Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management
Applied Quantitative Ecology Group (AQEG)

Philosophiae Doctor (PhD)
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Activity patterns in tropical forest mammals: a pantropical assessment using camera-trap data

Aktivitetsmønstre til tropiske skogpattedyr: en pantropisk vurdering ved bruk av viltkameradata

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To my son Camilo and the tropical rainforest

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__Article III__

Andrea F. Vallejo-Vargas, Douglas Sheil, Asunción Semper-Pascual, Marcela Guimarães Moreira Lima, Fernanda Santos, Richard Bischof. Spatiotemporal interactions between ocelots and agoutis in Neotropical protected forests. *Manuscript*

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Abstract

Diel activity of animals, the pattern of activity during the 24-hour day, is shaped by species interactions, as well as physiological and anatomical constraints. As such, diel activity patterns are a key expression of a species' ecological niche, and the fast-growing list of studies on this topic illustrates its interest to ecologists. Developments in wildlife monitoring methods and analytical frameworks have boosted our ability to study diel activity of wildlife in situ, with increasing detail and scope. In particular, research on the activity of terrestrial mammals has benefited from the growing popularity and widespread use of camera traps. Multiple studies have explored the role of biotic and abiotic factors in shaping the diel activity of mammals. However, most studies are local and focus on one or a few species; much remains to be learned about the factors explaining diel activity patterns in diverse communities and across large spatial scales. My thesis aimed to investigate patterns and determinants of diel activity in mammals using a large-scale comparative approach focused on terrestrial mammal communities across the tropics.

I explored the diel activity patterns of mammals in tropical forests using an extensive dataset of over 2.3 million camera trap pictures. These images were collected in 17 protected forests following standardized protocols by the Tropical Ecology Assessment Monitoring (TEAM) Network. My PhD thesis comprises four articles.

In **Article I,** I focused on characterizing the diel activity of mammal communities at the forest and biogeographic region levels. I identified two conspicuous activity peaks (i.e., rush hours) in most of these 17 mammal communities and pantropical regions. These peaks of activity coincide with the first and last hours of daylight.

In **Article II,** I looked for evidence indicating a role for top-down versus bottom-up processes, as well as temperature, in shaping the diel activity patterns of tropical forest mammals. I quantified the relationship between body mass and trophic groups in relation to diel activity. This analysis revealed a higher prevalence of nocturnal activity in large herbivores and insectivores (except in the Neotropics) than in smaller species; large species apparently minimize their activity during the warmest hours of the day. I also compared diel activity patterns within and between trophic groups to assess the influence of bottom-up and top-down processes on mammalian activity. My results suggest that species interactions, such as predator-prey relationships, are essential in determining the diel activity of carnivores, omnivores, and small

insectivores. Bottom-up processes, for instance, constrain the activity of large carnivores, whose activity patterns overlap those of herbivores. Simultaneously, top-down processes seem to regulate the diel activity of small omnivores and insectivores, with signals of temporal avoidance of larger carnivores.

Diving further into the effect of species interactions on diel activity, in **Article III**, I investigated the spatial and temporal distribution of activity of predator and prey species in three Neotropical forests. I explored whether agoutis (*Dasyprocta leporina*) respond to a sympatric predator, the ocelot (*Leopardus pardalis*), in space and time. In addition, I examined the degree to which the occurrence of the ocelot was influenced by that of the agouti. My analyses show that ocelots appear to frequent sites where agoutis occur. Conversely, agoutis exhibited reduced activity in sites where the predator occurred, especially during twilight. This behaviour likely minimizes predation risk during a period of peak ocelot activity. This study illustrates how both the spatial and temporal dimensions are required to shed light on the mechanisms facilitating species coexistence.

The last article of this thesis focuses on a particular abiotic factor: moonlight. Darkness dominates the forest floor beneath the canopy of tropical forests, especially at night. How do changes in lunar illumination influence this nocturnal environment for the species that occur there? **Article IV** quantified the prevalence and direction of activity responses to moonlight in tropical forest mammal communities. Of the 86 species with sufficient observations to be included in the study, 17 showed a significant response to moonlight. In these forests, apparent avoidance of moonlight (lunar phobia) is more common (14 species) than apparent attraction (lunar philia, three species). Strongly lunar phobic species, predominantly rodents, were less active during moonlit nights, which, in most cases, also decreased their total daily activity. These findings hold broader implications, especially considering escalating forest degradation and the spread of artificial light.

Data from camera traps spread throughout protected tropical forests were at the heart of this thesis. The TEAM data allowed me to test large-scale hypotheses and make comparisons across biogeographic regions. Findings in this thesis boost our knowledge about diel activity of tropical mammals and the factors shaping it. The consistent results from this thesis serve as a baseline of the diel activity of mammals in wildlife communities with comparatively low anthropogenic impacts. Consequently, general activity patterns and factors identified in this thesis can serve as valuable tools for monitoring temporal changes, such as those associated with global warming or heightened human activities, and contribute to comparative studies spanning forest disturbance gradients, various habitats, or latitudinal differences.

Norsk sammendrag

Dyrs døgnlige aktivitetsmønster formes av artsinteraksjoner så vel som fysiologiske og anatomiske begrensninger. Sånn sett er døgnlige aktivitetsmønstre et nøkkeluttrykk for en art sin økologiske nisje og den raskt voksende listen av forskningsstudier på dette emnet illustrerer økologers interresse i det. Utviklingen innen metoder for overvåking av dyreliv og analytiske rammeverk har styrket vår evne til å studere døgnlig aktivitet blant ville dyr i sitt naturlige miljø, med økende detaljrikhet og omfang. Særlig har forskning på aktiviteten til terrestriske pattedyr dratt nytte av den økende populariteten og utbredte bruken av kamerafeller. Flere studier har utforsket rollen til biotiske og abiotiske faktorer i utformingen av pattedyrs døgnlige aktivitet. Imidlertid er de fleste studier lokale og fokuserer på én eller noen få arter; det gjenstår mye å lære om faktorene som forklarer døgnlige aktivitetsmønstre i forskjellige dyresamfunn og over store romlige skalaer. Målet med min avhandling var å undersøke mønstre og påvirkende faktorer for pattedyrs aktivitet ved å bruke en storskala komparativ tilnærming med fokus på terrestriske pattedyrsamfunn i tropene.

Jeg utforsket døgnlige aktivitetsmønstre hos pattedyr i tropiske skoger ved hjelp av en omfattende datasett med over 2,3 millioner bilder fra kamerafeller. Disse bildene ble samlet inn i 17 vernede skoger etter standardiserte protokoller fra Tropical Ecology Assessment Monitoring (TEAM) nettverket. Min doktoravhandling består av fire artikler.

I **Artikkel I** fokuserte jeg på å karakterisere døgnlig aktivitet i pattedyrsamfunn på skog- og biogeografisk område- nivå. Jeg identifiserte to tydelige aktivitetstopper (rush hour) i de fleste av disse 17 pattedyrsamfunnene og pantropiske regionene. Disse aktivitetstoppene sammenfaller med de første og siste timene med dagslys.

I **Artikkel II** søkte jeg etter bevis som kan indikere en rolle for topp-ned eller bunn-opp prosesser, så vel som for temperatur, i utformingen av døgnlige aktivitetsmønstre hos pattedyr i tropiske skoger. Jeg kvantifiserte forholdet mellom kroppsvekt og trofiske grupper i forhold til daglig aktivitet. Denne analysen avslørte en høyere forekomst av nattlig aktivitet hos store planteetere og insektetere (unntatt i Neotropene) enn hos mindre arter; store arter ser ut til å minimere aktiviteten sin under de varmeste timene av døgnet. Jeg sammenlignet også døgnlige aktivitetsmønstre innenfor og mellom trofiske grupper for å vurdere innflytelsen av bunn-opp og topp-ned prosesser på pattedyraktivitet. Resultatene mine antyder at artsinteraksjoner, som rovdyr-byttedyr forhold, er avgjørende for å bestemme døgnlig aktivitet hos rovdyr, altetere og små insektetere. Bunn-opp prosesser begrenser for eksempel aktiviteten til store rovdyr, hvis aktivitetsmønstre verlapper med de hos planteetere. Samtidig ser det ut til at topp-ned prosesser regulerer daglig aktivitet hos små altetere og insektetere, som ser ut til å unngå større rovdyr i tidsdimensjonen.

Ved å dykke dypere inn i effekten av artsinteraksjoner på daglig aktivitet, undersøkte jeg i **Artikkel III** den romlige og tidsmessige fordelingen av aktivitet hos rovdyr- og byttedyrarter i tre neotropiske skoger. Jeg undersøkte om agoutier (*Dasyprocta leporina*) reagerer på en sympatrisk rovdyr, oceloten (*Leopardus pardalis*), i rom og tid. I tillegg undersøkte jeg i hvilken grad forekomsten av oceloten ble påvirket av agoutien. Mine analyser viser at oceloter ser ut til å oppsøke steder der agoutier forekommer. Omvendt viste agoutier redusert aktivitet på steder der rovdyret forekom, spesielt i skumringen. Denne atferden minimerer sannsynligvis risikoen for predasjon i en periode med økt ocelotaktivitet. Denne studien illustrerer hvordan både romlige og tidsmessige dimensjoner kreves for å belyse mekanismene som muliggjør arters sameksistens.

Den siste artikkelen i denne avhandlingen fokuserer på én spesifikk abiotisk faktor: månelys. Mørket dominerer skogbunnen under det tropiske skogtaket, spesielt om natten. Hvordan påvirker endringer i månebelysning dette nattlige miljøet for artene som finnes der? **Artikkel IV** kvantifiserte prevalensen og retningen på aktivitetsresponsene på månelys i pattedyrsamfunn i tropiske skoger. Av de 86 artene med tilstrekkelige observasjoner til å bli inkludert i studien, viste 17 en betydelig respons på månelys. I disse skogene er tilsynelatende unngåelse av månelys (lunær fobi) mer vanlig (14 arter) enn tilsynelatende tiltrekning (lunær fili, tre arter). Sterkt lunær fobiske arter, hovedsakelig gnagere, var mindre aktive under månelyse netter, noe som i de fleste tilfeller også reduserte den totale døgnlige aktiviteten deres. Disse funnene har brede implikasjoner, spesielt med tanke på økende skogforringelse og spredningen av kunstig lys.

Data fra kamerafeller fordelt over vernede tropiske skoger var hjertet av denne avhandlingen. TEAM-dataene tillot meg å teste hypoteser på stor skala og gjøre sammenligninger på tvers av biogeografiske regioner. Funnene i denne avhandlingen styrker vår kunnskap om døgnlig aktivitet hos tropiske pattedyr og faktorene som former den. De konsistente resultatene fra denne avhandlingen fungerer som en grunnlinje for døgnlig aktivitet hos pattedyr i dyresamfunn med relativ lav antropogen påvirkning. Derfor kan generelle aktivitetsmønstre og faktorer identifisert i denne avhandlingen tjene som verdifulle verktøy for overvåking av temporale endringer, slik som de knyttet til global oppvarming eller økt menneskelig aktivitet, og bidra til komparative studier som strekker seg over skogforstyrrelsesgradienter, ulike habitater eller breddegrader.

Synopsis

1. Introduction

In this thesis I endeavor to elucidate patterns and drivers of the diel activity of mammals in protected tropical forests across biogeographic regions. Mammals, being integral to ecosystem functioning through predation, herbivory, and nutrient cycling, significantly contribute to the biological diversity of tropical forests (Lacher Jr et al. 2019).

Despite the ubiquity of human interventions globally, tropical forests are among the least disturbed ecosystems worldwide (Belote et al. 2020). I used camera-trap data collected from 17 protected areas spanning four biogeographic regions to conduct an in-depth exploration of the ecology of forest mammal communities. This investigation delves into the intricacies of which, when, and why animals are active at specific times within the 24-hour day, shedding light on the coexistence dynamics among species in these diverse ecosystems. The findings of this thesis contribute to a comprehensive understanding of the daily life complexities in tropical forests. These results provide foundational baseline for monitoring changes over time, particularly in relation to biodiversity threats, such as global warming, the increase of artificial light, and habitat degradation. In the subsequent sections, I will explain the central concepts necessary for a through comprehension of the research presented in this thesis.

1.1. Ecological niche

The ecological niche represents the set of resources and environmental conditions, both biotic and abiotic, that a species requires to survive and reproduce (Hutchinson 1957). There are two important concepts related to the ecological niche: the fundamental and the realized niche. The fundamental niche is the theoretical set of abiotic conditions (e.g., humidity, temperature) required by a species to persist in the absence of competitors or limiting factors (e.g., resource availability, Grinnell 1917). On the other hand, the realized niche is shaped by species interactions. A realized niche comprises the conditions a species utilizes and can be restricted by competitors or predators, or expanded by interactions such as mutualism (Gause 1934, Hutchinson 1957). In essence, the fundamental niche is defined by the potential range of conditions suitable for a species to live in the absence of other species, while the realized niche is the observed and quantifiable range that accounts for species interactions.

A way to illustrate a species' niche is by considering two resources, such as space and food, and projecting them onto two axes. Figure 1 illustrates this by considering a subset of mammals inhabiting a Neotropical forest for which we can identify the ecological niche of a species. In Figure 1a, each mammal species has a specific niche characterized by its trophic group and forest strata. Trophic groups provide insights into the species' dietary preferences, while forest strata characterize the spatial environment where a species lives and moves.

Figure 1b shows the fundamental and realized niche for two armadillo species. All armadillo species have similar diet requirements (all consume insects), yet two species can coexist in a single forest. In this scenario, space becomes one niche axis. While the fundamental niche of one species may be broad individually, the presence of a second species in the same habitat reduces their respective niches. To avoid competition, these species occupy different parts of the forest. The nine-banded armadillo (*Dasypus novemcinctus*) occurs mainly in core areas of the Atlantic Forest of Brazil, while the six-banded armadillo (*Euphractus sexcinctus*) prefers forest edges (Ferreguetti, Tomas and Bergallo 2016). This spatial differentiation in habitat utilization by each of these species represents their realized niches. It also indicates that resource partition (niche partitioning), in terms of space, facilitates the coexistence of species.

Following Hutchison's (1957) definition, the niche is an "n-dimensional hypervolume" or hyper-space, where "every point corresponds to a state of the environment which would permit a species to exist indefinitely" (Hutchinson 1957). Therefore, the niche of a species is more complex than the two-dimensional representation used in the previous examples because all species have several environmental and resource requirements. However, to understand species' ecological niche and the mechanisms of coexistence between species, ecologists use the prominent dimensions of the niche: space, trophic position, and time, as discussed below (Chase and Leibold 2009, Hut et al. 2012).

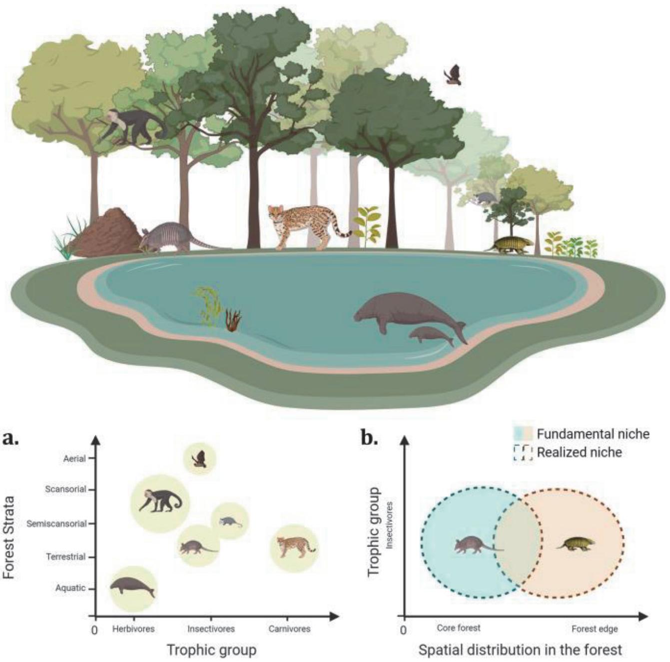


Figure 1. Example of the ecological niche of a subset of tropical mammal species. a) Two dimensions of the niche defined by forest strata and diet, b) Fundamental and realized niche of two species of armadillos (the nine-banded armadillo's niche is restricted by the presence of yellow armadillos). The illustration was created with BioRender.com and edited to include the yellow armadillo. The yellow armadillo was designed by rawpixel.com/Freepik (free license).

1.1.1. Time as a key dimension of the ecological niche

The variation of light and temperature driven by yearly, monthly, or daily natural cycles are prominent factors that yield a diverse array of adaptations in animals (Chesson 2000, Hut et al. 2012). Therefore, time is a key component of the ecological niche.

On a yearly basis, the rotation of the Earth around the sun leads to seasonal changes. Seasonal variations differ along the latitudinal gradient. While seasonality is strong in high latitudes, low latitudes have mild seasonality. Seasonal fluctuations in light and temperature exert variation on resource availability (Tonkin et al. 2017). Consequently, seasonality plays a major role in shaping the ecological niche of species. As a strategy to survival and reproduction many species give birth to their young at similar times of the year, when resources are abundant. In high latitudes, for instance, mammals synchronize births with spring or summer when food is abundant (Bronson 2009).

The lunar cycle, which last approximately 29 days, play a role in shaping the niche of some species. The amount of moonlight visible from the Earth contribute to differences in the night conditions, shaping the temporal niche of some species. For instance, the reproductive period of Eurasian badgers (*Meles meles*) coincides with the periods of new moon (Dixon et al. 2006).

1.2. Diel activity patterns

At a fine temporal scale, the Earth's rotation on its own axis results in the diel cycle of day and night. Animals distribute their activity along the continuum of the 24h day, known as **diel activity patterns** (a.k.a., daily activity timing, daily activity patterns, diel activity rhythms, Gilbert et al. 2022, Figure 2). The diel activity pattern reflects the times when animals forage, socialize, and perform other necessary tasks while also responding to risks and physiologic constraints (e.g., timescape of heat or fear, Veldhuis et al. 2020, Gilbert et al. 2022). Therefore, diel activity patterns represent an important aspect of the species realized niche.

1.1.2. Diel niche

The **diel niche** (i.e., temporal niche) is defined by the prevalent diel activity of a species during the 24h day. In other words, the diel niche is a high-level categorization of diel activity patterns assigned by standard definitions (Anderson and Wiens 2017, Gerber et al. 2023). Species are categorized in one of these four diel categories: diurnal (active solely or primarily during the day), nocturnal (active solely or primarily during the night), crepuscular (active solely or primarily during twilights), and cathemeral (active throughout the day). Each species with a particular diel niche possesses a set of traits (e.g., eye morphology) that enables it to exploit the diel cycle in different ways.

The traits allowing a species to be active at certain times of the day are outcomes of the evolution to biotic (competition or predation) and abiotic (light, temperature) factors (Hut et al. 2012, Baker and Venditti 2019). For example, nocturnal species are more sensitive to light by having larger corneas and pupils, diurnal species have longer focal distances to facilitate visual acuity (Hall and Ross 2007), and cathemeral species have intermediate eye shapes (Kirk 2004, 2006).

Research on the diel niches of species have broad ecological implications (Kronfeld-Schor and Dayan 2003, Hut et al. 2012). This is because the traits a species exhibits to be active during specific times of the day mirror its ecological function in the ecosystem. Notably, there is a widespread focus on studying the diel niche and diel activity patterns of mammals. This emphasis is due to mammals' integral role in ecosystem functioning and the advancements in monitoring wildlife and methodological frameworks to study the temporal niche of mammals.

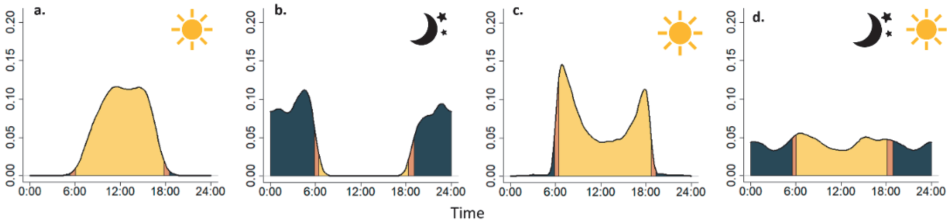


Figure 2. Diel activity patterns examples of the four diel niches: **a.** diurnal, **b.** nocturnal, **c.** crepuscular, **d.** cathemeral species.

Previous studies that explored the diel niche across terrestrial mammal species and biogeographic regions have broadened the understanding of the temporal component of the ecological niche. Such studies have shown the association of diel niches with species traits and their distribution across latitudes and biogeographic regions. Bennie and colleagues (2014) identified a correlation between the duration of daylight and darkness in relation to species diel niches. They predicted the distribution of mammal species' richness in each diel niche. Nocturnal mammals dominate worldwide; cathemeral species are more prevalent in the Holarctic region, where daylight and twilight hours are long. While the proportion of nocturnal species is high in arid regions and low at high elevations, there is a high proportion of diurnal and nocturnal species in tropical regions (Bennie et al. 2014).

Moreover, Cox and colleagues studied the diel niche of mammals worldwide. They assessed the relationship between mammal species traits (e.g., body mass, litter size) and diel niche. They reported that nocturnal mammal species have a larger set of unique trait combinations than diurnal and crepuscular species (Cox, Gardner and Gaston 2021). Additionally, the decline of mammal populations appears to be higher for diurnal mammals than for nocturnal, crepuscular and cathemeral species, indicating a higher extinction risk for diurnal mammals (Cox, Gardner and Gaston 2023). Furthermore, cathemeral species are likely to be more flexible in adapting to human interventions (Cox and Gaston 2023).

1.1.3. Circadian Rhythms

Internal circadian rhythms may regulate the diel activity patterns of wildlife. Circadian rhythms are persistent biological rhythms of ~24 hours, originating from clock gene expression triggered by cues such as light (day, night) or temperature

(Aschoff 1966). They regulate the daily organization of animal activity. While circadian rhythms are investigated in laboratory or controlled conditions, it is not plausible to confirm if wildlife diel activity emerges from these internal rhythms.

Furthermore, diel activity patterns of wildlife can be plastic and change with conditions such as food availability, rain, temperature, and the presence or absence of predators (Levy et al. 2019, Hart et al. 2020). Some species can display extreme activity shifts, transitioning from day to night or vice versa (Hut et al. 2012). However, it is unclear whether activity shifts are adaptive with low fitness costs or whether shifts and the unknown correlation with internal clocks could affect species' fitness (Riede, van der Vinne and Hut 2017, Gilbert et al. 2022).

Nonetheless, evidence from controlled studies (e.g., outdoor experimental enclosures) suggests that disruption of the circadian rhythms affects the fitness of individuals. For example, mice with disrupted circadian clocks have lower fitness (e.g., survival and reproduction) than control individuals (Spoelstra et al. 2016). Moreover, humans (primarily diurnal) who work at night or have high exposure to nighttime lights have a higher incidence of particular diseases (e.g., metabolic dysfunction, Bedrosian and Nelson 2017). Although there is little evidence on how shifts in the diel activity may affect species' fitness, basic knowledge of how wildlife distributes their activity is needed before the effects of diel activity changes can be assessed.

1.3. Biotic and abiotic factors shaping diel activity patterns.

Abiotic factors

Air temperature plays a crucial role in modulating body temperature and behavior. Animals that keep their body temperature stable by thermoregulation (i.e., heat production and dissipation) are called endotherms (e.g., mammals and birds). Endotherms can maintain their body temperature when the environmental temperature is within a certain range. However, when the temperature increases above or decreases below a threshold (i.e., thermoneutral zone), endotherms increase their metabolic rates to either dissipate heat by evaporative cooling or to produce heat. To decrease the risk of overheating or hypothermia, endothermic animals display distinct behaviors such as finding refuges, changing postures, or shifting their activity toward times during the day that are warmer or colder (Terrien, Perret and Aujard 2011). An example of such behavior is reported in the diel activity of giant anteaters (*Myrmecophaga tridactyla*) inhabiting the Brazilian Pantanal wetland: this species avoid overheating by extending its activity during the night and resting during the day (Giroux et al. 2023).

Another aspect that shapes the diel activity of animals is light. Natural light comes directly from the sun and by moonlight. Moon illumination has an impact on the diel niche of many species. It is reported that moonlight deters the activity of some species but boosts the activity of other species (Kronfeld-Schor et al. 2013, Prugh and Golden 2014). For example, the nine-banded armadillo (*Dasypus novencinctus*) decreases its activity (Harmsen et al. 2011), while nocturnal primates such as tarsiers (*Tarsius spectrum*) increase their activity during moonlit nights (Gursky 2003).

Biotic factors

Species interactions, such as predator-prey interactions, intraguild interactions (e.g., top predators and mesopredators), and competition shape species diel activity (Schoener 1974, Richards 2002). Predators and prey are in a constant arms race. Predators seek to overlap in time and space with their prey, while their prey tries to minimize spatial and temporal overlap with them (Sih 2005, Eriksen et al. 2011).

In other words, diel activity patterns of prey and predators may emerge from a combination of top-down and bottom-up behavioral processes, mirroring the way consumptive processes regulate food webs (Duffy 2002, Sinclair, Mduma and Brashares 2003, Beschta and Ripple 2009). Within predator-prey systems, some species show clear temporal avoidance to the activity of their predators (Tambling et al. 2015), suggesting a top-down effect on the prey behavior. For example, kudus (*Tragelaphus strepsiceros*) in South Africa are active during the day when nocturnal predators are present (Tambling et al. 2015). In other cases, predators such as jaguars overlap with the activity of their prey as giant anteaters (*Myrmecophaga tridactyla*) (Foster et al. 2013, Botts et al. 2020), suggesting a bottom-up effect on predator behavior.

In intraguild interactions, particularly within the carnivore guild, studies suggest that mesopredators (e.g., ocelots) exhibit low overlap to that of top predators (e.g., jaguars, Santos et al. 2019), suggesting a top-down effect on the activity of mesopredators.

Competition is another biotic factor that shapes the diel niche. Species with similar traits and requirements may coexist in a habitat by resource partitioning (e.g., time) (Schoener 1974, Kronfeld-Schor and Dayan 2003). For example, the margay (*Leopardus wiedii*) and the jaguarundi (*Herpailurus yagouaroundi*) have similar body sizes and sets of traits, yet they exhibit contrasting diel activity patterns in the Atlantic Forest, a subtropical region. The margay is primarily nocturnal, and the jaguarundi is primarily diurnal (Cruz et al. 2018). In this example, time serves as a resource that enables species to coexist -referred to as temporal partitioning-.

Biotic and abiotic factors are important drivers shaping the diel activity patterns of mammals, as previously shown. However, most studies investigate the effects of individual factors (e.g., biotic or abiotic) or their responses in a few species or locations.

1.4. The interplay between biotic and abiotic factors

The diel activity pattern of species results from balancing the responses to both biotic and abiotic factors. Consider, for example, the activity of herbivores that predators seek after. Herbivore diel activity is a balance of trade-offs between its traits to be active at specific times of the day (e.g., daytime), minimizing energy expenditure (e.g., avoiding extreme diurnal temperatures), foraging to meet energetic needs, and maximizing predator avoidance (Lima 1998).

For instance, in savannahs, herbivore activity reflects a trade-off between predation risk and thermoregulation. In sites where predators are present, prey species reduce their activity overlap with that of the predators. The time when prey is active to avoid predators coincides with hours of high temperature, resulting in high energy expenditure to thermoregulate. In areas where predators are absent, the same prey species are active during hours of low temperature (Veldhuis et al. 2020).

Thus, the observed activity pattern of a species results from the intertwined responses of both biotic and abiotic factors and is modulated by the context, such as the presence of predators. In the case of the prey in this example, if the temperature increases in savannahs due to climate change, prey species in areas with predators would be forced to balance their activity. They will either increase their overlap with the predator's activity to avoid overheating or increase their energetic expenditure for thermoregulation (Veldhuis et al. 2020). In both cases, individuals may experience reduced fitness.

Although both biotic and abiotic factors shape the diel activity pattern of animals, untangling the intertwined relationships between these factors is not always straightforward. Moreover, the variation of responses -such as prey exhibiting distinct diel patterns compared to their predator or displaying similar patterns- obscures the understanding of how important certain factors are compared to each other and how species coexist in the temporal dimension within a community. For instance, it is unclear whether the activity of prey (e.g., herbivores) is mostly shaped by the constant avoidance of the predators (top-down) or vice versa (bottom-up) and whether temperature is a stronger driver of activity than biotic interactions in mammals in other habitats such as tropical forests.

As community ecology seeks to identify general principles, a question emerges concerning the diel activity of mammals: are the processes or factors influencing the diel activity patterns of mammal similar across communities and biogeographic regions?

Convergence in factors shaping the diel activity could be expected, given that animals in different regions often fulfill similar functions in the ecosystem (e.g., predators consuming prey, herbivores consuming plants). The similarity in functions implies shared morphological characteristics resulting from convergent evolution, driven by similarities in the abiotic (e.g., light, temperature) and biotic (e.g., predation) factors shaping them (McGhee 2011). Hence, quantitative analysis of diel activity patterns at larger scales, such as pantropical analyses, is needed to unravel which processes and factors are prevalent in shaping diel activity of mammals among communities in distinct biogeographic regions.

1.5. Studying diel activity in wildlife

Our knowledge about wildlife activity patterns is constantly growing, thanks to the rapid development of methodological frameworks and new technologies such as passive detection devices (e.g. camera traps, acoustic sensors) (Frey et al. 2017, Oliver et al. 2023) and tracking devices (e.g., GPS tags, and accelerometers) (Brown et al. 2013, Whitford and Klimley 2019).

Before all these technological advancements, scientists relied on direct observations to make inferences on the diel activity patterns and diel niche of species (Belovsky and Slade 1986, Koprowski and Corse 2005). The drawback of using direct observation to describe diel niche lies in the potential bias associated with the presence of humans as a factor shaping the activity of animals and the difficulty of humans to observe individuals during the night and quantify their activity.

Tracking devices are suitable methods for extracting individual behavior data with a high level of detail but to limited extent. These methods allow researchers to obtain detailed information on the time of activity, movement, or body temperature (Feierabend and Kielland 2014, Hertel, Swenson and Bischof 2017). However, they are invasive as they require physical capture and are also costly and logistically challenging to implement on more than a few individuals from a given population.

Camera-traps, in contrast, provide low individual-level detail but cover entire populations and even communities. These non-invasive devices record the exact time when movement in front of the camera triggers the sensors. Camera-traps can reduce bias (e.g., human presence) on species behavior and enable surveys throughout all periods of the day, including nighttime (Bridges and Noss 2011). The drawback of camera traps is the lack of individual identification (at least in most cases), which prevents measuring species abundance of species without visual individual marks, such as agoutis. Additionally, camera trap detections can be biased depending on where the cameras are placed (e.g., trails or different heights) or by the different species detection probabilities. Some species may be curious about camera-traps in the forest, while other species may be shier (Rovero et al. 2013). Nevertheless, the records of animals captured in camera-traps are representative of the populations in a community. Therefore, tracking devices are more appropriate for addressing individual-specific questions, while camera-traps are more suitable for assessing population or community questions (Hebblewhite and Haydon 2010, Wearn and Glover-Kapfer 2019).

Originally, camera-trap surveys were introduced to determine species richness or abundance of species. However, as the use of camera-trap extended, it became a valuable tool for addressing knowledge gaps regarding species distribution in space and time (Burton et al. 2015, Frey et al. 2017). With the increasing availability of camera-trap data and the rapid development of ecological models, studies that quantitatively test hypotheses regarding diel activity patterns of mammals have proliferated in the last decade (Gilbert et al. 2022). Nevertheless, most studies assessing diel activity include few species and single communities or biogeographic regions.

Despite increased camera-trap monitoring over time and worldwide, biodiverse regions remain neglected. For instance, camera-trap monitoring in tropical forests, such as the Amazonian and Congo Forest basins, generally receives limited research allocation (Mugerwa et al. 2023). Consequently, research on diel activity in mammals in tropical regions is a notable research gap.

1.6. Tropical forest mammals

Tropical forests are considered the most productive terrestrial ecosystems on Earth (Huston and Wolverton 2009). Tropical forests are characterized by tall old-growth trees, dense canopies, high annual precipitation (>1500 mm), evergreen vegetation, and low variation of day and night lengths (Figure 2). These forests typically experience hot weather (over 20°C), and the dry season is either short or absent (Corlett and Primack 2011, Jacobs 2012). Such forests are found in different biogeographical regions: Neotropical, Afrotropical, Malagasy, Indo-Malayan, and Australasian. Tropical forests are also known for being the most diverse region in the world for all taxa and harbor all possible types of species interactions (Schemske et al. 2009). Despite the wide separation and distinct biotas, these regions share many related taxa (e.g. tapirs are present in the Americas and Southeast Asia, Ghazoul and Sheil 2010).

Figure 2. Examples of forest structure in tropical forests include evergreen forest (a), large trees (b), and canopy. a. Tortuguero National Park, Costa Rica (Photo: Andrea Vallejo-Vargas), b. Yasuní National Park, Ecuador (Photo: Andrea Vallejo-Vargas) & c., Bwindi Impenetrable Forest (Photo: Aida Cuni-Sanchez).

Notwithstanding their general characteristics, tropical forests harbor significant variation in species composition between biogeographical regions (Ghazoul and Sheil 2010, Corlett and Primack 2011). Concerning mammal species, notable differences exist. Malagasy forests, for instance, host a unique diversity of lemurs and few predators. The Afrotropical region features exclusively terrestrial lineages like ground-dwelling primates and large mammals. In the Neotropical region, there is a lower species richness of large mammals than in the Afrotropical region. Southeast Asia showcases isolated taxa in their islands and New Guinea has an absence of monkeys (Ghazoul and Sheil 2010). These contrasting differences in community structure and mammal species richness within tropical forests result from different biogeographic histories (evolutionary mechanisms of adaptation and speciation, Ghazoul and Sheil 2010, Gallery 2014). However, when considering the trophic composition (proportion of trophic groups) of mammals in protected areas, the differences across continents are minimal (Rovero, et al. 2019). The similarity in trophic composition is likely driven by shared conditions (biotic and abiotic) of tropical forests across biogeographic regions (McGhee 2011).

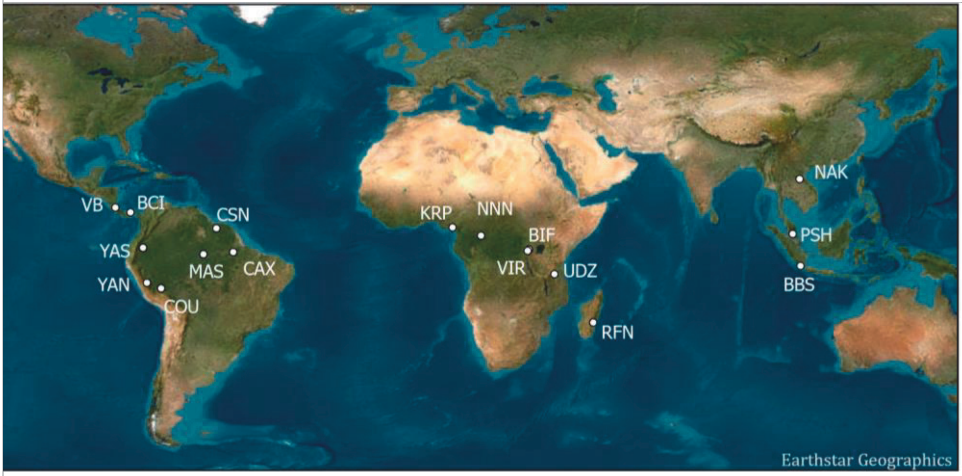
Despite hosting the highest terrestrial biodiversity, tropical forests experience fast habitat degradation and species extinction. Thus, protected areas are key elements for conservation across the tropics (DeFries et al. 2005). Although most forests have (or have had) human activities and some protected areas have experienced extinctions caused by human interventions (Benítez-López et al. 2019), some protected tropical forests are considered intact forests, assumed to be large enough to "maintain all native biodiversity, including viable populations of wide-ranging species" (Potapov et al. 2008).

Therefore, protected areas are representative examples of ecological communities and laboratories for ecologists that aim to study ecological processes. The protection of tropical forest and the existing camera-trap data collected in some of these forests provides a unique opportunity to test quantitatively hypotheses regarding diel activity of wildlife across forests and biogeographic regions.

1.7. TEAM database

I employed camera trap data collected in 17 protected areas across continents by the Tropical Ecology Assessment and Monitoring (TEAM) Network under a standard protocol (Box1). The TEAM Network was a cross-regional program designed in 2002 and implemented from 2007 onwards (see Box 1). Each study site was monitored and coordinated by a manager and a broad group of people, including biologists and local guides. The TEAM program was "designed as an early warning system for tropical rain forests" (Rovero and Ahumada 2017). TEAM aimed to assess trends of biodiversity change across protected areas through long-term camera-trap monitoring. The monitoring aimed to assess the diversity of birds and mammals in tropical forests under a systematic and standardized protocol to allow comparisons over time and space (Ahumada et al. 2011, Beaudrot et al. 2016). Therefore, the TEAM camera-trap data provides a unique opportunity for a robust comparative assessment of the diel activity patterns of tropical mammal species.

Box. 1. Tropical Ecology Assessment Monitoring (TEAM) camera trap data

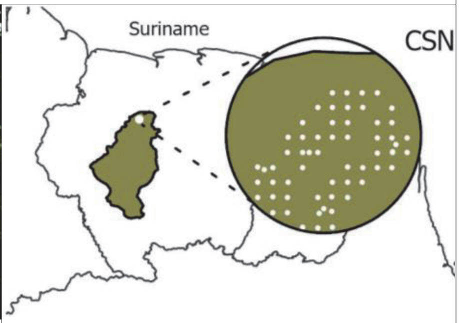


Earthstar Geographics

The TEAM database contains over 2.3 million images of mammals, including 270 species, 58 families, and 18 orders. The monitoring took place in 17 protected areas worldwide corresponding to four biogeographical regions (Neotropical, Afrotropical, Malagasy, and Indo-Malayan tropics) and gathered for over ten years (2007-2017). Camera-traps were deployed following a standardized protocol in all protected areas, mainly during the dry seasons. At each protected area, the monitoring ran from two to ten years with the deployment of 60 to 90 cameras annually. Camera-traps were placed at a density of 0.5–1 camera/km2 (1 camera every km2 or 1 camera every 2 km2) and remained active for ~30 consecutive days.

