

1 The moon's influence on the activity of tropical forest mammals

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48 **Open Research statement:** The data and code for performing the analyses described in this article are
49 available at <https://github.com/richbi/TropicalMoon>.

50 **Abstract**

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

57 We quantified the prevalence and direction of activity responses to the moon in tropical forest mammal
58 communities. Using custom Bayesian multinomial logistic regression models, we analyzed long-term
59 camera trapping data on 88 mammal species from 17 protected forests on three continents. We also tested
60 the hypothesis that nocturnal species are more prone to avoiding moonlight, as well as quantified diel
61 activity shifts in response to moonlight.

62 We found that, apparent avoidance of moonlight (lunar phobia, 16% of species) is more common than
63 apparent attraction (lunar philia, 3% of species). The three species exhibiting lunar philia followed diurnal
64 or diurnal-crepuscular activity patterns. Lunar phobia, detected in 14 species, is more pronounced with
65 higher degree of nocturnality, and is disproportionately common among rodents. Strongly lunar phobic
66 species were less active during moonlit nights, which in most cases also decreases their total daily
67 activity.

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

73 Introduction

74

75 The moon brightens the night. Changes in illumination associated with the 29-day lunar cycle alter the
76 conditions faced by wildlife (Kronfeld-Schor et al. 2013). For some mammal species, especially those
77 with limited night-vision or few nocturnal threats, the extra illumination provides periodic access to the
78 night and associated foraging (Fernández-Duque et al. 2010, Prugh and Golden 2014) or travel
79 opportunities (Gursky 2003). Other species are robbed of the cloak of darkness and become exposed to
80 predators (Prugh and Golden 2014) or visible to prey (Pratas-Santiago et al. 2016).

81 The daily pattern of activity or “diel activity” of an individual, a population, or a species constitutes a
82 fundamental part of its ecological niche and has been studied extensively (Bennie et al. 2014). Despite
83 intuitive expectations for attraction to the moonlight (lunar philia) or avoidance of moonlight (lunar
84 phobia) and accumulating evidence for each, our knowledge of wildlife responses to the moon and their
85 prevalence in nature is still disjoint. While some species seem to respond strongly to lunar illumination
86 (Kronfeld-Schor et al. 2013), others apparently do not respond at all (de Matos Dias et al. 2018, Zaman et
87 al. 2022), for reasons not fully understood. The most comprehensive assessment of species responses to
88 moonlight is a meta-analysis of 58 species that found that moonlight reduced the activity of species in
89 open habitats yet increased the activity of species in forested environments (Prugh and Golden 2014).
90 However, this meta-analysis combined temperate forest species with tropical forest species. Moreover,
91 the tropical forest species were predominately arboreal primates, which consistently responded positively
92 to moonlight leaving open questions about other tropical forest mammals – including those living in the
93 darkest part of forests - the forest floor. To date there has not yet been an assessment of the effects of
94 moonlight on animal activity patterns based on community-level data collected across multiple locations
95 and regions using standardized data collection and analytical methods.

96 There are both fundamental and applied reasons why we should identify responses to lunar phases and
97 associated changes in illumination. First, the recurrent change in potential risks and opportunities faced by
98 entire communities provides a testing ground for ecological theory about species adaptations (Bennie et
99 al. 2014), interactions (Kronfeld-Schor et al. 2017), and the temporal dimension of the ecological niche
100 (Kronfeld-Schor and Dayan 2003, Hut et al. 2012). Studies have tested for, and in some cases found,
101 evidence that lunar illumination triggers niche shifting, with animals modifying when and where they are
102 active dependent on the phase of the moon (Hut et al. 2012). Second, moonlight can serve as a model to
103 help make predictions about the potential effect of artificial illumination – which is already impacting a
104 substantial part of Earth (Cinzano et al. 2001, Falchi et al. 2016) – on wildlife behavior (Beier 2006,
105 Rotics et al. 2011, Gilbert et al. 2023) and community dynamics (Meyer and Sullivan 2013, Gaston et al.
106 2014). Finally, knowledge about the relationship between illumination and animal behavior in densely
107 canopied and less-impacted systems offers a baseline for detecting changes in human-modified habitats.
108 Even natural light regimes change because of human-driven habitat alteration. For example, tropical
109 forests, which harbor a substantial portion of earth’s biological diversity, are cleared, fragmented, and
110 degraded at an alarming rate (Hansen et al. 2013, Pillay et al. 2022). Not only does this result in direct
111 habitat modification, but also in reduced canopy cover which exposes forest-dwelling species to increased
112 and prolonged solar and lunar illumination.

113 What is the prevalence and direction of responses to lunar phases in wildlife communities in some of the
114 darkest places on earth, the floors of tropical forests? Do their inhabitants respond to moonlight like
115 species in other environments and regions? Camera trapping offers an opportunity to answer these
116 questions. If deployed long enough, camera traps record animal activity 24/7 throughout the lunar cycle
117 and may thus capture responses of wildlife to changing levels of moonlight. We used images from a
118 pantropical camera trap study in tropical forests across the globe. A standardized survey methodology
119 allowed us to simultaneously examine diel and nocturnal activity of 88 mammal species spread over 16
120 orders and 35 families. Camera traps are now widely used for monitoring and studying terrestrial

121 biodiversity (Burton et al. 2015, Steenweg et al. 2017, Semper-Pascual et al. 2022) and several studies
122 have relied on time-stamped camera trap images to quantify and study animal diel activity (Rowcliffe et
123 al. 2014, Frey et al. 2017, Vallejo-Vargas et al. 2022). We analyzed photographic detection data using a
124 novel framework – multinomial regression combined with ternary classification – for consistent
125 categorization and quantification of the temporal niche and shifts therein (see also Gerber et al. 2023).
126 The flexible framework allowed us to not only compare levels of activity associated with different lunar
127 phases, but also test hypotheses about how lunar illumination impacts activity beyond the night. Previous
128 studies have shown that lunar illumination can trigger shifts in overall diel activity (Kronfeld-Schor et al.
129 2013). These changes may come about in different ways. At one extreme (fully additive), animals can
130 reduce or increase their nocturnal activity during full moon, without a change in activity during day or
131 twilight. This strategy will result in a corresponding decrease or increase in overall net activity. On the
132 other extreme (fully compensatory), animals may shift activity into or out of the illuminated period, for
133 example by moving their activity from the twilight period into the night, without a change in overall net
134 activity.

