

Habitat disturbance trumps moonlight effects on the activity of tropical insectivorous bats

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Keywords

acoustic monitoring; anthropogenic impact; bat conservation; habitat fragmentation; light pollution; tropical forest; moonlight.

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Email: giu.appel@gmail.com

Editor: Karl Evans

Associate Editor: Thomas Tscheulin

Received 21 September 2020; accepted 29 April 2021

doi:10.1111/acv.12706

Abstract

Changes in moonlight intensity can affect predation risk and induce changes in habitat use and activity of nocturnal species. However, the effect of moonlight on animal activity is rarely evaluated in human-modified landscapes and can be of vital importance to understand possible changes in ecosystem services provided by light-sensitive taxa, such as insectivorous bats. Fragmentation changes forest structure and affects light penetration across the landscape. In this case, the effects of fragmentation on bat activity can be modulated by cyclical variations of moonlight intensity. We acoustically quantified the activity of nine aerial insectivorous bat species in relation to moonlight at the Biological Dynamics of Forest Fragments Project, Central Amazonia. We aimed to understand species-level variation in activity across habitats (continuous forest, fragments and secondary forest) at different temporal scales: lunar cycle, dark vs. bright nights and within nights. Amazonian aerial insectivorous bats responded more to habitat type than to moonlight, with two and six species showing reduced activity in fragments and secondary forest, respectively, compared to continuous forest. The lower activity in secondary forest suggests that despite *c.* 30 years of secondary forest regeneration, it is still less attractive as foraging habitat. An interactive effect of habitat type and moonlight on bat activity was most evident when contrasting dark and bright nights. Our results indicate that fragments have reduced bat activity on extremely bright nights, probably due to higher predation risk in small fragments. Species that emit constant-frequency calls (*Pteronotus* spp.) were the ones that most modulated their responses to habitat disturbance and moonlight. Otherwise, moonlight had little effect on hourly activity levels, irrespective of habitat type. Moonlight is capable of modulating the responses of some bat species in disturbed habitats, particularly in fragments.

Introduction

Anthropogenic habitat loss and fragmentation are key drivers of biodiversity change and erosion of ecological processes (Barlow et al., 2016; Pfeifer et al., 2017), especially in species-rich tropical regions such as the Amazon rainforest (Betts et al., 2019). Worryingly, forest fragmentation in the Brazilian Amazon is progressing faster than ever; in 2017, there was an increase of nearly 70% in the number of fragments (Montibeller et al., 2020) and this trend can be assumed to have worsened due to the high levels of forest loss in 2018–19 (Barlow et al., 2020). Forest fragmentation

results in the formation of isolated patches, surrounded by an anthropogenically modified matrix (Haddad et al., 2015). The type of human-made matrix can act as selective filter for the movements of species (Watling et al., 2011), altering the abundance, composition, phylogenetic and functional diversity of animal assemblages (Aninta et al., 2019; Mendenhall et al., 2014; Rutt et al., 2020).

Risk of predation is a major determinant of habitat use by animals (Atkins et al., 2019; Pringle et al., 2019). For nocturnal species, moonlight is an important source of information that affects foraging habitat selection (Waap et al., 2017). Prey species commonly curtail their activity under

bright moonlight, so as to reduce the probability of predation by visually oriented predators (Miranda *et al.*, 2020; Navarro-castilla and Barja, 2014). On the other hand, predator species can more easily locate prey under brighter conditions and thus increase their activity to maximize hunting success (Bhatt, Sarma and Lyngdoh, 2021; Pratas-Santiago *et al.*, 2016). However, species that are both prey and predators need to strike a balance between guaranteeing high foraging success and predator avoidance (Linley *et al.*, 2020; Penteriani *et al.*, 2011).

An increase in the perceived risk of predation during full moon nights can force prey species to forage in cluttered habitats such as primary forest, in which dense canopies limit the amount of moonlight reaching the understory (Gigliotti and Diefenbach, 2017). However, moonlight exposure in disturbed landscapes may differ from that in continuous primary forest. Canopy openness in forest fragments and continuous forest may be similar (Almeida *et al.*, 2019; Rocha *et al.*, 2020), resulting in comparable levels of moonlight reaching the undergrowth and consequently predation risk. However, the foraging area of a species may often be larger than the fragment area, forcing the animals to forage at fragment edges and in regrowth vegetation where exposure to bright light levels during moonlit nights is greater (Bernard and Fenton, 2003). Therefore, relative to continuous forest, predation risk can be expected to be higher in smaller fragments and in the surrounding matrix (Bowers and Dooley, 1993; Rocha *et al.*, 2020).

Bats are a group of essentially nocturnal animals which provide vital functions in the maintenance of tropical ecosystems through pollination, seed dispersal and insect population suppression (Kunz *et al.*, 2011). Studies involving the effect of moonlight on bats go back a considerable time, in fact the term “lunar phobia” was coined by Morrison (1978) for Neotropical frugivorous bats. Lunar phobia is a behavioural response to increased moonlight intensity and is probably an adaptation for reducing exposure to visually orientated nocturnal predators (Haeussler and Erkert, 1978; Morrison 1978). For aerial insectivorous bats, the relationship with moonlight is more complex because they simultaneously face the trade-off of being both prey and predator (Holland *et al.*, 2011; Roeleke *et al.*, 2018; Vásquez, Grez and Pedro, 2020). In Amazonian bats, moonlight seems to have species-specific effects, with some species either increasing or decreasing their activity in brighter nights, while others are unaffected (Appel *et al.*, 2017).