Box. 1. Tropical Ecology Assessment Monitoring (TEAM) camera trap data (continuation)

Camera trap deployment in Bwindi Impenetrable Forest (BIF) in Uganda. Photo by: Badru Mugerwa

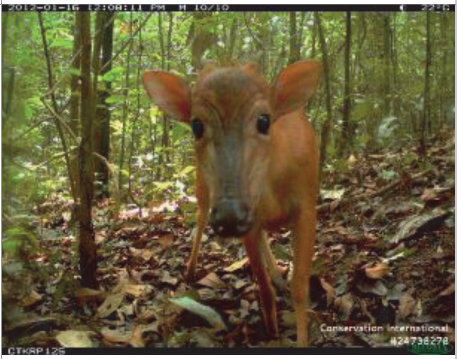


Central Surinam National Park (CSN) in Suriname and camera trap array.

Jaguar (*Panthera pardus*) in Caxiuanã National Forest

Forest elephants (*Loxodonta cyclotis*) in Noaubale-Ndoki National Park

Anteater (*Myrmecophaga trydactila*) in Yasuni National Park



Ogilby's duiker (*Cephalophus ogilbyi*) in Korup National Park

2. Thesis objectives

In this PhD thesis, I aimed to identify and quantify the drivers governing the diel activity patterns of mammal communities in protected areas across pantropical forests, employing data collected by the Tropical Ecology Assessment Monitoring (TEAM) Network. Specifically, this thesis had three main goals:

1) Assess the diel activity of tropical forest mammals quantitatively and determine whether activity patterns across communities and regions converge or diverge.
2) Deepen our understanding of how species coexist (species interactions) in space and time.
3) Deepen the understanding of how moonlight and temperature shape the diel activity of tropical forest mammals.

To achieve these goals, I established four main objectives:

1. Describe the diel activity pattern of the forest floor mammal communities detected with camera- traps (Article I).
    a. Compare the diel activity of mammal communities in different tropical regions to determine whether communities in distant regions are similar or diverge.
    b. Determine which species groups shape the activity of forest mammal communities.
2. Assess how diel activity patterns relate to species characteristics of tropical mammals across regions and the processes behind them (Article II).
    a. Identify the relationship between species characteristics (such as body mass and diet) and the diel activity of mammals.
    b. Determine the primary factor constraining the diel activity of tropical mammals, whether it be the energetic costs associated with thermoregulation or the influence of species interactions through top-down or bottom-up processes.
    c. Compare such patterns across regions.
3. Clarify mechanisms of coexistence of a predator and a prey in space and time (Article III).
    a. Estimate whether prey and predator spatial distribution is associated or segregated in three areas (Neotropical region).
    b. Estimate the diel activity of the prey and the predator and identify prey responses (e.g., changes in diel activity) to predator occurrence in space and time.

4. Examine and understand how tropical mammals respond to the lunar cycle (Article IV).
    a. Assess the prevalence of positive (lunar philia) or negative (lunar phobia) responses to moonlight quantitatively.
    b. Test the link between a species' degree of nocturnality and its propensity to avoid moonlight.
    c. Identify and quantify changes in activity (e.g., shifts, increase, decrease of activity) of lunarphilic or lunarphobic mammals.

3. Methods

To accomplish the objectives of this thesis, I used the time stamp and the location of camera-trap pictures from the data collected from the TEAM Network (See Box. 1) among tropical forests. To analyze the data, and clarify the underlying patterns, I used both frequentist and Bayesian frameworks.

Statistical frameworks

In Articles I and II, I used kernel density functions of the records of mammals to the 24 hours which allowed determining the diel activity patterns of species (Ridout and Linkie 2009). Kernel density functions are common methods used to assess the activity of animals (Box 2). However, to make inferences about processes shaping the diel activity of tropical mammals across communities and regions, I fitted generalized mixed models (Box 2) and multinomial logistic models that allowed me to incorporate the variation between the different protected areas studied.

For articles III and IV I fitted custom-built models in a Bayesian framework (Box 2). The transition from a Frequentist to a Bayesian framework in this thesis was driven by the complexity of the questions we sought to address and the enhanced flexibility that contemporary tools provide us as ecologists.

Box 2. Statistical methods employed in this thesis

Kernel density function in diel activity patterns estimates the concentration of events (i.e., pictures) in a given time during the 24h-day (Ridout and Linkie 2009, Rowcliffe et al. 2014). Generalized linear models (GLM) allow identification and quantification of the relation between one or more predictor variable(s) and a response variable. Generalized linear models allow non-normal distribution of the response variables, such as Multinomial or

Poisson distribution which arise from count data (Myers and Montgomery 1997). I fitted GLM models in Article II and submodels in Articles III and IV.

Generalized additive model (GAM) model allows a non-linear relationship between the predictor and the response variable. In its place, the response variable changes linearly with smooth functions of the predictor variables (Yee and Mitchell 1991). This is especially useful when the predictor variables are spatial or temporal. I employed GAM models in Article I.

Mixed models allow me to account for the variation in the data associated to repeated measures (i.e., random effects) when fitting a generalized model. Specifically, in this thesis, I used data from 17 protected areas, and each protected area represented one study site. We accounted for the variation between protected areas to extract the most prevalent pattern across protected areas. Therefore, in this study, I include random effects in the regional models in GLMM and GAMM models in Articles I and II.

Multinomial logit models are a generalization of logistic regression that allows the assessment of the relation between a response variable with more than two outcomes and the predictor variable (e.g., body mass). I used multinomial logit models (Article II, IV). In Article II, I used multinomial models to test the probability of mammals being active during the day, night, and twilight, given their body mass and diet. In Article IV, we employed multinomial models to test the probability of diel activity during the day, twilights, new moon, transition, and full moon in a Bayesian framework.

Bayesian framework allowed us to estimate parameters (e.g., occupancy or activity in moonlit nights) in Articles III and IV. The main motivations to use the Bayesian framework were: i) to build custom models to answer complex questions and build customized models, ii) the ability to easily propagate uncertainty to the final estimates using MCMC methods (see MCMC), and iii) the facility to provide a quantitative assessment of the probability of hypotheses to be true based on observed data (Royle and Dorazio 2008, de Valpine et al. 2017, Kéry and Royle 2017).

Hierarchical models allowed us to answer ecological questions from observations (e.g., camera-trap data) regarding where and when species are active. Hierarchical models in ecology are models that include submodels for both the ecological process (e.g., occupancy) and the observation process (e.g., photographic detection, Kéry and Royle 2017). In this example, the detection process implies that the data is imperfect due to variations from the monitoring methodology (e.g., camera trap model, height of placement of camera traps) or the intrinsic features of the species studied (e.g., arboreal, Rovero et al. 2013). Therefore, hierarchical models allow the estimation of parameters such as the occupancy of species accounting for the variation in the detection process and other variables of interest (e.g., time of the day). I employed a hierarchical model with a Bayesian framework in Article III.

Markov Chain Monte Carlo (MCMC): MCMC methods are random sampling algorithms used to draw simulations from the posterior distributions of a model's parameters (e.g., detection, occupancy). The samples from the posterior distribution using MCMC allow the characterization of a parameter, such as its mean and variance (de Valpine et al. 2017, Kéry and Royle 2017).

3.1. Methods for each study

Article I

We characterized the activity of forest mammal communities and across regions and defined general patterns in two steps. First, to identify patterns across the 17 protected areas, we fitted a Generalized Additive Mixed Model (GAMM) to all records of mammals aggregated by minute of the day for each tropical region. We analyzed 175,867 independent events (i.e., interval > 1 minute between pictures of one species in each camera trap site) of 270 mammal species and 10 identified to genus. To identify which species groups contributed the most to the community-level pattern within each region, we included data on the species characteristics (trophic group and body mass) from the PHYLACINE database (Faurby et al. 2018). We fitted GAMM models (Box 2) to all records of mammals aggregated by hour of the day and the interaction with the trophic guild to describe patterns at each tropical region. Second, to define the diel activity patterns of each community, we fitted a kernel density function to all records of mammals in each of the 17 protected areas.

Article II

To identify the relationship between species characteristics (trophic group and body mass) and diel activity, we analyzed the data from 16 protected areas, comprising 166 species and a total of 126,382 independent events (time interval between pictures > 1 h per camera for a given species). We fitted multinomial models with body mass and trophic groups as predictor variables and the number of records during the day, night, and twilight as response variables in each tropical region.

To test whether top-down or bottom-up processes shaped the activity of tropical mammals, we employed Generalized Linear Mixed Models (GLMMs, Box 2). These models allowed us to make pairwise comparisons between species groups. For instance, we fitted the number of records per hour of small herbivores as a response to the activity of large predators. By using the number of events in each hour, we investigated whether the activity of top predators drove or was driven by the activity of their prey. Additionally, we inspected whether the results aligned with pairwise comparisons in each of the 16 protected areas. To do so, we fitted Kernel density functions for each species group and extracted overlap estimates between the density functions for each pairwise comparison (Ridout and Linkie 2009). Finally, we visually compared whether the relationships between diel activity and species characteristics were consistent or divergent across biogeographic regions.

Article III

We used a custom-built single-season occupancy model for two interacting species (Kéry and Royle 2017) in three protected areas: (Central Suriname National Park (CSN), Caxiuanã National Forest (CAX) and Manaus (MAS). We used the data of the ocelot (*Leopardus pardalis*) and the red-rumped agouti (*Dasyprocta leporina*) with a total of 272 and 4013 observations (hours with at least one photographic detection at a given camera trap location), respectively. Occupancy models take into account the imperfect detection of species and thereby generate unbiased estimates of the probability of species occupancy (Mackenzie 2006, Burton et al. 2015). We used detection probability as a proxy for activity and included the effect of the three periods of the day (day, night and twilight) in the detection process. To test if the spatial distribution of the predator overlaps with that of the prey, we estimated the occupancy of the predator in sites where the prey was or absent. To identify temporal responses of the prey to the occupancy, we estimated the prey's detection during three diel niches (day, night, and twilights) in sites where the predator was present or absent.

Article IV

We used custom-built Bayesian multinomial models to determine the responses of tropical mammals to the moonlight in three main steps. First, we fitted a multinomial model that simultaneously allowed us to predict diel niche of the species (diurnal, crepuscular, and nocturnal) and the lunar responses to lunar activity patterns (full moon, transitional, new moon). We examined whether tropical mammals tend to be attracted (lunar philia) or avoid (lunar phobia) moonlight, using a dataset of 86 species in 17 protected areas (2.1M camera-trap pictures). Second, to identify the link between species nocturnality and lunar phobia, we fitted a modified version of the first model by incorporating a submodel to estimate the relationship between diel (diurnal, crepuscular) and lunar activity (full moon, new moon, transition). Finally, we used a third model to identify changes in activity (e.g., shifts, increase, decrease of activity) of lunar philic or lunar phobic mammals. This model included two submodels. Submodel 1 modelled the activity during 24-hour periods with and without full moon at night to identify changes in diel activity. Submodel 2 modelled the amount of activity during the same period to identify whether total activity increased or decreased during periods with moonlit nights.

For Articles III and IV, we fitted the models with Markov chain Monte Carlo (MCMC) with Numerical Inference for Statistical Models Using Bayesian and Likelihood Estimation NIMBLE (de Valpine et al. 2017).

4. Thesis summary

In this thesis, I quantified the diel and lunar activity of tropical forest mammals and determined patterns across regions and mammal communities. I focused on understanding how processes (bottom-up & top-down) and abiotic factors (temperature and moon illumination) shape the diel activity.

In Article I, we found that the diel activity of tropical forest mammal communities across continents was characterized by two activity peaks associated with sunrise and sunset. In addition, we identified that small and medium-sized herbivores were the main drivers of this pattern. The other guilds, such as omnivores or insectivores, had higher activity during the night. These two peaks appeared in most protected areas studied and across regions.

In Article II, we found that body mass and diet were predictors of diel activity patterns of mammals across all tropical forest regions. Large herbivores and insectivores (except in the Afrotropical region) had higher nocturnality than small herbivore species. We attributed this finding to the thermoregulatory constraint of large mammals to avoid overheating during day hours. We reported an opposite for carnivores and omnivores. We found evidence that both bottom-up and top-down processes shape the diel activity mammal communities. While bottom-up processes indicated that large carnivores matched the activity of large-size herbivores and small herbivores (except for the Afrotropical region), top-down processes shaped the activity of small omnivores and insectivores by reducing the overlap of activity with large carnivores. The divergent patterns in the Afrotropical region could be explained by differences in the abundance of prey or predators not assessed in this study.

In Article III, we teased apart the mechanisms of coexistence of a predator-prey system -the agouti (prey) and the ocelot (predator)- in both space and time. Ocelots appeared to seek sites where the agoutis occurred. On the other hand, agoutis appeared to decrease their activity in sites where the predator was present, especially during the twilights, to avoid the time when the predator was most active.

In Article IV, we found that 17 of the 86 species studied were responding to moonlight, even though we measured activity in the understory under the dense canopy of tropical forests. We found a higher prevalence of lunarphobia than of lunarphilia. Generally, lunar phobic species decreased their overall activity, and lunar philic increased their overall activity during periods with moonlit nights. Some of the species responded to the moonlight by shifting their activity. For example, the lunarphobic and nocturnal armadillos shifted their activity toward twilights.

5. Discussion

Overall, the findings of my thesis show that tropical forest mammal communities across continents converge in their diel activity patterns (Article I and II) and have similar processes and factors shaping these patterns (Article II, and IV). Moreover, a closer examination allowed me gain a deeper understanding of predator-prey coexistence in space and time (Article III) to tease apart the responses of mammal species to moonlight (Article IV).

5.1. Consistent patterns across continents and communities

Similarities among tropical regions are found in the morphological characteristics of the species (Corlett and Primack 2011), and community composition (Rovero and Ahumada 2017). These similarities result from convergent evolution. There are several examples of morphological convergences across the tropics. For instance, phylogenetically distant species such as the aardvarks (*Orcypteropus afer*) in the Afrotropical region and the anteaters (*Myrmecophaga tridactyla*) in the Neotropics have similar morphology and function in their ecosystems (McGhee 2011). Both species are terrestrial, placental mammals with long, strong claws and specialized snout morphology to consume ants (McGhee 2011). At the community level, the compositions of trophic groups across tropical regions are similar (Rovero et al. 2020). In line with morphological convergences and community similarities across regions, our analysis revealed consistent diel activity patterns of mammals across biogeographic. Across regions and in most communities, we found two peaks of activity associated with sunrise and sunset, a pattern similar to that of birds (Burivalova et al. 2018). Moreover, we found evidence of convergence in the processes shaping the diel activity of these communities (Article II). The convergence of diel activity across regions and communities likely resulted from the similar ecological factors that characterize tropical forests. For example, tropical forests have similar lengths of day, night and twilight and low seasonality compared to higher latitudes (Bennie et al. 2014).

My thesis contributes to the knowledge of the ecology of the diel activity of tropical mammals. The results from Articles I and II provide quantitative support for studies investigating the diel niche of species employing categorical data (e.g., diurnal, nocturnal). The study of Bennie and colleagues (2014) showed a consistent biogeographic distribution of mammal species with a prevalence of diurnal and nocturnal species across tropical regions. In this thesis, we found consistent patterns in other ways. First, there are two activity peaks at the community and regional levels

(Article I). Second, there is a similar direction on the relationship between the diel activity and species trophic groups and body size across biogeographic regions. For example, in all three regions the nocturnal activity was predicted to increase with body size (Article II). These similarities align with the association of mammal traits between body mass, diet, sociality, and species' diel niche, as reported by Cox and colleagues (2021). However, our quantitative analysis indicates the direction of the relationship between trophic groups and body mass and the diel activity of tropical mammals. Therefore, it provides a detailed understanding of when a tropical mammal is more likely to be active during the 24 hours of the day. For example, we could predict that small omnivores are generally more active at night than during the day.

Deepening our comprehension of the factors influencing the diel of forest mammal communities, we found evidence that for herbivores temperature constrain their activity. While biotic factors for other mammals' groups (e.g., carnivores) predator-prey interactions were the main constrain of their diel activity. Digging into the responses of individual species responses, moonlight influenced mainly the activity of nocturnal mammals.

5.2. Biotic factors – prey-predator interactions (Article II and III)

Species interactions between predators, prey, and competitors shape the activity of mammals (Schoener 1974). In this thesis, the primary focus was on the coexistence of predators and prey. There is evidence of predator activity overlapping prey activity (bottom-up) and of prey avoiding the activity of predators (top-down, Monterroso, Alves and Ferreras 2013, Ross et al. 2013, Veldhuis et al. 2020). In this thesis, I identified the importance of the two processes (bottom-up process and top-down) shaping the activity of tropical mammals (Article II).

Large predators appeared to match the activity of large and small herbivores in most regions (except for the Afrotropic large predators and small herbivores). The evidence on bottom-up processes shaping the activity of large predators is consistent with individual studies in Malaysia (Borneo) tropical forests and in Costa Rica (Talamanca Cordillera) montane forests (Ross et al. 2013, Botts et al. 2020). For instance, in Borneo Sunda clouded leopards' activity patterns overlapped with the activity of sambar deer (*Rusa unicolor*) and greater mouse deer (*Tragulus napu*) (Ross et al. 2013). In contrast, in habitats such as savannas and open habitats, most herbivores prey avoid the overlap with the activity of predators (e.g., lions and hyenas, Tambling et al. 2015, Veldhuis et al. 2020). The contrasting patterns between the activity of top predators and herbivore prey in tropical forests and savannahs may suggest that habitat differences may play a role in shaping the activity of communities.

The evidence of top-down processes shaping the diel activity of some species with intraguild (i.e., same trophic guild) interactions and predator-prey interactions is scattered. For example, in an intraguild interaction, mesopredators, such as the ocelot, avoid the overlap of activity to that of top predators (Santos et al. 2019). Similarly, in a predator-prey interaction, a prey such as the European rabbit has a low overlap with the activity of its predators (Monterroso, Alves and Ferreras 2013). In this thesis (Article II), I found evidence for top-down processes when looking at specific groups of species (large carnivores vs. small insectivores) in certain regions. For example, I found temporal avoidance of small omnivores and insectivores (e.g., Afrotropics) to the activity of large carnivores. Despite the indication that top-down processes shape the diel activity of small omnivores and insectivores, the simultaneous relationship between small carnivores and small omnivores is worth noting. Small carnivores overlapped small omnivores' activity, pointing to a bottom-up effect. These findings indicate that both processes, bottom-up and top-down, appear to shape the diel activity of the community simultaneously.

Despite finding a prevalence of specific processes, there is variation in the prevalence of bottom-up or top-down patterns or abiotic factors shaping the diel activity when looking into specific protected areas and among species (Supplementary material Article II). The variation may arise from different aspects, such as greater human activity outside the protected areas (Semper-Pascual et al. 2023).

Alternatively, the variation may have arisen from the spatial distribution of species in the studied forests. Despite this, our study shed light on the patterns of temporal coexistence in tropical forests; species coexistence depends on species' spatial distribution (Chesson 2008). Therefore, we zoomed in on a predator-prey system and accounted for the spatial occurrence of the species. We demonstrated a possible mechanism for how a predator (ocelot) and a prey (red-rumped agouti) coexist (Article III). Ocelots appeared to seek sites where the agouty occurred. The lowered activity of agoutis in sites where the predator occurred, especially during the twilights (to avoid the time when the predator was active) demonstrated that species coexist in complex ways.

5.3. Abiotic factors shaping the activity mammals (Article II, IV)

Temperature

A key predictor of animal activity appeared to be temperature, especially for large herbivores (Article II). The higher proportion of nocturnal activity in large herbivores compared to that of small herbivores pointed to a stronger effect of temperature on large herbivores and insectivores (except in the Afrotropics). Large herbivores, such as elephants, are active during day and night to forage and fulfill their energetic demands (van Schaik and Griffiths 1996). At the same time, large herbivores in warm environments with a low risk of predation may reduce overheating by being proportionally more active during the night than during the day to avoid the warmest periods of the day (e.g., diurnal hours) (Mccain and King 2014).

Moonlight

The second abiotic factor, moonlight (Article IV), appeared to predominantly reduce (i.e., lunar phobic) the activity of nocturnal tropical mammals. Only three species were categorized as lunar philic. Our results from tropical regions are consistent with those from the metanalysis published by (Prugh and Golden 2014). The decrease in activity of some prey species is likely explained by the predicted increase in predation risk during moonlit nights (Kronfeld-Schor et al. 2013). Indeed, most lunar phobic species are prey items of predators. For example, the lunar phobic lowland paca (*Cuniculus paca*) is a prey of jaguars (*Panthera onca*) (Foster et al. 2010, Harmsen et al. 2011).

We found two main categories of responses. On the one hand, most lunar phobic species decreased overall activity during the 24-hour day with moonlight, without corresponding activity changes during other periods (e.g., day). Other species respond to moonlight by a shift of activity into or out of the illuminated period. For example, some lunar phobic species shifted their activity from night to twilight without a change in net activity during elevated illumination at night. Some lunarphilic species increase their activity and shift it to the night (e.g., hare, *Lepus americanus*). Shifts in activity indicated that species are flexible to changes and can compensate for times when foraging may be dangerous or when they can increase their food intake (Hut et al. 2012).

5.4. Limitations of this study and future work

Tropical forest mammals show consistent diel activity patterns across regions (Articles I and II). How consistent these patterns are in other regions or how much season influences such patterns is unknown. Therefore, the study in the tropical forest represent a baseline to compare with the diel activity of mammals in different habitats to test whether the processes shaping the diel activity of mammals are similar or different. For example, in our analysis of tropical forest mammals, we show that the activity of large predators matches the activity of herbivore prey (Article II). Whereas in savannas the activity of prey show a clear avoidance to the activity of their predators (Veldhuis et al. 2020).

Another aspect to consider is seasonality in the diel activity of mammals. Tropical forest has low seasonality when compared with higher latitudes. However, tropical forests differ in precipitation and temperature between rainy and dry seasons (Jacobs 2012). In this thesis, we used camera-trap data from the dry season because monitoring with camera-trap is constrained to the driest months as floods and humidity damage the cameras. The effects of seasonality are reported to affect the diel activity patterns of some species (e.g., ocelots in Pantanal Brazil, Finnegan et al. 2021). Therefore, how mammal communities respond to the rainy season remains a knowledge research gap.

One aspect I did not cover in this Ph.D. thesis is the prevalence of competition shaping the diel activity patterns of species. Several studies have shown the importance of competition for species to shape their diel activity (de Satgé, Teichman and Cristescu 2017, Karanth et al. 2017). Evidence shows how mammals within the same trophic group, such as carnivores, coexist (Foster et al. 2013). Although we found small carnivores activity responding negatively to the activity of large carnivores, we did not find significant evidence of intraguild avoidance, and we did not test how mammals of similar size and trophic guild coexist (Article II). Therefore, studying competition is a possible research path to understand patterns on a larger scale in the tropical forest studied.

Forthcoming studies assessing the coexistence of species in space and time would benefit from including other species in the model to understand the community ecology better. For that, flexible models and data collected across different forests and regions have the potential to show how mammal communities coexist in time and space.

Finally, more studies will be needed to understand whether and how these mammal communities' diel activity patterns respond to human interventions (e.g., hunting, fragmentation, forest edges). Despite the protection status of the study sites, human activities such as hunting, illegal logging, or tourism are ongoing in some protected areas (Laudati 2010, Rovero et al. 2012, Espinosa and Salvador 2017). Moreover, there is evidence that the functional diversity and the occurrence of mammals in forest edges respond to human population density (Gorczynski et al. 2021, Gorczynski et al. 2022, Semper-Pascual et al. 2023). While not at the community level, shifts or variations in diel activity of tropical mammals due to human intervention as hunting, tourism, or forest fragmentation are reported for several species (e.g., *Tayassu pecari,* sun bear *Helarctos malayanus, Sus barbatus*) (Espinosa and Salvador 2017, Davison et al. 2019, Cremonesi et al. 2021).

5.5. Implications for conservation

In a rapidly changing world, it is crucial to provide baseline evidence that enable to predict the effects of changes in the ecosystems, and to try to prevent them. However, we still lack a comprehensive understanding of the ecology of many species and communities. This thesis contributes to our understanding of the patterns of coexistence and diel activity of mammal species in protected areas in tropical forests.

The pattern of each community with the two peaks of activity around sunrise and sunset (e.g., Article I) can be used as a community fingerprint to assess whether and how they change over time. Additionally, community diel activity of protected areas from this study can be compared to unprotected tropical mammal communities.

Given the ongoing threats to biodiversity worldwide, the primary environmental factors that are predicted to affect mammal behavior in tropical forests (beyond habitat loss) are temperature increases (related to global warming), human activity (e.g., tourism, hunting), and artificial light (Kronfeld-Schor et al. 2017, Gaynor et al. 2018).The rise of air temperature will strongly impact diurnal hours of the day. Hence the nocturnal activity reported for large herbivores and insectivore mammals in this thesis could increase due to global warming as a mechanism to decrease thermal stress during the hot hours of the day (Mccain and King 2014).

Another factor expected to exert changes in the diel activity of mammals is the increasing availability of artificial light (Kronfeld-Schor et al. 2017). If animals perceived artificial light similar to the moonlight, it could enable some diurnal species to shift their activity towards the night. Like the moonlight, artificial light enhances visibility during the night. Although few wildlife species exploit the moonlight niche (Article IV) (Prugh and Golden 2014), those that do are primarily diurnal or crepuscular. For example, the white-lipped peccary (*Tayassu pecari*), are mainly diurnal and active during full moon nights (Article IV). I speculate that the 29 days duration of the moon cycle, with only few illuminated nights in a month, may have prevented diurnal species from exploiting this niche. The increasing availability of artificial light could allow some species to exploit the night. If (diurnal, cathemeral) species shift or increase their activity towards the night, the already nocturnal species may experience increased competition.

For nocturnal species, moon phases represent different temporal niches. Among 14 species, dark nights are the time when they are the most active, and most species decrease their activity with moonlit nights (Article IV). These species appeared to be dark specialists. While some showed shifts towards crepuscular-nocturnal hours, none of the nocturnal lunarphobic species in this study shift their activity towards the day. Therefore, darkness may constitute an irreplaceable niche for certain species. If animals perceive artificial light as moonlight, they may respond similarly, affecting the time of activity and, consequently, their fitness.

The predicted changes mentioned above have the potential to have cascading effects on species communities and ecosystems. For example, if large herbivores shift their diel activity towards the night to avoid thermic stress, or to avoid the diurnal activity of humans, as previous studies suggest (Mccain and King 2014, Gaynor et al. 2018, Cox and Gaston 2023), top-predators (that in our analysis are more diurnal) are expected to maximize the overlap of their activity to that of their main prey and potentially become more nocturnal. Predator shifts may affect other trophic groups, such as small omnivores (that are more nocturnal) because predation risk will increase at night. For some species, the perceived risk can induce stress, reduce the time for foraging (e.g., agouti Article III), and reduce survival rates in prey populations. Therefore, the continuation of long-term monitoring of species activity patterns represent a crucial conservation tool for these tropical forests to identify changes in the diel activity of mammals over time and inform management strategies that prevent knock-on effects, such as biodiversity loss.

6. Concluding remarks

This PhD thesis contributes to ecological knowledge of tropical mammals' diel activity across four biogeographic regions. I quantified diel activity of mammals with data collected in 17 protected tropical forests. This research provided clear evidence of the prevalence of abiotic and biotic factors shaping the diel activity of mammals across tropical regions. The indication of both top-down and bottom-up processes shaping the diel activity of mammals in a community contributes to understanding how mammals coexist in diverse forests. Moreover, a closer look at a predator-prey system by integrating both space and time informed of detailed coexistence mechanisms. Abiotic factors, such as temperature, appeared to be the primary factor shaping the diel activity of herbivores, while moonlight affected mostly the diel activity of some nocturnal mammals and drove changes in their behavior. In this PhD

I have demonstrated that the diel activity patterns of tropical forest mammals in different communities and regions converge. Such responses likely arose from similar conditions in these forests. Therefore, the consistent patterns helped create a baseline, which can be used to monitor change over time (e.g., related to global warming or an increase in human activities) and contribute to comparative studies across forest disturbance gradients, habitats, or latitudes.

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Articles

ARTICLE I

Rush hour for tropical forests mammals

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Summary

Animal communities in species-rich tropical forests exhibit a hustle and bustle of feeding, foraging, mating, and socialising. Is there order in this exuberant diversity through the daily life of tropical mammals? A pantropical camera-trap network and standardised monitoring allowed us to study community-level activity patterns. This yielded over 2.3 million photos of 270 identified mammal species in 17 protected tropical forests and four realms (Neotropical, Afrotropical, Malagasy, and Indo-Malayan). We used these data to characterise overall patterns of daily or "diel" activity at forest and regional levels. We also assessed the contribution of different trophic groups to activity patterns. We detected two peaks– "rush hours". These peaks were broadly consistent across different forests and coincided with the first and last hours of daylight, which have comparatively cool temperatures. Small- and medium-sized herbivores were the primary contributors to the rush hour, while carnivores, omnivores, and insectivores showed varied activity. Community-level patterns identified in protected tropical forests can serve as a reference for comparison with less pristine communities. Localised divergence from the otherwise consistent pattern remains unexplained.

1 Results and Discussion

Species have distinct patterns for scheduling activity and rest throughout each 24-hour day, i.e., their daily or "diel" activity patterns(Rowcliffe et al. 2014). Some species are nocturnal, such as the Amazonian or Malayan tapirs (*Tapirus terrestris, T. indicus*, respectively), or diurnal, like the Southern pig-tailed macaque (*Macaca nemestrina*). Some species have peaks of activity that coincide with dusk and dawn (crepuscular), like the Indo-Malaya's chevrotain (*Tragulus kanchil*), a small ungulate. Yet other species, such as the African golden cat (*Caracal aurata*), may be active anytime during a 24-hour period, without consistent periods of rest (i.e., cathemeral). Previous tropical forest studies that recorded rainforest sounds produced by various animals e.g., birds, insects, and primates, revealed prominent bimodal patterns known as the "dawn and dusk choruses" (Staicer, Spector and Horn 1996, Hutchinson 2002, Burivalova et al. 2018, Gil and Llusia 2020). Indeed, dawn and dusk choruses involving a cacophony of birdsong are widespread across multiple continents and habitats and will be familiar to many readers, both in the tropics and elsewhere, around dawn and dusk (Gil and Llusia 2020).

A growing number of studies analyse the diel activity of mammals through camera-trap pictures around the world (Linkie and Ridout 2011, Monterroso, Alves and Ferreras 2013, Bischof et al. 2014, Cruz et al. 2014, Santos et al. 2019, Di Bitetti et al. 2020, Gilbert et al. 2022). Do photographic captures reveal a consistent diel activity pattern in in forest mammal communities similar to that found in forest sounds? The diel activity of animals reflects the trade-off between meeting their various needs (e.g., foraging), while managing various physiological constraints and the inherent risks of living in a habitat shared with other organisms (e.g., predators, competitors, and kleptoparasites, Schoener 1974, Kronfeld-Schor and Dayan 2003). Comparisons of community-level patterns among different forests and regions can indicate whether universal mechanisms shape mammal communities and their behavioural ecology (Frey et al. 2017). In addition, knowledge about community-level diel activity in protected tropical forest offers a baseline for future studies aiming to understand how activity patterns can change in more or less pristine contexts.

Here we used camera-trap data from 17 tropical protected areas in four realms (Neotropical, Afrotropical, Malagasy and Indo-Malayan) gathered by the Tropical Ecology Assessment and Monitoring (TEAM) Network following a consistent protocol (Jansen et al. 2014, Rovero and Ahumada 2017). Our objectives were to i) characterise the diel activity of mammal communities in each protected areas and realm and ii) assess how patterns differ between species groups with different traits (i.e., trophic guild, body size) and its contribution to the diel activity pattern of their communities. We analysed 175,867 independent events (i.e., interval > 1 minute between pictures of one species in each camera trap site) of 270 mammal species and ten identified to genus. We assessed diel activity patterns and how this varied with trophic guild, body size, protected area, and realm to characterise the daily activity of mammal communities. We fitted two generalised additive mixed models (GAMM) to data from each of the four realms to characterise the community diel activity among realms and the contribution of four main trophic guilds (herbivores, carnivores, insectivores, and omnivores). To predict the community activity distribution in each realm, we modelled the number of events per hour of the day (Figure 1, see Methods). We then ran a second set of models to describe the contribution of each trophic guild. We included protected area as a random effect in both sets of models to account for associated unmeasured variation. Finally, to describe the community diel activity for each protected area, we fitted a circular kernel density function to events in every minute in a given forest (see Methods).

Rush hours in the tropical forests

“Rush hour” typically refers to peak periods of people moving to and within a city during mornings and evenings, when roads and public transport are at their busiest. These activity peaks are the cumulative activity of numerous commuters going back and forth between their homes and workplaces. Camera traps revealed similar rush hours—periods of visible activity—in the daily life of tropical forest mammals.

Despite differences in fauna, location, environmental conditions, and anthropogenic influences among the forests in this study, we consistently identified two peaks of activity, “rush hours”. These peaks coincided with hours after sunrise and before sunset or overlapped the transition between light and dark periods of dawn and dusk (i.e., Malagasy tropics, Figure 1). The first peak was associated with the low temperatures around sunrise, and the second peak with the temperature decline preceding sunset (Figure 1, Figure 2). These results provide an additional way of viewing the similarity of mammal diel activity among tropical realms, likely reflecting similar responses to shared conditions (e.g., daylight duration, temperature, Vallejo-Vargas et al. 2022).

Second, our study extends the bimodal pattern previously reported for selected mammal species (Ashby 1972, Blake et al. 2012) and birds (Aschoff 1966, Burivalova et al. 2018, Gil and Llusia 2020) to the entire community of tropical mammals detected by camera traps. This bimodal pattern was visible in most protected areas (Figure 2). We did not find consistent evidence suggesting that the bimodal peaks around sunrise and sunset result from the overlap in activity among diurnal and nocturnal species. We observed such overlap in only five of 17 protected areas (Figure S4, see Methods).

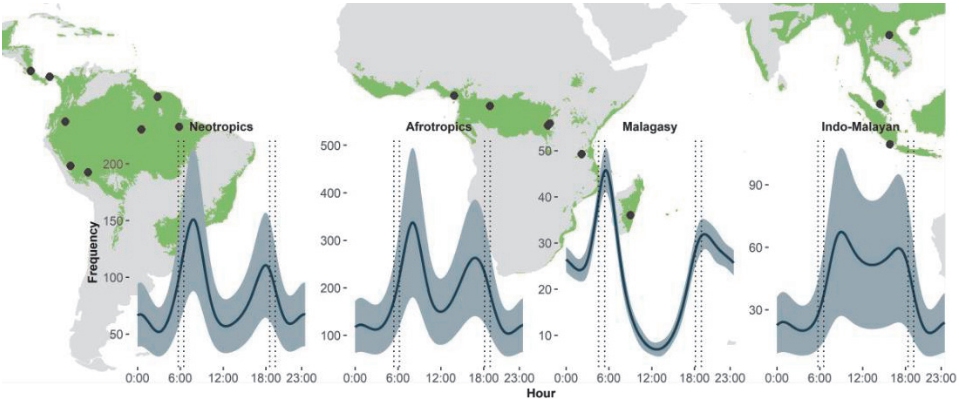

Figure 1. "Rush hours" in four tropical realms. Plots represent the frequency of independent events- photographic detections of mammals at camera traps - per hour predicted with realm-specific GAMM models. Grey bands represent confidence intervals, and vertical dashed lines the mean for dawn, sunrise, sunset, and dusk among protected areas in each realm. Grey dots on the maps represent the 17 protected areas where camera traps were systematically deployed. Green shading illustrates tropical forests distribution (Olson et al. 2001).

