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ORIGINAL RESEARCH

The importance of lakes for bat conservation in Amazonian rainforests: an assessment using autonomous recorders

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Keywords
Acoustic sampling, aerial insectivorous bats, Amazon, climate change, passive acoustic monitoring, tropical lakes

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Abstract

Recent studies predict a future decrease in precipitation across the tropics, particularly the Amazon, likely causing significant droughts that have negative consequences for Amazonian freshwater biomes, especially lakes. Furthermore, immediate consequences of global warming for terrestrial fauna associated with tropical lakes are poorly understood as the vast majority of studies come from temperate regions. Here, we assess the seasonal importance of lakes for the conservation of aerial insectivorous bats in the Central Amazon using passive bat recorders. We compared richness, general bat activity and foraging activity between lakes and adjacent forest. Of a total of 21 species/sonotypes recorded in both habitats, all were detected over lakes, and 18 were significantly more active over lakes than in forest. Only two species had significantly higher activity levels in the forest than at the lakes. Species richness and general bat activity over the lakes were higher in the dry than in the rainy season. Foraging activity was also greater over the lakes than within the forest in both seasons. Moreover, both variables were positively correlated with lake size, although the effect on activity was species-specific. Climate change-driven shrinking of lakes may have detrimental consequences for aerial insectivorous bats, especially for the most water-dependent species. Compared to permanent water bodies of other regions, the value of tropical lakes for functionally important taxa, such as bats, has been understudied. Higher bat activity levels over lakes than in forest in both seasons and comprising the whole ensemble of aerial insectivorous bats of the study region, indicate that lakes embedded in Amazonian terra firme forests deserve special attention for future bat conservation.

Introduction

The Amazon Basin, comprising 6.9 million km^2 of watershed (Macedo and Castello 2015), harbors both the Earth's largest river drainage system and largest contiguous area of rainforest. Throughout the Amazon Basin, lakes usually occur in areas that are seasonally flooded and are formed of two main elements: a body of open water that varies seasonally in extent and an area of inundated vegetation (Melack and Coe 2013). Upland forests (*terra firme*) cover an area of about 50% of the whole Amazonian wetland in the basin (Junk and Piedade 2010) and although they do not get flooded as other regions, streams and lakes are also present. Amazonian lakes face a series of threats due to (1) lack of agreement on their classification and management; (2) dam construction; (3) land-cover change; and (4) anthropogenic climate change (Melack and Coe 2013; Jiménez-Cisneros et al. 2014; Castello and Macedo 2016; Salvarina 2016).

Predicted temperature increases due to climate change are usually considered to be less important in the tropics than in boreal (Sala et al. 2000; Solomon 2007), arid (Root et al. 2003; Parmesan 2007) or temperate regions (Sala et al. 2000; Root et al. 2003). Tropical ecosystems are interannually influenced by El Niño events (Trenberth and Hoar 1996) which cause extreme climate variability in the form of floods and droughts (Williams et al. 2005; Marengo et al. 2013). Therefore, due to these marked, recurring fluctuations, it is generally accepted that within a safe threshold, tropical ecosystems will be less sensitive to future climatic changes than those at higher latitudes (Collins et al. 2013; IPCC, 2014). However, for the Neotropics, some climate models predict a decrease in precipitation and harsher droughts during the dry season (Beaumont et al. 2011; Marengo and Espinoza 2016), especially in the eastern and southern Amazon Basin (e.g. Shiogama et al. 2011; Staal et al. 2016; Aragão et al. 2018). This decrease in precipitation might have severe consequences for species that rely on lakes to fulfill their life cycles, especially during the dry season.

The vast majority of studies related to lakes and their associated fauna come from temperate habitats in Europe (Zacharias et al. 2007), Australia (Warwick and Brock 2003), Western USA (Kneitel and Lessin 2010) and South and North Africa (Rhazi et al. 2006, 2009). For Amazonia, studies on lakes have focused on those in floodplain forests and mainly targeted phytoplankton and fish (e.g. De Melo and Huszar 2000; Chellappa et al. 2005; Pazin et al. 2006; Moresco et al. 2017). Several studies have been conducted on a variety of taxa (e.g. birds and mammals) in flooded Amazonian forests (e.g. Haugaasen and Peres 2007, 2008; Beja et al. 2010), indicating for instance that the availability of water attracts more fauna than fruit presence (Paredes et al. 2017). For bats, Pereira et al. (2009) documented a large number of species associated with seasonally flooded forests, emphasizing the importance of this habitat for insectivorous bats. Almeida et al. (2014) demonstrated that open grassland habitat with scattered fruit trees with a water reservoir from a river dam had greater presence of insectivorous bats than open habitats without water in southeastern Brazil. Little is known about the abundance and distribution of lakes in unflooded *terra firme* forest (Sioli 2012) and no study yet has assessed the ecological importance of such lakes for aerial insectivorous bats.

