Tradition vs. innovation: comparing bioacoustics and mist-net results to bat sampling

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ABSTRACT

Bats are a complex and diverse group, making their study remarkably challenging. Several methods allow the study of bats, e.g. mist-nets and acoustic monitoring (AM). We compare the use of AM and mist-nets to inventory bats in a mountainous region of São Paulo state, Brazil. We provide a species list for the study area based on species registered with both methodologies, comparing with a species list known for the state, obtained from the literature. We calculated beta diversity between methodologies to evaluate the dissimilarity in species composition sampled with these methods. We also performed a PCA to evaluate if the bat fauna sampled with AM showed species-habitat associations. We recorded 15 species/sonotypes through AM and 22 species through mist-nets. Beta diversity revealed 97% of dissimilarity in species composition. The turnover component explained 96% of this dissimilarity. PCA revealed that Vespertilionidae bats were associated with border/cluttered habitats, while Molossidae bats were present in all habitat types. The species list for the state comprises eighty species. Our inventory recorded more than 25% of this fauna. Mist-nets are efficient for sampling low-flying/low-intensity echolocating bats. AM is crucial for sampling high-flying/high-intensity echolocating bats. This is the second study to use AM to inventory bats in this state.

Introduction

Brazil is a continental scale country with 181 bat species known, harbouring the secondhighest bat diversity in South America (Garbino et al. 2020). The majority of the bat surveys conducted in Brazil only employed traditional methods, such as mist-nets or roost search (Arias-Aguilar et al. 2018; Pedroso et al. 2020). Roost searches are mainly undertaken in caves and buildings, while mist-nets are mainly employed at ground level (3–4-m high). However, several bat species are not cave-dwellers, and eight of the nine bat families occurring in Brazil easily detect and avoid mist nets or fly high above them.
(O’Farrell and Gannon 1999; Rydell et al. 2002; Sampaio et al. 2003; Gardner 2008; Gregorin et al. 2017; Silva and Bernard 2017; Hintze et al. 2019). Consequently, knowledge about Brazilian bat fauna has a significant taxonomic bias, as demonstrated by Delgado-Jaramillo et al. (2020). For example, a review made by Bernard et al. (2011) showed that only 10% of the country is minimally sampled for bats. However, these authors did not mention acoustic monitoring in their study, and considering the small number of studies using this method in Brazil until 2011, it is possible that their review only considered traditional methods, and the scenario is even lower for the bat species that are underestimated with these. Therefore, the use of acoustic methodologies can provide important new information about the Brazilian bat fauna (Sampaio et al. 2003; Bernard et al. 2011; Silva and Bernard 2017).

Acoustic monitoring uses devices to record sounds emitted by animals, with the later identification and analysis of these sounds and their patterns to study animals’ distributions, behaviour, and ecology (see Blumstein et al. 2011 for a review of the applications of this method). Unlike temperate regions in the northern hemisphere, bat studies using bioacoustics in the Neotropics are still incipient (Arias-Aguilar et al. 2018). However, they have grown in number and have already brought significant contributions to bat biology. In the case of Brazil, acoustic monitoring has already brought important information about the aerial insectivore bat fauna (Portfors et al. 2000; Silva and Bernard 2017) as well as the detection and range extension of species previously considered rare or geographically restricted, respectively (Hintze et al. 2019). Acoustic information also contributed to describing a new species, Pteronotus alitonus (Pavan et al. 2018). Such information is essential to improve our knowledge about bat biology, diversity, and conservation, and in many cases, it can only be acquired using acoustic methodologies (Meyer et al. 2011; Silva and Bernard 2017). Considering the lack of information about bat fauna in Brazil (Bernard et al. 2011), the realisation of new studies using acoustic methodologies is of extreme importance to achieve greater completeness of the Brazilian bat fauna and to reduce the methodological bias towards mist-net sampling (Bernard et al. 2011; Silva and Bernard 2017).

Aiming to reduce these gaps, the present study focused on a bat inventory in a high altitude region in São Paulo state, southeastern Brazil, using mist-nets and acoustic monitoring simultaneously. This state is probably one of Brazil’s most sampled regions for bats; however, to our knowledge, only one study applied acoustic methodologies to inventory the bat fauna (Portfors et al. 2000). Moreover, this study was conducted more than 20 years ago, and since then, both acoustic recorders and knowledge about Neotropical bats’ echolocation have greatly advanced. Based on the results found by Silva and Bernard (2017) in the Caatinga biome, we aimed to test if acoustic monitoring is also providing new information in the Atlantic forest biome by comparing its results with the mist-net sampling and the historical records of the state. Additionally, we test if the bat species detected with acoustic monitoring are associated with elevation, habitat type, season, and time of detection. We work with the hypothesis that these two methodologies will sample different subsets of the bat community; with mist-net sampling most Phyllostomidae species, and acoustic monitoring sampling most aerial insectivore species (represented in our study by the families Molossidae and Vespertilionidae). For the species-habitat relationships, we expected that Vespertilionidae bats will be more associated with border and cluttered habitats, while
Molossidae bats will be associated with open habitats, as these families have acoustic adaptations suited to these habitat types, respectively (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013). We also expect more bat activity and richness at lower elevations and the beginning of the night, based on previous studies that detected a negative effect of temperature on bat activity (Barros et al. 2014; Appel et al. 2019) and a general pattern of increased bat activity after sunset (Hayes 1997; Appel et al. 2017).

