Comparing insectivorous bat community structure between locally defined forest types in the Ecuadorian Amazon

A project submitted in partial fulfilment of the requirements for the degree of BSc (Hons) Animal Behaviour

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Abstract

Deforestation is a widespread driver for a decline in biodiversity. Bats are particularly susceptible to changes in forest habitat due to their wing adaptation and foraging habits and have become a good indicator of environmental disturbance. Aerial insectivorous species can be sampled best with acoustic methods and species identification is possible due to the variability in call frequency. Ecuadorian bat fauna is rich but largely unsampled via acoustic techniques. Thirty two whole nights of data were recorded across 8 forest plots, consisting of locally defined primary and secondary forest types in the buffer zone of the Sumaco Napo-Glaeras national park. Using manually verified echolocation data, species richness, diversity and activity pattern variation were assessed to compare community structure across the two forest types. Ten species, 3 phonic groups and 2 unknown species were identified. There was no significant difference in the community structure between the two forest types, there was however a significant different amongst sites within forests. It is evident that complex site-specific habitat features are likely to have had a significantly effect on activity levels and species richness of the aerial insectivorous bat assemblages.

Keywords: Chiroptera, Ecuador, Neotropics, Acoustic monitoring, Echolocation, Community structure,

1. Introduction

Globally, over the past 300 years there has been a net forest loss of ~ 7-11 million km^2 primarily for logging and agricultural use (Foley et al. 2005). Deforestation is accounting for a disproportionate loss of biodiversity even in relatively unmarred areas of forest, with southeast Asia (Borneo), central-western Amazon and Congo Basin highlighted as high risk hot spots where the number of threatened forest-exclusive species is predicted to rise to ~121-219 over the next 30 years (Betts et al. 2017). Even 'preserved' patches of primary forest hold a lower conservation value (retaining 46-61%) than would be expected due to the impact of human disturbance (selective logging, wildfires, edge and isolation effects) meaning highly sensitive forest species are still under significant threat (Barlow et al. 2016). Loss of suitable habitat to sustain species populations is leading to an increased risk of extinction in vertebrates (Powers & Jetz 2015; Ceballos et al. 2015; Ceballos et al. 2017). The IUCN (International Union for Conservation of Nature) Red List of Threatened Species estimates that ~25% of land mammals (5282 spp.) are classified as threatened (Schipper et al. 2008; Hoffmann et al. 2011). Chiroptera is the 2nd largest Mammalia family with 1150 species and ~172 species of bat are considered threatened by extinction (Welch & Beaulieu 2018). These mammals have been on earth for over 50 million years, according to fossil records (Phil Richardson 2002), and play an active role in forest communities suppressing insect populations, pollinating flowers, and dispersing seeds as well as nutrient and energy cycling via their guano (Kunz et al. 2011). They have become popular indicators of environmental disturbance due to the species richness (Cunto & Bernard 2012) and this diversity peaks in the neotropics with at least 83 genera and 288 species represented (Mickleburgh et al. 2002) across 8 families: Emballonuridae, Phyllostomidae, Mormoopidae, Noctilionidae, Furipteridae, Thyropteridae, Molossidae and Vespertilionidae.

Bats have adapted to take advantage of different features and habitat types within neotropical forests. Fast flying bats (aerial insectivorous bats) have narrow wings which are adapted for foraging in open spaces and around forest edges where manoeuvrability requirements are low, and bats with high manoeuvrability, as a result of broad and short wings, are well adapted to inhibit the forest ground/sub canopy which is a cluttered environment (Heller & Volleth 1995; Kalko et al. 2008; Froidevaux et al. 2014). Selective deforestation can lead to more edges/forest fragments/open space which might be challenging for species with wing adaption suited to cluttered forest (Rocha, Ovaskainen, et al. 2017). Likewise open space/edge specialists might struggle in a cluttered environment (Marques et al. 2015). Changes in forest habitat is likely to result in a change in diversity and bat community, whilst secondary forest is significant to bat communities, primary forest is of irreplaceable value to tropical biodiversity (Rocha, López-Baucells, et al. 2017).

Echolocation calls are extremely variable and will differ depending on foraging tactics, habitat type, environmental conditions, present /absence of conspecifics (social calls), geographical location, age of the bat and sex (Biscardi et al. 2004). Aerial insectivorous bats will hawk/catch moving insects on the wing and produce low/intense frequency modulated (FM), constant frequency (CF), or quasi constant frequency (QCF) calls (Moss et al. 2011; López-Baucells et al. 2016) which allow them to detect prey at longer distances. The gleaners which pick static insects off vegetation or other surfaces generally produce high-frequency, short FM calls which delivers details on the near environment but has limited long range detection. The frequency of these calls makes them difficult to detect and the bats are so called ‘whispering’ bats because of this feature. This group is predominantly populated by bats of the Phyllostomidae family, the most species-rich accounting for 60-70% in neotropical bat assemblages (Rex et al. 2008), which are found foraging within the vegetation at sub canopy level (Brinkløv et al. 2009).