Freshwater bodies are essential for many bat species as they provide appropriate habitat for drinking and foraging (Seibold et al. 2013; Korine et al. 2016; Russo et al. 2017) as well as important habitats during their reproductive cycles (Mclean and Speakman 1999; Adams and Thibault 2006; Adams and Hayes 2008; Cisneros et al. 2015). Hence, a reduction in the number of lakes as a result of climate change might have potentially severe consequences for those bat species that depend on them.

The overarching aim of this study was to use bioacoustics to identify the ecological role of lakes for aerial insectivorous bats in Central Amazonian *terra firm*e rainforest and to establish whether their importance varies seasonally. Our specific objectives were to: (1) compare species richness, general bat activity and foraging activity between habitat types (forest and lakes) and between seasons (dry and rainy); (2) determine the influence of lake size on species richness and general bat activity; and (3) quantify differences in species-specific activity levels between habitats and seasons. We predicted higher levels of richness, general bat activity and foraging activity at lakes than in forest because, based on existing bibliography from other regions, bats commute to the former to drink and forage. Moreover, we expected richness and general bat activity to be higher at lakes during the dry months due to the lower water availability within the forest. Regarding our second objective, we predicted greater activity and species richness over larger lakes than small ones because, aside from providing more food resources, the former are structurally less complex habitats (open areas without overhanging foliage) and thus are also accessible to less maneuverable species. Thirdly, we hypothesized that although all species would be present at the lakes at least to drink, some species would forage more often in the forest (i.e. mormoopid bats), while others (molossid, emballonurid and vespertilionid bats), given their morphological adaptations for foraging in open habitats, would be more frequently recorded at the lakes.

Materials and Methods

Study area

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), 80 km north of Manaus, in the Brazilian Amazon (Fig. S1). The area encompasses approximately 1000 km^2 of primary and secondary unflooded upland (*terra firme*) rainforest surrounding forest fragments that were isolated between 1980 and 1984 (Marengo et al. 2013; Rocha et al. 2017a; Laurance et al. 2018). Average annual temperature is 25.8°C and there is a well-defined dry season from June to October when precipitation drops below 100 mm/month and a rainy season from November to May when precipitation can exceed 300 mm/month (Kunert et al. 2015, 2017; Ferreira et al. 2017). The topography of the surveyed terrain and its surroundings is relatively flat, divided by many small streams. Large rivers are almost absent; however, there are permanent lakes whose water level fluctuates seasonally (Laurance et al. 2018). The primary forest canopy is between 30 and 37 m tall, with emergent trees reaching up to 55 m. For a more detailed description of the study area, see Laurance et al. (2018).

Acoustic surveys

Bats were sampled at seven sites in primary forest (continuous forest and 100 ha forest fragments: *Forest 1* to *Forest 7*), located in the reserves Cabo Frio, Dimona, Porto Alegre and Km 41, and at eight adjacent lakes, one in Dimona (*Lake 1*), two in Porto Alegre (*Lake 2* and *3*), one close to the main BDFFP road (*Lake 4*), one in Colosso (*Lake 5*), and three in Km 41 (*Lakes 6*, *7* and *8*) (Figs. S1 and S2 and Table 1). Forest sites were selected based on their proximity to the known lakes in the study area. At each forest site, a passive bat recorder (Song Meter SM2Bat+) with an omnidirectional ultrasonic SMX-US microphone (Wildlife Acoustics, In. Maynard, Massachusetts, USA) was attached to the branches or the trunk of a tree at 1–2 m height, pointing in the direction with least vegetation clutter. At the lakes, the recorders were set at their shores, at the same height, attached to the branches or trunks of trees, with the microphone facing the center of the water body. During each sampling session, the detectors were programmed to continuously record from 18:00 h to 06:00 h, for a period of three consecutive nights. Recordings were made in real time, with a full spectrum (fs) resolution of 16-bit, a high-pass filter set at fs/32 (12 kHz) and a trigger level of 18 signal to noise ratio. Each site was sampled twice per season and acoustic surveys were conducted during the dry season (August to October) of 2013 and the rainy season (March to May) of 2014. The total number of nights surveyed was 72 for the lakes and 79 for the forest sites as we had to discard some of the data when the detectors only recorded during half of the night due to technical problems or intense rain.

Bioacoustic analysis

We defined our sample unit as a ‘bat pass’ – a sequence with a minimum of two recognizable echolocation pulses per species emitted by a flying bat within a 5-sec sound

Table 1. General information about the lakes surveyed, including the oscillation of the water level between the rainy and dry seasons, at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil.