**Materials and methods**

**Study area**

This study was carried out at Serra da Mantiqueira mountain range, more specifically in the municipalities of Pindamonhangaba, Piquete e Santo Antônio do Pinhal (São Paulo state – Figure 1). We defined three areas according to altitudinal strata (Figure 1, Supplementary Table 1). In each stratum, three to four forested sampling sites were selected in the field in a pilot expedition and took into consideration ease of access, availability to set up mist-nests, and authorisation by the landowners. In each site, the mist-nets were arranged in vegetation borders, clearings, and in pre-existing trails inside vegetation (Supplementary Table 1). All sampling sites are inside the protected area of Serra da Mantiqueira (Detzel Consulting 2018), an important protected area that covers many remnants of the Atlantic forest in Brazil. The vegetation is classified as a dense ombrophylous montane forest (IBGE 2012). The climate is the typical humid subtropical,

![Figure 1](image_url)

**Figure 1.** Upper left: Map from Southeastern Brazil with the São Paulo state highlighted. The red circles point to the municipalities surveyed in this study. In detail, the elevational maps of the study areas evidencing the sampling sites of the present study. Coordinates and precise elevations of each sampling point are provided in Supplementary Table 1.
with rains concentrated in the summer and dry in winter (Alvares et al. 2013). To increase the possible range of species detected and captured, our range of sampling sites covered 720 to 1600 m a.s.l., which encompassed most of the elevational gradients present in the area. We employed mist-netting and acoustic sampling concomitantly.

**Acoustic monitoring**

We employed active acoustic sampling using a Pettersson D-240X (Pettersson Elektronik, Sweden) ultrasound detector. We searched for bat calls at a fixed location by constantly scanning through the frequency range of the detector (10–120 kHz) in heterodyne mode. When detecting a bat call, we manually triggered the time expansion mode. This protocol was adopted based on the results of a previous study (Matos et al. 2013), which found that the manual mode has the potential to detect higher bat activity and richness. This is possible because the automatic mode can sometimes trigger a recording when a sound above the threshold is emitted by a non-bat source, which in turn precludes the detection of an echolocating bat during this time. This can especially be a problem in areas with a high acoustic activity of insects and amphibians, such as in ombrophylous tropical forests. In the manual mode, this limitation is not present if the operator has the minimum experience to distinguish an echolocating bat from another sound source. However, this advantage came with the drawback of reducing the total time sampled.

The time expansion mode was programmed to record for 1.7 seconds and to expand it by a 10x factor. We connected the ultrasound detector to a manual recorder ZOOM® H2n model (Zoom Corporation, Japan) and stored the recordings in .wav audio files. To avoid any sampling bias, the same person performed the acoustic sampling during nights with good weather conditions (temperature above 10°C and without rain or strong winds – Matos et al. 2013). We employed a recording scheme of 5 min recording/25 min interval, starting the recordings at sunset and finishing them six hours later. This resulted in a total of 13 recording events each night. We used this scheme because the recorder operator was also required to remove bats from mist-nets and for triage. Besides that, due to limitations in disk storage and available time to analyse the recordings, we were not able to set the detector recording in the automatic mode during the 25 minutes intervals. Sampling was done twice in each sampling site, one in the summer and one in winter, from March 2016 to April 2017. This resulted in a total of 130 minutes of sampling for each sampling point (5 minutes × 13 recording events during a sampling night × 2 sampling nights), and 1300 minutes for the entire study. A total of 81 recordings containing identifiable bat calls were made with this sampling effort. These recordings totalised 22 minutes and 57 seconds in expanded time (81 recordings × 17 seconds in expanded time = 1377 seconds = 22 minutes and 57 seconds). 21 recordings were made at the sampling point with higher bat activity (totalling 5 minutes and 57 seconds in expanded time), while only one recording was made at the sampling point with lower bat activity (totalling 17 seconds in expanded time). To avoid the influence of mist-nets on species detection, acoustic monitoring was always carried out at a distance of approximately 150–200 metres from the nets (Silva and Bernard 2017).
The recordings were analysed using Raven Pro v1.6© software (Cornell Lab of Ornithology, Ithaca). As spectrogram parameters, we used Fast Fourier Transformation size 1024 with 75% overlap in a Hanning window. For bat echolocation calls identification, we considered the following acoustic parameters: high frequency, low frequency, start frequency, end frequency, peak frequency, and call duration. Only recordings containing bat echolocation sequences with three or more good-quality pulses (signal-to-noise ratio >10 dB) were used (Jung et al. 2014; Lloyd et al. 2006). We used the available bibliography to identify the bat calls into species or acoustic groups (e.g. Jung et al. 2007, 2014; Barataud et al. 2013; López-Baucells et al. 2016; Arias-Aguilar et al. 2018).

