 m x 1^	$135	n/a
Rope bag 55 litre x 3^	$515 *($171.60 per unit)*	n/a
Harness x 2^	$659 *($329.50 per unit)*	n/a
Harness chest attachment x 2^	$110 *($55 per unit)*	n/a
Chest ascender (‘croll’) x 2^	$110 *($55 per unit)*	n/a
Hand ascender (‘jumar’) x 2^	$124 *($62 per unit)*	n/a
Descender (‘rig’) x 2^	$324 *($162 per unit)*	n/a
Fall-arrest (‘backup device’) x 2^	$384 *($192 per unit)*	n/a
Foot ascender (‘pantin’) x 2^	$117 *($58.50 per unit)*	n/a
Footcord (‘footloop’) x 2^	$55 *($27.50 per unit)*	n/a
Helmet x 2^	$176 *($88 per unit)*	n/a
Karabiners x 10^	$233 *($23.30 per unit)*	n/a
Slings x 5^	$51 *($10.20 per unit)*	n/a
Bigshot catapult x 1^	$165	n/a
Fishing rod x 1^	$96	n/a
Fishing line^	~$14 to set 50 cameras	n/a
Fishing weights^	~$14 to set 50 cameras	n/a
Pilot line 4 mm^	~$93 to set 50 cameras	n/a
Total	**$4,317**	**n/a**
Labour		
Ground crew (x1 person)	$30 per person per day	$30 per person per day
Canopy-trained crew (x1 person)	$60 per person per day	n/a
Total	**$90 per day**	**$30 per day**
Implementation (100 cameras)	**Realised Sampling Effort**	**Estimated Sampling Effort**
<u>Mt. Louisa sites (logged forest)</u>	<u>50 cameras, 25 locations</u>	<u>50 cameras, 50 locations</u>
Setup 2017:	39 days x $90 = $3,510	25 days* x $30 = $750
Collection 2018:	10 days x $90 = $900	20 days* x $30 = $600
Re-set 2019:	11 days x $90 = $990	22 days* x $30 = $660
Collection 2019:	8 days x $90 = $720	16 days* x $30 = $480
Total:	**57 days, $6,120**	**83 days*, $2,490**
<u>Maliau Basin sites (unlogged forest)</u>	<u>50 cameras, 25 locations</u>	<u>50 cameras, 50 locations</u>
Setup 2018:	22 days x $90 = $1,980	25 days* x $30 = $750
Maintenance check 2019:	15 days x $90 = $1,350	30 days* x $30 = $900
Collection 2019:	13 days x $90 = $1,170	26 days* x $30 = $780
Total:	**62 days, $4,860**	**81 days*, $2,430**
Total (all locations):	**50 canopy-and-terrestrial locations** **= 119 days, $10,980**	**100 terrestrial-only locations** **= 164 days*, $4,920**

2.4 Discussion

We describe the first canopy-based camera-trap inventory of arboreal mammals in Southeast Asia, and provide the first comparison of camera-trapping between terrestrial and canopy strata in this region. Our results reveal that arboreal mammals form a diverse community (Figure 2.2), comprising mainly species rarely or never detected at ground level (Figure 2.4, Supplementary Materials Table S2.2). This corroborates earlier findings on arboreal mammal communities from Peru (Gregory *et al.* 2017; Whitworth *et al.* 2019a), Brazil (Malcolm 1991), Rwanda (Moore *et al.* 2020), and Sri Lanka (Jayasekara *et al.* 2007), and emphasises the importance of effective monitoring protocols for arboreal species that are easily overlooked by traditional terrestrial-based sampling.

Contribution of canopy cameras to mammal inventories

Our results clearly indicate that a sizeable proportion of the mammal community is routinely missed if sampling is only conducted at ground-level. Species accumulation curves showed canopy camera-traps significantly increased the overall mammal inventory compared to using only terrestrial camera-traps, and this pattern held across unlogged and recovering-logged forest (Figure 2.4). Across all locations, canopy camera-traps recorded 18 species that were not detected at ground level, adding 32% more species to inventories than would have been recorded using terrestrial camera-traps alone (Figure 2.4, Supplementary Materials Table S2.2). The mammal fauna detected on terrestrial camera-traps was more consistent across sampling locations than that documented by canopy camera-traps (Figure 2.5), reflecting the greater patchiness in detections and slower accumulation of arboreal species (Supplementary Materials Figure S2.2). Differences between unlogged and recovering-logged forest were much weaker than those between terrestrial and canopy strata, and were largely driven by the greater number of species detected by terrestrial camera-traps in unlogged forest (Figure 2.2).

Despite high detections in both strata, 21 species known to be present and detectable in the landscape were not recorded (Supplementary Materials Table S2.2): nine terrestrial, six arboreal and six semi-arboreal (i.e. potentially detectable in either strata) taxa. This finding is common to all survey methods, including camera-trapping in canopy (Whitworth *et al.* 2016; Bowler *et al.* 2017; Moore *et al.* 2020) and terrestrial (e.g. Evans, Vickers, and Abu-Bakar 2016; Wearn *et al.* 2017) strata. Indeed, comparisons of the efficacy of visual surveys versus canopy camera-traps found both methods failed to detect some arboreal species that were picked up by the other (Whitworth *et al.* 2016; Bowler *et al.* 2017; Moore *et al.* 2020), and a similar pattern is reported for terrestrial versus canopy camera-traps elsewhere (Whitworth *et al.* 2019a; Moore *et al.* 2020). Possible reasons to explain this discrepancy in our study include low density or patchy distributions (e.g. bay cat *Catopuma badia*), preference for habitat conditions not represented (e.g. riverine areas, flat-headed cat *Prionailurus planiceps*), or population fluctuations linked to resource availability (e.g. rodents, Nakagawa *et al.* 2007).

Canopy camera-traps are most effective at detecting small- and medium-bodied species, gliding mammals and primates (Figure 2.3), reflecting the dominant arboreal taxa present in Borneo (Payne and Francis 2007). Previous canopy camera-trap studies in the Neotropics have focussed on medium- and large-bodied mammals (Cassano, Barlow, and Pardini 2012; Whitworth *et al.* 2016; Bowler *et al.* 2017), as have most terrestrial camera-trap surveys, since small-bodied species are often fast-moving or obscured by vegetation, making identification difficult (Jayasekara *et al.* 2007; Glen *et al.* 2013). It is therefore encouraging to find that smaller mammals, including the highly diverse gliding mammals, can be readily identified from canopy camera-trap images, especially given the prevalence of these groups in Bornean rainforests (Thorington *et al.* 2012). Both canopy and terrestrial camera-traps recorded relatively high detections of non-gliding rodents (Figure 2.3), with little overlap in the identity of these species present in each strata (Supplementary Materials Table S2.2), demonstrating the ability of canopy camera-traps to boost species inventories of often poorly-sampled taxa. Of the larger-bodied species, primates were well-sampled by canopy camera-traps, recording six of eight species known to be present, compared to only three species recorded by terrestrial cameras (Supplementary Materials Table S2.2). Consistently higher detection frequencies in the canopy for all recorded primates (Supplementary Materials Table S2.3) indicates that canopy camera-trapping may prove useful for studying the activity and behaviour of this group, which can be sensitive to human presence, in a manner that is minimally invasive and able to be deployed for long time periods across large spatial scales (see as example Whitworth *et al.* 2019b).

Conversely, terrestrial camera-traps were more effective at detecting medium- and larger-bodied species, particularly felids, civets and mustelids. Although many of these species are classified as semi-arboreal and therefore potentially detectable by cameras in either strata, we found they were more often detected on terrestrial camera-traps in our study area, indicating that they may be more habitually terrestrial than arboreal. However, this may also be a result of lower detection probability in the canopy, linked to the overall greater three-dimensional area of this stratum and the resultant slower accumulation of species. It is also possible that larger-bodied semi-arboreal species tend to utilise the lower canopy layers, or habitat features such as vine tangles (e.g. masked palm civet *Paguma larvata*, Chutipong *et al.* 2015) or tree holes (e.g. pangolin *Manis javanica*, Lim and Ng 2008), whereas most of our canopy camera-traps were set in the mid- to upper-canopy facing large branches or trunks.

These differences between presumed and detected arboreality serve to highlight that there is much we do not yet know about vertical space use by rainforest mammals.

Lower detections of threatened species by canopy camera-traps reflect the fact that fewer arboreal species in our sampling locations are categorised as threatened compared to terrestrial species (Supplementary Materials Table S2.2), particularly among rodents. However, canopy camera-traps at unlogged forest locations detected significantly higher numbers of threatened arboreal mammals than those in recovering-logged forest. In contrast, there was no significant difference in numbers of threatened terrestrial species between recovering-logged and unlogged forest. This may have implications for survey design where the aim is to monitor threatened species.

Species-specific insights

For most of the arboreal species we recorded, little is known about their ecology, geographic distribution and tolerance to habitat modification (Meijaard *et al.* 2005; Payne and Francis 2007). For example, our record of an arboreal squirrel not fitting any known description for Bornean species (*Callosciurus sp.*, Supplementary Materials Table S2.2, Supplementary Materials Figure S2.4), as well as our putative record of smoky flying squirrel *Pteromyscus pulverulentus*, for which no confirmed photographic image currently exists (Thorington *et al.* 2012; IUCN Red List: last assessed February 2016, accessed February 2021), suggests that much remains to be discovered about Borneo's little-known arboreal small mammals. Canopy camera-traps also documented interesting behavioural insights such as confirmed use of the canopy by plain treeshrews *Tupaia longipes*, a species previously considered strictly terrestrial (Payne and Francis 2007); probable branch scent-marking in tufted ground squirrels *Rheithrosciurus macrotis*, a threatened and poorly-known Borneo endemic; prevalence of 'branch-walking' rather than brachiating locomotion in Bornean gibbons *Hylobates funereus*, especially in unlogged forest locations; and canopy mating behaviour of the strictly arboreal small-toothed palm civet *Arctogalidia trivirgata* (Supplementary Materials Figure S2.4).

Effects of logging on rainforest mammals

Overall, our results suggest that the arboreal mammal community of recovering-logged forest is comparable in terms of species identity and diversity to that of unlogged forest (Figure 2.2, Table S2.2). This is encouraging from the perspective of species conservation, and corroborates similar findings from terrestrial mammal research (e.g. Brodie *et al.* 2014b; Jati *et al.* 2018). In contrast, we recorded lower terrestrial species diversity in recovering-logged versus unlogged forest (Figure 2.2), indicating that logged forest inventories are not artificially inflated by arboreal species more frequently descending to ground level, as sometimes proposed in the literature (e.g. Lambert, Malcolm, and Zimmerman 2005; Berry *et al.* 2010). However, these findings should be viewed in the context of the relative habitat quality of our recovering-logged forest locations, which underwent selective logging ten years prior to sampling and have been regenerating since that time. It is possible that there is a threshold of disturbance beyond which most arboreal species cannot persist (Deere *et al.* 2020a), and that this threshold had not been met in our study system. It is also important to note that our recovering-logged forest sampling area is subject to low hunting levels in the regional context (Wearn *et al.* 2017), whereas logging is often associated with a substantial increase in the hunting of mammals, due to easier forest access from logging roads (Brodie *et al.* 2014b).

Results from other locations are inconclusive, with canopy camera-trapping in the Neotropics showing medium- and large-bodied arboreal species to be more susceptible to habitat disturbance than their terrestrial counterparts (Cassano, Barlow, and Pardini 2012; Whitworth *et al.* 2019a), whereas live-trapping studies of small mammals documented varying responses to logging (e.g. Pardini 2004; Wells *et al.* 2007; Laurance *et al.* 2008). In our study, it is also notable that while arboreal species diversity was similar between unlogged and recovering-logged forest, the frequency of capture events for some arboreal primates and gliding mammals was substantially lower in recovering-logged forest, whereas that of more common species (e.g. Prevost's squirrel *C. prevostii*, pig-tailed macaque *M. nemestrina*) increased markedly in recovering-logged forest (Supplementary Materials Table S2.3). The causes of these differences warrant further examination. For now, they serve to highlight the fact that to fully understand the impacts of logging, we should not rely solely on species diversity. Changes in the relative abundance of mammals can impact ecosystem functioning, with declines in key species negatively affecting forest regeneration (Chazdon *et al.* 2009). What seems clear from the limited but increasing number of canopy-based studies is that habitat management strategies derived from terrestrial-only sampling risk overlooking the effect of logging on arboreal mammals, and thereby underestimating its true impact on rainforest ecosystems.

Methodological considerations

Species accumulated more slowly in canopy inventories compared to those on the ground, as reported by other studies (Gregory *et al.* 2014; Whitworth *et al.* 2016; Whitworth *et al.* 2019a). While terrestrial communities in both unlogged and recovering-logged forest reached an asymptote at a sampling period of 3,000-5,000 CTN (Figure 2.2), this increased to an estimated 12,000-13,000 CTN for arboreal communities, or up to 57,000 CTN when data from both unlogged and recovering-logged forest were combined (Supplementary Materials Figure

S2.2). Mammals utilising the terrestrial space are limited mostly to a horizontal distribution at ground level unless they exhibit arboreal tendencies. In the canopy space, however, mammals can be distributed both horizontally across branches and vertically across interlinked canopy strata (Nakamura *et al.* 2017; Hanya *et al.* 2020), which in Borneo can incorporate heights of up to 100 m in emergent trees (Shenkin *et al.* 2019). Mammal density in the canopy space is therefore much lower (i.e. animals per cubic kilometre). The passive infrared sensors on most camera-traps are designed to maximise the horizontal width of the detection zone (which may span 10+ m), but not the vertical height (typically spanning 1-2 m) (Wearn and Glover-Kapfer 2017). In addition, while terrestrial camera-traps sample within their detection zone relatively evenly up to their maximum trigger distance, canopy camera-traps facing a focal branch or trunk are effectively sampling only the width and length of that feature, with the rest of the surrounding sampling area comprising empty space. It is therefore intuitive that species will accumulate more slowly in canopy inventories, and this should be factored into study design.

It has become increasingly common in terrestrial camera-trapping studies to deploy multiple camera-traps per location to boost detection probabilities when they are low (Pease, Neilson, and Holzmueller 2016; O'Connor *et al.* 2017; Wong *et al.* 2019). There has been little research into whether this method is useful in canopy settings, although one study in Brazil deploying arrays of 2-8 canopy camera-traps found detection probabilities of primates increased with the number of camera-traps per sampling location (Kaizer 2019). Our trials deploying a second canopy camera-trap did not yield much improvement to new species detections (Figure 2.4, Supplementary Materials Figure S2.3); however, they were limited to a small subset of trees and a shorter sampling period. It is worth noting that the gains in unique species detections from additional canopy camera-traps came from unlogged forest locations, which makes sense in the context of the greater height and structural complexity – and therefore larger potential sampling area – of unlogged forest canopies (Deere *et al.* 2020a). Canopy camera-trapping as a sampling method is in its infancy, and forest canopies present a much more complex sampling space than the forest floor. While our results do not show strong support for prioritising additional canopy camera-traps per sampling location, we do not rule this out as an avenue for future research into maximising arboreal species detections, depending on study aims and resources available.

Costs

Research budgets are almost always a limiting factor in study design. Canopy camera-trapping is reported to be cost-effective when compared with alternative methods such as line transects (Whitworth *et al.* 2016; Kaizer 2019). However, for studies where camera-trapping alone is the preferred sampling method, we could find no information evaluating the extra expenses incurred by deploying camera-traps in the canopy. We found canopy-and-terrestrial camera-trapping to be approximately twice as expensive as equivalent sampling effort at ground-level only (Table 2.2), although exact costs will vary according to study design and field conditions. At our field sites, the greatest cost arose from the additional personnel needed to carry climbing equipment and access the canopy. This was due in part to our study design, with camera-trap locations widely spaced across difficult, off-trail terrain and therefore requiring substantial time to access regardless of the stratum in which our camera-traps were set. However, we note that for studies with easier access to sampling locations, the cost of canopy camera-trapping is likely to be proportionately higher in comparison to that of terrestrial-only sampling because once a location has been accessed, the greatest time cost of canopy camera-trapping arises from the process of canopy access itself. Selecting a suitable tree, rigging it with climbing ropes, ascending to the canopy and positioning a camera-trap took between 1.5-6 hours per tree (although this will vary with field conditions and, to some extent, experience). In contrast, once a location has been accessed, a terrestrial camera-trap can generally be set within 0.5-1 hours.

For these reasons, costs must be considered in the context of individual study aims and budget, and weighed against the value of the additional data likely to be obtained by canopy camera-traps (Figure 2.4, Supplementary Materials Table S2.2). For researchers wishing to implement canopy camera-trapping, we recommend the following ways of reducing costs: (1) Deploy camera-traps over one, longer period rather than two separate shorter periods, thus reducing the number of times locations need to be accessed to set-up, check and collect camera-traps; (2) Scout for suitable focal trees first with ground crew only and minimal equipment, marking positions and preparing access without the burden of heavy bags; (3) Leave pilot line (thin, inexpensive rope running from canopy to ground) in place in focal trees so that climbing ropes can then be easily re-installed upon subsequent visits, avoiding the lengthy rigging process; (4) Consider study longevity. Investment in climbing equipment and training is more cost-effective for multi-season studies as both last for several years; (5) Where possible, source equipment and training locally as this is often less expensive, reduces transport costs, and has the additional benefit of enabling familiarisation with location-specific climbing conditions (humidity, terrain, insects etc.).

Recommendations

Based on our findings, we recommend that studies aiming to inventory the entire, non-flying mammal community of a given area include canopy camera-traps alongside paired units at ground-level (although detection of very small-bodied species and bats may require additional live-trapping in both strata). Canopy camera-traps have shown comparative efficiency to ground-based visual surveys for inventorying arboreal mammal communities (Bowler *et al.* 2017; Moore *et al.* 2020). We provide evidence corroborating the ability of canopy camera-traps to reliably detect strictly arboreal and semi-arboreal species, and suggest that studies focussing on primarily arboreal species may consider deploying canopy camera-traps as a stand-alone method. However, consideration should be given to specific study aims, target species and resources available, as both camera-traps and visual surveys may miss a small proportion of the mammal community (see for example Whitworth *et al.* 2016). On the other hand, for studies concentrating on terrestrial and larger-bodied semi-arboreal species, it may be more cost-effective to deploy camera-traps only at ground-level. Behavioural studies of larger-bodied semi-arboreal species known to use both strata (e.g. orangutan *Pongo pygmaeus*, binturong *Arctictis binturong*) may benefit from camera-trapping at both levels as species likely utilise each stratum differently (Ancrenaz *et al.* 2014; Chutipong *et al.* 2015; Whitworth *et al.* 2019b).

2.5 Conclusion

We provide compelling evidence that the inclusion of canopy camera-trapping significantly increases overall rainforest mammal inventories. However, this survey method can incur substantial additional costs, which should be factored into project planning alongside consideration of study aims and design. There is great scope for further study in this field, including increasing knowledge of arboreal species’ geographic distributions, activity and vertical niche partitioning, tolerance to human-induced habitat disturbance, and optimal sampling methods for the canopy strata. Canopy camera-trapping also provides the potential for behavioural studies of species that are not easily observable from ground level. Our results add to the small but growing body of evidence that by overlooking arboreal communities, we are missing crucial insights into the true diversity and functional significance of rainforest mammals. Tropical rainforests are complex habitats covering vast horizontal and vertical areas, and with a high proportion of species utilising the canopy strata. In order to fully understand these ecosystems, and by extension effectively conserve them, it is vital that future research includes canopy-based sampling.

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Data Availability Statement. Data used for analyses in this study is available at: https://zenodo.org/record/5018280#.YNM-pehKiUk

Ethics Statement. The animal study was reviewed and approved by School of Anthropology and Conservation Research Ethics Committee, University of Kent.

Author Contributions. JKH, MJS, NJD and AM conceived and designed the study. JKH conducted the fieldwork and performed the statistical analysis under guidance from MJS, NJD and ORW. JKH, NJD and MJS wrote the manuscript. All authors contributed to manuscript revision and read and approved the submitted version.

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Conflict of Interest. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

2.7 Supplementary Materials

Table S2.1 Summary of all 75 peer-reviewed publications describing the use of canopy camera-traps to study arboreal mammals. Results obtained via Web of Knowledge in February 2021 using the search terms “camera trap” and “arboreal”, and, separately, “camera trap” and “canopy”, with time-period set to all years, and updated in July 2022 for the purposes of this thesis, to include additional studies that have taken place since the publication of Haysom *et al.* 2021. A summary of our study appears on the top row for comparison. Tildes (~) denote where number of camera-trap nights (CTN) was not stated, but could be estimated from the number of camera-traps and sampling period reported in the study.

	Reference	**Main focus**	**Country**	**Canopy camera-trap number (*N*), height range (H) & bait use**	**Other sampling**	**Forest type**	**No. CTN Canopy**	**No. CTN Terrestrial**	**No. mammal species detected (multi-species studies only)**
	This study (Haysom *et al.* 2021)	**Inventory, Method, Disturbance effects** Canopy & terrestrial camera traps to inventory mammal communities of unlogged & recovering-logged forest	Malaysia (Borneo)	*N* = 69 H = 9.8-52.3 m	Terrestrial cameras N = 49	Tropical lowland-hill rainforest	10565	6661	Total = 57 Canopy only = 18 Terrestrial only = 30 Both heights = 9
1	Agostini *et al*. 2022	**Inventory, Method** Surveyed arboreal and terrestrial mammal assemblages, detected brown-eared woolly opossum *Caluromys lanatus* not previously recorded in terrestrial surveys	Argentina	*N* = 19 H = 6-14.5 m	Terrestrial cameras *N* = 18	Atlantic forest	1141	625	Canopy = 6 (exclusive to canopy = 4) Terrestrial = 23
2	Garcia *et al.* 2022	**Bridge use** Testing wood, and rope, bridge designs for use by black lion tamarin *Leontopithecus chrysopygus* and other arboreal species	Brazil	*N* = 2 H = ~6 m	n/a	Atlantic Forest	1095	n/a	9

3	Gracanin & Mikac 2022	**Activity patterns** Arboreal and semi-arboreal mammal activity pattern overlap	Australia	*N* = 18 H = 2 m Baited	n/a	Subtropical rainforest & Eucalyptus forest	6517	n/a	10
4	Monteza-Moreno *et al*. 2022	**Plant-animal interactions** Seed dispersal of endemic cycad by mammal (northern olingo *Bassaricyon gabbii*)	Panama	*N* = 3 H = 15-20 m	Observations	Montane forest	271	n/a	Cameras = 7 mammal interactions Observations = 1 bird interaction
5	Seguine *et al*. 2022	**Frugivory, Multi-taxa** Birds & mammals at nutmeg trees. Frequent visits of kinkajou *Potos flavus*, likely important seed disperser	French Guiana	*N* = 34 H = 30-40m	n/a	Tropical forest	1320	n/a	24 vertebrate species
6	Chen *et al*. 2021	**Occupancy, Monitoring** Canopy camera traps to monitor threatened lemur species	Madagascar	*N* = 30 H = 6-14 m	Terrestrial cameras	Rainforest fragments	900	870	Canopy = 9 Terrestrial = 1
7	Honey *et al*. 2021	**Nest/cavity monitoring, Method, multi-taxa** Testing cameras to monitor mammals and birds using tree cavities	Australia	*N* = 80 H = 7-20 m	Observations	Dry /temperate forest	Not stated	n/a	Total = 21 Cameras = 21 Observations = 6
8	Kaizer *et al*. 2021	**Inventory** Cameras to inventory arboreal Atlantic Forest mammals, detected thin-spined porcupine *Chaetomys subspinosus* not previously known from area	Brazil	*N* = 24 H = 7.5-17 m	n/a	Atlantic Forest	4736	n/a	15
9	Randler & Kalb 2021	**Activity** Circadian activity of fat dormouse *Glis glis*	Germany	*N* = 41 H = 1.2-1.3 m Baited	n/a	Temperate woodland	Not stated	n/a	n/a
10	Scabin & Peres 2021	**Inventory, Hunting, Multi-taxa** Hunting affects composition & size structure of terrestrial & arboreal vertebrates. Highlights use of canopy cameras to record otherwise undetected taxa.	Brazil	*N* = 120 H = ~15 m	Terrestrial cameras *N* = 480	Amazon rainforest	5715	16290	(all taxa, incl. mammals & birds) Canopy only = 21 Terrestrial only = 30

11	Zhu *et al.* 2021	**Frugivory, multi-taxa** Plant-frugivore interactions in fruiting trees, birds & mammals	China	318 sites H not stated	n/a	Subtropical forest	Not stated	n/a	Not stated
12	Azcarraga *et al*. 2020	**Activity** Activity patterns of arboreal mammals	Mexico	*N* = 9 H = 8-12 m	n/a	Semi-deciduous tropical rainforest	2664	n/a	Total = 12
13	Chan *et al.* 2020	**Bridge use** Canopy bridge use by critically endangered Hainan gibbon *Nomascus hainanus*	China	*N* = 1 H = 7-10 m	n/a	Seasonal tropical rainforest	~1170	n/a	n/a
14	Debruille *et al*. 2020	**Species presence** Canopy cameras to improve detection of binturongs (*Arctictis binturong*)	Philippines	*N* = 15 H = 1.7-18 m	n/a	Logged tropical forest	2973	n/a	n/a
15	Fang *et al.* 2020	**Species presence** Canopy cameras confirm range extension for critically endangered western black crested gibbon *Nomascus concolor*	China	*N* = 30 H = 8-15 m	Line transects, interviews, call monitoring	Temperate montane forest	~5400	n/a	Presence suspected from call recordings & interviews, identity confirmed by cameras. Species not detected by transects.
16	Hongo *et al.* 2020	**Inventory** Using multi-layer (terrestrial, <15 m & >15 m) camera trapping to inventory mammals. Medium and large mammals only.	Cameroon	*N* = 150 H = 4-24 m	Terrestrial cameras *N* = 88	Evergreen & semi-deciduous rainforest	5404	2901	Total = 40 Canopy cameras only = 8* **incl. 4 previously unknown from area* Terrestrial cameras only = 22 Both heights = 10
17	Laughlin *et al*. 2020	**Behaviour** Seasonal behaviour of white-footed mouse, *Peromyscus leucopus* & deer mouse, *P. maniculatus*	USA	*N* not stated H = 8-24 m	Terrestrial live trapping to mark species	Temperate - pine	8491	n/a	n/a

18	Linden *et al*. 2020	**Bridge use** Canopy bridge use by samango monkey *Cercopithecus albogularis*	South Africa	*N* = 10 H = 3-4.5 m	Behaviour observations	Disturbed evergreen forest / road	480	n/a	n/a
19	Linnell & Lesmeister 2020	**Behaviour (multi-taxa)** Predator-prey interactions in the canopy (mammals & birds)	USA	*N* = 168 H = 12-20 m	n/a	Temperate forest	~110,595	n/a	4 mammal species 3 bird species
20	Moore *et al*. 2020	**Inventory, Method** Canopy camera traps, terrestrial camera traps & line transects *(see also Moore & Niyigaba 2018)*	Rwanda	*N* = 54 H = 4-17 m	Terrestrial cameras *N* = 50 Line transects (total distance = 118.23 km)	Montane tropical forest	~1620	~1560	Total = 35 Canopy cameras only = 7* **incl. 1 previously unknown from area* Terrestrial only = 15 Both heights = 10 Transects = 11
21	Nekaris *et al*. 2020	**Bridge use** Canopy bridge use between forest fragments	Indonesia (Java)	*N* = 20 H = 1-8 m	n/a	Agricultural/ montane rainforest	2206	n/a	19 species of mammals & birds, number in each category not stated
22	Tongkok *et al*. 2020	**Behaviour** Arboreal & terrestrial camera traps to monitor frugivory	China & Thailand	*N* not stated H not stated	Terrestrial cameras, number not stated	Tropical forest	Not stated	Not stated	Total = 26 Number on canopy vs terrestrial cameras not stated
23	Balbuena *et al*. 2019	**Bridge use** Canopy bridge use over gas pipeline	Peru	*N* = 14 H = 21.5-32.5 m	n/a	Tropical rainforest	4593	n/a	Canopy = 16
24	Birot *et al*. 2019	**Bridge use** Canopy bridge use by Javan slow loris *Nycticebus javanicus*	Indonesia (Java)	*N* not stated H = 2-8 m	Observations	Agroforest in montane rainforest	1561	n/a	n/a
25	Kaizer 2019 (PhD thesis)	**Method** Canopy camera traps vs line transects for primate monitoring	Brazil	*N* = 16 H = 7.5-16 m	Line transects (total distance ~200 km)	Montane forest	2613	n/a	Both methods detected 3 of 5 primate species

26	McComb *et al*. 2019	**Behaviour** Monitoring predation of critically endangered Leadbeater's possum *Gymnobelideus leadbeateri* at nest boxes by feral cats	Australia	Information not available	Stomach content analysis of cats	Information not available	n/a	n/a	n/a
27	Whitworth *et al*. 2019a	**Inventory, Disturbance effects** Canopy & terrestrial cameras in protected & non-protected areas. Med-large mammals only	Peru	*N* = 145 H = 3.5-30 m	Terrestrial cameras *N* = 77	Tropical rainforest	20364	11253	Total = 46 Canopy only =20 Terrestrial only = 22 Both heights = 4
28	Whitworth *et al*. 2019b	**Behaviour** Sleeping site use & role in seed dispersal of Geoffroy's spider monkey *Ateles geofroyii*	Costa Rica	*N* = 39 H not stated	Follows to find sleeping sites & Terrestrial cameras, *N* = 56	Tropical rainforest, varying disturbance levels	1055	2287	n/a
29	Suzuki & Ando 2019	**Species presence** Effective rapid survey for endangered Japanese flying squirrel *Pteromys momonga*	Japan	*N* = 154 H = 2-3 m	n/a	Temperate: conifer-broadleaf	4620	n/a	n/a
30	Godoy-Guinao *et al*. 2018	**Behaviour** Confirming arboreal habits & investigating functional role of small arboreal marsupial *Dromiciops gliroides*	Chile	*N* = 6 H = 12-21 m	n/a	Temperate forest	~720	n/a	n/a
31	Lama 2018 (Masters thesis)	**Species presence, Method, Activity** (as part of wider terrestrial camera study), comparing the effectiveness of canopy vs. terrestrial cameras to survey red panda *Ailurus fulgens*	Nepal	*N* = 19 H = <10 m	Terrestrial cameras *N* = 19	Montane forest	~810	~810	Canopy = 807 photos of target species Terrestrial = 96 photos of target species
32	Mella *et al*. 2018	**Behaviour** First evidence of tree climbing in red fox *Vulpes vulpes*	Australia	*N* = 10 H = 2.3 m	n/a	Not stated	Not stated	n/a	n/a

33	Moore & Niyigaba 2018	**Species presence** Canopy cameras provide first record of Central African oyan *Poiana richardsonii* in Rwanda	Rwanda	*N* = 54 H = 6-10 m	n/a	Montane rainforest	~4200	n/a	Records of up to 8 individual *P.richardsonii*
34	Ribeiro-Silva *et al.* 2018	**Behaviour (multi-taxa)** Canopy cameras a viable tool for monitoring nest predation of birds, by birds & mammals, in a tropical rainforest environment	Brazil	*N* = 68 H not stated	n/a	Atlantic Forest - submontane rainforest	2604	n/a	Predator species: 6 mammals (including small-bodied <1 kg) & 6 birds
35	Yang *et al.* 2018	**Species presence** Using canopy cameras with other methods to confirm the presence of, and study a new population of critically endangered Myanmar snub-nosed monkey *Rhinopithecus strykeri*	China	*N* not clear H = 15-20 m	Terrestrial cameras, n not stated; transects & follows, faeces analysis	Temperate montane forest	Not stated	Not stated	Images of species obtained, along with observations & faeces samples from follows
36	Fang *et al.* 2018	**Monitoring (multi-taxa)** Canopy & terrestrial cameras to monitor mammals & birds (abstract only – paper in Chinese language)	China	*N* = 10 H = 5-10 m	Terrestrial camera traps *N* = 10	Temperate montane forest	~1150	~1150	Total = 20 Canopy only = 3 Terrestrial only = 9 Both heights = 8
37	Aziz *et al.* 2017	**Behaviour** Canopy camera traps to confirm role of island flying fox *Pteropus hypomelanus* in durian pollination	Malaysia (Peninsular)	*N* = 13 H = 2-20 m	n/a	Fruit orchard (durian)	~702	n/a	Total = 5 (target + 4 additional species)
38	Bowler *et al.* 2017	**Inventory, Method** Canopy camera traps vs line transects. Medium-large arboreal mammals only.	Peru	*N* = 42 H = 16.6-29.9 m	Transects (total distance = 2014 km)	Lowland tropical rainforest, historic logging & hunting	3147	n/a	Total = 19 Canopy cameras only = 6 (*including 1 previously unknown from area)* Transects only = 1 Both methods = 12

39	Gregory *et al*. 2017	**Bridge use** Canopy bridge use over gas pipeline	Peru	*N* = 25 H = 13.5-33.7 m	Terrestrial cameras *N* = 112	Tropical rainforest	7102	7154	Total = 40 Canopy only = 19 Terrestrial only = 15 Both heights = 6
40	Loria & Mendez-Carvajal 2017	**Behaviour** Use of habitat and activity pattern of whitefaced monkey *Cebus imitator* (abstract only – paper in Spanish)	Panama	*N* not stated H = 8-10 m	Direct observations	Coffee agroforest	3233	n/a	n/a
41	Ortiz-Lozada 2017	**(Primarily terrestrial)** Multiple sampling methods to record mammals in a protected area	Mexico	*N* = 11 H = ~15 m	Terrestrial cameras Encounters Tracks Live traps Mist nets	Secondary tropical evergreen forest	90	80	Total = 32 Canopy cameras = 9 Terrestrial = 7 Encounters = 10 Tracks = 8 Live traps = 3 Mist nets = 13 bat spp
42	Suzuki & Ando 2017	**Activity** Seasonal changes in activity pattern of Japanese flying squirrel *Pteromys momonga*	Japan	214 locations H = 2-3 m	n/a	Temperate forest	7317	n/a	n/a
43	Boulerice & Van Fleet 2016	**Species presence** Canopy cameras & bait tubes to detect northern flying squirrel *Glaucomys sabrinus*	USA	*N* not stated H = 1.5 m bait used	n/a	Temperate pine	6640	n/a	n/a
44	Cotsell & Vernes 2016	**Behaviour (multi-taxa)** Examining tree hollow use by birds, mammals & reptiles	Australia	*N* = 80 H =< 25 m	n/a	Eucalyptus forest	1158		9 mammals 21 birds 8 reptiles
45	Goldingay & Taylor 2016	**Bridge use** Canopy bridge use in urban area by koala *Phascolarctos cinereus*	Australia	*N* = 10 H = 5 m	n/a	Eucalyptus	Not stated	n/a	Total = 4 (target + 3 additional species)
46	Mills *et al*. 2016	**Species presence** Cameras & footprint tracks for hazel dormouse *Muscardinus avellanarius* & wood mouse *Apodemus sylvaticus*	UK	*N* = 5 H = ~2.5 m bait used	n/a	Temperate oak/mixed woodland	405	n/a	n/a

47	Suzuki *et al*. 2016	**Activity** Diurnal activity of juvenile Russian flying squirrels *Pteromys volans*	Japan	*N* = 1 H = 2.6 m	n/a	Temperate forest	~26	n/a	n/a
48	Whitworth *et al*. 2016	**Inventory, Method** Canopy cameras vs line transects & incidental observations. Medium-large arboreal mammals only.	Peru	Total *N* = 30: H =10 m (*N* = 15) H = 18.4-33 m (*N* = 15)	Transects (total distance = ~78 km) & incidental observations from year-round surveys	Disturbed tropical rainforest – some logging & hunting	2929	n/a	Total = 24 Canopy cameras = 18 *(6 exclusive to method, 1 previously unknown from area)* Transects = 13 *(1 exclusive to method)* Observation = 18 *(5 exclusive to method)*
49	Gregory *et al*. 2015	**Species presence, Behaviour, Activity** Confirming range extension & describing activity & behaviours of streaked dwarf porcupine *Coendou ichillus*	Peru	*N* not clear (part of larger study, see Gregory *et al*. 2014, 2017) H not stated	Live trapping mid-canopy	Tropical rainforest	7198	n/a	Records represent range extension of 900 km
50	Rivas-Romero & Soto-Shoender 2015	**Behaviour (multi-taxa), Method** Canopy camera traps as a method of examining frugivory in birds and mammals	Guatemala	*N* = 8 H = 10-15 m	n/a	Tropical cloud forest	902	n/a	3 mammal species 9 bird species
51	Soanes *et al*. 2015	**Bridge use** Monitoring use of bridges & glider poles across a highway by arboreal marsupials	Australia	*N* = not clear H = 4-18 m	Transponder tags & readers	Agricultural land & multi-lane highway	3929	n/a	5 species confirmed to use crossing structures
52	Yokochi & Bencini 2015	**Bridge use** Rapid habituation to rope bridge by endangered western ringtail possum *Pseudocheirus occidentalis*	Australia	*N* = 1 H = 8.5 m	Live capture & transponder tagging	Peppermint trees across major road	270	n/a	n/a

53	Fonturbel *et al*. 2014	**Activity** Activity pattern of monito del monte, *Dromiciops gliroides* (small arboreal marsupial)	Chile	*N* = 25 H not stated bait used	n/a	Temperate rainforest & Eucalyptus plantations	5012	n/a	n/a
54	Gregory *et al*. 2014	**Method, Bridge use** First major study on canopy camera effectiveness in context of monitoring canopy bridges over gas pipeline	Peru	*N* = 25 H = 13.5-33.7 m	n/a	Tropical rainforest	3608	n/a	Total = 20
55	Harley *et al*. 2014	**Species presence** Canopy cameras to detect cryptic Leadbeater's possum, *Gymnobelideus leadbeateri*	Australia	*N* = 15 H = 3-4 m bait used	n/a	Eucalyptus forest	1519	n/a	Total = 5 (target + 4 additional species)
56	Mendez-Carvajal 2014	**Method** Testing system of setting canopy cameras without need to climb trees	Panama	*N* = 13 H = 8-18 m	n/a	Tropical montane forest	232	n/a	Canopy only = 10
57	Goldingay *et al*. 2013	**Bridge use** Arboreal mammals use of rope bridges across a major highway	Australia	*N* not stated H not stated	n/a	Not stated	Not stated	n/a	Total = 4
58	Soanes *et al*. 2013	**Bridge use** Effectiveness of road-crossing mitigation for squirrel glider *Petaurus norfolcensis*	Australia	*N* = 7 H = 6-14 m	Radio-tracking & transponder tags	Agricultural land & highway	1806	n/a	n/a
59	Tan *et al*. 2013	**Activity** Canopy cameras reveal nocturnal activity in presumptive diurnal primate: Guizhou snub-nosed monkey *Rhinopithecus brelichi*	China	*N* = 2 H = 5-6 m	n/a	Temperate evergreen & broadleaf forest	294	n/a	n/a
60	Teixeira *et al*. 2013	**Bridge use** Monitoring wildlife use of road overpasses in fragmented urban landscapes.	Brazil	*N* = 6 H not stated	Community observational monitoring	Semi-deciduous seasonal forest patches & roads	689	n/a	Camera traps = 3 Community observation = 2 (same species as cameras)