Site	Reserve	Size: rainy season (m^2)	Size: dry season (m^2)	Geographical coordinates
Lake 1	Dimona	~200	~200	−2.3398381°, −60.1016720°
Lake 2	Porto Alegre	~2500	~400	−2.3574670°, −59.9593178°
Lake 3	Porto Alegre	~2300	~1300	−2.3851464°, −59.9841295°
Lake 4	Km 21	~9600	~9600	−2.4051716°, −59.9704628°
Lake 5	Colosso	~2100	~440	−2.4109754°, −59.8690231°
Lake 6	Km 41	~2900	~860	−2.4305276°, −59.7741627°
Lake 7	Km 41	~60	~60	−2.4492385°, −59.7701420°
Lake 8	Km 41	~9700	~2400	−2.4476869°, −59.7505882°
Forest 1	Cabo Frio	–	–	−2.380979°, −59.928022°
Forest 2	Cabo Frio	–	–	−2.399757°, −59.900202°
Forest 3	Cabo Frio	–	–	−2.416985°, −59.926773°
Forest 4	Km 41	–	–	−2.416634°, −59.780269°
Forest 5	Km 41	–	–	−2.427005°, −59.749305°
Forest 6	Porto Alegre	–	–	−2.363252°, −59.975384°
Forest 7	Dimona	–	–	−2.343255°, −60.095072°

file (Azam et al. 2015; Millon et al. 2015) – which was used as a surrogate of activity levels. Species-specific activity was quantified as the number of bat passes per night recorded for each species and total activity as the sum of all bat passes per night. We also quantified foraging activity as the number of feeding buzzes detected per species (Kalko and Schnitzler 1989).

We used Kaleidoscope Pro Software (version 4.0.4.) (Wildlife Acoustics, Inc. Maynard, Massachusetts, USA) to analyze and classify the recordings. Call sequences were manually identified to species level or left as mixed-species groups, that is, sonotypes, when it was not possible to clearly assign a call to a particular species (Table S1). Classification was undertaken following López-Baucells et al. (2016), and by comparing our recordings with a local reference call library compiled in the same study area during 2011–2014. Species were manually identified based on a series of acoustic features and standard measurements: call shape, frequency of maximum energy (FME), start, end, maximum and minimum frequency, and call duration. If call sequences or pulses were too faint (<10 dB difference from the background noise) to obtain the information needed for reliable species identification they were discarded. Our analysis thus included a total of 21 sonotypes from the families *Emballonuridae*, *Furipteridae*, *Molossidae*, *Mormoopidae* and *Vespertilionidae* of which 14 were classified to species level, whereas seven sonotypes grouped several species (Table S1).

Statistical analysis

To assess the effect of habitat type (lakes vs. forest) and season (dry vs. rainy) on richness, total activity and foraging activity, we used Generalized Linear Mixed-effects Models (GLMMs) with a Poisson distribution, fitted in a Bayesian framework using Markov Chain Monte Carlo analysis (MCMC). Response variables in the GLMMs were richness (total number of sonotypes registered in a single night), bat activity (number of bat passes registered in a single night in total and per species) and foraging activity (number of feeding buzzes registered in a single night in total). Habitat type and season were used as fixed factors and reserve (Dimona, Porto Alegre, Km 21, Km 41, Colosso and Cabo Frio) was included as a random factor. We also included the interaction between both fixed-effect variables. Modeling was performed with the 'MCMCglmm' R package (Hadfield 2010), with default priors for the fixed effects (zero mean, high variance). Interaction effects were plotted with the 'effects' package (Fox 2003).

Lake sizes were estimated measuring their water surface areas with Google Earth. As the size of the lakes did not vary continuously (Table 1), we grouped them into three categories: 'Small' (<200 m^2); 'Medium' (2000–3000 m^2); and 'Large' (>9000 m^2). GLMMs were also used to analyze the effect of lake size (fixed effect) on richness and total bat activity. For this particular analysis, species from the family Molossidae were excluded as they are known to not forage in cluttered environments and over small lakes (Mora et al. 2004; Kalko et al. 2008a,b). All plots were built using the package 'ggplot2' in R (Wickham 2009) and all statistical analyses were performed with R version 3.3.2 for Windows (R Core-Team 2015).

Results

From a total of 290 899 sound files, we identified 353 099 bat passes and 69 454 feeding buzzes (Table S1). Although all 21 sonotypes were recorded at the lakes, only 15 were detected in the forest (Fig. 1). Specifically, only *Pteronotus* sp1, *Pteronotus rubiginosus* and *Furipterus horrens* were more often recorded in forest than at lakes (Fig. 1).

Effect of habitat type and season on aerial insectivorous bats

Richness, total activity and foraging activity

Species richness, total activity and the number of feeding buzzes were significantly higher at lakes than in forest sites ($P < 0.05$) (Fig. 2a and Table S2). In fact, habitat had a stronger effect than season for all response variables (Fig. 2b). Total bat activity and foraging activity were generally three and four times, respectively, higher over lakes than in forest sites, while richness was ca. 0.8 times greater over lakes than in forest (Fig. 2). Season and its interaction with habitat only had a significant effect on richness. While at the lakes richness increased during the dry season compared with the rainy season, in primary forest richness was higher in the rainy than in the dry season (Fig. 3).