Although there are many studies that evaluated the effect of moonlight on aerial insectivorous bat activity, these studies are concentrated in temperate regions (Perks and Goode-nough, 2020; Saldaña-Vázquez and Munguía-Rosas, 2013). While previous research has shown that some aerial insectivorous bat species respond to moonlight in undisturbed tropical rainforest (Appel *et al.*, 2017, 2019), such effects have rarely been evaluated in the context of human-modified landscapes (Jung and Kalko, 2011; Lima and O’Keefe, 2013; Kolkert *et al.*, 2020 but see Musila *et al.*, 2019). Assessing the effect of moonlight on the activity patterns of aerial insectivorous bats in human-modified landscapes is important

to understand possible changes in ecosystem services provided by this bat ensemble (Pianka, 1973; Presley *et al.*, 2009). In agricultural landscapes, this issue is relevant for the management of fragments because of the potential role of insectivorous bats in the suppression of agricultural pests (Kemp *et al.*, 2019).

Here, we used the experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon to evaluate the hypothesis that moonlight modulates the effects of habitat disturbance on aerial insectivorous bat activity at different temporal scales. We acoustically quantified bat activity in continuous forest and in disturbed habitats (forest fragments and within the intervening secondary forest matrix) to understand variation in species-level activity across these habitat types in relation to moonlight. We conducted our analyses at different temporal resolutions, focussing on variation in moonlight intensity: i) associated with the lunar cycle, ii) between dark and bright nights and iii) within nights. Accordingly, we predicted that:

- 1 Species sensitive to habitat disturbance and moonlight will respond negatively to moonlight intensity in fragments and secondary forest, as previous research indicates that some Amazonian aerial insectivorous bats respond to habitat disturbance (Núñez *et al.*, 2019) and moonlight (Appel *et al.*, 2017).
- 2 Species sensitive to habitat disturbance and moonlight will show increased activity in fragments and secondary forests on dark nights (associated with new moon) compared to bright nights (associated with full moon), whereas in continuous forest responses to moonlight will be species-specific.
- 3 In fragments and secondary forest, bat species will reduce activity in the early evening to avoid the time of greatest predation risk. In continuous forest, within-night activity will be concentrated in the early evening, both on bright and dark nights, to maximize foraging opportunities during the peak in prey abundance.

Materials and methods

Study site

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) (2°25’S; 59°50’W), located ~80 km north of Manaus, Brazil (Fig. 1), a long-term fragmentation experiment that has been running for ~40 years to study the effects of forest fragmentation on Amazonian biota (Laurance *et al.*, 2018). The climate is characterized by a dry season from July to November when precipitation drops below 100 mm/month and a rainy season from November to June, when precipitation can exceed 300 mm/month (Ferreira *et al.*, 2017). The study landscape consists of 11 forest fragments (five of 1 ha, four of 10 ha and two of 100 ha), surrounded at the time of the study by a matrix of tall secondary forest, and extensive areas of continuous primary forest that act as experimental controls (Laurance *et al.*,

2018). In the early 1980s, forest fragments were experimentally isolated and the vegetation around them has since been periodically cleared to maintain isolation, last in 2014 (Rocha *et al.*, 2017a), after data collection for this study. The site supports lowland evergreen *terra firme* rainforest at 50 to 100 m of elevation, and the temperature ranges from 19 to 39°C (Laurance and Williamson, 2001). The secondary forest is dominated by *Vismia* spp. in areas that were cleared and burned and dominated by *Cecropia* spp. in areas that were only cleared (Mesquita *et al.*, 2001). Percent canopy cover varies little between habitat types (continuous forest interiors: 85.4 ± 5.2 [mean \pm SD], fragment interiors: 87.4 ± 1 , secondary forest: 75.1 ± 6.7 ; Rocha *et al.*, 2017a). Canopy height in the largest fragments and continuous forest averages 28 m (Almeida *et al.*, 2019), while in the well-developed secondary forest the average canopy height is 15 m (Jakovac *et al.*, 2014; Mokross *et al.*, 2018).

Bat acoustic sampling

We sampled 13 sites across the BDFFP landscape between 2011 and 2013: three in continuous forest (Cabo Frio, Florestal and Km 41 camps), six forest fragments (3 fragments of 1 and 10 ha in Colosso, Dimona and Porto Alegre camps) and four in the secondary forest matrix (Cabo Frio, Colosso, Dimona, Florestal and Porto Alegre camps) (Fig. 1). Each

site was visited twice during both dry and rainy seasons. At each sampling site, we installed an automatic ultrasound recorder (Song Meter SM2Bat+) with an omnidirectional ultrasonic SMX-US microphone (Wildlife Acoustics, Inc., USA) placed at a height of 1.5 m above the ground (López-Baucells *et al.*, 2019). Ultrasound recorders were positioned in the centre of the fragments, in the secondary forest 100 m away from the edge of each fragment, and in the interior of continuous forest 1000 m away from the edge. The recorders were configured to passively register bat activity in real time, with a full spectrum resolution of 16 bit, a high-pass filter set at fs/32 (12 kHz), and an adaptive trigger level relative to noise floor of 18 SNR. The SM2Bat units were programmed to record bat activity between 18:00 and 06:00 for four to five consecutive nights per sampling site (Table S1). Total sampling effort was 727 nights, with 8,278 recording hours. The number of sampling nights in each season was similar in fragments and secondary forest (Table S1). Although for continuous forest sampling effort was higher in the dry season (Table S1), we contend that the number of nights sampled in the rainy season (77 nights) was sufficient to avoid seasonal biases, and differences in sampling effort were also accommodated in the analysis.