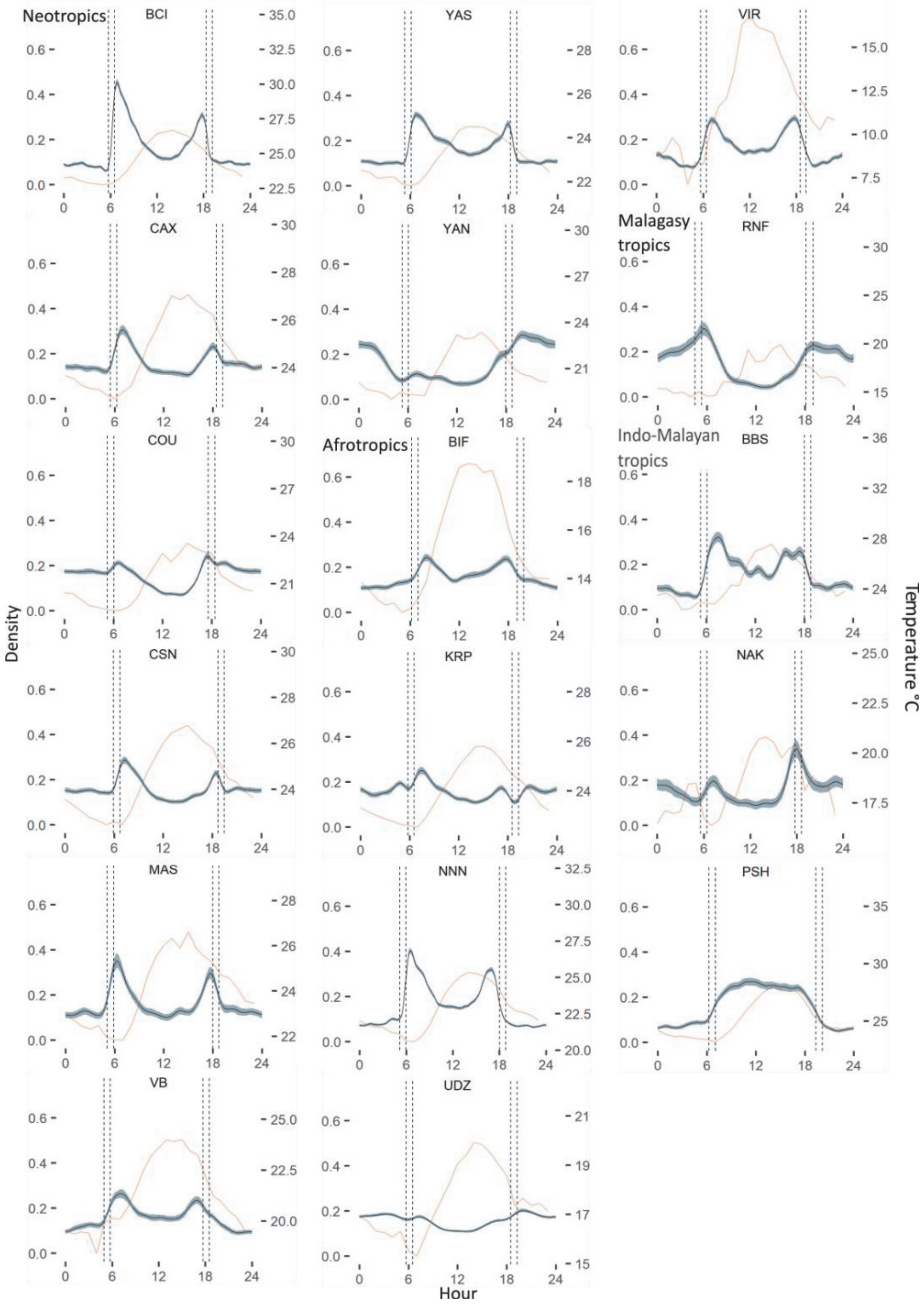

Figure 2. Community-level activity and mean temperature across four realms. Each plot displays the smoothed kernel density functions of activity at a given protected area (black line), with confidence intervals (grey shaded area). The orange line corresponds to the mean temperature every minute (°C) at each protected area. Vertical dashed lines represent the mean for dawn, sunrise, sunset, and dusk, standardised for each protected area.

Trophic guild contributions to rush hours

Each trophic guild made distinct contributions to the community diel activity patterns. Herbivores provided the most observations and evident bimodal activity in all domains (Figure 3). The dominant contribution of herbivores reflects the greater number of species, observation records (Figure S1, Figure S2), and implicit occurrences compared with other guilds (e.g., carnivores, insectivores)(Semper-Pascual et al. 2022).

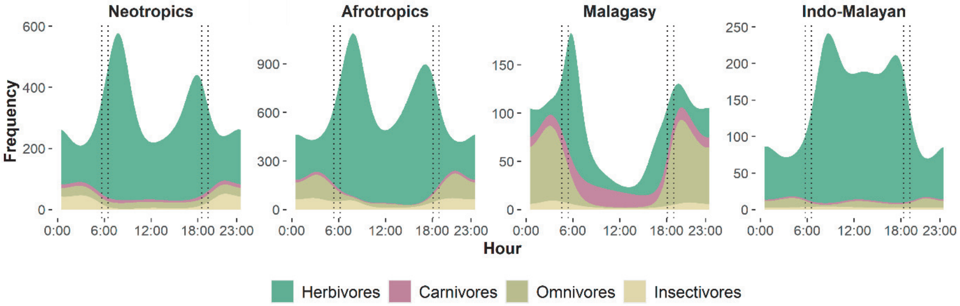

Figure 3. Contribution of each trophic guild to community-level diel patterns in events among realms. Vertical dotted lines correspond to the mean dawn, sunrise, sunset, and dusk standardised across protected areas in each realm. The frequency of events represents the predicted value from realm-specific GAMM models with hour of the day and trophic guild as independent variables and protected area as a random effect. Y-axis represents predicted frequencies and reflects the number of pictures collected throughout the camera-trap survey among protected areas in each realm. Note that the number of photographs in the Malagasy and Indo-Malayan realms was lower than in the Neotropics and Afrotropics. In addition, the proportion of carnivores in Madagascar is large but consists of just two species (*Cryptoprocta ferox*, *Galidia elegans*).

In our previous work, we found that body mass and trophic guild consistently explain shared patterns of tropical mammal diel activity (day, night, and twilight) in these same sites and regions (Vallejo-Vargas et al. 2022). Small herbivores are typically more active during the day than large herbivores in all realms. As expected, given that small and medium-sized mammals are typically more abundant than larger species (Damuth 1981), community-level patterns were mainly shaped by the activity of small and medium-sized herbivores (Figures S3a, S3b). Activity peaks around sunrise and sunset presumably coincide with the periods best suited for balancing foraging needs, predator avoidance, and thermal stress (Riede, van der Vinne and Hut 2017).

In contrast to the rush hours of herbivores, we found that carnivores, omnivores, and insectivores generally exhibited one or two nocturnal activity peaks (Figure 4). Carnivores in the Neotropics and Afrotropics showed higher activity during the night and one peak during the early morning and early night in the Malagasy realm. In the Indo-Malayan realm the model predicted a slight peak after sunrise, albeit with high uncertainty. The low contribution of carnivores to the rush hours may be related to their comparatively low abundance, their need to be active for extended periods to meet their energetic demands (Cid et al. 2020), to avoid each other due to the risks of intraguild killing and competition (Santos et al. 2019).

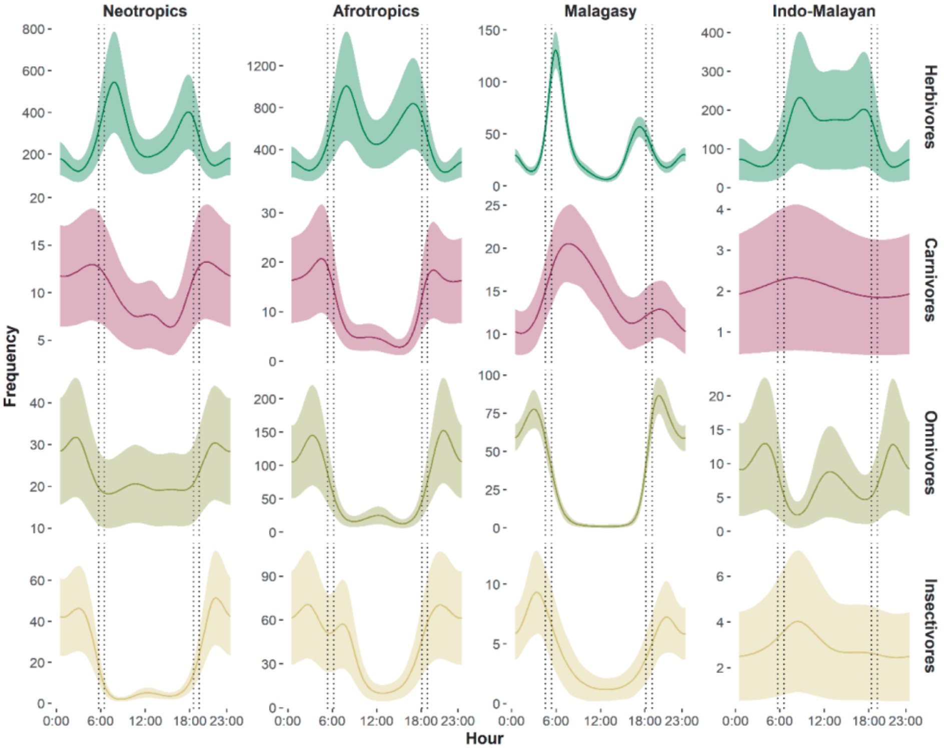

Figure 4. Predicted diel frequency (number of events) of each trophic guild among realms. Vertical dotted lines correspond to the mean dawn, sunrise, sunset, and dusk among protected areas in each realm. The frequency of events represents the predicted values from the GAMM model with hour of the day and trophic guild as independent variables and protected area as a random effect.

Omnivores and insectivores were predominantly nocturnal with activity peaks before dawn and after dusk. Indo-Malayan insectivores were an exception with one activity peak after dawn. The divergence of Indo-Malayan insectivores was mainly due to the presence of the diurnal shrews (genus *Tupaia*)(Meijer et al. 1990). Other insectivore taxa, such as the Malayan pangolin (*Manis javanica*)(Lim and Ng 2008) and *Hemigalus derbyanus* (the banded palm civet, Dunn et al. 2022), were primarily nocturnal.

2 Application

The behavioural patterns of near pristine wildlife communities and its deviations can inform wildlife ecology and conservation. Changes will result and simultaneously influence species interactions (e.g., predation, competition) that also determine ecosystem behaviour and functioning (Wilson et al. 2020). This general idea is already established for the analyses of soundscapes – the combined sounds detected in a forest by automated recording devices (Burivalova et al. 2018) – which reveal distinct patterns in degraded forests versus intact primary forests. Camera traps allow researchers to extend these observations and comparisons to other measures of activity (Kays et al. 2009). Photographic detection of movement can potentially inform the status of communities and their changes in broader ways.

While most protected areas studied here conformed to the general two-peaked rush hour pattern, four protected areas deviated (Figure 2). In the Neotropics, Yanachaga–Chemillén (YAN, Peru) rather showed a broad peak of nocturnal activity. In the Afrotropics, activity in the Udzungwa (UDZ, Tanzania) also peaked after dusk, while in Korup National Park (KRP, Cameroon), activity had four peaks, the first before dawn, the second after sunrise, while the next two peaks occurred about an hour before and after dusk. In the Indo-Malayan tropics, Pasoh (PSH, Malaysia) activity was concentrated in the daytime (after sunrise and before sunset) without marked peaks (Figure 2). We do not know the reason for the local differences but speculate that scarcity or absence of larger predators and herbivores, or that other legacies of human activity (e.g., tourism), are involved (Gaynor et al. 2018). Although these forests are protected, and the occurrence of mammals has generally declined less than in unprotected areas (Beaudrot et al. 2016), this protection is often imperfect, with many sites occasionally being subjected to illegal hunting, . Furthermore, all of these regions have experienced various other human interventions, with several species that would otherwise be part of the local fauna contributing to the observed activity being locally absent or entirely extinct. Impacts on the surrounding unprotected landscapes may also play a role (Gorczynski et al. 2022, Semper-Pascual et al. 2022), and animals may adapt to coexist with people, as noted for the arboreality and socialisation in orangutans (Spehar et al. 2018). For instance, various mammal species are known to increase nocturnal activity to avoid encounters with humans (Gaynor et al. 2018). Thus, changes in overall activity patterns may respond to human impacts, past and present.

3 Conclusion

Our study highlights the value of systematic camera trap surveys to reveal activity patterns within and among mammal communities. Despite their distinct evolutionary histories, the observed bimodal activity pattern among tropical forest mammal communities across biogeographic realms indicates shared responses arising under similar conditions. Small and medium-sized herbivore species were the primary cause of pronounced diel activity profiles of their communities. Both consistency and deviations from this pattern raise new questions and suggest novel avenues for comparative studies.

4 Methods

Study areas and camera trapping

We used camera-trap data from 17 tropical forest sites -all protected areas- located in four biogeographic realms (Neotropical, Afrotropical, Malagasy, and Indo-Malayan) collected by the Tropical Ecology Assessment and Monitoring (TEAM) Network (Network-TEAM 2011, Rovero and Ahumada 2017) (Figure 1). The TEAM Network employed a standardised protocol to deploy camera-traps across protected areas (Network-TEAM 2011). At each protected area, the monitoring occurred during the driest season between 2008 and 2017 with the deployment of cameras at 60 to 90 points annually. Camera-traps were placed at a density of 0.5 - 1 km2 (1 camera every km2 or 1 camera every 2 km2) and remained active for ~30 consecutive days

(Ahumada et al. 2011, Rovero and Ahumada 2017), yielding a total of 60-89 cameras per protected area (Figure 1, Table S1). We excluded 11 deployments with inconsistent date-time stamps.

A total of 2,428,030 camera-trap photos included mammals. We removed 46,168 records of domestic species (e.g., cow, dogs) and humans. A total of 280 species (270 identified species, and 10 unknown species identified to genus) belonging to 58 families, and 18 orders were included in our study (Table S1). Camera-traps are set to take multiple consecutive pictures of the same visit or individual to increase the chance of capturing animal in motion. To limit pseudo-replication of individuals and visits, we established independent events (time interval between pictures > 1-minute per camera for a given species, Peral, Landman and Kerley 2022). This resulted in 175,867 independent events.

To describe the diel activity in each community and realm, we double-anchored every independent event (Vazquez et al. 2019) to sunrise and sunset using the function ‘solartime’ from the 'activity' package (version 1.3.2, Rowcliffe et al. 2014, Rowcliffe 2022) in R (Team 2023) within each real and within each protected area. This accounted for the differences of day and night lengths among protected areas and over seasons (Figure S5, Vazquez et al. 2019). Once we standardised all the records to sunrise and sunset (anchored time), we summarised the number of independent events recorded within each hour (centred within half of an hour) to run the models (see Analysis below). By communities, we mean all the animals and their activities that our cameras recorded in the forest over the course of an average day: “community diel activity”.

To plot the sunrise, sunset, dawn, and dusk we extracted the time of each variable using the R library ‘maptools' version 1.1-4(Bivand et al. 2021) and the functions’ crepuscule’ and ‘sunriset' and calculated the mean of all independent events to plot the dotted lines of dawn, sunrise, dusk, and sunset (Figure 1, 2, 3, 4).

We extracted the species characteristics 1) diet, 2) body mass (g) from the PHYLACINE database (Faurby et al. 2018), and their activity pattern category from Cox et. al. (2023). We classified each mammal species into one of the four trophic guilds: carnivore, herbivore, insectivore, or omnivore. Categories were based on diet reported in the PHYLACINE database and we classified species feeding on ≥ 80% vertebrates as carnivorous, species feeding on ≥ 80 % plant material as herbivorous, species feeding on ≥ 80 % insects as insectivorous, the remaining species were categorised as omnivorous (e.g., feeding on vertebrates and fruits, Wilman et al. 2014, Faurby et al. 2018). Some independent events (N=748) were classified only to the genus level, thus we characterised the trophic guild with the known information from its genus. These events included records from the genus *Tragulus*, *Proechimys*, *Sciurus*, *Mazama*, *Cephalophus*, and *Leopardus*. Second, we categorised body size as follows: species with a body mass lower < 1 kg as small, 1 kg – 20 kg as medium, and > 20 kg as large (Benítez-López et al. 2019).

To characterize the rush hour, we used all 175,867 independent events associated with mammals. To assess the contribution of trophic guild, we used all independent events. To assess the contribution of body mass, we used events involving mammal species with data on body size and excluded events identified up to genus (N=748 independent events).

To assess whether the bimodal pattern reflected periods when diurnal, cathemeral, and nocturnal species overlap, we employed the species diel categories from Cox et. al. (2023). We filled the activity pattern of three missing species (*Cebus capucinus*, *Lagothrix cana*, and *Apodemus sylvaticus*) diel category with the information provided in Elton traits data base (Wilman et al. 2014). We plotted the number of independent events by hour of the day and colour coded them according to their diel category (Figure S4).

To represent the hourly temperature in each protected area, we calculated the average hourly temperature during the survey (Figure 2). To extract the temperature profile in each protected area, we only included camera-trap records with a temperature stamp generated by the camera-trap. When the temperature was recorded in degrees Fahrenheit, we converted it to degrees Celsius. From a total of 175,867 independent events, a total of 129,824 records included temperature.

Analysis

Description of the community diel activity among regions and protected areas

To characterise the activity among realms and the contribution of trophic guild to overall patterns, we fitted two generalised additive mixed models (GAMM) for each realm with the R package 'mgcv' version 1.8-42 (Wood and Wood 2015 , Figure 1 and 3, Wood, Pya and Säfken 2016). Then, we fitted the number of events to the 24-hour clock. Second, to assess the contribution of trophic guild to the community level, we fitted the number of independent events to the interaction between hour of the day and trophic guild. Except in Malagasy realm, which has a single protected area, we included protected area as a random effect to account for the nested study design in both models. To describe the community diel activity, we fitted a density kernel function to all independent events in each of the 17 protected areas. We used the function 'fitact' from the package 'activity' version 1.3.2 (Rowcliffe 2022 , Figure 4).

Finally, we plotted the number of events of each species and colour coded them by their diel activity category to qualitatively check whether the activity during the two peaks of activity coincided with the time when nocturnal species are going to rest and when diurnal species start their activity (Figure S3a, S3b).

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Article I: Supplementary Information

Figure S1. Number of independent events for each trophic guild among tropical realms.

Table S1. Additional information about the protected areas included in the study.

Figure S2. Predicted frequency (number of events) of each trophic guild by time of day in each protected area.

Figure S3a. Frequency distribution of independent events of trophic guild and body size categories in the Neotropics.

Figure S3b. Frequency distribution of independent events of trophic guild and body size categories in each protected area in the Afrotropics, Malagasy tropics, and Indo-Malayan realms.

Figure S4. Frequency of events for diurnal, nocturnal, cathemeral species, contributing to the total number of events in each protected area.

Figure S5. Day length in each protected area.

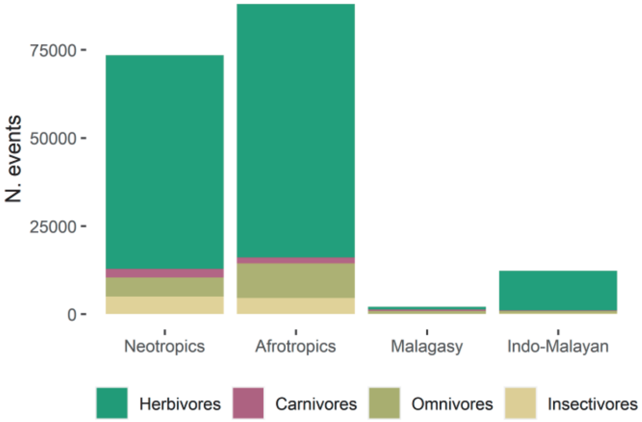

Figure S1. Number of independent events for each trophic guild in each tropical realm.

Table S1. Additional information about the protected areas included in the study.

Protected area	Code	N. sampling periods	Area (ha)*	Country	Number of cameras	Number of Families**	Number of Species**
Neotropical realm:							
Barro Colorado Nature Monument - Soberania National Park	BCI	6	4,890	Panama	60	21	31
Caxiuanã National Forest	CAX	6	317,945	Brazil	60	15	30
Central Suriname Nature Reserve	CSN	9	1,600,000	Suriname	65	16	37
Cocha Cashu - Manu National Park	COU	6	1,716,294	Peru	60	21	46
Manaus	MAS	2	1,198,944	Brazil	89	14	26
Volcán Barva (Brulio Carrillo National Park)	VB	10	49,921	Costa Rica	60	16	29
Yanachaga Chimillen National Park	YAN	6	122,000	Peru	63	19	31
Yasuni National Park	YAS	6	1,030,070	Ecuador	60	18	39
Afrotropical realm:							
Bwindi Impenetrable Forest	BIF	8	32,700	Uganda	60	19	42
Nouabalé Ndoki	NNN	7	423,870	Republic of Congo	64	18	38
Udzungwa Mountains National Park	UDZ	5	208,869	Tanzania	60	17	32
Korup National Park	KRP	5	125,900	Cameroon	60	15	27

Virunga Massif	VIR	4	16,000	Democratic Republic of the Congo	60	14	16
Malagasy realm:							
Ranomafana National Park	RNF	7	40,705	Madagascar	60	10	25
Indo-Malayan realm:							
Bukit Barisan	BBS	8	295,000	Indonesia	60	20	40
Nam Kading	NAK	6	169000	Laos	60	17	31
Pasoh Forest Reserve	PSH	6	13,610	Malaysia	60	20	45

*Area was extracted from the World Database on Protected Areas (WDPA). Pasoh Forest Reserve, Manaus, and Ranomafana were extracted from Beaudrot, et al. 2017(Beaudrot et al. 2016).

**Number of mammal families and species detected by camera traps and included in this study.

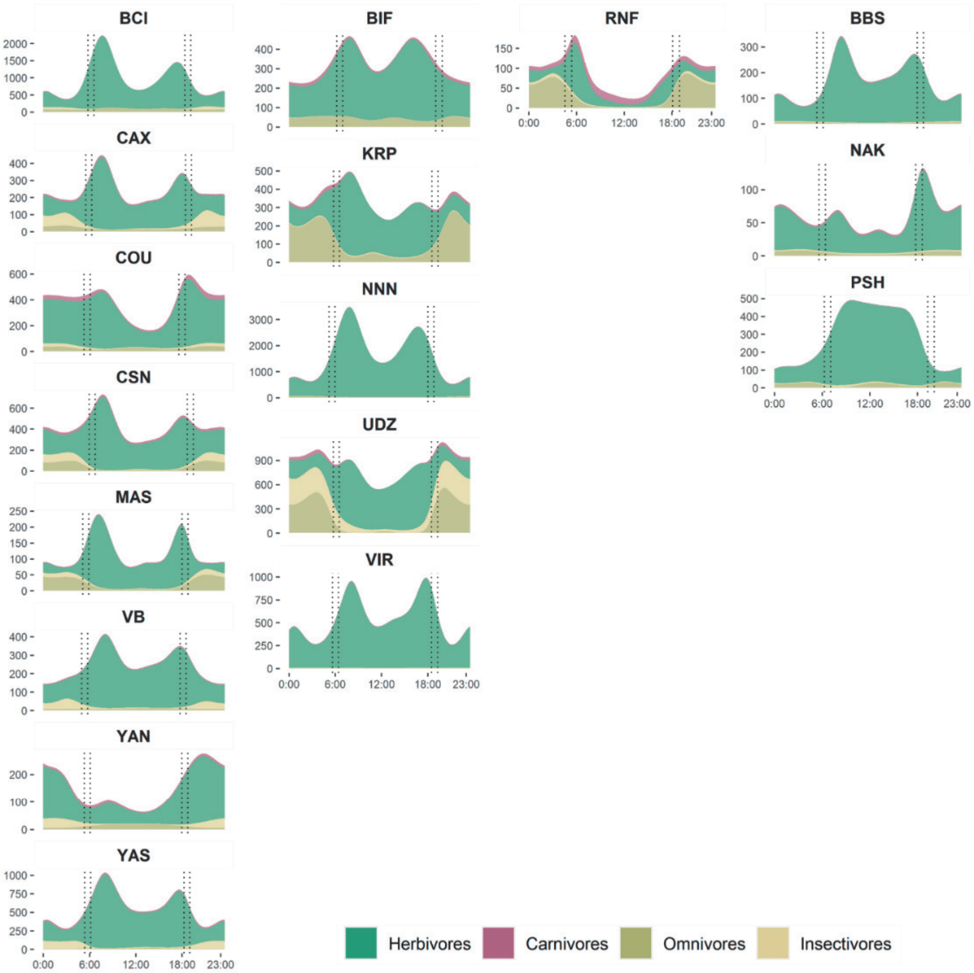

Figure S2. Predicted frequency (number of events) of each trophic guild by time of day in each protected area. Vertical dotted lines correspond to the mean dawn, sunrise, sunset, and dusk, anchored within protected areas. The frequency of events represents the predicted value fitted from the GAMM model to hour of the day and trophic guild.

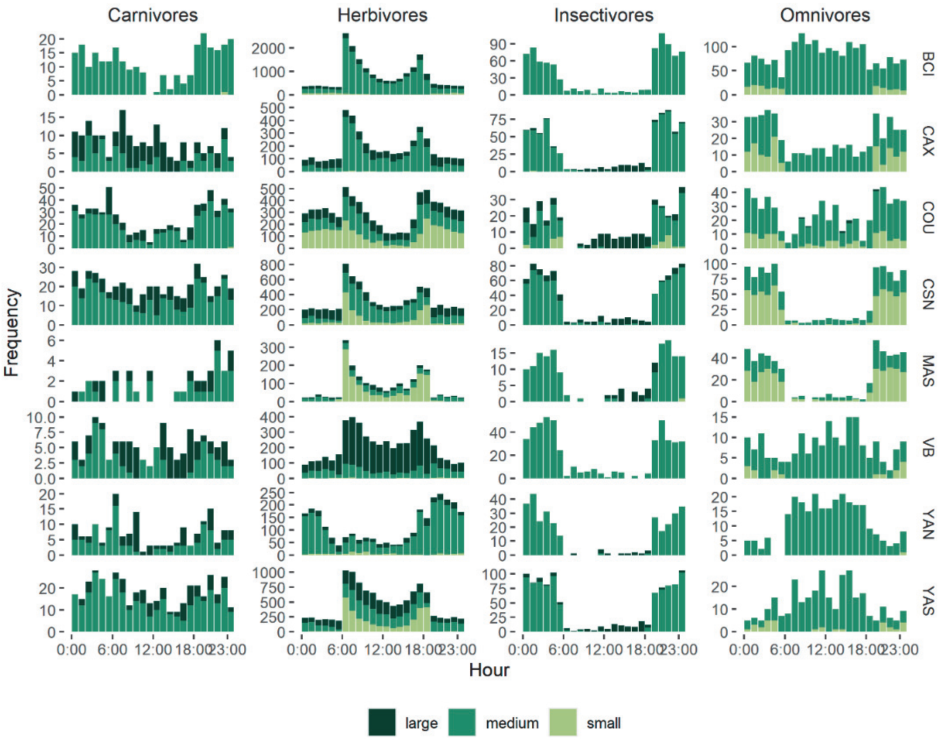

Figure S3a. Frequency distribution of independent events by trophic guild (columns) and body size categories (colours) in eight protected areas (rows) across the Neotropics.

Figure S3b. Frequency distribution of independent events by trophic guild (columns) and body size categories (colours) in five protected area (rows) in the Afrotropics, one in Malagasy tropics, and three in Indo-Malayan realm.

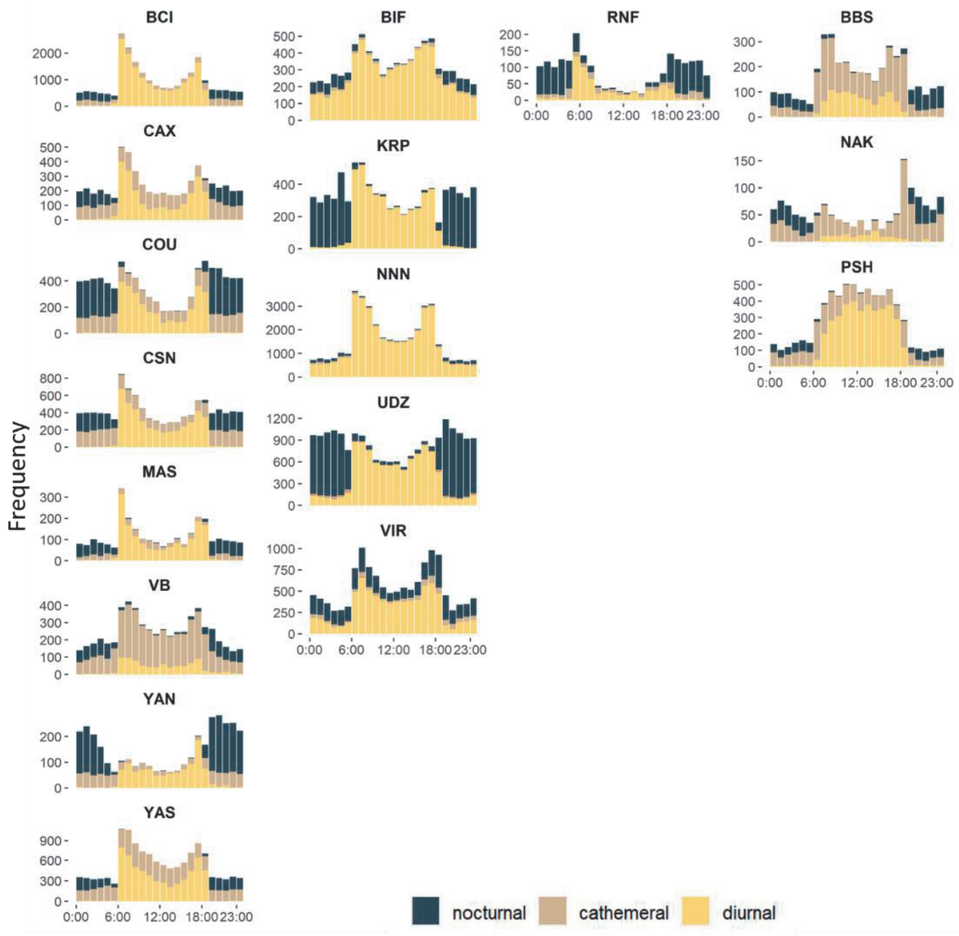

Figure S4. Frequency of events for diurnal, nocturnal, cathemeral species, contributing to the total number of events in each protected area.

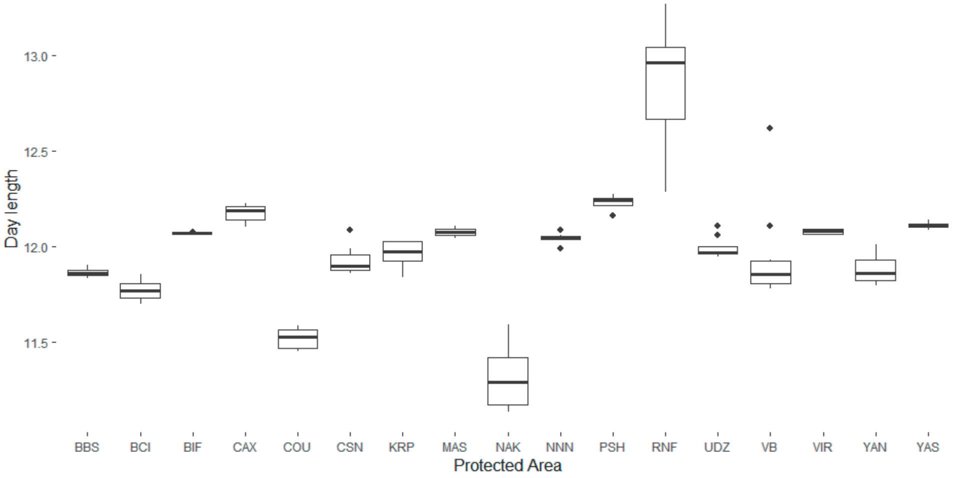

Figure S5. Day length (from sunrise to sunset) in each protected area. Boxplots show the distribution of day length during the data collection in each protected area.

ARTICLE II

nature communications

Article

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Consistent diel activity patterns of forest mammals among tropical regions

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An animal's daily use of time (their "diel activity") reflects their adaptations, requirements, and interactions, yet we know little about the underlying processes governing diel activity within and among communities. Here we examine whether community-level activity patterns differ among biogeographic regions, and explore the roles of top-down versus bottom-up processes and thermoregulatory constraints. Using data from systematic camera-trap networks in 16 protected forests across the tropics, we examine the relationships of mammals' diel activity to body mass and trophic guild. Also, we assess the activity relationships within and among guilds. Apart from Neotropical insectivores, guilds exhibited consistent cross-regional activity in relation to body mass. Results indicate that thermoregulation constrains herbivore and insectivore activity (e.g., larger Afrotropical herbivores are ~7 times more likely to be nocturnal than smaller herbivores), while bottom-up processes constrain the activity of carnivores in relation to herbivores, and top-down processes constrain the activity of small omnivores and insectivores in relation to large carnivores' activity. Overall, diel activity of tropical mammal communities appears shaped by similar processes and constraints among regions reflecting body mass and trophic guilds.

Diel activity patterns—how animals distribute their activity throughout the 24 h day—vary among and within species[1]. Some species and individuals maintain activity over extended periods while others exhibit brief peaks of activity[1]. Animals may be predominantly active at night (nocturnal), day (diurnal), twilight (crepuscular), or may lack pronounced nocturnal or diurnal peaks (cathemeral). These activity patterns reflect when organisms seek food, socialize, and perform other necessary tasks while also responding to risks and physiologic constraints[2,3]. How these underlying processes and constraints shape activity patterns has been studied in various contexts, yet their identification at the community level, and their generality among regions has remained scarce due to a dearth of comparable data.

Mammals possess diverse specializations, including morphological, physiological, and behavioural adaptations that reflect and influence their diel behaviours[4]. These adaptations, including eye forms[5], sensorial systems, and endothermy (i.e., generation and regulation of body temperature) evolved in response to various needs and constraints (e.g., light, temperature, predation risk). Endothermy facilitates activity during cold periods[6], and may have benefitted early mammals by permitting nocturnal activity to reduce predation by diurnal dinosaurs[7]. Furthermore, interactions between physiological

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characteristics, body size, and morphology may favour activity schedules that moderate exposure to thermal stress[8]. Large species may avoid overheating by limiting activity during warmer periods of the day[9,10]. By contrast, smaller species that can lose heat rapidly may favour activity in warmer periods of the day[11,12]. Moreover, activity patterns likely reflect a combination of processes and constraints. For example, small rodents may avoid diurnal predation through nocturnal behaviour, yet be active during daylight in response to food availability, temperature variation, or reduced competition or predation[2,13,14].

Species interactions—predation, competition—likely influence diel activity patterns within communities[15,16], yet, we lack a general understanding of how such interactions shape activity patterns. For instance, predators may favour periods where their prey are active, whereas prey species may avoid periods when their predators are active[17–19]. In other words, activity patterns could result from both top-down and bottom-up behavioural processes[2], analogous to the top-down and bottom-up consumptive processes that regulate food webs[20–22]. In a top-down process, one group of species (e.g., prey) adjusts their activity to avoid interacting with another group (e.g., predators or dominant competitors)[19,23]. For example, small carnivores may alter their activities to reduce their encounters with larger carnivores; similar avoidance behaviour is expected for prey (e.g., herbivores) to avoid their predators[18,23]. In a bottom-up process, on the other hand, predators may adjust their activity to facilitate encounters with their prey[24]. For instance, in four study areas in southwestern Europe, mesopredators match their activity to that of rodent prey[25]. Current evidence for bottom-up and top-down control of behaviour is restricted to scattered cases, regions, and communities[23–25]. For example, a top-down process was detected in African savannas where intermediate size-herbivores shifted their activity towards daytime when predation risk was high during the night[10]. The relative roles of top-down and bottom-up processes in shaping diel activity in mammal communities and the consistency of these processes among regions and biotas, therefore, remain uncertain.

Humid tropical forests provide an important context for exploring whether patterns in diel activity—thus potentially their main determinants—transcend biogeographical regions. In humid tropical forests the influence of seasonality is low, the environmental conditions across distinct regions are similar[8], and the maintenance of high species richness likely involves diverse interactions[26]. The trophic composition of mammal communities has been shown to be relatively consistent among regions[27]. If diel activity patterns are influenced by the same underlying processes as trophic guild composition, then we would expect consistency in diel activity patterns among regions.

Here, we study the diel activity patterns of ground-dwelling and scansorial (i.e., adapted to climb) mammals inhabiting protected tropical forests across the Neotropics, Afrotropics, and Indo-Malayan tropics. We examine patterns and test predictions associated with three alternative hypotheses (Fig. 1) for the main processes potentially

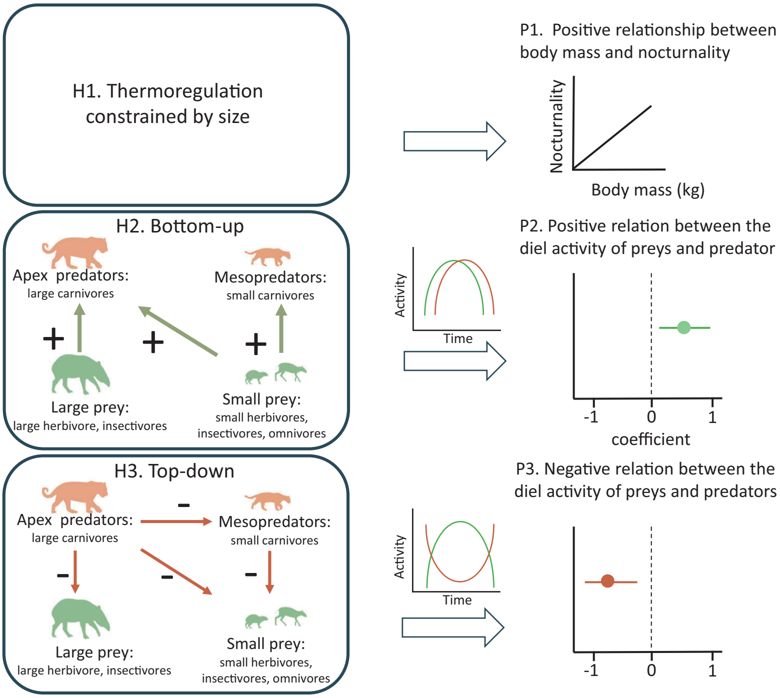

Fig. 1 | Hypotheses (H1–H3) to determine processes that shape diel activity patterns in tropical forest mammal communities, with associated predictions (P1–3). If the energetic cost of thermoregulation dominates (H1), we expect a positive relationship between body mass and nocturnality (1), regardless of trophic guild. If bottom-up regulation dominates (H2), predators will follow the diel activity of their prey (2). If top-down regulation dominates (H3), then we predict that small predators and potential prey species (herbivores and insectivores) will avoid top-predators (3). "+" represents a positive relationship between the activity of species groups (bottom-up process), and "–" represent a negative relationship between the activity of species groups (top-down process). Silhouettes from phylopic.org: jaguar, ocelot, and agouti by Gabriela Palomo-Munoz; tapir no license; browsing ruminant by Nobu Tamura (vectorized by T. Michael Keesey) http://creativecommons.org/licenses/by/3.0/.