Species-specific responses to habitat type and season

Only *Furipterus horrens* and *Pteronotus* sp1 had significantly higher activity levels in forest, whereas all other sonotypes, with the exception of *P. rubiginosus*, were detected significantly more often at lakes than in forest (Fig. 4 and Table S3). Thirty-five percent of sonotypes showed significant differences in activity levels depending on the season between lakes and forest. While the activity of *Centronycteris maximiliani*, *Peropteryx kappleri* and

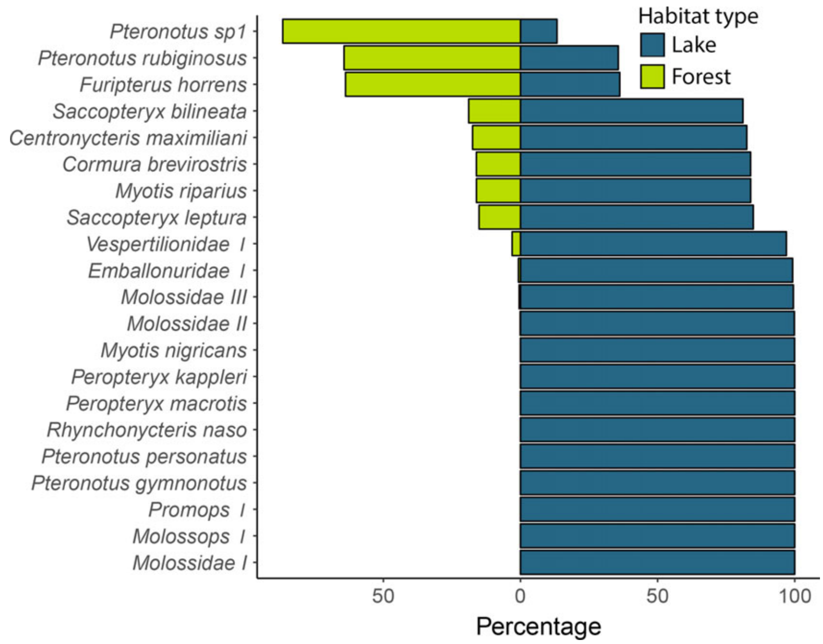

Figure 1. Percentage of bat species occurrence at eight lakes and in seven primary forest sites at the Biological Dynamics of Forest Fragments Project, Central Amazon.

Vespertilionidae I in the forest showed a significant peak in the rainy season, it remained almost constant along the year at the lakes (Figs. S4 and S7). The activity of *Myotis nigricans*, *Molossops I* and *Promops I* in the rainy season significantly increased at the lakes, and simultaneously decreased in forests (Figs. S5 and S7). *Pteronotus rubiginosus* and *Molossidae III* showed lower activity in the rainy season in both habitats, but more markedly so at the lakes (Figs. S5, S6 and Table S3).

Effect of lake size

Both richness and total activity scaled significantly and positively with lake size (Fig. 5 and Table S4). The variance associated with the reserve was minimal, and thus, its effect on the differences between lake size negligible (Table S2 and Table S5). *Myotis nigricans* and *Furipterus horrens* were detected significantly more often over large lakes than medium and small ones (Table S6). Others (*Rhynchonycteris naso, Saccopteryx bilineata*, *Emballonuridae I, Peropteryx kappleri*, *Peropteryx macrotis*) had greatest activity at both medium-sized and large lakes. In contrast, *Centronycteris maximiliani*, *Pteronotus rubiginosus*, *Pteronotus* sp1 and *Myotis riparius* were detected significantly more at the small than the large lakes (Fig. S3 and Table S6). Activity levels for *Cormura brevirostris*, *Pteronotus gymnonotus* and *Pteronotus personatus* did not vary among lake size categories (Fig. S3 and Table S6).

Discussion

As predicted, richness, general bat activity and foraging activity were significantly higher over lakes than in forest, especially during the dry season. This highlights the fundamental importance of lakes as key foraging habitat for aerial insectivorous bats and consequently for their conservation in Amazonian *terra firme* forests. As expected, all 21 species/sonotypes identified in the study area were detected over the lakes (either while foraging, drinking or commuting), whereas none was exclusively found in the forest. In fact, only two species were detected significantly more in forest than at the lakes, supporting the hypothesis that most of the species might at least to some extent be dependent on lakes and that their long-term persistence in *terra firme* forest thus might be strongly linked to the future of these aquatic habitats. Additionally, our results confirmed that sonotype richness and general bat activity were positively correlated with lake size.

Effect of habitat, season and lake size on richness and total activity

The lakes sampled had higher richness compared to the adjacent forests, including both open-space foragers and strict forest-dwelling species that were recorded while foraging. Pereira et al. (2009) undertook a similar study in Amazonian flooded forest and found that aerial insectivorous bats were more abundant in seasonally inundated