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

145

146 Methods

147 Data collection

148 **Camera trapping.** We derived observations of mammal activity in protected tropical forests from camera
149 trap data collected as part of the Tropical Ecology Assessment and Monitoring (TEAM) Network (Rovero
150 and Ahumada 2017). Following a common protocol (Jansen et al. 2014), cameras were deployed between
151 2008 and 2017 throughout 17 protected areas in Indomalaya, the Neotropics, and the Afrotropics. The
152 number of years of deployment varied between protected areas (2 years - 10 years; mean = 6.8 years), as
153 did the number of locations sampled (60-90 camera trap locations; total: 1062). Spatial configuration and
154 deployment were standardized, with cameras configured in either a 1x1km or 2x2km regular grid, at a
155 height of approximately 30-50 centimeters off the ground. On average cameras were active for 33.2 days
156 (SD=7.5). However, cameras were rotated sequentially until all sites were sampled within the wider
157 sampling season. As a result, multiple lunar cycles are recorded at each protected area within a sampling
158 season. For additional information about camera trapping protocols and species identification, see Rovero
159 and Ahumada (2017). In this analysis, we included 2.1M photographic detections from 88 mammal
160 species, i.e., species with ≥ 25 detections events during night (total across all protected areas;
161 Supplementary Information Tables S1-S3). Due to apparent inconsistent identification from photographs,
162 species in the genus *Tragulus* were considered jointly (*Tragulus sp.*)

163

164 Analysis 1: Prevalence of lunar phobia and philia

165 **Multinomial logistic regression** We use a Bayesian multinomial logistic regression model to
166 simultaneously assess diel (entire 24-hour period) and nocturnal (lunar) activity patterns. We
167 distinguished three diel periods (day, night, and twilight) and three lunar periods (full moon, transitional,
168 new moon). We chose discrete diel and lunar periods (see definitions below) instead of continuous values

169 based on illumination (Smielak 2023), as it enabled the multinomial analysis and an intuitive
170 categorization of activity (Figs 1 and 2).

171 This model contained two submodels, one for diel activity and one for lunar activity. The submodel for
172 diel activity consisted of a multinomial logistic regression model to estimate species-specific probability
173 of photographic capture in one of the three major diel periods (day, night, twilight; see also Gallo et al.
174 2022):

$$175 \quad y_i \sim \text{Multinomial}(p_i, N_i) \quad (1)$$

176

177 Here, y_i is the length-3 vector of the number of independent photographic capture events of species i in
178 each diel period, N_i the total number of detections ($N_i = \sum y_i$) of that species, and p_i the length-3 vector
179 of probabilities of detection in each diel period.

180 The multinomial probability vector can be defined using logistic regression:

$$181 \quad \log\left(\frac{p_{ik}}{p_{iK}}\right) = \beta_{0ik} + \sum_j^J \beta_{kj} x_{ij}, \quad \text{for } k = 1, \dots, K - 1 \quad (2)$$

182 where β_{i0k} is the species-specific intercept term associated with categorical outcome k (diel period) out
183 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
184 coefficients associated with predictor x_{ij} . The quotient on the left side of eq 2 signifies that the last
185 outcome (p_{iK}) serves as a reference value for the other $K - 1$ outcomes (p_{ik}).

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

$$189 \quad \log\left(\frac{p_{ik}}{p_{iK}}\right) = \beta_{0ik} + s_{ik} \quad (3)$$

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

201 The probabilities of interest are thus:

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

203

204 Where both \dot{p}_{ik} and p_{ik} are scaled to sum to 1 across the K multinomial outcomes.

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

213 sun touches the theoretical horizon). Dusk was delineated by the beginning of sunset and astronomical
214 sunset (sun 18° below the horizon). Night was delineated as the period between astronomical dusk and
215 dawn and day as the period between sunrise and sunset.

216 The submodel for lunar activity was structurally identical to the diel activity model described above. In
217 the lunar submodel, the three multinomial probabilities (p_{ik}) represent species-specific estimates of the
218 probability of photographic capture in one of the three major lunar periods, roughly corresponding to full
219 moon, new moon, and the combined intermediate phases. Moon phases were delineated for the night (as
220 defined above) using moon altitude (angular elevation) and illumination, again with R package ‘suncalc’.
221 Full moon was defined as the period when the moon had an altitude $\geq 18^\circ$ above the theoretical horizon
222 and was $\geq 90\%$ illuminated. New moon was defined as the period when the moon had an altitude $< 18^\circ$
223 above the theoretical horizon or was $< 10\%$ illuminated. All other nocturnal periods were designated as
224 transitional phases.

225 **Model fitting** We fitted multinomial models using Markov chain Monte Carlo (MCMC) simulation with
226 NIMBLE version 1.0.0 (de Valpine et al. 2017) in R version 4.3.0 (Team 2023). We ran 4 chains with
227 40000 iterations each, including a 20000-iterations burn-in period. Chains were thinned by a factor of 5.
228 We considered models as converged when the Gelman-Rubin diagnostics (Gelman 1996) was ≤ 1.1 for all
229 parameters and after visually inspecting trace plots.

230 **Designation of diel and lunar activity categories** For visual inspection, categorization, and presentation,
231 species-specific posterior samples of multinomial probabilities produced by the Markov chain Monte
232 Carlo MCMC analysis were plotted onto Ternary diagrams (Shepard 1954) using package ‘ternary’
233 (Smith 2017) in R. The diel and lunar activity pattern of each species was delineated with the help of the
234 ternary diagrams. We considered several alternative ternary configurations for categorization (Shepard
235 1954, Schlee 1973, Santini et al. 2005, Nakamura et al. 2018), but ultimately opted for a subdivision into
236 7 regions for diel activity and 4 regions for nocturnal activity as it relates to the lunar cycle. The lower
237 number of categories for nocturnal activity was motivated by the lower sample size (only observations

238 made during the night are considered for categorizing lunar activity) and ease of interpretation. For
239 categorizing diel activity, we divided the ternary diagram into these 7 regions (Fig. 2): 3 corner triangles
240 (each capturing cases that contain $>2/6$ of all activity) for the “pure” diel activity categories (e.g.,
241 diurnal), three transitional regions between pairs of corner regions for intermediate categories (e.g.,
242 diurnal-crepuscular), and one central triangle that indicates cathemerality (activity during all diel periods).
243 This classification follows Shepard’s (1954) approach for delineating soil categories, but without the
244 additional splitting of the intermediate regions along the sides of the ternary. We divided the ternary
245 diagram for lunar activity categorization into only these 4 regions (Fig. 2): one central triangle (identical
246 to the cathemeral region in the ternary diagram for diel activity) representing indifference (referred to as
247 “neutrality” by Gursky 2003) to the phase of the moon and 3 main lunar categories (activity during full
248 moon, new moon, and intermediate lunar phases).