All recordings were split into five-second segments and a bat pass was defined as a sequence with a minimum of two recognizable search phase calls per species in each five-

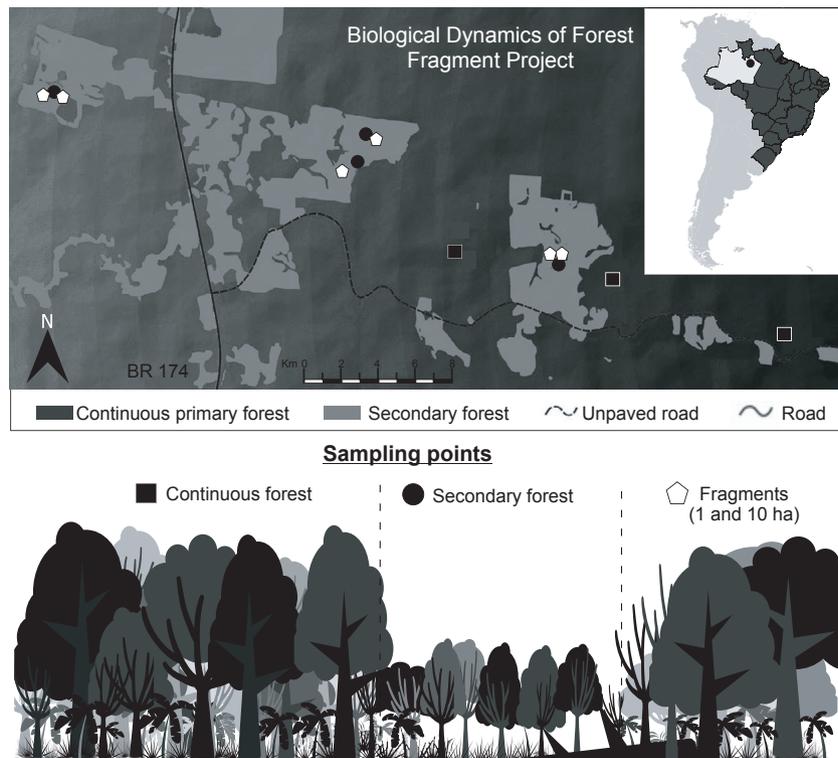


Figure 1 Location of the Biological Dynamics of Forest Fragments Project (BDFFP) and the distribution of sampling points in continuous forest, fragments of 1 and 10 ha, and secondary forest. Continuous forest is represented in dark grey and secondary forest (matrix) in light grey. The map in the upper right corner shows the location of the study area in the Central Amazon. The schematic figure illustrates the vegetation structure in the three habitat types

second segment (Appel *et al.*, 2019; Torrent *et al.*, 2018). All bat passes were manually identified to species or sonotype level following López-Baucells *et al.* (2016). We used Kaleidoscope Pro Software (version 4.0.4.) (Wildlife Acoustics, Inc. Maynard, Massachusetts, USA) for manual verification. Activity was calculated as the sum of five-second segments with bat passes per night (nightly activity) and per hour (hourly activity).

In the total of ~190,000 bat passes, we identified 18 aerial insectivorous bat species and four sonotypes. We minimized potential detection biases by focusing on species that were detected in at least 10% (73 nights) of the total nights and in all three sampling years. This resulted in the selection of nine species for analysis: *Pteronotus alitonus*, *P. rubiginosus* (revised by López-Baucells *et al.*, 2018; Pavan, Bobrowiec and Percequillo, 2018), *Furipterus horrens*, *Centronycteris maximiliani*, *Cormura brevirostris*, *Saccopteryx bilineata*, *S. leptura*, *Myotis riparius* and *Eptesicus brasiliensis* (Table S2).

Moonlight intensity

Moonlight intensity for each night was estimated using the “sunmoon” software (Kyba, Conrad and Shatwell, 2020), a robust method for quantifying the amount of sunlight reflected by the moon. This software employs the illuminance model of Janiczek & DeYoung (1987). To test whether bat activity varied between dark and bright nights, we classified those nights with 0–30% moon illuminated as dark and those with 70–100% as bright, following Appel *et al.* (2017, 2019). We used this broad categorization instead of the moon phase because moonlight intensity can vary greatly within the same moon phase (e.g. moonlight intensity in the waning phase can vary from 3% to 55%, Appel *et al.*, 2017). Indeed, we used this categorization because these nights are characterized by little variation in moon presence (during bright nights) and absence (during dark nights) in order to avoid the influence of moonrise and moonset times on bat activity (Appel *et al.*, 2017).

Cloud presence can influence the amount of moonlight that penetrates the forest, and thus potentially distort bat activity responses to moonlight. In order to test for an effect of cloud presence, we used data on cumulative rainfall per hour collected at the meteorological tower of the Large-scale Biosphere–Atmosphere Experiment in Amazonia (LBA) ZF-3 installed at KM 34 within the BDFFP. Nights were considered “cloudy” when rainfall ranged from 0.1 to 10 mm/h, generally classified as weak to moderate rain (Appel *et al.*, 2019; Vásquez *et al.*, 2020). Nights with more than 10 mm rain per hour were nights with heavy rain, therefore were removed from the analyses (Carvalho *et al.*, 2011).