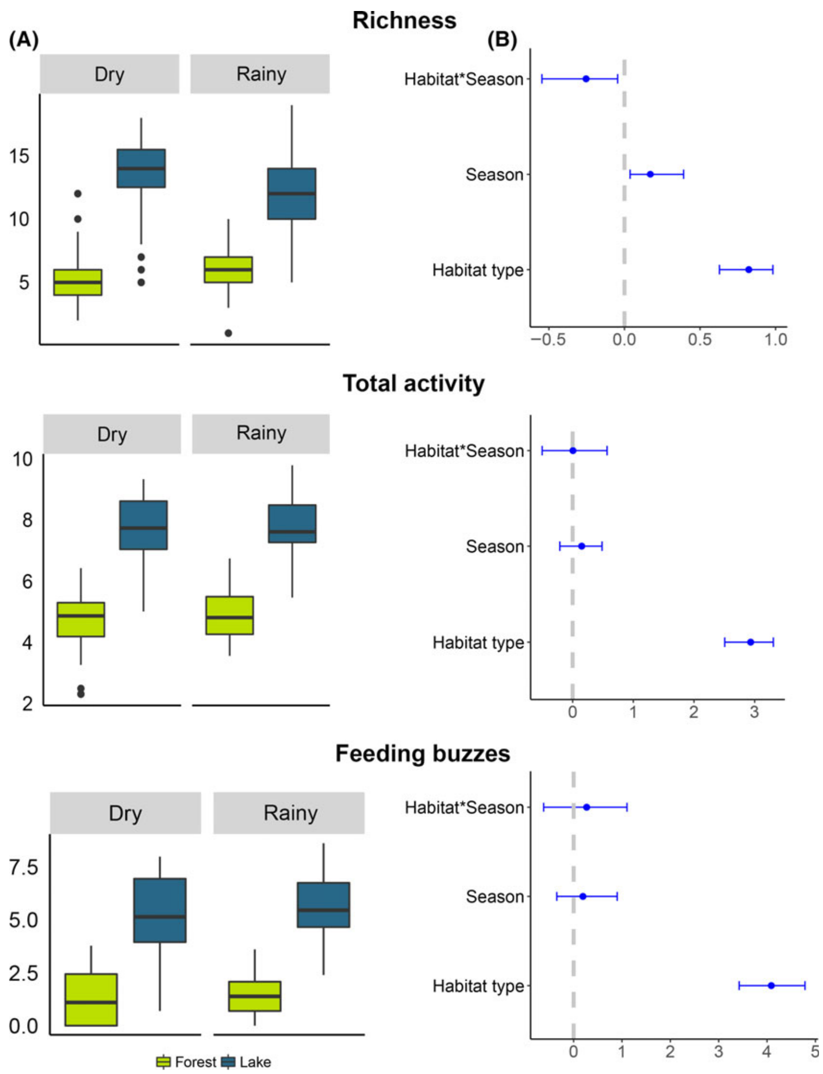

Figure 2. (A) Richness, total bat activity and feeding buzzes per night in primary forest and at lakes for each season at the Biological Dynamics of Forest Fragments Project, Central Amazon. (B) Parameter estimates of the fixed effects habitat type and season as well as their interaction.

than in *terra firme* forest. During both seasons, the total number of feeding buzzes recorded in our study was four times higher over the lakes than within the forest (Fig. 2). This adds to previous evidence that most Neotropical aerial insectivorous bats actively forage over water bodies (MacSwiney et al. 2009; Costa et al. 2012; Staal et al. 2016). In general, riparian habitats and water bodies in the tropics are characterized by higher insect abundances than dense forests (Fukui et al. 2006; Chan et al. 2008; Hagen and Sabo 2011), especially during the rainy season (Dudgeon 1997; Chan et al. 2008). However, as lakes do not provide as much vegetation cover as forests during moonlit nights, they also expose bats to increased risk of predation (Appel et al. 2017). Therefore, higher richness in forest during the rainy season than during the driest months suggests that some species (probably strict forest-dwelling bats) might not need to commute to the lakes if enough resources are available within the forest. In contrast, richness at the lakes was higher during the dry than the rainy season, probably because some species were forced to commute to the lakes for drinking due to the lack of smaller water sources within the forest. Activity levels of some Neotropical bat species vary seasonally in response to higher energetic requirements associated with pregnancy and lactation in females (Cisneros et al. 2015; Rocha et al. 2017b). Greater abundance of insects over lakes might offer better foraging opportunities to female bats during their reproductive season. However, lack of phenological data for the species included in this study and the impossibility to disentangle males and females based on acoustic data precludes a sex-specific analysis in relation to reproductive patterns.

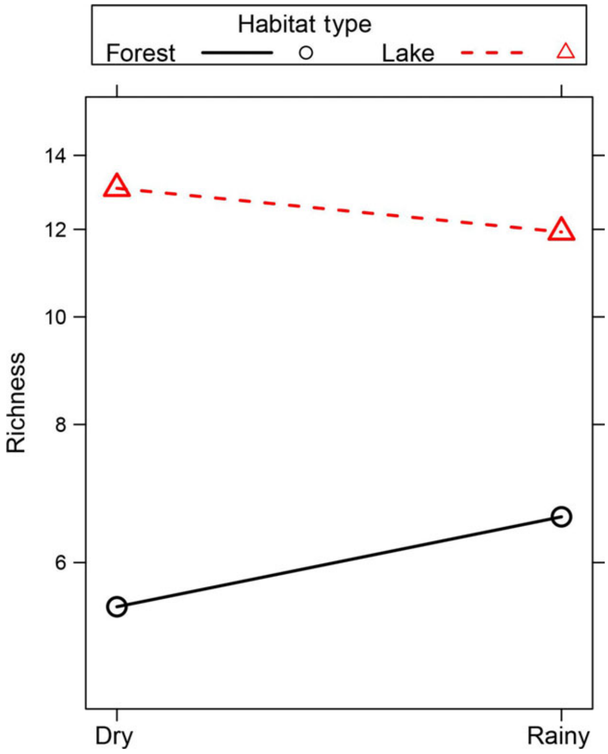

Figure 3. Interaction plot illustrating the inter-dependence of habitat type (forest and lake) and season (dry and rainy) in determining richness of aerial insectivorous bats at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil.