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

254

255 Analysis 2: Link between nocturnality and lunar phobia

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

$$258 \quad \log\left(\frac{\bar{p}_{il}}{\bar{p}_{il}}\right) = \bar{\beta}_{0il} + \bar{\beta}_{night,l} \hat{p}_{i,night} + \bar{s}_{il} \quad (5)$$

259 Where $\hat{p}_{i,night}$ is the strength of selection for nocturnal activity estimated in the diel submodel and
260 $\beta_{night,l}$ is its effect on the multinomial probability associated with lunar period l out of a total of L lunar

261 periods. Whereas $\hat{p}_{i,night}$ is species specific, we estimate one coefficient $\underline{\beta}_{night,l}$ in this analysis, across
262 the entire species data set. Model fitting proceeded as in Analysis 1. We used the posterior distribution of
263 $\bar{\beta}_{night,l}$ and species-specific $\bar{\beta}_{oil}$ to derive fitted values (means) and associated 95% Bayesian credible
264 intervals (BCI) of the link between nocturnality and the probability of association with new moon and full
265 moon periods.

266

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

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

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

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

$$281 \quad \log(\lambda_i) = \check{\beta}_{0i} + \check{s}_i \quad (6)$$

$$282 \quad n_i \sim \text{Poisson}(\lambda_i) \quad (7)$$

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

$$289 \quad \lambda_i = e^{\beta_{0i}} \quad (8)$$

290 The multinomial model for diel activity was identical to the model defined with equations 1 and 3. The
291 main difference between the diel activity model in analyses 1, 2, and 3 was in the design: whereas in
292 analyses 1 and 2 we estimated the multinomial probabilities of being active during the three diel periods
293 (day, night, twilight) at any point during monitoring, in analysis 3 we estimated separate multinomial
294 probabilities for periods (multiple days) with and without at least 1 hour of full moon at night (Fig. 1).
295 Model fitting and assessment of convergence/mixing was performed as in analysis 1 and 2. Diel activity
296 was categorized using the ternary approach described earlier. Changes in diel activity during periods with
297 full moon that resulted in a change of activity category were considered evidence of temporal niche
298 switching. Changes in diel activity without a change in activity category but a difference in the posteriors
299 for p_{night} associated with new moon vs. all other phases whose 95% BCI did not include zero were
300 considered activity timing shift, a term also used in (Gilbert et al. 2023). We subtracted the posterior
301 sample for $\hat{\lambda}_i$ for periods without moonlit nights from those with to derive species-specific posteriors of
302 the effect of full moon on overall activity levels. We considered a species to show evidence of altered
303 overall activity levels in response to lunar illumination when the 95% BCI of this derived variable did not
304 include zero.

305

306 Results

307 Diel activity and overview

308 Of the 88 species included in the analysis, we categorized 20 species as predominantly nocturnal and nine
309 as diurnal, following the multinomial regression analysis controlling for temporal availability and the
310 ternary classification scheme (Fig. 2, Supplementary Information Tables S1-S3). Only one species
311 (common tapeti, *Sylvilagus brasiliensis*) was categorized as predominantly crepuscular. Most species (42)
312 fell into one of the two intermediate categories involving crepuscularity (Fig. 3). All remaining species
313 (16) were categorized as cathemeral (Supplementary Information Tables S1-S3). Cathemeral designation,
314 by nature of its position within the ternary, is associated with greater uncertainty (Gerber et al. 2024). In
315 data-sparse situations it may be difficult to distinguish between a species being truly cathemeral and the
316 model not having enough information to assign the species to another category. However, all species
317 categorized as cathemeral in this analysis had more than 100 observations (hours with at least one
318 detection; mean = 770, range = 136– 3250; Supplementary Information Tables S1-S3).

319 Prevalence of lunar phobia and philia

320 Of the 88 species included in the analysis, 14 were categorized as lunar phobic and three as lunar philic
321 (Fig. 3, Supplementary Information Tables S1-S3). Only one species (Forest giant squirrel, *Protoxerus*
322 *stangeri*) was categorized as selecting for intermediate lunar phases (“transitional”). Rodents were the
323 most common lunar phobic species (11), followed by armadillos (2), and one opossum (gray four-eyed
324 opossum, *Philander opossum*). The representation of rodents among lunar phobic species (79%) was
325 disproportional to their prevalence (25%) among the species in our sample. The three mammal species
326 exhibiting lunar philia were the white-lipped peccary (*Tayassu pecari*, order Artiodactyla) and the
327 common tapeti (order Lagomorpha) in the Neotropics, and the four-toed elephant shrew (*Petrodromus*
328 *tetradactylus*, order Macroscelidea) in the Afrotropics. The remaining 70 species were categorized as
329 indifferent towards lunar phases, either because their nocturnal activity was not impacted by lunar

330 illumination or because their data had such a high noise-to signal ratio that it prevented designation to one
331 of the peripheral ternary regions (Supplementary Information Tables S1-S3). In our dataset, 14 (20%) of
332 the species categorized as indifferent towards lunar phases had less than 50 observations during the night
333 and we consider these species as data-sparse. Nonetheless the sample size was relatively high with an
334 average of 445 nocturnal observations (range: 25 – 4189; Supplementary Information Tables S1-S3) of
335 species categorized as indifferent towards lunar phases.

336

337 [Link between nocturnality and lunar phobia](#)

338 Species with a greater probability of being active at night were more likely to be more active also at new
339 moon ($\beta_{night,new\ moon} = 1.55$, 95% CrI: 1.46 to 1.64, Fig. 5) and, conversely, less likely to be active at
340 full moon ($\beta_{night,full\ moon} = -1.12$, 95% CrI: -1.25 to -0.99, Fig. 5). This effect was also reflected in our
341 categorization of diel activity of species identified as lunar phobic. Thirteen of the fourteen species
342 categorized as lunar phobic also exhibited a nocturnal or nocturnal-crepuscular diel activity pattern, and
343 only one was categorized as diurnal-crepuscular (Fig. 3). Of the lunar philic species, one was diurnal, one
344 diurnal-crepuscular, and one nocturnal-crepuscular (Fig. 3).