Data analysis

To model the effects of habitat type (continuous forest, fragments and secondary forest) and moonlight on species-specific bat activity levels, we performed generalized linear mixed models (GLMMs) using the function `glmmTMB` from

the package “`glmmTMB`” (Bolker *et al.*, 2020). The response variable in the GLMM models was the number of bat passes recorded in a single night per species. Models were fitted using a negative binomial distribution and, whenever the respective activity distribution showed a signal of zero inflation, were implemented as zero-inflated models (Zuur *et al.*, 2009). For each model, habitat type was specified as categorical fixed effect and moonlight as a continuous fixed effect (percentage of moonlight intensity) and sampling night nested within research camp as a random effect. We chose to model moonlight intensity only jointly with habitat type because we were interested in evaluating the effect of moonlight for each habitat and not its independent effect. The aforementioned random effects structure was chosen to account for not only the spatial but also the temporal autocorrelation of the data – moonlight intensity of one night depends on the moonlight intensity of the previous night. To compensate for differences in sampling effort between habitat types (Table S2), we used the log-transformed sampling effort per habitat type as offset in all models. Parameter estimates were visualized using R package “`ggstatsplot`” (Patil, 2020). We used the full dataset of the 727 sampling nights in the GLMMs. To test if cloud presence affects bat activity, we performed GLMMs analysing bat activity in relation to moonlight, cloud presence and their interaction effect. There was no effect of cloud presence on the activity of any of the focal bat species (Table S3).

For each habitat type, differences in bat activity levels between dark and bright nights were visualized using Gardner–Altman estimation plots and statistically evaluated using non-parametric permutation tests with 1000 bootstrap samples to estimate effect sizes and 95% confidence intervals for the difference of means using R package “`dabestr`”. Statistical significance of the difference between dark and bright nights was determined based on the lack of overlap in the frequency distributions of the datasets (Ho *et al.*, 2019).

Hourly activity levels between dark and bright nights for each habitat type were compared using Kolmogorov–Smirnov 2-sample tests. Bat activity was pooled into 12 sampling intervals (hourly intervals) – for example, bat passes recorded between 18:00 and 18:59 were assigned to the same time interval (18:00). For comparisons between dark and bright nights, we used data from 206 nights in continuous forest (118 dark, 88 bright), 124 nights in fragments (65 dark, 59 bright) and 195 nights in secondary forest (97 dark, 98 bright). All analyses were conducted in softwares R 4.0.2 and R Studio 4.0.2 (R Core Team, 2020; RStudio Team, 2020).

Results

Bat activity responses to habitat type

Based on the GLMM results, habitat type had by far the greatest effect on bat activity. Most significant responses were observed for secondary forest, followed by fragments (Fig. 2). Six species (*S. bilineata*, *S. leptura*, *C. maximiliani*, *C. brevirostris*, *E. brasiliensis* and *F. horrens*) exhibited reduced activity in secondary forest, whereas *P. alitonus* and

P. rubiginosus showed elevated activity levels in this habitat (Fig. 2). On the other hand, two species (*P. alitonus* and *F. horrens*) had significantly lower activity in fragments than in continuous forest (Fig. 2).

Bat activity responses to habitat type and moonlight intensity

The activity of three species (*P. rubiginosus*, *S. bilineata* and *E. brasiliensis*) in fragments was negatively affected by moonlight as suggested by the significant interaction effect (Fig. 2). Similarly, moonlight significantly curtailed activity levels of *P. alitonus* and *P. rubiginosus* in secondary forest, albeit the effect was small (Fig. 2).

In relation to habitat-specific comparisons of activity between dark and bright nights, all species, except *S. leptura*, showed changes in activity between dark and bright nights in some habitat type (Fig. 3). In continuous forest, *P. rubiginosus* and *P. alitonus* were more active on bright nights, whereas *F. horrens* had greater activity during dark nights (Fig. 3). *Pteronotus rubiginosus*, *S. bilineata*, *C. maximiliani*, *C. brevirostris*, *M. riparius* and *E. brasiliensis* exhibited greater activity during dark than bright nights in fragments (Fig. 3). In secondary forest, only *P. alitonus* and *P. rubiginosus* showed greater activity on dark nights, opposite to the pattern in continuous forest (Fig. 3).

Hourly activity varied little between dark and bright nights and only five species exhibited some change in activity pattern between dark and bright nights in the same habitat (Table 2; Fig. S1). In continuous forest, *P. rubiginosus* and *S. leptura* were more active on bright nights. On the other hand, hourly activity of *C. maximiliani* and *F. horrens* steadily decreased on bright nights in continuous forest. In these two species, activity on dark nights increased at the end of the night. In fragments, *M. riparius*, *P. rubiginosus* and *C. maximiliani* increased their activity on dark nights, with greater activity in the middle of the night in the latter two species. In secondary forest, only *P. rubiginosus* showed significant differences, with an elevated activity during dark nights (Fig 4).