The lakes sampled during this study were less encroached by overhanging vegetation than other aquatic habitat associated with rainforests, such as streams or small ponds. Less overhanging vegetation allows less maneuverable species, such as molossid bats, to use these lakes for drinking and foraging, giving them enough space to maneuver, despite their wing morphology (Greif and Siemers 2010). Species-specific bat activity levels are greatly influenced by habitat complexity (Sleep and Brigham 2003; Farneda et al. 2015). When foraging, bats receive information about both potential prey and their immediate surroundings (Schnitzler and Kalko 2001). As a consequence, flight costs to navigate and to detect and catch prey are higher within structurally complex forest habitats than over lakes and other open areas. Moreover, open, deep (1–1.5 m), smooth and calm surfaces of water have been suggested to be ideal for all types of bats to drink compared to flowing rivers and streams (Almenar et al. 2006; Linton et al. 2011; Seibold et al. 2013). As some of the lakes surveyed were also partially connected to streams, bats could have also used these linear corridors as commuting routes (Palmeirim and Etheridge 1985; Meyer et al. 2005). Although detectability in open spaces should be higher than in cluttered environments, we tested ultrasound attenuation between forests and lakes and found the difference at distances up to 10 m to be so negligible, that we assumed they could be directly compared (Fig. S8).

Species-specific responses to habitat type, season and lake size

Emballonuridae

Rhynchonycteris naso was the emballonurid bat most strongly associated with lakes, as it was never recorded in the forest. As described by Ceballos (2014), this species tends to forage and roost over water bodies. The other emballonurids identified were also more commonly detected over lakes, in agreement with existing literature which considers *Saccopteryx leptura* an open-space forager (Jung et al. 2007) and *S. bilineata*, *Centronycteris maximilani*, *Peropteryx kappleri* and *P. macrotis* edge specialists (Jung et al. 2007; Kalko et al. 2008b; Barboza-Marquez et al. 2014). However, in contrast to previous studies, *Cormura brevirostris,* a forest interior forager (Estrada-Villegas et al. 2010), was also detected significantly more over lakes, probably because higher densities of aquatic insects during the rainy season accumulated above water bodies (Chan et al. 2008).

Molossidae

Our results agree with previous studies in which molossids were commonly found over water bodies (Costa et al. 2012), especially above larger lakes that allow them to easily maneuver near the water surface (Adams and Simmons 2002; Costa et al. 2012). Although *Promops*, *Molossops* and other rare molossid species are widely distributed across Central and South America, little is known about these genera (González-Terrazas et al. 2016; López-Baucells et al. 2018) and our study provides new information about their presence and feeding behavior at Amazonian lakes.

Mormoopidae

The species complex *Pteronotus* cf. *parnellii* includes two sympatric sister species in our study area (López-Baucells et al. 2017). Our data provide the first comparative quantification of species-specific activity and occurrence of these species (*Pteronotus rubiginosus* and *P.* sp1) and suggest that both are associated with highly cluttered habitats. *Pteronotus personatus* and *P. gymnonotus* were rarely recorded and only over lakes, which agrees with previous literature where they are defined as edge specialists (Kalko et al. 2008b).