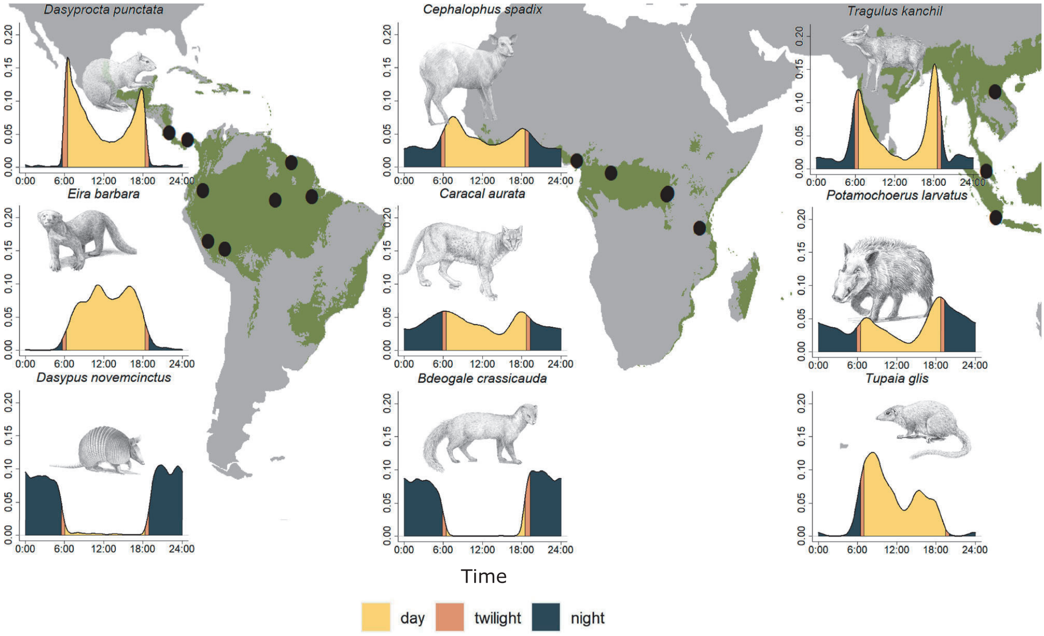

Fig. 2 | Map of the study areas and activity density examples. Mammal activity data were collected using the standardized TEAM camera-trapping protocol in 16 protected areas (black dots in background) situated in 14 countries and tropical forests (areas shaded green on the map in the background) in three biogeographic regions. Activity density plots in each column show examples of species in each region (from left to right: Neotropics, Afrotropics, and Indo-Malayan tropics). Illustrations by John Meaghan.

driving them. First, if the energetic cost of thermoregulation constrains diel activity (H1), then (1) larger mammals should be more active during the night when it is colder and smaller mammals more active during the day when it is warmer, irrespective of the dietary functional group. If bottom-up processes regulate diel activity (H2), then activity patterns of predators (e.g., carnivores) should match that of prey species (e.g., herbivores, insectivores). Finally, if top-down processes regulate the diel activity of animals in a community (H3), (3a) prey species such as herbivores should exhibit diel activity patterns contrasting those of predators of a similar size, and (3b) small carnivores should exhibit diel activity patterns that avoid large carnivores (Fig. 1). Here, we examine the diel activity pattern of distinct forest mammal communities using standard data collected from multiple sites across multiple regions. We show that diel activity appears remarkably consistent in relation to trophic guilds and body mass, which implicates multiple factors. First, herbivore activity and insectivores in two regions appears to be determined by thermoregulation. Second, smaller prey species (i.e., insectivores, and omnivores) and small carnivores reflect some top-down avoidance of top predators. Third, top-predators show bottom-up regulation of their activity in response to herbivores prey.

Results

We used time-stamped images from standardized large-scale camera-trap surveys implemented by the Tropical Ecology Assessment and Monitoring (TEAM) Network in 16 protected areas (Fig. 2 and Table S1)[28] to examine and test our hypotheses. First, to identify if there were consistent patterns across regions, we used multinomial analysis with random intercepts (protected area) for each biogeographical region to investigate how diurnal, nocturnal, and crepuscular activity was related to the trophic guild and body size. The best model based on the lowest Akaike information criterion (AIC) contained an interaction between body mass and guild and best explained the activity of mammals in all regions. We extracted the probability of being active during the day, night, and twilight, and the correspondent upper (UCI) and lower (LCI) 95% confidence intervals for the given range of body mass and trophic guild derived from the best multinomial model. Second, to test how top-down and bottom-up processes shape diel activity, we divided species into small and large categories for each trophic guild and tested whether the hourly activity of prey (e.g., large herbivores) or subordinate species (e.g., small carnivores) was correlated with the activity of predators (e.g., large carnivores). We tested the top-down and bottom-up hypotheses for all protected areas where top predators had been detected ($N = 11$, Table S1), and utilized generalized linear mixed models (GLMM) with the protected area as a random intercept. Positive coefficients were interpreted as an overlap of activity, while negative coefficients were interpreted as a temporal avoidance between the activity of the groups compared. We further assessed how top-down, and bottom-up processes shaped the diel activity of tropical mammals by plotting the density distribution of all species groups (prey/subordinate species vs. predators) and estimating the coefficients of overlap ("Dhat", see "Methods") for each protected area. This coefficient ranges from 0 to 1 with higher and lower values interpreted as bottom-up and top-down influences, respectively.

Consistent patterns of diel activity

Diel activity, as analyzed with multinomial models, was generally well explained by the interaction between body mass and trophic guild in all three regions (Fig. 3 and Tables S2, S3), despite substantial variation in diel activity patterns among species (Figs. 1 and S4). The probability of nocturnal activity by herbivores increased with increasing body

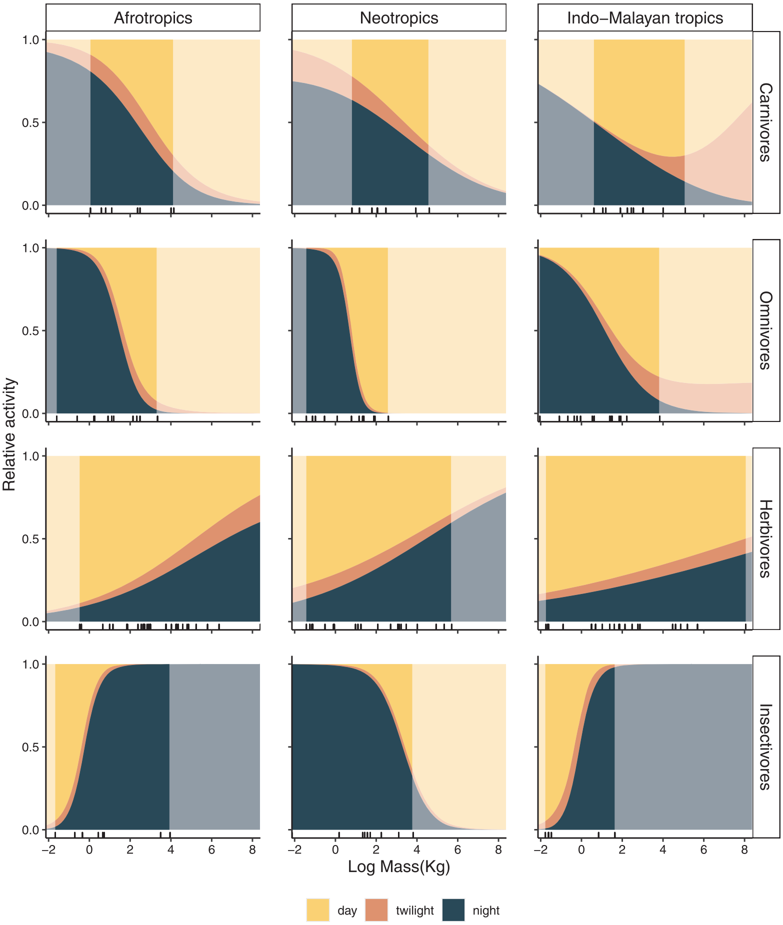

Fig. 3 | Diel activity in relation to body size and trophic guilds of tropical ground-dwelling and scansorial mammals in three regions. Estimates correspond to the probability of activity during the day, night, and twilight extracted from the multinomial logit models fitted to TEAM camera-trap data ($n = 126{,}382$). Tick marks above the x-axis indicate the body mass of species included in the analysis. Lighter colours indicate model predictions for body masses that are below or above the range for species included in the analysis in each region. "n" represents the number of independent events. $n_{\text{carnivores\_Neotropics}} = 2182$, $n_{\text{carnivores\_Afrotropics}} = 1474$, $n_{\text{carnivores\_Indo-Malayan\_tropics}} = 152$, $n_{\text{omnivores\_Neotropics}} = 4656$, $n_{\text{omnivores\_Afrotropics}} = 4656$, $n_{\text{omnivores\_Indo-Malayan\_tropics}} = 435$, $n_{\text{herbivores\_Neotropics}} = 45{,}839$, $n_{\text{herbivores\_Afrotropics}} = 47{,}458$, $n_{\text{herbivores \_Indo-Malayan\_tropics}} = 7803$, $n_{\text{insectivores\_Neotropics}} = 4399$, $n_{\text{insectivores\_Afrotropics}} = 3886$, $n_{\text{insectivores\_Indo-Malayan\_tropics}} = 212$.

mass in all regions (Fig. 3). For example, the largest herbivore in the Neotropics was 4.6 times more likely to be nocturnal than the smallest herbivore (e.g., large: $p_{\text{night}} = 0.60$, CI: 0.48–0.71, body mass = 210 kg; small: $p_{\text{night}} = 0.13$, CI: 0.08–0.21, body mass = 0.24 kg, Fig. 3). The opposite relationship occurred for carnivores and omnivores in all regions. For example, a 61 kg carnivore in the Afrotropics was 3.9 times less likely of being active at night ($p_{\text{night}} = 0.21$, CI: 0.14–0.28) than a 1 kg carnivore ($p_{\text{night}} = 0.81$, CI: 0.74–0.87).

Insectivores in the Neotropics were an exception from the general pattern (Fig. 3, Fig. S1, and Table S2). Whereas Afrotropical and Indo-Malayan insectivores exhibited a positive relationship between body mass and the probability of nocturnal activity (e.g., in the Indo-Malayan region nocturnal probability increased from 0.01 to 0.98), in the Neotropics nocturnality decreased with increasing body mass, from a probability of 0.99 (CI: 0.99–0.99, body mass = 0.12 kg) to 0.32 (CI: 0.22–0.44, body mass = 43.30 kg, Fig. 3).

Thermoregulation constrains the activity of herbivores and insectivores

The positive relation between nocturnality and body mass for herbivores and insectivores (Afrotropics and Indo-Malayan tropics) was congruent with the prediction for H1. Nevertheless, carnivores, omnivores, and insectivores in the Neotropics showed the opposite relationship.

Top-down and bottom-up processes shape the diel activity of tropical mammals

Our GLMM analyses of the relationship between the activity of different trophic groups and different sizes (large and small) suggests that a combination of bottom-up (H2) and top-down (H3) processes shaped the diel activity of mammalian groups among regions. Consistent with H2 (bottom-up), we found evidence of a positive relationship between the activity of large herbivores and large carnivores across the three

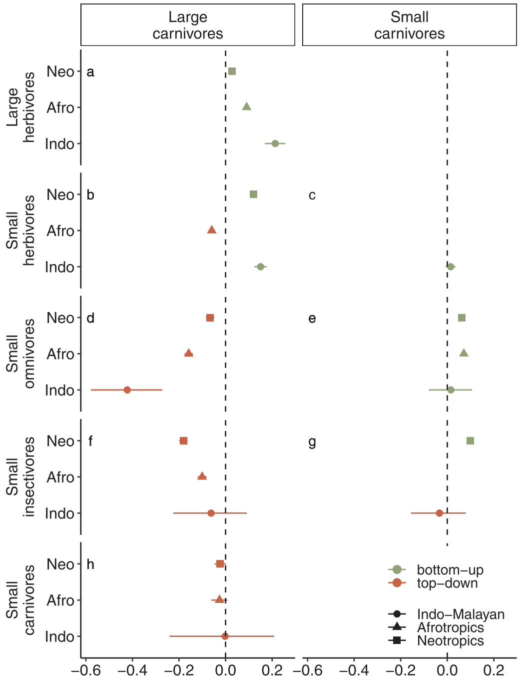

Fig. 4 | Bottom-up and top-down processes as determinants of the diel activity of tropical mammals. Centre of bars represent the mean coefficient estimates and bars show the 95% confidence intervals of the (GLMM) fitted to assess the relationship between the activity of species groups. The first column includes the relationship between the activity of large carnivores ($n = 747$) and prey (**a** large herbivores $n = 191{,}294$, **b** small herbivores $n = 58392$, **d** small omnivores $n = 8098$, and **f** small insectivores $n = 7120$) and **h** the relationship between the activity of large carnivores and small carnivores ($n = 2280$). The second column includes the relationship between small carnivores and potential prey (**c** small herbivores, **e** small omnivores, and **g** small insectivores). Note that n represents the total number of independent events for each species group and size. Green symbols illustrate a positive effect (bottom-up) and brown symbols illustrate a negative (top-down) relationship. Effects were considered significant when the 95% CI did not overlap zero (dashed horizontal lines). Neotropical sites "Neo" are denoted with squares, Afrotropical sites "Afro" with triangles, and Indo Malayan "Indo" with circles.

regions studied (e.g., Neotropics: $\beta = 0.03$, CI: 0.02–0.04; Indo-Malayan: $\beta = 0.21$, CI: 0.17–0.26, Fig. 4a). Similarly, we detected a positive relationship between the activity of small herbivores and the activity of large carnivores in the Neotropics and Indo-Malayan tropics (e.g., Neotropics: $\beta = 0.12$, CI: 0.13–0.13, Fig. 4b). The activity of small carnivores in the Afrotropics and Neotropics exhibited a significant positive relationship with the activity of small omnivores (e.g., Afrotropics: $\beta = 0.07$, CI: 0.07–0.07, Fig. 4e) and small insectivores in the Neotropics ($\beta = 0.10$, CI: 0.09–0.11, Fig. 4g). Inconsistent with the bottom-up hypothesis, the activity of large carnivores vs. small herbivores showed a negative relationship (Fig. 4b) in the Afrotropics.

Consistent with top-down processes (H3), we detected a negative relationship between the activity of large carnivores vs. small omnivores across all regions (Fig. 4d) and for the activity of large carnivores vs. small insectivores in two regions as indicated by the GLMMs (Neotropics, $\beta = -0.18$, CI: −0.20 to −0.16; Afrotropics: $\beta = -0.10$, CI: −0.12 to −0.09, Fig. 4f). Additionally, albeit no-significant support for H3 was suggested by the GLMM, the activity of small and large carnivores tended to be negatively correlated (Fig. 4h).

Overlap estimates varied depending on the species groups compared as well as the protected area. The lowest variability among protected areas was found for the overlap estimates between the activity of large carnivores and large herbivores (10 out of 11 protected areas was higher than 0.78, CI:0.67–0.82, Fig. S5). These results provide support for the bottom-up hypothesis (H2). In contrast, the overlap estimates for the rest of the species group comparisons were less consistent (Figs. S6–S12). For example, overlap estimates between the activity of small omnivores and large carnivores ranged from Dhat1 = 0.39 (CI: 0.29–0.5) to Dhat4 = 0.85 (CI: 0.76–0.92, Fig. S8).

We did not detect significant relationships between the activity of large insectivores and large predators, and the data were too sparse to include models comparing large omnivores with other groups.

Discussion

Our study revealed similar relationships of trophic guild and body mass with diel activity patterns of tropical forest mammals in distant biogeographic regions despite the variation in species-specific activity patterns (Fig. S3). These results suggest convergent ecological and/or evolutionary responses in diel activity among tropical regions. Such convergence, despite the considerable taxonomic differences in regional biotas, likely reflects the results of adaptations to similar environments. Among carnivores and omnivores, larger species were less likely to be nocturnal than smaller ones. In contrast, larger herbivores, tended to be more nocturnal. Insectivores were an exception because they showed a negative relationship between body size and nocturnality in the Neotropics but a positive relationship in the Afrotropics and Indo-Malayan regions.

Despite the overall consistency in diel activity patterns across the pantropics, our analysis did not point towards a single dominant driver for the observed patterns. Instead, it appears that multiple factors may have acted simultaneously. Thermal constraints (H1), bottom-up (H2), and top-down (H3) processes all seemed to contribute to the configuration of activity within tropical forest mammal communities (Figs. 3, 4). Increasing nocturnality with body mass for herbivores and insectivores (Afrotropics and Indo-Malayan tropics) is consistent with the hypothesis on thermoregulatory constraints (H1). Furthermore, trophic interactions, known to influence species richness and biodiversity[26,29], appear in our study to be important influences on diel activity patterns through both top-down and bottom-up processes. Although multiple factors (e.g., predation risk, prey abundance) appear to have influenced interactions, there was nonetheless some uniformity observed among regions. Carnivores tended to match the diel activity of potential prey species, supporting the bottom-up hypothesis (H2). On the other hand, in some regions the activity of small insectivores, small omnivores, and small carnivores was best explained by the top-down hypothesis because these groups seemed to avoid periods when larger carnivores were active (H3).

Consistent with the thermoregulatory constraint hypothesis (H1), we found that larger-bodied herbivores and insectivores were more likely to be nocturnal than smaller-bodied ones. While diel temperature is more stable in tropical rainforests than in many other ecosystems, it does vary[30]. Most tropical mammals are adapted to survive in a narrow thermal tolerance range[31,32], thus both high and low temperatures can increase energy expenditure[33]. Small-bodied species can reduce energy loss by being active during warmer periods of the day[11], while large-bodied animals (e.g., tapirs[34], aardvark[35]) can reduce thermal stress by focusing their activity during cooler periods of the day[9,34,36]. For example, in the Neotropics the probability of being active during the night was two times higher for a 290 kg herbivore (e.g., *Tapirus bairdii*) than for one weighing 1 kg (e.g., *Myopracta acouchi*).

If thermoregulatory constraints were the sole or primary driver of diel activity, we would anticipate the relationship between mass and activity to manifest across all trophic guilds and regions. This was not the case. Carnivores and omnivores did not exhibit a positive relationship between size and diurnality. This may in part be explained by the lack of large species in those groups or less severe risk of thermal stress. Alternatively, our study suggests that there is a greater role of species interactions (bottom-up and top-down processes) influencing diel activity patterns for carnivores and omnivores in humid tropical forests. Another group exhibiting behaviours inconsistent with the thermoregulatory constraint hypothesis was the Neotropical insectivores. The higher diurnal activity of larger versus smaller Neotropical insectivore species was dominated by just three species (*Myrmecophaga tridactyla, Tamandua tetradactyla, and Tamandua mexicana*)—all of which reflect the distinct South American native lineages that persisted after the great interchange[37]. The different behaviour in this group may be due to chance, the low number of species, or characteristics neglected by our guild categories. For example, among large insectivores, Neotropical anteaters live above ground unlike the fossorial aardvarks of the paleotropics. Another possibility beyond the scope of our current study is that there may be differences in the presence and temporal availability of insect prey.

The positive correlation in the diel activity of large carnivores and large herbivores was relatively consistent among regions (Fig. 4) and overlapped more than expected by chance among protected areas (Fig. S6). Similarly, small carnivores seemed to match their activity to that of small potential prey (e.g., small omnivores and small insectivores, Fig. 4). We infer that these carnivores sought to increase encounters with prey. Previous studies have reported a similar match between predator and prey activity[25,38–40]. For example, the activity of the Borneo Sunda clouded leopard (*Neofelis diardi*), a top-predator, overlaps with its preferred prey species, the sambar deer (*Rusa unicolor*) and small herbivore greater mouse deer (*Tragulus napu*)[41]. We also found evidence to the contrary: the activity of small herbivores in the Afrotropics indicated temporal avoidance of large carnivores (Fig. 4b), potentially due to the abundance or richness of prey or predator species in the Afrotropics. For example, when predator abundance increases, prey have been observed to adjust their activity to reduce interactions with predators[23]. We speculate that the temporal avoidance we reported in the Afrotropics may reflect lower prey availability or higher predator abundance that resulted in higher predation risk and a resulting shift in the activity of herbivore prey. We do not have reliable estimates on abundance to evaluate these nuances directly.

Our analysis revealed apparent temporal avoidance of the activity of large carnivores by small omnivores in the Indo-Malayan tropics and Afrotropics and by small insectivores in the Neotropics and Afrotropics. Avoidance of large carnivores could decrease antagonistic interactions (e.g., predation, interguild killing) with large predators[19,42], which exert top-down behavioural control. We detected a signal of temporal avoidance from the negative relationship between the activity of small and large carnivores in two regions (Neotropics and Indo-Malayan tropics) consistent with previous studies demonstrating temporal avoidance among species pairs. For instance, an earlier study[43] in some of our Neotropical study areas, revealed that ocelots (*Leopardus pardalis*) exhibited a low overlap with the activity of the larger jaguar (*Panthera onca*) and puma (*Puma concolor*). The present study suggests that, overall, the activity of smaller carnivores in protected tropical forests is to a large extent motivated by bottom-up processes (H2)—i.e., facilitate encounters with potential prey such as small omnivores and insectivores—rather than top-down processes (H3)—i.e., avoidance of intraguild interactions with larger carnivores. Nonetheless, there is likely substantial variation among species in the relative importance of top-down and bottom-up processes, with both potentially playing a role. For example, ocelot activity overlaps with various omnivorous prey species, such as opossums, raccoons[44], insectivores as armadillos[45], while it also avoids jaguars[43].

Despite some consistency between the GLMM and the overlap analysis, there was also variation between them. For example, comparing the activity of large carnivores and herbivores, most protected areas exhibited high overlap coefficients consistent with the bottom-up hypothesis (H2), yet one protected area differed (e.g., Manaus, Fig. S6). In other cases, the overlap coefficients among protected areas varied greatly and limited us from inferring general mammalian diel activity patterns. Thus, the use of GLMM allowed a more formal assessment of bottom-up and top-down processes at the regional level while accounting for variation among protected areas.

Although all study areas were relatively well-protected, none were completely free of human impacts[28] raising the question of how this may have influenced our observations. Human presence and activities can have pronounced impacts on wildlife activity; for example, species may become more nocturnal to avoid hunters[46]. This has been observed in Yasuní, one of our study areas, where ungulates became more nocturnal as hunting increased[47]. Our study cannot clarify the role of hunters in determining the specific details of our results and we are wary of such attempts. Simple approaches using human activity may be misleading as evasive responses among mammals are not universal and can change over time (for example, the gorillas in Bwindi have been habituated to humans). At some of the study areas, certain large predators that were previously present are now scarce or absent (e.g., leopards in Bwindi[48])[49,50], raising questions concerning how the prey community (e.g., omnivores and insectivores) may respond.

Despite distinct origins, biogeographic histories, and taxonomic compositions, community level diel activity patterns for tropical forest mammals exhibited consistent patterns in relation to trophic guild and body size across three tropical biogeographic regions. Convergent responses—ecological and/or evolutionary—to similar conditions among regions appear manifested in similar diel activity strategies within these diverse communities. Furthermore, our analysis pinpoints different determinants depending on trophic guild. Herbivore and insectivore activity appears to be shaped by thermoregulatory constraints while predator-prey interactions appear to be influenced by the temporal behaviour of their members. Thus, bottom-up processes dominate the activity of carnivores, and top-down processes dominate the activity of prey (mainly omnivores and insectivores).

Methods

Study areas and camera trapping

We used camera-trap data from the Tropical Ecology Assessment and Monitoring (TEAM) Network[49]. TEAM data comprise data from three tropical biogeographic regions (Neotropics, Afrotropics, and Indo-Malayan tropics) and 16 protected areas (TEAM Network, 2011) (Fig. 1). Camera-traps were deployed following a standardized protocol in all protected areas during the dry seasons between 2008 and 2017. At each protected area, the monitoring ran from two to ten years with the deployment of 60 to 90 cameras annually. Camera-traps were placed at a density of 0.5–1 camera/km^2 (1 camera every km^2 or 1 camera every 2 km^2) and remained active for ~30 consecutive days[28,49]. We excluded data from camera-trap sites with inconsistent date-time stamps, yielding a total of 60–89 cameras per protected area (Fig. 1 and Table S1).

Data

A total of 2,312,635 camera-trap photos included mammals. We further filtered the dataset to include only species with a body mass greater than 75 g (smaller species have high uncertainty of identification and are difficult to detect) and strictly terrestrial or scansorial species (i.e., we excluded all arboreal and aquatic species)[27,51]. A total of 166 species, 38 families, and 15 orders of ground-dwelling and scansorial species were included in our study (Table S1). Since camera-traps often take multiple consecutive pictures of the same visit or individual, we avoided pseudo-replication of individuals by establishing independent events (time interval between pictures > 1 h per camera for a given species). This resulted in a total of 126,382 independent events. To analyze diel activity, we used the time-stamp recorded in each independent event[52]. To test whether activity was consistent among tropical regions and to test H1, we summarized the number of events for each of the following three categories (1) day, (2) twilight, or (3) night. Each event was classified by protected area, location, time, and date to specify the sunrise, sunset, nautical dawn, and dusk using the R library 'maptools' version 1.1–4[53] and the functions 'crepuscule' and 'sunriset'. Twilight was defined as the interval between dawn and sunrise and between sunset and "nautical dusk"[54]. Day was defined as the interval between sunrise and sunset. Night was the interval between nautical dusk and nautical dawn. To test H2 and H3, and to plot species-specific activity profiles, every independent event was anchored to sunrise and sunset to correct for differences in the delimitation of day, night, and twilights between protected areas and across seasons[55] using the 'activity' package[56,57].

We extracted (1) diet, (2) body mass (g), and forest strata from the PHYLACINE database[58] and updated reviewed data on forest strata of mammals in the protected areas studied[51] (Fig. S2). We excluded the arboreal species and only included ground-dwelling and scansorial species in our study. Then, we classified each mammal species into one of four trophic guilds: carnivore, herbivore, insectivore, or omnivore. Categories were based on diet reported in the PHYLACINE database and we classified as carnivore species feeding on ≥80% vertebrates, herbivore species feeding on ≥80% plant materials, insectivore feeding on ≥80% insects, the remaining species were categorized as omnivores (e.g., feeding on vertebrates and fruits)[58,59].

Analysis

To test how trophic guild (discrete variable: carnivores, herbivorous, insectivores, and omnivores) and body mass (continuous variable: log-transformed) were associated with the number of independent events of each diel activity (day, night, twilight) of tropical ground-dwelling and scansorial mammals we fitted a multinomial logit model[60] using the package 'mclogit' version 0.9.4.2[61]. Multinomial modelling allowed us to assess three response classes (day, night, and twilight), as opposed to two responses classes in logistic regression models. We fit a set of candidate models for each tropical region (Neotropics, Afrotropics, Indo-Malayan tropics) using maximum likelihood (ML) and with a convergence tolerance (Ɛ) of 1e−6 (Table S1). To account for potential non-independence in activity patterns of species detected in a given protected area, we included protected areas as a random intercept effect within all models. We selected the best model for each tropical region using Akaike information criterion (AIC)[62]. We ranked models using ΔAIC and considered models with a $\Delta AIC < 2$ to be equally supported. Once we selected the best models, we ran the models with a restricted maximum likelihood (REML) to arrive at final estimates for each tropical region. We predicted relative activity with the package 'mpred' version 0.2.4.1[61]. This allowed us to extract the predicted probability of activity falling into each diel category for the range of body masses, for each trophic guild, and region.

To test if the diel activity of tropical mammals showed indication of arising from top-down or bottom-up processes, we classified trophic guilds by size to test how the hourly activity (number of independent events), anchored to sunrise and sunset, of large and small groups (cut-up of 20 kg[63]) respond to the activity of large and small predators. We excluded species with very low risk of predation, the African buffalo *Syncerus craffer*, and elephant species[64] (body mass >580 kilograms). We used a log link and a Poisson distribution in package "lme4" version 1.1–29 for each region to assess the relationship between the activity of a) large and small herbivores, insectivores, omnivores, carnivores (response variable) and b) large and small carnivores (predictor variable). Significant negative and positive model coefficients were interpreted as evidence for top-down and bottom-up effects, respectively. We did not include the comparison between large omnivores and large carnivores in our models because there were not sufficient detections to test this combination. We also excluded models that did not converge (small carnivores vs. small herbivores in the Neotropics and Afrotropics, and small carnivores vs. small insectivores in the Afrotropics). We employed the data of 11 protected areas where large carnivores were present (Table S1) and set protected area in the models as a random intercept.

In addition, we plotted the kernel density distribution of the activity of each trophic guild and size and (e.g., prey-predator) extracted the overlap estimates in each protected area to exemplify our results from the GLMM models assessing the bottom-up and top-down processes on diel activity. To compare the activity of prey species (e.g., herbivores) and predators (i.e., carnivores) with different sizes, we extracted the coefficient of overlap (Δ "Dhat") between the two kernel density distributions with the package 'overlap' version 0.3.4[65]. If the sample size was ≥75 independent events, we extracted the coefficient of overlap type "Dhat1", if the sample size was higher than 75 we extracted the "Dhat4"[66]. In addition, we tested the probability that the fitted distributions of the activity among pairwise groups (e.g., large herbivores vs. large carnivores) came from the same distribution by employing 500 bootstrap iterations, and obtained 95% confidence intervals (CI) and the 'probability observed index arose by chance' (*P* pNull) using the package 'activity' version 1.3.2[57]. Low values of this coefficient indicate avoidance between groups of species and *P* is the probability that the overlap between groups arose by chance (Supplementary Material PDF). It is worth mentioning that, we did not run a regional model to extract the coefficient of overlap among groups of species because pooling data from different study areas may overestimate the coefficient of overlap and lead to biased inferences[66].

To plot the activity patterns of species from Fig. 2 and Fig. S3, we gathered the data of all protected areas in each tropical region and characterized species-specific activity patterns when the number of independent events was 25 or more[66] (Fig. S3). Then we plotted species activity with the package 'overlap', which employs kernel density estimation that circumvents the conflation of data required for histograms[66]. The map for Fig. 2 was prepared in ArcGIS 10.8.1, and the composed Fig. 2 was prepared in Inkscape 1.1.1. All statistical analyses and plots were made in R-4.2.1[67].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data generated in this study have been deposited in the DataverseNO database is available online at https://doi.org/10.18710/BIGEO7. The raw camera-trap data employed in this study can be found in Wildlife Insights (www.wildlifeinsights.org). Species characteristics extracted from PHYLACINE 1.2 are available online at https://doi.org/10.5061/dryad.bp26v20. Species list with reviewed forest strata data are available at https://doi.org/10.5061/dryad.f1vhhmgv0.

Code availability

The code to analyze and reproduce this study has been deposited in the DataverseNO and is available online at https://doi.org/10.18710/BIGEO7.

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Author contributions

D.S. and R.B. proposed the study and accessed funding. A.F.V.-V., R.B., and D.S. developed the approach and hypotheses presented here. A.F.V.-V. developed and performed the analyses. R.B. verified the analysis. A.F.V.-V. wrote the manuscript with support from R.B., D.S., A.S.-P., and L.B. The authors D.S. J.A., E.A., R. Bitariho, S.E., V.E., P.A.J., C.K., E.H.M., M.G.M.L., B.M., F.R., J.S., F.S., W.R.S., and E.U. were responsible for camera trap data collection in the TEAM study areas. A.F.V.-V., R.B., and D.S. finalized the manuscript with input and approval from all authors.

Competing interests

The authors declare no competing interests.

Additional information

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Article II: Supplementary Information

Table S1. Additional information about the protected areas included in the study.

Table S2. Candidate multinomial models ranked according to Akaike information criterion (AIC) for each biogeographic region.

Table S3. Summary from the multinomial logit model on each biogeographic area.

Figure S1. Multinomial model coefficient estimates by each region.

Figure S2. a) Distribution of body mass for the three different biogeographic regions. b) Number of species in each trophic guild and each biogeographic region.

Figure S3. Examples of Kernel density activity of species by tropical region and trophic group.

Figure S4. Extended predicted probability of being diurnal (a), crepuscular (b) and nocturnal (b) for a sequence of body mass values by trophic guild and continent.

Figure S5 to Figure S12. Kernel density plots of the activity of all species groups and overlap estimates.

Table S1. Additional information about protected areas included in the study.

Protected area	Code	Area (ha)*	Country	Tropical region	Number of cameras	Number of Families**	Number of Species**	Presence of top-predators
Barro Colorado Nature Monument - Soberania National Park	BCI	4,890	Panama	Neotropical	60	15	24	No
Bukit Barisan	BBS	295,000	Indonesia	Indo-Malayan	60	18	32	Yes
Bwindi Impenetrable Forest	BIF	32,700	Uganda	Afrotropical	60	13	22	No
Caxiuanã National Forest	CAX	317,945	Brazil	Neotropical	60	12	23	Yes
Central Suriname Nature Reserve	CSN	1,600,000	Suriname	Neotropical	65	13	30	Yes
Cocha Cashu - Manu National Park	COU	1,716,294	Peru	Neotropical	60	15	32	Yes
Korup National Park	KRP	125,900	Cameroon	Afrotropical	60	11	17	No
Manaus	MAS	1,198,944	Brazil	Neotropical	89	11	22	Yes
Nam Kading	NAK	169000	Laos	Indo-Malayan	60	16	25	No
Nouabalé Ndoki	NNN	423,870	Republic of Congo	Afrotropical	64	16	30	Yes
Pasoh Forest Reserve	PSH	13,610	Malaysia	Indo-Malayan	60	18	34	Yes
Udzungwa	UDZ	208,869	Tanzania	Afrotropical	61	15	24	Yes
Virunga Massif	VIR	16,000	Rwanda-Uganda	Afrotropical	60	7	10	No
Volcán Barva (Brulio Carrillo National Park)	VB	49,921	Costa Rica	Neotropical	60	13	22	Yes
Yanachaga Chimillen National Park	YAN	122,000	Peru	Neotropical	63	14	25	Yes

Yasuni National Park	YAS	1,030,070	Ecuador	Neotropical	60	13	28	Yes

*Areas were extracted from the World Database on Protected Areas (WDPA). Pasoh Forest Reserve, and Manaus were extracted from Beaudrot et al. 2017 67.

**Number of mammals families and species detected by camera traps and included in this study. Species with a body mass >=75 g, ground dwelling and scansorial species

Table S2. Candidate multinomial models ranked according to Akaike information criterion (AIC) for each biogeographic region. LR= Likelihood ratio, AIC=Akaike Information Criterion, N= sample size (number of independent events), and ΔAIC= delta AIC.