**Mist-nets**

Sampling was carried out with the use of eight mist-nets (ECOTONE®, 12 m × 2.5 m) positioned at the understory level (approximately 2.5–3-m high), concomitantly with the acoustic monitoring. A total of seven field expeditions were made between 2016 and 2017, each one with eight consecutive days of duration. There was a sampling interval of 2 months between the field expeditions. Mist-nets were opened at sunset and remained sampling for 6 hours. This resulted in a sampling effort of 2,880 m².h for each sampling site (calculated as mist-net area = 30 m² × 8 mist-nets x 6 hours per sampling night x 2 sampling nights) and 28,800 m².h for the entire study. Mist-nets were checked at 30-minute intervals. During the intervals, the researchers kept a distance of approximately 100 metres from the nets to avoid human interference. After capture, we identified the bats to species level with the support of the taxonomic keys available in Díaz et al. (2016). Bats were fitted with aluminium rings before release.

**Literature information**

We used the bat species list provided by Garbino (2016) as a reference for São Paulo state. We also searched on Web of Science, Scielo, and Scholar Google platforms for studies of bats in São Paulo state from 2015 to 2020, to check if some new species were recorded in the state after the compilation of Garbino (2016).

**Data analysis**

To test the hypothesis that mist-net and acoustic monitoring samples different subsets of the bat community, we calculated the beta diversity between these two methodologies (Baselga and Orme 2012). First, we compiled all species sampled with the same method in a unique list, to obtain a species list of the study area provided by each one of the methodologies used. After this step, we calculated the ‘methodological’ beta diversity of these two methods and partitioned this diversity into two components, turnover and nestedness (Baselga and Orme 2012). The turnover component indicates the proportion of dissimilarity that is explained by species substitutions between methods, while nestedness indicates the proportion of dissimilarity that is explained by species losses between methodologies (Baselga and Orme 2012). We estimated the beta diversity using the Jaccard distance, which accounts only for changes in species composition (but not in
species abundance). This was done due to the different unit samples of the methods used, which are not comparable (abundance of individuals for mist-nets versus frequency of occurrence for acoustic sampling).

To test the hypothesis of species-habitat relationships, we did a Principal Component Analysis (PCA – Abdi and Williams 2010). First, we defined a bat pass as our unit sample. We considered as a bat pass any good-quality echolocation sequence (see ‘Acoustic monitoring’ section) that was found in a 1.7-second recording in expanded time. When two different sonotypes were present in the same 1.7-second recording, we considered this recording as having two bat passes. Although this method can lead to counting the same individual more than once, this frequency of occurrence measure reflects the time spent by a bat in habitat and thus can be used as a proxy for habitat use (Kerbiriou et al. 2019). We obtained a total of 95 bat passes in the entire study. We then used the following explanatory variables to build a vectorial space: elevation, time of detection, season (wet and dry), and habitat type (open, border, and cluttered habitat – Supplementary Table 1). After the ordination of these variables in the principal components, we plotted all the bat passes obtained in the study, so we could evaluate if the species are associated with specific habitats, seasons, and time. As we worked with variables in different scales, the explanatory variables were standardised by log-transformation before the application of the PCA. All analyses were performed in R v4.0.5 (http://www.r-project.org). We used the default R to perform the PCA, and the betapart package (Baselga and Orme 2012) to perform the beta diversity analysis.

Results

Inventory with acoustic monitoring and mist-nets

Our acoustic monitoring resulted in an inventory of 15 species/sonotypes for the entire study (Table 1, Figure 2). The local richness in sampling sites ranged from 1 to 7 (Figure 3). On the other hand, our mist-netting sampling resulted in an inventory of 22 species for the entire region (Table 1), with richness in sampling sites ranging from 2 to 13 species (Figure 3). Altogether, we had a total of 36 bat species recorded, of which 25 of those are species with precise identification, and 11 are species that could not be precisely identified (acoustic groups composed of two species, ‘cf’. and ‘sp’. notes – Table 1). From the total species sampled in this study, only one (E. brasiliensis) was recorded by both methodologies. The remaining taxa were only registered by one type of method.