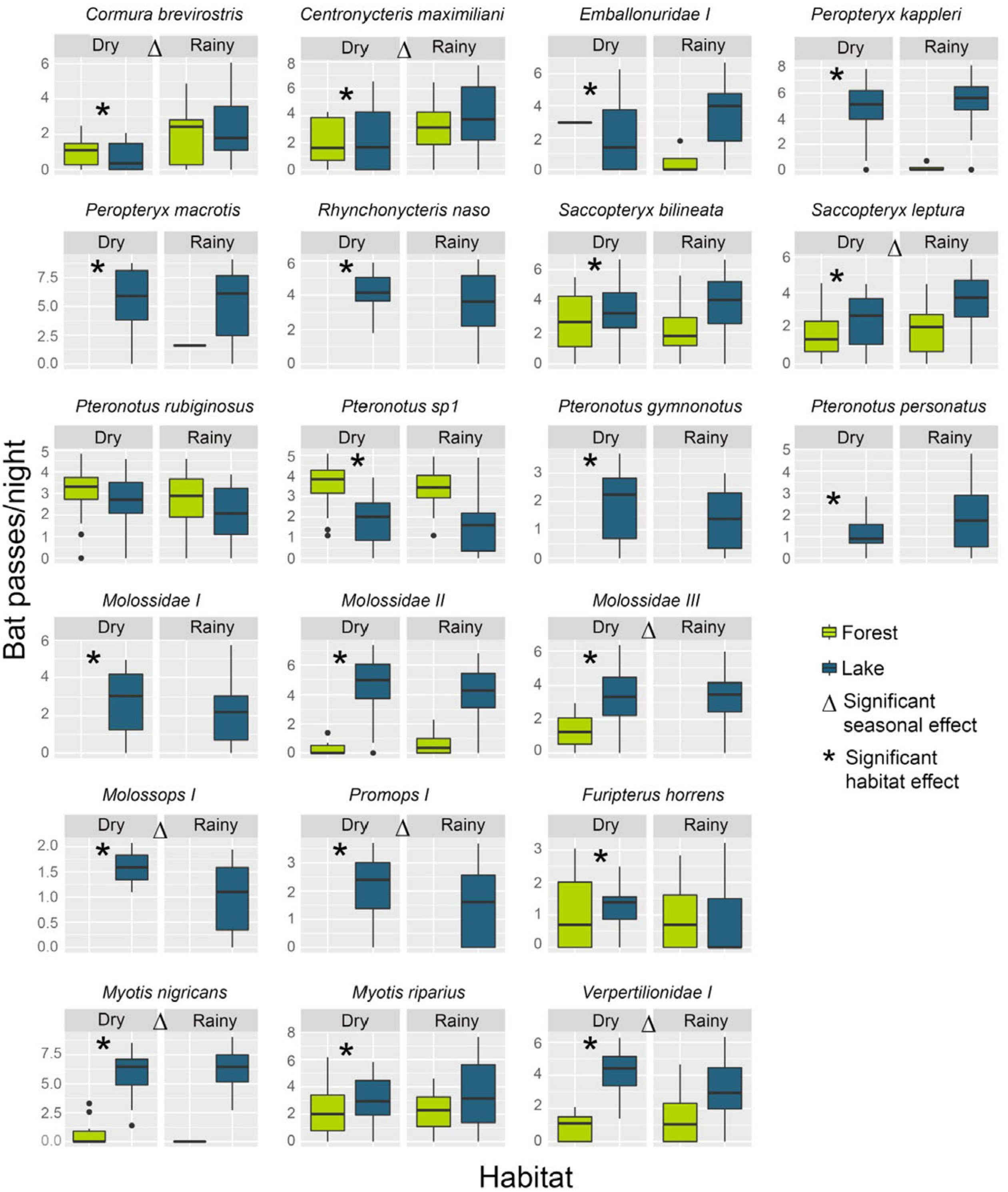

Figure 4. Comparison of the number of bat passes per species per night between primary forest and lakes for each season at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil. Significant differences ($P < 0.05$) are indicated with an asterisk (habitat effect) or triangle (seasonal effect).

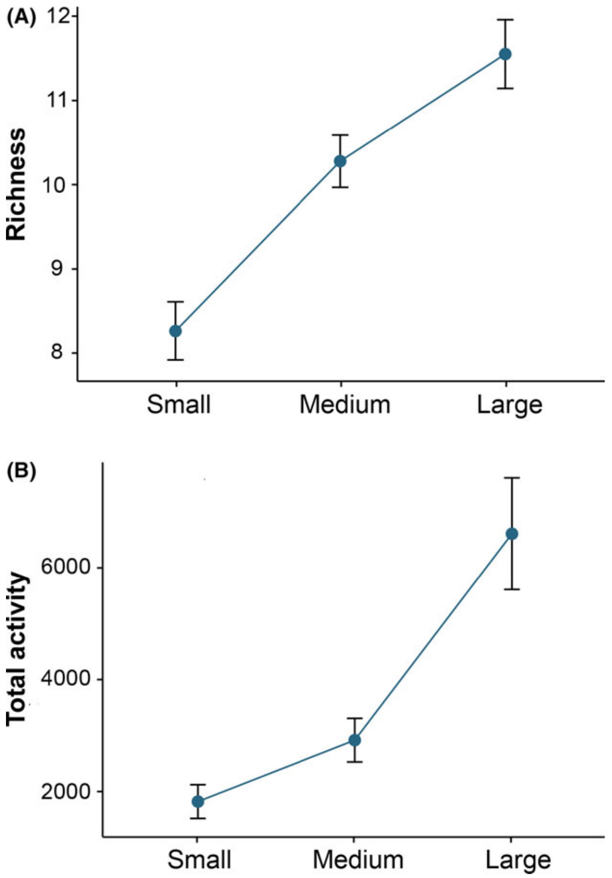

Figure 5. Richness and total activity (mean ± 95% CI) of aerial insectivorous bats (excluding molossids) per site and night for 'small' (up to 200 m^2), 'medium' (2000–3000 m^2) and 'large' (>9000 m^2) lakes at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil.

Furipteridae

Furipterus horrens is one of the least known insectivorous species in the Neotropics due to its elusiveness and the difficulty to detect it acoustically or with capture techniques (Falcão et al. 2015). The species was only captured once in our study area during extensive mist netting surveys that were conducted parallel to this study (Rocha et al. 2017a). Using bioacoustics, we passively and more efficiently monitored presence and activity of *F. horrens*, whereby our data suggest greater activity within the forest than over lakes.