345

346 [Temporal niche shifting and changes in overall activity](#)

347 Eleven of the 14 lunar phobic species significantly reduced their overall activity level during periods with
348 moonlit nights and eight of these shifted their diel behavior to become less nocturnal (Figs 3 and 5;
349 Supplementary Information Fig. S2). Three species classified as lunar phobic (*Philander opossum*,
350 *Hoplomys gymnurus*, *Tylomys watsoni*) reduced their overall activity without a significant shift in diel
351 behavior, and two species (*Nesomys rufus*, *Protoxerus stangeri*) shifted their diel behavior to be less
352 nocturnal without a significant reduction in overall activity (Fig. 6). Of the three species identified as
353 lunar philic, one (*Sylvilagus basiliensis*) shifted to more nocturnal activity and increased its overall

354 activity, one (*Tayassu pecari*) only shifted its activity to become more nocturnal, and one (*Petrodomus*
355 *tetradactylus*) only increased its overall activity during periods with moonlit nights (Fig. 6). Following
356 our categorization of diel behavior, 9 of the 14 lunar phobic species switched their temporal niche from
357 nocturnal to nocturnal-crepuscular during periods with full moon. See Supplementary Information Figures
358 S1 and S2 for detailed results for all species classified as lunar phobic or philic.

359

360 Discussion

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

371

372 Lunar philia and lunar phobia in tropical forest mammal communities

373 Unlike prior meta-analysis results showing that forest dwelling species increased activity during
374 moonlight (Prugh and Golden 2014), our standardized assessment shows that the most common tropical
375 terrestrial mammal response to moonlight is reduced activity. Lunar philia is rare among terrestrial
376 tropical forest mammals. Only three species, among the 88 species studied here, significantly increased
377 their exposure to camera traps during hours filled with moonlight (Fig. 3). Lunar philia has previously

378 been reported as comparatively rare and has been associated with species, such as arboreal primates,
379 relying on visual cues for foraging and predator avoidance (Prugh and Golden 2014). The only species
380 classified as lunar philic in our study were a peccary (white-lipped peccary, *Tayassu pecari*), a rabbit
381 (common tapeti, *Silvilagus brasiliensis*), and an elephant shrew (four-toed elephant shrew, *Petrodromus*
382 *tetradactylus*). Apparent lunar philia in the common tapeti has previously been reported in Argentina
383 (Huck et al. 2017), and contrasts lunar phobic behavior reported in another lagomorph, the snowshoe hare
384 (*Lepus americanus*, Griffin et al. 2005). Lunar philia in elephant shrews is consistent with descriptive
385 studies on the order (Woodall et al. 1989). Similarly, white-lipped peccary have been reported to change
386 routes and increase movement in the forest during full moon (Serrano et al. 2010, Hernández 2015). *T.*
387 *pecari* is a large group-living mammal (40 kg) which may make it less vulnerable predators.

388 Lunar phobia, in contrast, was common. It was exhibited primarily by small-to-medium sized mammals
389 that are prey of carnivores such as ocelots (*Leopardus pardalis*) or jaguars (*Panthera onca*, Moreno et al.
390 2006, Pratas-Santiago et al. 2016). Nevertheless, the fact that lunar phobia was disproportionately found
391 in rodents, suggests that there are evolutionary differences among prey groups that influence responses to
392 moonlight above and beyond ecological responses to predators as prey, potentially related to their sensory
393 ecology. The paca, one of the largest lunar phobic rodents in our study (8000g) has been classified as
394 lunar phobic in other study areas (but see Michalski and Norris 2011), as were armadillos (Harmsen et al.
395 2011, Pratas-Santiago et al. 2017). Pacas and armadillos need to avoid natural predators but also hunting
396 by rural and indigenous communities (Redford and Robinson 1987, Pires Mesquita et al. 2018). Although
397 Harmsen et al. (2011) detected no changes in the activity of the common opossum (*Didelphis*
398 *marsupialis*) in response to moonlight, evidence on lunar phobia in the gray four-eyed opossum
399 (*Philander opossum*) in our study matches findings for members of the Didelphimorphia order reported in
400 other studies (e.g., *Didelphis aurita*, *Calouromys philander*; Julien-Laferrrière 1997, Tripodi et al. 2023).

401 We simultaneously analyzed activity data from many species using one standardized approach. Across
402 that diverse community of mammals, some species were observed more frequently than others.

403 Technically, all activity data, no matter how sparse, can be designated to one of the categories represented
404 by the areas delineated in the ternary diagram. However, observation of activity is imperfect in nature,
405 either because not all individuals are observed or individuals are not observed all of the time, or both. The
406 probability of making an erroneous designation (i.e., an activity category other than the true one) is liable
407 to increase as sample size decreases. Designation to the cathemeral (diel activity) and indifferent (lunar
408 activity) categories, by nature of their position within the ternary, are probably the most error prone and
409 most vulnerable to data paucity. Determination of cathemerality was less ambiguous, as all species in this
410 study had more than 100 observations for diel activity categorization, with an average of 796 observations
411 per species. However, 22% and 44% of species categorized indifferent to lunar phases had < 50 and < 100
412 hourly observations respectively. At least for these, we cannot reliably distinguish true indifference to
413 lunar phases from an insufficient sample size for making a designation.

414

415 [The link between lunar phobia and nocturnality](#)

416 The more nocturnal species are, the more likely they are to exhibit lunar phobic behavior (Fig. 5). Lunar
417 phobia has been explained as a behavioral adaptation by nocturnal species, intended to avoid the elevated
418 predation risk during periods with higher illumination (Daly et al. 1992, Kronfeld-Schor et al. 2013). The
419 large number of species included in our study and a standardized classification approach yielded support
420 for this explanation. The avoidance of moonlight could reduce vulnerability to detection by visually-
421 hunting predators or, in the case of lunar phobic predators, detection by prey. Rodents, for example,
422 generally seem to reduce foraging activity during bright nights (Price et al. 1984, Longland and Price
423 1991, Prugh and Golden 2014). Conversely, we found that lower nocturnality was associated with higher
424 activity during full moon periods (Fig. 5). The three species identified as lunar philic were diurnal,
425 crepuscular, and crepuscular-nocturnal. Two of these species significantly increased their overall level of
426 activity during moonlit periods (Fig. 6). Meanwhile, 13 of the 14 lunar phobic species were nocturnal or

427 nocturnal-crepuscular, and only one was categorized as diurnal-crepuscular (Fig. 3). Thus, moonlight
428 appears to give species adapted to daylight and twilight better visual access to the night.