Mist-netting was the only method by which Phyllostomidae bats were recorded (Table 1). In fact, of the 311 individuals recorded with mist-nets, only 10 were non-Phyllostomidae bats. These individuals were of the species Eptesicus brasiliensis (1 individual), Molossops neglectus (1 individual), and species of the genus Myotis (8 individuals – Table 1). The most abundant species recorded with mist-nets were Carollia perspicilata (111 individuals), followed by Sturnira lilium (82 individuals), and Artibeus planirostris (25 individuals). Acoustic sampling recorded Molossidae and Vespertilionidae bats only (Table 1). Of the 81 recordings made, in 34 we found echolocation calls of Molossidae bats (Table 1, Figure 2), while echolocation calls of Vespertilionidae bats were found in 60 recordings (Table 1, Figure 2). The most frequent sonotypes were Lasiurus/Eptesicus (20 recordings), followed by Lasiurus ega/egregius (16 recordings) and Myotis sp2 (12 recordings).
The review made by Garbino (2016) provided a list of 78 species belonging to 8 of the 9 bat families found in Brazil (the Mormoopidae family is restricted to northern and northeastern regions). Our search found two additional species that were not registered by Garbino (2016): *Molossus currentium* and *Micronycteris schmidtorum* (Cláudio et al. 2020), totalling 80 known bat species in São Paulo state. The updated list is provided in Supplementary Table 2.

**Table 1.** Species/acoustic groups recorded in the present study. Numbers represent abundance registered with mist-nets, and ‘A’ indicates the presence of the species registered through acoustic monitoring. Numbers in parenthesis after ‘A’ indicates the number of recordings each species was detected in each sampling site. Sampling site numbers are as follows in Figure 1. Species citations are included in Supplementary Table 2.

| Species | Sampling site |
|---------|---------------|
|         | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 |
| **Phyllostomidae** |     |     |     |     |     |     |     |     |     |     |
| Anoura caudifer | 1  | 2  | 3  | 1  | 1  | 1  | 2  |     |     |     |
| Anoura geoffroyi | 1  | 1  |     |     | 5  | 5  |     |     |     |     |
| Artibeus fimbriatus | 1  |     |     |     |     |     |     |     |     | 5  |
| Artibeus lituratus | 3  | 8  | 2  | 2  |     |     |     |     |     |     |
| Artibeus planirostris | 4  | 5  | 2  | 5  | 1  | 8  |     |     |     |     |
| Carollia perspicilata | 37 | 25 | 18 | 5  | 6  | 9  | 5  | 4  | 2  |     |
| Desmodus rotundus |     |     | 3  | 1  | 4  |     |     |     |     |     |
| Glossophaga soricina | 1  | 12 | 2  |     |     |     |     |     |     |     |
| Micronycteris megalotis |     |     |     |     |     | 2  |     |     |     |     |
| Phyllostomus hastatus | 1  |     |     |     |     |     |     |     |     |     |
| Platyrhinus lineatus | 1  | 1  |     |     |     |     |     |     | 3  |     |
| Platyrhinus recifinus | 1  |     |     |     |     |     |     |     | 1  |     |
| Pygoderma bilabiatum |     |     |     |     |     |     |     |     | 3  |     |
| Stenura lilium | 5  | 5  | 16 | 4  | 14 | 4  | 17 | 16 | 1  |     |
| Vampyressa pusilla |     | 1  | 1  |     |     |     |     |     |     |     |
| **Molossidae** |     |     |     |     |     |     |     |     |     |     |
| Cynomops cf. planirostris |     |     |     | A(1) |     |     |     |     |     |     |
| Eumops sp.1 | A(5) | A(4) | A(1) |     |     |     |     |     |     |     |
| Molossidae sp. 1 | A(1) |     |     | A(2) |     |     |     |     |     |     |
| Molossops neglectus |     |     |     |     |     | 1  |     |     |     |     |
| Molossus cf. currentum |     | A(2) |     |     | A(2) | A(5) | A(1) |     |     |     |
| Molossus molossus |     |     |     |     | A(1) |     |     |     |     |     |
| Molossus rufus* | A(1) |     | A(1) |     |     |     |     |     |     | A(1) |
| Promops centralis | A(1) |     |     | A(3) |     |     |     |     |     |     |
| Tadarida brasiliensis /Nyctinomops sp. |     |     |     |     |     |     |     |     |     | A(1) |
| **Vespertilionidae** |     |     |     |     |     |     |     |     |     |     |
| Eptesicus brasiliensis | 1  |     |     |     |     |     |     |     | A(1) |     |
| Eptesicus cf. chiriquinus |     |     |     |     |     |     |     |     | A(1) |     |
| Eptesicus furinalis |     |     |     |     | A(4) | A(3) | A(2) |     |     |     |
| Lasiurus/Eptesicus | A(12) | A(3) | A(1) | A(2) | A(1) | A(1) | A(1) |     |     |     |
| Lasiurus ega/egregius | A(2) | A(1) | A(11) | A(1) | A(1) |     |     |     |     |     |
| Myotis nigricans |     |     | 2  |     |     |     |     |     |     | 1  |
| Myotis sp.1 |     |     |     |     |     |     |     |     | 1  |     |
| Myotis sp.2 | A(1) | A(1) |     | A(10) |     |     |     |     |     |     |
| Myotis levis |     |     | 1  |     |     |     |     |     |     | 1  |
| Myotis riparius |     |     | 1  |     |     |     |     |     |     | 1  |
| Myotis ruber |     |     | 1  |     |     |     |     |     |     | A(1) |
| Vespertilionidae sp.1 |     |     |     |     |     |     |     |     |     |     |