61	Wahyudi & Stuebing 2013	**(Primarily terrestrial)** Wildlife monitoring in mixed use landscape	Indonesia (Borneo)	*N* = 17 H = 10-12 m lure used	Terrestrial cameras *N* = 40 lure used	Disturbed forest & oil palm	424	8204	Total = 33 Canopy only = 8 Terrestrial only = 23 Both heights = 2
62	Cassano *et al*. 2012	**Disturbance effects** Mammal use of agroforest vs forest: canopy & terrestrial camera traps. Large-bodied species only.	Brazil	*N* = 18 H = 3-4 m bait used	Terrestrial cameras *N* = 18	Logged forest & agroforest	~2000	~2000	Total = 22 Canopy = 6 Terrestrial = 16
63	Dalloz *et al*. 2012	**Behaviour** Climbing behaviour in bare-tailed woolly opossum, *Caluromys philander*	Brazil	*N* = 10 H = 2.5-5 m	n/a	Montane forest	~3650	n/a	Total = 10 (target + 9 additional species)
64	Olson *et al*. 2012	**Species presence** Validate sightings of greater bamboo lemur, *Prolemur simus* (critically endangered)	Madagascar	*N* = 7 H = 2-14 m	n/a	Tropical rainforest	231	n/a	n/a
65	Van Berkel *et al*. 2012	**(Primarily terrestrial)** Biodiversity survey	Indonesia (Borneo)	*N* = 2 H not stated	Terrestrial cameras *N* = 25	Tropical rainforest	7	570	Total = 26 Canopy only = 2 Terrestrial only = 24
66	Weston *et al*. 2011	**Bridge use** Canopy bridge use over roads	Australia	*N* not stated H = 7-8 m	Observation, scat collection, hair funnels	Tropical rainforest	Not stated	n/a	Total on cameras = 7 Detected by other methods but not cameras = 2
67	Oliveira-Santos, Tortato & Graipel 2008	**Activity** Activity patterns of small arboreal mammals	Brazil	*N* = 3 H = 3-6 m bait used	Terrestrial cameras (data from different study) *N* = 14	Atlantic Forest	Not stated	Not stated	Canopy cameras = 11 (Terrestrial cameras targeted only 1 species)
68	Forsman & Swingle 2007	**Behaviour (multi-taxa)** Use of arboreal tree vole *Arborimus spp.* nests by amphibians	USA	*N* = 3 H not stated	n/a	Temperate forest	Not stated	n/a	n/a

69	Jayasekara *et al*. 2007	**Behaviour** Using canopy and terrestrial camera traps to study frugivory at fruiting trees	Sri Lanka	*N* = 15 h <35 m bait used	Terrestrial cameras *N* = 15	Tropical lowland rainforest	Not stated	Not stated	Total = 14 Canopy only = 5 Terrestrial only = 6 Both = 3
70	Malt & Lank 2007	**Behaviour, Activity (multi-taxa)** Nest predation & activity patterns of marbled murrulet *Brachyramphus marmoratus*, red squirrel *Tamiasciurus hudsonicus* & deer mice *Peromyscus spp.*	Canada	*N* = 136 H = 25 ± 7 m	Artificial nests constructed	Temperate forest	Not stated	n/a	n/a
71	Schipper 2007	**Method** Camera trap avoidance by kinkajous, *Potos flavus*	Costa Rica	*N* = 1 H = 15 m	n/a	Moist forest	20	n/a	n/a
72	Goosem *et al*. 2005	**Bridge use** Testing the effectiveness of rope overpasses & faunal underpasses for wildlife connectivity across a road	Australia	*N* = ~3 H = 7-7.5 m	Spotlighting, hair & scat collection; sand-tracks; roadkill; some terrestrial cameras	Highland rainforest & road	Not stated	Not stated	6 arboreal species detected by cameras, 7 detected by scat collection, 4 by spotlighting, 2 by hair sample
73	Hirakawa 2005	**Method** Testing a new bat lure	Japan	*N* = 40 H = 1.5 m lure used	n/a	Temperate forest	~400	n/a	n/a
74	Kierulff *et al*. 2004	**Species presence** Surveying buff-headed capuchin, *Cebus xanthosternos* (endangered & elusive)	Brazil	*N* not stated H = 2 m bait used	n/a	Atlantic Forest	Not stated	n/a	n/a
75	Otani 2001	**Behaviour** Measuring fig foraging by Yakushima macaque, *Macaca fuscata yakui*	Japan	*N* = 7 H = 10 m	n/a	Temperate forest	~77	n/a	n/a

Table S2.2 Mammal species recorded by camera-traps in terrestrial and canopy strata in unlogged and recovering-logged forest. Species names in parentheses are those detected only by our experimental second canopy camera-traps (Bornean pygmy squirrel and Temminck’s flying squirrel). Species shaded grey are those thought to be present at our sampling locations and likely detectable using camera-traps, but not detected in this study. Assumption of presence and detectability was based on known body size, geographic distribution, elevation range, habitat preferences (information obtained from Payne and Francis 2007, and the IUCN Red List, accessed February 2021), as well as data from live-trapping studies at our sampling locations (S. Heon, *pers. comm.*). *Asterisks denote species endemic to Borneo. Brooke’s squirrel was previously known only from mountains outside of our sampling locations, and our records here likely reflect a range expansion. We define a species as ‘arboreal’ if it was detected exclusively by canopy camera-traps, ‘terrestrial’ if detected exclusively by camera-traps at ground level, or ‘semi-arboreal’ if detected by cameras in both strata (and we note in parentheses where these definitions contradict available knowledge from field guides). Three species frequently detected by canopy camera-traps, but recorded once each on terrestrial camera-traps, were classed as arboreal in line with available knowledge and considering the one-off nature of these records in the context of our extensive sampling period. These species were: Thomas’ flying squirrel (1 terrestrial record, 58 canopy records), Sabah grey langur (1 terrestrial record, 98 canopy records) and maroon langur (1 terrestrial record, 230 canopy records). Likewise, while banded civets have been noted as sleeping in tree holes (Payne and Francis 2007), and we obtained one canopy record on our experimental second canopy cameras, we include this species with terrestrial mammals here in light of the relative frequency of detections (1 canopy record, 159 terrestrial records). Species are grouped according to: IUCN threat status (‘threatened’ = categories Vulnerable, Endangered, or Critically Endangered; ‘not threatened’ = Near Threatened, Least Concern, or Data Deficient); body size (small <1 kg, medium 1-5 kg, large >5 kg); and broad taxonomic group (with elephant included in ‘ungulates’ and pangolin with ‘Insectivora’, according to closest relatives and/or feeding strategy).

Order	**Family**	**Species**	**Unlogged or logged forest: Detected vs. (presumed, where different)**	**Strata: Detected vs. (presumed, where different)**	**IUCN Threat Status**	**Body Size**	**Taxonomic Group**
Carnivora	Felidae	*Catopuma badia** Borneo bay cat*	n/a (both)	n/a (terrestrial)	threatened	medium	Carnivora
		Neofelis diardi Sunda clouded leopard	both	terrestrial (semi-arboreal)	threatened	large	Carnivora
		Pardofelis marmorata Marbled cat	both	terrestrial (semi-arboreal)	not threatened	medium	Carnivora

	Prionailurus bengalensis Leopard cat	both	terrestrial	not threatened	medium	Carnivora
	Prionailurus planiceps Flat-headed cat	n/a (both)	n/a (terrestrial)	threatened	medium	Carnivora
Herpestidae	*Herpestes brachyurus* Short-tailed mongoose	both	terrestrial	not threatened	medium	Carnivora
	Herpestes semitorquatus Collared mongoose	unlogged (both)	terrestrial	not threatened	medium	Carnivora
Mustelidae	*Martes flavigula* Yellow-throated marten	both	semi-arboreal	not threatened	medium	Carnivora
	Mustela nudipes Malay weasel	n/a (both)	n/a (terrestrial)	not threatened	medium	Carnivora
	Mydaus javanensis Sunda stink badger	both	terrestrial	not threatened	medium	Carnivora
Viverridae	*Arctictis binturong* Binturong	both	semi-arboreal	threatened	large	Carnivora
	Arctogalidia trivirgata Small-toothed palm civet	both	arboreal	not threatened	medium	Carnivora
	Cynogale bennettii Otter civet	n/a (both)	n/a (terrestrial)	threatened	medium	Carnivora
	Hemigalus derbyanus Banded civet	both	terrestrial (semi-arboreal?)	not threatened	medium	Carnivora
	*Hemigalus hosei** Hose's civet*	n/a (both)	n/a (terrestrial)	threatened	medium	Carnivora
	Paguma larvata Masked palm civet	both	terrestrial (semi-arboreal)	not threatened	medium	Carnivora
	Paradoxurus hermaphroditus Common palm civet	unlogged (both)	terrestrial (semi-arboreal)	not threatened	medium	Carnivora

		Viverra tangalunga Malay civet	both	terrestrial	not threatened	medium	Carnivora
	Prionodontidae	*Prionodon linsang* Banded linsang	n/a (both)	n/a (semi-arboreal)	not threatened	medium	Carnivora
	Ursidae	*Helarctos malayanus* Sun bear	both	terrestrial (semi-arboreal)	threatened	large	Carnivora
Cetartiodactyla	Suidae	*Sus barbatus* Bearded pig	both	terrestrial	threatened	large	Ungulates
	Tragulidae	*Tragulus kanchil* Lesser mousedeer	both	terrestrial	not threatened	medium	Ungulates
		Tragulus napu Greater mousedeer	both	terrestrial	not threatened	medium	Ungulates
	Cervidae	*Muntiacus atherodes** Bornean yellow muntjac*	both	terrestrial	not threatened	large	Ungulates
		Muntiacus muntjak Red muntjac	both	terrestrial	not threatened	large	Ungulates
		Rusa unicolor Sambar deer	both	terrestrial	threatened	large	Ungulates
	Bovidae	*Bos javanicus* Banteng	logged (both)	terrestrial	threatened	large	Ungulates
Dermoptera	Cynocephalidae	*Galeopterus variegatus* Sunda colugo	both	arboreal	not threatened	medium	Gliding mammals
Eulipotyphla	Erinaceidae	*Echinosorex gymnura* Moonrat	both	terrestrial	not threatened	small	Insectivora
Pholidota	Manidae	*Manis javanica* Sunda pangolin	both	terrestrial (semi-arboreal)	threatened	medium	Insectivora
Primates	Cercopithecidae	*Presbytis rubicunda** Maroon langur*	both	arboreal	threatened	large	Primates

		*Presbytis sabana** Sabah grey langur*	unlogged (both)	arboreal	threatened	large	Primates
		Macaca fascicularis Long-tailed macaque	unlogged (both)	semi-arboreal	threatened	large	Primates
		Macaca nemestrina Pig-tailed macaque	both	semi-arboreal	threatened	large	Primates
	Hylobatidae	*Hylobates funereus** Bornean gibbon*	both	arboreal	threatened	large	Primates
	Lorisidae	*Nycticebus menagensis* Philippine slow loris	n/a (both)	n/a (arboreal)	threatened	small	Primates
	Pongidae	*Pongo pygmaeus** Bornean orangutan*	logged	semi-arboreal	threatened	large	Primates
	Tarsiidae	*Cephalopacus bancanus* Horsfield's tarsier	n/a (both)	n/a (arboreal)	threatened	small	Primates
Proboscidea	Elephantidae	*Elephas maximus* Asian elephant	logged (both)	terrestrial	threatened	large	Ungulates
Rodentia	Sciuridae	*Aeromys tephromelas* Black flying squirrel	both	arboreal	not threatened	medium	Gliding mammals
		*Aeromys thomasi** Thomas' flying squirrel*	both	arboreal	not threatened	medium	Gliding mammals
		*Callosciurus adamsi** Ear-spot squirrel*	logged (both)	arboreal (semi-arboreal)	not threatened	small	Non-gliding Rodents
		Callosciurus notatus Plantain squirrel	n/a (both)	n/a (semi-arboreal)	not threatened	small	Non-gliding Rodents
		Callosciurus prevostii Prevost's squirrel	both	arboreal	not threatened	small	Non-gliding Rodents
		Callosciurus sp. (?) Large mystery squirrel	logged (both?)	arboreal	?	small	Non-gliding Rodents

(Exilisciurus exilis)* (Bornean pygmy squirrel*)	unlogged (both)	arboreal	not threatened	small	Non-gliding Rodents
Hylopetes spadiceus Red-cheeked flying squirrel	n/a (both)	n/a (arboreal)	not threatened	small	Gliding mammals
Iomys horsfieldi Horsfield's flying squirrel	logged (both)	arboreal	not threatened	small	Gliding mammals
*Lariscus hosei** Four-striped ground squirrel*	n/a (both)	n/a (terrestrial)	not threatened	small	Non-gliding Rodents
*Petaurillus hosei** Hose's pygmy flying squirrel*	n/a (unlogged)	n/a (arboreal)	not threatened	small	Gliding mammals
Petaurista petaurista Red giant flying squirrel	unlogged (both)	arboreal	not threatened	medium	Gliding mammals
Petinomys genibarbis Whiskered flying squirrel	n/a (both)	n/a (arboreal)	threatened	small	Gliding mammals
(Petinomys setosus) (Temminck's flying squirrel)	unlogged (both)	arboreal	threatened	small	Gliding mammals
Pteromyscus pulverulentus Smoky flying squirrel	unlogged	arboreal	threatened	small	Gliding mammals
Ratufa affinis Giant squirrel	both	arboreal	not threatened	medium	Non-gliding Rodents
*Rheithrosciurus macrotis** Tufted ground squirrel*	both	semi-arboreal	threatened	medium	Non-gliding Rodents
*Sundasciurus brookei** Brooke's squirrel*	both (unlogged)	arboreal	not threatened	small	Non-gliding Rodents
Sundasciurus lowii Low's squirrel	both	semi-arboreal	not threatened	small	Non-gliding Rodents
Sundasciurus hippurus Horse-tailed squirrel	both	semi-arboreal	not threatened	small	Non-gliding Rodents

	Muridae	*Chiropodomys major** Large pencil-tailed tree mouse*	n/a (both)	n/a (arboreal)	not threatened	small	Non-gliding Rodents
		*Haeromys margarettae** Ranee mouse*	n/a (both)	n/a (semi-arboreal)	not threatened	small	Non-gliding Rodents
		Leopoldamys sabanus Long-tailed giant rat	unlogged (both)	terrestrial	not threatened	small	Non-gliding Rodents
		*Maxomys baeodon** Small spiny rat*	n/a (both)	n/a (terrestrial)	not threatened	small	Non-gliding Rodents
		*Maxomys ochraceiventer** Chestnut-bellied spiny rat*	n/a (both)	n/a (terrestrial)	not threatened	small	Non-gliding Rodents
		Maxomys rajah Brown spiny rat	unlogged	terrestrial	threatened	small	Non-gliding Rodents
		Maxomys surifer Red spiny rat	logged	terrestrial	not threatened	small	Non-gliding Rodents
		Maxomys whiteheadi Whitehead's rat	unlogged (both)	terrestrial	threatened	small	Non-gliding Rodents
		Niviventer cremoriventer Dark-tailed tree rat	n/a (both)	n/a (semi-arboreal)	not threatened	small	Non-gliding Rodents
		Sundamys muelleri Muller's rat	n/a (both)	n/a (semi-arboreal)	not threatened	small	Non-gliding Rodents
	Hystricidae	*Hystrix brachyura* Malay porcupine	both	terrestrial	not threatened	medium	Non-gliding Rodents
		*Hystrix crassispinis** Thick-spined porcupine*	both	terrestrial	not threatened	medium	Non-gliding Rodents
		Trichys fasciculata Long-tailed porcupine	both	terrestrial	not threatened	medium	Non-gliding Rodents
Scandentia	Ptilocercidae	*Ptilocercus lowii* Pentail treeshrew	logged (both)	arboreal	not threatened	small	Insectivora

Tupaiidae	*Tupaia dorsalis** Striped treeshrew*	n/a (both)	n/a (terrestrial)	not threatened	small	Insectivora
	*Tupaia gracilis** Slender treeshrew*	n/a (both)	n/a (semi-arboreal)	not threatened	small	Insectivora
	*Tupaia longipes** Plain treeshrew*	both	semi-arboreal (terrestrial)	not threatened	small	Insectivora
	Tupaia tana Large treeshrew	unlogged (both)	terrestrial	not threatened	small	Insectivora
	Tupaia minor Lesser treeshrew	unlogged (both)	terrestrial (semi-arboreal)	not threatened	small	Insectivora

Table S2.3 Community structure of mammals between canopy and terrestrial strata, and unlogged and recovering-logged forest, according to capture events per 100 camera trap nights (CTN). Canopy data are from single canopy camera-traps, except records of Bornean pygmy squirrel, Temminck's flying squirrel and horse-tailed squirrel in unlogged forest, and banded civet in recovering-logged forest, which were only detected by our additional canopy camera-traps at those sites (marked by parentheses). Orangutans are known to be absent from Maliau Basin, our unlogged site. Asterisks denote species endemic to Borneo. Grey shading denotes no captures in that stratum or area. Indicator species analyses utilised data from the first 91 CTN at each camera location to visualise similarities or dissimilarities between mammal community structure across unlogged and recovering-logged forest and, separately, across strata. No indicator species were identified that could be aligned with unlogged or recovering-logged forest since the community-level differences between these habitats were weak. Species reported are therefore indicators of terrestrial or canopy strata (denoted 'T' or 'C') according to vector fitting (envfit) or Pearson's coefficient of association based on the ordination and species detection data. Significant values are in bold.

	Capture Events per 100 CTN				**Indicator species**		**Indicator species**	
Species	**Canopy Cameras**		**Terrestrial Cameras**		**(Envfit test)**		**(Pearson association)**	
	Unlogged	**Logged**	**Unlogged**	**Logged**	**R^2**	**P-value**	**Φ**	**P-value**
Sunda clouded leopard, *Neofelis diardi borneensis*			0.48	0.04	0.03	0.348	0.21	0.082
Marbled cat, *Pardofelis marmorata*			0.08	0.08	0.03	0.237	0.17	0.193
Leopard cat, *Prionailurus bengalensis*			0.28	0.41	0.07	0.045	**0.33**	**0.002 (T)**
Short-tailed mongoose, *Herpestes brachyurus*			0.63	0.34	0.05	0.116	**0.26**	**0.002 (T)**
Collared mongoose, *Herpestes semitorquatus*			0.13					
Yellow-throated marten, *Martes flavigula*	0.18	0.19	0.25	0.30	0.03	0.325	0.02	0.924
Sunda stink badger, *Mydaus javanensis*			0.05	0.04				
Binturong, *Arctictis binturong*	0.25	0.16	0.08	0.08	0.01	0.833	0.05	0.713
Small-toothed palm civet, *Arctogalidia trivirgata*	0.31	1.73			**0.19**	**0.001 (C)**	**0.42**	**<0.001 (C)**
Banded civet, *Hemigalus derbyanus*		(0.01)	2.88	1.39	**0.15**	**0.004 (T)**	**0.47**	**<0.001 (T)**
Masked palm civet, *Paguma larvata*			0.23	0.11	0.07	0.063	**0.25**	**0.031 (T)**
Common palm civet, *Paradoxurus hermaphroditus*			0.08					
Malay civet, *Viverra tangalunga*			3.58	5.14	**0.27**	**0.001 (T)**	**0.60**	**<0.001 (T)**
Sun bear, *Helarctos malayanus*			1.20	2.14	**0.17**	**0.003 (T)**	**0.39**	**<0.001 (T)**
Bearded pig, *Sus barbatus*			9.61	28.84	**0.12**	**0.010 (T)**	**0.43**	**<0.001 (T)**

Lesser mousedeer, *Tragulus kanchil*			2.73	8.18	0.08	0.058	**0.28**	**<0.001 (T)**
Greater mousedeer, *Tragulus napu*			14.62	11.97	**0.18**	**0.001 (T)**	**0.53**	**<0.001 (T)**
Bornean yellow muntjac*, *Muntiacus atherodes**			14.59	21.91	**0.19**	**0.002 (T)**	**0.51**	**<0.001 (T)**
Red muntjac, *Muntiacus muntjak*			13.29	9.00	**0.20**	**0.001 (T)**	**0.53**	**<0.001 (T)**
Sambar deer, *Rusa unicolor*			1.18	3.98	0.08	0.047	**0.36**	**<0.001 (T)**
Banteng, *Bos javanicus*				1.16	0.02	0.306	0.13	0.199
Sunda colugo, *Galeopterus variegatus*	0.05	0.03			0.03	0.213	0.11	1.000
Moonrat, *Echinosorex gymnurus*			0.58	0.11	0.06	0.105	**0.28**	**0.007 (T)**
Sunda pangolin, *Manis javanica*			0.23	0.04	0.03	0.312	0.17	0.194
Bornean gibbon*, *Hylobates funereus**	0.71	1.03			0.05	0.128	**0.25**	**0.011 (C)**
Orangutan*, *Pongo pygmaeus**		0.93		0.83	0.01	0.587	0.03	0.811
Maroon langur*, *Presbytis rubicunda**	3.41	0.61			0.04	0.186	**0.14**	**0.043 (C)**
Sabah grey langur*, *Presbytis sabana**	1.57				**0.09**	**0.029 (C)**	0.22	0.060
Long-tailed macaque, *Macaca fascicularis*	1.16		0.15		**0.12**	**0.014 (C)**	0.12	0.407
Pig-tailed macaque, *Macaca nemestrina*	0.63	1.93	20.33	12.00	**0.14**	**0.004 (T)**	**0.46**	**<0.001 (T)**
Asian elephant, *Elephas maximus*				0.08				
Black flying squirrel, *Aeromys tephromelas*	0.15	0.19			0.01	0.726	0.15	0.255
Thomas' flying squirrel*, *Aeromys thomasi**	0.81	0.03			**0.20**	**0.001 (C)**	0.18	0.104
Ear-spot squirrel*, *Callosciurus adamsi**		0.42			0.03	0.295	0.13	0.250
Prevost's squirrel , *Callosciurus prevostii*	1.39	4.91			**0.08**	**0.035 (C)**	**0.32**	**<0.001 (C)**
Large mystery squirrel, *Callosciurus sp.?*		0.03						
Bornean pygmy squirrel*, *Exilisciurus exilis**	(0.01)							
Horsfield's flying squirrel, *Iomys horsfieldi*		0.03						
Red giant flying squirrel, *Petaurista petaurista*	0.53				**0.08**	**0.033 (C)**	0.21	0.126
Temminck's flying squirrel, *Petinomys setosus*	(0.01)							
Smoky flying squirrel, *Pteromyscus pulverulentus*	0.02							
Giant squirrel, *Ratufa affinis*	0.38	0.90			0.03	0.238	**0.20**	**0.001 (C)**

Tufted ground squirrel*, *Rheithrosciurus macrotis**	0.02		1.08	0.34	**0.11**	**0.017 (T)**	**0.35**	**<0.001 (T)**
Brooke's squirrel*, *Sundasciurus brookei**	0.08	0.13			0.04	0.161	0.15	0.498
Low's squirrel, *Sundasciurus lowii*		0.03	0.03					
Horse-tailed squirrel, *Sundasciurus hippurus*	(0.04)	0.13	0.05	0.19	0.01	0.990	0.02	1.000
Long-tailed giant rat, *Leopoldamys sabanus*			0.53		0.03	0.316	0.20	0.080
Brown spiny rat, *Maxomys rajah*			0.88		0.03	0.266	**0.21**	**0.034 (T)**
Red spiny rat, *Maxomys surifer*				0.15	0.02	0.555	0.17	0.1895
Whitehead's rat, *Maxomys whiteheadi*			0.08					
Malay porcupine, *Hystrix brachyura*			2.33	2.89	**0.08**	**0.049 (T)**	**0.31**	**<0.001 (T)**
Thick-spined porcupine*, *Hystrix crassispinis**			3.70	0.64	0.03	0.306	**0.21**	**<0.001 (T)**
Long-tailed porcupine, *Trichys fasciculata*			1.05	0.38	0.06	0.109	**0.25**	**0.002 (T)**
Pentail treeshrew, *Ptilocercus lowii*		0.06			0.04	0.183	0.15	0.504
Plain treeshrew*, *Tupaia longipes**	0.02		0.08					
Large treeshrew, *Tupaia tana*			0.08					
Lesser treeshrew, *Tupaia minor*			0.05					

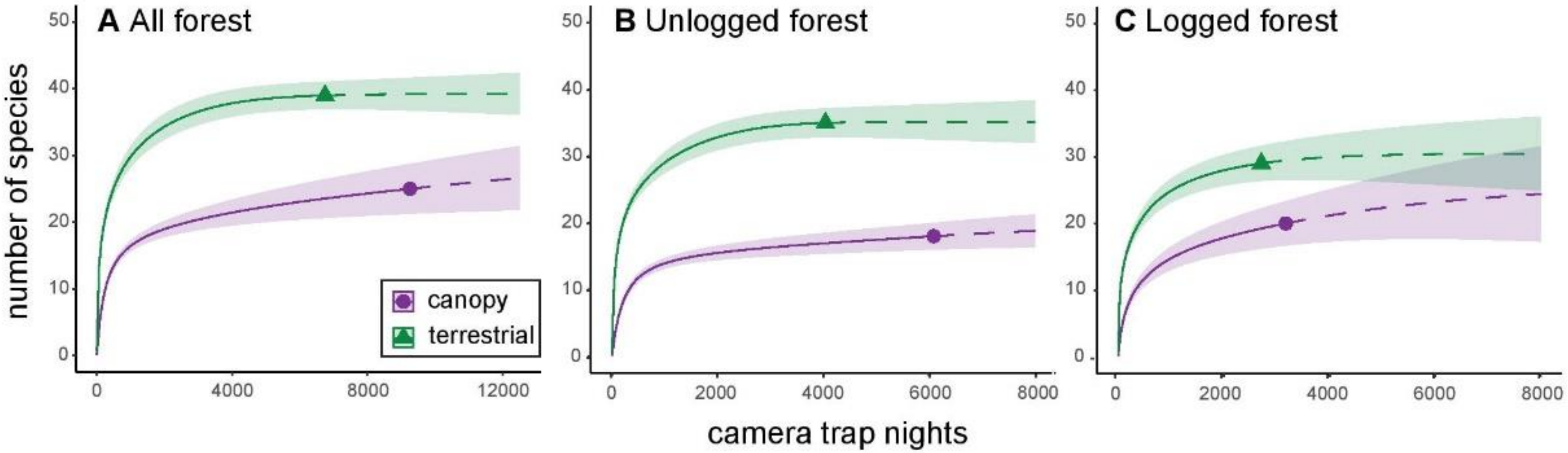

Figure S2.1 (A-C). Rarefied species accumulation curves for arboreal and terrestrial mammal communities in (A) both unlogged and recovering-logged forest combined, (B) unlogged forest only, and (C) recovering-logged forest only. Curves were extrapolated (dashed line) to approximately double the minimum observed sample size in each comparison. Confidence intervals were set at 95% and are represented by shaded areas around the curves.

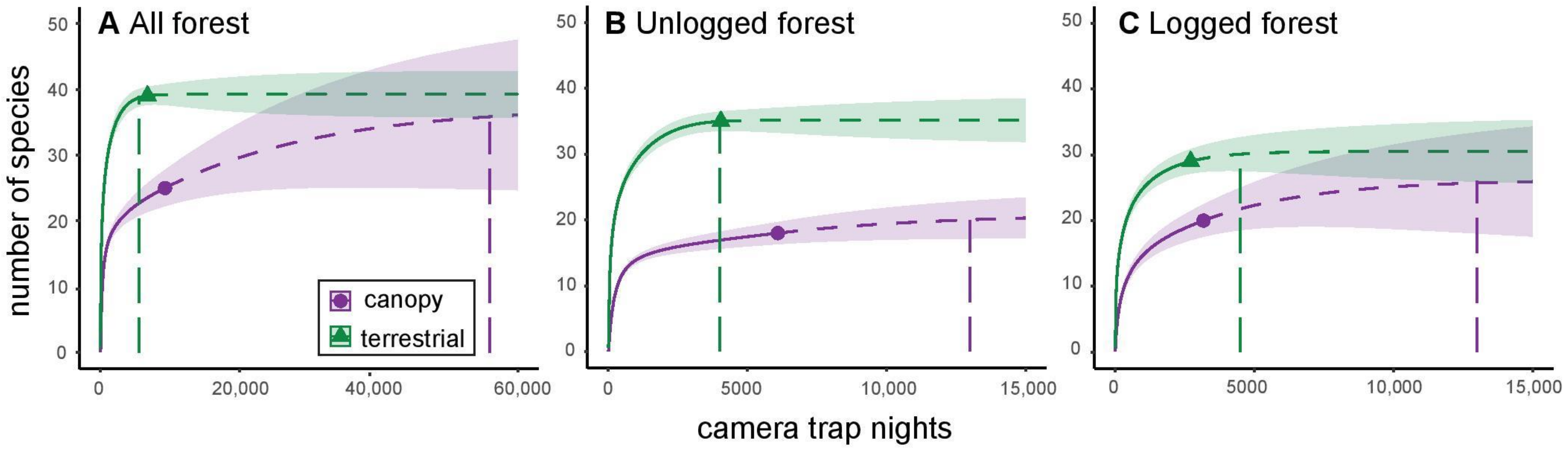

Figure S2.2 (A-C). Rarefied species accumulation curves for arboreal and terrestrial mammal communities in (A) both unlogged and recovering-logged forest combined, (B) unlogged forest only, and (C) recovering-logged forest only. Curves were extrapolated (dashed line) to the point of asymptote for arboreal communities. Approximate sampling effort required to reach asymptote is marked by vertical dashed lines. Confidence intervals were set at 84% and are represented by shaded areas around the curves.

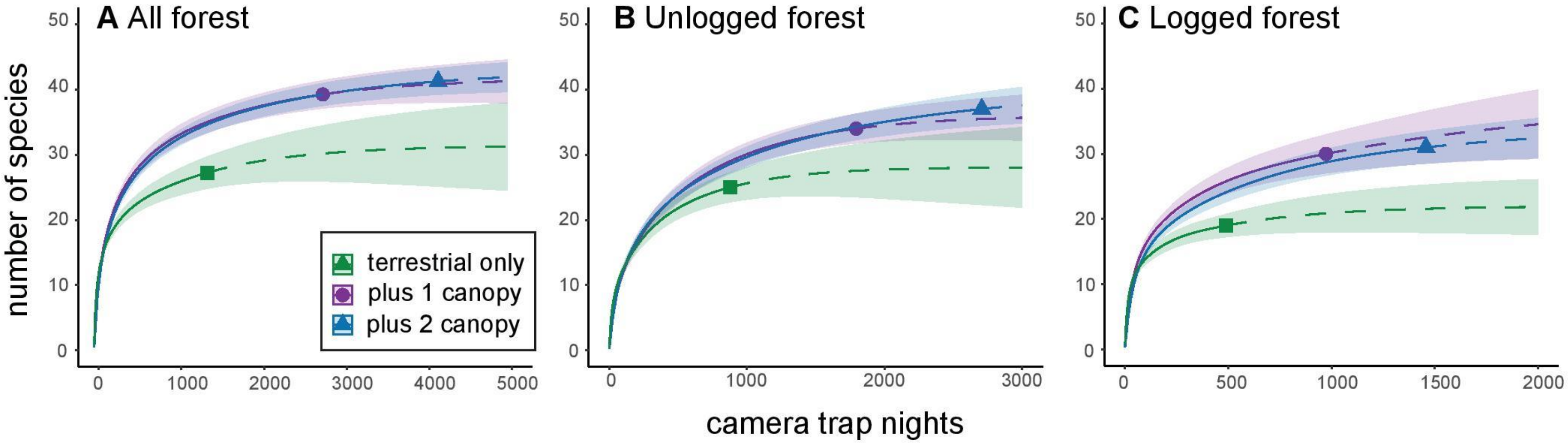

Figure S2.3 (A-C). Control species accumulation curves for a standardised subset of the sampling period, in order to directly compare additions from 19 second canopy-cameras, which functioned for 1,409 CTN in total. Curves here show species accumulation for only the sampling locations with three cameras (one terrestrial, two canopy), for (A) both unlogged and recovering-logged forest combined, (B) unlogged forest and (C) recovering-logged forest; comparing overall species numbers obtained from a standardised sampling period of 1,409 CTN for each group (terrestrial-only cameras, terrestrial- plus one canopy camera-trap, terrestrial- plus two canopy camera-traps). Confidence intervals were set at 84% and are represented by shaded areas around the curves.

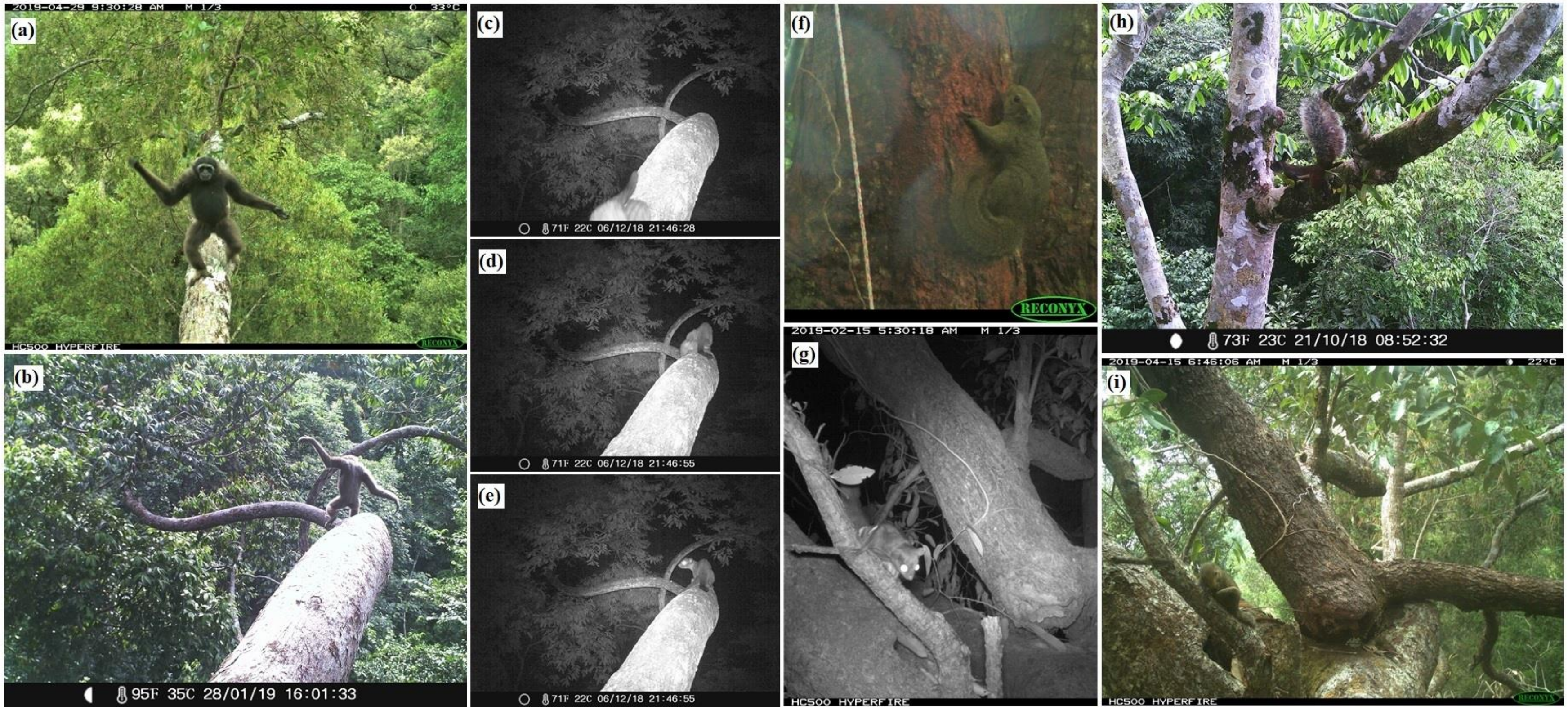

Figure S2.4 Examples of new insights from canopy camera-traps: (a), (b) branch-walking locomotion in Bornean gibbon *Hylobates funereus*; (c)-(e) likely mating event of the strictly arboreal small-toothed palm civet *Arctogalidia trivirgata* at 33.6 m height; (f) squirrel not fitting any known description for Bornean species (image cropped for clarity); (g) putative record of smoky flying squirrel *Pteromyscus pulverulentus*, for which no confirmed photographic image currently exists (Thorington *et al.* 2012, IUCN Red List); (h) likely scent-marking behaviour in tufted ground squirrel *Rheithrosciurus macrotis*, a rarely-seen Borneo endemic thought to be largely terrestrial; (i) use of the canopy strata (camera-trap at 22 m height) by plain treeshrew *Tupaia longipes*, a species previously considered strictly terrestrial (Payne and Francis 2007).