Region	Model	N	LR	AIC	ΔAIC
Afrotropics	trophic_guild * b_mass + 1|Protected.area	60704	51357.51	82054.81	0.00
Afrotropics	trophic_guild + b_mass+ 1|Protected.area	60704	47432.70	85967.62	3912.80
Afrotropics	trophic_guild+ 1|Protected.area	60704	45910.99	87485.33	5430.52
Afrotropics	b_mass+ 1|Protected.area	60704	33107.59	100280.73	18225.92
Afrotropics	1+ 1|Protected.area	60704	29922.11	103462.21	21407.40
Indo-Malayan	trophic_guild * b_mass+ 1|Protected.area	8602	6102.54	12829.98	0.00
Indo-Malayan	trophic_guild + b_mass+ 1|Protected.area	8602	5677.21	13243.32	413.33
Indo-Malayan	trophic_guild+ 1|Protected.area	8602	5639.64	13276.88	446.90
Indo-Malayan	b_mass+ 1|Protected.area	8602	5318.54	13589.99	760.01
Indo-Malayan	1+ 1|Protected.area	8602	5299.85	13604.68	774.69
Neotropics	trophic_guild * b_mass+ 1|Protected.area	57076	37722.82	87717.97	0.00
Neotropics	trophic_guild + b_mass+ 1|Protected.area	57076	31624.34	93804.45	6086.48
Neotropics	trophic_guild+ 1|Protected.area	57076	30988.40	94436.39	6718.42
Neotropics	b_mass+ 1|Protected.area	57076	24355.06	101061.73	13343.76
Neotropics	1+ 1|Protected.area	57076	24044.83	101367.96	13649.99

Table S3. Summary from the multinomial logit model on each biogeographic area. Values represent the mean coefficient from the model and the significance, the p-value from the Wald-test, standard error are within parenthesis.

a) **Neotropics**

	night/day	twilight/day
(Intercept)	1.613***	0.095
	(0.336)	(0.337)
logmassk	−0.503***	−0.539***
	(0.053)	(0.092)
trophic_guild: Herbivores/Carnivores	−2.888***	−2.159***
	(0.157)	(0.257)
trophic_guild: Insectivores/Carnivores	4.333***	0.600
	(0.231)	(0.410)
trophic_guild: Omnivores/Carnivores	1.562***	0.210
	(0.190)	(0.289)
logmassk x trophic_guild: Herbivores/Carnivores	0.846***	0.587***
	(0.053)	(0.093)
logmassk x trophic_guild: Insectivores/Carnivores	−1.240***	−0.363*
	(0.087)	(0.170)
logmassk x trophic_guild: Omnivores/Carnivores	−3.651***	−1.911***
	(0.118)	(0.156)
night/day x VCov(~1,~1)	0.704	0.171
	(0.212)	(0.096)
twilight/day x VCov(~1,~1)	0.171	0.383
	(0.096)	(0.052)
Groups by Site.Code	8	
Deviance	84205.7	
N	57076	

Significance: *** = p < 0.001; ** = p < 0.01; * = p < 0.05

b) Afrotropics

	night/day	twilight/day
(Intercept)	2.341***	0.176
	(0.212)	(0.235)
logmassk	−0.845***	−0.521***
	(0.053)	(0.070)
trophic_guild: Herbivores/Carnivores	−4.406***	−3.585***
	(0.120)	(0.157)
trophic_guild: Insectivores/Carnivores	−1.347***	−1.212***
	(0.130)	(0.168)
trophic_guild: Omnivores/Carnivores	1.090***	−0.406*
	(0.133)	(0.175)
logmassk x trophic_guild: Herbivores/Carnivores	1.216***	0.889***
	(0.053)	(0.071)
logmassk x trophic_guild: Insectivores/Carnivores	3.744***	1.823***
	(0.133)	(0.160)
logmassk x trophic_guild: Omnivores/Carnivores	−1.300***	−0.271**
	(0.082)	(0.102)
night/day x VCov(~1,~1)	0.158	0.007
	(0.003)	(0.002)
twilight/day x VCov(~1,~1)	0.007	0.165
	(0.002)	(0.003)
Groups by Site.Code	5	
Deviance	81612.5	
N	60704	

Significance: *** = p < 0.001; ** = p < 0.01; * = p < 0.05

c) Indo-Malayan tropics

	night/day	twilight/day

(Intercept)	0.585	−4.295***
	(0.661)	(1.252)
logmassk	−0.375**	0.601*
	(0.135)	(0.271)
trophic_guild: Herbivores/Carnivores	−1.877***	1.781
	(0.332)	(1.140)
trophic_guild: Insectivores/Carnivores	0.418	3.945**
	(0.625)	(1.267)
trophic_guild: Omnivores/Carnivores	0.976**	2.641*
	(0.355)	(1.185)
logmassk x trophic_guild: Herbivores/Carnivores	0.551***	−0.465
	(0.136)	(0.273)
logmassk x trophic_guild: Insectivores/Carnivores	3.540***	0.824
	(0.454)	(0.448)
logmassk x trophic_guild: Omnivores/Carnivores	−0.570***	−0.556
	(0.163)	(0.306)
night/day x VCov(~1,~1)	0.987	0.474
	(1.372)	(1.115)
twilight/day x VCov(~1,~1)	0.474	0.831
	(1.115)	(1.032)
Groups by Site.Code	3	
Deviance	12459.6	
N	8602	

Significance: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$

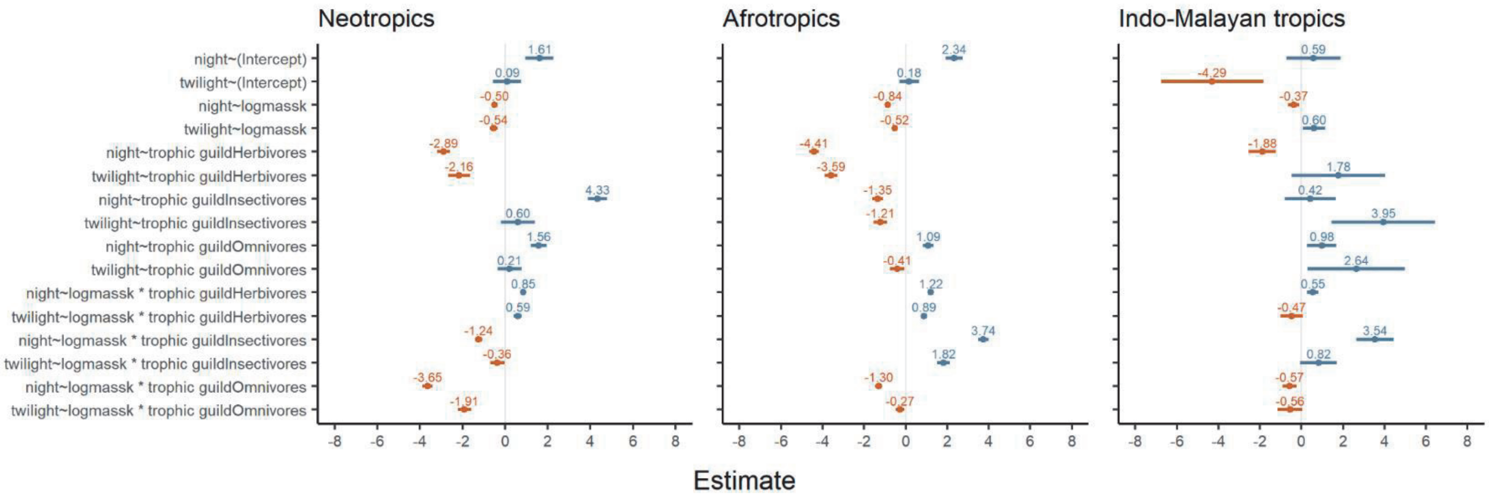

Figure S1. Multinomial model coefficient estimates by each region. The intercept (vertical line at 0) is represented with Carnivores as the reference group. Bars represent the 95% confidence intervals. Significance was considered when the 95 % CI did not overlap zero (horizontal lines). Neotropics n=57076, Afrotropics n=60704, Indo-Malayan tropics n=8602. n represent the number of independent events employed to fit the multinomial models at the regional level.

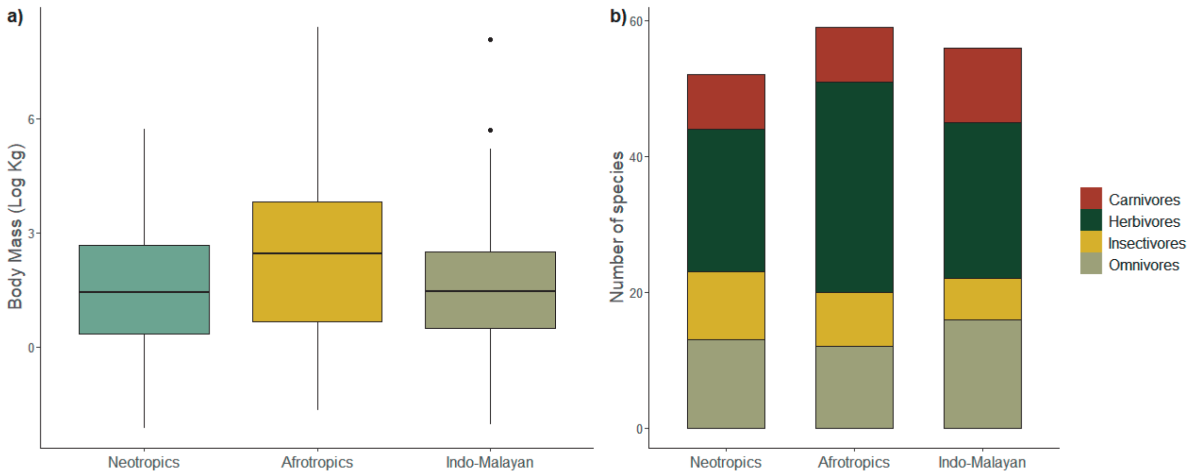

Figure S2. a) Distribution of body mass values (log scale kg) of ground-dwelling mammals for the three different biogeographic regions, boxplot centres represent the median, hinges represent the 25th and 75th percentiles, whisker extend from the hinges to the largest and smallest value no further than 1.5 times the interquartile from the hinge. b) Number of species in each trophic guild and each biogeographic region. Neotropics n=52, Afrotropics n= 59, Indo-Malayan tropics n= 56 (n= number of species).

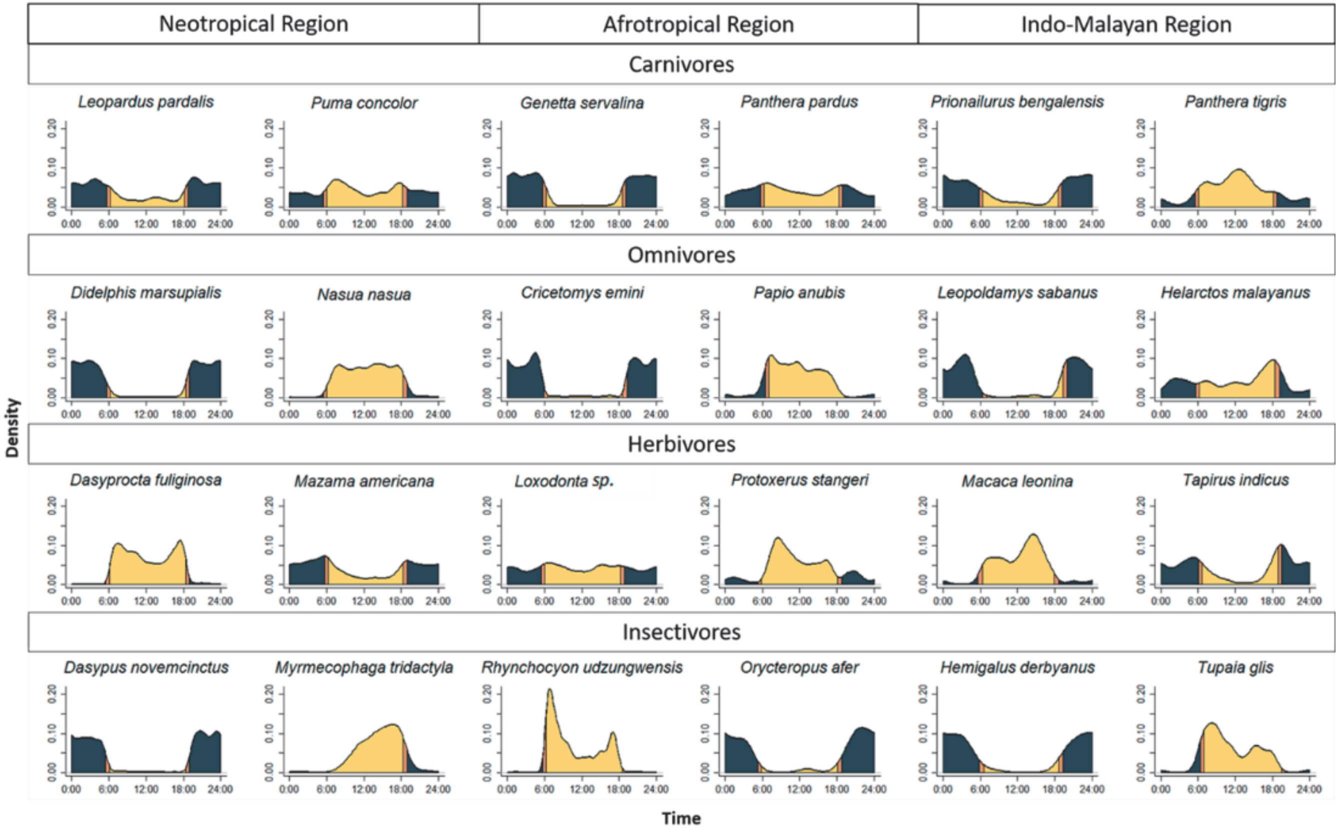

Figure S3. Examples of Kernel density activity of species by tropical region and trophic group. Yellow, dark blue, and orange represents day, night, and twilight, respectively.

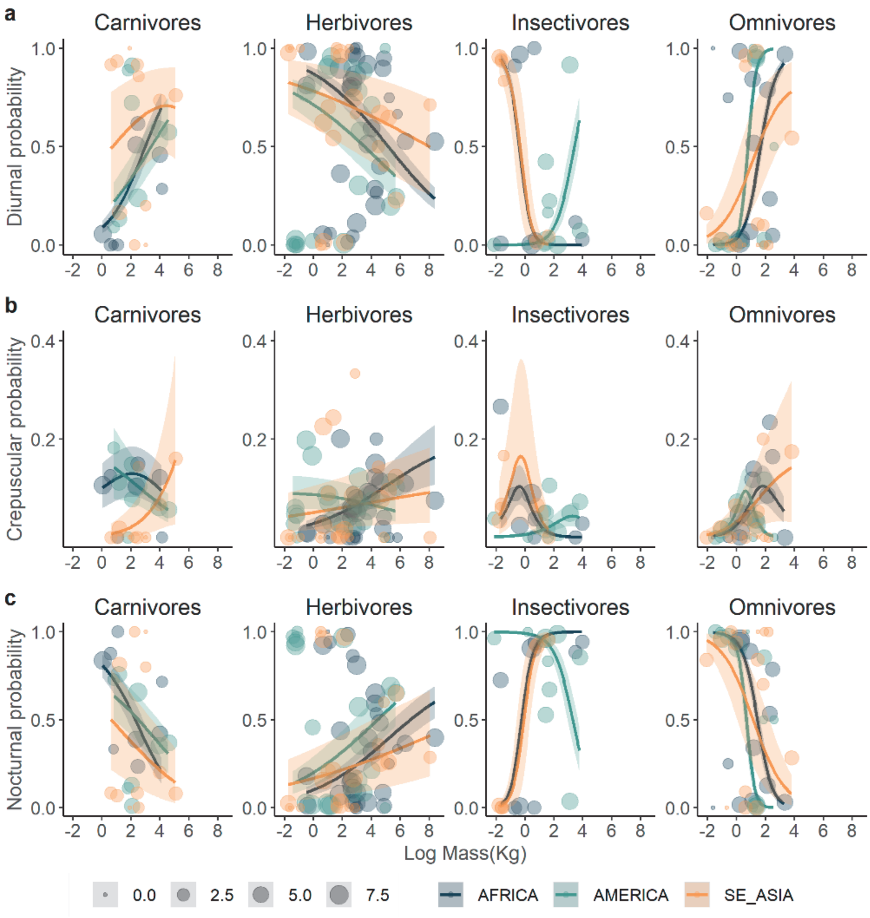

Figure S4. Extended predicted probability of being diurnal (a), crepuscular (b) and nocturnal (b) for a sequence of body mass values by trophic guild and continent. Lines represent continuous predictions along a range of body mass values extracted from the fitted multinomial logit models. Lighter regions correspond to the upper and lower 95% confidence intervals. Circles represent raw proportions of diurnal, crepuscular, and nocturnal activity for species included in this study are based on the number of independent events (log-scaled), with the smallest circle corresponding to 1 and the biggest to 1055 events. Total number of independent events: 126 382. $n_{\text{carnivores\_Neotropics}}$= 2182, $n_{\text{carnivores\_Afrotropics}}$= 1474, $n_{\text{carnivores\_Indo-Malayan\_tropics}}$ = 152, $n_{\text{omnivores\_Neotropics}}$ = 4656, $n_{\text{omnivores\_Afrotropics}}$= 4656, $n_{\text{omnivores\_Indo-Malayantropics}}$= 435, $n_{\text{herbivores\_Neotropics}}$= 45839, $n_{\text{herbivores\_Afrotropics}}$= 47458, $n_{\text{herbivores \_Indo-Malayan\_tropics}}$= 7803, $n_{\text{insectivores\_Neotropics}}$= 4399, $n_{\text{insectivores\_Afrotropics}}$ = 3886, $n_{\text{insectivores\_Indo-Malayan\_tropics}}$ = 212

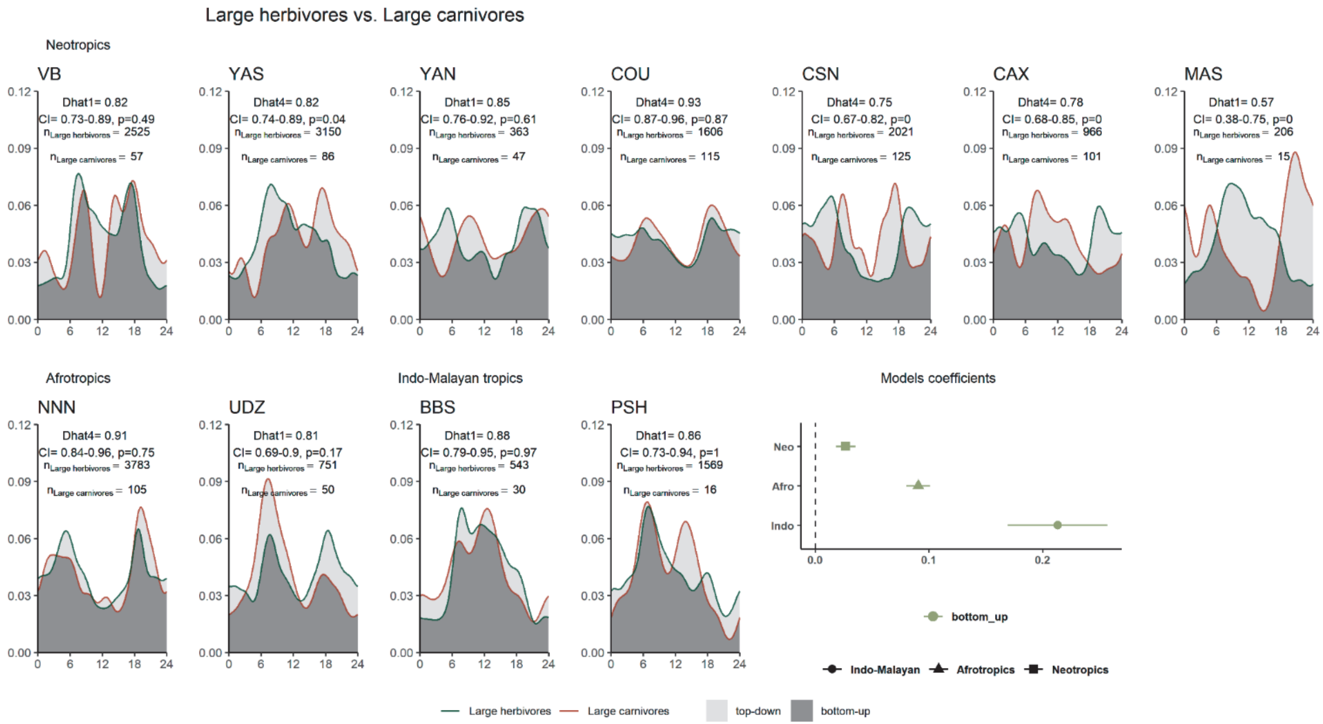

Figure S5. Fitted kernel density distribution and coefficient of overlap (Dhat) between the activity of large carnivores vs. large herbivores at the protected area level. Lines: Fitted kernel density distribution of each group, Dhat1: coefficient of overlap type 1 if the sample size was lower than 75, and Dhat4: type 1 if the sample size was higher than 75. CI: 95% confidence intervals, p-value: probability that the fitted distributions of the activity among these groups came from the same distribution. “n” represents the number of independent events in each trophic guild and size. Bottom right panel represents the results at the regional level Figure 4.

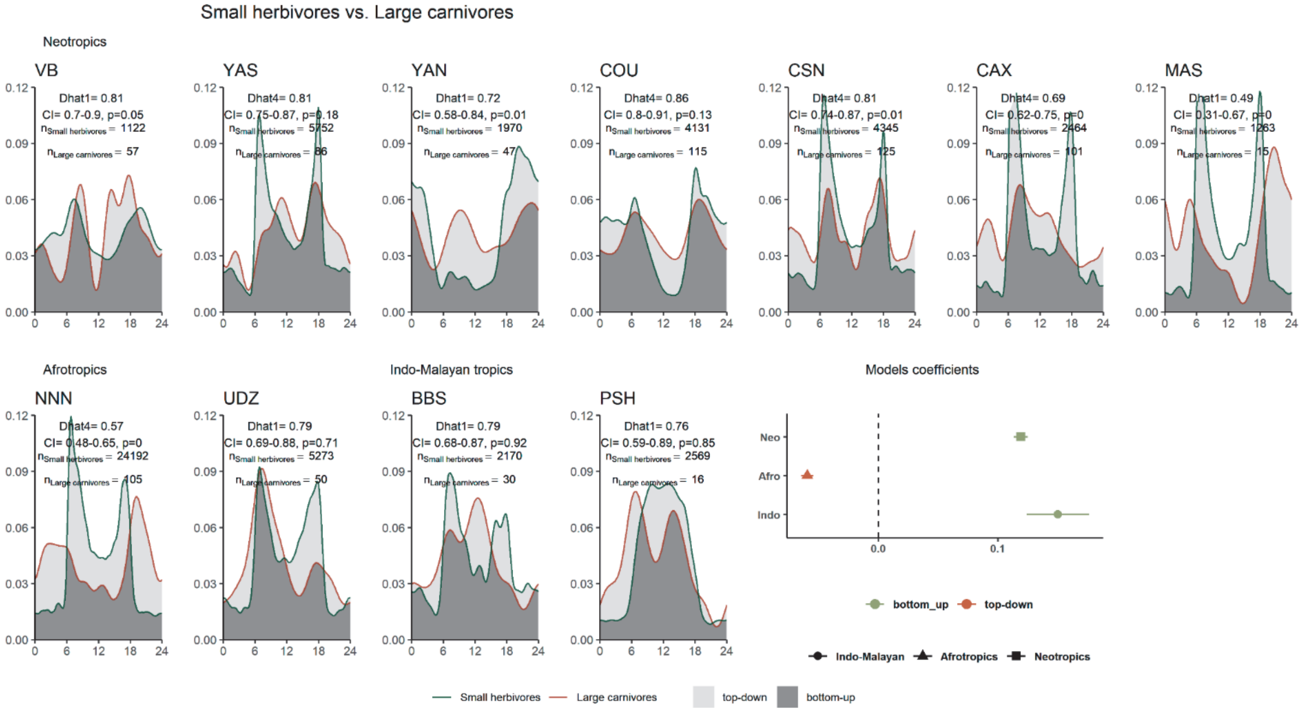

Figure S6. Fitted kernel density distribution and coefficient of overlap (Dhat) between the activity of large carnivores vs. small herbivores at the protected area level. Lines: Fitted kernel density distribution, Dhat1: coefficient of overlap type 1 if the sample size was lower than 75, and Dhat4: type 1 if the sample size was higher than 75, CI: 95% confidence intervals, p-value: probability that the fitted distributions of the activity among these groups came from the same distribution. “n” represents the number of independent events in each trophic guild and size. Bottom right panel represents the results at the regional level Figure 4.

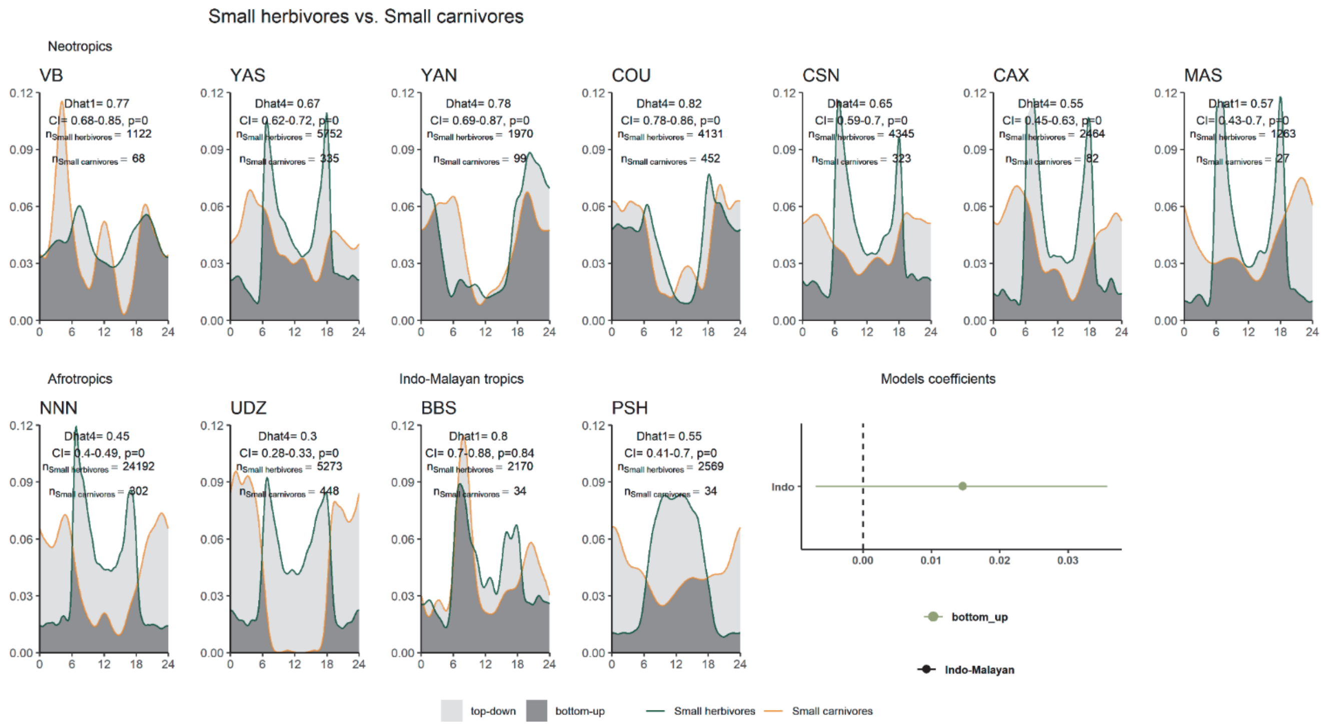

Figure S7. Fitted kernel density distribution and coefficient of overlap (Dhat) between the activity of small carnivores vs. small herbivores at the protected area level. Lines: Fitted kernel density distribution, Dhat1: coefficient of overlap type 1 if the sample size was lower than 75, and Dhat4: type 1 if the sample size was higher than 75, CI: 95% confidence intervals, p-value: probability that the fitted distributions of the activity among these groups came from the same distribution. "n" represents the number of independent events in each trophic guild and size. Bottom right panel represents the results at the regional level Figure 4.

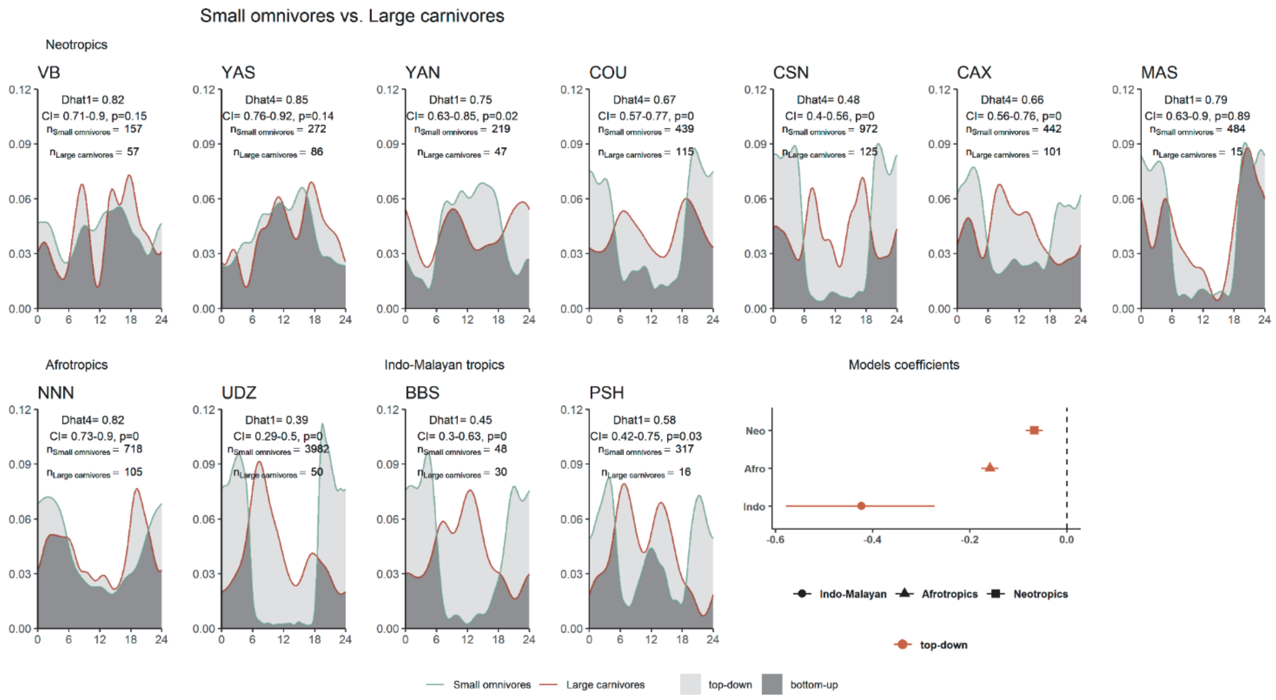

Figure S8. Fitted kernel density distribution and coefficient of overlap (Dhat) between the activity of large carnivores vs. small omnivores at the protected area level. Lines: Fitted kernel density distribution, Dhat1: coefficient of overlap type 1 if the sample size was lower than 75, and Dhat4: type 1 if the sample size was higher than 75, CI: 95% confidence intervals, p-value: probability that the fitted distributions of the activity among these groups came from the same distribution. "n" represents the number of independent events in each trophic guild and size. Bottom right panel represents the results at the regional level Figure 4.

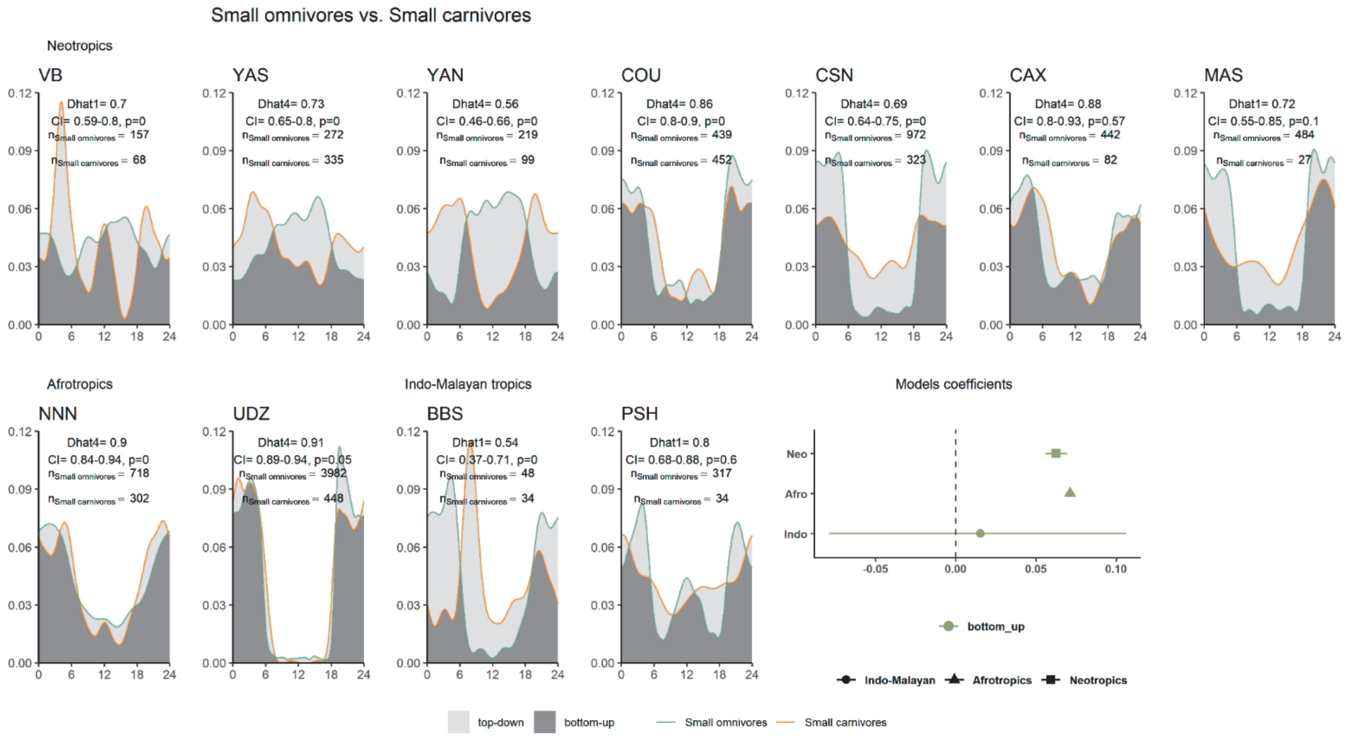

Figure S9. Fitted kernel density distribution and coefficient of overlap (Dhat) between the activity of small omnivores vs. small carnivores at the protected area level. Lines: Fitted kernel density distribution, Dhat1: coefficient of overlap type 1 if the sample size was lower than 75, and Dhat4: type 1 if the sample size was higher than 75, CI: 95% confidence intervals, p-value: probability that the fitted distributions of the activity among these groups came from the same distribution. "n" represents the number of independent events in each trophic guild and size. Bottom right panel represents the results at the regional level Figure 4.

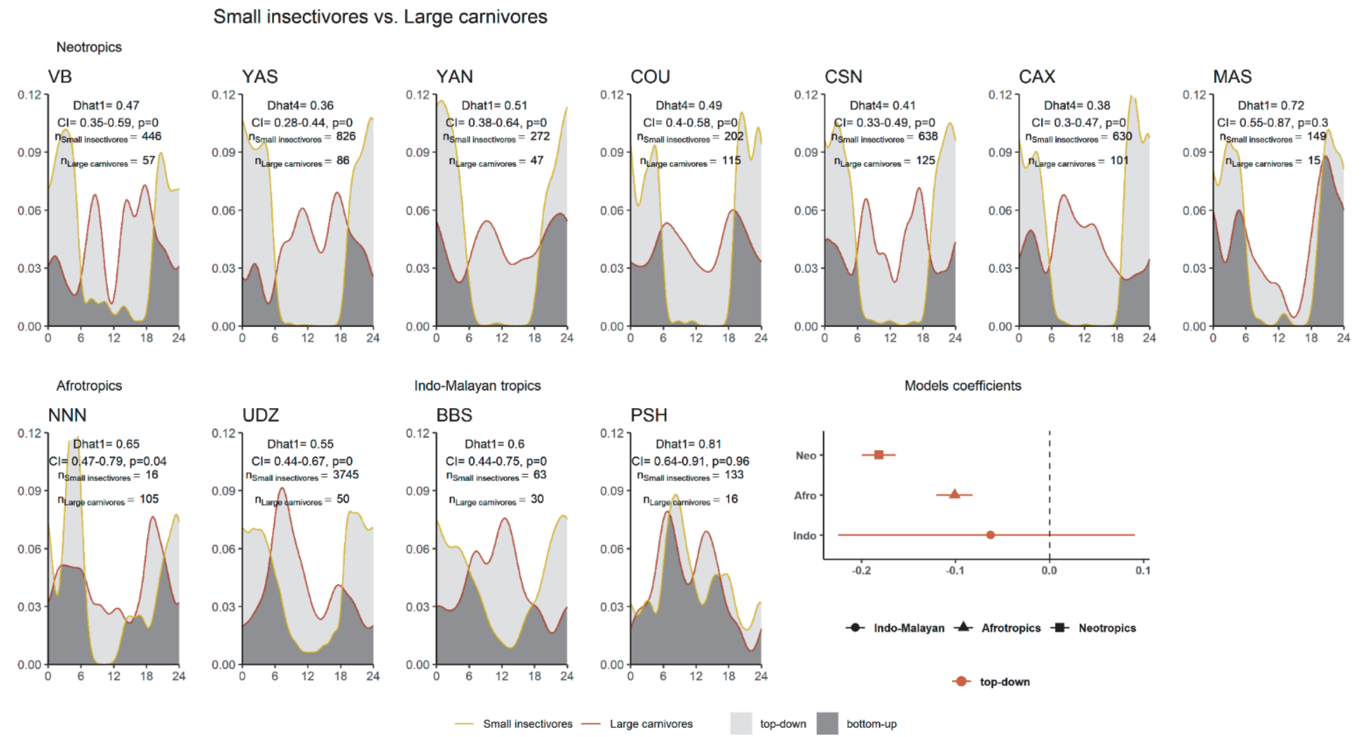

Figure S10. Fitted kernel density distribution and coefficient of overlap (Dhat) between the activity of large carnivores vs. small insectivores at the protected area level. Lines: Fitted kernel density distribution, Dhat1: coefficient of overlap type 1 if the sample size was lower than 75, and Dhat4: type 1 if the sample size was higher than 75, CI: 95% confidence intervals, p-value: probability that the fitted distributions of the activity among these groups came from the same distribution. "n" represents the number of independent events in each trophic guild and size. Bottom right panel represents the results at the regional level Figure 4.

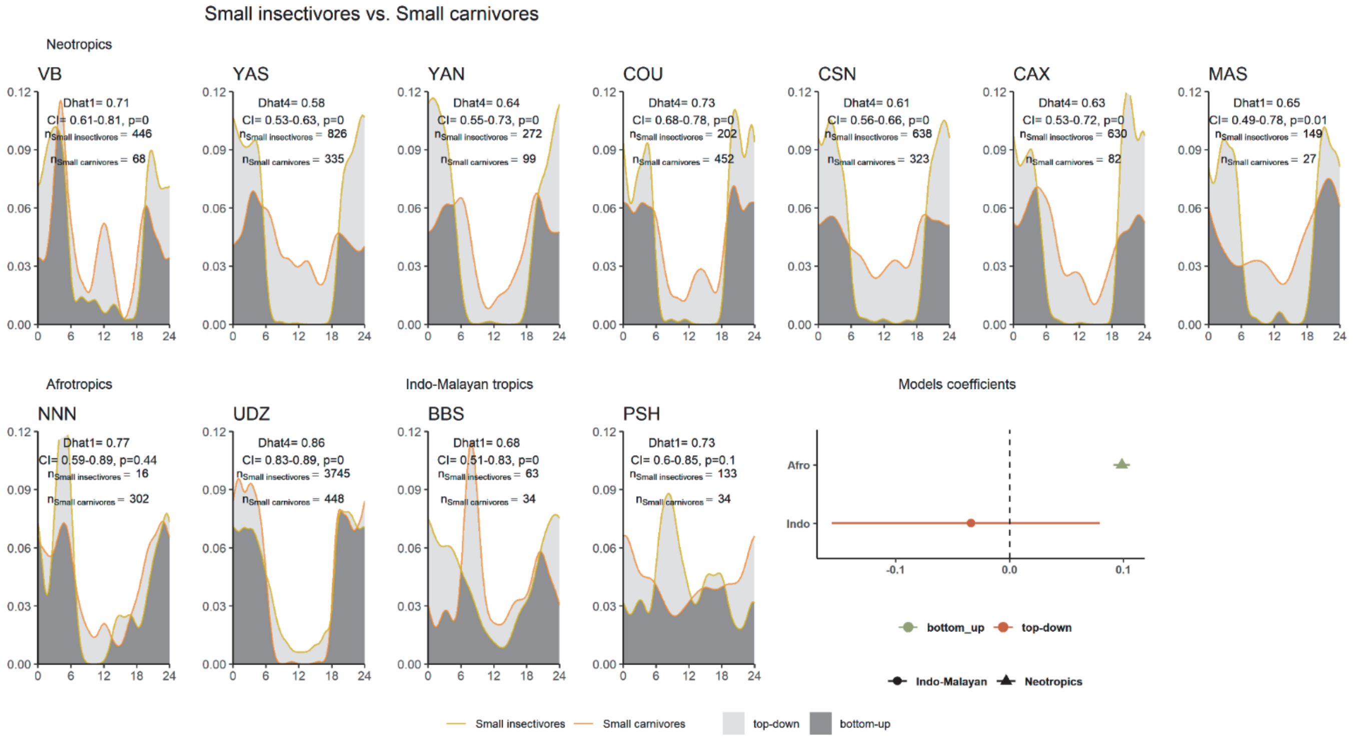

Figure S11. Fitted kernel density distribution and coefficient of overlap (Dhat) between the activity of small carnivores vs. small insectivores at the protected area level. Lines: Fitted kernel density distribution, Dhat1: coefficient of overlap type 1 if the sample size was lower than 75, and Dhat4: type 1 if the sample size was higher than 75, CI: 95% confidence intervals, p-value: probability that the fitted distributions of the activity among these groups came from the same distribution. “n” represents the number of independent events in each trophic guild and size. Bottom right panel represents the results at the regional level Figure 4.