429

430 Temporal niche shifting in response to moon phases

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

449

450 Methodological insights and other considerations

451 In this study, we adjusted and deployed a novel framework to delineate diel and nocturnal activity
452 categories using multinomial probability distributions, and ternary diagrams (Gallo et al. 2022, Gerber et
453 al. 2024). This approach is both visually intuitive and quantitative, facilitating detection of ecological
454 patterns related to activity, such as temporal niche partitioning and niche shifting/switching in response to
455 moonlight. Any analytical approach that can estimate the probability of designation and the associated
456 uncertainty can be substituted for the Bayesian multinomial approach used here. The advantage of the
457 latter is that it produces posterior samples of multinomial probabilities, which readily allow propagation
458 of uncertainty to the ternary projection and subsequent classification.

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

473

474 Implications

475 The influence of natural and artificial light is an increasingly important topic in wildlife conservation and
476 ecosystem functioning (Gaston et al. 2017, Hirt et al. 2023). Yet we still know too little about the
477 implications of artificial light on the activity of mammals (Hoffmann et al. 2022). The prevalence of lunar
478 phobia in our study suggests there may be more losers than winners when illumination increases in
479 tropical forests. Moreover, most lunar phobic species in our study reduced their overall activity during
480 periods with new moon. If these results extend to artificial light, a loss of dark nights could curtail the
481 amount of time some species invest into foraging and other important activities. Strong responses to
482 artificial light have already been observed in nocturnal mammals (Prugh and Golden 2014). For example,
483 the common spiny mouse (*Acomys cahirinus*) shows a clear reduction in the overall activity and time for
484 foraging when exposed to artificial light (Rotics et al. 2011). The constant reduction of activity, for
485 example due to permanent human light sources, may, affect individuals, populations and even
486 communities. However, predicting fitness consequences of artificial light based on responses to lunar
487 phases is challenging. Seemingly indifferent species without adaptations to changing nocturnal light
488 conditions may not be impacted at all or could bear the brunt of brighter nights resulting from canopy loss
489 and light pollution if they are made vulnerable by increased visibility. Species that change their overall
490 activity level in response to nocturnal illumination may be more strongly impacted than species that can
491 maintain their level of activity by adjusting its timing. Along those lines, lunar phobic species could be
492 expected to cope better with artificial light if they follow a cathemeral diel activity pattern as this is
493 indicative of behavioral plasticity that may be advantageous in a changing world ((temperature changes,
494 artificial light; Cox and Gaston 2023). However, in tropical regions cathemerality is less reportedly less
495 common than in higher latitudes (Bennie et al. 2014).

496 Our research describes responses to moonlight on the forest floor. It would be interesting for future
497 studies to examine responses in the canopy of tropical forest, where lunar illumination likely has more
498 pronounced effects on animal behavior. It is also worthwhile to extend research into the effects of

499 moonlight and artificial light to birds, another prominent class of both ground and canopy-dwelling
500 species in tropical forests.

501

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509

510 Conflict of interest statement

511 The authors declare no conflicts of interest.

512

513 Data availability statement

514 The data and code for performing the analyses described in this article are available at:

515 <https://github.com/richbi/TropicalMoon>.

516

517 Supplementary information

518 Appendix S1

519

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692

693 Figure captions

694 **Figure 1.** Illustration of the study design. Time-stamped camera trap images (A) are aggregated into 15-
695 minute intervals and mapped onto available site-specific diel and lunar periods (B). Red dots in the
696 example belong to the nine-banded armadillo (*Dasypus novemcinctus*), an apparently lunar phobic
697 species. Multinomial logistic regression models are used to quantify the probability of a species using a
698 given diel or lunar period. Three analyses explore 1) the prevalence of lunar phobia and lunar philia
699 during nocturnal activity (C), 2) the effect that the level of nocturnality of a species (D) has on its
700 propensity to exhibit lunar phobia (E), and 3) changes in diel activity patterns and total activity levels
701 during periods with full moon (F) vs. other lunar phases (G). The blue boxes delineate the part of the diel
702 region involved in each assessment or comparison. Photos: TEAM network.

703 **Figure 2.** Posterior samples (dots) of multinomial probabilities mapped onto ternary diagrams. Shown are
704 example posterior samples for diel activity (left; activity during day, night, and twilight periods) and lunar
705 activity (right; nocturnal activity during full moon, new moon, and transitional phases). The ternary
706 diagrams are divided into seven and four regions for diel and lunar activity delineation respectively.
707 Designation to activity categories (grey text) is made according to the region into which the majority
708 (colored dots) of posterior samples are mapped. The examples show a diurnal-crepuscular (left) and a
709 lunar phobic species (right).