Discussion

Numerous studies have targeted the effects of forest fragmentation on tropical bats (Mendes and Srbek-Araujo, 2020; Meyer, Struebig and Willig, 2016). Yet, in the Neotropics, most research has been limited to the impacts of fragmentation on phyllostomid bats (e.g. Klingbeil and Willig, 2009; Rocha *et al.*, 2017b, 2018), and fragmentation effects on aerial insectivores remain poorly explored (but see Estrada-Villegas, Meyer and Kalko, 2010; Núñez *et al.*, 2019). Over the past two decades, intensive research at the BDFFP has provided valuable information about taxonomic, functional, phylogenetic and behavioural responses of bats to the dynamic nature of fragmented landscapes (e.g. Aninta *et al.*, 2019; Bobrowiec and Gribel, 2010; Farneda *et al.*, 2015; Rocha *et al.*, 2018, 2020; Silva *et al.*, 2020). Although less researched than their phyllostomid counterparts, aerial

insectivorous bats at the BDFFP were found to exhibit trait-related responses to fragmentation, with understory and constant-frequency and frequency-modulated echolocating bats being particularly vulnerable to forest disturbance (Núñez *et al.*, 2019). Here, we further advance current understanding about the responses of aerial insectivorous bats to fragmentation, by analysing how temporal activity patterns of this bat ensemble are molded by variation in moonlight intensity. As hypothesized, we found that moonlight can modulate responses to habitat disturbance but only in extremely bright nights. Importantly, a joint effect of moonlight and habitat disturbance was most evident only in species that emit constant-frequency calls (*Pteronotus* spp.).

Our results show that Amazonian aerial insectivorous bats respond more to habitat type than to the interaction between habitat and moonlight. Most species had lower activity in secondary forest and two showed lower activity in fragments compared to continuous forest. This suggests that despite *c.* 30 years of secondary forest regeneration, secondary forest is still less attractive as foraging habitat for most aerial insectivorous bat species. These results are consistent with those commonly reported for gleaner animalivorous bats, whose capture rates typically decrease in disturbed habitats (Rocha *et al.*, 2017b; Webala *et al.*, 2019; Willig *et al.*, 2019), probably due to being poorer foraging and roosting areas (Carballo-Morales, Saldaña-Vásquez and Villalobos, 2021; Meyer and Kalko, 2008). Yet, they contrast with results from nectarivorous and frugivorous bats, which normally increase in abundance in fragments and in secondary forest due to the higher density of food resources (Bobrowiec and Gribel, 2010; Farneda *et al.*, 2015).

The effect of moonlight on activity differed between habitat types for *P. alitonus*, *P. rubiginosus*, *S. bilineata* and *E. brasiliensis*. These four species exhibit a flexible behaviour, changing their activity in disturbed environments when light conditions are not favourable. The interaction between fragmentation and moonlight shows that for some species the effects of fragmentation can be more acute than expected, since at least during part of the lunar cycle their activity in fragments may be suppressed.

Bat activity over the lunar cycle is shaped by predator-prey interactions, as aerial insectivorous bats are simultaneously predators and prey (Lang *et al.*, 2006; Vásquez, Grez and Pedro, 2020). *Pteronotus rubiginosus* and *P. alitonus* increase their activity with moonlight in continuous forest probably due to higher foraging success, as some insect orders increase their activity in nights of high moon illumination (Kolkert *et al.*, 2020). The observed lunar philia of *P. rubiginosus* agrees with the pattern found in other areas of Amazonian continuous forest (Appel *et al.*, 2017; Durán and Oviedo Morales, 2019). On the other hand, the observed decrease in the activity of *Pteronotus* spp. with increasing moonlight indicates that in disturbed areas the perceived risk of predation is probably greater. These bats may avoid leaving fragments as some visually oriented avian predators forage preferentially along fragment edges and open areas (Chalfoun, Thompson and Ratnaswamy, 2002; Spanhove *et al.*, 2009).