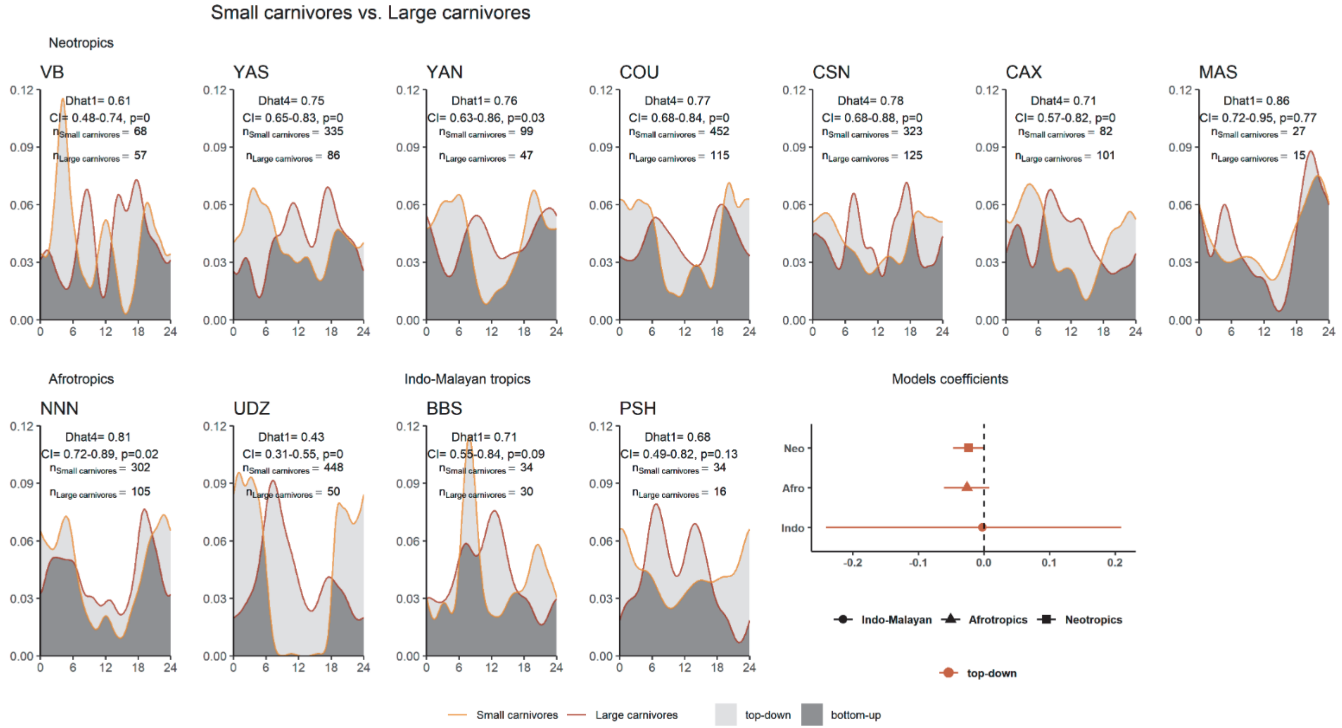

Figure S12. Fitted kernel density distribution and coefficient of overlap (Dhat) between the activity of large carnivores vs. small carnivores at the protected area level. Lines: Fitted kernel density distribution, Dhat1: coefficient of overlap type 1 if the sample size was lower than 75, and Dhat4: type 1 if the sample size was higher than 75, CI: 95% confidence intervals, p-value: probability that the fitted distributions of the activity among these groups came from the same distribution. “n” represents the number of independent events in each trophic guild and size. Bottom right panel represents the results at the regional level Figure 4.

ARTICLE III

Spatiotemporal interactions between ocelots and agoutis in Neotropical protected forests

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Abstract

Understanding how predators and their prey coexist in space and time is of core interest in ecology. Increased access to camera trap data allows the study of species interactions in space and time. Here, we investigated the spatiotemporal distribution of activity of predator-prey species in protected areas. We explored whether agouti (*Dasyprocta leporina*) respond to predation risks by adjusting their activity to the occurrence of a potential predator, the ocelot (*Leopardus pardalis*), and whether ocelot occurrence responds to that of the prey. Using a custom Bayesian occupancy model for two species, we analyzed camera-trap data collected over three protected tropical forests from Brazil and Suriname. This model distinguishes between occupancy (i.e., spatial distribution) and detection (i.e., activity). We found a positive spatial association between predator and prey, suggesting that ocelots seek places where agouti are present. Instead of segregating in space, the diurnal agouti appeared to respond to predation risk by reduced activity. The most pronounced reduction in agouti activity was during twilight in sites where ocelots, nocturnal and crepuscular predators, occurred. Our approach of jointly modelling interactions in space and time helped identify mechanisms of predator and prey coexistence.

Keywords: predator-prey, predation risk, diel activity, spatiotemporal interactions.

1 Introduction

Studying the mechanisms that allow predator and prey to coexist is a central topic in ecology and conservation. This is because predator-prey interactions can determine community structure, dynamics, and ecosystem stability (Holt 1984). Predator-prey interactions represent an arms race, where prey try to minimize spatial and temporal overlap, and predators maximize such overlap (Sih 2005). One particularly interesting aspect gaining interest is how prey realize their spatiotemporal niche in relation to that of the predator (and vice versa). For instance, the prey's diel activity pattern—when activity occurs within the 24-hour daily cycle—may be an adaptive response to avoid predators and their activity peaks (Tambling et al. 2015). Alternatively, sites occupied (i.e., spatial distribution) by prey may be sought by predators (Bischof et al. 2014).

To gain a deeper understanding of how predator and prey interact and coexist, ecologists usually employ data from passive detection devices (camera traps) or tracking devices (GPS tags, trap-based loggers, and accelerometers). While tracking devices (e.g., GPS tags) can reveal spatiotemporal predator-prey interactions with a high level of detail (Kohl et al. 2018), the focus remains on a few instrumented individuals that may or may not represent the population. On the other hand, camera trap studies can help capture the spatial distribution and activity patterns of wildlife communities in situ and with low disturbance (Beaudrot et al. 2016, Semper-Pascual et al. 2022, Vallejo-Vargas et al. 2022). To investigate the mechanisms of species coexistence on the species spatial distribution and diel activity using camera-trap data, ecologists employ spatial (MacKenzie, Bailey and Nichols 2004, Mackenzie 2006, Richmond, Hines and Beissinger 2010, Rota et al. 2016) and temporal models (Meredith and Ridout 2014, Rowcliffe et al. 2014) separately, or jointly (Niedballa et al. 2019, Kellner et al. 2022, Suraci et al. 2022).

The increasing availability of camera trap data and analytical methods for exploiting them have already yielded insights into mechanisms facilitating the coexistence of predators and prey. Studies have reported several mechanisms by which prey decreases predation risk in space or time. Prey species avoid sites where predators occur (Esparza-Carlos, Íñiguez-Dávalos and Laundré 2018, Pudyatmoko

2019), increase movement (Kellner et al. 2022), likely to decrease encounters (Sih et al. 1985), or shift their diel activity patterns (e.g., from night to day)(Bischof et al. 2014, Tambling et al. 2015). For example, in sites where top predators went extinct (like lions, *Panthera leo* and hyaenas, *Crocuta crocuta*), prey such as kudu (*Tragelaphus strepsiceros*) or buffalo (*Syncerus caffer*) are more active at night, than in sites where predators remain (Tambling et al. 2015). Yet, studies that jointly assess interactions in space and time remain scarce and tend to focus on the effect of anthropogenic factors (Murphy et al. 2021, Kellner et al. 2022) and carnivore guild interactions (Karanth et al. 2017) or do not account for the true occurrence of the species (Niedballa et al. 2019), potentially leading to biased inferences (Burton et al. 2015).

Here, we test for and quantify the spatiotemporal relationship between a predator and a prey inhabiting protected areas in tropical forests. Our analysis has three key features: 1) it treats space and time jointly, 2) it accounts for imperfect detection, and 3) it focuses on protected areas, which are still only minimally impacted by people. We employed data collected from protected tropical rainforests in Brazil and Suriname and two species, red-rumped agouti (*Dasyprocta leporine)* and one of its predators, the ocelot *Leopardus pardalis*). We used a customized single-season occupancy model for our two species to assess their spatiotemporal relationship in protected tropical forests. Specifically, we tested how prey activity during day, night, and twilight relates to the occurrence and activity of the predator. In addition, we tested for and quantified potential response in predator occupancy to that of the prey. We hypothesized that: i) predator occupancy would be positively related with prey occupancy, ii) prey would be less active in places where predators are present, and iii) where predators and prey both occur, the prey will modify its activity to avoid overlap with the predator.

2 Methods

2.1 Study area and camera trap data

We used camera-trap data from three protected areas in the Neotropical rainforest collected by the Tropical Ecology Assessment Monitoring (TEAM) Network (Network-TEAM 2011, Rovero and Ahumada 2017) (Figure 1). We used data from one protected area in Suriname (Central Suriname Nature Reserve, CSN) and two protected areas in Brazil (Caxiuanã National Forest, CAX and Manaus, MAS). In CSN, was sampled during nine years (2008-2017), CAX during six years (2010-2016), and MAS for two years (2010-2011) (Table S1). CSN and CAX had low population density in a 10 km buffer around them, 0.00006, and 0.009 people per square kilometer, respectively. Meanwhile, MAS has the highest population density among the three study areas, 4.7 (Figure 1). The climate in these protected forests is characterized by one rainy season and one wet season (Text S1).

Camera-trap data was mainly collected in the three protected areas during the dry season. On average, 58 camera traps were deployed in each protected area at a density of one camera per 0.5 - 1 km^2 and were active ~38 consecutive days in each sampling period (min = 1 day, max = 80 days). We excluded observations where detections had errors in the date-time stamps or the camera did not work properly (e.g., blanks).

We defined a visit as when a species was detected in an hour clock in each camera trap site and sampling season. We defined three diel periods using local (study area specific) astronomical sunrise, sunset and twilight times, obtained using the R package ‘suncalc’ (Thieurmel, Elmarhraoui and Thieurmel 2019). Dawn was delineated by the beginning of astronomical twilight (sun 18° below the horizon) and sunrise (when the bottom edge of the sun touches the horizon). Dusk was delineated by the beginning of sunset and astronomical sunset (sun 18° below the horizon). Night was defined as the period between astronomical dusk and dawn and day between sunrise and sunset. Twilights were defined as the activity in the periods of dawn and dusk. Day, night, and twilight had an average duration of 11.8, 9.6, 2.6 hours, respectively. The total number of hours available for detection was the difference between the date and hour when the camera was deployed and the date and hour when the cameras was collected.

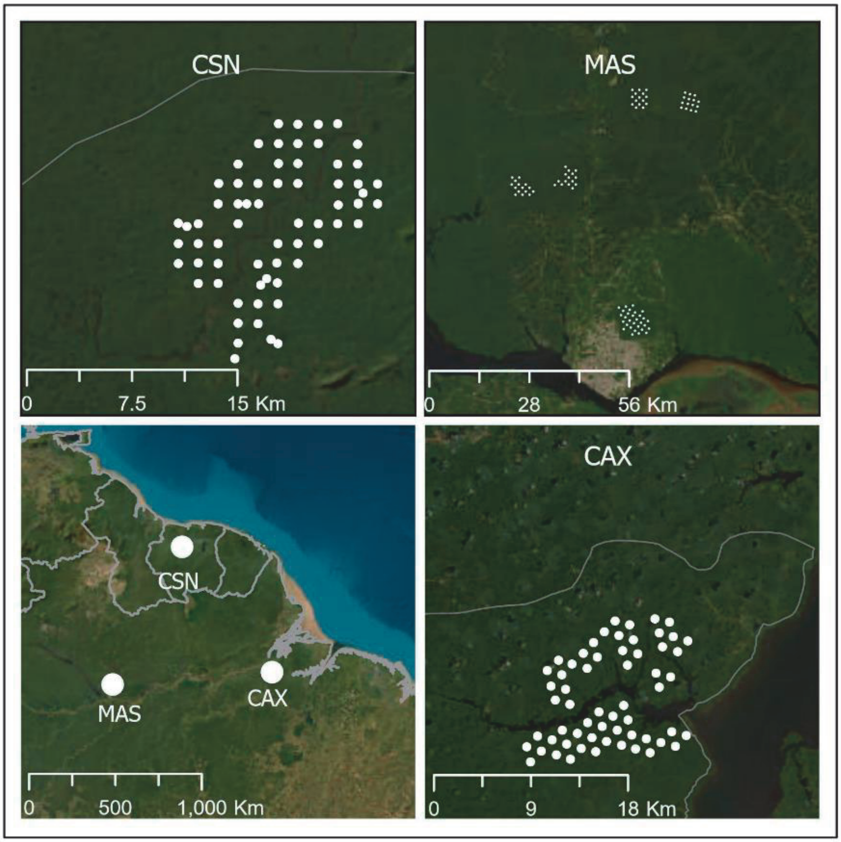

Figure 1. Map of the study area. Left-bottom: location of the three protected areas in the Neotropics. Panels show the camera trap arrays in each protected area. In CSN and CAX, grey lines represent the protected area border. The map was created in ArcGisPro 3.1.2, and the satellite imagery was extracted from Earthstar Geographics.

2.2 Spatiotemporal interaction model

We built a Bayesian single-single season 2-species occupancy model that allowed us to analyse data from multiple protected areas and sampling periods. Occupancy models takes into account species imperfect detection to estimate the probability of species occupancy (Mackenzie 2006, Burton et al. 2015, Kéry and Royle 2017). Our custom model included separate ecological and observation process models for both the prey and the predator. To model interactions, we included an effect of prey occupancy on the occupancy of the predator and an effect of predator occupancy on prey detection probability, which we interpreted as a proxy of activity. In addition, we tested for differences in prey activity between diel periods (day, night, twilight), modulated by predator presence/absence (Supplementary Text 2).

Ecological model – occupancy. Site occupancy z_i of the prey at site i was modelled as the outcome of a Bernoulli trial:

$$z_i \sim Bernoulli(\psi)$$

where ψ is the occupancy probability of the prey. Overall occupancy probability, and thus site occupancy, was allowed to vary between protected areas and seasons; indices are omitted here for readability.

Similarly, site occupancy $\dot{z}_i$ of the predator was modelled as:

$$\dot{z}_i \sim Bernoulli(\dot{\psi}_i)$$

The occupancy probability $\dot{\psi}_i$ of the predator at site i is the result of a logistic regression:

$$logit(\dot{\psi}_i) = \dot{\beta}_{\psi_0} + \dot{\beta}_{\psi_1} z_i$$

Where $\dot{\beta}_{\psi_0}$ is the intercept and $\dot{\beta}_{\psi_1}$ the effect of site occupancy z_i by the prey on the occupancy probability of site i by the predator.

Observation process model – detection. The number of hours $y_{i,d}$ with detections of the prey at site i during diel period d (day, night, twilight) was modelled as the outcome of a Binomial process:

$$y_{i,d} \sim Binomial(p_{i,d} z_i, n_{i,d})$$

Where $p_{i,d}$ is the probability of detecting the prey at least once in a given hour at site i and during diel period d and $n_{i,d}$ the number of hours the camera trap was active at that site during diel period d. Detection at a site is conditional on the prey being present at that site, hence the multiplier z_i.

Detection probability of the prey is the result of a logistic regression:

$$log\imath\dot{t}(p_{\imath,d}) = \beta_0 + \beta_d I_{d_i} + \beta_1 \dot{z}_i + \beta_2 I_{d_i} \dot{z}_i$$

Where β_0 is the intercept, β_d the effect of diel period (dummy variable I_{d_i}, with day serving as the contrast for night and twilight), β_1 the effect of the predator's presence at site i, and β_2 the effect of the interaction between diel period and predator presence. We chose the above formulation (shared intercept across all diel periods) to allow direct estimation of the effect of diel activity instead of having to derive it from the posterior of $p_{i,d}$.

Predator detections were similarly modelled as:

$$\dot{y}_{i,d} \sim Binomial(\dot{p}_{i,d} \dot{z}_i, n_{i,d})$$

Where $\dot{p}_i$ is the probability of detecting the prey at least once in a given hour at site i and $n_{i,d}$ the number of hours the camera trap was active at that site during diel period d. Predator and prey shared the same n_i, as all cameras could detect either species.

Detection probability of the predator is the result of a logistic regression:

$$log\imath\dot{t}(\dot{p}_{\imath,d}) = \dot{\beta}_0 + \dot{\beta}_d I_{d_i}$$

Where β_0 is the intercept, β_d the effect of diel period (dummy variable I_{d_i}, with day serving as the contrast for day and twilight).

2.3 Model fitting

We fitted the model using a Markov chain Monte Carlo (MCMC) approach within the Numerical Inference for Statistical Models Using Bayesian and Likelihood Estimation (NIMBLE) package (de Valpine et al. 2017) in R version 4.2.3. We used uninformative priors, ran three chains of 50000 MCMC iterations each, discarded the first 10000 iterations, and recorded samples in intervals of 5. To assess MCMC convergence and chain mixing, we visually examined trace plots and calculated the Gelman-Rubin statistic for each parameter, where values < 1.1 indicated convergence (Gelman et al. 2013). We used posterior distributions of parameters of interest to derive fitted values (means) and associated 95% Bayesian credible intervals (BCI).

3 Results

A total of 214 sites were established across the three protected areas. Ocelots were detected in 99 sites over the duration of the study, and red-rumped agouti were detected at 195 sites (Table S1). The ocelot was recorded in a total of 272 hours, and the agouti in 4013 hours out of a total number of 2910298 hours across the three protected areas (More detail Table S1).

Occupancy and spatial association between predator and prey

Ocelot occupancy was positively related to prey occurrence $\dot{\beta}_{\psi_1} z_i$ = 2.87 (BCI= 2.18; 3.60). Site occupancy varied between years and protected areas (Figure S1, S2). Agouti mean occupancy ranged from 0.65(BCI: 0.52-0.79) to 0.96 (BCI:0.89-0.99). Ocelot mean occupancy in sites where the prey was present varied from 0.69 (BCI:0.51-0.84) to 0.97 (BCI: 0.90-0.99). In sites where the prey was absent, ocelot occupancy varied from 0.13 (BCI: 0.04-0.32) to 0.72 (BCI: 0.34-0.98). The highest mean ocelot occupancy was estimated in MAS in 2010 ($\dot{\psi}$ = 0.97; BCI: 0.90-0.99) and the lowest in CAX in 2014 ($\dot{\psi}$ = 0.13; BCI: 0.04-0.32).

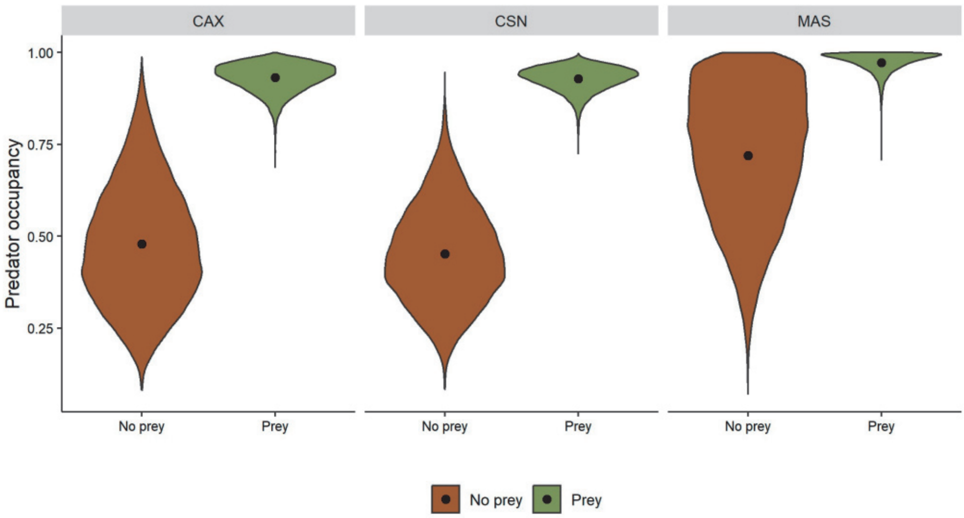

Figure 2. Predator occupancy ($\dot{\psi}_\iota$) predicted in sites where prey was absent and present z in the first sampling period. Limits along the y-axis reflect the upper and lower detection probabilities. Violins show the continuous distribution of the posterior parameter of ($\dot{\psi}_\iota$) from our model.

Predator-prey detection probability

The mean detection probability for the red-rumped agouti was higher than that for the ocelot. For example, in CSN the mean detection (hourly) probability of the agouti in the first sampling period was $p =$ 0.05 (BCI: 0.04; 0.06), and the mean detection of the ocelot was $\dot{p}$ = 0.0004 (BCI: 0.0003; 0.0006).

Inferred agouti activity (detection probability) was highest during the day and twilight, while ocelots were most active at twilight and night (Fig. 3a). Agouti activity was lower at sites also occupied by the ocelot (Fig. 3). The depressing effect on prey activity was particularly pronounced during twilight (-0.41, BCI: -0.622- -0.18, Fig. 3a).

Table 2. Coefficient estimates from our model with its confidence intervals.

Coefficient	**Mean (BCI)**
Prey detection probability:	
$\beta_1 \dot{z}_i$	-1.62 (-1.72; -1.53)*
$\beta_d(night)$	- 4.30 (-5.03; -3.68)*
$\beta_d(twilight)$	0.02 (-0.17; 0.20)
$\beta_2 I_{d_i} \dot{z}_i\ (night)$	0.19 (-0.57; 1.03)
$\beta_2 I_{d_i} \dot{z}_i\ (twilight)$	-0.41 (-0.64; -0.18)*
Predator detection probability:	
$\dot{\beta}_d I_{d_i}\ (night)$	0.47 (0.22;0.73)*
$\dot{\beta}_d I_{d_i}\ (twilight)$	0.68 (0.32; 1.02)*
Predator occupancy probability:	
$\dot{\beta}_{\psi_1} z_i$	2.87 (2.18; 3.60)*

*Note: * β coefficients statistically different from 0 when the 95% confidence interval did not overlap 0.*

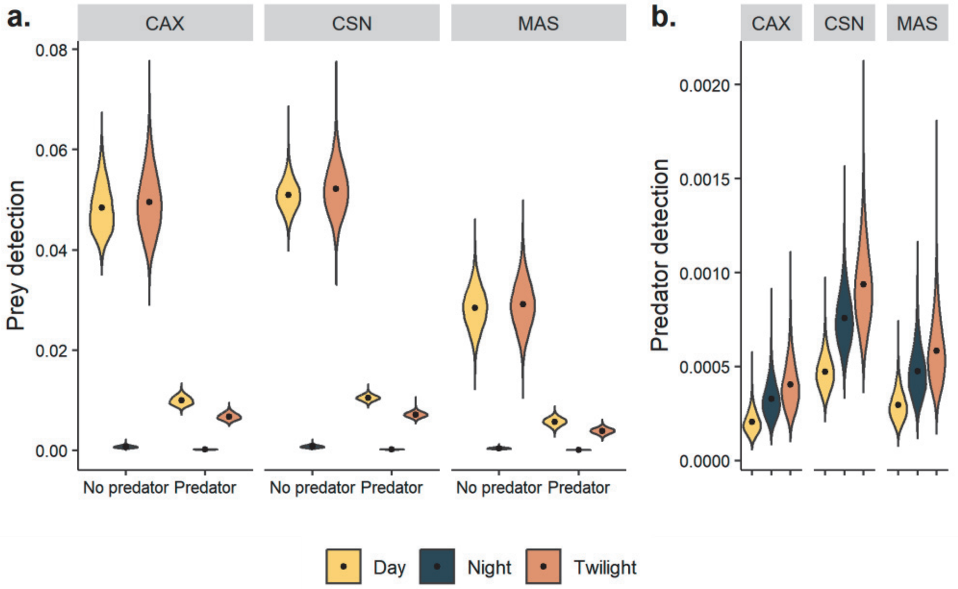

Figure 3. Detection of prey and predator. a. predicted agouti detection p by predator presence $\dot{z}$ during day, night and twilight, b. predicted ocelot detection $\dot{p}$ during day, night and twilight. Violins show the continuous distribution of the posterior parameter of p *and* $\dot{p}$ from our model; points indicate the mean of the estimate.

4 Discussion

We jointly investigated the spatial distribution and diel activity in a predator-prey system to better understand the mechanisms of coexistence. Our results showed evidence of spatial association and temporal segregation. The agouti, which is active predominantly during day and twilight, appeared to respond to predator presence by decreasing its activity. In particular, the activity during twilights was lower in sites where the predator occurred, suggesting a shift of activity to avoid the crepuscular activity of the predator.

4.1 Spatial association between agoutis and ocelots

The positive relationship between the occupancy of both predator and prey highlights spatial overlap. This finding suggests that the predator seeks sites where the prey is present. The results are congruent with a study in Panama, where ocelots were attracted to areas with agouti (*Dasyprocta punctata*) dens (Emsens et al. 2014). Similarly, the occupancy of ocelots in some of the forests we studied was positively associated with the availability of small prey (Santos et al. 2019), consistent with ocelots seeking sites where their prey is present. Co-occurrence of prey and predator at fine spatial scales (e.g., camera trap site) has also been observed in other ecosystems. For example, in temperate regions, coyotes and their main prey (white-tailed deer and eastern cottontails) in urbanised and rural regions occupy the same areas(Gallo et al. 2019). In these anthropogenic landscapes (e.g., urban areas), it is suggested that the need for food may outweigh predator avoidance behaviour and explain the lack of spatial segregation between prey and predator (Magle et al. 2014). However, our study showed that even in protected areas, where resources and space is more available than in urbanized habitats, prey and predator exhibit positive spatial association at local scales.

4.2 Reduction and shifts in agouti activity when ocelots are present

Consistent with our expectations, we found that the red-rumped agouti had distinct patterns of activity in sites where the ocelot was and was not present (Figure 3a). Notably, agouti activity during the day and twilight was lower in sites with the ocelots. This finding is consistent with the predation risk allocation hypothesis, which predicts that in sites with high predation risk, the prey would reduce the time it spent active (Lima and Bednekoff 1999). Similarly, in another study, the photographic detection probability of Mexican agouti was lower in sites where ocelots were present (Flores-Martínez et al. 2022). Additionally, in sites where the ocelot was present, agouti activity, as measured by detections, shifted from diurnal-crepuscular towards diurnal. This seems likely to be an adaptation to prevent encounters with ocelots. The ocelot exhibits a nocturnal-crepuscular activity pattern, thus leaving the twilight period as the most likely time of encounter between the two species if the prey takes no evasive action. Shifts of activity due to changes in the level of predation risk from day to night or vice versa have been reported in experiments with rabbits (Bakker et al. 2005) and rodents (Fenn and Macdonald 1995). Under natural conditions, for example, in savannahs, sites where predation risk is low due to the absence of lions, gemsbok (*Oryx gazella*) and zebras (*Equus quagga*) switched their activity from day to night (Veldhuis et al. 2020).

Our model allowed us to assess how predator-prey coexist in space and time (during day, night and twilights). This enabled us to identify potential prey responses to predation risk and the effect of prey presence on the spatial distribution of the predator. The advantage of our analysis is its flexibility and its potential for integrating more species to understand interactions at higher levels (i.e., communities). Still, there are limitations. First, the different detection values may be determined by various other factors unrelated to predator-prey relationships that differ among locations. Sites, where prey detection was low may result from differences in the landscape that promote lower species detection and may not be identifiable as a response to predation risk. For instance, agoutis can concentrate their foraging around preferred fruit trees (Silvius and Fragoso 2003), and the low detection may respond to sites with low food availability. Additionally, even though our study was conducted in protected areas, impacts in the surroundings can impact species occupancy, especially close to the edge (Semper-Pascual et al. 2023), and may also impact species activity. We recommend including habitat structure around camera trap sites and other spatial variables to reduce such uncertainties (Gorczynski et al. 2023).

5 Conclusions

Predator-prey interactions are a fundamental ecological phenomenon with repercussions for population and community dynamics. They are also highly cryptic and challenging to study in situ, particularly so of population or landscape-scale inferences are sought. Using non-invasive data and a hierarchical modelling approach, we find evidence of spatial-temporal configuration of prey activity that facilitates coexistence despite strong spatial association with the predator. Our results provide a baseline for comparison with future studies in more human-impacted systems.

6 Acknowledgements

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Article III: Supplementary Information

Text S1. Climatic characteristics of the sites of study

Table S1. Details of number of camera traps deployed, and number of cameras where ocelot and prey was detected by protected area and sampling periods.

Text S2. Model script fitted to the data.

Figure S1. Predicted occupancy $\left(\dot{\psi}_{\iota}\right)$ probability of the predator.

Figure S2. Predicted occupancy (ψ) probability of the prey.

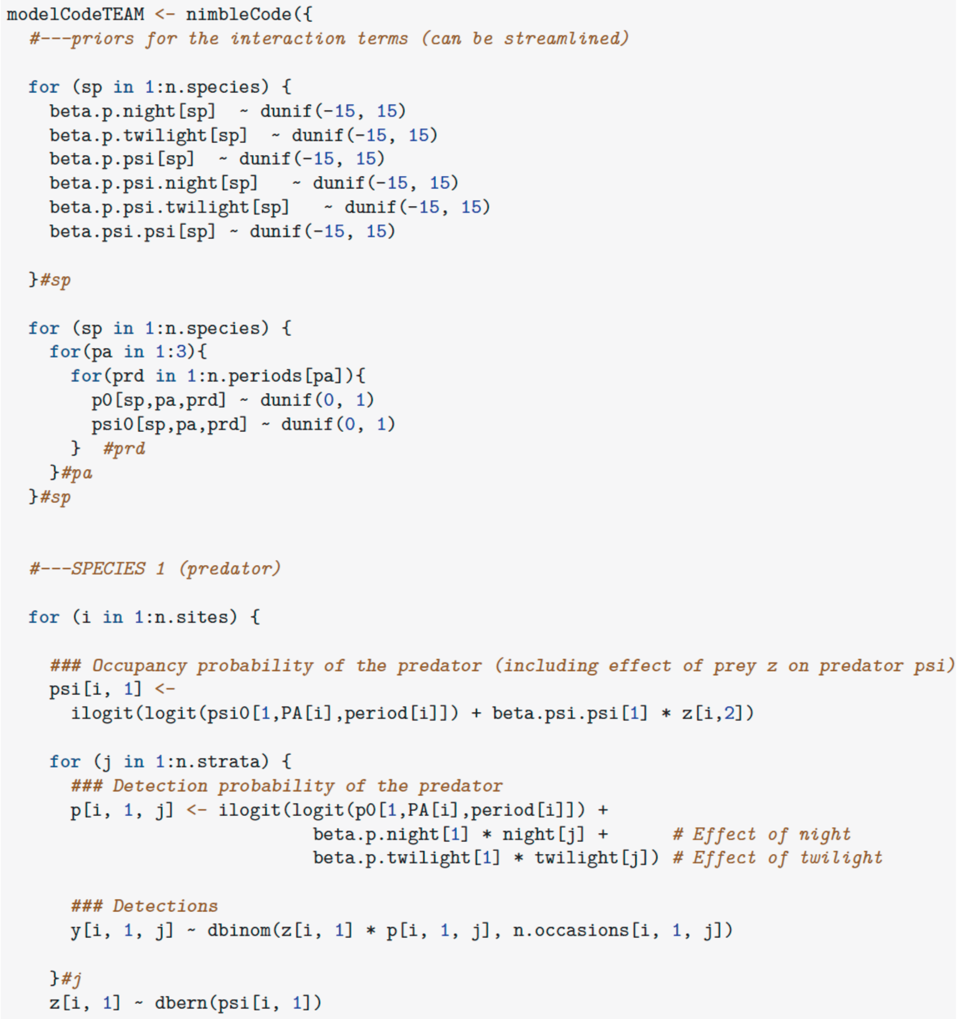
Text S1. Climatic characteristics of the sites of study

Among the three sites we studied, CSN is considered a primary rainforest with trees that can rich up to 60 m (Vath 2008), with an altitude of 30-360 m.a.s.l(Convention). CSN has a main dry season from September to November (monthly precipitation <100 mm) and a rainy season from April to November. In average, the annual rainfall in Suriname is in average 2,200 mm, with an average annual temperature of 27.5°C (Hendrison and De Graaf 2011). CAX vegetation is predominantly non-flooded (terra firme forest), with less flooded forest (várzea and igapó), and aquatic vegetation (Lisboa 2002). CAX dry season is between July to November, and the rainy season is between December to June (monthly precipitation >100 mm). The annual rainfall averages 2,272 (±193) mm and the mean annual temperature is 25.7 °C (Fisher et al. 2006). MAS is characterised by terra firme forest with an elevation of 40-110 m.a.s.l.(Braga-Neto et al. 2008). In average, the annual rainfall 2,436 (±332) mm. MAS has a rainy season during November and June and the dry season between July and September (Marques Filho et al. 1981, Braga-Neto et al. 2008).

Table S1. Details of number of camera traps deployed, and number of cameras where ocelot and prey was detected by protected area and sampling periods, CT: camera-traps.

Site Code	Sampling Period	Year(s)	Number of CTs	Ocelot CTs detected	Agouti CTs detected	Agouti n. hourly detections	Ocelot n. hourly detections
CAX	2010	2010	59	11	56	363	12
CAX	2012	2012	59	7	48	246	8
CAX	2013	2013	60	9	51	460	11
CAX	2014	2014	57	6	46	248	7
CAX	2015	2015-2016	55	5	37	188	5
CAX	2016	2016-2017	42	3	33	220	3
CSN	2008	2008-2009	57	21	49	391	31
CSN	2009	2009	58	14	46	257	26
CSN	2010	2010-2011	50	18	38	198	28
CSN	2011	2011-2012	49	16	39	145	20
CSN	2012	2012-2013	43	9	34	197	16
CSN	2013	2013-2014	54	20	47	255	36
CSN	2014	2014	46	6	31	112	6
CSN	2015	2015-2016	50	12	38	230	23
CSN	2016	2017	43	15	38	240	23
MAS	2010	2010	59	13	36	103	15
MAS	2011	2011	88	2	58	160	2

Text S2. Model script fitted to the data



```
modelCodeTEAM <- nimbleCode({
  #---priors for the interaction terms (can be streamlined)

  for (sp in 1:n.species) {
    beta.p.night[sp]  ~ dunif(-15, 15)
    beta.p.twilight[sp]  ~ dunif(-15, 15)
    beta.p.psi[sp]  ~ dunif(-15, 15)
    beta.p.psi.night[sp]   ~ dunif(-15, 15)
    beta.p.psi.twilight[sp]   ~ dunif(-15, 15)
    beta.psi.psi[sp] ~ dunif(-15, 15)

  }#sp

  for (sp in 1:n.species) {
    for(pa in 1:3){
      for(prd in 1:n.periods[pa]){
        p0[sp,pa,prd] ~ dunif(0, 1)
        psi0[sp,pa,prd] ~ dunif(0, 1)
      }  #prd
    }#pa
  }#sp


  #---SPECIES 1 (predator)

  for (i in 1:n.sites) {

    ### Occupancy probability of the predator (including effect of prey z on predator psi)
    psi[i, 1] <-
      ilogit(logit(psi0[1,PA[i],period[i]]) + beta.psi.psi[1] * z[i,2])

    for (j in 1:n.strata) {
      ### Detection probability of the predator
      p[i, 1, j] <- ilogit(logit(p0[1,PA[i],period[i]]) +
                           beta.p.night[1] * night[j] +      # Effect of night
                           beta.p.twilight[1] * twilight[j]) # Effect of twilight

      ### Detections
      y[i, 1, j] ~ dbinom(z[i, 1] * p[i, 1, j], n.occasions[i, 1, j])

    }#j
    z[i, 1] ~ dbern(psi[i, 1])
```

```
  }#i

  #---SPECIES 2 (prey)

  for (i in 1:n.sites) {
    ### Occupancy probability of the prey
    psi[i, 2] <-
      ilogit(logit(psi0[2,PA[i],period[i]]))

    for (j in 1:n.strata) {
      ### Detection probability of the prey
      p[i, 2, j] <- ilogit(
        logit(p0[2,PA[i],period[i]]) +
          beta.p.night[2] * night[j]   +           # Effect of night
          beta.p.twilight[2] * twilight[j] +      # Effect of twilight
          beta.p.psi[2] * z[i, 1]  +               # Effect predator occurrence
          beta.p.psi.night[2] * z[i, 1] * night[j] +       # Effect of the interaction
                                                       # predator occurrence and night

          beta.p.psi.twilight[2] * z[i, 1] * twilight[j]   # Effect of the interaction
                                                    # predator occurrence and twilight
      )

      ### Detections
      y[i, 2, j] ~ dbinom(z[i, 2] * p[i, 2, j], n.occasions[i, 2, j])

    }#j
    z[i, 2] ~ dbern(psi[i, 2])

  }#i
})
```

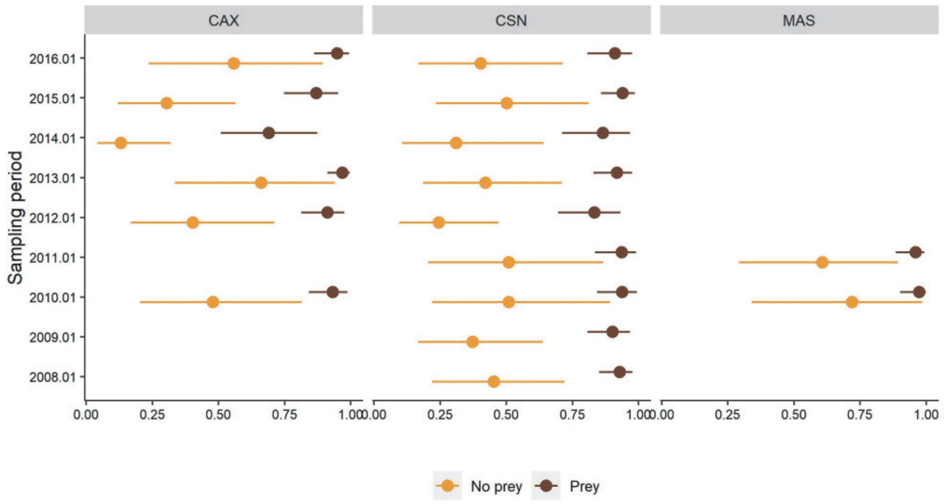


Figure S1. Predicted occupancy $(\dot{\psi})$probability of the predator. Estimates from the fitted model for each year of sampling in the three protected areas for sites where prey is present and absent (z). Dots correspond to mean estimates and lines correspond to lower and upper confidence intervals.