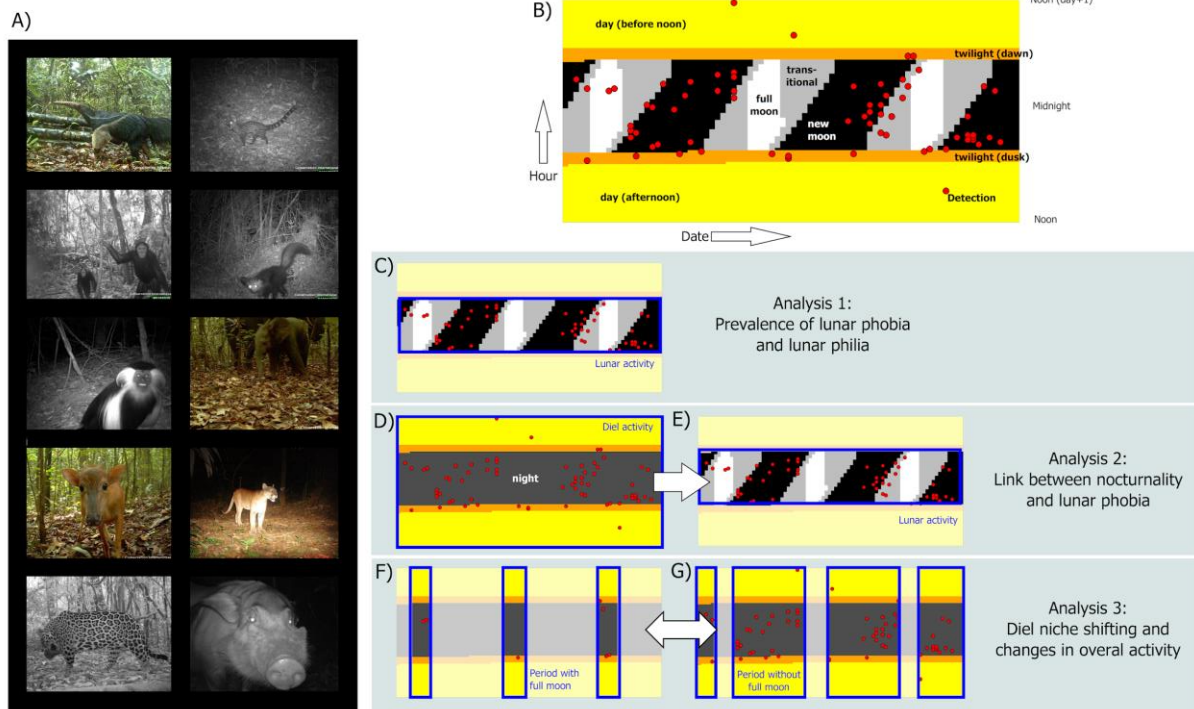
710 **Figure 3.** Diel and lunar categorization charted across phylogenetic trees of tropical forest mammals in
711 three realms. The distribution of tropical moist broadleaf forest (green regions) and location of study areas
712 (black dots) included in this analysis are shown on the map. Lunar category is only indicated for species
713 that were unambiguously designated as either lunar phobic or lunar philic. Lunar phobia, manifested as
714 reduced activity during moonlit nights, was more common than lunar philia, increased activity during
715 moonlit nights. Rodents, particularly nocturnal species, were overrepresented among lunar phobic
716 species, followed by members of the Cingulata (including armadillos) and Didelphimorphia (opossums).
717 Phylopic silhouettes credits: *Cuniculus paca*, *Dasypus novemcinctus*, *Silvilagus brasiliensis* and *Tayassu*

718 *pecari* by Gabriela Palomo-Munoz; *Philander opossum* by Milena Cavalcanti, Patricia Pilatti & Diego
719 Astúa; *Hopломys gymurus*, *Atherurus africanus*, *Cricetomys emini*, *Hystrix brachyura* and *Leopoldamys*
720 *sabanus* provided by Andrea F. Vallejo Vargas; *Petrodromus tetradactylus* under universal public domain
721 license.

722 **Figure 4.** Overview of ternary classifications for diel and lunar activity (columns 1-2) and responses to
723 lunar phases (column 3 and 4) for four example species (rows). The species shown in the top row
724 (common tapeti or forest cottontail) was classified as lunar philic, whereas the bottom three rows show
725 lunar phobic species. Column 1: ternary plots of diel activity posteriors. Column 2: ternary plot of lunar
726 activity posteriors. Column 3: ternary plots showing difference of diel activity (potential temporal niche
727 shifting) between periods with full moon (green) and without moonlit nights (orange). Column 4:
728 posterior distribution of the difference between overall activity (related to the number of photographic
729 detection events) during periods with vs. without full moon. Negative (red) and positive (blue) values
730 indicate a reduction or an increase, respectively, in overall activity during periods (multiple 24-hour
731 periods, Fig. 1) with full moon. See Supplementary Information Figures S1-S3 for results for all species
732 classified as either lunar phobic or philic.

733 **Figure 5.** Effect of the probability of nocturnal activity on the probability of activity during new moon
734 (blue) and full moon (magenta). The plot shows posterior predictions, with the intensity of shading
735 (opaqueness) corresponding to the posterior distribution of \hat{p}_{night} (x-axis, eq 3), $\hat{p}_{full\ moon}$ (left y-axis),
736 and $\hat{p}_{new\ moon}$ (right y-axis) across all 88 species included in the analysis.

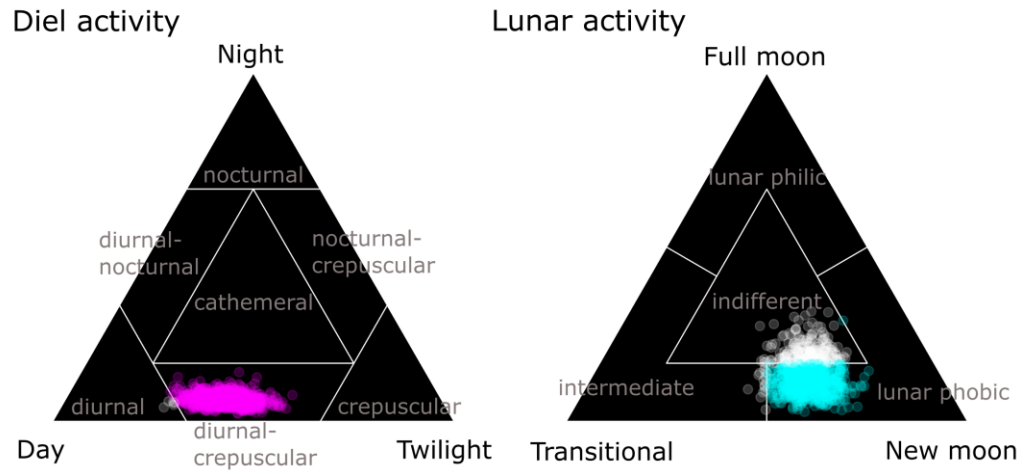
737 **Figure 6.** Changes in nocturnality (left) and overall diel activity levels (right) of forest mammals during
738 periods with and without full moon. Responses (“Effect”) are represented by the posterior distributions of
739 coefficient estimates shown as violins. Species names are shown on color-coded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