Vespertilionidae

As expected, *Myotis nigricans* and *M. riparius* were both significantly more active over lakes (Costa et al. 2012) than in forest, particularly during the rainy season when insect availability is greater (Chan et al. 2008). Despite both species foraging over the water, our results indicate differential preferences regarding lake size. Although *M. nigricans* was frequently detected over large lakes, *M. riparius* was more often recorded over small lakes in closed environments. These are cryptic species whose identification in the field is far from easy due to similarities in morphology and echolocation. Their capacity to forage in lower forest strata, over water and both in open spaces and edge-and-gap situations (Siemers et al. 2001; Sampaio et al. 2003) as well as their diet (Siemers et al. 2001; Laval and Rodríguez 2002) should be further investigated to unveil what factors allow such similar species to coexist.

Conservation implications

Studies indicate that climate change can affect the emergence of aquatic insects and also cause physiological changes in tropical insects (Greig et al. 2012; Jonsson et al. 2015). Hence, longer drought periods associated with climate change might imperil tropical fauna that exploit insects associated with freshwater ecosystems. As insectivorous bats extensively use lakes in the tropics to forage and drink, it is essential to study their response to seasonal fluctuations in water levels. In fact, not only aerial insectivorous bats but also other guilds, such as gleaning animalivorous, frugivorous and nectarivorous bats (Giannini and Kalko 2004; Meyer and Kalko 2008) might be seasonally relying on Amazonian lakes. During the rainy season, lakes may be good foraging areas for animalivorous bats for two main reasons: (1) their prey, such as terrestrial arthropods and frogs, migrate to escape the water (Adis and Junk 2002) and (2) lakes are more accessible habitats than dense forest as they have less obstacles which facilitates maneuverability and prey detection (Schnitzler and Kalko 2001; Bobrowiec et al. 2014). Lakes can accumulate nutrient-rich sediments during rainy periods, enhancing the productivity of flowers and fruits of pioneer trees (Haugaasen and Peres 2007; Pereira et al. 2009), which could attract frugivorous and nectarivorous bats. The available evidence therefore seems to suggest that potentially negative consequences of anthropogenic climate change upon Neotropical lakes will not only affect aerial insectivorous bats but also various other Neotropical bat guilds.

A better understanding of bat phenology would allow us to more reliably predict the consequences of climate change for this species-rich group. Our findings indicate that the climate change-driven shrinking or disappearance of many lakes across the Amazon Basin will have negative repercussions for aerial insectivorous bats, probably leading to local population declines, if not extinctions, of the most water-dependent species. Compared to permanent lakes in other regions of the world, the role of Amazonian lakes for bat conservation so far has clearly been underappreciated. Higher levels of bat activity over lakes than in forest sites in both seasons and comprising the whole ensemble of aerial insectivorous bats of the study region, indicate that lakes, although seasonally variable in terms of water surface and sparsely distributed in unflooded Amazonian rainforest, deserve special attention for conservation. In the face of anthropogenic climate change, protection of floodplains and riparian forest, as well as buffer zones along rivers and lakes should be encouraged across the Amazon Basin to sustain populations of not only aerial insectivorous bats, but the whole diversity of taxa associated with these aquatic ecosystems.

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Supporting Information

Additional supporting information may be found online in the supporting information tab for this article.

Figure S1. Location of the Biological Dynamics of Forest Fragments Project and the lakes (*Lake 1* to *8*) and primary forest sites (*Forest 1* to *7*) sampled in the Central Amazon, Brazil.
Figure S2. Photos of each lake surveyed for bat activity in this study at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil. Numbers correspond to each lake in Figure S1.
Figure S3. Species/sonotype activity per site per night between lakes of different size for all bat families except Molossidae, at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil.
Figure S4. Interaction effect between habitat type and season as determinants of species-specific activity of emballonurid bats.
Figure S5. Interaction effect between habitat type and season as determinants of species-specific activity of molossid bats.
Figure S6. Interaction effect between habitat type and season as determinants of species-specific activity of mormoopid bats.
Figure S7. Interaction effect between habitat type and season as determinants of species-specific activity of vespertilionid and furipterid bats.
Figure S8. Ultrasound attenuation along 30-m transects at the different habitats (forest interior, clearings and secondary forest) in the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil.
Table S1. Bat echolocation call sonotypes detected at the Biological Dynamics of Forest Fragments Project, Central Amazon, and their frequency ranges.
Table S2. Summary of the MCMC-GLMMs testing for the effect of habitat type (forest vs. lake) and season (dry vs. rainy) on bat sonotype richness and total bat activity.
Table S3. Summary of the results of MCMC-GLMMs modeling species-specific acoustic bat activity in relation to habitat type (forest vs. lake), season (dry vs. rainy) and the interaction of both.
Table S4. Results of multiple comparison tests following MCMC-GLMMs assessing differences between bat sonotype richness and total bat activity and the three size categories of lakes.
Table S5. Variance for the confidence intervals on the obtained points in Figure 5.
Table S6. Results of multiple comparison tests following MCMC-GLMMs, assessing differences in activity levels of individual bat species between lake size categories.