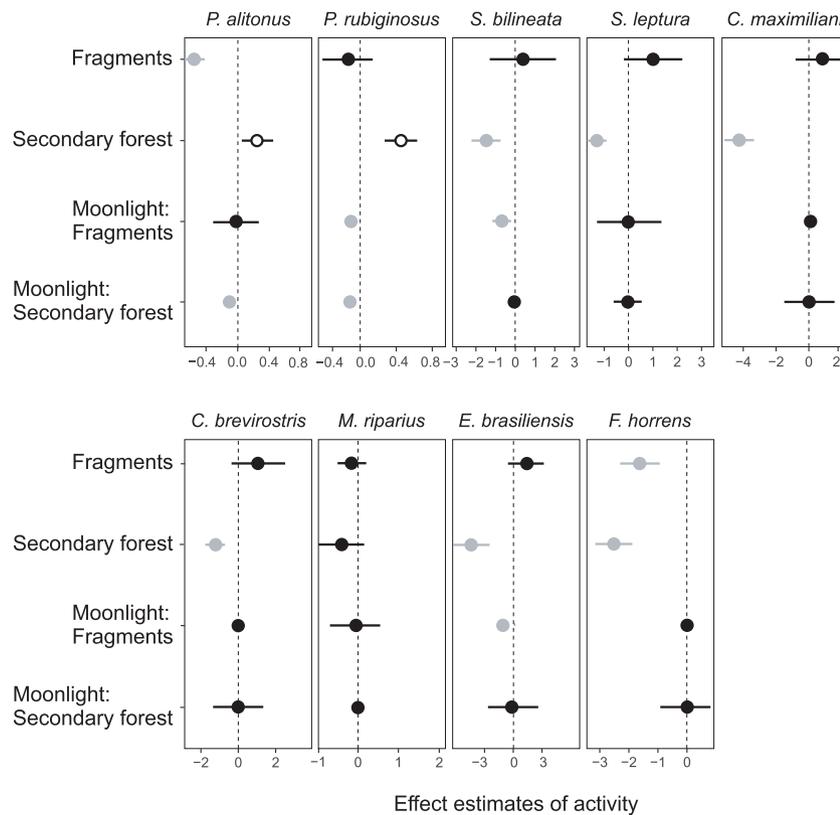


Figure 2 Effects of moonlight, habitat type and their interaction on activity of the nine focal species in the BDFP evaluated using generalized linear mixed models. Effect estimates are based on the fixed effect posterior distribution, characterized by its mean (dot) and credible intervals (95% CI, lines). Grey circle estimates indicate significant negative effects, white circle estimates significant positive effects and black estimates non-significant effects

Although the interactive effect of moonlight and habitat type on bat activity was weak, our analyses showed that the effects of habitat type were most evident when evaluated at the extremes of the lunar cycle (dark vs. bright nights). In fragments, the activity of six species decreased on very bright nights, whereas, with the exception of *P. alitonus* and *P. rubiginosus* (which showed greater activity on bright nights in continuous forest), it was unaltered in continuous forest. The home ranges of aerial insectivorous bats (e.g. *P. parnelli* and *S. bilineata*) are generally much greater than the size of fragments studied (≤ 10 ha; Bradbury and Vehrencamp, 1976; Estrada, Coates-Estrada, and Meritt, 1993; Hoffmann *et al.*, 2007). As such, bats inhabiting forest fragments might need to forage/commute in the surrounding matrix, which on brighter nights, may increase exposure to predators. This increase in predation risk may therefore reduce bat activity in small fragments during nights with more intense moonlight (Bowers and Dooley, 1993). Thus, on bright nights probably bats reduced their home range avoiding the edges of the fragments, specially *Peronotus* spp., since they are less active in secondary forest on bright nights.

The two extremes of the lunar cycle, bright vs. dark nights, had little effect on hourly activity levels indicating that bats do not respond to changes in moonlight during short periods of

time. Yet, two species had higher hourly activity on bright nights in continuous forest and two species were more active at the end of dark nights. However, in fragments, hourly activity only changed for three species, all exhibiting lower activity at dusk on bright nights, which might be a strategy to reduce predation risks (Appel *et al.*, 2017). A similar result was found for phyllostomids in early successional forest, small agricultural fields and forest subjected to reduced-impact logging in the Amazon (Castro-Arellano *et al.*, 2009; Presley *et al.*, 2009). *Cormura brevirostris* and *S. bilineata* did not change the hourly activity between the extremes of brightness. This may relate with their foraging strategies (Gomes, Appel and Barber, 2020), as both species have been suggested to feed closer to vegetation in brighter nights (Jung and Kalko, 2010). The apparent absence of a moon effect on hourly activity of insectivorous bats was also found by Appel *et al.*, (2017) in a continuous forest location in Central Amazonia and by Thomas and Jacobs (2013) in South Africa.

Our results show that moonlight is an abiotic variable that can modulate bat activity levels in tropical human-altered landscapes, but for most aerial insectivorous species the effect is either weak or absent, and responses are more evident only in extremely bright nights in fragments. Species that emit constant frequency calls such as *P.*