* Currently known as *Molossus fluminensis.*

**Literature information**

The review made by Garbino (2016) provided a list of 78 species belonging to 8 of the 9 bat families found in Brazil (the Mormoopidae family is restricted to northern and northeastern regions). Our search found two additional species that were not registered by Garbino (2016): *Molossus currentium* and *Micronycteris schmidtorum* (Cláudio et al. 2020), totalling 80 known bat species in São Paulo state. The updated list is provided in Supplementary Table 2.
**Methodological beta diversity**

Our analysis of beta diversity between mist-netting and acoustic monitoring detected a dissimilarity of 97.1% between the species composition sampled with these methods. When partitioned, the turnover component explained 96.5% of the dissimilarity in species composition between methods, while the nestedness component explained only 0.6% of the dissimilarity.

**Species-habitat associations**

The PCA revealed that our explanatory variables had great explanatory power for the data distribution. The PC1 alone explained 51% of the data variance, while the PC2 explained 26.3% of this pattern (Figure 4). Together, the two first PCs accounted for 77% of the data variance. The majority of bat passes were recorded in the first hours of the night in cluttered and border habitats located at lower elevations. The sonotypes *E. furinalis* and *M. rufus* showed a more scattered distribution in the vectorial space.
and were recorded at different habitat types, elevations, and times. On the other hand, the sonotypes *Myotis* sp2, *Lasiurus ega/egregious*, *Promops centralis*, *Eumops sp1*, and Molossidae 1 appeared to be more associated with border and cluttered habitats at low elevations.

**Discussion**

**Acoustic monitoring vs. mist-nets**

Together with previous studies (MacSwiney et al. 2008; Meyer et al. 2011; Silva and Bernard 2017) the results from our sampling with mist-nets and acoustic monitoring corroborate our first hypothesis, evidencing there are significant differences in species detection between these methodologies. Our beta diversity analysis showed a high dissimilarity between methods (97%), with the turnover component explaining the majority of this pattern (96%). This indicates that the methodologies used here are highly complementary, and each one can sample a subset of the bat community that is not ‘available’ to the other. For example, it is well known that Phyllostomidae bats are well sampled with mist-nets, as these bats commonly forage in the understory stratum, where mist-nets are normally positioned (O’Farrell and Gannon 1999; Sampaio et al. 2003; Meyer et al. 2011). On the other hand, these bats are undersampled with acoustic monitoring because these species usually emit low-intensity echolocation calls that cannot be recorded easily (Portfors et al. 2000; Silva and Bernard 2017). Conversely,
Molossidae and Vespertilionidae bats are undersampled with mist-nets due to their high-flight behaviour and the capacity to detect and avoid mist-nets (O’Farrell and Gannon 1999; MacSwiney et al. 2008). For these bats, the use of acoustic monitoring is more appropriate, as they normally emit high-intensity echolocation calls (Rydell et al. 2002). These results evidence the importance of employing varied methods in biological inventories, particularly the use of acoustic monitoring, because this procedure is still underused in Brazil (Mendes and Srbek-Araujo 2021).

Indeed, all species recorded here with acoustic monitoring are aerial insectivore bats (Figure 2), which are rarely captured by mist-nets hung in the understory level (Rydell et al. 2002; Sampaio et al. 2003; Gregorin et al. 2017; Silva and Bernard 2017). Therefore, the richness and abundance of those groups are always markedly underestimated or even not recorded in studies using mist-nets only (Cunto and Bernard 2012; Marques et al. 2016; Arias-Aguilar et al. 2018). This has strongly influenced the knowledge and conservation of bats in Brazil. For example, eight of the nine bat families occurring in Brazil still have a significant knowledge gap in their ecology and distribution (Arias-Aguilar et al. 2018), and bat fauna inventories for the country are certainly underestimated and biased (Bernard et al. 2011; Cunto and Bernard 2012; Arias-Aguilar et al. 2018). These facts highlight the need for acoustic monitoring to be implemented in future studies, so a more holistic knowledge about the Brazilian bat fauna can be reached.

In this study, Phyllostomidae bats were only registered through the use of mist-nets. Together with them, one individual of Eptesicus brasiliensis and some Myotis species (as well Molossops neglectus among molossid bats) were also netted when mist-nets were arranged in forest borders or clearings. Species from the genus Eptesicus and Myotis are
known to forage in vegetation borders or even in open trails inside vegetation (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013), thus it is understandable that some individuals of these species were caught by mist-nets here and in other studies (MacSwiney et al. 2008; Silva and Bernard 2017; Hoppe et al. 2020). Moreover, some of our sampling sites are next to water bodies, which are frequently used by these bats as foraging habitats due to the high insect abundance and the absence of obstacles in these sites (Laurindo et al. 2020). These species emit echolocation calls characterised by the presence of a frequency-modulated component, which is suitable for habitat recognition and obstacle avoidance in flight (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013). This frequency-modulated component is characteristic of species that forage next to vegetation (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013) and can also be an explanation why an individual of *M. neglectus* was caught in mist-nets. This species is one of the few Molossidae that emits echolocation calls with frequency-modulated components (Jung et al. 2014). In contrast, the majority of Molossidae bats emit quasi-constant frequencies that are suited to hunt for prey in open areas, as these calls are less affected by atmospheric attenuation (Schnitzler and Kalko 2001).