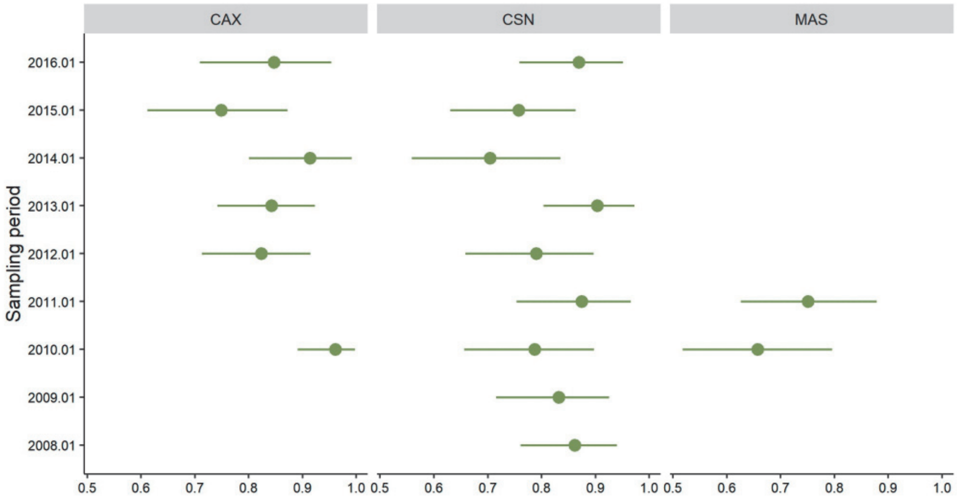


Figure S2. Predicted occupancy (ψ) probability of the prey. Estimates from the fitted model for each year of sampling in the three protected areas. Dots correspond to mean estimates and lines correspond to lower and upper confidence intervals.

ARTICLE IV

The moon’s influence on the activity of tropical forest mammals

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Abstract

Changes in lunar illumination alter the balance of risks and opportunities for animals at night, influencing activity patterns and species interactions. Our knowledge about behavioural responses to moonlight is incomplete, yet it can serve to assess and predict how species respond to environmental changes such as light pollution or loss of canopy cover. As a baseline, we wish to examine if and how wildlife responds to the lunar cycle in some of the darkest places inhabited by terrestrial mammals: the floors of tropical forests.

We quantified the prevalence and direction of activity responses to the moon in tropical forest mammal communities. Using custom Bayesian multinomial logistic regression models, we analyzed long-term camera trapping data on 86 mammal species from 17 protected forests on three continents. We also tested the hypothesis that nocturnal species are more prone to avoiding moonlight, as well as quantified diel activity shifting in response to moonlight.

We found that, apparent avoidance of moonlight (lunar phobia) is more common than apparent attraction (lunar philia). The three species exhibiting lunar philia followed diurnal or diurnal-crepuscular activity patterns. Lunar phobia, detected in 14 species, is associated with nocturnality, and is particularly common among rodents. Strongly lunar phobic species were less active during moonlit nights, which in most cases also decreases their total daily activity.

Our findings indicate that moonlight influences animal behavior even beneath the forest canopy. This suggests that such impacts may be exacerbated in degraded and fragmented forests. Additionally, the effect of artificial light on wild communities is becoming increasingly apparent. Our study offers empirical data from protected tropical forests as a baseline for comparison, together with a robust approach for detecting activity shifts in response to environmental change.

Key words: Lunar phases, diel activity, lunar philia, lunar phobia, camera trapping

1. Introduction

The effect of the solar day – Earth's 24-hour rotation around its axis – is reflected in the periods of rest and activity exhibited by most animals (Bennie et al. 2014). Often species-specific, the daily pattern of activity or "diel activity" of a species or population constitutes a fundamental part of its ecological niche. Critically, and yet with impacts far less well understood, the moon brightens the night. Changes in illumination associated with the 29-day lunar cycle alter the conditions faced by wildlife (Kronfeld-Schor et al. 2013). For some mammal species, especially those with limited night-vision or few nocturnal threats, the extra illumination provides periodic access to the night and associated foraging (Fernández-Duque et al. 2010, Prugh et al. 2014) or travel opportunities (Gursky 2003). Some species are robbed of the cloak of darkness and become exposed to predators (Prugh and Golden 2014) or visible to prey (Pratas-Santiago et al. 2016).

Despite intuitive expectations for attraction to the moonlight (lunar philia) or avoidance of moonlight (lunar phobia) and accumulating evidence for each, our knowledge of wildlife responses to the moon and their prevalence in nature is still disjoint. While some species seem to respond strongly to lunar illumination (Kronfeld-Schor et al. 2013), others apparently do not respond at all (de Matos Dias et al. 2018, Zaman et al. 2022), for reasons not fully understood. Furthermore, responses to moonlight may also differ according to latitudinal gradients, geographic regions, or habitats (Taylor et al. 2023). For instance, during illuminated nights, species living in open habitats (e.g., savannah, desert) may show a more pronounced decrease in activity (Prugh and Golden 2014). Nonetheless, insights about the direction, strength, and prevalence of mammal responses to moonlight remain hard to compile into a consistent framework, owing to the species-focus of most studies and methodological differences between them. Is the moon's influence on wildlife activity a persistent phenomenon across regions and phyla or is it a curiosity?

There are both fundamental and applied reasons why we should identify responses to lunar phases and associated changes in illumination. First, the recurrent change in potential risks and opportunities faced by entire communities provides a testing ground for ecological theory about species adaptations (Bennie et al. 2014), interactions (Kronfeld-Schor et al. 2017), and the temporal dimension of the ecological niche (Kronfeld-Schor and Dayan 2003, Hut et al. 2012, Prugh et al. 2014). Studies have tested for, and in some cases found, evidence that lunar illumination triggers niche shifting in animals with animals modifying when and where they are active dependent on the phase of the moon (Hut et al. 2012). Second, moonlight can serve as a model to help make predictions about the potential effect of artificial illumination – which is already impacting a substantial part of Earth (Cinzano et al. 2001, Falchi et al. 2016) – on wildlife behavior (Beier 2006, Rotics et al. 2011, Kronfeld-Schor et al. 2017, Gilbert et al. 2023) and community dynamics (Meyer and Sullivan 2013, Gaston et al. 2014). Finally, knowledge about the relationship between illumination and animal behavior in densely canopied and less-impacted systems offers a baseline for detecting changes in human-modified habitats. Even natural light regimes change because of human-driven habitat alteration. For example, tropical forests, which harbor a substantial portion of earth's biological diversity, are cleared, fragmented, and degraded at an alarming rate (Hansen et al. 2013, Pillay et al. 2022). Not only does this result in direct habitat modification, but also in reduced canopy cover which exposes forest-dwelling species to increased and prolonged solar and lunar illumination.

What is the prevalence and direction of responses to lunar phases in wildlife communities in some of the darkest places on earth, the floors of tropical forests? Can we expect their inhabitants to respond to moonlight like species in other environments and regions? Are they more vulnerable to changes in nocturnal illumination?

We used images from a pantropical camera trap study in tropical forests across the globe. A standardized survey methodology allowed us the simultaneously examine diel and nocturnal activity of 86 mammal species spread over 16 orders and 34 families. Camera traps are now widely used for monitoring and studying terrestrial biodiversity (Burton et al. 2015, Frey et al. 2017) and several studies have relied on time-stamped camera trap images to quantify and study animal diel activity (Rowcliffe et al. 2014). We used a novel framework –multinomial regression combined with ternary classification – for consistent categorization and quantification of the temporal niche and shifts therein (see also Gerber et al. 2023). The flexible framework allowed us to not only compare levels of activity associated with different lunar phases, but also test hypotheses about how lunar illumination impacts activity beyond the night. Previous studies have shown that lunar illumination can trigger shifts in overall diel activity (Kronfeld-Schor et al. 2013). These changes may come about in different ways. At one extreme ("fully additive"), animals can reduce or increase their nocturnal activity during full moon, without a change in activity during day or twilight. This strategy will result in a corresponding decrease or increase in overall net activity. On the other extreme ("fully compensatory"), animals may shift activity into or out of the illuminated period, for example by moving their activity from the twilight period into the night, without a change in overall net activity.

The aim of this study was to better understand impacts of moonlight on animal activity. We investigated whether and how tropical forest mammals alter their diel activity in response to changing lunar phases. Specifically, we first assessed the prevalence of lunar philia and lunar phobia. Which species exhibit lunar philia or lunar phobia, and is one response to moonlight more prevalent than the other among mammals living under the dense canopy of tropical forests? Second, we tested for a link between a species' degree of nocturnality and the response to lunar phases. Are nocturnal species more likely to manifest lunar phobia? Third, we quantified the extent to which mammals altered their diel activity in response to changes in lunar illumination. Do species responding to the different phases of the moon solely shift activity into or out of the night during moonlit periods without a change in overall activity levels (compensation) or do overall activity levels also change (additivity)?

2. Methods

2.1. Data collection

Camera trapping. We derived observations of mammal activity in protected tropical forests from camera trap data collected as part of the Tropical Ecology Assessment and Monitoring (TEAM) Network (Rovero and Ahumada 2017). Following a common protocol (Jansen et al. 2014), cameras were deployed between 2008 and 2017 throughout 17 protected areas in Indomalaya, the Neotropics, and the Afrotropics. The number of years of deployment varied between protected areas (2 years - 10 years; mean = 6.8 years), as did the number of locations sampled (60-90 camera trap locations; total: 1062). Spatial configuration and deployment were standardized, with cameras configured in either a 1x1km or 2x2km regular grid, at a height of approximately 30-50 centimeters off the ground. On average cameras were active for 33.2 days (SD=7.5). For additional information about camera trapping protocols and species identification, see (Rovero and Ahumada 2017). In this analysis, we used 2.1M camera trap pictures and filtered the data from 86 mammal species, (i.e., species with ≥ 25 detections events during night; Supplementary Information Tables S1-S3).

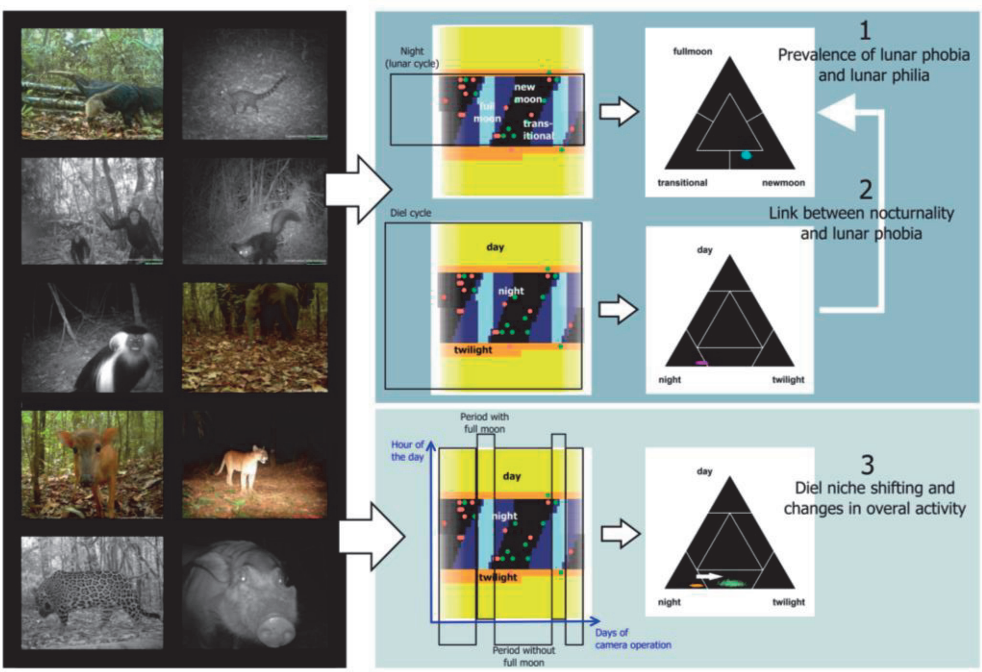

Figure 1. Illustration of the study design. From left to right: Time-stamped camera trap images are summarized as hourly observations (dots, different colors for two species) and mapped onto available site-specific diel and lunar periods (color coded raster plots). Multinomial logistic regression models are used to quantify the probability of using a given diel or lunar period (categorization performed with the aid of ternary diagrams) and to test hypotheses about the link between diel and lunar activity. Photos: TEAM Network.

2.1. Analysis

Analysis 1: Prevalence of lunar phobia and philia

Multinomial logistic regression We use a Bayesian multinomial logistic regression model to simultaneously assess diel (entire 24-hour period) and nocturnal (lunar) activity patterns. We distinguished three diel periods (day, night, and twilight) and three lunar periods (full moon, transitional, new moon). We chose discrete diel and lunar periods instead of continuous values based on illumination (Smielak 2023), as it enabled the multinomial analysis and an intuitive categorization of activity (Figs 1 and 2, Gerber et al. 2023).

This model contained two submodels, one for diel activity and one for lunar activity. The submodel for diel activity consisted of a multinomial logistic regression model to estimate species-specific probability of photographic capture in one of the three major diel periods (day, night, twilight; (see also Gallo et al. 2022)):

$$y_i \sim \text{Multinomial}\left(p_i, N_i\right) \tag{1}$$

Here, y_i is the vector of the number of independent photographic capture events of species i in each diel period, N_i the total number of detections ($N_i = \sum y_i$) of that individual, and p_i the length-3 vector of probabilities of detection in each diel period. The multinomial probability vector can be defined using logistic regression:

$$\log\left(\frac{p_{ik}}{p_{iK}}\right) = \beta_{0ik} + \sum_{j}^{J} \beta_{kj} x_{ij}\,, \qquad \text{for k} = 1, \dots, \text{K} - 1 \tag{2}$$

where β_{i0k} is the species-specific intercept term associated with categorical outcome k (diel period) out of the total possible number of outcomes K (i.e., 3: day, night, twilight), β_{kj} the j’th out of a set of J coefficients associated with predictor x_{ij}. The quotient on the left side of eq 2 signifies that the last outcome (p_{iK}) serves as a reference value for the other $K - 1$ outcomes (p_{ik}).

Predictor variables and associated coefficients shown in eq 2, were omitted in our multinomial logistic regression model for diel activity as we were primarily interested in estimating intercepts and corresponding probabilities:

$$\log\left(\frac{p_{ik}}{p_{iK}}\right) = \beta_{0ik} + s_{ik} \tag{3}$$

In addition to species-specific intercepts, we incorporated an offset variable s_{ik} defined as the proportion of time (rounded to number of hours in our analysis) during which cameras where active (available for making photographic captures) within each diel period k, relative to the reference period K. The offset variable serves the purpose to account for differences in “availability” (see also Gallo et al. 2022), and has the effect of adjusting the estimated intercept according to the amount of camera trap effort in each observational record. For example, the crepuscular period is significantly shorter than periods of daylight and night. Similarly, the period of full moon only makes up a small proportion of total nighttime (Figure 1). The relative “availability” of different diel periods also changes over the course of seasons, particularly at more northern latitudes. The model thus produces comparable estimates of selection for or against a given period, reflecting “density” of activity (hours with photographic captures per total hours of camera operation during a period) rather than pure activity volume.

The probabilities of interest are thus:

$$\log\left(\frac{\dot{p}_{ik}}{\dot{p}_{iK}}\right) = \beta_{0ik} \tag{4}$$

Where both $\dot{p}_k$ and p_k are scaled to sum to 1 across the K multinomial outcomes.

Detection data (y_i) used in the analysis constituted the number of hours with at least one detection of a given species in each diel period (daylight, twilight, and night) at each camera trap site, summed across all sites. The sum of the period-specific activity of a species makes up its total activity N_i. Availability (to calculate the offset s_k) was derived as the number of hours that fell into a given diel period at each camera trap site, summed across all camera trap sites. Diel periods were delineated using local (study area specific) astronomical sunrise, sunset and twilight times, assuming a flat landscape and obtained using R package 'suncalc' (Thieurmel and Elmarhraoui 2022). Dawn was delineated by the beginning of astronomical twilight (sun 18° below the theoretical horizon) and sunrise (when the bottom edge of the sun touches the theoretical horizon). Dusk was delineated by the beginning of sunset and astronomical sunset (sun 18° below the horizon). Night was delineated as the period between astronomical dusk and dawn and day as the period between sunrise and sunset.

The submodel for lunar activity was structurally identical to the diel activity model described above. In the lunar submodel, the three multinomial probabilities ($\dot{p}_{ik}$) represent species-specific estimates of the probability of photographic capture in one of the three major lunar periods, roughly corresponding to full moon, new moon, and the combined intermediate phases. Moon phases were delineated for the night (as defined above) using moon altitude and illumination, again with R package 'suncalc'. Specifically, full moon was defined as the period when the moon had an altitude ≥ 18° above the theoretical horizon and was ≥90% illuminated. New moon was defined as the period when the moon had an altitude < 18° above the theoretical horizon and was <10% illuminated. All other nocturnal periods were designated as transitional phases.

Model fitting We fitted multinomial models using Markov chain Monte Carlo (MCMC) simulation with NIMBLE version 1.0.0 (de Valpine et al. 2017) in R version 4.3.0 (Team 2023). We ran 4 chains with 40000 iterations each, including a 20000-iterations burn-in period. Chains were thinned by a factor of 5. We considered models as converged when the Gelman-Rubin diagnostics (Gelman 1996) was ≤ 1.1 for all parameters and after visually inspecting trace plots.

Designation of diel and lunar activity categories For visual inspection, categorization, and presentation, species-specific posterior samples of multinomial probabilities produced by the Markov chain Monte Carlo MCMC analysis were plotted onto Ternary diagrams (Shepard 1954) using package 'ternary' (Smith 2017) in R. The diel and lunar activity pattern of each species was delineated with the help of the ternary diagrams. We considered several alternative ternary configurations for categorization (Shepard 1954, Schlee 1973, Santini et al. 2005, see also Nakamura et al. 2018), but ultimately opted for a subdivision into 7 regions for diel activity and 4 regions for nocturnal activity as it relates to the lunar cycle. The lower number of categories for nocturnal activity was motivated by the lower sample size (only observations made during the night are considered for categorizing lunar activity) and ease of interpretation. For categorizing diel activity, we divided the ternary diagram into these 7 regions (Fig. 2): 3 corner triangles (each capturing cases that contain >2/6 of all activity) for the "pure" diel activity categories (e.g., diurnal), three transitional regions between pairs of corner regions for intermediate categories (e.g., diurnal-crepuscular), and one central triangle that indicates cathemerality (activity during all diel periods). This classification follows Shepard's (1954) approach for delineating soil categories, but without the additional splitting of the intermediate regions along the sides of the ternary. We divided the ternary diagram for lunar activity categorization into only these 4 regions (Fig. 2): one central triangle (identical to the cathemeral region in the ternary diagram for diel activity) representing indifference to the phase of the moon and 3 main lunar categories (activity during full moon, new moon, and intermediate lunar phases).

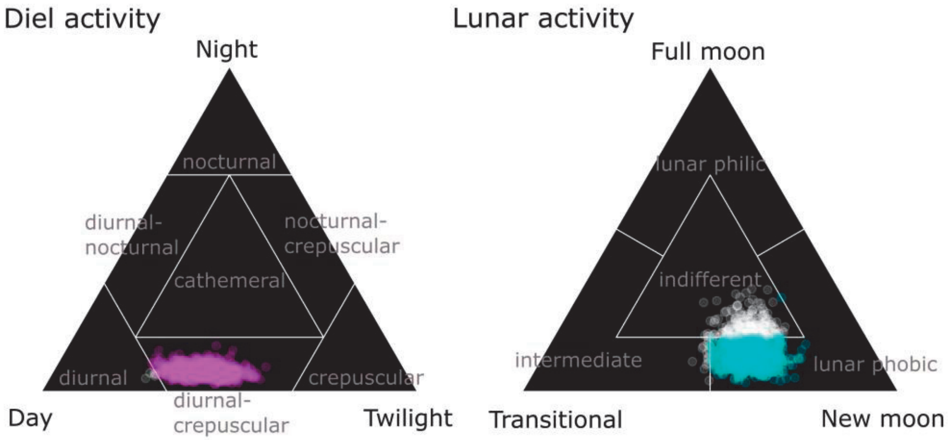

Figure 2. Posterior samples (dots) of multinomial probabilities mapped onto ternary diagrams. Shown are example posterior samples for diel activity (left; activity during day, night, and twilight periods) and lunar activity (right; nocturnal activity during full moon, new moon,

and transitional phases). The ternary diagrams are divided into seven and four regions for diel and lunar activity delineation respectively. Designation to activity categories (grey text) is made according to the region into which the majority (colored dots) of posterior samples are mapped. The examples show a diurnal-crepuscular (left) and a lunar phobic species (right).

Species activity is categorized based on the position of the posterior distribution of multinomial probabilities ($\dot{p}_k$) within the ternary space. As a species-level designation (diel and lunar activity category/strategy/niche), we based designation on the region that contained the majority of the posterior samples of the multinomial hyperparameter, depending on which one of the seven (diel) and four (lunar) regions the majority of posterior samples fell into.

Analysis 2: Link between nocturnality and lunar phobia

To estimate the relationship between diel and lunar activity we used the model from Analysis 1 as a starting point, but now linking the lunar activity submodel with the diel activity submodel:

$$\log\left(\frac{\overline{p}_{il}}{\overline{p}_{iL}}\right) = \overline{\beta}_{0il} + \overline{\beta}_{night,l}\,\dot{p}_{i,night} + \overline{s}_{il} \tag{5}$$

Where $\dot{p}_{i,night}$ is the strength of selection for nocturnal activity estimated in the diurnal submodel and $\beta_{night,l}$ is its effect on the multinomial probability associated with lunar period l out of a total of L lunar periods. Whereas $\dot{p}_{i,night}$ is species specific, we estimate one community-level coefficient $\bar{\beta}_{night,l}$ in this analysis. Model fitting proceeded as in Analysis 1. We used the posterior distribution of $\bar{\beta}_{night,l}$ and species-specific $\bar{\beta}_{0il}$ to derive fitted values (means) and associated 95% Bayesian credible intervals (BCI) of the link between nocturnality and the probability of association with new moon and full moon periods.

Analysis 3: Diel activity shifting and changes in overall activity levels

We used a third Bayesian model to assess whether and how animals altered their diel activity in response to changes in lunar illumination (Fig. 1). Specifically, we tested whether species categorized as lunar phobic during the first analysis 1) reduced their overall activity (number of photographic capture events) during the period (multi-day lunar phases, Fig. 1) that contained nights with full moon and/or 2) shifted their diel activity towards daylight or twilight. Conversely, for species categorized as lunar philic, we tested whether they 1) increased their overall activity during the multi-day time periods containing bright nights and/or 2) shifted their diel activity towards the night.

We used two submodels, one for modelling the number of photographic detection events during 24-hour periods with and without at least one hour of full moon at night and a multinomial logistic model for overall diel activity during the same time periods.

The model for the total number of photographic detection events n_i for species i during a given period (days with vs without full moon at night) was formulated as a generalized linear model with a log-link (Poisson regression):

$$\log(\lambda_i) = \ddot{\beta}_{0i} + \ddot{s}_i \tag{6}$$

$$\mathrm{n}_i \sim \mathrm{Poisson}(\lambda_i) \tag{7}$$

Where λ_i is the parameter of the Poisson distribution (expected number of events) and $\ddot{\beta}_{0i}$ the species-specific intercept. As in the multinomial models (equations 3 and 5), we included an offset term $\ddot{s}_i$ to account for differences in availability, provided as the total operational camera trap hours associated with a given lunar phase over all camera trap sites and sampling seasons in protected areas where species i was detected at least once. This allowed direct comparison of periods with and without moonlit nights via $\dot{\lambda}_i$, derived as

$$\dot{\lambda}_i = e^{\ddot{\beta}_{0i}} \tag{8}$$

The multinomial model for diel activity was identical to the model defined with equations 1 and 3. The main difference between the diel activity model in analyses 1, 2, and 3 was in the design: whereas in analyses 1 and 2 we estimated the multinomial probabilities of being active during the three diel periods (day, night, twilight) at any point during monitoring, in analysis 3 we estimated separate multinomial probabilities for periods (multiple days) with and without at least 1 hour of full moon at night (Fig. 1).

Model fitting and assessment of convergence/mixing was performed as in analysis 1 and 2. Diel activity was categorized using the ternary approach described earlier. Changes in diel activity during periods with full moon that resulted in a change of activity category were considered evidence of temporal niche switching. Changes in diel activity without a change in activity category but a difference in the posteriors for $\dot{p}_{night}$ associated with new moon vs. all other phases whose 95% BCI did not include zero were considered activity timing shift, a term also used in (Gilbert et al. 2023). We subtracted the posterior sample for $\dot{\lambda}_i$ for periods without moonlit nights from those with to derive species-specific posteriors of the effect of full moon on overall activity levels. We considered a species to show evidence of altered overall activity levels in response to lunar illumination when the 95% BCI of this derived variable did not include zero.

3. Results

3.1. Diel activity and overview

We categorized 20 species as predominantly nocturnal and two as diurnal, following the multinomial regression analysis controlling for temporal availability and the ternary classification scheme (Fig. 2). Only one species (common tapeti, *Sylvilagus brasiliensis*) was categorized as predominantly crepuscular. Most species (45) fell into one of the two intermediate categories involving crepuscularity (Fig. 3). All remaining species (18) were categorized as cathemeral (Supplementary Information Tables S1-S3). Cathemeral designation, by nature of its position within the ternary, is associated with greater uncertainty (Gerber et al. 2023). In data-sparse situations it may be difficult to distinguish between a species being truly cathemeral and the model not having enough information to assign the species to another category. However, all species categorized as cathemeral in this analysis had more than 100 observations (hours with at least one detection; mean = 816, range = 123 – 4097; Supplementary Information Tables S1-S3).

3.2. Prevalence of lunar phobia and philia

Of the 86 species included in the analysis, 14 were categorized as lunar phobic and three as lunar philic (Fig. 3). Only one species (Forest giant squirrel, *Protoxerus stangeri*) was categorized as selecting for intermediate lunar phases ("transitional"). Rodents where the most common lunarphobic species (11), followed by armadillos (2), and one opossum (gray four-eyed opossum, *Philander opossum*). The representation of rodents among lunar phobic species (79%) was disproportional to their prevalence (24%) among the species in our sample. The three mammal species exhibiting lunar philia were the white-lipped peccary (*Tayassu pecari*, order Artiodactyla) and the common tapeti (order Lagomorpha) in the Neotropics, and the four-toed elephant shrew (*Petrodromus tetradactylus*, order Macroscelidea) in the Afrotropics. The remaining 68 species were categorized as indifferent towards lunar phases, either because their nocturnal activity was not impacted by lunar

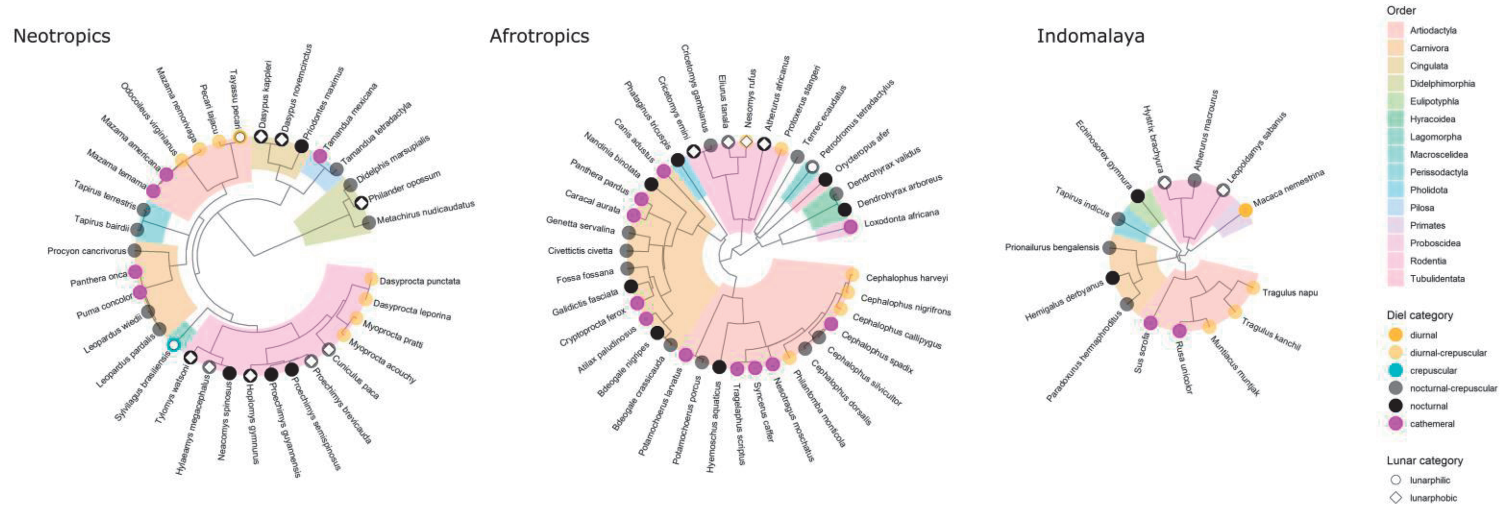

Figure 3. Diel and lunar categorization charted across phylogenetic trees of tropical forest mammals. Lunar category is only indicated for species that were unambiguously designated as either lunar phobic or lunar philic. Lunar phobia, manifested as reduced activity during moonlit nights, was more common than lunar philia, increased activity during moonlit nights. Rodents, particularly nocturnal species, were overrepresented among lunar phobic species, followed by members of the Cingulata (including armadillos) and Didelphimorphia (opossums).

illumination or because their data had such a high noise-to signal ratio that it prevented designation to one of the peripheral ternary regions (Supplementary Information Tables S1-S3). In our dataset 15 (22%) of the species categorized as indifferent towards lunar phases had less than 50 observations during the night and we consider these species as data-sparse. Nonetheless the sample size was relatively high with an average of 409 nocturnal observations (range: 25 – 3775; Supplementary Information Tables S1-S3) of species categorized as indifferent towards lunar phases.

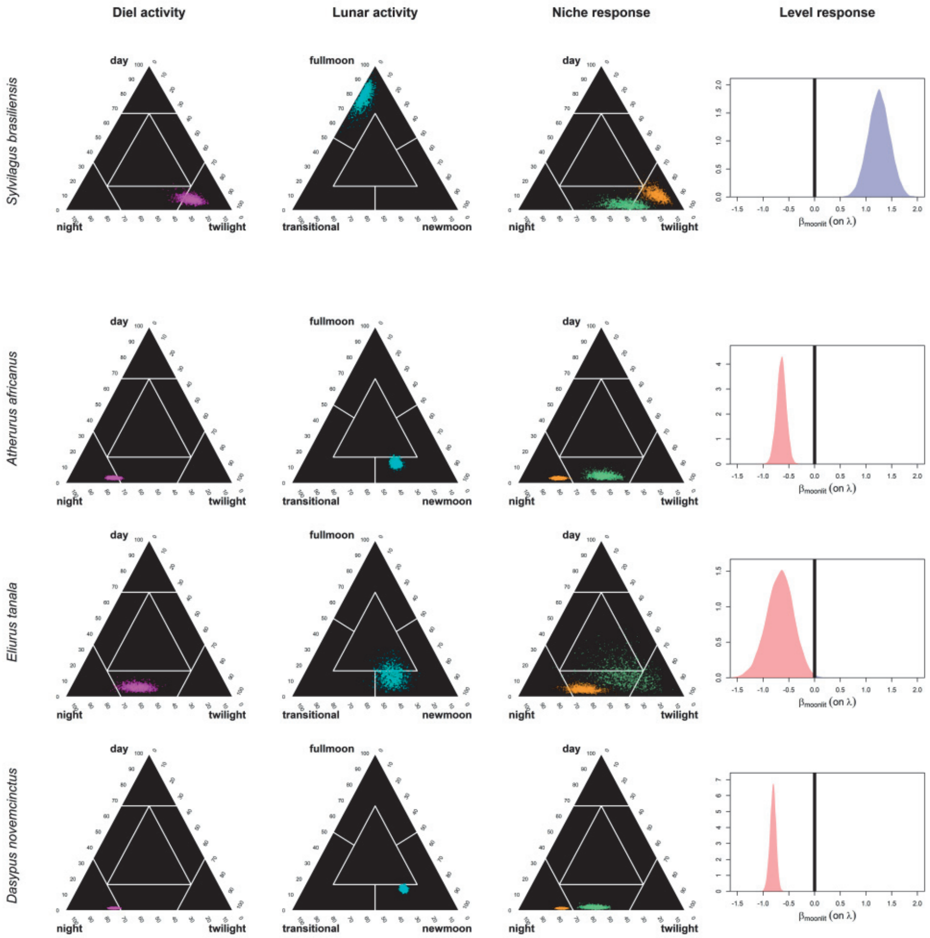

Figure 4. Overview of ternary classifications for diel and lunar activity (columns 1-2) and responses to lunar phases (column 3 and 4) for four example species (rows). The species shown in the top row (common tapeti or forest cotton tail) was classified as lunar philic, whereas the bottom three rows show lunar phobic species. Column 1: ternary plots of diel activity posteriors. Column 2: ternary plot of lunar activity posteriors. Column 3: ternary plots showing difference of diel activity (potential temporal niche shifting) between periods with full

moon (green) and without moonlit nights (orange). Column 4: posterior distribution of the difference between overall activity (related to the number of photographic detection events) during periods with vs. without full moon. Negative (red) and positive (blue) values indicate a reduction or an increase, respectively, in overall activity during periods (multiple 24-hour periods, Fig. 1) with full moon. See Supplementary Information Figures S1 and S2 for results for all species classified as either lunar phobic or philic.

3.3. Link between nocturnality and lunar phobia

Species with a greater probability of being active at night were more likely to be more active also at new moon ($\beta_{night,new\ moon}$ = 1.51, 95% CrI: 1.41 to 1.62, Fig. 5) and, conversely, less likely to be active at full moon ($\beta_{night,full\ moon}$ = -1.11, 95% CrI: -1.24 to -0.973, Fig. 5). This effect was also reflected in our categorization of diel activity of species identified as lunar phobic. Thirteen of the fourteen species categorized as lunar phobic also exhibited a nocturnal or nocturnal-crepuscular diel activity pattern, and only one was categorized as diurnal-crepuscular (Fig. 3). Of the lunar philic species, one was diurnal, one diurnal-crepuscular, and one nocturnal-crepuscular (Fig. 3).

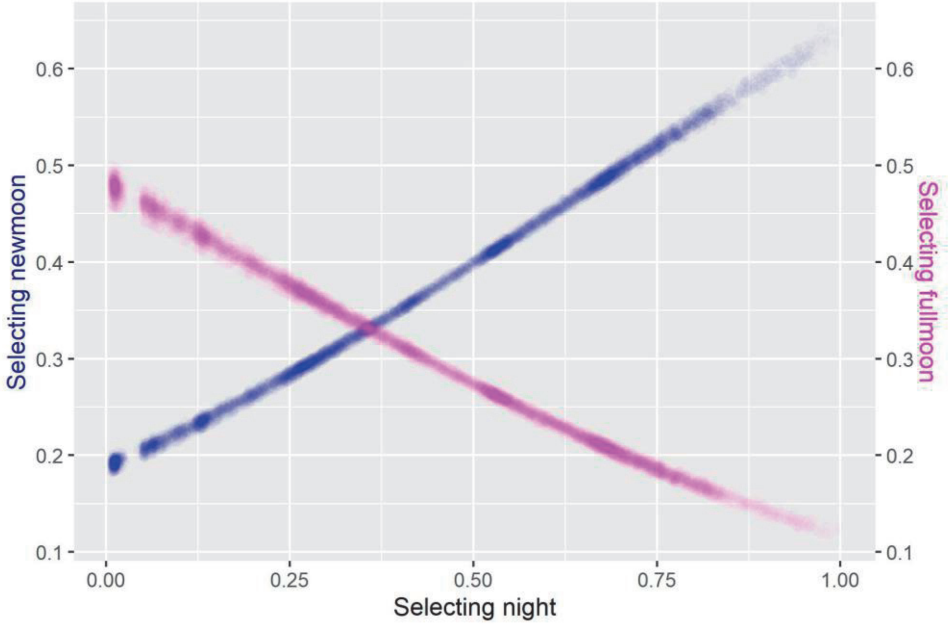

Figure 5. Effect of the probability of nocturnal activity on the probability of active during new moon (blue) and full moon (magenta). The plot shows posterior predictions, with shading corresponding to the posterior distribution of $\dot{p}_{night}$(x-axis, eq 3), $\dot{p}_{full\ moon}$ (left y-axis) , and $\dot{p}_{new\ moon}$ (right y-axis) across all 86 species included in the analysis.