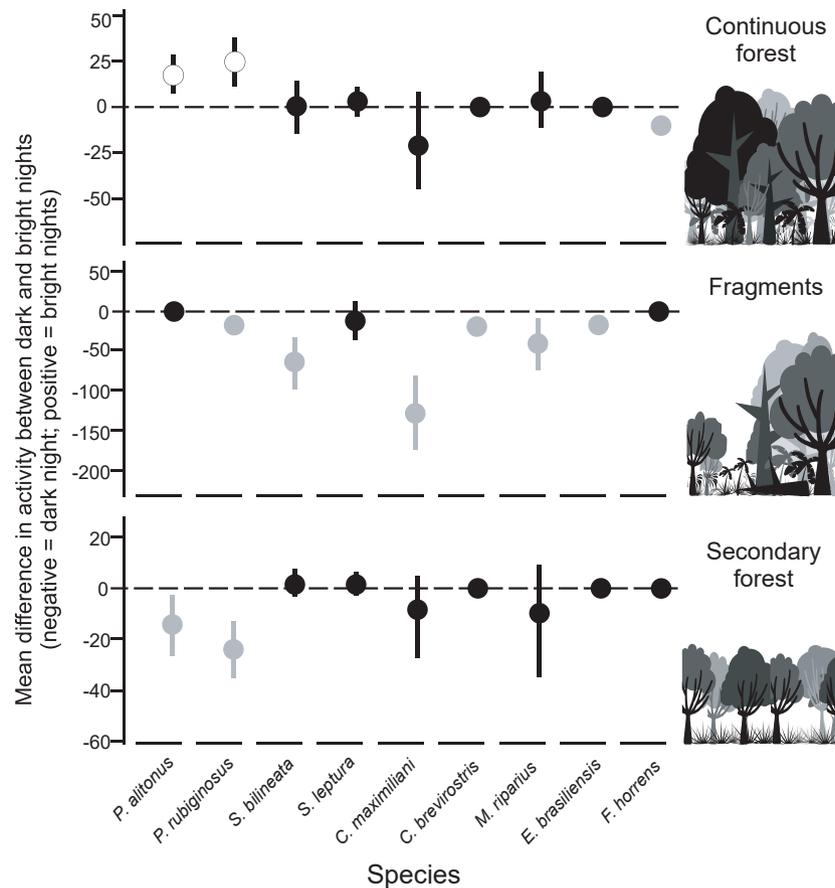


Figure 3 Gardner–Altman estimation plots showing the effect size (mean difference) of bat activity between dark and bright nights in each type of forest - continuous, fragments and secondary forest at the BDFPP. Dark nights were considered those with between 0 and 30% moonlight intensity and bright nights those above 70%. The mean is indicated by a dot, error bars represent the 95% confidence interval. Grey circle estimates indicate significant negative effects (higher activity on dark nights), white circle estimates significant positive effects (higher activity on bright nights) and black estimates non-significant effects

rubiginosus and *P. alitonus* showed the strongest response in activity levels as manifested by a change from a positive relationship with moonlight in continuous forest to a negative one in fragments and secondary forest. Therefore, moonlight can augment the effects of fragmentation on the activity of bats that echolocate using constant frequency calls. This is concerning because habitat disturbance might reduce the temporal window in which foraging conditions are favourable and thus limit the ability of species to meet their daily dietary requirements (Castro-Arellano *et al.*, 2009; Rocha *et al.*, 2020; Vásquez, 1994). This physiological stress may increase exposition to pathogens (Turmelle and Olival, 2009), and there are several examples of how anthropogenic land-use change can have a major impact on the infection and circulation of zoonoses (Gibb *et al.*, 2020; White and Razgour, 2020). Future research investigating how behavioural responses translate into fitness consequences (e.g. mortality and reproductive success) in fragmented landscapes is needed to better understand long-term population persistence.

Conservation implications

Fragmentation and forest disturbance have been identified as the major causes of biodiversity loss in the tropics. Some of the insectivorous bat species studied here are fragmentation-sensitive (Núñez *et al.* 2019). In our study, habitat disturbance was the main factor underlying decreases in the activity of aerial insectivorous bats, but moonlight accentuated reductions in activity for some species in fragments and might impact their capacity to provide their crucial ecosystem services as insect predators. Insectivorous bats are key suppressors of herbivorous insects in both humanized and natural habitats and they can prevent rice loss at an estimated cost of \$1.2 million/year and more than \$3.7 billion/year in general agricultural losses (Boyles *et al.*, 2011; Kemp *et al.*, 2019; Wanger *et al.*, 2014). However, it is important to mention that the BDFPP fragments are surrounded by secondary forest at an advanced stage of succession, which can buffer the impacts of fragmentation and create better foraging conditions for aerial insectivorous bats than in other