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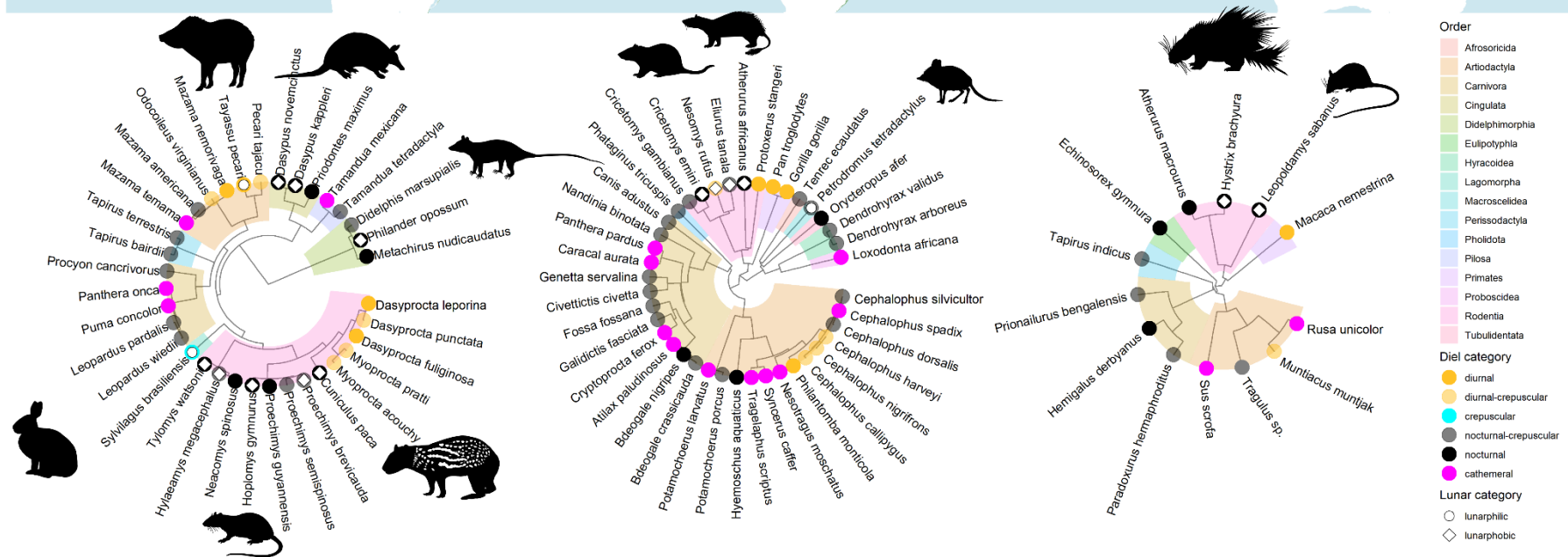
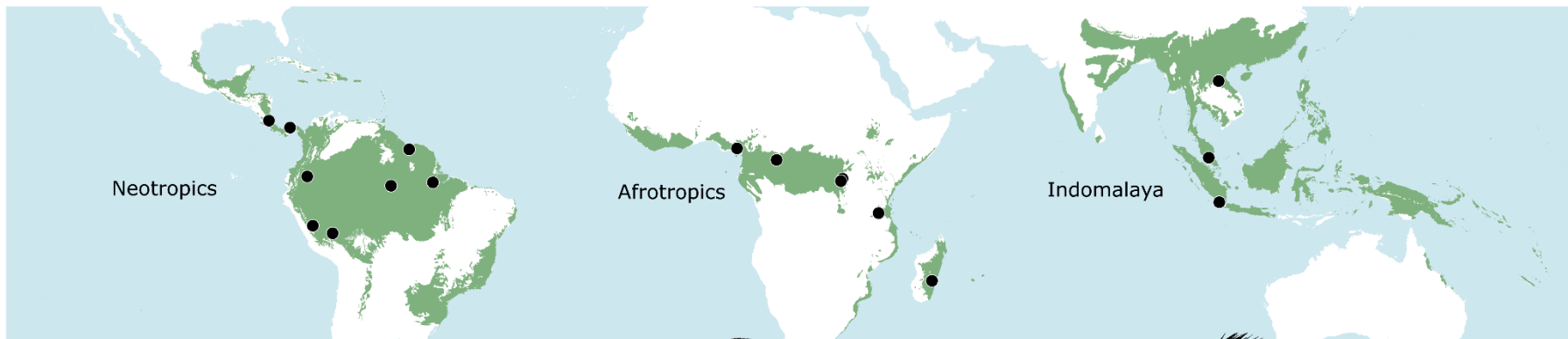
743 **Figure 1**

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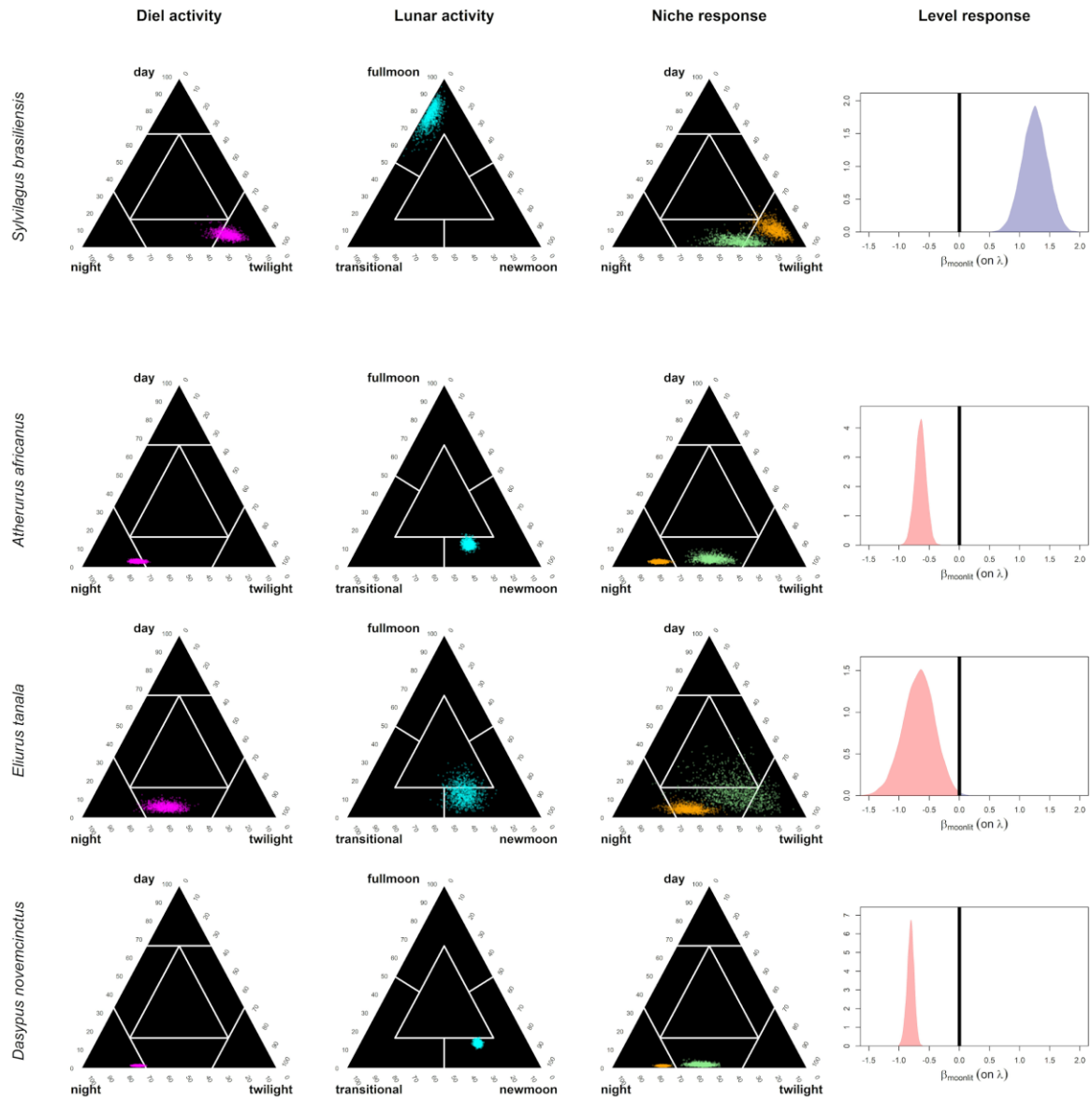
745