We also highlight the presence of the sonotypes *E. cf. chiriquinus* and *M. cf. currentium*. The first is an insectivore species with scarce records in Brazil (Gregorin and Loureiro 2011; Zortéa et al. 2013), while the second was only recently recorded at São Paulo state with the use of mist-nets (Cláudio et al. 2020). We cannot precisely affirm that these calls belong to these species because of the lack of acoustic information about congener species. However, this information is indicative that these species may occur in the region as Gregorin and Loureiro (2011) recorded *E. chiriquinus* not far from our study’s region and Cláudio et al. (2020) recently registered *M. currentium* in the state. Another interesting record was *P. centralis*, an undersampled insectivore species that had its vocalisations repertoire and distribution updated recently using acoustics (Hintze et al. 2019).

Together with the differences in species composition, there are also important differences in costs and efforts between these two methodologies. For example, the costs to acquire an ultrasound detector are normally high, especially if importation is required. On the other hand, mist-nets are relatively inexpensive (Zamora-Gutierrez et al. 2021). However, mist-nets demand that researchers be well trained to safely remove bats from nets without injuring them (Zamora-Gutierrez et al. 2021). This also makes mist-nets a very invasive method (Zamora-Gutierrez et al. 2021). In the case of acoustic monitoring, researchers normally need to be trained only to programme and set the equipment in the field. It is also a non-invasive method, as it does not require direct observation or manipulation of animals to document bat activity (Zamora-Gutierrez et al. 2021). In terms of effort, mist-nets demand much more effort while in the field, as nets need to be carried, erected, and checked, and bats need to be removed and analysed. This also adds costs to sustain the human resources, such as food and water, at a minimum. After fieldwork, the only effort that is still needed when inventorying bats with nets is to organise the data in a spreadsheet so it can be saved. In the case of acoustic monitoring, the efforts are the opposite. The data collection at the field requires less effort, as researchers only need to be there to install/uninstall the detector. A little more effort is necessary if the detector or the sampling protocol demands an operator (such as in our study). However, acoustic monitoring requires much more effort after the fieldwork,
when the recordings need to be analysed. The storage of the recordings also demands additional costs with storage devices or cloud storage, as audio files are much larger than simple spreadsheets and demand more storage space (Frick 2013; Zamora-Gutierrez et al. 2021). Researchers should also keep these differences in mind when choosing the sampling method of their study.

It is important to consider that the still incipient knowledge about Brazilian bats’ echolocation (Arias-Aguilar et al. 2018) could have influenced the detected richness in the present study. For example, there are many species that still lack an acoustic description of their echolocation calls (e.g. Myotis levis and Eptesicus diminutus – Arias-Aguilar et al. 2018). Moreover, many acoustic descriptions available were made based on few individuals sampled in a few specific areas (e.g. Histiotus velatus – Fenton et al. 1999; Arias-Aguilar et al. 2018), which makes intra-specific and intra-individual variability highly underestimated. This lack of information directly affects detected richness, as a researcher can classify two different species in the same sonotype due to the lack of enough acoustic data to distinguish them. Another problem would be richness overestimation, if the researcher recognises two different echolocation calls of the same species (as the high variable P. centralis – Hintze et al. 2019) as two distinct taxa. Some insectivorous bats can also change their echolocation calls depending on the habitat in which they are foraging (Schnitzler and Kalko 2001), which can also be a problem if the researcher recognises these calls as belonging to two different species. To avoid this mistake, researchers must keep in mind that some echolocation parameters of the bat calls tend to be more constant (of course inside a variation range). For the families detected here, for example, the minimum frequency and the frequency of maximum energy are two parameters that can help researchers to detect if two bat calls are from the same sonotype foraging at different habitats (Arias-Aguilar et al. 2018). Alternatively, call duration and bandwidth are parameters expected to show higher variation as a bat changes its foraging habitat (Schnitzler and Kalko 2001).