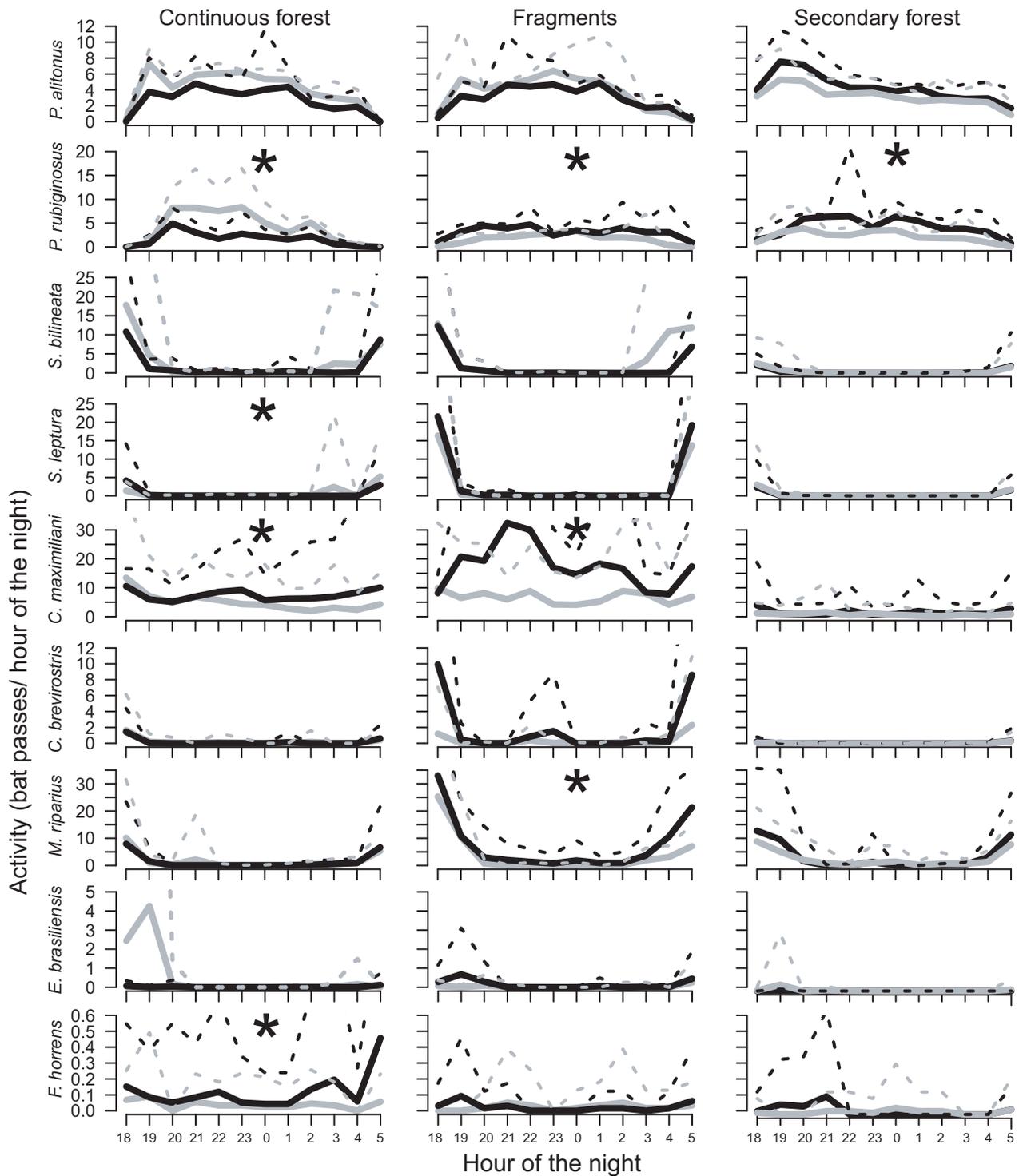


Figure 4 Hourly activity of nine species of aerial insectivorous bat in each habitat type (continuous forest, fragments and secondary forest) on dark nights (0-30% of moonlight intensity) and bright nights (70-100% of moonlight intensity). Black lines denote dark nights, grey lines bright nights. The solid line is the average activity and the dotted line represents the standard deviation of activity. * indicates a significant difference between dark and bright nights based on Kolmogorov–Smirnov 2-sample tests

human-modified landscapes (Rodríguez-San Pedro and Simonetti, 2015). Fragments in landscapes dominated by large-scale agriculture commonly exhibit abrupt margins, are embedded within a homogeneous matrix and suffer additional anthropogenic disturbances (e.g. effects of roads and artificial illumination) which may considerably reduce the ecological services provided by light-sensitive bat species (Put, Fahrig and Mitchell, 2019).

Artificial light at night has been increasing over time in biodiversity hotspots (Guetté *et al.*, 2018) and this is concerning because the increasing human pressure in the periphery of forested areas can leave forest fragments in a state of constant illumination during the night. Although artificial light attracts insects consumed by insectivorous bats, some bat species studied here are sensitive to urbanization (Alpizar, Rodríguez-Herrera, and Jung, 2019; Jung and Kalko, 2010). It is known that lit areas can influence the quality of roosts and fragment commuting routes for some bat species with negative consequences for the reproduction and behaviour of bats (Downs *et al.*, 2003; Laforge *et al.*, 2019; Straka *et al.*, 2019). In view of the recent increase of fragmentation and artificial light at night in the Brazilian Amazon due the development of cities, agricultural areas and expanding road networks (Haddad *et al.*, 2015; Lovejoy and Nobre, 2018; Vilela *et al.*, 2020), the protection of undisturbed forests is crucial for the conservation of light-sensitive aerial insectivorous bats. Moreover, bats actively prey on mosquitoes responsible for disease transmission (Puig-Montserrat *et al.*, 2020) and as tropical urban areas have a proliferation of these insects, the promotion of large forest fragments in urban areas can be an alternative to attract more activity of insectivorous bats.

Acknowledgements

We would like to thank the field assistants and volunteers that participated in data collection, as well as the Biological Dynamics of Forest Fragments Project (BDFFP), specially José Luis Camargo, Rosely Hipólito and Ary Jorge Ferreira for logistical support. We would like to thank Jeff Conrad, who allowed us to use the Sunmoon program. GA was supported by a Coordenação de Aperfeiçoamento Pessoal Nível Superior (CAPES) scholarship (Finance code 1) and Sandwich fellowship CAPES Process (PDSE) (88881.362190/2019-0). PEDB was supported by a postdoctoral scholarship from PNP/CAPES (88887.370067/2019-00). CFJM (PTDC/BIA-BIC/111184/2009), RR (SFRH/BD/80488/2011) and ALB (PD/BD/52597/2014) acknowledge funding from the Portuguese Foundation for Science and Technology (FCT) and RR was also supported by an ARDITI – Madeira's Regional Agency for the Development of Research, Technology and Innovation Fellowship (M1420-09-5369-FSE-000002). Data collection was conducted under permit 26877-2 issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/Brazil). Additional funding was provided by Bat Conservation International to ALB and RR. We would like to thank the LBA Program (Large-scale Biosphere–Atmosphere Experiment in Amazonia) for providing

weather data. We also thank the two anonymous reviewers and the Senior Editor Karl Evans and Associate Editor Elina Rantanen that helped us improve our manuscript with valuable comments. This is publication 813 in the Technical Series of the BDFFP.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Number of hours recorded in each habitat type and each season sampled.

Table S2. Number of bat passes recorded for the nine aerial-insectivorous bat species studied.

Table S3. Summary of GLMMs examining the influence of cloud presence, moonlight and their interaction on bat activity.

Table S4. Number of bat passes in dark and bright nights for the nine aerial-insectivorous bat species studied.

Table S5. Summary of GLMMs examining the influence of habitat type and the interaction between moonlight and habitat type on bat activity.

Table S6. Results of Kolmogorov–Smirnov 2-sample tests comparing the hourly activity between dark and bright nights in each habitat type sampled.