3.4. Temporal niche shifting and changes in overall activity

Eleven of the 14 lunar phobic species significantly reduced their overall activity level during periods with moonlit nights and eight of these shifted their diel behavior to become less nocturnal (Figs 3 and 5; Supplementary Information Fig. S2). Three species classified as lunar phobic (*Philander opossum, Hoplomys gymnurus, Tylomys watsoni*) reduced their overall activity without a significant shift in diel behavior, and two species (*Nesomys rufus, Protoxerus stangeri*) shifted their diel behavior to be less nocturnal without a significant reduction in overall activity (Fig. 6). Of the three species identified as lunar philic one (*Sylvilagus basiliensis*) shifted to more nocturnal activity and increased its overall activity, one (*Tayassu pecari*) only shifted its activity to become more nocturnal, and one (*Petrodomus tetradactylus*) only increased its overall activity during periods with moonlit nights (Fig. 6). Following our categorization of diel behavior, 9 out of 14 lunar phobic species switched their temporal niche, all from nocturnal to nocturnal-crepuscular during periods with full moon. Two of the three lunar philic species also switched, one from crepuscular to nocturnal-crepuscular and one from diurnal to diurnal crepuscular. See Supplementary Information Figures S1 and S2 for detailed results for all species classified as lunar phobic or philic.

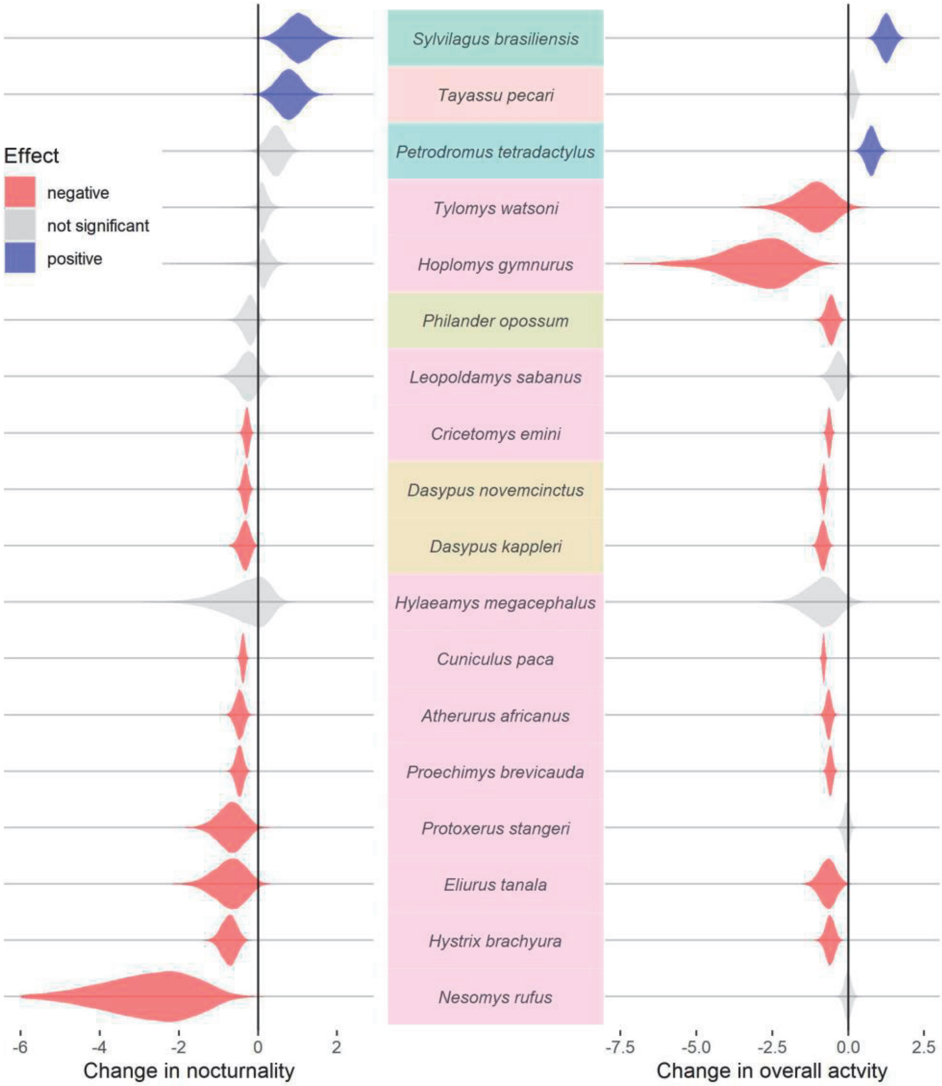

Figure 6. Changes in nocturnality (left) and overall diel activity levels (right) of forest mammals during periods with and without full moon. Responses ("Effect") are represented by the posterior distributions of coefficient estimates shown as violins. Species names are shown on color-coded backgrounds according to the order they belong to (see Fig. 3 for key). The top 3 species were categorized as lunar philic, the remainder as lunar phobic.

4. Discussion

Wildlife responses to moon phases are still poorly understood. We applied a novel analysis of activity patterns to data from standardized camera trapping in 17 tropical forests across the globe. We found that even in the understory of protected tropical forests, characterized by densely-shaded habitats, the moon's phases impact the activity of mammal species. Lunar phobia was more common than lunar philia, with rodents being the most common lunar phobic taxonomic group. Additionally, we found that nocturnal species are more active during new moon than during other lunar phases. Finally, our quantitative study revealed that species may avoid bright moonlight by shifting their activity towards other parts of the diel cycle, by reducing overall activity, or both. These findings indicate that changes in illumination (e.g., through deforestation or artificial illumination) could affect species activity, and ultimately interactions in tropical forest communities.

4.1. Lunar philia and lunar phobia in tropical forest mammal communities

Our results suggest that lunar philia is rare among tropical forest mammals. Only three species, among the 86 species studied here, significantly increased their exposure to camera traps during hours filled with moonlight (Fig. 3). Lunar philia has previously been reported as comparatively rare and has been associated with species relying on visual cues for foraging and predator avoidance (Prugh and Golden 2014). The only species classified as lunar philic in our study were a peccary (*Tayassu pecari*), a rabbit (common tapeti, *Silvilagus brasiliensis*), and an elephant shrew (*Petrodromus tetradactylus*). Apparent lunar philia in the common tapeti has previously been reported in Argentina (Huck et al. 2017), and contrasts lunar phobic behavior reported in another lagomorph, the snowshoe hare (*Lepus americanus*, Griffin et al. 2005). Lunar philia in elephant shrews is consistent with descriptive studies on the order (Woodall et al. 1989). Similarly, white-lipped peccary have been reported to change routes and increase movement in the forest during full moon (Serrano et al. 2010, Hernández 2015).

Lunar phobia, in contrast, was common. It was exhibited primarily by small-to-medium sized mammals that are prey of carnivores such as ocelots (*Leopardus pardalis*) or jaguars (*Panthera onca*, Moreno et al. 2006, Pratas-Santiago et al. 2016). This is the case for rodents, although armadillos and opossums were also reported as lunar phobic. The paca, one of the largest lunar phobic rodents in our study (8000g) has been classified as lunar phobic in other study areas, as were armadillos (Harmsen et al. 2011, Pratas-Santiago et al. 2017). Although Harmsen et al. (2011) detected no changes in the activity of the common opossum (*Didelphis marsupialis*) in response to moonlight, evidence on lunar phobia in the gray four-eyed opossum (*Philander opossum*) in our study matches findings for members of the Didelphimorphia order reported in other studies (e.g., *Didelphis aurita*, *Calouromys philander*) (Julien-Laferrière 1997, Tripodi et al. 2023).

One of the strengths of our study is that it simultaneously analyzed activity data from a large number of species using one standardized approach. Across that diverse community of mammals, some species were observed more frequently than others. Technically, all activity data, no matter how sparse, can be designated to one of the categories represented by the areas delineated in the ternary diagram. However, observation of activity is imperfect in nature, either because not all individuals are observed or individuals are not observed all of the time, or both. The probability of making an erroneous designation (i.e., an activity category other than the true one) is liable to increase as sample size decreases. Designation to the cathemeral (diel activity) and indifferent (lunar activity) categories, by nature of their position within the ternary, are probably the most error prone and most vulnerable to data paucity. Determination of cathemerality was less ambiguous, as all species in this study had more than 100 observations for diel activity categorization, with an average of 409 hours of observations per species. However, 22% and 44% of species categorized indifferent to lunar phases had < 50 and < 100 hourly observations respectively. At least for these, we cannot reliably distinguish true indifference to lunar phases from an insufficient sample size for making a designation.

4.2. The link between lunar phobia and nocturnality

The more nocturnal species are, the more likely they are to exhibit lunar phobic behavior (Fig. 5). Lunar phobia has been explained as a behavioral adaptation by nocturnal species, intended to avoid the elevated predation risk during periods with higher illumination (Daly et al. 1992, Kronfeld-Schor et al. 2013). The avoidance of moonlight could reduce vulnerability to detection by visually-hunting predators or, in the case of lunar phobic predators, detection by prey. Our results are in line with those reported in previous studies. For instance, rodents generally seem to reduce foraging activity during bright nights (Price et al. 1984, Longland and Price 1991, Prugh and Golden 2014). Conversely, lower nocturnality was associated with higher activity during full moon periods (Fig. 5). In fact, all three species identified as lunar philic in this study were crepuscular-diurnal. Meanwhile, 13 of the 14 lunar phobic species were nocturnal or nocturnal-crepuscular, and only one was categorized as diurnal-crepuscular (Fig. 3). Thus, moonlight appears to give species adapted to daylight and twilight better visual access to the night.

4.3. Temporal niche shifting in response to moon phases

Lunar illumination can trigger changes in diel activity. We found that during periods with full moon, eight species (all classified as lunar phobic) changed their diel activity from nocturnal to crepuscular-nocturnal. These species also decreased their overall activity level. These results are in line with observations on snowshoe hares (*Lepus americanus*, Studd et al. 2019) and Marriam's kangaroo rats (*Dipodomys merriani*, Daly et al. 1992), which reduce their activity during moonlit nights and increase their diurnal and crepuscular activity, respectively. Potentially indicative of compensatory response to lunar illumination, two species reduced their nocturnal activity without an apparent reduction on overall activity during periods with full moon. Conversely, three species reduced their overall activity without a clear shift in nocturnality, suggesting a response closer to the additive end of the spectrum. One of the three lunar philic species increased its overall activity levels during periods with illuminated nights and shifted from diurnal or crepuscular towards more nocturnal activity. This echoes the findings from studies on owl monkeys (*Aotus azarai*) a generally nocturnal species, which increases its activity during full moon, and, during new moon, shifts its activity from night towards day (Erkert 2008, Fernández-Duque et al. 2010). Regardless of the strategy chosen in response to changing lunar illumination, our results showed evidence of temporal niche shifting. Two lunar phobic species in our study exhibited a reduction in overall activity levels without a noticeable shift towards crepuscular behavior. We could speculate that this is a result of behavioral inflexibility (i.e., strict nocturnality); although it may be purely a result of insufficient statistical power or reflect a shift to habitat strata less well-covered by camera traps.

4.4. Methodological insights and other considerations

In this study, we adjusted and deployed a novel framework to delineate diel and nocturnal activity categories using multinomial probability distributions, and ternary diagrams (Gallo et al. 2022, see also Gerber et al. 2023). This approach is both visually intuitive and quantitative, facilitating detection of ecological patterns related to activity, such as temporal niche partitioning and niche shifting/switching in response to moonlight. Any analytical approach that can estimate the probability of designation and the associated uncertainty can be substituted for the Bayesian multinomial approach used here. The advantage of the latter is that it produces posterior samples of multinomial probabilities, which readily allow propagation of uncertainty to the ternary projection and subsequent classification.

We recorded species' diel activity detectable with camera traps. Camera trap data lend themselves to comparative and comprehensive diel activity studies as they monitor entire communities (Cid et al. 2020, Vallejo-Vargas et al. 2022) and are non-invasive, or at least less invasive than traditional methods such as direct observation and telemetry. The rapidly expanding spatial and temporal scope of camera trapping in wildlife ecology offers opportunities for revising and filling gaps in our understanding of the temporal niche of wildlife and its dynamics (Gerber et al. 2023). Nonetheless, camera trapping has limitations and inferences should be drawn with caution. For example, if arboreal or scansorial animals shift their activity to lower forest strata during moonlit periods or if species move into more densely vegetated areas from beyond forest edges, lunar phobia may increase terrestrial activity as detected through photographic captures by understory cameras. In our study, however, all but one of the species with lunar responses are classified as terrestrial (Wilman et al. 2014). Yet, other sampling methods (or sampling in other strata; Bowler et al. 2017, Haysom et al. 2021) may in some situations and for certain species be more suitable to obtain reliable data on activity. Any sampling approach that does not influence activity itself and produces timestamped observations can be used.

4.5. Implications

The influence of natural and artificial light is an increasingly important topic in wildlife conservation and ecosystem functioning (Hirt et al. 2023). Yet we still know too little about the implications of artificial light on the activity of mammals (Hoffmann et al. 2022). The prevalence of lunar phobia in our study suggests there may more be more losers than winners when illumination increases in tropical forests. Moreover, most lunar phobic species in our study reduced their overall activity during periods with new moon. If these results extend to artificial light, a loss of dark nights could curtail the amount of time some species invest into foraging and other important activities. Strong responses to artificial light have already been observed in nocturnal mammals. For example, the common spiny mouse (*Acomys* *cahirinus*) shows a clear reduction in the overall activity and time for foraging when exposed to artificial light (Rotics et al. 2011). The constant reduction of activity, for example due to permanent human light sources, may, affect individuals, populations and even communities. However, predicting fitness consequences of artificial light based on responses to lunar phases is challenging. Seemingly indifferent species without adaptations to changing nocturnal light conditions may not be impacted at all or could bear the brunt of brighter nights resulting from canopy loss and light pollution if they are made vulnerable by increased visibility. Species that change their overall activity level in response to nocturnal illumination are more strongly impacted than species that can maintain their level of activity by adjusting its timing. Along those lines, lunar phobic species could be expected to cope better with artificial light if they follow a cathemeral diel activity pattern as this is indicative of behavioral plasticity that may provide advantages in a changing world (temperature changes, artificial light) (Cox and Gaston 2023). However, in tropical regions cathemerality is less reportedly less common than in higher latitudes (Bennie et al. 2014).

Our research describes responses to moonlight on the forest floor. It would be interesting for future research to examine responses in the canopy of tropical forest, where lunar illumination likely has a more pronounced effects on behavior. It is also worthwhile to extend research into the effects of moonlight and artificial light to birds, another prominent class of both ground and canopy-dwelling species in tropical forests.

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Article IV: Supplementary Information

Table S1. Designation of forest mammals in the Afrotropics to diel and lunar categories.
Table S2. Designation of forest mammals in the Neortropics to diel and lunar categories.
Table S3. Designation of forest mammals in the Indomalayan tropics to diel and lunar categories
Figure S1. Overview of ternary classifications for diel and lunar activity and responses to lunar phases for three mammal species identified as lunar philic.
Figure S2. Overview of ternary classifications for diel and lunar activity and responses to lunar phases for 14 mammal species identified as lunar phobic.

Table S1. Designation of forest mammals in the Afrotropics to diel and lunar categories based on multinomial logistic regression and ternary classification. Also shown are the number of observations (hours with at least one photographic detection at distinct camera trap locations).

		Designation		**Number of observations**						
Species	**Order**	**Diel category**	**Lunar category**	**Full moon**	**Tran-sition**	**New moon**	**Night**	**Twilight**	**Day**	**Total**
Tenrec ecaudatus	Afrosoricida	nocturnal-crepuscular	indifferent	7	9	21	37	13	8	58
Cephalophus callipygus	Artiodactyla	diurnal-crepuscular	indifferent	131	210	327	668	1438	7684	9790
Cephalophus dorsalis	Artiodactyla	nocturnal-crepuscular	indifferent	309	498	746	1553	301	269	2123
Cephalophus harveyi	Artiodactyla	diurnal-crepuscular	indifferent	72	132	168	372	271	2911	3554
Cephalophus nigrifrons	Artiodactyla	diurnal-crepuscular	indifferent	155	264	402	821	651	4743	6215
Cephalophus silvicultor	Artiodactyla	nocturnal-crepuscular	indifferent	477	780	1008	2265	965	858	4088
Cephalophus spadix	Artiodactyla	cathemeral	indifferent	30	49	61	140	56	292	488
Hyemoschus aquaticus	Artiodactyla	nocturnal	indifferent	18	28	24	70	1	1	72
Nesotragus moschatus	Artiodactyla	cathemeral	indifferent	146	163	171	480	211	513	1204
Philantomba monticola	Artiodactyla	diurnal-crepuscular	indifferent	162	295	407	864	1898	11653	14415
Potamochoerus larvatus	Artiodactyla	cathemeral	indifferent	36	54	76	166	73	175	414
Potamochoerus porcus	Artiodactyla	nocturnal-crepuscular	indifferent	81	96	129	306	130	182	618
Syncerus caffer	Artiodactyla	cathemeral	indifferent	33	41	71	145	57	225	427
Tragelaphus scriptus	Artiodactyla	cathemeral	indifferent	182	285	356	823	358	1305	2486
Atilax paludinosus	Carnivora	cathemeral	indifferent	9	16	31	56	37	90	183
Bdeogale crassicauda	Carnivora	nocturnal-crepuscular	indifferent	445	826	1281	2552	360	108	3020
Bdeogale nigripes	Carnivora	nocturnal	indifferent	21	40	82	143	16	12	171
Canis adustus	Carnivora	cathemeral	indifferent	18	15	20	53	31	42	126
Caracal aurata	Carnivora	cathemeral	indifferent	20	34	60	114	55	172	341

Civettictis civetta	Carnivora	nocturnal-crepuscular	indifferent	9	16	14	39	15	6	60
Cryptoprocta ferox	Carnivora	cathemeral	indifferent	14	19	28	61	30	63	154
Fossa fossana	Carnivora	nocturnal-crepuscular	indifferent	79	153	233	465	112	32	609
Galidictis fasciata	Carnivora	nocturnal	indifferent	6	7	12	25	3	0	28
Genetta servalina	Carnivora	nocturnal-crepuscular	indifferent	104	214	376	694	147	63	904
Nandinia binotata	Carnivora	nocturnal	indifferent	24	44	67	135	18	7	160
Panthera pardus	Carnivora	cathemeral	indifferent	12	17	21	50	23	69	142
Dendrohyrax arboreus	Hyracoidea	nocturnal	indifferent	9	18	31	58	6	8	72
Dendrohyrax validus	Hyracoidea	nocturnal-crepuscular	indifferent	45	97	140	282	31	34	347
Petrodromus tetradact.	Macroscelidea	nocturnal-crepuscular	lunarphilic	33	33	25	91	23	16	130
Phataginus tricuspis	Pholidota	nocturnal	indifferent	9	25	37	71	6	2	79
Loxodonta africana	Proboscidea	cathemeral	indifferent	70	115	126	311	146	451	908
Atherurus africanus	Rodentia	nocturnal	lunarphobic	51	220	631	902	110	57	1069
Cricetomys emini	Rodentia	nocturnal	lunarphobic	116	462	1595	2173	159	71	2403
Cricetomys gambianus	Rodentia	nocturnal-crepuscular	indifferent	357	937	2481	3775	580	92	4447
Eliurus tanala	Rodentia	nocturnal-crepuscular	lunarphobic	6	26	63	95	25	16	136
Nesomys rufus	Rodentia	diurnal-crepuscular	lunarphobic	0	5	27	32	117	290	439
Protoxerus stangeri	Rodentia	diurnal-crepuscular	NA	6	38	38	82	45	449	576
Orycteropus afer	Tubulidentata	nocturnal	indifferent	5	12	14	31	1	2	34

Table S2. Designation of forest mammals in the Neortropics to diel and lunar categories based on multinomial logistic regression and ternary classification. Also shown are the number of observations (hours with at least one photographic detection at distinct camera trap locations).

		Designation		**Number of observations**						
Species	**Order**	**Diel category**	**Lunar category**	**Full moon**	**Tran-sition**	**New moon**	**Night**	**Twilight**	**Day**	**Total**
Mazama americana	Artiodactyla	cathemeral	indifferent	509	734	913	2156	712	1229	4097
Mazama nemorivaga	Artiodactyla	diurnal-crepuscular	indifferent	17	36	35	88	88	982	1158
Mazama temama	Artiodactyla	cathemeral	indifferent	55	117	158	330	94	578	1002
Odocoileus virginianus	Artiodactyla	diurnal-crepuscular	indifferent	17	15	29	61	30	233	324
Pecari tajacu	Artiodactyla	diurnal-crepuscular	indifferent	190	259	392	841	606	4542	5989
Tayassu pecari	Artiodactyla	diurnal	lunarphilic	17	16	9	42	28	444	514
Leopardus pardalis	Carnivora	nocturnal-crepuscular	indifferent	133	236	341	710	191	301	1202
Leopardus wiedii	Carnivora	nocturnal-crepuscular	indifferent	23	30	50	103	20	19	142
Panthera onca	Carnivora	cathemeral	indifferent	16	30	29	75	19	120	214
Procyon cancrivorus	Carnivora	nocturnal-crepuscular	indifferent	9	22	31	62	12	2	76
Puma concolor	Carnivora	cathemeral	indifferent	20	32	45	97	36	169	302
Dasypus kappleri	Cingulata	nocturnal	lunarphobic	55	159	531	745	62	4	811
Dasypus novemcinctus	Cingulata	nocturnal	lunarphobic	151	489	1772	2412	264	68	2744
Priodontes maximus	Cingulata	nocturnal	indifferent	16	29	101	146	11	9	166
Didelphis marsupialis	Didelphimorphia	nocturnal-crepuscular	indifferent	273	421	657	1351	226	55	1632
Metachirus nudicaudatus	Didelphimorphia	nocturnal-crepuscular	indifferent	56	153	445	654	89	19	762
Philander opossum	Didelphimorphia	nocturnal	lunarphobic	23	79	213	315	29	3	347
Sylvilagus brasiliensis	Lagomorpha	crepuscular	lunarphilic	26	10	4	40	35	17	92
Tapirus bairdii	Perissodactyla	nocturnal-crepuscular	indifferent	33	73	94	200	53	82	335

Tapirus terrestris	Perissodactyla	nocturnal-crepuscular	indifferent	189	269	394	852	244	290	1386
Tamandua mexicana	Pilosa	cathemeral	indifferent	18	17	45	80	13	62	155
Tamandua tetradactyla	Pilosa	nocturnal-crepuscular	indifferent	7	9	30	46	15	13	74
Cuniculus paca	Rodentia	nocturnal-crepuscular	lunarphobic	338	1400	3912	5650	862	104	6616
Dasyprocta leporina	Rodentia	diurnal-crepuscular	indifferent	7	18	20	45	552	3416	4013
Dasyprocta punctata	Rodentia	diurnal-crepuscular	indifferent	35	63	82	180	1595	9725	11500
Hoplomys gymnurus	Rodentia	nocturnal	lunarphobic	1	8	31	40	2	0	42
Hylaeamys megaceph.	Rodentia	nocturnal-crepuscular	lunarphobic	0	8	23	31	5	0	36
Myoprocta acouchy	Rodentia	diurnal-crepuscular	indifferent	3	9	18	30	528	1483	2041
Myoprocta pratti	Rodentia	diurnal-crepuscular	indifferent	8	13	24	45	599	1945	2589
Neacomys spinosus	Rodentia	nocturnal	indifferent	3	8	18	29	2	0	31
Proechimys brevicauda	Rodentia	nocturnal-crepuscular	lunarphobic	74	293	824	1191	183	46	1420
Proechimys guyannensis	Rodentia	nocturnal	indifferent	14	36	76	126	12	0	138
Proechimys semispinosus	Rodentia	nocturnal	indifferent	59	144	309	512	49	11	572

Table S3. Designation of forest mammals in the Indomalayan tropics to diel and lunar categories based on multinomial logistic regression and ternary classification. Also shown are the number of observations (hours with at least one photographic detection at distinct camera trap locations).

		Designation		**Number of observations**						
Species	**Order**	**Diel category**	**Lunar category**	**Full moon**	**Tran-sition**	**New moon**	**Night**	**Twilight**	**Day**	**Total**
Muntiacus muntjak	Artiodactyla	diurnal-crepuscular	indifferent	44	65	80	189	197	828	1214
Rusa unicolor	Artiodactyla	cathemeral	indifferent	6	13	13	32	23	68	123
Sus scrofa	Artiodactyla	cathemeral	indifferent	72	143	231	446	297	1186	1929
Tragulus kanchil	Artiodactyla	diurnal-crepuscular	indifferent	24	25	34	83	123	376	582
Tragulus napu	Artiodactyla	diurnal-crepuscular	indifferent	8	11	12	31	51	73	155
Hemigalus derbyanus	Carnivora	nocturnal	indifferent	7	17	28	52	5	3	60
Paradoxurus hermaphr.	Carnivora	nocturnal-crepuscular	indifferent	10	15	23	48	11	4	63
Prionailurus bengalensis	Carnivora	nocturnal-crepuscular	indifferent	7	13	15	35	12	6	53
Echinosorex gymnura	Eulipotyphla	nocturnal	indifferent	7	14	20	41	4	0	45
Tapirus indicus	Perissodactyla	nocturnal-crepuscular	indifferent	23	39	48	110	61	54	225
Macaca nemestrina	Primates	diurnal	indifferent	9	9	24	42	113	2443	2598
Atherurus macrourus	Rodentia	nocturnal-crepuscular	indifferent	32	65	186	283	49	7	339
Hystrix brachyura	Rodentia	nocturnal-crepuscular	lunarphobic	27	85	257	369	66	7	442
Leopoldamys sabanus	Rodentia	nocturnal-crepuscular	lunarphobic	17	19	110	146	24	2	172

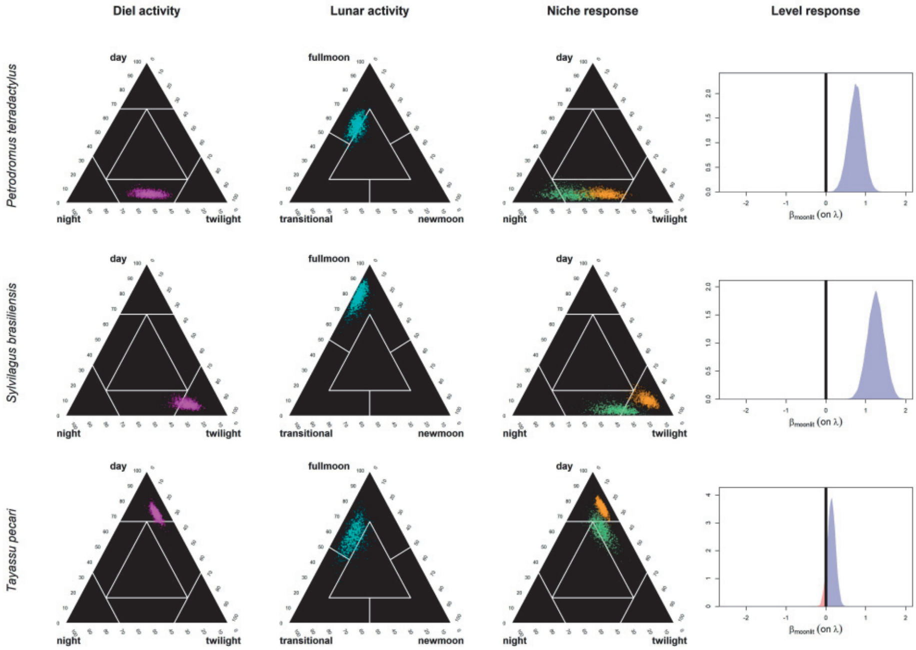
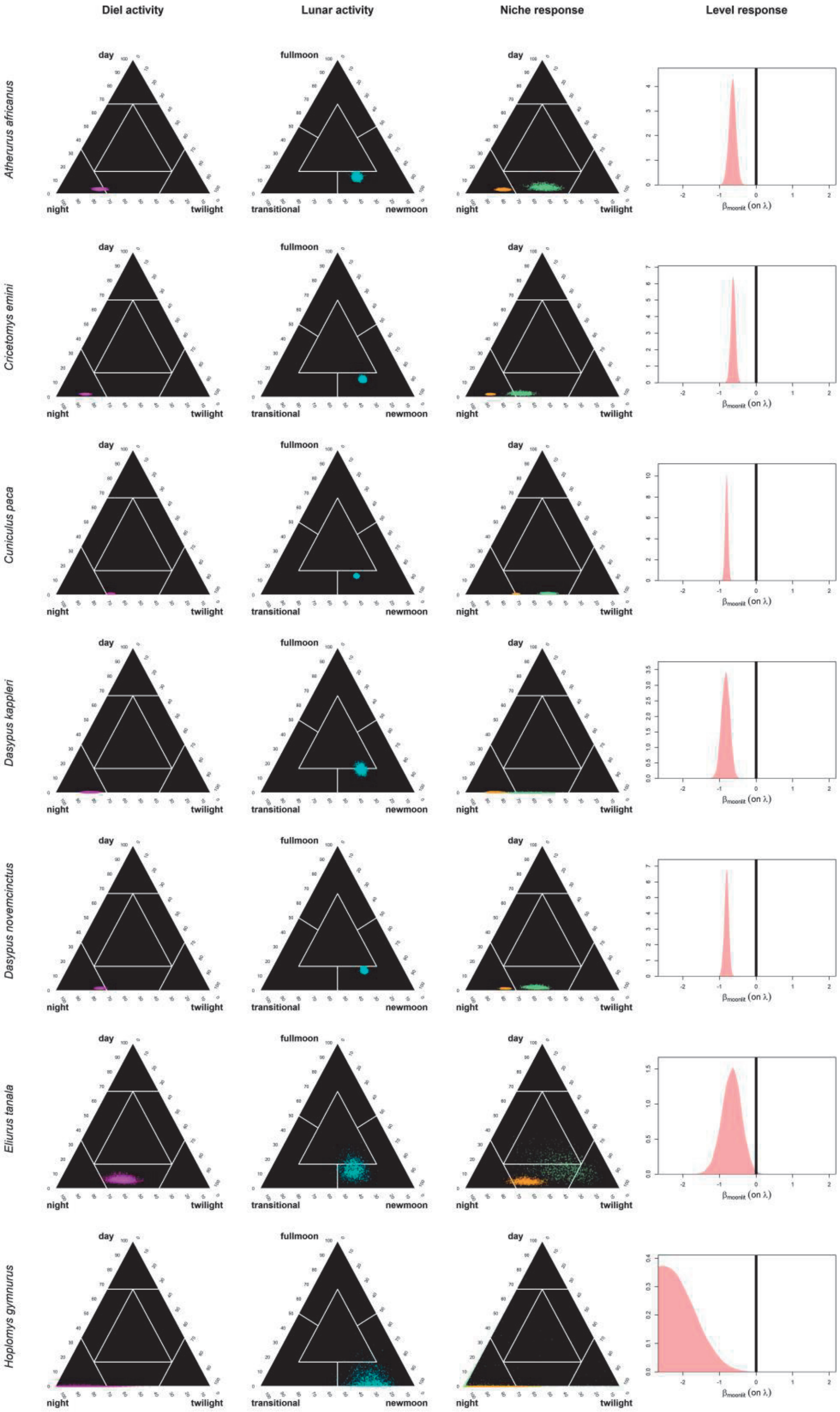


Figure S1. Overview of ternary classifications for diel and lunar activity (columns 1-2) and responses to lunar phases (column 3 and 4) for three mammal species identified as lunar philic. Column 1: ternary plots of diel activity posteriors. Column 2: ternary plot of lunar activity posteriors. Column 3: ternary plots showing difference of diel activity (potential temporal niche shifting) between periods with full moon (green) and without moonlit nights (orange). Column 4: posterior distribution of the difference between overall activity (related to the number of photographic detection events) during periods with vs. without full moon. Negative (red) and positive (blue) values indicate a reduction or an increase, respectively, in overall activity during periods (multiple 24-hour periods, Fig. 1 in the main text) with full moon.


Diel activity
Lunar activity
Niche response
Level response
Atherurus africanus
Cricetomys emini
Cuniculus paca
Dasypus kappleri
Dasypus novemcinctus
Eliurus tanala
Hoplomys gymnurus
day
night
twilight
fullmoon
transitional
newmoon
$\beta_{moonlit}$ (on λ)

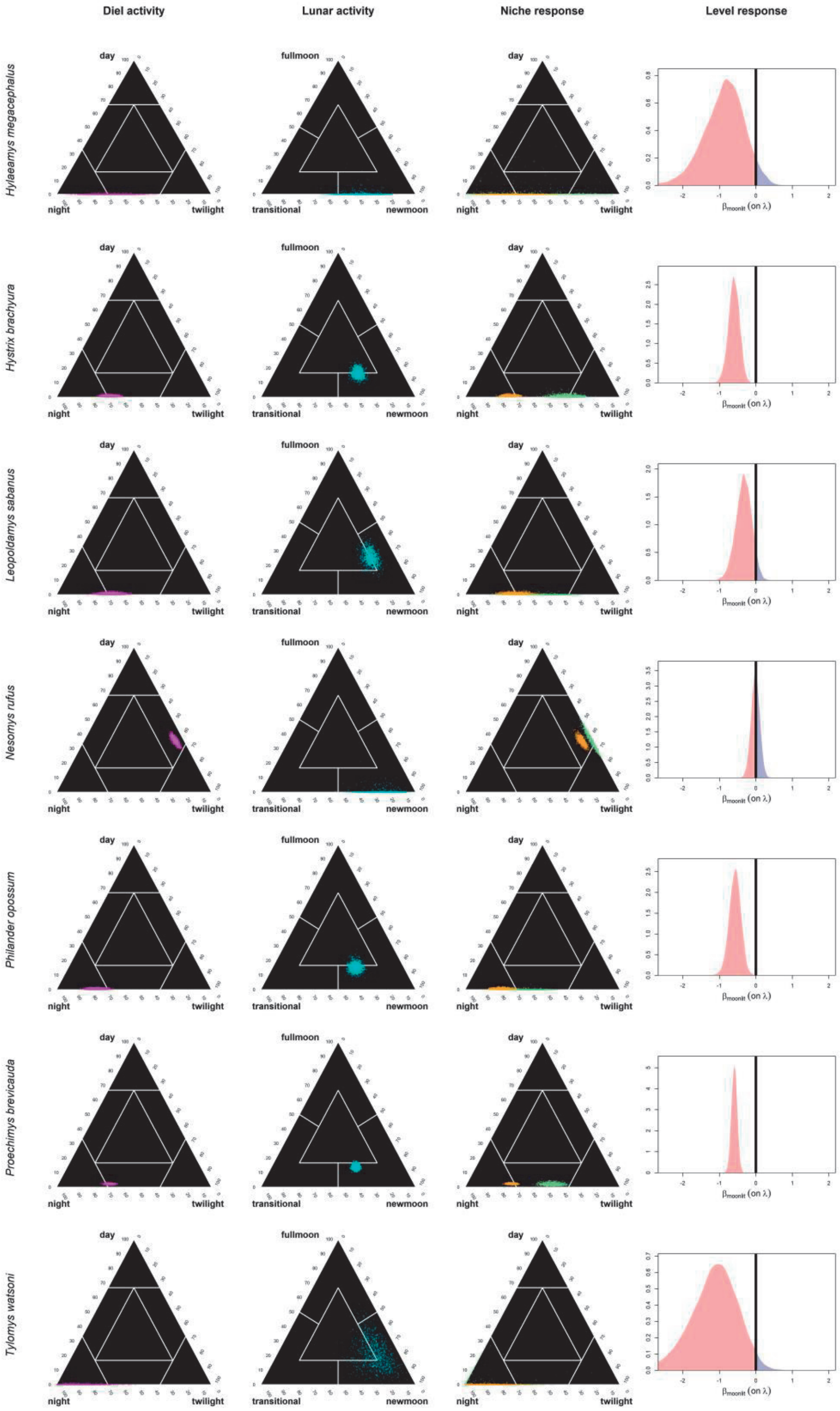

Diel activity
Lunar activity
Niche response
Level response
Hylaeamys megacephalus
Hystrix brachyura
Leopoldamys sabanus
Nesomys rufus
Philander opossum
Proechimys brevicauda
Tylomys watsoni
day
night
twilight
fullmoon
transitional
newmoon
$\beta_{moonlit}$ (on λ)

Figure S2. Overview of ternary classifications for diel and lunar activity (columns 1-2) and responses to lunar phases (column 3 and 4) for 14 mammal species identified as lunar phobic. Column 1: ternary plots of diel activity posteriors. Column 2: ternary plot of lunar activity posteriors. Column 3: ternary plots showing difference of diel activity (potential temporal niche shifting) between periods with full moon (green) and without moonlit nights (orange). Column 4: posterior distribution of the difference between overall activity (related to the number of photographic detection events) during periods with vs. without full moon. Negative (red) and positive (blue) values indicate a reduction or an increase, respectively, in overall activity during periods (multiple 24-hour periods, Fig. 1 in the main text) with full moon.

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