Chapter 3 Stratified activity: Vertical partitioning of the diel cycle by rainforest mammals in Borneo

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Abstract

Animal activity is driven by the environmental conditions and physical structure of a habitat, as well as the need to interact with, or avoid, other animals. Knowledge of the proportion of the 24-hour cycle spent active (activity level), and the times of day in which activity is concentrated (activity pattern), can therefore inform our understanding of species' ecology and community dynamics. However, community-wide analyses of activity are challenging to obtain, particularly in biodiverse tropical forests. In these ecosystems, habitat space extends both horizontally and vertically, and arboreal (tree-dwelling) and semi-arboreal taxa comprise up to three-quarters of vertebrate assemblages; yet, wildlife surveys are often only conducted at ground level. Here, we describe the first time that paired ground- and canopy-level camera-traps have been used to assess and compare animal activity across strata in a tropical rainforest. We conducted our research in Borneo, and by sampling in both unlogged and previously-logged areas we were further able to evaluate whether the activity of terrestrial (ground-dwelling) and arboreal communities changes in response to logging. We focussed our investigation on mammals, and report activity metrics for 37 species overall, as well as comparisons across strata for six semi-arboreal species, and across unlogged and recovering-logged forest for 25 species detected in both. Our results show that while activity varied substantially between the ground and the canopy, differences between unlogged and recovering-logged forest were minimal. We discuss these findings in light of what they may reveal about the varying opportunities and constraints present within each stratum. Our study further demonstrates that the inclusion of canopy-based camera-traps provides a much more complete picture of rainforest mammal activity throughout the diel cycle than can be achieved by terrestrial sampling alone.

3.1 Introduction

Activity – the movement from one place to another to forage, seek shelter, or engage in social behaviour – is essential for all mobile animals. Knowledge of activity is therefore fundamental to understanding animal ecology and informing conservation actions (Lashley *et al.* 2018). How and when species acquire the necessary food and shelter, encounter mates, and avoid predation or competition, are questions that can be informed by examining activity and how it overlaps with, or is mediated by, that of other species occupying the same habitat (Bridges and Noss 2011).

All activity incurs an energetic cost, as well as increased risks of exposure to predators, competitors, and environmental stresses (Rowcliffe *et al.* 2014). The activity of a given species may be influenced by intrinsic biological traits (e.g. body size, Van Schaik and Griffiths 1996), and environmental factors such as temperature, rainfall, moon-phase, and season. The monito del monte, an arboreal nocturnal marsupial of South America, shows reduced activity during brighter moon-phases that is likely linked to increased predation risk (Fonturbel, Candia, and Botto-Mahan 2014), while Japanese flying squirrels exhibit seasonal fluctuations in activity related to temperature changes (Suzuki and Ando 2017). Interactions with other species may also affect diel patterns. Nocturnal Malay civets increase daytime activity in the absence of other diurnal competitors (Cheyne *et al.* 2010); the times of activity of jaguar and puma overlap significantly with those of their main prey (Harmsen *et al.* 2011); and bearded pigs reduce night-time activity when their main predator, the predominantly nocturnal clouded leopard, is present (Ross *et al.* 2013).

Characterising activity in the context of these multiple influences can thus help shed light on the drivers and constraints a particular species or population may be subject to, while showing how different species sharing the same habitat may use temporal partitioning to facilitate co-existence (Azcarraga, Tessaro, and Delfin-Alfonso 2020). However, for most wild animals, patterns of activity are not well known due to the difficulties of consistent and accurate quantification in non-captive settings (Bridges and Noss 2011; Rowcliffe *et al.* 2014). In these situations, animals are often not readily observed (Jayasekara *et al.* 2007), almost never observable across the entire 24-hour cycle, and the presence of human observers is likely to influence the activity itself (Van Schaik and Griffiths 1996; Whitworth *et al.* 2016).

A further limitation is that most activity research focusses on a restricted set of taxa, such as studies of competition between primate species (e.g. Hanya *et al.* 2020), or predator-prey dynamics between a limited subset of species (e.g. Dias *et al.* 2018; Shukor *et al.* 2018), rather than considering a community as a whole. This approach risks overlooking the impact of other key relationships such as competition for resources between less closely-related taxa (e.g. primates and squirrels, Beaudrot *et al.* 2013), or predator-prey dynamics across forest strata, when predators are able to access both the canopy and ground (Grassman, Tewes, and Silvy 2005). In the reality of wild ecosystems, every animal is potentially subject to multiple influences from multiple other species, as well as from members of their own species. Although this adds complexity, studies of activity that consider these multiple influences may present a more complete view of the animal community.

Community perspectives of animal activity are perhaps most challenging in tropical rainforests, which are renowned for their high biodiversity, and where resources are partitioned over vertical as well as horizontal space. Mammals are one of the most diverse vertebrate taxa in rainforest ecosystems, comprising species of wide-ranging body sizes and ecological roles (Nakabayashi *et al.* 2019), utilising the entire three-dimensional habitat space from forest floor to the uppermost tree crowns (Kays and Allison 2001). Indeed, arboreal (tree-dwelling) taxa comprise a substantial portion of rainforest mammal communities (Emmons, Gautier-Hion and Dubost 1983; Whitworth *et al.* 2016; Moore *et al.* 2020; Haysom *et al.* 2021). However, most of our knowledge of these communities comes from studies of terrestrial (ground-dwelling) species, or observations of arboreal species made from ground level (Whitworth *et al.* 2016). Consequently, the activity of many arboreal and semi-arboreal mammals is poorly characterised (see as examples Van Schaik and Griffiths 1996; Oliveira-Santos, Tortato, and Graipel 2008). Community-wide investigations of arboreal mammal activity are particularly lacking; we could find only two such studies (Azcarraga, Tessaro, and Delfin-Alfonso 2020; Gracanin and Mikac 2022), although the use of bait in the latter could influence species detections.

The pervasive presence of logging across tropical regions (Watson *et al.* 2018) alters the vertical structure and biotic conditions of rainforests by removing the largest trees, resulting in reduced canopy height and connectivity (Deere *et al.* 2020a), increased light penetration (Fauset *et al.* 2017) and warmer temperatures (Hardwick *et al.* 2015). Given that animal activity reflects the ecological constraints and requirements of each species, and that these in turn are influenced by the physical environment, habitat disturbances such as logging could be expected to substantially impact animal activity (Johns 1986). Indeed, this has been shown for some terrestrial mammals, particularly larger-bodied ungulates, which were observed to shift towards greater night-time activity in logged habitats (Chapman 2019; Davison *et al.* 2019; Lewton 2020). The structural changes caused by logging may be most noticeable in the canopy, and thus may disproportionately affect arboreal species, with lower canopy heights and reduced density of canopy-level vegetation effectively reducing the vertical niche space available. Evidence suggests that arboreal taxa such as primates and rodents vertically partition the canopy space by preferentially using different heights (e.g.

Sushma and Singh 2006; Nakagawa *et al.* 2007; Hanya *et al.* 2020). This raises the question of whether a reduced ability to spatially partition resources in logged forests would lead to a more pronounced temporal separation of activity by arboreal species. However, while some studies have noted changes at the species level (e.g. the monito del monte significantly reduced its hours of activity as habitat degradation increased, Rodriguez-Gomez and Fonturbel 2020), we could find no research investigating the impact of logging on arboreal mammal activity at the community level.

Advances in camera trapping technology and canopy access techniques provide a means to study animal activity patterns in the upper forest strata (Whitworth *et al.* 2016). Camera-trapping enables non-invasive 24-hour monitoring of an environment, and the collection of data on many species simultaneously (Van Schaik and Griffiths 1996; Bridges and Noss 2011), while canopy access facilitates direct investigations of arboreal species in their natural habitat. Canopy-based camera-traps have revealed novel insights on activity, for example, frequent nocturnal behaviour of the Guizhou snub-nosed monkey in China, a primate previously thought to be strictly diurnal (Tan, Yang, and Niu 2013). Although few studies to date have utilised camera-traps to compare both canopy and terrestrial wildlife, those that have showed mammal communities in each strata are comprised mainly of different species, with a smaller subset of semi-arboreal mammals that use both heights. These findings are broadly consistent across locations in the Neotropics (Whitworth *et al.* 2016), Africa (Moore *et al.* 2020), and Southeast Asia (Haysom *et al.* 2021). It is therefore important, and timely, that studies of community-wide mammal activity patterns include arboreal taxa, most of which are rarely detected by terrestrial camera-traps, and not at sufficient levels to enable analysis of activity metrics. In addition, terrestrial-only camera-trap studies risk providing incomplete information on the diel activity of semi-arboreal species (Wong, Servheen and Ambu 2004). The increased energetic cost of movement in a disrupted canopy (Davies *et al.* 2017) may lead to semi-arboreal mammals using the ground more frequently in logged forests (Berry *et al.* 2010); alternatively, the reduced energetic cost of accessing a lower canopy from the ground may have the opposite effect. However, almost no research exists on whether semi-arboreal mammals change their amount of terrestrial activity in logged forests (see as example Ancrenaz *et al.* 2014, who found similar amounts of ground-level activity in logged and unlogged areas for orangutan *Pongo pygmaeus*). The application of paired canopy and terrestrial camera-traps could thus help to shed light on these cross-strata species.

Here, we conducted the first community-wide investigation of mammal activity across both canopy and terrestrial strata and in both unlogged and recovering-logged tropical rainforest. We undertook our assessment in Borneo, known for its high mammal diversity, with at least 135 non-volant species, over half of which are arboreal or semi-arboreal (Payne and Francis 2007). Borneo's distinct arboreal and terrestrial mammal assemblages make sampling only at ground-level insufficient to reliably depict whole community activity (Haysom *et al.* 2021). Further, almost half of the island's remaining rainforest has undergone at least one round of logging (Gaveau *et al.* 2016), and so it is important to investigate what impact this may have had on mammalian activity. We deployed camera-traps on the ground and in the canopy of unlogged and recovering-logged forest, and used detection data to quantify activity metrics for 37 mammal species. We also investigated whether, and to what extent, activity varied between (i) canopy and terrestrial strata (for six semi-arboreal species) and (ii) unlogged and recovering-logged forest (for 25 species present in both).

3.2 Methods

3.2.1 Study site

Research was undertaken in and around the Stability of Altered Forest Ecosystems Project (Ewers *et al.* 2011) in Sabah, Malaysian Borneo. We sampled mammals in unlogged forest at Maliau Basin Conservation Area, which has experienced very little disturbance, and in recovering-logged forest in the Mt. Louisa Forest Reserve, which experienced multiple rounds of logging between 1978 and 2008, but has since been formally protected.

3.2.2 Camera trapping

Camera-traps (Hyperfire HC500, Reconyx, WI, USA) were deployed across 50 locations between October 2017 and September 2019 following methods outlined in Haysom *et al.* (2021). Locations were divided equally between unlogged and recovering-logged forest (mean distance between locations 1.26 km; range 0.5-4.0 km). Each location comprised one terrestrial camera-trap set 0.3 m above the ground, paired with either one or two canopy camera-traps in the mid- or upper-canopy of the focal tree, which was within 10 m of the ground placement. After accounting for malfunction, sampling comprised a total of 17,226 camera-trap nights (CTN): 6,661 terrestrial CTN (3,995 in unlogged forest, 2,666 in logged) and 10,565 canopy CTN (6,944 in forest, 3,621 in logged).

Prior to analysis, we expressed site-specific camera-trap encounters as independent mammal detections, with independence defined as photographic captures of different species, or of the same species separated by ≥30 minutes (Ridout and Linkie 2009; Laughlin *et al.* 2020). Where focal trees contained two canopy camera-traps, these were treated as one unit so that detections of a given species on one were excluded from data analysis if the same species had been detected on the other within the 30 minute cut-off period.

3.2.3 Characterising mammal activity

We used all independent detections of each species to characterise two core features of diel activity for mammals with sufficient sample sizes (≥10 detections, Ridout and Linkie 2009; Azcarraga, Tessaro, and Delfin-Alfonso 2020). ‘Activity level’ quantifies the proportion of the 24-hour cycle spent active (Rowcliffe *et al.* 2014); and ‘activity pattern’ describes the time or times of activity across the 24-hour cycle (Vazquez *et al.* 2019). We used the R package ‘activity’ to calculate an average activity level per species, given as a figure between 0 and 1 that represents the proportion of time spent active, e.g. 0 would indicate no activity, 0.2 would indicate a species was active 20% of the 24-hour cycle, and 1 would indicate constant activity. Uncertainty was expressed using 95% confidence intervals. Activity pattern is typically assessed by building a visual profile of independent detections across the diel cycle. Activity patterns are commonly divided into four main categories: diurnal (predominantly or exclusively active during daylight hours); nocturnal (predominantly or exclusively active during the hours of darkness); crepuscular (where a majority of activity occurs during twilight, usually defined as one hour before and after dawn and dusk, Aschoff 1966); and cathemeral (where substantial amounts of activity occur during daylight and darkness, with no clear majority in one time period, Tattersall 2006).

For each species, activity patterns were categorised by calculating the proportion of detections during daylight, darkness, and twilight, following Gomez *et al.* (2005) (Supplementary Materials Tables S3.1, S3.2). Once primary activity patterns had been defined, we assessed the significance of the deviation from expected proportions using a binomial test (following Van Schaik and Griffiths 1996). Any secondary patterns were noted where, after the primary pattern had been determined, a species showed a clear tendency by proportion of remaining detections towards activity during another period. For example, a species with the majority of detections during twilight and the remainder during daylight would be categorised as ‘crepuscular with diurnal tendencies’. We used the ‘dplyr’ and ‘activity’ packages in R to first determine the number of independent detections per species, then align these with solar time (the deviation of clock time from sunrise and sunset) specific to geographic location. Failing to account for solar time can create inaccuracies in how activity patterns are categorised between periods of light, dark and twilight (Vazquez *et al.* 2019). Kernel density functions were fitted to detection data using the R packages ‘activity’ and ‘overlap’ (Ridout and Linkie 2009; Rowcliffe 2016), and we produced activity pattern plots for each species from all detections of that species across canopy and terrestrial strata and unlogged and recovering-logged forest.

Table 3.1 Activity pattern definitions used throughout our study. As sunrise and sunset times in Sabah varied across the year by 30 and 45 minutes, respectively, we defined the crepuscular period to encompass one hour before and one hour after the maximum variation (05:00-07.30 and 16:50-19:25); with diurnal and nocturnal periods between these times.

Category	Definition	Time period in our study region
Nocturnal	Strictly = ≥90% detections in darkness	19.26 – 04.59
	Mostly = ≥70% detections in darkness	
Diurnal	Strictly = ≥90% detections in daylight	07.31 – 16.49
	Mostly = ≥70% detections in daylight	
Crepuscular	≥50% detections during twilight	05.00 – 07.30 & 16.50 – 19.25
Cathemeral	>10% but <70% detections in both daylight and darkness	n/a

3.2.4 Activity comparisons between strata and unlogged/recovering-logged forest

Activity levels and patterns were compared between (i) strata, for six species with sufficient detections on both canopy and terrestrial camera-traps, and (ii) unlogged and recovering-logged forest, for 25 species with sufficient detections in both, using the R package ‘overlap’ (Ridout and Linkie 2009). To achieve this, we first produced average activity levels, and quantified activity patterns, split by strata and unlogged/logged forest for each species (i.e. using detections from only canopy camera-traps, only terrestrial camera-traps, only unlogged forest camera-traps and only recovering-logged forest camera-traps). To compare activity levels between strata and unlogged and recovering-logged forest, we used a Wald test to evaluate statistical differences between two estimates. For activity patterns, we calculated the coefficient of overlap with 95% bootstrapped confidence intervals using the estimator Δ1 (dhat1) for comparisons where the minimum number of detections was <75, and Δ4 (dhat4) where the minimum number of detections was >75 (Ridout and Linkie 2009). Overlap of two patterns is measured on a scale from 0 to 1, where 0 indicates no overlap, and 1 indicates identical patterns. We produced overlap plots for each comparison.

3.2.5 Activity within groups

As activity can be influenced by species’ traits, we categorised mammals according to body size, taxonomy, and feeding strategy to examine any differences between groups (Supplementary Materials Table S3.1). Body size categories were defined as: small <1 kg, medium 1-5 kg, large >5 kg. Broad taxonomic groups were defined as: Carnivora (viverrids, mustelids, felids, bear), Insectivora (moonrat, Sunda pangolin), Primates (macaques, langurs, gibbon, orangutan), Ungulates (deer, mousedeer, pig, and banteng), and Rodents (flying and non-flying squirrels, murid rodents, porcupines). Sunda pangolin was included within Insectivora to keep the number of groups reasonable. Functional (feeding strategy) categories were: omnivores, insectivores, carnivores, and herbivores. As the largest functional group, and because for many herbivores, specific food-item preferences are known and are starkly different in terms of nutritional value (e.g. leaves vs. seeds, Mitsuzuki and Oshida 2018), we further divided herbivores into frugivores, folivores, and granivores (i.e. those that predominantly consume fruit, leaves, and seeds, respectively). Species were categorised using available information from Payne and Francis 2007 and the IUCN Red List. The number of species in each group is stated in Table 3.3.

3.3 Results

Fifty-seven mammal species were recorded across 17,226 camera-trap nights (CTN), and 37 species with ≥10 total independent detections were retained for analyses (Ridout and Linkie 2009, Azcarraga, Tessaro, and Delfin-Alfonso 2020) (Supplementary Materials Tables S3.1, S3.2). Community composition between strata was largely distinct, with 10 species detected only by canopy camera-traps (hereafter referred to as ‘arboreal species’), 21 only by terrestrial camera-traps (‘terrestrial species’), and six by camera-traps in both strata (‘semi-arboreal species’), all with sufficient canopy and terrestrial detections to allow separate analyses across strata: Section 3.3.3). In contrast, community composition between unlogged and recovering-logged forest was very similar, with five species detected only in unlogged forest, two only in recovering-logged, and 30 in both (25 of which had sufficient detections in both unlogged and recovering-logged forest to allow separate comparative analyses: Section 3.3.3).

3.3.1 Activity level

On average across all species, mammals were active for approximately 35% of the 24-hour cycle (mean 0.35, range 0.14-0.59) (Table 3.2, Supplementary Materials Table S3.1). Generally, arboreal mammals were less active than terrestrial species, and this was most pronounced in recovering-logged forest (difference between arboreal and terrestrial activity levels: all data -8%, unlogged forest -8%, recovering-logged forest -14%, Table 3.2). In contrast, logging itself did not appear to have a large effect on mammal activity (difference between mean activity levels in unlogged and recovering-logged forest: all species +1%, arboreal species -4%, terrestrial species +2%). Semi-arboreal species showed similar activity levels across strata (-1% in the canopy) and between unlogged and recovering-logged forest (+4% in recovering-logged forest).

Table 3.2 Mean activity levels for arboreal, terrestrial, and semi-arboreal mammals, compared across strata, and unlogged and recovering-logged forest, and the proportion of species in each grouping that were nocturnal, diurnal, crepuscular, and cathemeral, given as a percentage of the total number of species in that grouping. Mean values and percentages were calculated from information in Supplementary Materials Table S3.2. Where abbreviations are used, UL = unlogged forest only, RL = recovering-logged forest only, C = canopy camera-traps only, T = terrestrial camera-traps only.

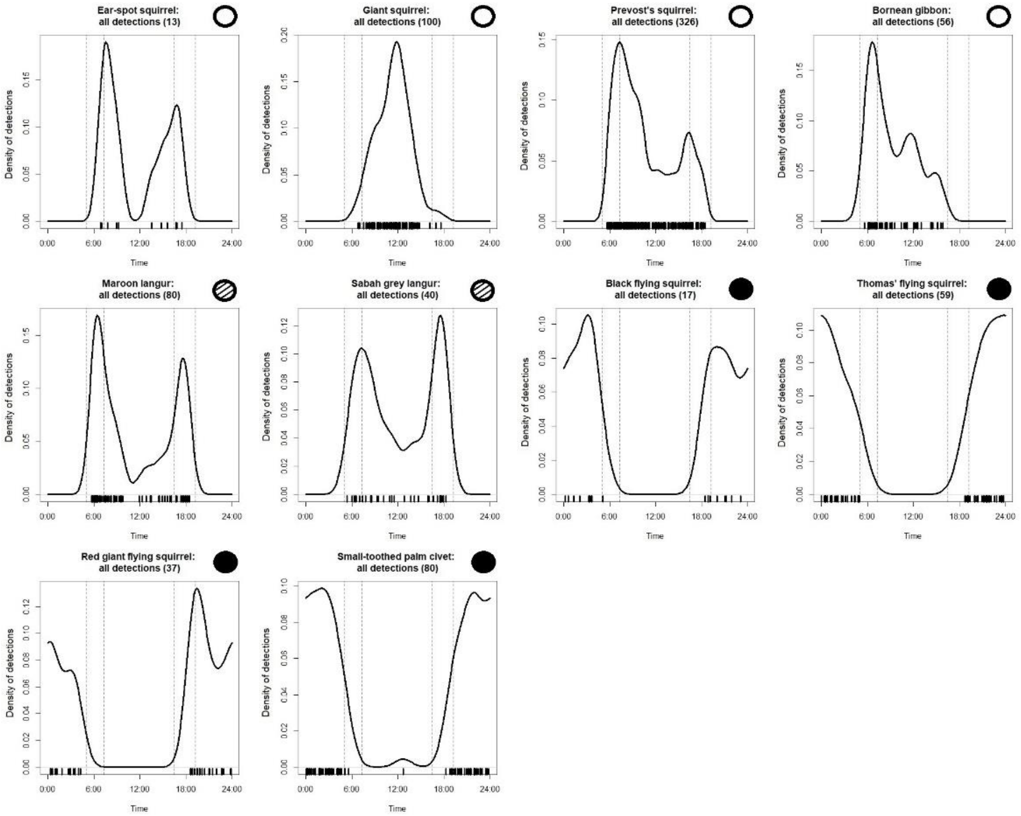
Dataset	Activity level		Activity pattern (% species)			
	mean	range	nocturnal	diurnal	crepuscular	cathemeral
all data	0.35	0.14 – 0.59	41	24	13	22
all arboreal species	0.30	0.22 – 0.42	40	40	20	0
all terrestrial species	0.38	0.19 – 0.59	52	10	5	33
all semi-arboreal species	0.37	0.14 – 0.52	0	50	33	17
all species UL	0.36	0.09 – 0.50	32	32	20	16
all species RL	0.37	0.17 – 0.61	32	28	16	24
arboreal species UL	0.30	0.18 – 0.44	33	50	17	0
terrestrial species, UL	0.38	0.29 – 0.50	40	27	13	20
semi-arboreal species, UL	0.35	0.09 – 0.48	0	25	50	25
arboreal species, RL	0.26	0.17 – 0.37	33	50	17	0
terrestrial species, RL	0.40	0.30 – 0.61	40	20	7	33
semi-arboreal species, RL	0.39	0.19 – 0.58	0	25	50	25
semi-arboreal species, C	0.29	0.04 – 0.45	0	50	33	17
semi-arboreal species, T	0.30	0.19 – 0.42	17	66	17	0

3.3.2 Activity pattern

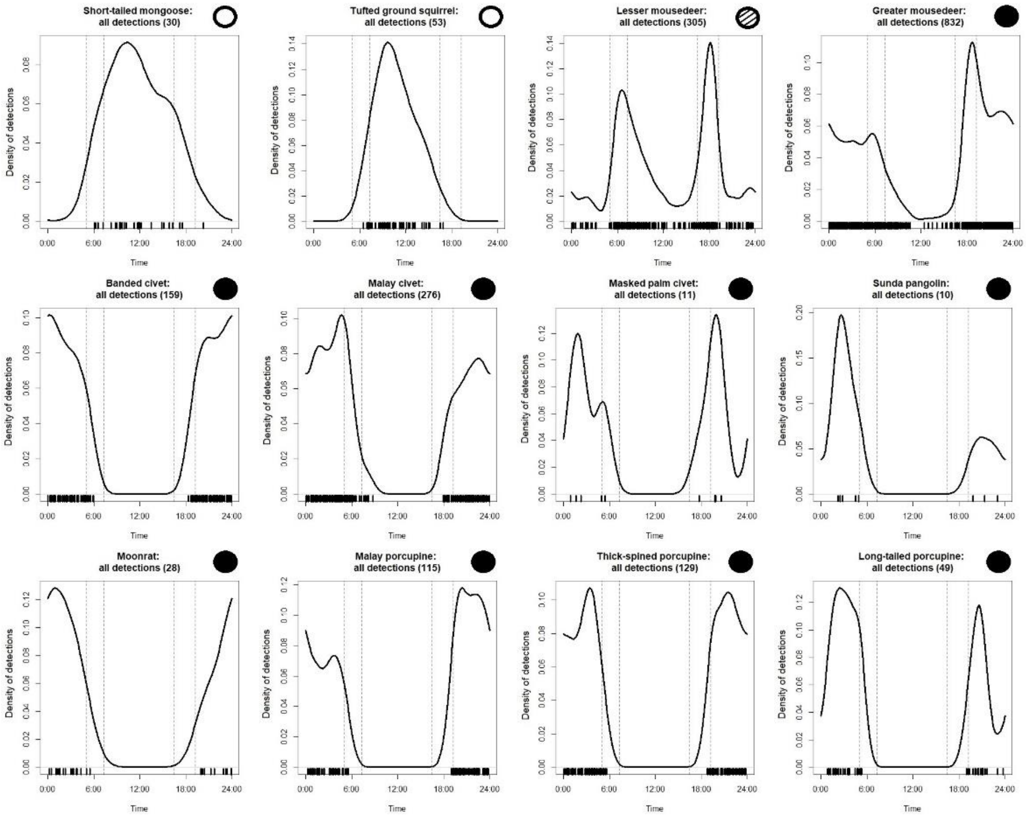
Across all species, nocturnality was the most common activity pattern, (15 of 37 species, 41%), and diurnality the second most common (9 species, 24%). Eight species (22%) were cathemeral, and five (13%) crepuscular (Figure 3.1, Supplementary Materials Tables S3.1, S3.2). Activity patterns are often not clear-cut (Van Schaik and Griffiths 1996) and indeed almost half of mammals detected (17 species, 46%) exhibited secondary patterns (Supplementary Materials Table S3.1).

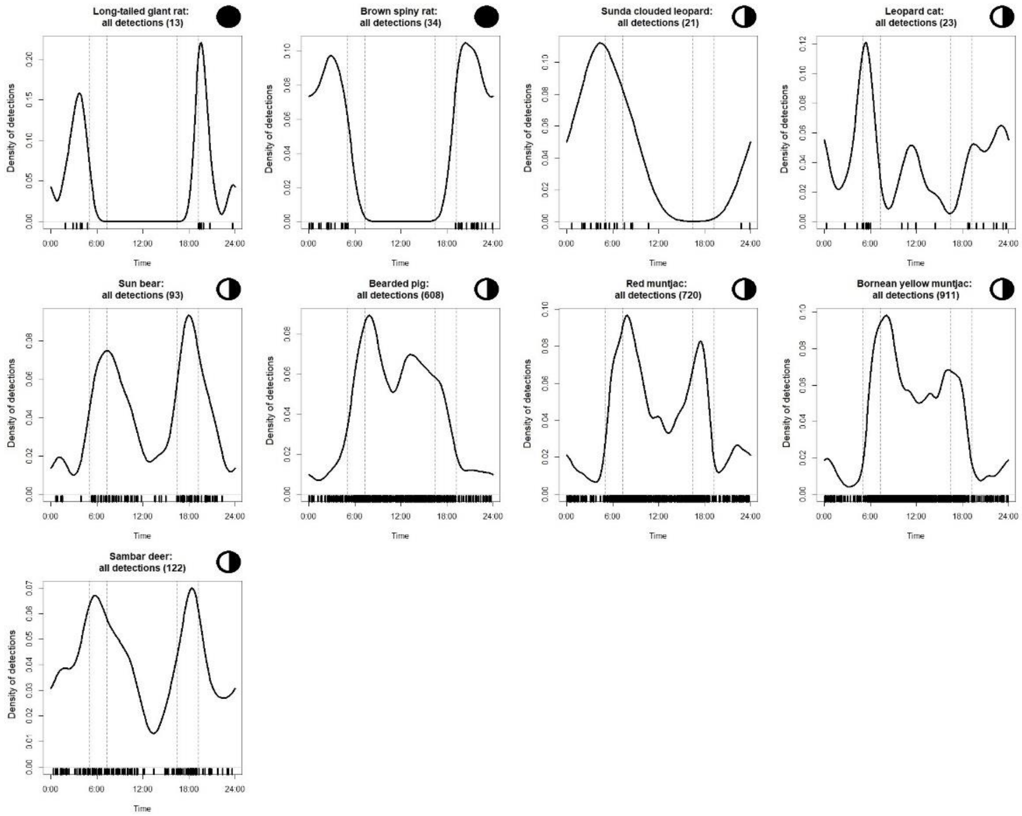
Arboreal mammals were nocturnal (4 of 10 species, 40%), diurnal (4 species, 40%), or crepuscular (2 species, 20%) (Figure 3.1, Table 3.2, Supplementary Materials Table S3.1), but not cathemeral. Terrestrial mammals showed all activity patterns, but were predominantly nocturnal (11 of 21 species, 52%) or cathemeral (7 species, 33%); few were diurnal (2 species, 10%) or crepuscular (1 species, 5%). When detection data were pooled across strata and unlogged and recovering-logged forest, semi-arboreal mammals were mainly diurnal (3 of 6 species, 50%) or crepuscular (33%, 2 species), with one species (17%) cathemeral, and none nocturnal. However, see Figure 3.2, Section 3.3.3, and Supplementary Materials Table S3.3, as a majority of semi-arboreal mammals showed different primary activity patterns across strata, while patterns in unlogged and recovering-logged forest did not change.

arboreal mammals



terrestrial mammals





semi-arboreal mammals

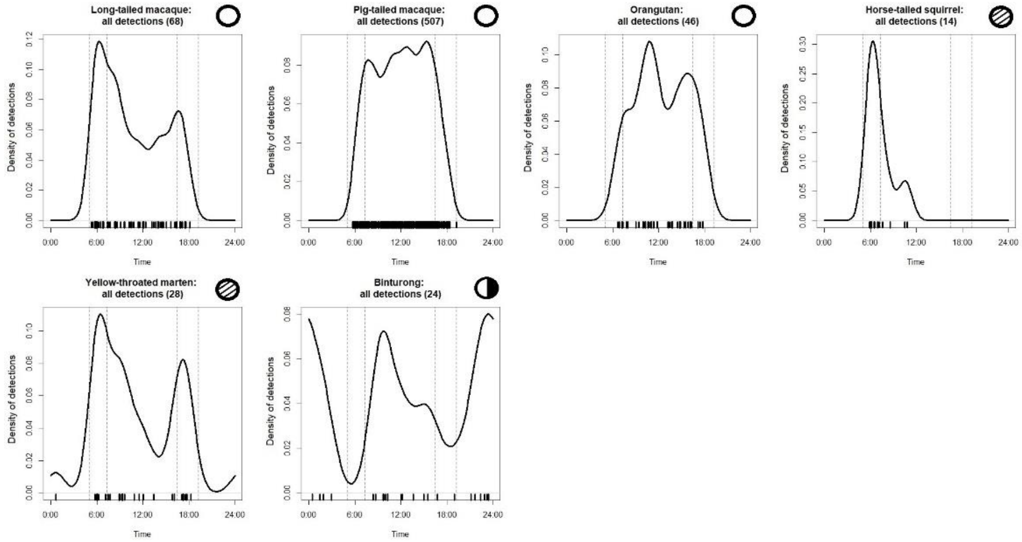


Figure 3.1 Activity plots for 37 mammal species showing times of activity across the 24-hour cycle, using data pooled from all detections of each species across all camera-trap locations. Dashed vertical lines indicate the crepuscular period around dawn and dusk. Symbols denote primary activity pattern: ○ = diurnal, ▨ = crepuscular, ● = nocturnal, ◐ = cathemeral (see Supplementary Materials Table S3.2 for calculations). Total number of independent detections is stated in parentheses after species' names, and is also indicated by the density of black vertical bars along x axes. Plots are grouped by: arboreal species (those detected exclusively by canopy camera-traps), terrestrial species (those detected exclusively by cameras on the ground), and semi-arboreal species (those detected by cameras in both strata).

3.3.3 Effect of strata and disturbance on mammal activity

Activity level. Of six semi-arboreal species, two (33%) had significantly lower activity levels in the canopy (horse-tailed squirrel *Sundasciurus hippurus* and pig-tailed macaque *Macaca nemestrina*) and none had significantly higher (Supplementary Materials Table S3.3). Of the remaining non-significant changes, one species had lower canopy activity levels and three had higher. Four of 25 (16%) species with sufficient detections in both unlogged and recovering-logged forest had significantly lower activity levels in recovering-logged forest (two arboreal: Prevost's squirrel *Callosciurus prevostii*, black flying squirrel *Aeromys tephromelas*; and two terrestrial: Malay porcupine *Hystrix brachyura*, and Malay civet *Viverra tangalunga*), and three (12%) had significantly higher (one arboreal: giant squirrel *Ratufa affinis*; and two terrestrial: red muntjac *Muntiacus muntjak*, and greater mousedeer *Tragulus napu*). Of the remainder, eight species had lower activity in recovering-logged forest and ten had higher, all non-significant.

Activity pattern. Activity patterns of individual species mostly differed between strata but were mostly consistent between unlogged and recovering-logged forest. Four of six semi-arboreal species (67%) had a different activity pattern in the canopy than on the ground (yellow-throated marten *Martes flavigula*, binturong *A. binturong*, pig-tailed macaque *M. nemestrina*, horse-tailed squirrel *S. hippurus*), while only two (8%) of 25 species had different activity patterns in unlogged versus recovering-logged forest (Bornean yellow muntjac *Muntiacus atherodes*, sun bear *Helarctos malayanus*). Statistical comparisons corroborated these findings, highlighting an overall trend towards dissimilarity in activity patterns between strata (average coefficient of overlap 0.47, range 0.16-0.68), but a strong trend towards similarity between unlogged and recovering-logged forest (average coefficient of overlap 0.74, range 0.52-0.90) (Figure 3.2, Supplementary Materials Table S3.3).

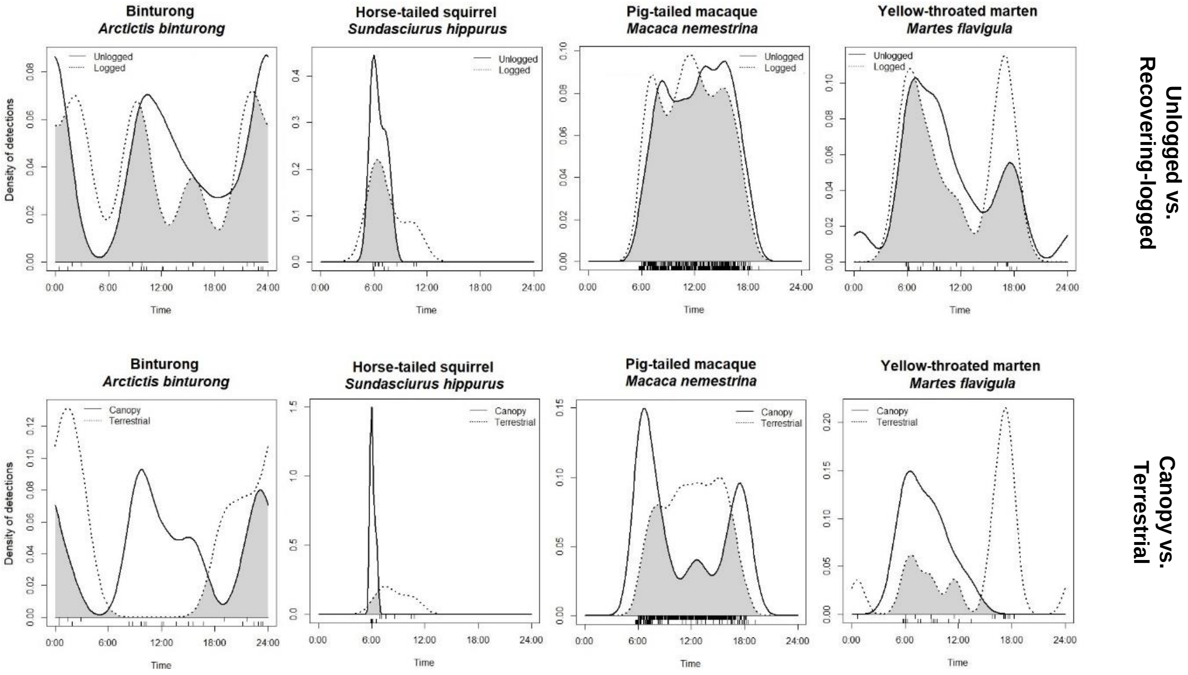


Figure 3.2 Overlap plots showing comparisons of activity patterns for four mammal species detected in both: unlogged vs. recovering-logged forest (top row), and both canopy vs. terrestrial strata (bottom row). The degree of overlap between patterns is represented by grey shaded areas, and black bars on the x axes show the independent detections from which the patterns derive. These illustrate the trend towards similarity in patterns between unlogged and recovering-logged forest, but dissimilarity between strata (quantified by coefficient of overlap statistics: Supplementary Materials Table S3.3). See also Supplementary Materials Figure S3.1 for overlap plots of a further 23 species with comparisons only between strata (*N*=2) or between unlogged and recovering-logged forest (*N*=21).

3.3.4 Activity within groups

The lowest activity levels were in small-bodied rodents and Insectivora, species of which spent on average 11-20% less of the 24-hour cycle active than large-bodied ungulates and Carnivora (Table 3.3). Activity levels within functional groups were less variable, although for herbivores, differences between sub-groups were more defined, with folivores 11% more active than granivores. For activity patterns, the clearest trends were also observed across size groups, with small- and medium-bodied mammals predominantly nocturnal, while large-bodied mammals were predominantly cathemeral. Most ungulates were cathemeral (and the remainder showed cathemerality as a secondary activity pattern, Supplementary Materials Table S3.1), while primates were exclusively diurnal or crepuscular. Both carnivore species were cathemeral, while omnivores and insectivores were most likely to be nocturnal, and herbivores were equally likely to be diurnal or nocturnal.

Table 3.3 Summary of mean activity levels, and prevalence of activity patterns (*asterisks denote dominant pattern/s per group). Results here derive from metrics for individual species, presented in Supplementary Materials Table S3.2. Species groupings are defined in Supplementary Materials Table S3.1. Feeding preferences of two herbivores are unknown, so the total number of folivores, frugivores and granivores does not equal that of herbivores.