746 **Figure 2**



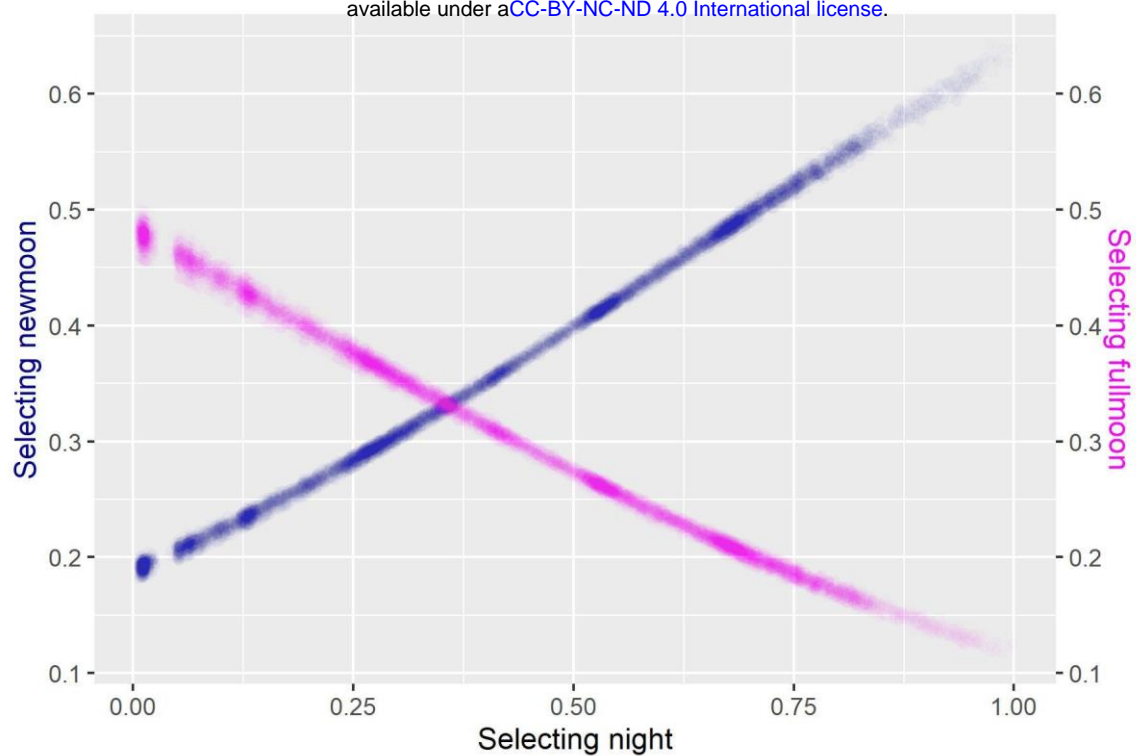
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748 **Figure 3**



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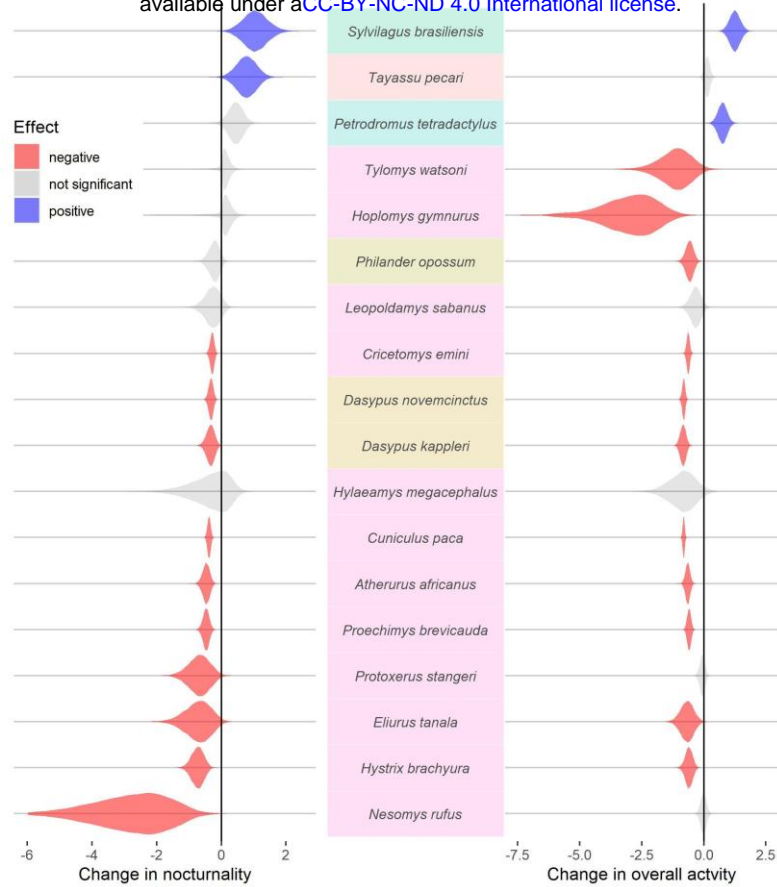
750 **Figure 4**



751

752 **Figure 5.**

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754

755 **Figure 6**

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