Together with the incipient knowledge about Brazilian bats’ echolocation (Arias-Aguilar et al. 2018), other factors may have influenced the scarcity of bat surveys using bioacoustics in Brazil. For example, the high prices of ultrasound detectors, allied with the fact that these devices need to be imported from other countries, probably worked as a limitation. Moreover, acoustic methodologies in Neotropics are time-consuming for two reasons. First, the high species diversity of the region together with the high plasticity of the echolocation calls demand that researchers invest time in identification courses, which are still rare in Brazil. Second, the analysis of acoustic data obtained by acoustic monitoring is often (if not always) time-consuming due to the high levels of bat activity, which frequently includes many species foraging at the same time. Although these limitations still exist, some steps have already been taken to reduce them. For example, there is an increasing number of ultrasound detectors becoming more accessible, and the Brazilian Society for the Study of Bats (SBEQ) has already delivered an educational course focused on bat bioacoustics in 2021. These factors should be seen as stimuli for studies using bioacoustics, especially studies focused on describing echolocation calls of species with little or no recordings. This information is highly desirable as they will certainly improve the knowledge about Brazilian bat fauna and echolocation, making species identification and richness estimates more accurate.
Species-habitat associations

Our PCA showed that the variables habitat type, season, hour of activity, and elevation have a high explanatory power on the aerial insectivore bats' distribution (Figure 4). First, we observed a higher number of bat passes and species richness at low-elevated areas. The elevation is highly correlated with temperature (McCain and Grytnes 2010), and previous studies already have found that lower temperatures can have significant negative effects on the activity of aerial insectivore bats and their prey (Estrada-Villegas et al. 2012; Barros et al. 2014; Appel et al. 2019). Thus, the higher bat activity and richness found at lower elevations in this study is probably a result of the temperature’s effects on these aspects of the aerial insectivore bat fauna. We also found higher activity and richness at cluttered and border habitats, possibly because in these habitats it is possible to sample both open-area and forest species (Ethier and Fahrig 2011; Falcão et al. 2021). This is especially true in our study area, as we were able to record open-space bats (such as Promops centralis and Eumops sp1) even when sampling in large trails inside vegetation (classified here as a cluttered habitat). This probably occurred because molossid bats usually explore the open space above the canopy (Marques et al. 2016), and emit high-intensity echolocation calls (Rydell et al. 2002). Moreover, the fact that the vegetation canopy in our study area reaches about 20 metres (IBGE 2012) also explains why we recorded these species in cluttered habitats.

We found a higher number of bat passes from vespertilionid bats (triangles in Figure 4) at the border and cluttered habitats, in accordance with the second hypothesis of this study. For example, although the sonotype E. furinalis was also recorded in open habitats, other sonotypes, such as Myotis sp2, Lasiurus/Eptesicus, and Lasiurus ega/egregious, were recorded almost exclusively in border/cluttered habitats (Figure 4). This is in agreement with the previous studies of Schnitzler and Kalko (2001) and Denzinger and Schnitzler (2013), which had described the echolocation calls of vespertilionid bats as suited to explore these habitats due to their frequency-modulated components, which enable habitat recognition and obstacle avoidance (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013). In contrast, molossid bats were more scattered in the vectorial space, indicating they were detected in all habitat types. As stated above, it probably occurred because these animals also explore the space above the canopy, which is not very high in our study area. Moreover, molossid bats also exhibit wing and echolocation adaptations that make it difficult for these animals to explore cluttered habitats, such as less manoeuvrable flight (Norberg and Rayner 1987) and quasi-constant frequency echolocation calls (Schnitzler and Kalko 2001; Denzinger and Schnitzler 2013).

Seasonality and time of detection were also important aspects of species detection (Figure 4). Although many species were recorded in both seasons and through the night, one sonotype (P. centralis) was only recorded in the dry season, while other two were recorded only in the wet season (M. molossus and Eumops sp1). Moreover, the sonotype P. centralis was recorded only in the early hours of the night, while the other two sonotypes were mainly detected 3 hours after sunset. These results suggest that sampling schemes that encompass seasonality and are conducted through the maximum number of hours possible would provide a more detailed picture of the aerial insectivore bat fauna (Estrada-Villegas et al. 2010). Unfortunately, the potential effect of seasonality on the composition of the aerial insectivore bat fauna is another knowledge gap in Brazil and the
Neotropics. For example, Estrada-Villegas et al. (2010, 2012) argued that they used acoustic sampling through seasons to account for possible seasonal differences, but they did not test this question. In Brazil, Barros et al. (2014) evaluated aerial insectivore bat activity between seasons, but they also did not evaluate changes in species composition. Barros et al. (2014) found that bat activity was lower in colder seasons, which is contrary to our findings (Figure 4). However, their study was conducted in Brazil’s southernmost region, which has relatively lower mean temperatures than our study area.

In our study, the higher bat activity detected at the dry/winter season may reflect of how seasonality affects insect prey. For example, as insect activity and abundance are positively related to temperature (Barros et al. 2014; Stangler et al. 2015; Appel et al. 2019), it is possible that a lower prey availability in winter forces bats to forage more frequently or over greater distances to fulfil their energetic demands. These options should not be too expensive energetically to aerial insectivore bats, as most species have wings adapted to high-speed and low-energetic cost flights (Norberg and Rayner 1987). Any of these scenarios could lead to a higher detection in the dry/winter season. However, these are only hypotheses, as the relationships between insect prey and aerial insectivore bats are poorly understood in tropical regions (Appel et al. 2019). The knowledge about the hourly activity of specific aerial insectivore bat species is also scarce in these regions (but see Appel et al. 2017), even considering there is a consensus in the literature that the first hours of the night show higher bat activity (Rydell et al. 1996; Hayes 1997; Appel et al. 2017; our data). This study is one of the few in the Neotropics that explicitly found differences in species detection in aerial insectivore bats between seasons and throughout the night. Therefore, future studies with aerial insectivore bats in the Neotropical region are expected to sample entire nights at different seasons if they are proposed to sample the highest bat richness possible. Moreover, the results of this study also highlight the need for conducting more studies on how seasonality and time of activity affect the detection of specific bat species.