Group	No. species	Mean activity level	Predominant activity pattern & no. species in each category			
body size						
Large	13	0.46	nocturnal: 0	diurnal: 4	crepuscular: 2	cathemeral: **7***
medium	18	0.35	nocturnal: **12***	diurnal: 3	crepuscular: 2	cathemeral: 1
Small	6	0.26	nocturnal: **3***	diurnal: 2	crepuscular: 1	cathemeral: 0
taxonomic order						
Ungulates	6	0.43	nocturnal: 1	diurnal: 0	crepuscular: 1	cathemeral: **4***
Carnivora	10	0.41	nocturnal: **4***	diurnal: 1	crepuscular: 1	cathemeral: **4***
Primates	6	0.33	nocturnal: 0	diurnal: 4	crepuscular: 2	cathemeral: 0
Rodents	13	0.30	nocturnal: **8***	diurnal: 4	crepuscular: 1	cathemeral: 0
Insectivora	2	0.27	nocturnal: **2***	diurnal: 0	crepuscular: 0	cathemeral: 0
functional group						
omnivores	12	0.40	nocturnal: **6***	diurnal: 2	crepuscular: 1	cathemeral: 3
carnivores	2	0.36	nocturnal: 0	diurnal: 0	crepuscular: 0	cathemeral: **2***
insectivores	4	0.35	nocturnal: **3***	diurnal: 1	crepuscular: 0	cathemeral: 0
herbivores	19	0.32	nocturnal: **6***	diurnal: **6***	crepuscular: 4	cathemeral: 3
folivores	*7*	*0.37*	*nocturnal: 1*	*diurnal: 1*	*crepuscular: 2*	*cathemeral:**3****
frugivores	*6*	*0.32*	*nocturnal: **3****	*diurnal: 2*	*crepuscular: 1*	*cathemeral: 0*
granivores	*4*	*0.26*	*nocturnal: 1*	*diurnal: **2****	*crepuscular: 1*	*cathemeral: 0*

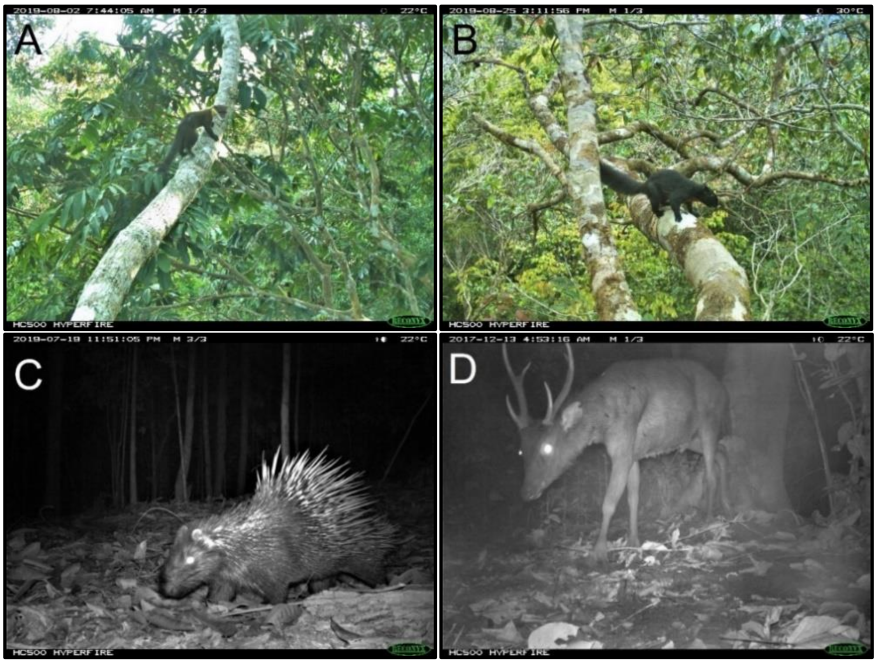


Figure 3.3 Examples of different activity patterns. (A) yellow-throated marten *M. flavigula*, a predominantly crepuscular semi-arboreal member of the Carnivora; (B) Prevost's squirrel *C. prevostii*, a diurnal arboreal rodent; (C) Malay porcupine *H. brachyura*, a nocturnal terrestrial rodent; (D) sambar deer *Rusa unicolor*, a cathemeral ungulate. Time stamps (top left of each image) are indicative of the most common period of activity for these species.

3.4 Discussion

We present information on activity levels and patterns for 37 Bornean mammal species, and compare these metrics across canopy and terrestrial strata in unlogged and recovering-logged rainforest. Mean community activity levels were consistently lower for arboreal mammals than terrestrial mammals, with the difference most pronounced in recovering-logged forest. However, there was more variation at the species level, with both increased and decreased activity in recovering-logged forest for both arboreal and terrestrial mammals. Activity patterns, on the other hand, showed clear differences between strata, but remained largely consistent across unlogged and recovering-logged forest.

Activity levels

To our knowledge, this is the first study to investigate the proportion of the diel cycle that arboreal mammals spend active, and to compare this to their counterparts at ground level. As such, it is not yet clear whether the consistently lower activity levels of arboreal mammals (Table 3.2, Supplementary Materials Table S3.1) is a trend common to tropical regions. The amount of time animals spend active represents a compromise between the need to find food and engage in social behaviour, and to rest and avoid predation or competition. Thus, it will vary depending on species' characteristics, and the opportunities and constraints of a given habitat. Lower activity levels observed in the canopy may be related to the differing environmental conditions between strata. Climbing among branches requires more energy than walking across flat ground and poses an additional danger of injury or death from falling (Dial 2003). Arboreal species may spend less time travelling than terrestrial species in order to conserve energy and minimise risk. Reduced canopy activity levels may also reflect the smaller effective sampling area of each canopy camera-trap and longer sampling period required to detect all species compared to camera-traps at ground level, and/or a lower density of species in the three-dimensional canopy space than on the forest floor (i.e. animals per cubic kilometre) (Haysom *et al.* 2021). Sampling period and sampling environment should therefore be considered when comparing the amount of time different communities spend active, and caution is advised when making direct comparisons between the activity of arboreal and terrestrial mammals.

Although logging appears to have a negligible effect on overall activity levels (with a difference across all species of 1% between unlogged and recovering-logged forest, Table 3.2), when communities were split by strata, the greatest differences were observed in recovering-logged forest, with arboreal mammals 14% less active than their terrestrial counterparts, potentially indicating that arboreal communities are more affected by habitat changes. Disruption of the canopy architecture caused by logging reduces lateral movement pathways for arboreal species, and navigating within logged forest canopies likely requires greater energy expenditure than within the more uniform and connected canopies of unlogged forest (Davies *et al.* 2017). Thus, arboreal species in recovering-logged forest may reduce the overall amount of time they spend active in order to balance the increased energetic cost of movement in this habitat. However, there was no consistent or predictable effect for individual species, corroborating a separate study on Bornean terrestrial mammals that showed species' activity levels were approximately equally as likely to increase or decrease in logged forests (Wearn *et al.* 2022). We extend this result across strata: for the seven species with significant changes between unlogged and recovering-logged forest, the amount of time spent active was equally as likely to increase or decrease, for both arboreal and terrestrial mammals, with non-significant changes also evenly split in direction (Supplementary Materials Table S3.3). There was no obvious trend in the type of species affected, with those showing significant changes belonging to a range of body sizes, functional and taxonomic groups (Supplementary Materials Table S3.3). In addition, care should be taken when interpreting changes in activity level, as a reduction is not necessarily negative. For example, an animal that needs to travel less to forage due to a high concentration of resources nearby (e.g. because of new vegetation growth in canopy gaps) is arguably at an energetic advantage to one that has to travel further to fulfil its daily energy requirements.

Data pooled across unlogged and recovering-logged forest for six semi-arboreal mammals revealed three species were more active on the ground (long-tailed macaque *Macaca fascicularis*, pig-tailed macaque *M. nemestrina*, and horse-tailed squirrel *S. hippurus*; the latter two significantly), while three were more active in the canopy (orangutan *P. pygmaeus*, yellow-throated marten *M. flavigula*, and binturong *Arctictis binturong*) (Supplementary Materials Table S3.3). These findings may reflect species-specific preferences between strata and might thus be useful for researchers to inform where to concentrate sampling. We did not detect any significant increase in terrestrial activity levels of semi-arboreal species in recovering-logged forest (Supplementary Materials Table S3.3), suggesting that these species are not descending to the ground more often because of structural changes post-logging (e.g. as suggested in Berry *et al.* 2010). That semi-arboreal mammals were frequently detected in both strata, do not appear to become more terrestrial in recovering-logged forest, and tended to have different activity patterns between strata (Supplementary Materials Tables S3.1, S3.3), underlines the importance of including canopy-based sampling for these species. Studies utilising only ground-based camera-traps may mischaracterise the amount of time and the times of day that semi-arboreal mammals are active, which will in turn restrict our ability to understand their behaviour, ecology and inter-specific interactions.

Activity patterns

Ninety-two percent of all species retained the same activity pattern in unlogged and recovering-logged forest, corroborating similar findings for terrestrial mammals in Sarawak, Borneo (Maiwald, Mohd-Azlan, and Brodie 2021). In contrast, there was a clear divergence in activity pattern trends between terrestrial and canopy strata. Terrestrial mammals were predominantly nocturnal or cathemeral, with very few species diurnal or crepuscular. Arboreal and semi-arboreal species displayed a more even spread of activity patterns across time categories, with the exceptions that no arboreal mammals were cathemeral, and no semi-arboreal mammals were nocturnal (Table 3.2).

Across all species, nocturnality was the dominant activity pattern, which may be common for rainforest mammals (Charles-Dominique 1975). Evidence suggests that primitive mammals evolved in a nocturnal environment (Maor *et al.* 2017) and all extant species are thought to be descended from these nocturnal ancestors with most, except anthropoid primates, retaining a nocturnal eye shape (Heesy and Hall 2010). It may be that the environmental conditions of the rainforest today (e.g. high daytime temperatures, Curtis and Rasmussen 2006), together with intrinsic and extrinsic biotic factors, e.g. eye morphology; and the need to avoid competitors such as diurnal frugivorous birds (Jayasekara *et al.* 2007; Nakabayashi, Ahmad and Kohshima 2016), mean that nocturnality remains advantageous for many species in both strata. Semi-arboreal mammals were a notable exception to this trend. Given the prevalence of nocturnality among terrestrial and arboreal mammals, it may be that few nocturnal niches exist for semi-arboreal species.

Cathemerality appears by its prevalence to have advantages for ground-dwelling mammals. The ability to be active at any time during the 24-hour cycle affords greatly increased hunting or foraging opportunities compared to animals only active during one period (Van Schaik and Griffiths 1996), as well as the flexibility to concentrate activity during times that either minimise predation or competition risk, or maximise the likelihood of encountering prey (Curtis and Rasmussen 2006). On the other hand, cathemerality may represent an infeasible strategy for strictly arboreal mammals, potentially due to a greater need for sharp vision in the canopy. No arboreal species displayed cathemeral activity (Table 3.2, Figure 3.1), a finding consistent with other studies (Van Schaik and Griffiths 1996; Oliveira-Santos, Tortato, and Graipel 2008; Azcarraga, Tessaro, and Delfin-Alfonso 2020). Visual acuity in mammals has evolved to be optimum in either bright or dark light (Van Schaik and Griffiths 1996; Heesy and Hall 2010; Veilleux and Kirk 2014). While animals moving on a flat plane at ground level may be able to contend with sub-optimal vision, and therefore be active across a wider temporal niche, for those travelling along branches at height, the risk of a fall associated with poor vision may lead to behavioural adaptations that favour activity during a defined light period.

Diurnality was rare among terrestrial mammals but was the most common primary pattern for arboreal and semi-arboreal species, especially primates and non-gliding squirrels (Supplementary Materials Table S3.1), in line with global trends (Thorington *et al.* 2012; Tan, Yang, and Niu 2013). These taxa were among the first to evolve the ability to be active during daylight (Maor *et al.* 2017), and so may be more able to take advantage of brighter light conditions, particularly in the canopy, which stays illuminated longer per day than the more shaded forest floor (Wong, Servheen and Ambu 2004). Differing light levels between strata may also help explain why four of five crepuscular species were arboreal or semi-arboreal (Figure 3.1, Supplementary Materials Table S3.1), as the canopy presents extended foraging opportunities around dawn and dusk compared to ground level. Twilight may additionally represent a relatively safe time to travel, for example to move into or away from sleeping sites. Lower light conditions than full daylight reduce the risk from visually-hunting predators such as raptors (Becker, Leighton, and Payne 1985), while background noise from the insect chorus, which is loudest around dawn and dusk (Gogala and Riede 1995), may afford some protection against predators with acute hearing, such as felids (Van Schaik and Griffiths 1996). Thus, although twilight represents the shortest time-period in which to be active, it may be that for species with adaptations to daylight or darkness that do not translate well to the opposite conditions, the transition between the two offers an advantageous compromise period.

Semi-arboreal mammals

Semi-arboreal mammals appeared to fill the niches least used in either strata (Table 3.2, Supplementary Materials Table S3.1). In the canopy, binturong *A. binturong* followed a cathemeral activity pattern not shown by any arboreal species, while on the ground, semi-arboreal primates (pig-tailed macaque *M. nemestrina*, long-tailed macaque *M. fascicularis*, and orangutan *P. pygmaeus*) filled the diurnal niche under-utilised by terrestrial mammals. These cross-strata analyses offer more complete insights into the diel activity of semi-arboreal mammals, which is missing from terrestrial-only studies (Wearn *et al.* 2022), and the opportunity to examine possible reasons behind the differential use of each stratum. For example, both long-tailed and pig-tailed macaques – and to a lesser extent orangutan – are predominantly crepuscular in the canopy, but diurnal on the ground (Figure 3.2). All three species sleep in the trees (Ashbury *et al.* 2015; Otani *et al.* 2020), explaining peaks in their canopy activity around dawn and dusk as they move from and to sleeping sites, while strong diurnal activity on the ground indicates that they mainly use this stratum to travel and forage.

For other semi-arboreal species, the ability to utilise both strata may allow them to avoid both arboreal and terrestrial competitors. Horse-tailed squirrels *S. hippurus* were most active in the early morning in both strata (Figure 3.2). This small-bodied rodent specialises on consuming hard-shelled nuts (MacKinnon 1978), and likely competes with the strictly arboreal giant squirrel *R. affinis* and the predominantly terrestrial tufted ground squirrel *Rheithrosciurus macrotis*, both of which have similar diets (Marshall, Meijaard and Leighton 2020), but are larger and more strongly diurnal, with activity concentrated between late morning and midday (Figure 3.1). As the latter two species mainly utilise different strata, they are unlikely to directly compete with each other, whereas the semi-arboreal horse-tailed squirrel could conceivably compete with both and, due to its smaller size, be at a disadvantage. Temporal avoidance of competitors has been noted in temperate squirrel species (Di Cerbo and Biancardi 2013), and Bornean felids at ground level (Hearn *et al.* 2018), while spatial niche partitioning along vertical gradients has been observed in tropical rodent assemblages (Nakagawa *et al.* 2007). In a similar way, it may be that a crepuscular activity pattern allows horse-tailed squirrels to avoid potentially harmful competitive interactions at both ground- and canopy-level, while maintaining the ability to optimise foraging across strata.

Overall, our findings indicate that the vertical dimension of the rainforest environment has a greater influence on mammal activity than selective logging, underlining the stark differences between canopy and terrestrial habitats, and suggesting that the structural changes caused by logging do not have a clear or predictable effect on animal activity across strata. Our results imply that the major ecosystem components driving mammal activity patterns (e.g. physical structure, food availability, inter-species interactions) are not sufficiently altered in recovering-logged forest, in either strata, to result in significant changes to animal activity. This is particularly encouraging for the arboreal community, which could be expected to be disproportionately impacted by logging (but see Caveats, below).

Activity within groups

Activity may vary predictably with species traits such as body size, taxonomic order, and feeding strategy (Van Schaik and Griffiths 1996; Heesy and Hall 2010; Rowcliffe *et al.* 2014; Cid *et al.* 2020), although some studies contradict this (e.g. Clauss *et al.* 2021). To evaluate any trends in our data, we compared activity metrics according to these groups (Table 3.3, Supplementary Materials Table S3.1). The number of species within each group varied, and some had a particularly low number. Therefore, caution should be exercised when interpreting differences in activity metrics between groups with low and high numbers of species. With that in mind, we report the main differences observed as they can help inform our understanding of species' activity, as well as providing useful comparisons for future studies.

We found average activity levels of small-bodied mammals were 14% lower than those of large-bodied species, providing support to hypotheses that small mammals maintain lower activity levels to conserve energy that is more easily lost due to their high metabolic rate (Hazlerigg and Tyler 2019). Most small-bodied species were nocturnal, which may also aid energy conservation as thermoregulatory pressures are reduced at night (Crompton *et al.* 1978; Heesy and Hall 2010). Large-bodied species, on the other hand, may need to spend more time actively foraging in order to meet the energetic demands of a bigger body (Cid *et al.* 2020), particularly carnivores, whose prey may be patchily distributed across space or time (Azlan and Sharma 2006), and herbivores, who may need to spend more time consuming food due to the low nutritional quality of their diet (Shafique *et al.* 2006). Most cathemeral species were large-bodied carnivores and herbivores (e.g. Sunda clouded leopard *Neofelis diardi*, sambar deer *R. unicolor*) (Supplementary Materials Table S3.1), potentially corroborating these suggestions. Furthermore, when herbivores were split into folivorous, frugivorous, and granivorous sub-groups, leaf-eaters spent 11% more of the 24-hour cycle active than seed-eaters, which may be explained by the poor nutritional value of leaves compared to seeds (Mitsuzuki and Oshida 2018). The durability of seeds may also be a factor as they can be cached in a convenient location for later consumption (e.g. Becker, Leighton, and Payne 1985), which could reduce overall foraging time, and therefore activity level, for granivores.

Caveats

While analysis of animal activity can be informative for species and community ecology, in any ecosystem there are multiple variables at play. Inter-species relationships extend outside the mammalian taxon (Sushma and Singh 2006; Beaudrot *et al.* 2013), and environmental variables can fluctuate with season and across geographic location (e.g. Cheyne *et al.* 2010; Suzuki and Ando 2017). Even at the regional level, activity within a species may vary across locations, e.g. other studies in Sabah reported cathemeral and diurnal activity patterns, respectively, for greater and lesser mousedeer *T. napu and T. kanchil* (Matsubayashi and Sukor 2005), whereas we found these species to be nocturnal and crepuscular, respectively.

It is also important to note that our recovering-logged forest site was of relatively high quality, with logging having ceased a decade prior to sampling, and low levels of hunting (Wearn *et al.* 2017). Time since cessation of logging may be an important factor for some species such as bearded pig *Sus barbatus* (Chapman 2019) and sun bear *H. malayanus* (Meijaard *et al.* 2005), which may significantly alter their activity immediately after disturbance, taking several years to return to pre-logging levels. Likewise, the presence of humans can cause some mammals, especially those targeted by hunters, to shift activity patterns (e.g. Chapman 2019; Davison *et al.* 2019). Locations with higher levels of disturbance may report greater shifts in the diel activity of resident wildlife.

Finally, certain species may be more noticeable by their absence, e.g. our negligible records of two of the three large flying squirrels (Thomas' flying squirrel *Aeromys thomasi*, red giant flying squirrel *Petaurista petaurista*) in recovering-logged forest, and our failure to record Sabah grey langur *Presbytis sabana* in this habitat (Supplementary Materials Tables S3.1, S3.2). Activity analyses do not extend to examination of abundance changes, but these differences serve as a reminder that missing species may also be informative. Therefore, although our finding that past selective logging has a minimal effect on animal activity is encouraging, it should not be interpreted as a message that logging has no effect on mammals. While it may not greatly alter diel activity for mammals that are present in both unlogged and recovering-logged forest, there may be species that simply cannot persist in viable numbers in post-logging environments.

3.5 Conclusion

Our study represents the first community-wide investigation of rainforest mammal activity encompassing both canopy and terrestrial strata in both unlogged and recovering-logged forest. Our findings add to previous work suggesting that mammal communities are more similar across unlogged and recovering-logged forest than across strata (Haysom *et al.* 2021), with differences between arboreal and terrestrial activity likely arising from species' adaptations to these structurally different habitats. We further show that within the rainforest mammal community, all temporal niches across the 24-hour cycle are filled, and this is most evident when species utilising the vertical dimension are taken into account. In this complex and biodiverse ecosystem, cross-strata sampling enables a much more complete understanding of mammal community dynamics, revealing how species interact and partition activity temporally and spatially.

3.6 Acknowledgements

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3.7 Supplementary Materials

Table S3.1 Characteristics of fifty-seven mammal species detected during our study. Species endemic to Borneo are marked with an asterisk. Species excluded from activity analyses due to insufficient detections (<10) are shaded grey (*N*=20). For species retained (*N* =37), primary activity pattern, any secondary pattern (in italics), and mean activity level are stated. These derive from all detections of each species: for species' metrics between strata and unlogged/logged forest, see Supplementary Materials Table S3.2. 'Strata' refers to whether a species was detected exclusively by canopy camera-traps ('arboreal'), exclusively by terrestrial camera-traps ('terrestrial'), or by camera-traps in both strata ('semi-arboreal'). Two species (banded civet *Hemigalus derbyanus*, and tufted ground squirrel *Rheithrosciurus macrotis*) were detected by canopy camera-traps, but for the purposes of our analyses have been categorised as terrestrial due to the very low number of canopy detections in the context of high terrestrial detections (1 vs. 159 and 2 vs. 53, respectively). Similarly, three species (maroon langur *Presbytis rubicunda*, Sabah grey langur *P. sabana* and Thomas' flying squirrel *A. thomasi*) were detected once each by terrestrial camera-traps but categorised as arboreal in the context of frequent canopy detections (80, 40, and 59, respectively).). Information on body size, taxonomic group and functional group are from Payne and Francis 2007 and the IUCN Red List.

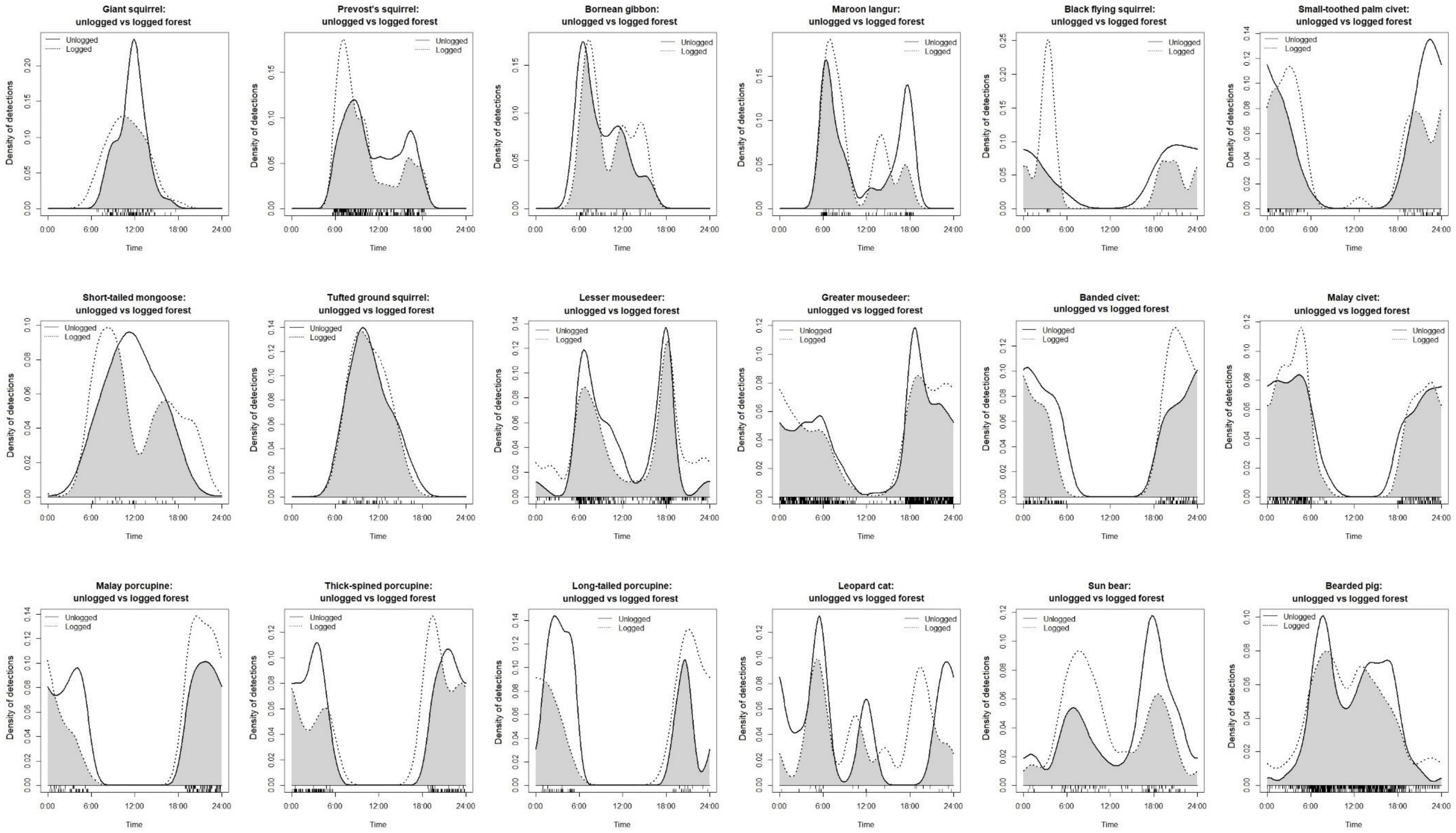
Family	**Species**	**Forest**	**Strata**	**Body size**	**Taxonomic group**	**Functional group**	**Primary & secondary activity pattern (all data)**	**Mean activity level (all data)**
Felidae	*Neofelis diardi* Sunda clouded leopard	both	terrestrial	large	Carnivora	carnivore	cathemeral *nocturnal tendencies*	0.37
	Pardofelis marmorata Marbled cat	both	terrestrial	medium	Carnivora	carnivore	-	-
	Prionailurus bengalensis Leopard cat	both	terrestrial	medium	Carnivora	carnivore	cathemeral *nocturnal tendencies*	0.34
Herpestidae	*Herpestes brachyurus* Short-tailed mongoose	both	terrestrial	medium	Carnivora	insectivore	diurnal	0.46
	Herpestes semitorquatus Collared mongoose	unlogged	terrestrial	medium	Carnivora	carnivore	-	-
Mustelidae	*Martes flavigula* Yellow-throated marten	both	semi-arboreal	medium	Carnivora	omnivore	crepuscular *diurnal tendencies*	0.38
	Mydaus javanensis Sunda stink badger	both	terrestrial	medium	Carnivora	insectivore	-	-

Viverridae	*Arctictis binturong* Binturong	both	semi-arboreal	large	Carnivora	omnivore	cathemeral	0.52
	Arctogalidia trivirgata Small-toothed palm civet	both	arboreal	medium	Carnivora	omnivore	nocturnal	0.42
	Hemigalus derbyanus Banded civet	both	semi-arboreal	medium	Carnivora	insectivore	nocturnal	0.41
	Paguma larvata Masked palm civet	both	terrestrial	medium	Carnivora	omnivore	nocturnal	0.31
	Paradoxurus hermaphroditus Common palm civet	unlogged	terrestrial	medium	Carnivora	omnivore	-	-
	Viverra tangalunga Malay civet	both	terrestrial	medium	Carnivora	omnivore	nocturnal	0.50
Ursidae	*Helarctos malayanus* Sun bear	both	terrestrial	large	Carnivora	omnivore	cathemeral *crepuscular tendencies*	0.45
Suidae	*Sus barbatus* Bearded pig	both	terrestrial	large	Ungulates	omnivore	cathemeral *diurnal tendencies*	0.47
Tragulidae	*Tragulus kanchil* Lesser mousedeer	both	terrestrial	medium	Ungulates	herbivore *(frugivore)*	crepuscular *cathemeral tendencies*	0.30
	Tragulus napu Greater mousedeer	both	terrestrial	medium	Ungulates	herbivore *(frugivore)*	nocturnal *crepuscular tendencies*	0.37
Cervidae	*Muntiacus atherodes** Bornean yellow muntjac*	both	terrestrial	large	Ungulates	herbivore *(folivore)*	cathemeral *diurnal tendencies*	0.42
	Muntiacus muntjak Red muntjac	both	terrestrial	large	Ungulates	herbivore *(folivore)*	cathemeral *diurnal tendencies*	0.43
	Rusa unicolor Sambar deer	both	terrestrial	large	Ungulates	herbivore *(folivore)*	cathemeral *crepuscular tendencies*	0.59
Bovidae	*Bos javanicus* Banteng	logged	terrestrial	large	Ungulates	herbivore	-	-

Cynocephalidae	*Galeopterus variegatus* Sunda colugo	both	arboreal	medium	Insectivora	herbivore	-	-
Erinaceidae	*Echinosorex gymnura* Moonrat	both	terrestrial	small	Insectivora	insectivore	nocturnal	0.32
Manidae	*Manis javanica* Sunda pangolin	both	terrestrial	medium	Insectivora	insectivore	nocturnal	0.21
Cercopithecidae	*Presbytis rubicunda** Maroon langur*	both	arboreal	large	Primates	herbivore *(folivore)*	crepuscular *diurnal tendencies*	0.25
	*Presbytis sabana** Sabah grey langur*	unlogged	arboreal	large	Primates	herbivore *(folivore)*	crepuscular *diurnal tendencies*	0.33
	Macaca fascicularis Long-tailed macaque	unlogged	semi-arboreal	large	Primates	omnivore	diurnal *crepuscular tendencies*	0.35
	Macaca nemestrina Pig-tailed macaque	both	semi-arboreal	large	Primates	omnivore	diurnal	0.45
Hylobatidae	*Hylobates funereus** Bornean gibbon*	both	arboreal	large	Primates	herbivore *(folivore)*	diurnal *crepuscular tendencies*	0.23
Pongidae	*Pongo pygmaeus** Bornean orangutan*	logged	semi-arboreal	large	Primates	herbivore *(frugivore)*	diurnal	0.39
Elephantidae	*Elephas maximus* Asian elephant	logged	terrestrial	large	Ungulates	herbivore	-	-
Sciurdiae	*Aeromys tephromelas* Black flying squirrel	both	arboreal	medium	Rodents	herbivore *(granivore)*	nocturnal	0.40
	*Aeromys thomasi** Thomas' flying squirrel*	both	arboreal	medium	Rodents	herbivore *(frugivore)*	nocturnal	0.38
	*Callosciurus adamsi** Ear-spot squirrel*	logged	arboreal	small	Rodents	herbivore *(unknown)*	diurnal *crepuscular tendencies*	0.22
	Callosciurus prevostii Prevost's squirrel	both	arboreal	small	Rodents	herbivore *(frugivore)*	diurnal *crepuscular tendencies*	0.28

	Callosciurus sp. Large mystery squirrel	logged	arboreal	small	Rodents	herbivore?	-	-
	*Exilisciurus exilis** Bornean pygmy squirrel*	unlogged	arboreal	small	Rodents	herbivore?	-	-
	Iomys horsfieldi Horsfield’s flying squirrel	logged	arboreal	small	Rodents	herbivore?	-	-
	Petaurista petaurista Red giant flying squirrel	unlogged	arboreal	medium	Rodents	herbivore *(folivore)*	nocturnal	0.31
	Petinomys setosus Temminck’s flying squirrel	unlogged	arboreal	small	Rodents	herbivore?	-	-
	Pteromyscus pulverulentus Smoky flying squirrel	unlogged	arboreal	small	Rodents	herbivore?	-	-
	Ratufa affinis Giant squirrel	both	arboreal	medium	Rodents	herbivore *(granivore)*	diurnal	0.22
	*Rheithrosciurus macrotis** Tufted ground squirrel*	both	semi-arboreal	medium	Rodents	herbivore *(granivore)*	diurnal	0.30
	*Sundasciurus brookei** Brooke’s squirrel*	both	arboreal	small	Rodents	herbivore?	-	-
	Sundasciurus lowii Low’s squirrel	both	semi-arboreal	small	Rodents	herbivore?	-	-
	Sundasciurus hippurus Horse-tailed squirrel	both	semi-arboreal	small	Rodents	herbivore *(granivore)*	crepuscular *diurnal tendencies*	0.14
Murdiae	*Leopoldamys sabanus* Long-tailed giant rat	unlogged	terrestrial	small	Rodents	herbivore *(frugivore)*	nocturnal	0.19
	Maxomys rajah Brown spiny rat	unlogged	terrestrial	small	Rodents	herbivore *(unknown)*	nocturnal	0.40
	Maxomys surifer Red spiny rat	logged	terrestrial	small	Rodents	herbivore	-	-

	Maxomys whiteheadi Whitehead’s rat	unlogged	terrestrial	small	Rodents	insectivore	-	-
Hystricidae	*Hystrix brachyura* Malay porcupine	both	terrestrial	medium	Rodents	omnivore	nocturnal	0.35
	*Hystrix crassispinis** Thick-spined porcupine*	both	terrestrial	medium	Rodents	omnivore	nocturnal	0.39
	Trichys fasciculata Long-tailed porcupine	both	terrestrial	medium	Rodents	omnivore	nocturnal	0.32
Ptilocercidae	*Ptilocercus lowii* Pentail treeshrew	logged	arboreal	small	Insectivora	insectivore	-	-
Tupaiidae	*Tupaia longipes** Plain treeshrew*	both	semi-arboreal	small	Insectivora	insectivore	-	-
	Tupaia tana Large treeshrew	unlogged	terrestrial	small	Insectivora	insectivore	-	-
	Tupaia minor Lesser treeshrew	unlogged	terrestrial	small	Insectivora	insectivore	-	-


Giant squirrel: unlogged vs logged forest
Prevost's squirrel: unlogged vs logged forest
Bornean gibbon: unlogged vs logged forest
Maroon langur: unlogged vs logged forest
Black flying squirrel: unlogged vs logged forest
Small-toothed palm civet: unlogged vs logged forest
Short-tailed mongoose: unlogged vs logged forest
Tufted ground squirrel: unlogged vs logged forest
Lesser mousedeer: unlogged vs logged forest
Greater mousedeer: unlogged vs logged forest
Banded civet: unlogged vs logged forest
Malay civet: unlogged vs logged forest
Malay porcupine: unlogged vs logged forest
Thick-spined porcupine: unlogged vs logged forest
Long-tailed porcupine: unlogged vs logged forest
Leopard cat: unlogged vs logged forest
Sun bear: unlogged vs logged forest
Bearded pig: unlogged vs logged forest
Unlogged
Logged
Density of detections
Time
0:00
6:00
12:00
18:00
24:00

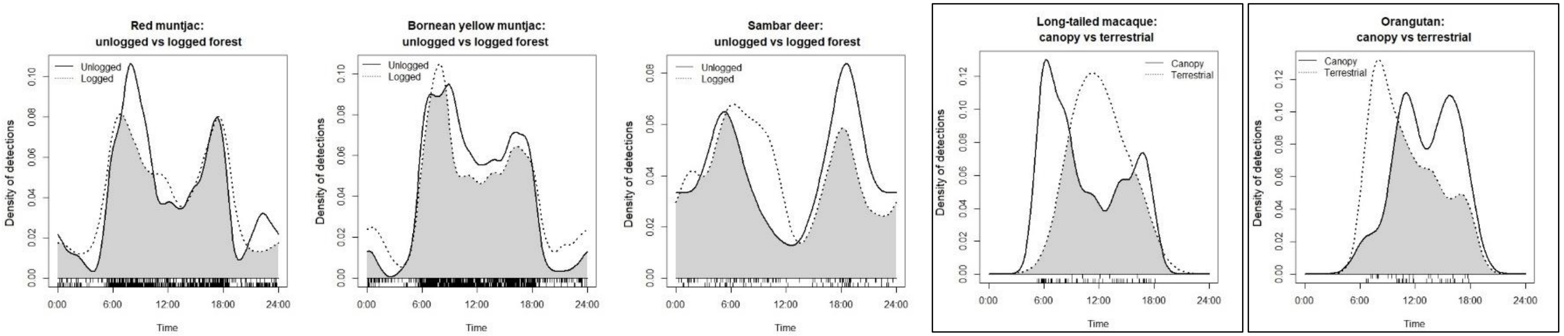


Figure S3.1 Overlap plots showing comparisons of activity patterns for 23 mammal species in: unlogged vs. recovering-logged forest (*N*=21: no border around plot), or canopy vs. terrestrial strata (*N*=2: solid border). Grey shaded areas show the degree of overlap between patterns, black bars on the x axes show the independent detections from which the patterns derive. These plots visualise trends quantified by coefficient of overlap statistics (Table S3.3 below), i.e. that activity patterns between unlogged and recovering-logged forest tended towards similarity, whereas those between canopy and terrestrial strata tended towards dissimilarity. (See also main text Figure 3.2 for four species detected in both unlogged and recovering-logged forest and both canopy and terrestrial strata.)

Table S3.2 Detection data for 57 mammal species recorded during our study. Asterisks denote Bornean endemics; grey shading indicates species excluded from analyses due to insufficient detections. For all 37 species retained, the number and percentage of detections per time period are given. Daylight was defined as between the hours of 07:30:00-16:49:59, darkness between 19:26:00-04:59:59, twilight between 05:00:00-07:29:59 or 16:50:00-19:25:00. Following Gomez *et al.* (2005), strictly diurnal or strictly nocturnal species had ≥90% detections during daylight or darkness, respectively; mostly diurnal or mostly nocturnal species had ≥70% detections during daylight or darkness, respectively; crepuscular species had ≥50% detections during twilight; and cathemeral species had <70% but >10% detections during both daylight and darkness. Once primary patterns were defined, they were tested for deviation from expected proportions using a binomial test with significance at p<0.05 (in bold font if significant) (Van Schaik and Griffiths 1996). We noted secondary patterns where, after the primary pattern, a species showed a clear tendency (by proportion of detections) towards activity during another period. For four species (greater mousedeer, long-tailed macaque, Bornean gibbon, Prevost's squirrel), the proportion of time active in each period did not fit any category as defined above and so we re-calculated using a two-way split between daylight and darkness, defining daylight as 05:45:00-17:34:59, and darkness as 17:35:00-05.44:59 (dividing the twilight period equally). In all cases, this allowed us to confirm the apparent primary pattern. Where relevant, this is noted in italics as 'confirmed by 2-way split' and with the 2-way number and proportion of detections stated. Detection data and resultant activity patterns are given for: all data combined ('all' in dataset column); unlogged forest only ('unlogged'), recovering-logged forest only ('logged'), canopy cameras only ('canopy') and terrestrial cameras only ('terrestrial').

Species	Dataset	Total no. detections	No. detections per time period			% detections per time period			Primary activity pattern, per dataset	Any secondary pattern, per dataset
			daylight	twilight	darkness	daylight	twilight	darkness		
Neofelis diardi Sunda clouded leopard	all:	21	5	4	12	24	19	57	cathemeral	nocturnal tendencies
Pardofelis marmorata Marbled cat	all:	5								
Prionailurus bengalensis Leopard cat	all:	23	5	8	10	22	35	43	cathemeral	nocturnal tendencies
	unlogged:	11	2	4	5	18	36	45	cathemeral	nocturnal tendencies
	logged:	12	3	4	5	25	33	42	cathemeral	nocturnal tendencies
Herpestes brachyurus Short-tailed mongoose	all:	30	21	8	1	70	27	3	mostly diurnal	n/a
	unlogged:	23	18	5	0	78	22	0	mostly diurnal	n/a
	logged:	7	3	3	1	43	43	14	mostly diurnal	crepuscular tendencies
Herpestes semitorquatus Collared mongoose	all:	4								
Martes flavigula Yellow-throated marten	all:	28	12	15	1	43	54	4	crepuscular	diurnal tendencies
	unlogged:	18	8	9	1	44	50	6	crepuscular	diurnal tendencies
	logged:	10	4	6	0	40	60	0	crepuscular	diurnal tendencies
	canopy:	15	8	7	0	53	47	0	mostly diurnal	crepuscular tendencies
	terrestrial:	13	4	8	1	31	62	8	crepuscular	diurnal tendencies
Mydaus javanensis Sunda stink badger	all:	3								
Arctictis binturong Binturong	all:	24	12	1	11	50	4	46	cathemeral	n/a
	unlogged:	17	9	1	7	53	6	41	cathemeral	n/a
	logged:	7	3	0	4	43	0	57	cathemeral	n/a
	canopy:	19	12	0	7	63	0	37	cathemeral	n/a
	terrestrial:	5	0	1	4	0	20	80	mostly nocturnal	n/a
Arctogalidia trivirgata Small-toothed palm civet	all:	80	1	10	69	1	13	86	**mostly nocturnal**	n/a
	unlogged:	34	0	3	31	0	9	91	strictly nocturnal	n/a
	logged:	46	1	7	38	2	15	83	**mostly nocturnal**	n/a
Hemigalus derbyanus Banded civet	all:	159	0	26	133	0	16	84	**mostly nocturnal**	n/a
	unlogged:	121	0	24	97	0	20	80	**mostly nocturnal**	n/a
	logged:	38	0	2	36	0	5	95	strictly nocturnal	n/a

Paguma larvata Masked palm civet	all:	11	0	2	9	0	18	82	mostly nocturnal	n/a
Paradoxurus hermaphroditus Common palm civet	all:	3								
Viverra tangalunga Malay civet	all:	276	6	65	205	2	24	74	**mostly nocturnal**	n/a
	unlogged:	144	4	37	103	3	26	72	mostly nocturnal	n/a
	logged:	132	2	28	102	2	21	77	**mostly nocturnal**	n/a
Helarctos malayanus Sun bear	all:	93	33	42	18	35	45	19	cathemeral	crepuscular tendencies
	unlogged:	46	12	23	11	26	50	24	crepuscular	cathemeral tendencies
	logged:	47	21	19	7	45	40	15	cathemeral	diurnal tendencies
Sus barbatus Bearded pig	all:	608	379	161	68	62	27	11	cathemeral	diurnal tendencies
	unlogged:	224	141	66	17	63	29	5	mostly diurnal	crepuscular tendencies
	logged:	284	238	95	51	84	33	14	mostly diurnal	cathemeral tendencies
Tragulus kanchil Lesser mousedeer	all:	305	90	168	47	30	55	15	**crepuscular**	cathemeral tendencies
	unlogged:	103	39	60	4	38	58	4	**crepuscular**	diurnal tendencies
	logged:	202	51	108	43	25	53	22	crepuscular	cathemeral tendencies
Tragulus napu Greater mousedeer	all:	832	56	309	467	7	37	56	mostly nocturnal	crepuscular tendencies
			162	-	*670*	*19*	-	*81*	*Confirmed by 2-way split*	
	unlogged:	552	42	215	295	8	39	53	mostly nocturnal	crepuscular tendencies
	logged:	280	1	94	172	0	34	61	mostly nocturnal	crepuscular tendencies
*Muntiacus atherodes** Bornean yellow muntjac*	all:	911	554	267	90	61	29	10	cathemeral	diurnal tendencies
	unlogged:	449	293	132	24	65	29	5	diurnal	crepuscular tendencies
	logged:	462	261	135	66	56	29	14	cathemeral	diurnal tendencies
Muntiacus muntjak Red muntjac	all:	720	375	242	103	52	34	14	cathemeral	diurnal tendencies
	unlogged:	514	279	160	75	54	31	15	cathemeral	diurnal tendencies
	logged:	206	96	82	28	47	40	14	cathemeral	diurnal tendencies
Rusa unicolor Sambar deer	all:	122	36	47	39	30	39	32	cathemeral	crepuscular tendencies
	unlogged:	41	8	19	14	20	46	34	cathemeral	crepuscular tendencies
	logged:	81	28	28	25	35	35	31	cathemeral	n/a
Bos javanicus Banteng	all:	9								
Galeopterus variegatus Sunda colugo	all:	4								

Echinosorex gymnura Moonrat	all:	28	0	2	26	0	7	93	strictly nocturnal	n/a
Manis javanica Sunda pangolin	all:	10	0	0	10	0	0	100	strictly nocturnal	n/a
*Presbytis rubicunda** Maroon langur*	all:	80	27	53	0	34	66	0	**crepuscular**	diurnal tendencies
	unlogged:	71	23	48	0	32	68	0	**crepuscular**	diurnal tendencies
	logged:	9	4	5	0	44	56	0	crepuscular	diurnal tendencies
*Presbytis sabana** Sabah grey langur*	all:	40	19	21	0	48	53	0	**crepuscular**	diurnal tendencies
Macaca fascicularis Long-tailed macaque	all:	68	41	27	0	60	40	0	mostly diurnal	crepuscular tendencies
			55	-	*0*	*81*	-	*19*	*Confirmed by 2-way split*	
	canopy:	63	36	27	0	57	43	0	mostly diurnal	crepuscular tendencies
	terrestrial:	5	5	0	0	100	0	0	strictly diurnal	n/a
Macaca nemestrina Pig-tailed macaque	all:	507	399	108	0	79	21	0	**mostly diurnal**	n/a
	unlogged:	326	264	62	0	81	19	0	**mostly diurnal**	n/a
	logged:	181	135	46	0	75	25	0	**mostly diurnal**	n/a
	canopy:	64	24	40	0	79	21	0	crepuscular	diurnal tendencies
	terrestrial:	443	375	68	0	85	15	0	mostly diurnal	n/a
*Hylobates funereus** Bornean gibbon*	all:	56	33	23	0	59	41	0	mostly diurnal	crepuscular tendencies
			50	-	*6*	*89*	-	*11*	*Confirmed by 2-way split*	
	unlogged:	43	24	19	0	56	44	0	mostly diurnal	crepuscular tendencies
	logged:	13	9	4	0	69	31	0	mostly diurnal	crepuscular tendencies
*Pongo pygmaeus** Bornean orangutan*	all:	46	35	11	0	76	24	0	mostly diurnal	n/a
	canopy:	28	22	6	0	79	21	0	mostly diurnal	n/a
	terrestrial:	18	13	5	0	72	28	0	mostly diurnal	n/a
Elephas maximus Asian elephant	all:	2								
Aeromys tephromelas Black flying squirrel	all:	17	0	4	13	0	24	76	mostly nocturnal	n/a
	unlogged:	10	0	3	7	0	30	70	mostly nocturnal	n/a
	logged:	7	0	1	6	0	14	86	mostly nocturnal	n/a
*Aeromys thomasi** Thomas' flying squirrel*	all:	59	0	7	52	0	12	88	**mostly nocturnal**	n/a
*Callosciurus adamsi** Ear-spot squirrel*	all:	13	10	3	0	77	23	0	mostly diurnal	crepuscular tendencies

Callosciurus prevostii Prevost's squirrel	all:	326	217	109	0	67	33	0	mostly diurnal	crepuscular tendencies
			299	-	*27*	*92*	-	*8*	*Confirmed by 2-way split*	
	unlogged:	154	114	40	0	74	26	0	mostly diurnal	n/a
	logged:	172	103	69	0	60	40	0	mostly diurnal	crepuscular tendencies
Callosciurus sp. Large mystery squirrel	all:	1								
*Exilisciurus exilis** Bornean pygmy squirrel	all:	1								
Iomys horfieldi Horsfield’s flying squirrel	all:	2								
Petaurista petaurista Red giant flying squirrel	all:	37	0	7	30	0	19	91	mostly nocturnal	n/a
Petinomys setosus Temminck’s flying squirrel	all:	1								
Pteromyscus pulverulentus Smoky flying squirrel	all:	1								
Ratufa affinis Giant squirrel	all:	100	95	5	0	95	5	0	strictly diurnal	n/a
	unlogged:	68	67	1	0	99	1	0	**strictly diurnal**	n/a
	logged:	32	28	4	0	88	13	0	**mostly diurnal**	n/a
*Rheithrosciurus macrotis** Tufted ground squirrel*	all:	53	46	7	0	87	13	0	**mostly diurnal**	n/a
	unlogged:	44	37	7	0	84	16	0	**mostly diurnal**	n/a
	logged:	9	9	0	0	100	0	0	strictly diurnal	n/a
*Sundasciurus brookei** Brooke’s squirrel*	all:	8								
Sundasciurus lowii Low’s squirrel	all:	2								
Sundasciurus hippurus Horse-tailed squirrel	all:	14	4	10	0	29	71	0	**crepuscular**	diurnal tendencies
	unlogged:	5	1	4	0	20	80	0	crepuscular	diurnal tendencies
	logged:	9	3	6	0	33	67	0	crepuscular	diurnal tendencies
	canopy:	8	0	8	0	0	100	0	**crepuscular**	n/a
	terrestrial:	6	4	2	0	67	33	0	mostly diurnal	crepuscular tendencies
Leopoldamys sabanus Long-tailed giant rat	all:	13	0	2	11	0	15	85	mostly nocturnal	n/a

Maxomys rajah Brown spiny rat	all:	34	0	2	32	0	6	94	strictly nocturnal	n/a
Maxomys surifer Red spiny rat	all:	5								
Maxomys whiteheadi Whitehead's rat	all:	3								
Hystrix brachyura Malay porcupine	all:	115	0	12	103	0	10	90	strictly nocturnal	n/a
	unlogged:	66	0	7	59	0	11	89	**mostly nocturnal**	n/a
	logged:	49	0	5	44	0	10	90	strictly nocturnal	n/a
*Hystrix crassispinis** Thick-spined porcupine*	all:	123	0	14	115	0	11	89	**mostly nocturnal**	n/a
	unlogged:	117	0	10	107	0	9	91	strictly nocturnal	n/a
	logged:	12	0	4	8	0	33	67	mostly nocturnal	n/a
Trichys fasciculata Long-tailed porcupine	all:	49	0	8	41	0	16	84	**mostly nocturnal**	n/a
	unlogged:	41	0	8	33	0	20	80	mostly nocturnal	n/a
	logged:	8	0	0	8	0	0	100	strictly nocturnal	n/a
Ptilocercus lowii Pentail treeshrew	all:	2								
*Tupaia longipes** Plain treeshrew*	all:	5								
Tupaia tana Large treeshrew	all:	3								
Tupaia minor Lesser treeshrew	all:	2								

Table S3.3 Activity metrics and comparative statistics for 37 mammal species with ≥ 10 independent detections. Metrics are based on: all data combined, or partitioned by unlogged/recovering-logged forest and canopy/terrestrial strata, as denoted in dataset column ('recovering-logged' has been shortened to 'logged' for space purposes). Grey shading indicates species that did not have sufficient records in a particular category to allow comparisons. Asterisks denote species endemic to Borneo. Statistically significant differences (p<0.05) as indicated by Wald tests for activity level, and binomial tests for activity pattern, are in bold font. Coefficient of overlap between activity patterns is measured on a scale from 0-1 (0 indicates no overlap, 1 indicates identical patterns).

		Activity Levels		**Activity Patterns**	
Species	**Dataset**	**Mean & range (±2.5 and 97.5 CL)**	**Change between unlogged/logged forest or strata (Wald statistic & p-value)**	**Primary pattern**	**Change between unlogged/logged forest or strata (coefficient of overlap with ±95% CI)**
Neofelis diardi Sunda clouded leopard	all:	0.37 (0.21-0.45)		cathemeral	
Prionailurus bengalensis Leopard cat	all:	0.34 (0.17-0.53)		cathemeral	
	unlogged:	0.31 (0.10-0.45)	logged vs unlogged	cathemeral	logged vs unlogged
	logged:	0.42 (0.17-0.55)	0.106 (p > 0.1)	cathemeral	0.52 (0.35-0.78)
Herpestes brachyurus Short-tailed mongoose	all:	0.46 (0.28-0.53)		mostly diurnal	
	unlogged:	0.43 (0.24-0.49)	logged vs unlogged	mostly diurnal	logged vs unlogged
	logged:	0.42 (0.11-0.50)	-0.011 (p > 0.1)	mostly diurnal	0.61 (0.48-0.97)
Martes flavigula Yellow-throated marten	all:	0.38 (0.22-0.48)		crepuscular	
	unlogged:	0.41 (0.19-0.52)	logged vs unlogged	crepuscular	logged vs unlogged
	logged:	0.36 (0.09-0.48)	-0.045 (p > 0.1)	crepuscular	0.64 (0.52-0.97)
	canopy:	0.28 (0.13-0.36)	canopy vs terrestrial	mostly diurnal	canopy vs terrestrial
	terrestrial:	0.19 (0.09-0.39)	0.086 (p > 0.1)	crepuscular	0.34 (0.09-0.59)
Arctictis binturong Binturong	all:	0.52 (0.26-0.61)		cathemeral	
	unlogged:	0.48 (0.20-0.58)	logged vs unlogged	cathemeral	logged vs unlogged
	logged:	0.58 (0.10-0.60)	0.099 (p > 0.1)	cathemeral	0.57 (0.49-0.96)
	canopy:	0.45 (0.21-0.52)	canopy vs terrestrial	cathemeral	canopy vs terrestrial
	terrestrial:	0.32 (0.07-0.38)	0.132 (p > 0.1)	mostly nocturnal	0.36 (0.17-0.64)
Arctogalidia trivirgata Small-toothed palm civet	all:	0.42 (0.30-0.43)		**mostly nocturnal**	
	unlogged:	0.31 (0.20-0.38)	logged vs unlogged	strictly nocturnal	logged vs unlogged
	logged:	0.37 (0.24-0.43)	0.059 (p > 0.1)	**mostly nocturnal**	0.75 (0.60-0.90)

Hemigalus derbyanus Banded civet	all:	0.41 (0.33-0.44)	logged vs unlogged -0.095 ($p > 0.05$)	**mostly nocturnal**	logged vs unlogged 0.79 (0.65-0.91)
	unlogged:	0.40 (0.33-0.44)		**mostly nocturnal**	
	logged:	0.31 (0.19-0.37)		strictly nocturnal	
Paguma larvata Masked palm civet	all:	0.31 (0.12-0.38)		mostly nocturnal	
Viverra tangalunga Malay civet	all:	0.41 (0.33-0.47)	logged vs unlogged **-0.138 ($p < 0.05$)**	**mostly nocturnal**	logged vs unlogged 0.88 (0.83-0.97)
	unlogged:	0.50 (0.37-0.53)		mostly nocturnal	
	logged:	0.36 (0.27-0.44)		**mostly nocturnal**	
Helarctos malayanus Sun bear	all:	0.45 (0.32-0.54)	logged vs unlogged 0.092 ($p > 0.1$)	cathemeral	logged vs unlogged 0.77 (0.53-0.85)
	unlogged:	0.35 (0.21-0.52)		crepuscular	
	logged:	0.45 (0.29-0.55)		cathemeral	
Sus barbatus Bearded pig	all:	0.47 (0.40-0.54)	logged vs unlogged 0.107 ($p > 0.05$)	cathemeral	logged vs unlogged 0.86 (0.81-0.92)
	unlogged:	0.41 (0.32-0.51)		mostly diurnal	
	logged:	0.52 (0.43-0.58)		mostly diurnal	
Tragulus kanchil Lesser mousedeer	all:	0.30 (0.24-0.36)	logged vs unlogged 0.027 ($p > 0.1$)	**crepuscular**	logged vs unlogged 0.79 (0.73-0.88)
	unlogged:	0.30 (0.21-0.36)		**crepuscular**	
	logged:	0.33 (0.25-0.41)		crepuscular	
Tragulus napu Greater mousedeer	all:	0.37 (0.32-0.43)	logged vs unlogged **0.139 ($p < 0.01$)**	mostly nocturnal	logged vs unlogged 0.89 (0.84-0.94)
	unlogged:	0.35 (0.29-0.43)		mostly nocturnal	
	logged:	0.49 (0.37-0.53)		mostly nocturnal	
*Muntiacus atherodes** Bornean yellow muntjac*	all:	0.42 (0.37-0.47)	logged vs unlogged -0.041 ($p > 0.1$)	cathemeral	logged vs unlogged 0.87 (0.83-0.92)
	unlogged:	0.44 (0.36-0.48)		diurnal	
	logged:	0.40 (0.33-0.47)		cathemeral	
Muntiacus muntjak Red muntjac	all:	0.43 (0.37-0.48)	logged vs unlogged **0.120 ($p < 0.05$)**	cathemeral	logged vs unlogged 0.86 (0.83-0.93)
	unlogged:	0.39 (0.33-0.46)		cathemeral	
	logged:	0.51 (0.38-0.57)		cathemeral	
Rusa unicolor Sambar deer	all:	0.59 (0.39-0.65)	logged vs unlogged 0.116 ($p > 0.1$)	cathemeral	logged vs unlogged 0.77 (0.69-0.94)
	unlogged:	0.50 (0.28-0.65)		cathemeral	
	logged:	0.61 (0.41-0.68)		cathemeral	
Echinosorex gymnura Moonrat	all:	0.32 (0.21-0.39)		strictly nocturnal	
Manis javanica Sunda pangolin	all:	0.21 (0.09-0.36)		strictly nocturnal	

_Presbytis rubicunda_* Maroon langur*	all:	0.25 (0.17-0.31)		**crepuscular**	
	unlogged:	0.25 (0.17-0.31)	logged vs unlogged	**crepuscular**	logged vs unlogged
	logged:	0.22 (0.08-0.35)	-0.030 (p > 0.1)	crepuscular	0.64 (0.51-0.91)
_Presbytis sabana_* Sabah grey langur*	all:	0.33 (0.20-0.43)		**crepuscular**	
Macaca fascicularis Long-tailed macaque	all:	0.35 (0.25-0.46)		mostly diurnal	
	canopy:	0.32 (0.22-0.43)	canopy vs terrestrial	mostly diurnal	canopy vs terrestrial
	terrestrial:	0.34 (0.08-0.39)	-0.021 (p > 0.1)	strictly diurnal	0.63 (0.33-0.86)
Macaca nemestrina Pig-tailed macaque	all:	0.45 (0.38-0.46)		**mostly diurnal**	
	unlogged:	0.44 (0.36-0.45)	logged vs unlogged	**mostly diurnal**	logged vs unlogged
	logged:	0.42 (0.33-0.44)	-0.014 (p > 0.1)	**mostly diurnal**	0.90 (0.84-0.95)
	canopy:	0.28 (0.19-0.37)	canopy vs terrestrial	crepuscular	canopy vs terrestrial
	terrestrial:	0.42 (0.35-0.43)	**-0.14 (p < 0.01)**	mostly diurnal	0.62 (0.48-0.68)
_Hylobates funereus_* Bornean gibbon*	all:	0.23 (0.15-0.35)		mostly diurnal	
	unlogged:	0.24 (0.15-0.35)	logged vs unlogged	mostly diurnal	logged vs unlogged
	logged:	0.24 (0.10-0.37)	-0.003 (p > 0.1)	mostly diurnal	0.74 (0.48-0.93)
_Pongo pygmaeus_* Bornean orangutan*	all:	0.39 (0.26-0.44)		mostly diurnal	
	canopy:	0.37 (0.21-0.41)	canopy vs terrestrial	mostly diurnal	canopy vs terrestrial
	terrestrial:	0.32 (0.16-0.44)	0.058 (p > 0.1)	mostly diurnal	0.68 (0.49-0.89)
Aeromys tephromelas Black flying squirrel	all:	0.40 (0.18-0.44)		mostly nocturnal	
	unlogged:	0.44 (0.17-0.31)	logged vs unlogged	mostly nocturnal	logged vs unlogged
	logged:	0.17 (0.04-0.40)	**-0.275 (p < 0.05)**	mostly nocturnal	0.53 (0.29-0.91)
_Aeromys thomasi_* Thomas' flying squirrel*	all:	0.38 (0.27-0.41)		**mostly nocturnal**	
_Callosciurus adamsi_* Ear-spot squirrel*	all:	0.22 (0.10-0.30)		mostly diurnal	
Callosciurus prevostii Prevost's squirrel	all:	0.28 (0.24-0.32)		mostly diurnal	
	unlogged:	0.35 (0.27-0.41)	logged vs unlogged	mostly diurnal	logged vs unlogged
	logged:	0.22 (0.18-0.27)	**-0.124 (p < 0.01)**	mostly diurnal	0.79 (0.70-0.88)
Petaurista petaurista Red giant flying squirrel	all:	0.31 (0.18-0.40)		mostly nocturnal	
Ratufa affinis Giant squirrel	all:	0.22 (0.17-0.26)		strictly diurnal	
	unlogged:	0.18 (0.12-0.26)	logged vs unlogged	**strictly diurnal**	logged vs unlogged
	logged:	0.32 (0.21-0.38)	**0.145 (p < 0.01)**	**mostly diurnal**	0.76 (0.62-0.90)

*Rheithrosciurus macrotis** Tufted ground squirrel*	all:	0.30 (0.20-0.37)		**mostly diurnal**	
	unlogged:	0.30 (0.20-0.38)	logged vs unlogged	**mostly diurnal**	logged vs unlogged
	logged:	0.30 (0.13-0.36)	0.005 (p > 0.1)	strictly diurnal	0.78 (0.71-1.08)
Sundasciurus hippurus Horse-tailed squirrel	all:	0.14 (0.06-0.24)		**crepuscular**	
	unlogged:	0.09 (0.03-0.11)	logged vs unlogged	crepuscular	logged vs unlogged
	logged:	0.19 (0.06-0.27)	0.095 (p > 0.1)	crepuscular	0.64 (0.33-0.92)
	canopy:	0.04 (0.03-0.05)	canopy vs terrestrial	**crepuscular**	canopy vs terrestrial
	terrestrial:	0.20 (0.06-0.27)	**-0.166 (p < 0.01)**	mostly diurnal	0.16 (-0.002-0.35)
Leopoldamys sabanus Long-tailed giant rat	all:	0.19 (0.06-0.34)		mostly nocturnal	
Maxomys rajah Brown spiny rat	all:	0.40 (0.22-0.42)		strictly nocturnal	
Hystrix brachyura Malay porcupine	all:	0.35 (0.26-0.40)		strictly nocturnal	
	unlogged:	0.41 (0.27-0.42)	logged vs unlogged	**mostly nocturnal**	logged vs unlogged
	logged:	0.30 (0.20-0.35)	**-0.112 (p < 0.05)**	strictly nocturnal	0.76 (0.64-0.90)
*Hystrix crassispinis** Thick-spined porcupine*	all:	0.39 (0.28-0.41)		**mostly nocturnal**	
	unlogged:	0.37 (0.27-0.40)	logged vs unlogged	strictly nocturnal	logged vs unlogged
	logged:	0.31 (0.12-0.45)	-0.058 (p > 0.1)	mostly nocturnal	0.71 (0.54-0.92)
Trichys fasciculata Long-tailed porcupine	all:	0.32 (0.20-0.33)		**mostly nocturnal**	
	unlogged:	0.29 (0.18-0.32)	logged vs unlogged	mostly nocturnal	logged vs unlogged
	logged:	0.31 (0.11-0.37)	0.024 (p > 0.1)	strictly nocturnal	0.60 (0.39-0.86)

Chapter 4 Whole-community conservation: Assessing the value of recovering-logged forests for arboreal and terrestrial mammals

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Keywords: occupancy | arboreal mammal | LiDAR | Circuitscape | forest structure | disturbance effects | logging | community assessment | vertical stratification | 3-dimensional niche

Abstract

Selective logging is pervasive across the tropics, causing significant changes to forest structure that are most noticeable at canopy-level. Many terrestrial (ground-dwelling) species can persist in disturbed areas, yet the effects of logging on arboreal (tree-dwelling) taxa – which comprise a substantial proportion of rainforest communities – remain poorly understood. We describe the first comprehensive assessment of terrestrial and arboreal mammal responses to logging in Southeast Asia, using detection data from camera-traps deployed on the ground and in the canopy of unlogged and recovering-logged rainforests in Malaysian Borneo. Multi-species occupancy models accounted for differences in abundance and detection probability, providing robust estimates of occurrence that we compared across canopy and terrestrial strata and unlogged and recovering-logged forest. Furthermore, an understanding of the specific structural attributes important for species' persistence can shed light on precisely what constitutes valuable versus degraded habitat, helping to inform conservation and management plans. We thus incorporated a suite of remotely-sensed vegetation covariates, including a bespoke measure of canopy connectivity, to quantify the importance of forest structure to mammal communities in both strata. Most arboreal and terrestrial species were able to persist in recovering-logged forest, providing a 'whole community' perspective to the value of disturbed habitats for biodiversity conservation. Canopy connectivity was the only structural covariate retained across unlogged and recovering-logged forest; we demonstrate its importance for arboreal mammals at both site- and landscape-level scales, and suggest that this was the predominant factor underpinning arboreal species' persistence in recovering-logged forest. However, while only 3% of terrestrial mammals substantially declined in occupancy in recovering-logged forest, 21% of arboreal mammals did, highlighting the increased vulnerability of this community. Our findings demonstrate the need to include arboreal taxa in logging impact assessments, as failing to do so risks overlooking declines in species that are often unseen, but ecologically important.

4.1 Introduction

Tropical rainforests are one of the most biodiverse and threatened ecosystems in the world (Barlow *et al.* 2018). Knowledge of how animals use these complex habitats and respond to human disturbances is crucial to guide effective conservation strategies. Yet most studies have focussed on the fauna at ground level (Whitworth *et al.* 2019a), despite tree-dwelling (arboreal) wildlife comprising a substantial proportion of rainforest communities (Kays and Allison 2001; Ellwood and Foster 2004). An improved understanding of arboreal species' occurrence and responses to disturbance could have important implications for the management and restoration of tropical forests.

Habitat structure underpins species diversity (Davies and Asner 2014), determining how animals travel, forage, and avoid predation (Palminteri *et al.* 2012), and, ultimately, whether they can persist in a given area. Human disturbance of tropical forests, for example through selective logging – which targets large, mature trees – leads to an overall structural simplification of the habitat that particularly affects the upper vegetation layers (Deere *et al.* 2020a; Milodowski *et al.* 2021). Consequently, logged forests are characterised by reduced tree height and size, and an increase in the number of canopy gaps, resulting in fewer canopy pathways, fewer environmental niches across the vertical column, and reduced vegetation density at canopy level (Deere *et al.* 2020a). On the forest floor, increased light penetration allows a proliferation of herb and shrub growth (Fauset *et al.* 2017). These effects may be apparent over a decade after logging has ceased, with full canopy recovery expected to take several decades longer (Milodowski *et al.* 2021). Nevertheless, many studies investigating disturbance impacts on wildlife indicate that recovering-logged forests (i.e. those that have been logged in the past, but where logging has since ceased) can retain high species diversity (Putz *et al.* 2012; Chaudhary *et al.* 2016), although forest specialists may be disproportionately affected (Newbold *et al.* 2014), and the quality of the remaining habitat is often important (Wearn *et al.* 2017; Deere *et al.* 2020a).

As a large and taxonomically diverse group, mammals play important functional roles in rainforest ecosystems as seed dispersers, pollinators, and within predator-prey dynamics (Corlett 1998; 2017; Kays and Allison 2001). Many species are also of high conservation concern (IUCN 2022). Arboreal mammals represent a distinct and diverse community in their own right, comprising up to 60% of non-volant taxa (Emmons, Gautier-Hion and Dubost 1983; Malcolm and Lowman 2004), and while many species may be physiologically capable of descending to the ground, the majority do not habitually do so (Whitworth *et al.* 2019a; Moore *et al.* 2020; Haysom *et al.* 2021). The canopy space encompasses a vast and structurally complex three-dimensional area, especially in tall and floristically diverse tropical rainforests

(Dudley and DeVries 1990). Arboreality – the ability to live in or utilise the canopy – is an evolutionary adaptation that provides access to resources unavailable at ground level (Scheffers *et al.* 2017), and facilitates the co-existence of a high diversity of species by allowing niche partitioning along vertical, as well as horizontal, gradients (Oliveira and Scheffers 2018). Staying within the canopy has clear advantages for arboreal mammals, as descending and re-ascending individual trees is energetically more costly than horizontal movement along branches, and incurs an increased risk of predation by terrestrial (i.e. ground-dwelling) predators (Thorpe *et al.* 2007; Makin *et al.* 2012; McLean *et al.* 2016). Thus, arboreal mammals rely on intact canopy architecture; high connectivity at canopy level facilitates lateral movement (e.g. in primates, McLean *et al.* 2016; Davies *et al.* 2017), and is an important determinant of habitat selection for a variety of taxa (e.g. rodents, Wells *et al.* 2004b; Fedyn *et al.* 2021; civets, Mudappa 2006; lemurs Chen *et al.* 2021; gibbons, Hankinson *et al.* 2021).

Logging reduces the interconnectedness and complexity of the canopy environment, disrupting movement pathways, and compacting the available niche space via a reduction in canopy height, which may intensify competition between species that vertically partition resources (e.g. small mammals, Saiful *et al.* 2001; Vieira and Monteiro-Filho 2003; primates, Hanya *et al.* 2020; primates and squirrels, Sushma and Singh 2006). Arboreal mammals may therefore be more sensitive to structural disturbances resulting from logging than their terrestrial counterparts, with structural simplification potentially reducing species diversity in the canopy and/or causing arboreal species to descend more frequently to the ground, and negative implications for energy budgets and predation risk. Indeed, research in Peru found medium- and large-bodied arboreal mammals experienced greater occupancy declines post-logging than terrestrial species (Whitworth *et al.* 2019a), while other studies in Latin America revealed arboreal mammal diversity to be positively associated with measures of habitat quality (Cudney-Valenzuela *et al.* 2021), and strictly arboreal species to be more likely to decline as habitat disturbance increased (Almeida-Maues *et al.* 2022). Yet, detailed studies of how changes to forest structure affect arboreal mammals lag behind those of terrestrial species, largely due to the challenges of accessing the canopy and of quantifying ecologically meaningful measures of forest structure that account for the multidimensional nature of forest ecosystems.

The advent of airborne LiDAR (Light Detection And Ranging) has provided a potential solution to generating the type of structural data much needed for studying habitat-biodiversity relationships in tall tropical forests. LiDAR uses light-emitting sensors to quantify three-dimensional high-resolution images of vegetation and forest structure at landscape scales (Lefsky *et al.* 2002). Combined with biodiversity monitoring data, this approach can help identify the physical features most important for species' persistence in vertical as well as horizontal planes, which is key to our understanding of what constitutes valuable habitat. In Borneo, LiDAR datasets demonstrated that orangutans can persist in logged areas if canopy height and uniformity are maintained (Davies *et al.* 2017). Separately, terrestrial mammals were found to be more prevalent in recovering-logged forests that retained a high degree of structural integrity, although semi-arboreal species (i.e. those that also use the canopy) showed greater sensitivity to degradation that may be linked to their reliance on canopy elements (Deere *et al.* 2020a). LiDAR has begun to be utilised in arboreal research, revealing the dependence of some canopy-dwelling species on the structural attributes typically associated with mature forests (e.g. large, tall trees for red tree voles *Arborimus longicaudus* and northern spotted owls *Strix occidentalis caurina*, Johnston and Moskal 2016; Hagar *et al.* 2020; tree cavities for savanna gliders *Petaurus ariel*, Stobo-Wilson *et al.* 2021). Nevertheless, the potential application of combining species' occurrence data with highly-detailed measures of forest structure throughout the vertical column has yet to be fully attempted for tropical arboreal communities.

Here, we present the first in-depth appraisal of rainforest biodiversity across vertical strata that couples mammal detection data from ground- and canopy-level camera-traps with high-resolution habitat information derived from LiDAR. We utilise 19 covariates to characterise fine-scale forest structure across horizontal and vertical dimensions, and relate these to occupancy estimates of arboreal and terrestrial communities. We further develop a bespoke measure of canopy connectivity, in order to quantify its relevance for arboreal taxa at the landscape scale. With both unlogged and recovering-logged forest represented in our sampling locations, we are able to investigate changes in the arboreal community due to selective logging, and compare these to changes in the community at ground level. Our findings highlight the need to consider the whole community in forest biodiversity assessments, i.e. incorporating species from the forest floor to the upper canopy, to avoid underestimating logging impacts, and inform the development of conservation and management strategies.

4.2 Methods

4.2.1 Study site

The study was based in the rainforests of Borneo, which are the tallest and most structurally complex tropical forests in the world (Dudley and DeVries 1990; Shenkin *et al.* 2019; Ehbrecht *et al.* 2021), and support high levels of biodiversity. The island is home to 135 species of non-volant mammal, over half of which are arboreal or semi-arboreal (Payne and

Francis 2007). Although pristine areas are retained, at least 45% of Borneo's rainforests have undergone at least one round of logging (Gaveau *et al.* 2016), making this an ideal system in which to investigate the impacts of logging on arboreal wildlife. Additionally, LiDAR-derived vegetation covariates have been mapped across large areas of Sabah, Borneo's northernmost state (Milodowski *et al.* 2021), allowing the integration of mammal detection data and detailed measures of forest structure.

Research took place in and around the Stability of Altered Forest Ecosystems Project (Ewers *et al.* 2011) in Sabah. Fieldwork was undertaken in unlogged forest at Maliau Basin Conservation Area, and recovering-logged forest in the Mt. Louisa Forest Reserve, which experienced multiple rounds of selective logging between 1978 and 2008 but has since been protected. Sampling locations in both areas covered comparable elevations (mean 482 m, range 225-933 m). The landscape was monitored via an airborne LiDAR campaign in 2014, conducted by the Natural Environment Research Council's Airborne Research Facility (Milodowski *et al.* 2021).

4.2.2 Biodiversity monitoring

Camera-trapping is well-established as an effective sampling method for terrestrial mammals (Tobler *et al.* 2015) and has recently been extended to the canopy, with a high degree of success in detecting arboreal species across the tropics (e.g. Bowler *et al.* 2017; Moore *et al.* 2020; Haysom *et al.* 2021). We deployed camera-traps (Hyperfire HC500, Reconyx, WI, USA) at 50 locations between October 2017 and September 2019 following methods outlined in Haysom *et al.* (2021). Locations were divided equally between unlogged and recovering-logged forest (mean distance between locations: 1.26 km; range: 0.5-4.0 km). Each location comprised one terrestrial camera-trap set approximately 0.3 m above the ground, paired with either one or two canopy camera-traps, set at heights of 9.8-52.3 m above the ground (mean = 25.9 m) (total = 120 camera-traps: 50 terrestrial, 70 canopy). For locations with two canopy camera-traps, the second was set at a different height (mean difference 3.6 m, range 0.5-9.0 m) and facing a different focal branch. Focal trees were selected based on safety considerations for climbing, and were located within 10 m of the terrestrial camera-trap. We did not target any particular habitat feature, e.g. trails at ground level, or particular tree species, height or branch architecture type in the canopy.

4.2.3 Vegetation Structure

We defined 19 vegetation covariates to test associations with mammal detection data; 16 of which were LiDAR-derived, and three measured in the field (Supplementary Materials Table

S4.2). We used R packages rgdal, sf, rgeos, plyr, and raster (R version 4.0.3) to extract values for each covariate at each camera-trap location, at specified spatial scales (see Section 2.4.1). Our aims were to: (i) quantify precisely how forest structure changes between unlogged and recovering-logged areas and; (ii) test for associations between forest structure covariates and community occupancy of arboreal and terrestrial mammals.

Remotely-sensed covariates. To quantify forest structure in the vicinity of our sampling locations, we developed a canopy height model and three-dimensional plant area distributions for our study sites from LiDAR-derived data. LiDAR surveys used a Leica ALS50-II sensor attached to a light aircraft, flown in multiple transects over the target landscape at a height of 1.4-2.4 km above sea level and a velocity of 120-240 knots. The sensor emits a laser pulse, and evaluates the time elapsed between transmission and reflection to quantify the distances to target features, returning a data point-cloud (density: 25-50 points m^{-2}). Point-cloud data were then processed, and the following structural covariates were extracted around camera locations: vegetation density, uniformity, and distribution in the vertical column, amount of vegetation matter, number of environmental niches, and number of contiguous canopy layers in the vertical column, and canopy height. We further developed covariates for elevation, aboveground biomass (a proxy for forest maturity), terrain ruggedness, variability in canopy height (the latter three derived from LiDAR values of aboveground carbon density, elevation, and canopy height, respectively), and canopy connectivity (Supplementary Materials Table S4.2). For a full description of LiDAR protocols, see Milodowski *et al.* (2021).

The high-resolution of the LiDAR point cloud allows vegetation within the vertical column to be visualised within specified height layers. We defined 10 m as the minimum scale to do this since vertical niche separation in small-bodied arboreal mammals has been identified across heights of this distance (Vieira and Monteiro-Filho 2003; Nakagawa *et al.* 2007). Values were extracted for the total amount of vegetation matter within the entire vertical column, and separately for vegetation within each 10 m vertical slice (i.e. 2-10 m, 10-20 m, 20-30 m, 30-40 m, 40-50 m, 50-60 m). This allowed us to generate covariates for vegetation matter and connectivity (as connectivity values derived from vegetation matter values, see below) for the specific height layer in which a given camera was deployed (‘height-calibrated covariates’), as well as the overall value across the vertical column. For height-calibrated covariates, we tested ‘HC1’, which selected the value for the height layer in which the camera-trap was set, and ‘HC2’, which took an average of values for the height layer in which the camera-trap was set, the layer above and the layer below. Given that the height of Borneo’s rainforests is commonly 45-60 m, with emergent trees exceeding 70 m (Dudley and DeVries 1990), and the possibility that arboreal species may preferentially use particular heights as a method of niche separation (e.g. Saiful *et al.* 2001; Nakagawa *et al.* 2007; Hanya *et al.* 2020), our height-calibrated covariates were designed to provide an accurate representation of vegetation matter and connectivity relevant to the immediate placement of the camera-trap.