Our inventory vs. literature information

Our literature review provided a list of 80 bat species occurring in São Paulo state (Garbino 2016; Cláudio et al. 2020). In this study, a short-time inventory in three municipalities of São Paulo state using acoustic and mist-net methodologies provided a list of 25 identifiable species, more than 25% of all bat diversity known in the entire state. This highlights the importance of short-time inventories, as they can provide important information about bat fauna and its occurrence. It is also important to emphasise that this is the second study carried out in São Paulo state using acoustic methodologies to inventory bat fauna, the first one being the one carried out by Portfors et al. (2000) at Fazenda Intervales. The 20-year gap between studies offers additional evidence of how bioacoustics has been underused in Brazil. As a consequence, the picture of the aerial insectivore bat fauna at São Paulo state was outdated, as both the acoustic monitoring devices and the knowledge about bats’ echolocation had greatly advanced. For example, at the time of of the study of Portfors et al. (2000), there were no echolocation keys available for Neotropical bats (López-Baucells et al. 2016; Arias-Aguilar et al. 2018), so these authors were limited to identify only the species they were able to record from individuals sampled with mist-nets. Moreover, the ultrasound
detector used by the authors was a Zero-crossing detector, which is not able to store some information about bats' echolocation that can be useful to species identification, such as amplitude and harmonics (Corben 2002).

Looking at the species recorded by Portfors et al. (2000), who recorded 17 species, only three species were not recorded in our study (Peropteryx macrotis, Furipiterus horrens, and Histiotus velatus). However, the authors recorded all three species with mist-nets and harp traps erected at buildings and caves that were used as roosts, a methodology not used in this study. This highlights the importance of using the most varied sampling methods possible to have a complete picture of the local bat fauna (MacSwiney et al. 2008; Silva and Bernard 2017). When the use of many different methodologies is not possible, researchers should try at least to include acoustic monitoring, as this method can provide consistent information about aerial insectivore bats (Rydell et al. 2002; Silva and Bernard 2017). Another alternative would be the deployment of specialists’ teams to survey in the same area with different methods. There are advantages and disadvantages in both cases. Using two different methodologies at the same time is resource-saving, but it requires researchers able to work with both methods and higher involvement of these researchers to deal with the triage and data analysis of both methods. If there are specialists’ teams focused on individual methodologies, researchers need to have experience only with the sampling method they are working on. However, this alternative is much more expensive as it demands a higher quantity of human resources specialised in different fields of study.

Considering the scarce number of acoustic studies in São Paulo state, it is probable that future studies using this methodology will obtain new information about bats, not only species new to the state but also other ecological meaningful data on foraging activity and behaviour, for example (Bernard et al. 2011). Another fact that is important to be mentioned is the acoustic sampling effort of this study. Time expansion detectors (as the one used here) cannot sample echolocating bats while reproducing/storing a detected ultrasound, resulting in a useful sampling of only ~10% of the active monitoring time (Limpens and McCracken 2002). In this study, for example, with 2 hours of active monitoring in each sampling site (130 min) we had only ~13 minutes of effective acoustic sampling in each site. This means that the aerial insectivore bat fauna of São Paulo state remains under-represented. Future studies using real-time detectors and passive monitoring are expected to record much more activity and diversity of these animals, as they are capable of sampling the acoustic environment for several hours (Oliveira et al. 2015; Appel et al. 2019). Unfortunately, only a few studies using acoustic monitoring in Brazil have used passive real-time monitoring (Oliveira et al. 2015; Appel et al. 2019). This scenario is expected to change as real-time detectors become more accessible, and considering the advantages these devices provide in time sampled and resource-saving at the field. However, as observed in this study, even with a small sampling effort it is possible to detect a representative portion of the bat assemblage. We therefore hope future studies will focus on acoustic monitoring of aerial insectivore bats in São Paulo and other Brazilian states, as knowledge of this subset of the bat fauna is still underrepresented in the country.
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Ethical statement

This study followed the animal bioethics protocols proposed by the American Society of Mammalogists (Sikes 2016). A licence to collect and handle bats was also obtained with Brazilian legal authorities (ICMBIO process: 50363-2).

Data Availability Statement

The data that support the findings of this study are available at Figshare and can be accessed via the link <https://figshare.com/projects/The_tradition_vs_innovation_comparing_bioacoustics_and_mist-net_results_to_bat_sampling/122656>.

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