Canopy connectivity. We integrated LiDAR outputs with electronic circuit theory and random walk modelling, using the open-source Circuitscape programme (McRae *et al.* 2013), to develop novel metrics that specifically describe canopy connectivity. Circuit theory accounts for the possibility of multiple pathways for movement in all directions across a landscape, as opposed to methods that define one path of least resistance. Thus, landscapes are visualised as conductive surfaces, with pixels assigned conductance values that represent ease or difficulty of movement. The approach is typically applied to model landscape or genetic connectivity between populations or habitat patches (Phillips *et al.* 2021) but, to date, has not been employed to model the structural connectivity of canopy vegetation.

We utilised LiDAR-derived values of vegetation matter throughout the vertical column to represent ease of movement across the landscape (i.e. 'conductance'). As LiDAR values account for all vegetation matter, including trunks, branches, stems, vines, and leaves, we assumed that higher vegetation matter values reflect more movement pathways at canopy level, and therefore greater canopy connectivity. Throughout, conductance values are relative, i.e. a negative value does not necessarily indicate low conductance; rather, the meaning of the value is dependent on the context of all other values for all other sites. To quantify connectivity relative to vegetation density, we calculated pairwise current flow between nodes (i.e. the points at which the theoretical current is injected) and derived conductance values using the Circuitscape algorithm (McRae *et al.* 2013). To define focal nodes, we used a point-based omnidirectional connectivity method appropriate for modelling multispecies connectivity across large landscapes (Phillips *et al.* 2021). This method models conductance in all directions between nodes placed around the outer edge of a sampling area. We placed 25 nodes at regularly spaced intervals across a minimum convex hull around our sampling points, extended using a 1 km buffer to avoid boundary effects (e.g. Figure 4.1). Conductance values were extracted for each camera-trap location, providing bespoke canopy connectivity covariates: (i) across the entire vertical column ('overall connectivity') and; (ii) specific to the height layer of each camera-trap ('height-calibrated connectivity').

Field-measured connectivity. To ground-truth remotely-sensed approximations of canopy connectivity, we also quantified a fine-scale, field-derived measure representing the number of connections of the focal branch (i.e. the branch along which the canopy camera-trap faced). One connection was defined as one point where the focal branch touches a branch, trunk or vine of an adjacent tree ('adjacent connection'); or another branch or vine in the focal tree ('focal connection').

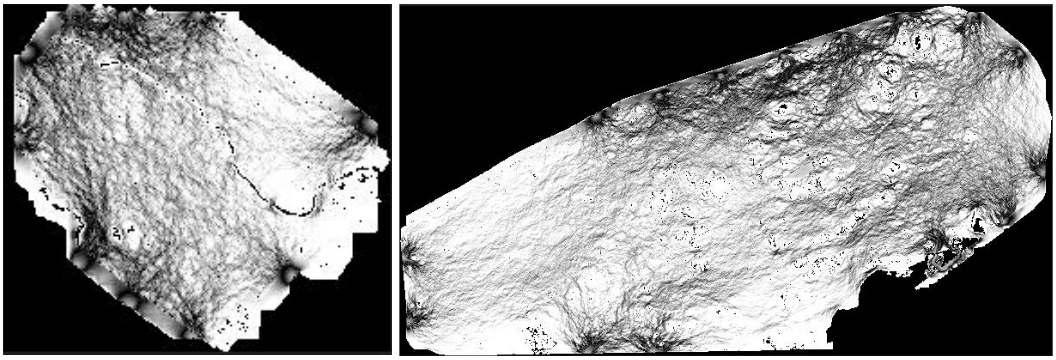


Figure 4.1 Characterisation of overall canopy connectivity using circuit theory modelling for unlogged (left) and recovering-logged (right) forest sampling areas. Current injection nodes can be seen as dark circular areas with white centres around the perimeter. Areas of high conductance (=connectivity) are represented by darker shading, visualising the network of likely canopy pathways based on LiDAR-derived vegetation density data.

4.2.4 Modelling species' habitat use

We constructed species-specific detection histories by pooling data from each camera-trap into seven-day sampling occasions, which were summarised across locations and species. Each of our 50 sampling locations comprised one terrestrial camera, and one or two cameras in the canopy. To minimise pseudoreplication, detection data were pooled for trees with two canopy camera-traps. Camera-traps that were not operational for a minimum sampling period of 14 days were excluded from analysis (N=3), resulting in 47 terrestrial locations (comprising a total 6,643 camera-trap nights (hereafter, CTN): 3,995 in unlogged forest, 2,648 in recovering-logged forest), and 50 canopy locations (10,565 CTN: 6,944 in unlogged forest, 3,621 in recovering-logged). Of 57 mammal species detected, we excluded five (two terrestrial, two arboreal, one semi-arboreal) with ≤ 3 independent detections as differences in occupancy and detection cannot be reliably uncoupled when detection data are sparse (Brodie *et al.* 2014b). We further grouped four small-bodied flying squirrel species that had ≤ 2 independent detections each, into one species group, thereby retaining 49 species for analysis (Supplementary Materials Table S4.1).

We estimated mammal occurrence using hierarchical Royle-Nichols multispecies occupancy models, specified within a Bayesian framework (Royle and Nichols 2003). Hierarchical models separate the ecological processes underpinning the state variable (i.e. species occurrence), from the observation processes describing the sampling procedure (i.e. given that a species is present at a location, it will be detected), allowing true absence to be distinguished from non-detection. Moreover, this modelling framework explicitly accounts for abundance-induced heterogeneity in detection rates, and additional sources of bias relating to the non-random movement of animals (Tobler *et al.* 2015).

We constructed independent models for the arboreal and terrestrial communities to account for differences in life history traits (adaptations to climbing vs. walking), and in the time needed to achieve sampling completeness using camera-traps (Haysom *et al.* 2021). Detections of semi-arboreal species (those recorded in both strata) were divided according to strata, so that only detections of these species from canopy camera-traps were included in arboreal models, and only detections from terrestrial camera-traps were included in terrestrial models. To accommodate multi-year data collected over multiple sampling seasons and account for the longer sampling periods necessary for arboreal species within a coherent modelling framework, we implemented a stacked design, where sampling locations across different years were treated as unique locations and a random effect for season was added to account for temporal dependencies. Within this framework, we initially modelled the abundance of species *i* at site *j* (λij) within either the arboreal or the terrestrial community as a function of the structural environment:

Arboreal and terrestrial:

$$\log\left(\lambda_{ij}\right) = \beta_0(Season_j)_i + \beta_{1i} Structural\ Covariate_j + \gamma(ForestType_j)_i + \delta(Tree_j)_i$$

and detection of species *i* at site *j* (p_{ij}) as a linear combination of arboreal or terrestrial-specific covariates considered to influence the likelihood of encountering a species given it occupies the area in the immediate vicinity of the sampling location:

Arboreal:

$$logit(p_{ij}) = \alpha_0(Season_j)_i + \alpha_{1i} sampling\ period_j + \alpha_{2i} cameratrap\ height_j + \alpha_{3i} vegetation\ density_j$$

Terrestrial:

$$logit(p_{ij}) = \alpha_0(Season_j)_i + \alpha_{1i} sampling\ period_j + \alpha_{2i} vegetation\ density_j$$

Abundance and detection were modelled on the log and logit scales respectively, with species-specific slopes and intercepts. Species effects were drawn as realisations from a common distribution, described by estimable hyperparameters that indicate community-level responses to covariates. This framework improves estimation precision, particularly for rare or elusive species encountered infrequently during sampling (Pacifici *et al.* 2014). We specified additional random effects structures on the abundance component of the model to account for broad habitat classifications (*ForestType:* unlogged versus recovering-logged forest) and non-independence induced by multiple camera deployments in the same tree

(*Tree*). Throughout, we derive occupancy of species *i* at site *j* (ψ_{ij}) as a deterministic function of abundance using the equation: $\psi_{ij} = 1 - \exp(-\lambda_{ij})$.

We tested 19 occupancy covariates: 18 in arboreal models, and 12 in terrestrial models (Supplementary Materials Table S4.2). We excluded terrain ruggedness from arboreal models as this specifically relates to the evenness or unevenness of the ground surface so is not relevant for arboreal species. Likewise, height-calibrated covariates of vegetation matter and connectivity, the number of adjacent and focal connections to the focal branch, and camera-trap height were excluded from terrestrial models as they are not relevant to ground-dwelling species. Due to high levels of multi-collinearity between structural covariates ($|r| > 0.7$; VIF > 5), we ran single covariate models while keeping forest type (i.e. unlogged or recovering-logged forest), season and site terms constant. Detection covariates were kept constant to control for factors that may influence the detectability of species in either stratum. In terrestrial and arboreal models, we controlled for sampling period, which can affect the likelihood of rare or patchily-distributed species being detected, and overall amount of vegetation matter, which can indicate visual obstruction in front of the camera-trap. In arboreal models, we additionally controlled for camera-trap height, which may affect detectability of species preferentially using the lower, mid- or upper canopy. All detection covariates were tested at the 50 m spatial scale, as this is the smallest scale compatible with our model and is most relevant to the detection zone around the camera-trap. All covariates were standardised prior to modelling to ensure comparability and improve model convergence.

Spatial scale optimisation. To avoid overlooking key associations, habitat covariates need to be defined at spatial scales that are relevant to the study species. However, the spatial ecology of many species is not known (Niedballa *et al.* 2015). We therefore extracted the data for each at three spatial scales (circular buffer around the camera-trap with radii: 100 m, 250 m, and 500 m) in both terrestrial and arboreal models. We additionally tested each covariate at 50 m in the arboreal model, as initial tests suggested this may be most relevant to arboreal species. For each covariate, we selected the most appropriate spatial scale by comparing model performance using WAIC (Watanabe-Akaike Information Criterion, Watanabe 2010), a relative measure of model predictive power, with lower values denoting better statistical support. We also assessed which scales species were generally most responsive to, as indicated by whether the covariate had a substantial association with mammal occupancy at the community level (demonstrated by 2.5th and 97.5th percentiles of the posterior distribution [95% BCI] not overlapping zero) (Supplementary Materials Table S4.3). Where a covariate was strongly associated with community occupancy at more than one spatial scale, we selected the scale with substantial associations for the greatest number of individual species.

Final model selection. All covariates showing substantial associations with occupancy at the community level (*N*=8 for terrestrial species; *N*=6 for arboreal species, Supplementary Materials Table S4.2) were compared using delta WAIC values (Supplementary Materials Table S4.3) in order to select the top-performing model for the terrestrial and arboreal communities separately. While field-measured adjacent connections had the overall strongest association for arboreal species according to WAIC values, we selected the top-performing LiDAR-derived covariate in order to be comparable with terrestrial models. Throughout, we present findings from the top-performing canopy and terrestrial models.

Model specification and predictive performance. All models were run using JAGS version 4.3.0 via the jagsUI package in R version 4.0.3. We specified three Markov chains per parameter, each consisting of 150,000 iterations, thinned at a rate of 100 following a burn-in period of 50,000. We inspected parameter convergence visually via trace plots to confirm adequate mixing, and numerically using the Gelman-Rubin statistic, where values <1.1 indicate convergence. Model fit was assessed using Bayesian *P* values, which were summarised by species for each model. Bayesian *P* values of 0.5 indicate perfect model fit, while values <0.05 or >0.95 suggest poor model fit. For both arboreal and terrestrial communities, and all individual species, model fit was within acceptable thresholds (Supplementary Materials Tables S4.2, S4.4). Throughout, we consider substantial statistical support for species responses to covariates if the 95% BCI for the associated parameter did not overlap zero, and moderate statistical support if the 75% BCI (12.5th and 87.5th percentiles of the posterior distribution) did not overlap zero.

4.3 Results

We recorded 3,559 detections of 57 mammal species from all camera-traps across vertical strata in unlogged and recovering-logged forest. Of these, 3,550 detections of 49 mammal species were retained for analysis (Supplementary Materials Table S4.1). As our occupancy models require species' detection histories to be constructed by pooling data for each species from each camera-trap location into seven-day sampling occasions, here, detection totals refer to the number of sampling occasions per camera-trap location at which a species was recorded. For example, if a bearded pig was detected at location [x] five times during sampling occasion one, one time during sampling occasion two, and nine times during sampling occasion three, this would total three detections.

Of the 49 species retained for analyses, 14 were detected exclusively on canopy-camera-traps ('strictly arboreal'), 29 exclusively on camera-traps at ground-level ('strictly terrestrial'), and six on camera-traps in both strata ('semi-arboreal'). As semi-arboreal species appeared on both canopy and terrestrial camera-traps, they were included in both arboreal and terrestrial models, but with only the detections deriving from canopy camera-traps included in arboreal models, and only those deriving from terrestrial camera-traps in terrestrial models. Thus, arboreal models, and references hereafter to 'arboreal species' or 'the arboreal community', encompass 20 mammal species overall (14 strictly arboreal + canopy detections of six semi-arboreal), and terrestrial models, and references hereafter to 'terrestrial species' or 'the terrestrial community', encompass 35 species overall (29 strictly terrestrial + terrestrial detections of six semi-arboreal).

4.3.1 Community occupancy and detection probability

We recorded 2,816 mammal detections on terrestrial camera-traps and 734 detections on cameras in the canopy. Mean occupancy of the terrestrial mammal community was almost four times higher than that of the arboreal mammal community, although the overlap of Bayesian Credible Intervals (BCI) suggests these differences are not substantial (terrestrial mean occupancy 0.29, 95% BCI 0.15 – 0.53; arboreal mean occupancy 0.08, 95% BCI 0.02 – 0.42) (Table 4.1). Overall mean detection probability was very similar for arboreal (0.04, 95% BCI = 0.02 – 0.06) and terrestrial mammal communities (0.04, 0.02 – 0.05). Camera-trap height had no effect on the detection probability of arboreal mammals, vegetation matter in the vertical column had a weakly positive relationship with the arboreal community, but a strongly negative relationship with the terrestrial community, and sampling period had a slight positive relationship with detection probability in both communities (Table 4.1).

4.3.2 Vegetation structure

Unlogged forest was characterised by higher values of covariates linked with greater habitat quality - i.e. taller canopies, with vegetation distributed towards the top of the canopy rather than the ground; more vegetation matter and greater variation in vegetation density throughout the vertical column; giving rise to a greater number of environmental niches; and greater aboveground biomass (a proxy for the structural integrity associated with mature forest, i.e. more, and larger trees). In contrast, recovering-logged forest was associated with lower habitat quality values with the exception of canopy connectivity, which was largely retained in recovering-logged forest, with values for both height-calibrated connectivity and overall connectivity throughout the vertical column showing similar levels to those of unlogged forest, although with less variation in recovering-logged locations (Figure 4.2).

Table 4.1 Occupancy and detection probability of arboreal and terrestrial communities, showing overall estimates, and how these changed in recovering-logged forest, and including model fit (values between 0.05-0.95 indicate acceptable fit). Community responses to covariates are summarised for the top-performing canopy model (height-calibrated connectivity) and terrestrial model (canopy height). Symbols + or – indicate a substantially positive or negative community response (95% BCI), respectively; (+) or (–) indicate the direction of weak responses, and na indicates that covariate was not tested in that model.

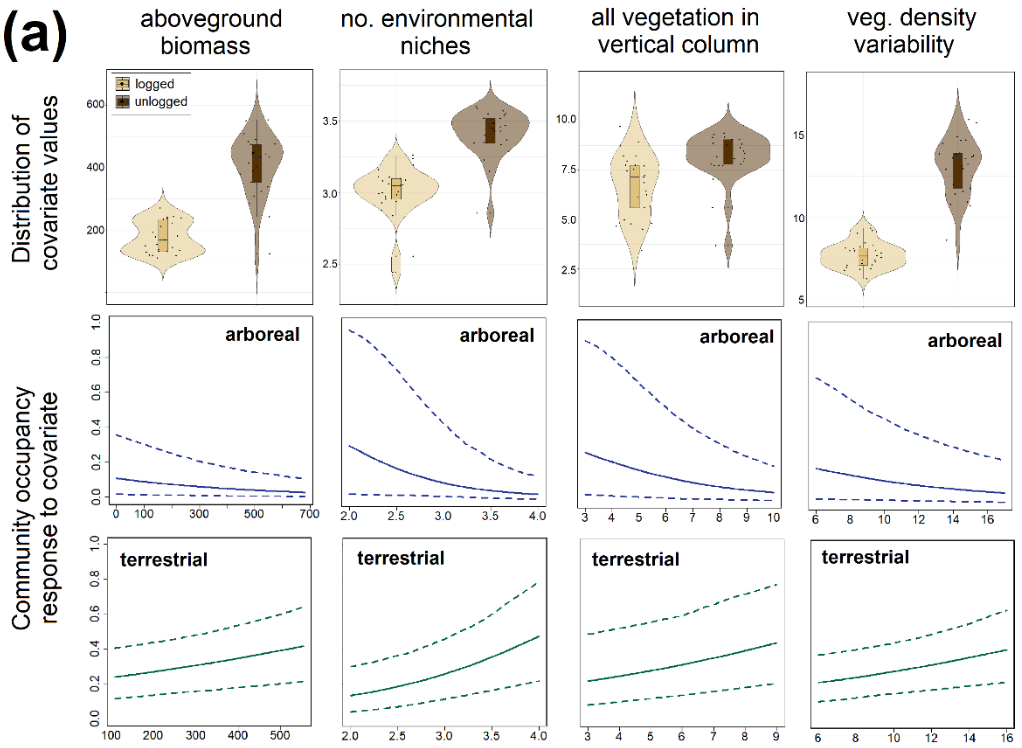
	arboreal	**terrestrial**
community occupancy		
overall mean:	0.08	0.29
2.5th and 97.5th percentiles:	0.02 – 0.42	0.15 – 0.53
change in recovering-logged forest mean:	0.00	0.03
2.5th and 97.5th percentiles:	-0.10 – 0.10	-0.14 – 0.21
community detection probability		
overall mean:	0.04	0.04
2.5th and 97.5th percentiles:	0.02 – 0.06	0.02 – 0.05
change in recovering-logged forest mean:	-0.003	0.002
2.5th and 97.5th percentiles:	-0.00003 – 0.003	0.001 – 0.004
model fit (Bayesian p-value)	0.18	0.26
community response to covariates		
occupancy		
height-calibrated connectivity:	+	na
canopy height:	na	+
detection probability		
sampling period:	(+)	(+)
vegetation matter:	(+)	**–**
camera-trap height:	(–)	na

4.3.3 Occupancy changes in recovering-logged forest

Community. Overall mean community occupancy did not change for arboreal mammals in recovering-logged forest (mean across species 0.004, 95% BCI -0.10 – 0.10), and increased slightly for terrestrial mammals (0.03, -0.14 – 0.21) (Table 4.1, Supplementary Materials Table S4.1). Detection probability did not change in recovering-logged forest compared to unlogged forest for either arboreal (mean across species -0.003, 95% BCI -0.00003-0.003) or terrestrial mammals (for both communities: mean across species 0.002, 95% BCI 0.001-0.004) (Table 4.1). Three species (two strictly terrestrial: red spiny rat *Maxomys surifer*, brown spiny rat *Maxomys rajah*, and one semi-arboreal: orangutan *Pongo pygmaeus*) were excluded from these calculations as they occur exclusively at either our unlogged or recovering-logged forest sampling areas, leaving 19 arboreal species and 32 terrestrial species.

Terrestrial. Of 32 terrestrial species, one (3%) showed a substantial decrease in occupancy in recovering-logged forest (Sunda clouded leopard *Neofelis diardi*), and eight (25%) showed increased occupancy (five substantially increased: lesser mousedeer *Tragulus kanchil*, sambar deer *Rusa unicolor*, Bornean yellow muntjac *Muntiacus atherodes*, red muntjac *Muntiacus muntjak*, bearded pig *Sus barbatus*; and three moderately: sun bear *Helarctos malayanus*, Malay civet *Viverra tangalunga*, banteng *Bos javanicus*). For the remainder, 10 species (31%) showed slight decreases, seven (22%) slight increases, and six (19%) showed no change between unlogged and recovering-logged forest (Figure 4.3, Supplementary Materials Table S4.1).

Arboreal. Of 19 arboreal species, four (21%) exhibited substantial declines in occupancy in recovering-logged forest (long-tailed macaque *Macaca fascicularis*, Sabah grey langur *Presbytis sabana*, Thomas' flying squirrel *Aeromys thomasi* and red giant flying squirrel *Petaurista petaurista*). A further four species (21%) showed increases in recovering-logged forest (two substantial: ear-spot squirrel *Callosciurus adamsi* and pig-tailed macaque *Macaca nemestrina*; two moderate: Prevost's squirrel *Callosciurus prevostii* and small-toothed palm civet *Arctogalidia trivirgata*). Of the remainder, one species (5%) showed a slight occupancy decrease, four (21%) a slight increase, and six (32%) did not change (Figure 4.3, Supplementary Materials Table S4.1).



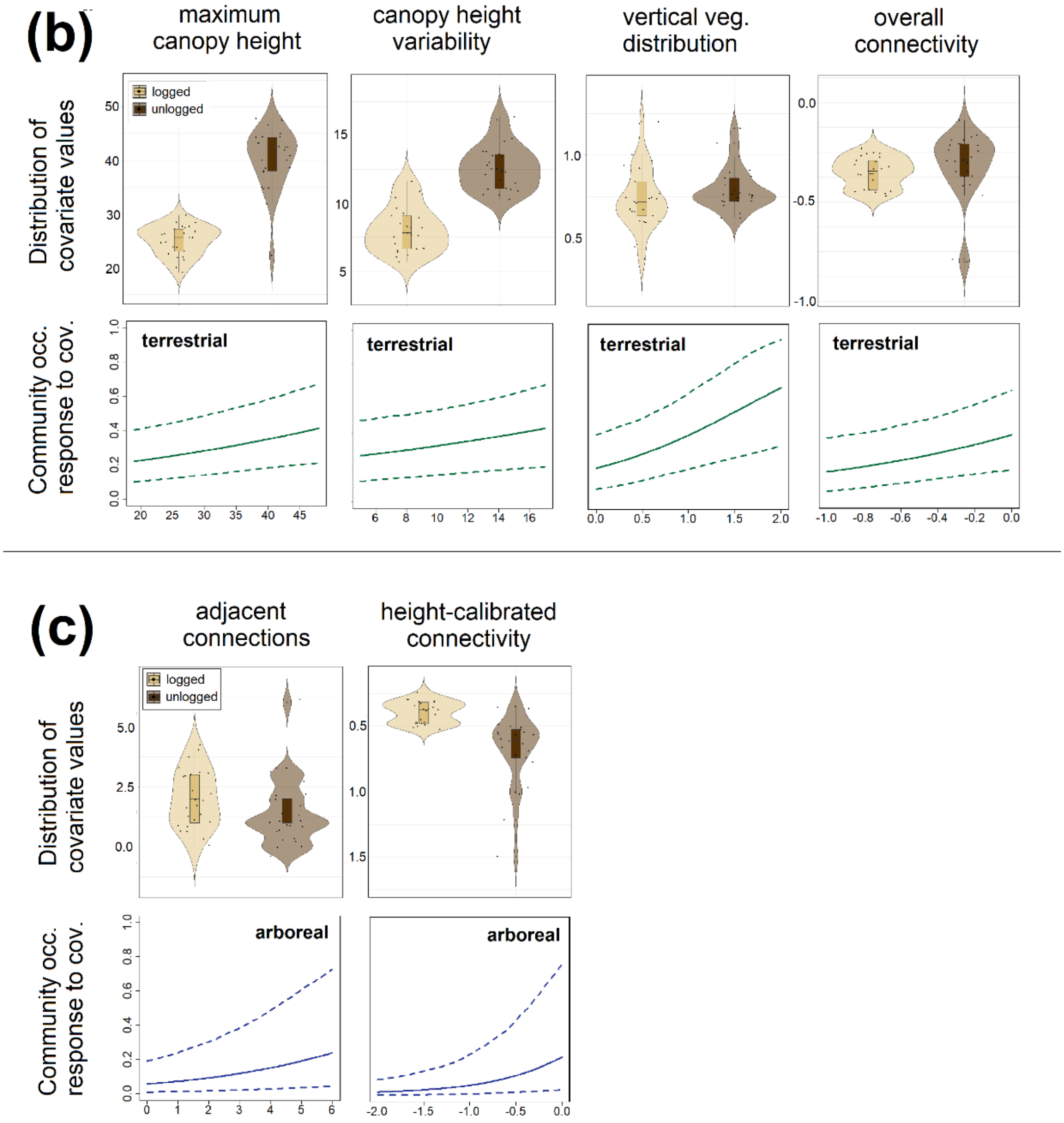


Figure 4.2 The distribution of values for vegetation covariates that had a substantial (95% BCI) association with mammal community occupancy for (a) both arboreal and terrestrial communities; (b) the terrestrial community only; (c) the arboreal community only (see also Supplementary Materials Table S4.2). Violin plots show covariate values in unlogged forest (dark brown) and recovering-logged forest (pale brown). Community occupancy responses to each covariate are below the relevant violin plot, and show mean community response (solid line) and 95% BCI (dashed lines) for arboreal (blue) and terrestrial (green) communities (also labelled within plots). Note that covariate values (y axes of violin plots) are relative rather than absolute, i.e. the meaning of the value is dependent on the context of all other values, except for maximum canopy height (panel b), which is measured by LiDAR in metres above ground level and adjacent connections (panel c), which were counted in the field.

4.3.4 Response to covariates

Terrestrial and arboreal mammal communities were both sensitive to changes in the structural environment, although responses were notably different between communities in each stratum (Figures 4.2, 4.5, Supplementary Materials Tables S4.1, S4.2). Terrestrial mammals, in line with expectations (e.g. Deere *et al.* 2020a), showed positive associations with forest quality covariates, most strongly to increased canopy height. Terrestrial occupancy increased in areas with taller, larger trees, where vegetation density was concentrated towards tree crowns, and with greater structural integrity – indicated by vegetation matter, number of niches, and overall connectivity – throughout the vertical column. Arboreal mammals had substantially higher occupancy in well-connected trees and in areas retaining high levels of canopy connectivity. However, this community had negative relationships to all other covariates of habitat quality, with decreased occupancy in areas that had taller canopies, greater amounts of vegetation matter within the vertical column, and greater availability of environmental niches.

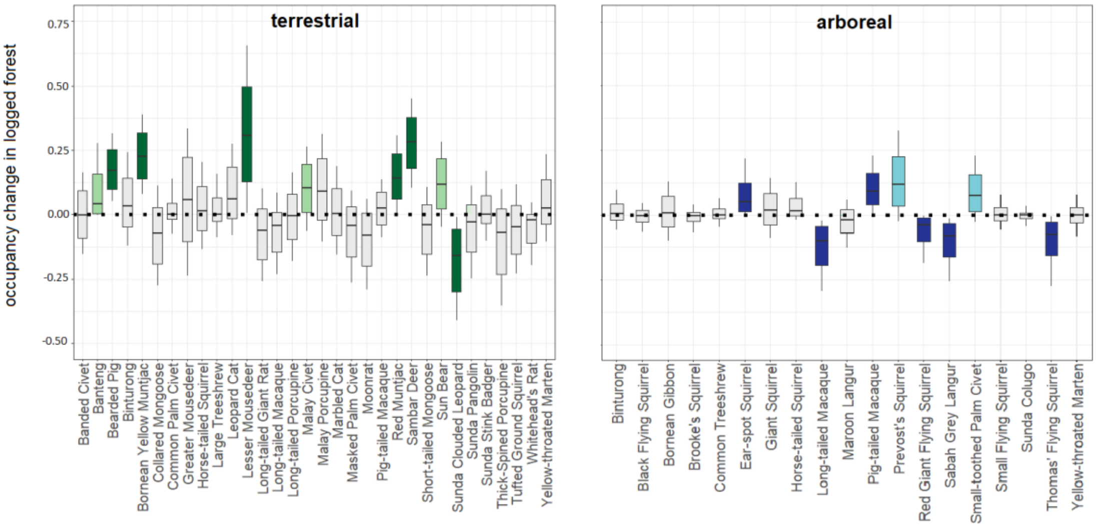
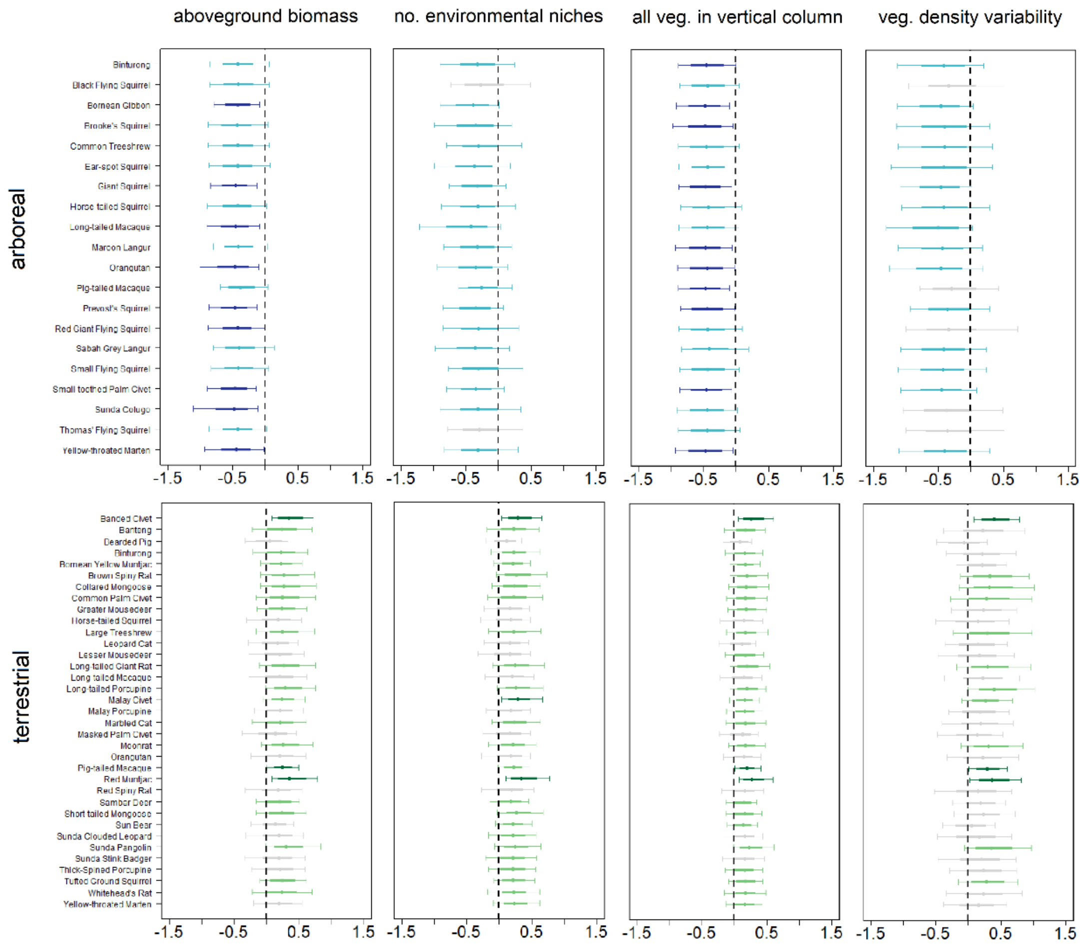


Figure 4.3 Relative changes in occupancy in recovering-logged forest for terrestrial (left panel) and arboreal (right panel) species. Occupancy increases or decreases are shown by median lines (central black line of each box plot) above or below zero, respectively. Whiskers show the 2.5th and 97.5th Bayesian credible intervals (BCI). Substantial changes (BCI 95%) are indicated where whiskers do not cross the zero line, and by dark highlighting of boxes (green for terrestrial species, blue for arboreal species). Moderate changes (BCI 75%) are highlighted pale green or blue, for terrestrial or arboreal species, respectively, and weak responses are shown in grey.

Figure 4.4 Arboreal mammals with substantial (BCI 95%) occupancy declines in recovering-logged forest. From top left, clockwise: red giant flying squirrel *P. petaurista*, Thomas' flying squirrel *A. thomasi*, long-tailed macaque *M. fascicularis*, Sabah grey langur *P. sabana*.



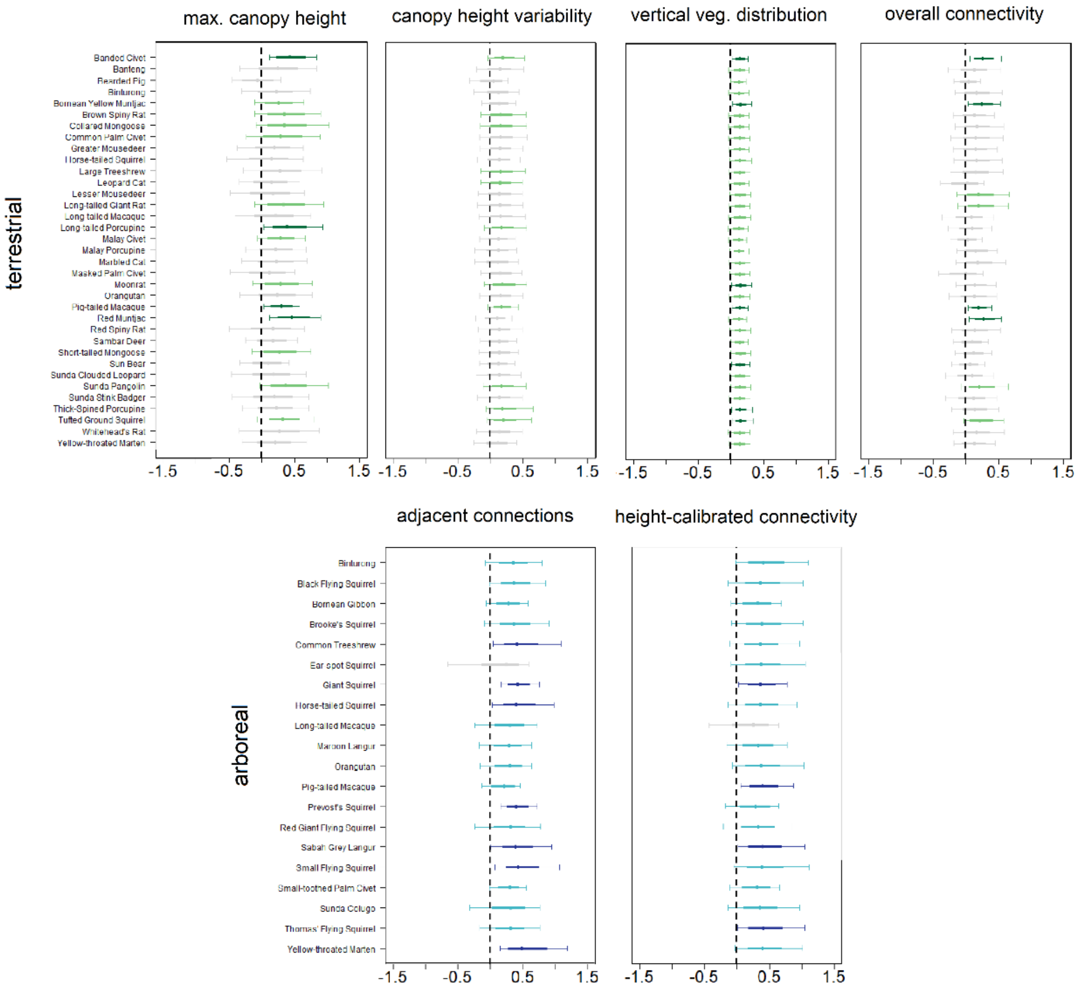


Figure 4.5 Caterpillar plots showing arboreal (blue) and terrestrial (green) species' responses to vegetation covariates, with substantial (BCI 95%) responses in dark colours, moderate (BCI 75%) responses in light colours, and weak responses in grey. The top two panels show covariates substantially associated with occupancy for both arboreal and terrestrial mammals, the middle panel shows covariates with substantial associations for terrestrial mammals only, the bottom panel shows those with substantial associations for arboreal mammals only. Positive and negative responses are indicated by values to the right or left of the zero line (dashed black), respectively.

4.4 Discussion

We provide the first evaluation of how an arboreal mammal community responds to habitat disturbance by coupling occupancy analyses with high-resolution LiDAR data. Combining field-measures with our novel application of connectivity modelling demonstrates that arboreal mammals rely upon canopy connections at both local and landscape scales. We extend the findings of terrestrial research by highlighting the value of recovering-logged forests for tropical mammals across vertical strata (i.e. from ground to canopy). However, we draw attention to the increased vulnerability of some arboreal species, with primates and gliding mammals at particular risk. Our results highlight that, although arboreal and terrestrial communities inhabit the same forest environment, there are clear structural differences between canopy- and ground-level niches that should be explicitly accounted for in order to gain more complete insights into wildlife responses to disturbance, understanding of which ultimately underpins effective forest management.

The importance of connectivity

Arboreal community occupancy estimates were positively associated with both field-measured and LiDAR-derived connectivity metrics (Figure 4.2, Figure 4.5, Supplementary Materials Table S4.2), clearly demonstrating the importance of canopy continuity for arboreal mammals at both local- and landscape-level scales. This relationship was mirrored for individual species, with the occupancy of all arboreal taxa increasing together with connectivity values (Figure 4.5). Well-connected canopies allow arboreal animals to move around at height without incurring the energetic cost and increased predation risk of descending to ground level (McLean *et al.* 2016). Even gliding mammals such as flying squirrels likely benefit from canopy connectivity, as the energetic advantages of gliding increase with glide distance, particularly for larger-bodies species (Dial 2003), and so the ability to move along canopy pathways is still energetically advantageous when travelling across short distances, e.g. between closely-spaced feeding trees. Other studies have described positive associations between site-level connectivity and occupancy of arboreal assemblages (e.g. Whitworth *et al.* 2019a; Chen *et al.* 2021; Hankinson *et al.* 2021). Furthermore, the frequent use of artificial canopy bridges by a wide range of species in fragmented forests (e.g. Chan *et al.* 2020; Nekaris *et al.* 2020), points to the importance of interconnected canopies for non-volant arboreal wildlife. We provide the first demonstration that canopy connectivity can be quantified over wide areas via remotely-sensed technology in a way that retains details relevant to biodiversity sampling at the scale of an individual site, thereby providing evidence that canopy continuity is equally crucial for arboreal communities at the landscape-scale.

Further, the ability of LiDAR to quantify vegetation values in specified height layers demonstrated that arboreal mammals respond to structural differences within the vertical column itself. Of our bespoke connectivity covariates, neither overall connectivity throughout the vertical column nor ‘HC2’ (an average value across three height layers) were associated with arboreal mammal occupancy (Supplementary Materials Table S4.2). In contrast, ‘HC1’ (the value for the same height layer as the camera-trap) had a substantial positive association with both community and species-level occupancy (Figures 4.2, 4.5), highlighting the variability and complexity of the canopy space even across vertical distances as small as 10 metres, and the relevance of these fine-scale changes for canopy-dwelling wildlife.

The value of recovering-logged forest

At the community-level, mean occupancy did not change substantially in recovering-logged forest for arboreal or terrestrial mammals (Table 4.1). This corroborates previous studies that show terrestrial biodiversity is often retained in recovering-logged forests in Borneo (e.g. Brodie *et al.* 2014b; Granados *et al.* 2016; Wearn *et al.* 2017; Maiwald, Mohd-Azlan, and Brodie 2021), and provides a meaningful extension by including, for the first time across Southeast Asia, the arboreal community. Terrestrial-only sampling may fail to detect important changes in arboreal assemblages (Almeida-Maues *et al.* 2022), and it has been suggested that high apparent terrestrial diversity in logged forests may be partly due to semi-arboreal species descending more frequently to the ground (e.g. Berry *et al.* 2010). However, to date this has been largely speculative, as detections of semi-arboreal species derived from terrestrial-only surveys have no canopy-level equivalent with which to draw comparisons. Here, we show that recovering-logged forest is indeed valuable habitat for both terrestrial and arboreal mammals, and that terrestrial assemblages are not artificially inflated by ground-level detections of canopy species (i.e. no semi-arboreal mammals showed substantial increases in ground-level occupancy in recovering-logged forest, and no arboreal species were detected on the ground in this habitat, Supplementary Materials Table S4.1). This is particularly encouraging in the context of Borneo, where almost half of lowland rainforests have already been logged (Gaveau *et al.* 2016), and where the arboreal fauna is highly diverse (Payne and Francis 2007). Furthermore, our vegetation analyses help to explain the persistence of arboreal mammals in recovering-logged forest, as we demonstrate that connectivity is by far the most important predictor of mammal occupancy at canopy-level, and that this structural feature was retained in recovering-logged forest (Figures 4.2, 4.5, Supplementary Materials Table S4.3).

Although overall community occupancy did not change between unlogged and recovering-logged forest (Table 4.1), at the species level, arboreal mammals were more likely to undergo post-logging declines than those on the ground (Figure 4.3, Supplementary Materials Table S4.1). This trend was driven by substantial decreases in occupancy in two of five primates and two of three large-bodied flying squirrels in recovering-logged forest (Figure 4.3), which contrasts with substantial increases in this habitat of most terrestrial ungulates (six of seven species, Supplementary Materials Table S4.1) as well as two facultative carnivores (Malay civet *V. tangalunga*; sun bear *H. malayanus*). Logging reduces the number of large trees, resulting in more canopy gaps, greater light penetration, and more dense understorey vegetation (Fauset *et al.* 2017; Milodowski *et al.* 2021, Figure 4.2). In areas with low hunting pressure (as in our sampling locations, Deere *et al.* 2020b), the resultant increase in foraging opportunities can benefit generalist species, such as those seen to increase here (Wong, Servheen and Ambu 2004; Meijaard and Sheil 2008; Granados *et al.* 2016). At ground level, only Sunda clouded leopard *N. diardi* experienced a substantial decline in recovering-logged forest, consistent with this species' habitat preferences (Brodie *et al.* 2015; Haidir *et al.* 2021). Ungulates in our study system, as key prey species, may then also benefit from the decreased presence of their main predator.

For arboreal mammals, structural simplification of the canopy architecture caused by logging disrupts movement pathways and reduces the availability of environmental niches across the vertical column. Thus, we expect this group to experience greater impacts from selective logging than mammals at ground level. Indeed, this was evidenced by the declines seen in 21% of arboreal species, with those most affected likely to be highly dependent on specific elements of the canopy associated with large, tall trees. Both long-tailed macaque *M. fascicularis* and Sabah grey langur *P. sabana* preferentially use the upper forest strata (Nijman 2009; Hanya *et al.* 2020), and may be less able to shift their activity downwards in forests with lower canopies. Similarly, as two of the largest-bodied gliding species (Payne and Francis 2007), both Thomas' flying squirrel *A. thomasi*, and red giant flying squirrel *P. petaurista* require trees of sufficient height to launch energetically efficient glides (Dudley and DeVries 1990; Dial 2003), and of sufficient size and age to provide cavities for shelter and nesting (Thorington *et al.* 2012; Krishna *et al.* 2019). These taxa play important roles in seed dispersal, regulation of vegetation growth via herbivory, and possibly pollination (Yumoto *et al.* 2000; Chapman *et al.* 2013; McConkey 2018), and their loss may therefore have implications for long-term forest regeneration and ecosystem functioning (Chazdon *et al.* 2009; Gardner *et al.* 2019; Whitworth *et al.* 2019b). Arboreal species that showed no change or an increase in occupancy in recovering-logged forest may be more able to adapt to disturbed habitats. For example, diurnal squirrels that climb rather than glide and build nests rather than relying on cavities (Payne and Francis 2007), or semi-arboreal mammals such as such as pig-tailed macaque, *M. nemestrina,* for which the energetic cost of accessing the canopy is reduced in areas where tree heights are lower.

Response to forest quality covariates

Almost all measures of habitat quality had lower values in recovering-logged forest, demonstrating the reduced height, tree size, number of niches, and density of canopy-level vegetation that is characteristic of degraded habitats (Figure 4.2). Canopy connectivity was the only exception, with similar values across unlogged and recovering-logged forest for field-measured and remotely-sensed covariates, suggesting that structural integrity was largely retained at canopy-level, albeit distributed across a lower height layer in recovering-logged forest. Negative associations observed between arboreal mammal occupancy and all habitat quality covariates except connectivity (Figures 4.2, 4.5, Supplementary Materials Table S4.2) are somewhat surprising considering that arboreal taxa are thought to be more reliant on vegetation structure than terrestrial species (Whitworth *et al.* 2019a). We consider possible reasons for these seemingly counter-intuitive responses.

(1) Arboreal mammals are less reliant on structural attributes than expected. If this were the case, we would expect species with occupancy declines in recovering-logged forest to show positive relationships with habitat quality, but this was not observed.

(2) Species poorly detected by cameras are the ones more sensitive to habitat change, in which case we would expect more records of rare taxa in unlogged forest. This again was not supported by our data; of arboreal species excluded due to low detections, one (Bornean pygmy squirrel *Exilisciurus exilis*) was recorded only in unlogged forest and three (pentail treeshrew *Ptilocercus lowii*, Low's squirrel *Sundasciurus lowii*, and an unidentified squirrel *Callosciurus sp.*) only in recovering-logged forest.

(3) A potential influx effect in response to new vegetation growth in canopy gaps as a result of increased light penetration in a disrupted canopy. If so, we might expect stronger responses to covariates from herbivores (e.g. langurs *Presbytis sp.*) than omnivores (e.g. small-toothed palm civet *A. trivirgata*), but the strength of the relationship was similar across all species (Figure 4.5).

(4) A potential 'compaction' effect. Arboreal mammal occupancy was negatively associated with measures of habitat quality that, together, translate to a reduction in recovering-logged forest of available habitat space for canopy-dwelling species to occupy (Figure 4.2, Supplementary Materials Tables S4.2). Therefore, similar to the 'crowding' effect seen in forest fragments (e.g. Cudney-Valenzuela *et al.* 2021; Pang *et al.* 2022), species in these 'compacted' post-logging environments may see a 'crowding from above' effect, where a similar number of individuals occupy a smaller area, resulting in occupancy estimates that are a product of reduced habitat availability rather than direct responses to reduced habitat quality. If there is a compaction effect, it may be masking declines in relative arboreal occupancy (i.e. occupancy per cubic metre) in recovering-logged forest and could lead to an underestimation of disturbance impacts on arboreal communities. Future studies could investigate this by standardising the number of canopy camera-traps to forest height (e.g. one unit per 10 metre vertical height increase) and by sampling across a gradient of increasing habitat degradation.

Methodological considerations

Detection probability in the canopy was not strongly influenced by camera-trap height (Table 4.1). Variable results have been reported from other studies: detection probability modestly increasing with camera height (Bowler *et al.* 2017); significantly increasing or decreasing, depending on species, for a third of mammals (Whitworth *et al.* 2019a); or slightly decreasing (Moore *et al.* 2020). Along with other authors, at this relatively early stage of canopy camera-trapping we suggest not preferentially targeting a certain height, as this may bias detections depending on species-specific preferences (Bowler *et al.* 2017). For terrestrial mammals, amount of vegetation matter was substantially negatively associated with detection probability, but this relationship was reversed in the canopy, likely reflecting the different meanings of increased vegetation matter in each stratum. On the ground, a greater density of herbs, shrubs and stems reduces animal visibility and therefore likelihood of detection. Conversely in the canopy, more vegetation in the form of branches and vines represents higher availability of movement pathways, increasing the likelihood of an animal travelling in front of the camera-trap. Sampling period showed a weakly positive association with detection probability for both arboreal and terrestrial communities, reflecting an increased likelihood of detection during longer surveys. Similarly, lower occupancy estimates for arboreal communities (Table 4.1) is consistent with other research (Bowler *et al.* 2017) and likely reflects the longer deployments needed in the canopy to achieve inventory completeness, as the effective sampling area of each canopy camera-trap is much smaller than that of each unit at ground level (Haysom *et al.* 2021). While use of the same sampling protocol on the ground and in the canopy facilitates direct comparisons, differences in the sampling environment between strata should be taken into account when interpreting results.

4.5 Conclusion

Here, we describe the first study to quantify the occupancy of an arboreal mammal community in Southeast Asia, and the first comparison between arboreal and terrestrial mammal responses to logging in this region. We demonstrate the importance of canopy connectivity for arboreal mammals, at both local and landscape scales, and develop a novel approach to quantify this relationship. Previous work has shown the value of recovering-logged forests for terrestrial mammals; we extend this to arboreal species, and highlight the importance of conserving this habitat for the entire mammal community, from ground to canopy. However, our finding that arboreal mammals are more likely to undergo occupancy declines than their terrestrial counterparts, alongside similar results from the Neotropics, should serve as a timely warning.

Failing to specifically monitor canopy communities is likely to lead to an underestimation of the true impact of logging on rainforest biodiversity, and may ultimately result in the silent disappearance of poorly known but ecologically important taxa. Our results have implications for logging practices, and the management of recovering-logged habitats, prompting consideration of how to effectively retain or restore structural features that are of vital importance to arboreal wildlife.

4.6 Acknowledgements

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4.7 Supplementary Materials

Table S4.1 Occupancy estimates for 57 mammal species detected during terrestrial and canopy sampling campaigns in Sabah, and these species' characteristics according to body size, taxonomic group, and functional group (information from Payne & Francis 2007 and the IUCN Red List). Asterisks next to species' names denote those endemic to Borneo. 'Strata' refers to whether a species was detected exclusively by canopy camera-traps ('arboreal'), exclusively by terrestrial camera-traps ('terrestrial'), or by camera-traps in both strata ('semi-arboreal'). Species excluded from occupancy analyses due to insufficient detections (<3) are shaded grey (*N*=8). For species retained (*N*=49), occupancy in unlogged forest (U) and recovering-logged forest (L) is given. For semi-arboreal species, occupancy is given per stratum, i.e. (C) refers to occupancy estimates derived only from detections on canopy camera-traps and (T) refers to occupancy estimates derived only from detections on terrestrial camera-traps. Detections of small-bodied flying squirrels were too infrequent to analyse separately, however these species are poorly-known and therefore of interest, and ecologically similar in terms of body size, taxonomy, likely functional group, and nocturnality. We created a species group ("small flying squirrel"), consisting of Temminck's flying squirrel *Petinomys setosus* (No. independent detections = 1), Horsfield's flying squirrel *Iomys horsfieldi* (*N*=2), and smoky flying squirrel *Pteromyscus pulverulentus* (*N*=1). Changes in occupancy between unlogged and recovering-logged forest are stated, except for three species that are each not known from one sampling area (marked 'na'). Substantial changes, i.e. where the 2.5th and 97.5th Bayesian credible intervals (BCI) did not overlap zero are marked with a double asterisk (**). Moderate changes, i.e. where the 12.5th and 87.5th BCI did not overlap zero are marked with a single asterisk (*). Changes indicating an occupancy decrease in recovering-logged forest have a negative symbol (–) before the number.

Species	**Strata**	**Body Size**	**IUCN Threat Status**	**Taxonomic Group**	**Functional Group**	**Occupancy by forest & strata**	**Occupancy change unlogged to recovering-logged forest**
Neofelis diardi Sunda clouded leopard	terrestrial	large	threatened	Carnivora	carnivore	U: 0.22 L: 0.03	–0.16 **
Pardofelis marmorata Marbled cat	terrestrial	medium	not threatened	Carnivora	carnivore	U: 0.19 L: 0.20	0.00
Prionailurus bengalensis Leopard cat	terrestrial	medium	not threatened	Carnivora	carnivore	U: 0.29 L: 0.36	0.06
Herpestes brachyurus Short-tailed mongoose	terrestrial	medium	not threatened	Carnivora	insectivore	U: 0.38 L: 0.33	–0.04

Herpestes semitorquatus Collared mongoose	terrestrial	medium	not threatened	Carnivora	carnivore	U: 0.20 L: 0.12	–0.07
Martes flavigula Yellow-throated marten	semi-arboreal	medium	not threatened	Carnivora	omnivore	C: U: 0.06 L: 0.06 T: U: 0.25 L: 0.29	C: 0.00 T: 0.02
Mydaus javanensis Sunda stink badger	terrestrial	medium	not threatened	Carnivora	insectivore	U: 0.03 L: 0.04	0.00
Arctictis binturong Binturong	semi-arboreal	large	threatened	Carnivora	omnivore	C: U: 0.06 L: 0.07 T: U: 0.18 L: 0.22	C: 0.01 T: 0.03
Arctogalidia trivirgata Small-toothed palm civet	arboreal	medium	not threatened	Carnivora	omnivore	U: 0.16 L: 0.24	0.08 *
Hemigalus derbyanus Banded civet	terrestrial	medium	not threatened	Carnivora	insectivore	U: 0.57 L: 0.57	0.00
Paguma larvata Masked palm civet	terrestrial	medium	not threatened	Carnivora	omnivore	U: 0.30 L: 0.24	–0.04
Paradoxurus hermaphroditus Common palm civet	terrestrial	medium	not threatened	Carnivora	omnivore	U: 0.00 L: 0.01	0.00
Viverra tangalunga Malay civet	terrestrial	medium	not threatened	Carnivora	omnivore	U: 0.62 L: 0.73	0.10 *
Helarctos malayanus Sun bear	terrestrial	large	threatened	Carnivora	omnivore	U: 0.53 L: 0.65	0.12 *
Sus barbatus Bearded pig	terrestrial	large	threatened	Ungulates	omnivore	U: 0.73 L: 0.91	0.17 **
Tragulus kanchil Lesser mousedeer	terrestrial	medium	not threatened	Ungulates	herbivore	U: 0.14 L: 0.46	0.31 **

Tragulus napu Greater mousedeer	terrestrial	medium	not threatened	Ungulates	herbivore	U: 0.67 L: 0.73	0.06
Muntiacus atherodes* Bornean yellow muntjac*	terrestrial	large	not threatened	Ungulates	herbivore	U: 0.65 L: 0.89	0.23 **
Muntiacus muntjak Red muntjac	terrestrial	large	not threatened	Ungulates	herbivore	U: 0.72 L: 0.87	0.14 **
Rusa unicolor Sambar deer	terrestrial	large	threatened	Ungulates	herbivore	U: 0.45 L: 0.73	0.28 **
Bos javanicus Banteng	terrestrial	large	threatened	Ungulates	herbivore	U: 0.00 L: 0.05	0.04 *
Galeopterus variegatus Sunda colugo	arboreal	medium	not threatened	Insectivora	herbivore	U: 0.01 L: 0.01	0.00
Echinosorex gymnura Moonrat	terrestrial	small	not threatened	Insectivora	insectivore	U: 0.33 L: 0.24	–0.08
Manis javanica Sunda pangolin	terrestrial	medium	threatened	Insectivora	insectivore	U: 0.28 L: 0.24	–0.03
Presbytis rubicunda* Maroon langur*	arboreal	large	threatened	Primates	herbivore	U: 0.13 L: 0.11	–0.02
Presbytis sabana* Sabah grey langur*	arboreal	large	threatened	Primates	herbivore	U: 0.09 L: 0.00	–0.08 **
Macaca fascicularis Long-tailed macaque	semi-arboreal	large	threatened	Primates	omnivore	C: U: 0.11 L: 0.00 T: U: 0.11 L: 0.04	C: –0.10 ** T: –0.04
Macaca nemestrina Pig-tailed macaque	semi-arboreal	large	threatened	Primates	omnivore	C: U: 0.16 L: 0.26 T: U: 0.75 L: 0.77	C: 0.09 ** T: 0.02

*Hylobates funereus** Bornean gibbon*	arboreal	large	threatened	Primates	herbivore	U: 0.19 L: 0.20	0.01
*Pongo pygmaeus** Bornean orangutan*	semi-arboreal	large	threatened	Primates	herbivore	C: U: na L: 0.17 T: U: na L: 0.55	na
Elephas maximus Asian elephant	terrestrial	large	threatened	Ungulates	herbivore	na	na
Aeromys tephromelas Black flying squirrel	arboreal	medium	not threatened	Rodents (gliding)	herbivore	U: 0.03 L: 0.03	0.00
*Aeromys thomasi** Thomas' flying squirrel*	arboreal	medium	not threatened	Rodents (gliding)	herbivore	U: 0.10 L: 0.02	–0.07 **
*Callosciurus adamsi** Ear-spot squirrel*	arboreal	small	not threatened	Rodents	herbivore	U: 0.00 L: 0.06	0.05 **
Callosciurus prevostii Prevost's squirrel	arboreal	small	not threatened	Rodents	herbivore	U: 0.19 L: 0.32	0.12 *
Callosciurus sp. Large mystery squirrel	arboreal	small	?	Rodents	herbivore?	na	na
See table legend above Small flying squirrel	arboreal	small	threatened	Rodents (gliding)	herbivore?	U: 0.04 L: 0.04	0.00
Petaurista petaurista Red giant flying squirrel	arboreal	medium	not threatened	Rodents (gliding)	herbivore	U: 0.05 L: 0.00	–0.04 **
Ratufa affinis Giant squirrel	arboreal	medium	not threatened	Rodents	herbivore	U: 0.19 L: 0.21	0.02
*Rheithrosciurus macrotis** Tufted ground squirrel*	terrestrial	medium	threatened	Rodents	herbivore	U: 0.40 L: 0.34	–0.05
*Sundasciurus brookei** Brooke’s squirrel*	arboreal	small	not threatened	Rodents	herbivore?	U: 0.02 L: 0.02	0.00

Sundasciurus lowii Low’s squirrel	semi-arboreal	small	not threatened	Rodents	herbivore?	na	na
Sundasciurus hippurus Horse-tailed squirrel	semi-arboreal	small	not threatened	Rodents	herbivore	C: U: 0.03 L: 0.05 T: U: 0.15 L: 0.17	C: 0.02 T: 0.01
Leopoldamys sabanus Long-tailed giant rat	terrestrial	small	not threatened	Rodents	herbivore	U: 0.20 L: 0.12	–0.06
Maxomys rajah Brown spiny rat	terrestrial	small	threatened	Rodents	herbivore	U: 0.35 L: na	na
Maxomys surifer Red spiny rat	terrestrial	small	not threatened	Rodents	herbivore	U: na L: 0.19	na
Maxomys whiteheadi Whitehead’s rat	terrestrial	small	threatened	Rodents	insectivore	U: 0.03 L: 0.00	–0.02
Hystrix brachyura Malay porcupine	terrestrial	medium	not threatened	Rodents	omnivore	U: 0.40 L: 0.49	0.09
*Hystrix crassispinis** Thick-spined porcupine*	terrestrial	medium	not threatened	Rodents	omnivore	U: 0.36 L: 0.27	–0.07
Trichys fasciculata Long-tailed porcupine	terrestrial	medium	not threatened	Rodents	omnivore	U: 0.33 L: 0.32	0.00
Ptilocercus lowii Pentail treeshrew	arboreal	small	not threatened	Insectivora	insectivore	na	na
*Tupaia longipes** Plain treeshrew*	arboreal	small	not threatened	Insectivora	insectivore	U: 0.02 L: 0.02	0.00
Tupaia tana Large treeshrew	terrestrial	small	not threatened	Insectivora	insectivore	U: 0.01 L: 0.02	0.00
Tupaia minor Lesser treeshrew	terrestrial	small	not threatened	Insectivora	insectivore	na	na

Table S4.2 Summary statistics for all vegetation covariates across all spatial scales tested in the occupancy component of our arboreal and terrestrial models. Bayesian p-value (Bpv) is a measure of model fit, where 0.5 would be perfect fit, and any value >0.05 and <0.95 is acceptable. WAIC is a relative measure of predictive model power, with lower values denoting greater statistical support. Covariates where the 2.5th and 97.5th percentile did not overlap zero were deemed to have substantial associations with mammal occupancy at the community level, denoted by ‘Y’, and the direction of the response indicated by + (positive) or – (negative). ‘n’ denotes no strong association between a covariate and mammal community occupancy. Our model outputs also returned response values for individual species, and the number of species with a strong association to each covariate is given. For final model testing, we selected covariates with substantial associations at the community level (highlighted blue for arboreal models and green for terrestrial models), providing Bpv was within acceptable parameters. Where one covariate had substantial associations at more than one spatial scale, we selected the scale with strong relationships for the greatest number of species. Due to differences between the canopy and terrestrial space, and the ecology of, and required sampling period for, arboreal and terrestrial species, we developed separate models for each community. We later ranked selected covariates according to WAIC in order to select one top-performing model each for arboreal and terrestrial communities (Supplementary Materials Table S4.3, 4.4). Field-measured covariates were only tested at the 50 m spatial scale, as these were not linked to LiDAR data so could not be extrapolated. The direction and strength of community and species’ relationships with highlighted covariates are visualised in main text Figures 4.2 and 4.5.

			ARBOREAL				**TERRESTRIAL**			
Covariate abbreviation & derivation	**Description**	**Spatial scale (m)**	**Bpv**	**WAIC**	**Substantial community response?**	**No. species with strong association**	**Bpv**	**WAIC**	**Substantial community response?**	**No. species with strong association**
agb LiDAR	Aboveground biomass. Derived from LiDAR acd (aboveground carbon density) value. Higher values denote larger, taller trees, indicating older forest and greater structural complexity.	50	0.17	3183	Y –	9	na	na	na	na
		100	0.18	3467	n	0	0.21	5779	n	0
		250	0.16	3374	Y –	1	0.24	6124	n	0
		500	0.19	3398	n	0	0.23	5738	Y +	3
chm LiDAR	Canopy height measured as the highest point in discrete space above ground level.	50	0.16	3374	n	0	na	na	na	na
		100	0.19	3391	n	1	0.24	5727	n	1
		250	0.18	3153	n	1	0.25	6120	n	2
		500	0.18	3387	n	0	0.25	5701	Y +	4
chm_st LiDAR	Variability in canopy height around each camera-trap. Higher values denote greater variability.	50	0.17	3298	n	0	na	na	na	Na
		100	0.18	3417	n	0	0.22	5673	Y +	0
		250	0.18	3322	n	0	0.23	5979	n	0
		500	0.18	3342	n	0	0.22	5718	n	0

dtm LiDAR	Digital terrain model, approximately equivalent to elevation in metres above sea level.	50	0.16	3335	n	1	na	na	na	na
		100	0.18	3301	n	1	0.25	5686	n	8
		250	0.17	3307	n	1	0.28	5937	n	10
		500	0.16	3339	n	1	0.26	5695	n	8
tri LiDAR	Terrain ruggedness index. Calculated from dtm, measures how flat/uniform or uneven/hilly is the terrain around the camera-trap.	50	na	na	na	na	na	na	na	na
		100					0.26	5750	n	1
		250					0.25	6024	n	0
		500					0.25	5756	n	0
padmean LiDAR	Plant area density central height, calculated for discrete 1 m vertical layers.	50	0.17	3372	n	0	na	na	na	na
		100	0.18	3386	n	0	0.23	5788	n	0
		250	0.19	3326	n	1	0.23	6069	n	0
		500	0.20	3317	n	0	0.23	5758	n	2
padnlayer LiDAR	Number of contiguous canopy layers with a plant area density greater than a user-defined threshold of 0.1m^2 m^{-2}. A basic measure of connectivity.	50	0.18	3357	n	0	na	na	na	na
		100	0.19	3349	n	0	na	na	na	na
		250	0.19	3311	n	2	0.24	5808	n	0
		500	0.20	3307	n	2	0.25	5743	n	0
padshannon LiDAR	Number of environmental niches available throughout the vertical column.	50	0.26	3459	n	0	na	na	na	na
		100	0.18	3426	n	0	0.22	5726	Y +	3
		250	0.21	3174	Y –	0	0.23	6118	Y +	2
		500	0.19	3359	n	0	0.24	5746	Y +	2
padskew LiDAR	Distribution of vegetation matter in the vertical column. Positive values denote vegetation distributed towards the top of the canopy, lower or negative values towards the ground.	50	0.17	3314	n	0	na	na	na	na
		100	0.20	3360	n	0	0.21	5718	n	0
		250	0.18	3381	n	0	0.20	5868	Y +	7
		500	0.18	3345	n	0	0.21	5709	Y +	4
padstd LiDAR	Standard deviation of plant area density calculated across 1 m vertical layers, i.e. how uniform or variable is the vegetation in the vertical column. Higher values denote greater variability.	50	0.19	3433	n	0	na	na	na	na
		100	0.21	3360	n	0	0.23	5730	n	0
		250	0.18	3175	Y –	0	0.24	6132	N	0
		500	0.20	3323	n	0	0.23	5704	Y +	3
pai LiDAR	Plant area index: all vegetation matter in the vertical column (trunks, stems, leaves, etc.).	50	0.16	4683	n	0	na	na	na	na
		100	0.17	3192	Y –	10	0.23	5779	n	0
		250	0.19	3528	n	1	0.26	6314	Y +	2
		500	0.19	3350	n	0	0.25	5808	Y +	3

HC1_pai LiDAR	Plant area index values are given overall (=pai), and per 10 m height layer. Height-calibrated pai (1) is thus the vegetation matter value in the height layer in which the camera-trap was set.	50	0.18	3147	n	0	na	na	na	na
		100	0.17	3343	n	0				
		250	0.17	3412	n	0				
		500	0.17	3332	n	0				
HC2_pai LiDAR	Height-calibrated pai (2) was calculated as an average of vegetation matter values for the three height layers closest to the camera-trap.	50	0.18	3134	n	0	na	na	na	na
		100	0.17	3406	n	0				
		250	0.18	3411	n	0				
		500	0.17	3337	n	0				
cnt_all LiDAR & Circuitscape	Connectivity throughout the vertical column, calculated in Circuitscape using LiDAR plant area index values.	50	0.16	3170	n	0	na	na	na	na
		100	0.17	3147	n	0	0.23	5704	Y +	3
		250	0.18	3159	n	0	0.23	5699	Y +	3
		500	0.19	3141	n	0	0.23	5750	Y +	4
HC1_cnt LiDAR & Circuitscape	Height-calibrated connectivity (1): Circuitscape value for the height layer in which the camera-trap was set.	50	0.17	3134	n	0	na	na	na	na
		100	0.17	3155	n	0				
		250	0.18	3162	n	0				
		500	0.18	3136	Y +	4				
HC2_cnt LiDAR & Circuitscape	Height-calibrated connectivity (2), calculated as an average of Circuitscape values for the three height layers closest to the camera-trap.	50	0.18	3151	n	0	na	na	na	na
		100	0.18	3179	n	0				
		250	0.17	3149	n	0				
		500	0.19	3178	n	0				
cnx_adj field-measure	Number of connections of focal branch to adjacent trees or vines. One connection = one point of contact.	50	0.18	3124	Y +	7	na	na	na	na
cnx_focal field-measure	Number of connections of focal branch to other branches or vines of the focal tree. One connection = one point of contact.	50	0.21	3281	n	1	na	na	na	na
trap_height field-measure	Height of canopy camera-trap in metres, obtained using tape measure extending from climber at exact height of camera-trap, to ground crew at base of the focal tree.	50	0.18	3280	n	0	na	na	na	na

Table S4.3 Selected covariates with substantial associations at the community level and ranked by WAIC values to determine the best performing model for the arboreal community, and separately for the terrestrial community. Models are listed in order of lowest to highest WAIC, with delta (Δ) WAIC values calculated by subtracting each model WAIC value from the WAIC value of the model with the lowest WAIC. Any models within 2 delta points of the top performing model would be deemed to have equivalent statistical support; any within 2-10 points would have moderate statistical support. No models in either the arboreal or the terrestrial comparison were within these thresholds, indicating that our selected models (highlighted in bold font) far out-performed any others in terms of their ability to describe arboreal and terrestrial mammal occupancy.

Selected covariate & spatial scale (m)	WAIC	ΔWAIC	Exp(0.5*ΔWAIC)	WAIC weight	Evidence ratio
arboreal models					
height-calibrated connectivity (500 m)	**3136.22**	**0**	**1.0**	**1.0**	**1**
no. environmental niches (250 m)	3173.76	37.54	0.00	0.00	141810185
veg. density variability (250 m)	3174.76	38.54	0.00	0.00	233805469
aboveground biomass (50 m)	3182.90	46.68	0.00	0.00	13690938122
all veg. in vertical column (100 m)	3191.81	55.59	0.00	0.00	1178189436266
terrestrial models					
canopy height (500 m)	**5690.77**	**0.00**	**1.00**	**1.00**	**1**
canopy height variability (100 m)	5725.26	34.49	0.00	0.00	30860882
veg. density variability (500 m)	5726.44	35.67	0.00	0.00	55672674
veg. vertical distribution (250 m)	5728.43	37.66	0.00	0.00	150579237
no. environmental niches (100 m)	5745.91	55.14	0.00	0.00	940803373629
aboveground biomass (500 m)	5748.90	58.13	0.00	0.00	4195358873066
connectivity in vertical column (500 m)	5749.51	58.74	0.00	0.00	5691528743797
all veg. in vertical column (500 m)	5769.82	79.05	0.00	0.00	146382579957921000

Table S4.4 Community and species' responses to occupancy and detection probability covariates. Substantial positive or negative responses are indicated by + or – respectively, and the direction of weak community responses by (+) or (–). Na indicates a covariate was not tested in that model. Model fit is given (Bpv). Semi-arboreal species appear in arboreal and terrestrial models, using data from canopy-only and terrestrial-only cameras, respectively.

	Bpv	**Occupancy covariate: height-calibrated connectivity**	**Detection covariate: sampling period (CTN)**	**Detection covariate: vegetation matter**	**Detection covariate: camera-trap height**
ARBOREAL					
Community response	**0.18**	+	(+)	(+)	(–)
Species' responses					
Binturong	0.60				
Black flying squirrel	0.45				
Bornean gibbon	0.31				
Brooke's squirrel	0.56				
Ear-spot squirrel	0.49				
Giant squirrel	0.23	+			
Horse-tailed squirrel	0.36				
Long-tailed macaque	0.55				
Maroon langur	0.38				
Orangutan	0.38				
Plain treeshrew	0.68				
Pig-tailed macaque	0.47	+			
Prevost's squirrel	0.15		+		
Red giant flying squirrel	0.45				
Sabah grey langur	0.30	+			
Small flying squirrel	0.83				
Small-toothed palm civet	0.28				
Sunda colugo	0.51				
Thomas' flying squirrel	0.55	+			
Yellow-throated marten	0.58				

TERRESTRIAL		**Occupancy covariate: Canopy height**	**Detection covariate: sampling period (CTN)**	**Detection covariate: vegetation matter**	
Community response	**0.26**	+	(+)	–	**na**
Species' responses					
Banded civet	0.26	+			
Banteng	0.60				
Bearded pig	0.61		+	–	
Binturong	0.86				
Bornean yellow muntjac	0.27			–	
Brown spiny rat	0.18				
Collared mongoose	0.84			–	
Common palm civet	0.70				
Greater mousedeer	0.09		+		
Horse-tailed squirrel	0.20			–	
Large treeshrew	0.48				
Leopard cat	0.64			–	
Lesser mousedeer	0.24		+	–	
Long-tailed giant rat	0.51				
Long-tailed macaque	0.53			–	
Long-tailed porcupine	0.55	+		–	
Malay civet	0.27			–	
Malay porcupine	0.30			–	
Marbled cat	0.67			–	
Masked palm civet	0.80			–	
Moonrat	0.58			–	
Orangutan	0.67			–	
Pig-tailed macaque	0.25	+		–	
Red muntjac	0.32	+	+		
Red spiny rat	0.35				

Sambar deer	0.48	–
Short-tailed mongoose	0.51	–
Sun bear	0.49	–
Sunda clouded leopard	0.70	–
Sunda pangolin	0.91	
Sunda stink badger	0.41	
Thick-spined porcupine	0.50	
Tufted ground squirrel	0.30	–
Whitehead’s rat	0.42	
Yellow-throated marten	0.63	

Chapter 5 Discussion

In this thesis, I explored the efficacy of using canopy-based camera-traps to study Borneo's diverse and little-known arboreal mammal community. To the best of my knowledge, this work represents the first application of the method in Borneo, where tropical rainforests are substantially taller and more structurally complex than those of other regions, and selective logging rates are among the highest globally. It also represents the first comprehensive comparison of the terrestrial and arboreal mammal community in Southeast Asia, providing insights into the differing patterns of community composition (**Chapter 2**), diel activity (**Chapter 3**), and responses to logging (**Chapter 4**) between strata. The evidence presented here can be practically applied to guide further arboreal mammal research, with the dual aims of increasing baseline knowledge on this understudied but functionally important group, and creating more effective conservation and habitat management strategies that take into account 'whole forest' diversity, i.e. from the ground to the canopy.

5.1 Contributions to the research field

5.1.1 Application of the method: Borneo as a proving ground

Arboreal mammals comprise a substantial proportion of the diversity and biomass of tropical rainforests (Kays and Allison 2001; Malcolm and Lowman 2004), but remain globally understudied compared to terrestrial taxa due to the practical difficulties of canopy-based sampling, and the detection biases inherent in ground-based surveys (Lowman and Moffett 1993; Whitworth *et al.* 2016). Although studies deploying camera-traps at height have increased in recent years, the method is still in its infancy, and most research originates from sites in the Neotropics, Africa, and Australia (Moore *et al.* 2021). In Borneo, dipterocarp-dominated rainforests have given rise to a structurally distinct environment with a unique and diverse arboreal fauna (Emmons and Gentry 1983; Dudley and DeVries 1990). However, comprehensive ecological information for most of the island's arboreal mammals is lacking (Payne and Francis 2007). The immense height of Borneo's forest canopies presents significant barriers to detecting and accurately identifying arboreal taxa from ground level, and terrestrial camera-traps do not provide sufficient detection records for these species (Brodie *et al.* 2014b).

Camera-traps in this study were deployed up to 52.3 metres above the ground, to my knowledge representing the greatest reported height at which the method has yet been tested.

This is simply a function of tree architecture, as most large branches occur in the mid- to upper-canopy, which in Borneo is on average 10-15 metres taller than in other regions (Dudley and DeVries 1990). However, it is encouraging in the context of a significantly greater risk of false triggers in the canopy due to increased wind and light exposure (Otani 2001; Gregory *et al.* 2014), and serves to reinforce the efficacy of canopy camera-trapping even in ultra-tall forests.

Overall, results presented in **Chapters 2-4** demonstrate the viability of canopy camera-trapping to obtain detailed information on Bornean arboreal mammals, including robust estimates of species diversity, species accumulation, activity metrics, and occupancy, across both unlogged and recovering-logged forest. In addition, data from paired ground-level cameras negate the issue of differential sampling biases arising from different methods (e.g. camera-traps for terrestrial species, which can be effective in the detection of elusive wildlife versus transects for arboreal species, which, due to the necessary presence of human observers, often are not (Whitworth *et al.* 2016)). Thus, employing a standard sampling protocol across strata facilitates direct comparisons between arboreal and terrestrial communities, as well as the investigation of cross-strata forest use by semi-arboreal mammals.

5.1.2 The whole-community perspective

The different structural architecture (Lowman and Rinker 2004), light levels (Fauset *et al.* 2017) and microclimate (Nakamura *et al.* 2017) of the canopy present different environmental conditions for species utilising this space than for those restricted to the forest floor. Animal activity is driven by the opportunities and constraints of the physical habitat, as well as the need to interact with, or avoid, other animals (e.g. for breeding or cooperative foraging, and avoidance of competitors or predators). Knowledge of activity can thus shed light on how species adapt to environmental challenges, and the community dynamics that facilitate species' co-existence (Bridges and Noss 2011; Azcarraga, Tessaro, and Delfin-Alfonso 2020). Diel activity is often not well characterised for mammal communities, although camera-trapping lends itself to this type of study as it allows 24-hour monitoring of multiple species simultaneously (Van Schaik and Griffiths 1996; Bridges and Noss 2011). **Chapter 3** demonstrates how data obtained from ground- and canopy-level camera-traps can be used in community-wide activity analyses that help to shed light on temporal niche partitioning across strata. Mammals active at ground level tended to be nocturnal or cathemeral, whereas the daylight and twilight periods were under-utilised in this stratum. In the tropics, day length and climatic conditions are stable across the year (Oliveira and Scheffers 2018), and Bornean forests have likely remained little-changed over evolutionary timescales (Wilf *et al.* 2022). It would therefore be surprising if these factors had not given rise to species able to exploit all temporal niches. Indeed, the inclusion of canopy-derived detection data revealed arboreal and semi-arboreal mammals were much more likely to be diurnal or crepuscular than their terrestrial counterparts, illustrating how sampling in both strata can provide a more in-depth insight into whole forest community dynamics.

Paired terrestrial and canopy camera-trap studies from across the tropics have demonstrated that strictly arboreal mammals are a distinct group, and not a nested subset of those at ground-level (Whitworth *et al.* 2019a, Peru; Hongo *et al.* 2020, Cameroon; Moore *et al.* 2020, Rwanda; Kaizer *et al.* 2021, Brazil; Agostini *et al.* 2022, Argentina). Despite this, arboreal species are often not included in surveys (Bowler *et al.* 2017), meaning that many studies describing mammal community assessments in fact only encompass the terrestrial element of the community, leading to an incomplete picture of overall vertebrate biodiversity. In **Chapter 2**, I demonstrate that the inclusion of canopy-based sampling alongside standard ground-based camera surveys increased mammal inventories in Borneo by 32%, detecting eighteen unique species and adding significantly to estimates of overall mammal richness.

Additionally, in **Chapter 2**, comparisons between unlogged and recovering-logged forest show that although mammal community composition was notably different across strata, it does not vary greatly between unlogged and recovering-logged forest. However, reporting species richness data alone can conceal important details such as abundance changes (Wearn *et al.* 2017) e.g. a species may be present in both unlogged and recovering-logged forest, but significantly less abundant in one habitat. Quantifying changes in abundance underpins our ability to interpret species' responses to habitat disturbance and, by extension, to implement appropriate conservation actions for those at risk of decline. Occupancy can be used as a proxy for abundance (MacKenzie and Nichols 2004), and in **Chapter 4**, I employed multi-species occupancy models, which statistically evaluate patterns of detection for all species across all sampling locations, to provide the first comparative assessment of how arboreal and terrestrial mammal communities in Borneo are affected by logging. Results from these analyses extend those of terrestrial assessments (e.g. Putz *et al.* 2012; Maiwald, Mohd-Azlan, and Brodie 2021) by demonstrating that recovering-logged forests offer valuable habitat for arboreal mammals, giving a whole-community perspective to the importance of previously-logged areas for biodiversity conservation in Borneo (Meijaard and Sheil 2007). This included threatened species such as the Endangered Bornean gibbon *Hylobates funereus* (IUCN Red List), corroborating findings from Peninsular Malaysia that show gibbon density did not change in logged forest (Pang *et al.* 2022). The persistence of gibbons in disturbed areas may reflect the ability of these frugivores to utilise potentially increased food resources at canopy level, as well as to leap across relatively large canopy gaps (Cannon and Leighton

1994). Similarly, the small-toothed palm civet *Arctogalidia trivirgata* is almost never detected on the ground (Chutipong *et al.* 2014), which could lead to the assumption that it is rare, but detection data from canopy camera-traps revealed it to be common across both unlogged and recovering-logged forest and to increase in occupancy in recovering-logged forest. Canopy-level sampling of strictly arboreal mammals can thus provide information on species that, perhaps contrary to expectations, may be less sensitive to habitat disturbance, and avoid misdirected conservation actions (Gerber *et al.* 2014).

However, while 21% of arboreal species increased in occupancy in recovering-logged forest, the same proportion substantially declined in this habitat, whereas for terrestrial mammals, 25% increased and only 3% declined. Arboreal species with the greatest declines were all primates or gliding mammals – taxa which may be more dependent than others on the presence of large, tall trees to access resources and/or avoid competitors. Both long-tailed macaque *Macaca fascicularis* and Sabah grey langur *Presbytis sabana* are thought to preferentially use the upper canopy strata (Nijman 2009; Hanya *et al.* 2020), and may be less able to shift their activity downwards in forests with lower canopies. For example, for long-tailed macaques, use of the lower strata may incur a greater risk of harmful interactions with their closest ecological competitor, the larger and more strongly terrestrial pig-tailed macaque *M. nemestrina* (Mohd-Azlan *et al.* 2017; Hanya *et al.* 2020). Pig-tailed macaques on the other hand, showed substantially increased occupancy at canopy level in recovering-logged forest, but not on the ground, suggesting that they may benefit from the reduced presence of their main competitor in this habitat, alongside the reduced energetic costs of accessing a lower canopy.

As two of the largest-bodied gliding mammals (Payne and Francis 2007), both Thomas' flying squirrel *Aeromys thomasi*, and red giant flying squirrel *Petaurista petaurista* may be reliant on trees of sufficient height to launch energetically efficient glides (Dudley and DeVries 1990; Dial 2003), and of sufficient size and age to provide cavities for shelter and nesting (Cockle *et al.* 2011; Thorington *et al.* 2012; Krishna *et al.* 2019). In contrast, non-gliding squirrel species showed either no change or an increase in occupancy in recovering-logged forest. Their mode of locomotion (climbing rather than gliding), small body size (allowing use of thin branches), and nesting habits (building nests of twigs and leaves rather than using cavities, Payne and Francis 2007), may mean that they are more able to adapt to recovering-logged habitats with a lower density of mature trees.

Collectively, analyses and results presented in **Chapters 2-4** serve to demonstrate that the inclusion of canopy camera-trapping alongside standard terrestrial protocols offers a feasible and successful sampling method that significantly enhances our knowledge of mammalian species richness, ecology, and sensitivity to habitat disturbance compared to data obtained only from terrestrial cameras. Arboreal mammals play important roles in ecosystem processes such as seed dispersal, regulation of vegetation growth via herbivory, and pollination (Yumoto *et al.* 2000; Chapman *et al.* 2013; McConkey 2018), and their loss would likely have negative implications for the long-term regeneration of tropical forests. Explicitly accounting for this group is thus crucial to our understanding of rainforest mammal communities, and, by extension, to the development of effective conservation and habitat management plans that encompass ground-to-canopy biodiversity.

5.1.3 Semi-arboreal species

Terrestrial camera-trap studies often record detections of semi-arboreal species, and indeed this may be the most effective sampling method for some of the largest-bodied and widest-ranging, such as clouded leopard *Neofelis diardi*, marbled cat *Pardofelis marmorata*, sun bear *Helarctos malayanus*, and pangolin *Manis javanica* (**Chapter 2**). However, the ability of terrestrial cameras to detect these species may lull us into a false sense of security by giving the impression that the information obtained is comprehensive. In fact, for many semi-arboreal mammals, data and conclusions are likely to be limited if the canopy aspect of their ecology is not accounted for (Mohd-Azlan *et al.* 2020). For example, canopy camera-trapping in the Philippines provided a much higher detection rate for binturong *Arctictis binturong* compared to results from 30 other terrestrial-only studies (Debruille *et al.* 2020).

Comparative detection records from terrestrial and canopy camera-traps in my study clearly demonstrate that the inclusion of canopy sampling alongside terrestrial protocols can provide more reliable relative abundance estimates for semi-arboreal mammals, and improve our understanding of their distribution across the sampling landscape (Appendix II). Of nine species recorded in both strata, six had an equal or greater proportion of detections in the canopy than on the ground. Excluding pig-tailed macaque *M. nemestrina*, which had a disproportionately high number of total detections (1230, compared to <80 per species for all other semi-arboreal mammals), canopy camera-traps accounted for 56% of all semi-arboreal detections, and increased the number of separate locations where each species was detected by an average of four (range 1 – 7).

The ability to compare data across strata further revealed that semi-arboreal mammals preferentially use the ground and the canopy at different times of day, likely for different purposes (**Chapter 3**), and that structural simplification in recovering-logged areas does not result in greater occurrence at ground-level (**Chapter 4**), as has been previously hypothesised (Malcolm and Ray 2000; Berry *et al.* 2010). This latter finding is important in the context of the ecological value of recovering-logged forests, because it indicates that high recorded levels of terrestrial biodiversity are robust, rather than an artefact of increased detections of semi-arboreal species. More anecdotally, interesting observations of semi-arboreal mammals in the canopy include a pair of usually solitary tufted ground squirrels *Rheithrosciurus macrotis* travelling together and, separately, an individual appearing to scent-mark a branch (**Chapter 2**); providing insights into social aspects of this enigmatic species' behaviour that were not apparent from terrestrial detections.

Taken together, these findings illustrate that for mammals habitually using both the canopy and the ground in the Bornean rainforest, data derived solely from terrestrial surveys provide a restricted view into their ecology and distribution, and show how future research could benefit from incorporating canopy-derived data for semi-arboreal species, particularly those which are infrequently detected (e.g. binturong *A. binturong*), or of conservation concern (e.g. orangutan *P. pygmaeus*).

5.1.4 The importance of a connected canopy

LiDAR-derived vegetation metrics quantify forest structure at high resolution and are widely used as indicators of habitat quality (Simonson, Allen and Coomes 2014), although most studies to date focus on temperate regions (Acebes, Lillo and Jaime-González 2021). While the integration of these metrics with animal detection data shows great potential to describe species-habitat associations for arboreal mammals, its applications have been limited to a few single-species studies (e.g. Johnston and Moskal 2016; Stobo-Wilson *et al.* 2021). Previous research using field-measured metrics have shown arboreal mammals rely on site-level canopy connectivity for movement and habitat selection (e.g. McLean *et al.* 2016; Chen *et al.* 2021). In **Chapter 4**, I combined occupancy estimates with a bespoke, LiDAR-derived measure of canopy connectivity to demonstrate for the first time the importance of connectivity at height for arboreal communities at the landscape scale.

These findings have implications for our understanding of arboreal mammal responses to logging, as canopy connectivity was the only vegetation covariate retained in recovering-logged forest, likely underpinning the ability of most arboreal species in our study to persist in this otherwise structurally-altered habitat. They add to those of Deere and colleagues (2020a) by highlighting the benefits of taking a more nuanced examination of forest structure than simply categorising areas as 'unlogged' or 'logged': here, the principal message is that recovering-logged forest is valuable for most arboreal species as long as canopy-level connectivity is maintained. This provides a clear basis on which to make habitat management decisions as recovering-logged areas that retain canopy connectivity have added value for biodiversity conservation across strata. Furthermore, it helps inform the type of mitigation strategy that may be useful for the restoration of severely degraded areas. For example, the success of artificial canopy bridges to connect habitat fragments for arboreal mammals has been well-documented in several countries (e.g. Gregory *et al.* 2014; Nekaris *et al.* 2020), and could equally be applied in Borneo in forests where canopy connectivity has been lost. A caveat is the requirement for LiDAR surveys to have been carried out in a target location, but as use of this technology becomes more widespread, it is hoped that obtaining the necessary data should become easier. In the meantime, my findings also corroborate the importance of site-level connectivity, which can be assessed in the field in areas without LiDAR data.

5.2 Caveats, limitations, and methodological considerations

5.2.1 Sampling sites

Logged forest quality. Our recovering-logged forest sampling area, while quantifiably different on a structural level to unlogged forest, is of relatively good habitat quality compared to other logged forests in Borneo (i.e. logging ceased a decade prior to sampling, the area remains dominated by trees, albeit of reduced height and size, and largely retains canopy connectivity). However, terrestrial research shows that mammal occupancy declines as the degree of forest degradation increases (Wearn *et al.* 2017; Deere *et al.* 2020a), and in more highly degraded areas, canopy connectivity is likely to be more severely disrupted (Pinard and Putz 1996). Therefore, arboreal assemblages in logged forests that are more degraded, with less connected canopies, than those in our study system are likely to suffer correspondingly greater declines than observed here. Further, our study system has low levels of hunting in the context of the overall landscape (Deere *et al.* 2020b), and arboreal mammals may be less able to persist in areas with high hunting pressure (Scabin and Peres 2021), especially species targeted for food or body parts (e.g. langurs hunted for bezoar stones, Nijman 2005).

Pseudoreplication. Fieldwork logistics and equipment availability restricted the scope of this study to one unlogged and one recovering-logged forest sampling area, limiting the ability to extrapolate results. However, the spatial pairing of terrestrial and canopy units provides robust community-level comparisons across strata, which have not been previously available in Borneo except for in live-trapping studies of small mammals (Wells *et al.* 2004a; Nakagawa *et al.* 2007). I also took care to ensure that spacing between sampling points was appropriate for an occupancy-focused analysis (i.e. within home range sizes of target species). Methods described here are replicable, and include an assessment of likely costs (**Chapter 2**); and the data presented provide a useful reference point on which future researchers can compare findings.

5.2.2 Camera deployment

Canopy camera-trapping studies in other regions have found field-measured connectivity of the focal tree to be a strong predictor of occupancy (Whitworth *et al.* 2019a, Chen *et al.* 2021). Results in **Chapter 4** show an even more fine-scale relationship: that connectivity of the focal branch is important. For the moment, for researchers in the field, this may be the most easily quantifiable predictor of arboreal mammal occurrence. However, in this relatively early stage of canopy research, it may not be advisable to completely exclude placements that face branches without connections. First, as with terrestrial camera-traps exclusively targeting trails, preferential placement of canopy camera-traps may unwittingly bias species detections (Wearn *et al.* 2013), as optimum camera positioning will vary across species (Bowler *et al.* 2017). Camera images also show that some species will utilise unconnected branches (e.g. long-tailed macaques and flying squirrels). Additionally, it is worth noting the importance of using infrared flash in canopy camera-trap studies, as white flash can cause temporary blindness, which for arboreal species could lead to a fall and possible death (Schipper 2007). Care should also be taken during tree climbing to minimise damage to canopy vegetation such as epiphytes, as these provide important habitat for a number of invertebrate and vertebrate taxa (Ellwood and Foster 2004).

5.2.3 Missing taxa

All sampling methods will inevitably miss a proportion of species (Whitworth *et al.* 2019a). While I did not investigate other techniques such as transects, camera-derived inventories compared with available information on species' distributions (Payne and Francis 2007) indicate that the proportion of arboreal species present in the landscape but not detected by canopy camera-traps was similar to that of terrestrial species not detected by ground-level units (**Chapter 2**), suggesting equivalent efficacy across strata. In contrast, some arboreal species appeared to be common and frequently-detected across sampling locations (e.g. Prevost's squirrel *Callosciurus prevostii*, and small-toothed palm civet *Arctogalidia trivirgata*). This is similar to certain species at ground level (e.g. bearded pig *Sus barbatus* and muntjac deer *Muntiacus atherodes* and *M. muntjak*) and in neither stratum appeared to be a barrier to sampling – i.e. while there were instances where a camera's field of view was dominated by an individual or individuals of a common species either for a continuous time-period, or by frequent re-visits, this did not appear to preclude visits by, and detections of, other species during other time periods.

The success in detecting and identifying several small-bodied arboreal mammals to species level (**Chapter 2**) is encouraging. However, some taxa known to utilise the canopy were not recorded, for example pencil-tailed tree mice *Chiropodomys sp.*, tarsier *Cephalopachus bancanus*, and slow loris *Nycticebus menagensis*. Species accumulation curves had not fully reached an asymptote for arboreal communities (**Chapter 2**), suggesting that longer sampling periods may yet return detections of these species. Alternatively, some may require targeting specific heights (e.g. 2-3 metres above ground for tarsiers), or habitat features (e.g. vine tangles or trunks for slow loris). For the very smallest species such as murid rodents, it may be necessary to either deploy cameras specifically designed to target this group (e.g. the 'selfie trap', Gracanin, Gracanin, and Mikac 2019) or, for species that may be distinguished predominantly by hind-foot measurements, conduct supplementary live-trapping (e.g. Wells *et al.* 2004a; 2004b). In addition, bats are one of the most diverse groups in tropical canopies (Kays and Allison 2001), but are poorly sampled by camera-traps (although see Hirakawa 2005; Aziz *et al.* 2017). Acoustic monitoring has shown promise for sampling tropical bat assemblages (e.g. Yoh *et al.* 2021), and future studies wishing to include both volant and non-volant arboreal mammals could perhaps set both camera-traps and audio-recording equipment at canopy level.

5.2.4 Species identification & classification

Although there were challenges in identifying a limited number of individuals, these should reduce over time as canopy camera-trapping studies become more commonplace. One diurnal squirrel (referred to as *Callosciurus sp.*, but which could be *Sundasciurus sp*.) could not be identified either by reference books or by seeking the opinions of several Borneo-mammal experts, and indeed may be a previously unrecorded species or hybrid. Similarly, two small-bodied flying squirrels (smoky flying squirrel *Pteromyscus pulverulentus* and Horsfield's flying squirrel *Iomys horsfieldi*) were assigned the most likely identity given their appearance. The records were retained for analyses in **Chapters 2** and **4** on the basis that our purpose was to examine community composition and responses of different species to logging, and so it was important to consider all data points that could be confidently assessed to be distinct species. Additionally, in an attempt to reduce complications and keep definitions clear, I classified species as, 'terrestrial' = detected exclusively on ground-level camera-traps in this study, 'arboreal' = detected exclusively on canopy-level camera-traps in this study, 'semi-arboreal' = detected by camera-traps in both strata in this study. Given the number of species under analysis and the purposes of my research (to directly compare the methodology and results of terrestrial and canopy camera-trapping), I felt that consistently defining species according to my observed data was the most relevant and practical system. However, I recognise that in some cases these classifications were contrary to known behaviour, for example I defined sun bear *Helarctos malayanus* as terrestrial although in general it is known to be semi-arboreal, and I defined plain treeshrew *Tupaia longipes* as semi-arboreal although it was previously thought to be terrestrial (see Chapter 2, Supplementary Materials Table 2.2 for the full species list including any classification discrepancies). For many Bornean mammals, their degree of arboreality remains unclear and in **Chapter 2** I discuss possible reasons that larger mammals known to be semi-arboreal were only detected at ground-level under my sampling design. I raise the point here because it is worth considering for future research, particularly as canopy camera-trapping becomes more widespread. How do we define 'semi-arboreal'? What factors influence a species' arboreality, e.g. habitat structure, location, gender (for example female clouded leopards are hypothesised to be more arboreal than males, Cheyne *et al.* 2016), or perceived arboreality, e.g. sampling method – with a smaller effective sampling area per camera in the canopy, larger semi-arboreal mammals may be more likely to be detected on terrestrial cameras, but does this accurately reflect proportional habitat use? Would changing the sampling design help to mitigate these issues, e.g. by increasing vertical coverage to account for the disproportionately larger three-dimensional area (see Section 5.3.1 below)?

Together, these identification and classification challenges, the unrecognised squirrel, and the consideration that our likely smoky flying squirrel would represent the only known photograph of this species – all revealed by canopy camera-trapping – serve to emphasise how little is known about Bornean arboreal mammals, while at the same time providing a viable means to increase that knowledge.

5.3 Recommendations for future research

5.3.1 Optimal sampling period

As with terrestrial mammals (e.g. Tobler *et al.* 2015) and other canopy research (e.g. Bowler *et al.* 2017), species accumulation curves for arboreal mammals in this study increased rapidly during the first 500-1000 days of sampling – a rate comparable to communities at ground level (**Chapter 2**). However, after this initial phase, species accumulated more slowly in canopy inventories than in those on the ground. Extrapolated curves predicted that while terrestrial inventories were complete for this sampling design (i.e. further species detections would likely require deployments in different habitat types such as riverine), achieving inventory completeness (i.e. detection of all species able to be recorded by this sampling design) would likely take substantially longer for arboreal mammals, corroborating results of other studies in the Neotropics (Gregory *et al.* 2014; Whitworth *et al.* 2016, 2019a; Bowler *et al.* 2017). As slower species accumulation in the canopy appears to be common across tropical locations, future research investigating the minimum sampling time necessary to comprehensively inventory arboreal mammal communities would be very useful to help plan efficient surveys that maximise species detections while keeping labour and equipment costs reasonable.

5.3.2 Vertical stratification

This work documents the differences between mammal communities on the ground and in the canopy, with 'canopy' encompassing heights of 9.8-52.3 metres. Sampling locations comprised one terrestrial camera-trap and one canopy camera-trap (except a small subset of sites with an experimental second canopy camera, see **Chapter 2**), as the primary aims were to test the ability of canopy camera-traps to inventory Bornean arboreal mammals, and compare results to terrestrial inventories. However, forest canopies have a much greater three-dimensional area than the forest floor; reflected in the longer sampling periods needed to achieve inventory completeness for arboreal species. Furthermore, several tropical studies have demonstrated vertical stratification of mammal occurrence and activity within the canopy itself (e.g. Malcolm 1991; Saiful *et al.* 2001; Sushma and Singh 2006; Nakagawa *et al.* 2007; Hanya *et al.* 2020). Canopy camera-trapping is rapidly being established as an effective sampling method (both in Borneo and elsewhere) (**Chapters 2-4**; Moore *et al.* 2021), and there is much further scope for optimising its applications. For example, studies aiming to inventory arboreal communities while simultaneously investigating vertical stratification could consider a design whereby sampling locations are widely-spaced (i.e. >1 km apart), thereby ensuring independence between sites, but with each location rigged with multiple camera-traps along a vertical gradient from ground-level to the upper canopy (e.g. one or two units per 10-metre height increase). This approach would clearly necessitate a robust research budget, as well as prior consideration of statistical methods to account for non-independence of vertical camera-traps. However, a scaled-down pilot study with a small number of locations should be feasible and there are potentially high knowledge gains for our understanding of vertical niche partitioning within the canopy, and optimal survey design.

5.3.3 Behavioural studies and other taxa

Gregory and colleagues identified the ability of camera-traps to provide information on arboreal mammal behaviour and group dynamics (Gregory *et al.* 2014), and anecdotal observations from my study (e.g. scent-marking by Prevost's squirrel *C. prevostii* and tufted ground squirrel *R. macrotis*, mating of small-toothed palm civets *A. trivirgata*, and orangutan *P. pygmaeus* family groups comprising mother, dependent baby and independent juvenile) corroborate this. Behavioural studies may be particularly feasible for territorial species such as gibbons (McConkey and Chivers 2007), or those using tree cavities (e.g. Cotsell and Vernes 2016). A further possibility may be the installation within cavities of very small video cameras of the type used in wildlife documentaries, with the potential to provide detailed information on social and breeding behaviour. A high proportion of tropical species are classified 'Data Deficient' by the IUCN (Dirzo *et al.* 2014), thus, behavioural studies facilitated by canopy cameras could provide much-needed insights that help guide population assessments and threat status. Furthermore, while this research focussed on mammals, canopy camera-traps also recorded relatively frequent detections of large birds including five hornbill species, eagles, and owls. There is then perhaps scope for testing the method in studies of certain avian taxa (e.g. Schrul *et al.* 2012).

5.3.4 Responses to structural degradation

Arboreal mammals were more vulnerable to occupancy declines in recovering-logged forest than terrestrial species, and are highly reliant on canopy-level connectivity, although showed counter-intuitive responses to all other measures of forest quality (i.e. occupancy increased as quality decreased) (**Chapter 4**). This may hint at a more complex relationship with forest structure than expected, which warrants further investigation as it has implications for our understanding of the vulnerability of arboreal species to the structural alterations caused by logging. In forest fragments, some birds will vertically expand their territory to compensate for the loss of horizontal habitat area (Bierregard and Lovejoy 1989). Perhaps here, the reverse is true – arboreal mammals in forests that are compacted vertically by reduced tree height may be forced to restrict their vertical range of movement. Thus, activity levels that remain relatively stable in recovering-logged forest (**Chapter 3**), but within a compacted canopy space could produce what appears to be a positive occupancy response to lower habitat quality (**Chapter 4**), but is in fact a response to reduced total habitat area (similar to the horizontal 'crowding effect' seen in forest fragments, e.g. Cudney-Valenzuela *et al.* 2021). Substantiating this hypothesis would require comparative studies in more highly degraded forests, where we would expect the strength of the relationship to increase as degradation increases, up to a threshold beyond which most arboreal species cannot persist. Indeed, regardless of whether compaction occurs, it is important to identify this threshold as it has relevance for the prioritisation of conservation areas that retain sufficient structural integrity to maximise biodiversity retention across strata.

5.4 Conclusion

Throughout this thesis, I demonstrate that canopy camera-trapping provides a robust and replicable sampling method for Bornean arboreal mammals, and that the data obtained add significantly to our understanding of the overall diversity, ecology, and vulnerability to habitat change of rainforest mammal communities. In this exciting new era for tropical canopy research, advanced canopy-access techniques and remote-sensing technologies are facilitating in-depth investigations of one of the least explored ecosystems on Earth. As canopy camera-trapping becomes more widespread, it is my hope that the findings presented here can be used to help inform and develop standard monitoring protocols for tropical forest mammals that take into account the vast three-dimensionality of their habitat. By doing so, I further hope that the knowledge gained will facilitate the implementation of progressive conservation and landscape management policies, that encompass the full biodiversity of rainforest ecosystems, from forest floor to tree crowns.

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Appendix I   Co-authored publications

I provide the titles and abstracts for peer-reviewed journal articles to which I contributed during the course of my PhD, and which are supplementary to the research presented in the main thesis text. These are presented in reverse chronological order and full texts are available online.

In addition, I contributed as lead author of six chapters for WWF Malaysia's Wildlife Atlas of Sabah, due to be published in September 2022. This documents the distribution of wildlife species across Sabah, synthesising all available occurrence, distribution, and ecological information. I contributed all detection records for all mammal species deriving from my PhD fieldwork, and I wrote the species accounts for: black flying squirrel *Aeromys tephromelas*; Thomas' flying squirrel *Aeromys thomasi*; red giant flying squirrel *Petaurista petaurista*; Prevost's squirrel *Callosciurus prevostii*; giant squirrel *Ratufa affinis*; and tufted ground squirrel *Rheithrosciurus macrotis*.

Research article: Estimating animal density for a community of species using information obtained only from camera-traps

Methods in Ecology and Evolution, May 2022, doi:10.1111/2041-210X.13930

Oliver R. Wearn, Thomas E.M. Bell, Adam Bolitho, James Durrant, **Jessica K. Haysom**, Sahil Nijhawan, Jack Thorley, J. Marcus Rowcliffe

Abstract

1. Animal density is a fundamental parameter in ecology and conservation, and yet it has remained difficult to measure. For terrestrial mammals and birds, camera-traps have dramatically improved our ability to collect systematic data across a large number of species, but density estimation (except for species with natural marks) is still faced with statistical and logistical hurdles, including the requirement for auxiliary data and large sample sizes, and an inability to incorporate covariates.

2. To fill this gap in the camera-trapper's statistical toolbox, we extended the existing Random Encounter Model (REM) to the multi-species case in a Bayesian framework. This multi-species REM can incorporate covariates and provides parameter estimates for even the rarest species. As input to the model, we used information directly available in the camera-trap data. The model outputs posterior distributions for the REM parameters—movement speed, activity level, the effective angle and radius of the camera-trap detection zone, and density—for each species. We applied this model to an existing dataset for 35 species in Borneo, collected across old-growth and logged forest. Here, we added animal position data derived from the image sequences in order to estimate the speed and detection zone parameters.

3. The model revealed a decrease in movement speeds, and therefore day-range, across the species community in logged compared to old-growth forest, whilst activity levels showed no consistent trend. Detection zones were shorter, but of similar width, in logged compared to old-growth forest. Overall, animal density was lower in logged forest, even though most species individually occurred at higher density in logged forest. However, the biomass per unit area was substantially higher in logged compared to old-growth forest, particularly among herbivores and omnivores, likely because of increased resource availability at ground level. We also included body mass as a variable in the model, revealing that larger-bodied species were more active, had more variable speeds, and had larger detection zones.

4. Caution is warranted when estimating density for semi-arboreal and fossorial species using camera-traps, and more extensive testing of assumptions is recommended. Nonetheless, we anticipate that multi-species density estimation could have very broad application.

Research article: The potential and practice of arboreal camera trapping

Methods in Ecology and Evolution, June 2021, doi: 10.1111/2041-210X.13666

Jennifer F. Moore, Kylie Soanes, Diego Balbuena, Christopher Beirne, Mark Bowler, Farah Carrasco-Rueda, Susan M. Cheyne, Opale Coutante, Pierre-Michel Forget, **Jessica K. Haysom**, Peter R. Houlihan, Erik R. Olson, Stacy Lindshield, Jonathan Martin, Mathias Tobler, Andrew Whitworth, Tremaine Gregory

Abstract

1. Arboreal camera trapping is a burgeoning method providing a novel and effective technique to answer research questions across a variety of ecosystems, and it has the capacity to improve our understanding of a wide range of taxa. However, while terrestrial camera trapping has received much attention, there is little guidance for dealing with the unique challenges of working in the arboreal realm.

2. Our review draws on the expertise of researchers from six continents and the broader literature to investigate the advantages and disadvantages of arboreal camera trapping, and challenges to consider when using this technology. We also include mini-guides with detailed information on the current arboreal camera trap literature, mounts used to install arboreal cameras, tree climbing pointers and safety tips, methods for deploying cameras without climbing, and tips for managing interference with camera function.

3. We find that arboreal camera traps have been most commonly used in the study of mammals in forests; however, there is potential for this method to be applied to a broad range of habitats including urban areas, and taxa such as birds, amphibians, invertebrates, and plants. Methods in arboreal camera trapping could be improved by developing a greater understanding of the factors affecting detection of species. The most common challenges of arboreal camera trapping are camera placement and camera site access. These can be overcome by understanding correct camera orientation, managing potential sources of interference in front of cameras, utilizing appropriate cameras mounts and training researchers properly.

4. Given the benefits and opportunities presented by arboreal camera trapping, it is likely to become an ever-more popular method of studying arboreal species and systems. The information synthesized in this review provides guidance for future studies to help direct more reliable and robust ecological inferences from arboreal camera trapping.

Research article: Implications of zero-deforestation commitments: Forest quality and hunting pressure limit mammal persistence in fragmented tropical landscapes

Conservation Letters, December 2019, doi: 10.1111/conl.12701

Nicolas J. Deere, Gurutzeta Guillera-Arroita, Philip J. Platts, Simon L. Mitchell, Esther L. Baking, Henry Bernard, **Jessica K. Haysom**, Glen Reynolds, Dave J.I. Seaman, Zoe G. Davies, Matthew J. Struebig

Abstract

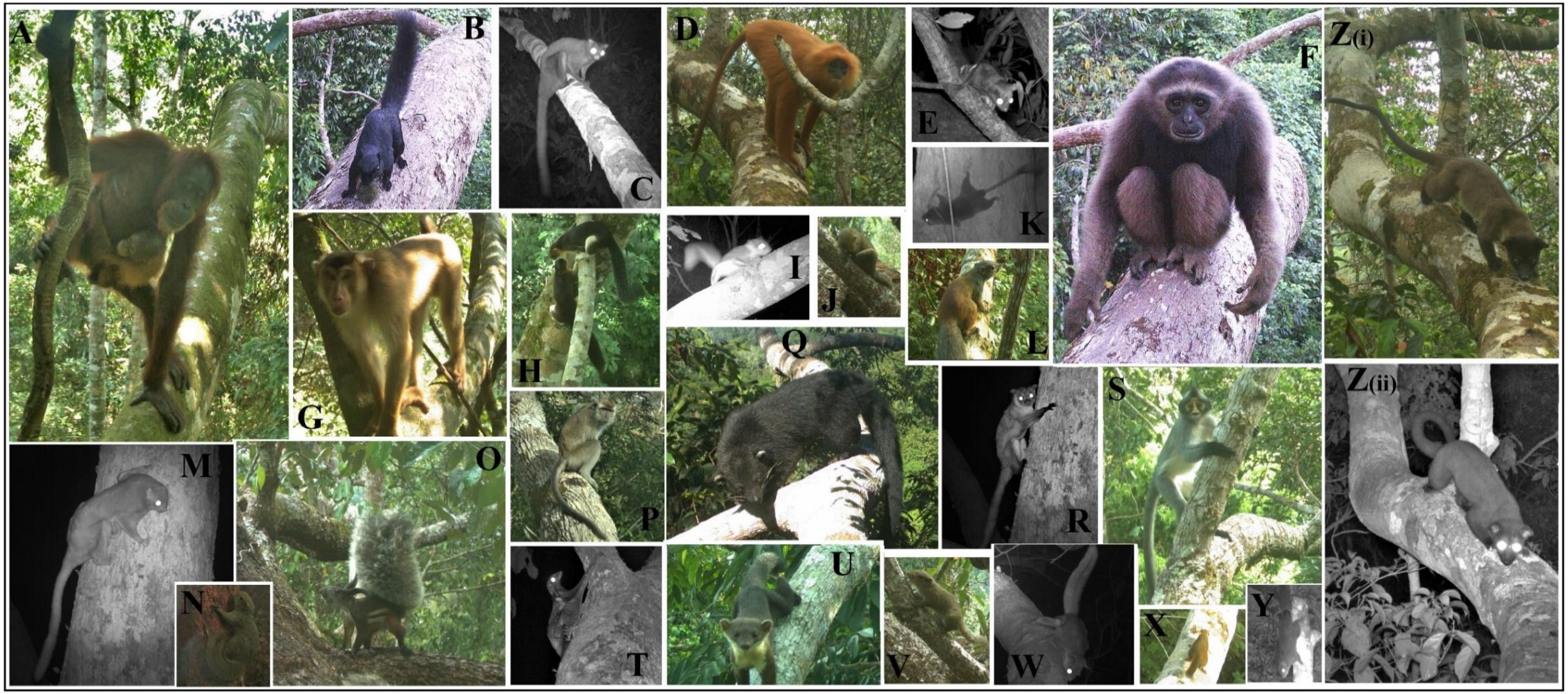
Zero-deforestation commitments seek to decouple agricultural production and forest loss to improve prospects for biodiversity. However, the effectiveness of methods designed to meet these commitments is poorly understood. In a highly fragmented tropical landscape dominated by oil palm, we tested the capacity for the High Carbon Stock (HCS) Approach to prioritize forest remnants that sustain mammal diversity. Patches afforded high priority by HCS protocols (100 ha core area) provided important refuges for IUCN-threatened species and megafauna. However, patch-scale HCS area recommendations conserved only 35% of the mammal community. At least 3,000 ha would be required to retain intact mammal assemblages, with nearly 10 times this area needed if hunting pressure was high. While current HCS protocols will safeguard patches capable of sustaining biodiversity, highly fragmented tropical landscapes typical of zero-deforestation pledges will require thinking beyond the patch toward strategically configured forest remnants at the landscape level and enforcing strict controls on hunting.

Appendix II Comparison of ground and canopy detections of semi-arboreal species

Supplementary Table S5.1 The additional contribution of canopy sampling to presence and distribution data for semi-arboreal mammals. Figures given here exclude detections from the experimental second canopy camera-traps, in order to provide a direct comparison between data obtained from one terrestrial unit versus one canopy unit per sampling location. Total independent detections = 1489 (all cameras): 1246 (84%) from terrestrial units, 243 (16%) from canopy units. Excluding pig-tailed macaque, total detections = 259: 114 (44%) from terrestrial units, 145 (56%) from canopy units.

	No. independent detections				**Distribution across sampling locations**				
Species	**Total, all cameras**	**Terrestrial cameras**	**Canopy cameras**	**Proportion of detections from canopy cameras only**	**Total no. locations detected at (of 50)**	**No. locations detected by cameras in both strata**	**No. locations detected by terrestrial cameras only**	**No. locations detected by canopy cameras only**	**Proportion of locations from canopy cameras only**
Binturong *Arctictis binturong*	25	5	20	80 %	10	2	3	5	50 %
Yellow-throated marten *Martes flavigula*	35	18	17	49 %	16	1	8	7	44 %
Orangutan *Pongo pygmaeus*	51	22	29	57 %	20	2	11	7	35 %
Pig-tailed macaque *Macaca nemestrina*	1230	1132	98	8 %	44	21	22	1	2 %
Long tailed macaque *Macaca fascicularis*	76	6	70	92 %	8	3	0	5	63 %
Horse-tailed squirrel *Sundasciurus hippurus*	11	7	4	36 %	7	0	5	2	29 %
Low's squirrel *Sundasciurus lowii*	2	1	1	50 %	2	0	1	1	50 %
Tufted ground squirrel *Rheithrosciurus macrotis*	53	52	1	2 %	19	1	18	0	0 %
Plain treeshrew *Tupaia longipes*	6	3	3	50 %	4	0	2	2	50 %

Appendix III Arboreal and semi-arboreal mammals recorded in the canopy



Supplementary Figure S5.2. All arboreal and semi-arboreal mammal species recorded on canopy cameras, except Bornean pygmy squirrel *Exilisciurus exilis* due to poor quality image. Images have been cropped for clarity, but all are original camera-trap photographs from this study. (A) orangutan mum and baby, *Pongo pygmaeus* – this image sequence also showed an independent juvenile with the family group; (B) Prevost's squirrel *Callosciurus prevostii* – here carrying fruit in its mouth, possibly to consume away from the source crown, or cache; (C) black flying squirrel *Aeromys tephromelas;* (D) maroon langur *Presbytis rubicunda;* (E) likely smoky flying squirrel *Pteromyscus pulverulentus* – if identification is correct, this record represents the first known photograph of this species; (F) Bornean gibbon *Hylobates funereus;* (G) pig-tailed macaque *Macaca nemestrina;* (H) two giant squirrels *Ratufa affinis* in what appears to be a social interaction – very little is known of the social behaviour of this species*;* (I) Temminck's flying squirrel *Petinomys setosus;* (J) plain treeshrew *Tupaia longipes* – recorded in field guides as strictly terrestrial*;* (K) pentail treeshrew *Ptilocercus lowii;* (L) horse-tailed squirrel *Sundasciurus hippurus;* (M) Thomas' flying squirrel *Aeromys thomasi;* (N) mystery squirrel *Callosciurus sp.* or *Sundasciurus sp.;* (O) tufted ground squirrel *Rheithrosciurus macrotis* – an enigmatic Bornean endemic*;* (P) long-tailed macaque *Macaca fascicularis;* (Q) binturong *Arctictis binturong;* (R) red giant flying squirrel *Petaurista petaurista;* (S) Sabah grey langur *Presbytis sabana;* (T) Sunda colugo *Galeopterus variegatus;* (U) yellow-throated marten *Martes flavigula;* (V) Brooke's squirrel *Sundasciurus brookei* – previously known only from mountains outside of this study's sampling locations, so records here represent a likely range expansion; (W) Horsfield's flying squirrel *Iomys horsfieldi;* (X) ear-spot squirrel *Callosciurus adamsi;* (Y) Low's squirrel *Sundasciurus lowii;* (Zi) a rare daytime record of small-toothed palm civet *Arctogalidia trivirgata;* (Zii) *A. trivirgata* at night.