Species which are adapted for foraging in the forest are best sampled with mist netting (Phyllostomidae family species plus *Pteronotus parnellii* from the Mormoopidae family). The aerial insectivorous species (hawkers) which forage in open space, above the canopy and at forest edges are notoriously difficult to catch with mist nets and so acoustic surveying is the most suitable sampling method for these bats (Silva & Bernard 2017; Arias-Aguilar et al. 2018). Mist netting was the only sampling technique (used for over 100 years; MacSwiney G et al. 2008), before acoustics sampling was available which has resulted in a sampling and research bias towards Phyllostomidae bats. Acoustic monitoring of neotropical bats was rare 10 years ago but has started to gain some popularity due to improvements in technology with passive acoustic detectors (Kalko et al. 2008). However, studies are still limited to a few localities in Central and South America (Mexico, Panama, Costa Rica, Honduras, French Guiana, Ecuador, Chile and Brazil) (Arias-Aguilar et al. 2018). Ecuador ranks 4th highest in terms of South American mammalian diversity (McDonough et al. 2011) with bats accounting for ~40% of this with 160 species. Proportionally, Ecuadorian bat communities are unstudied in terms of globally accessible literature (Webster & Jones 1984; Rex et al. 2008; McDonough et al. 2011) although limited local research is available (Tirira & Burneo 2012).

Further research is needed to identify if species rely on undisturbed forest or have adapted to disturbed habitats within the forest (Sampaio et al. 2003). Acoustic data provides valuable insight into the understudied aerial insectivorous bat communities, informing activity patterns, use of space and resources, species richness and distribution (Skalak et al. 2012; Froidevaux et al. 2014). This is the first acoustic study of the aerial insectivorous bat community in the San Jose de Payamino district which will compare community structure across locally defined forest types and contribute to Ecuadorian bat research.

1.1 Aims & objectives

This project compared bat assemblage structure across locally defined primary and secondary forest in the Ecuadorian Amazon. Specifically, the objectives were:

1. Primary: To compare community structure of aerial insectivorous bats between the two forest types, specifically by;
    a. Comparing community structure using multivariate analysis of all species data
    b. Comparing simple richness and diversity measures
    c. Compare activity patterns of species across the night
2. Secondary: To validate acoustic identification of aerial insectivorous species / phonic group echolocation calls.

2. Methods

2.1 Study area and site selection

Field surveys were conducted in July 2018 in the San Jose de Payamino district (UTM: 18M 0028983 07717102) located in the buffer zone of the Sumaco Napo-Glaeras national park (SNGNP), an IUCN category II PA (Oldekop et al. 2012), within the Sumaco Biosphere Reserve (SBR)(Fig.1.). The local indigenous (Kichwa) community (Torres et al. 2018) defined the primary and secondary forest types. Primary forest was undisturbed fragments and secondary forest was exposed to varying levels of human disturbance (selective logging, walkways, near human inhabitations, agricultural plots etc.) Each forest plot was 0.5km^2. Four consecutive nights monitoring was conducted in each plot at two randomly selected sampling sites within the plot. Primary and secondary plots were sampled concurrently. (Primary forest plots were existing research sites. To enable reference to other studies using those sites, plot naming convention has been retained here. Plot P1 was not surveyed during this project due to its proximity to plot P2.)

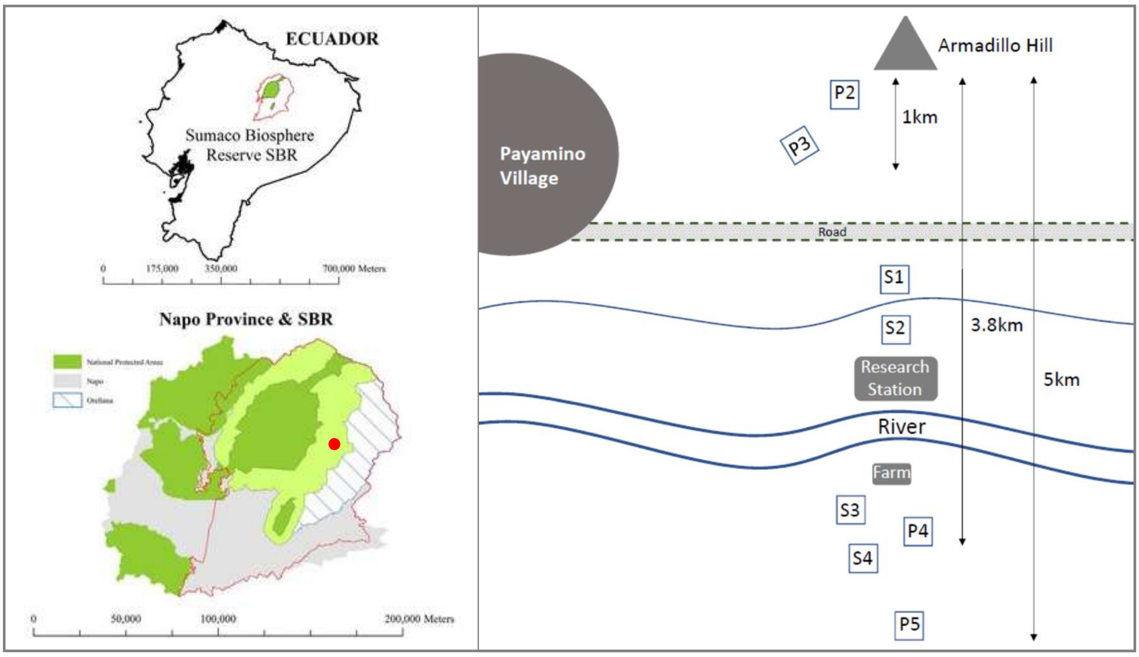

Fig. 1. Locally defined primary (P) and secondary (S) sampling plots located within the district San Jose de Payamino (red dot) in the buffer zone of the Sumaco Galeras National Park. Ecuador & Napo Province Map (Torres et al. 2018).

2.2 Acoustic surveys

Bat echolocation calls were captured using Song Meter SM4Bat FS paired with omnidirectional ultrasonic SMX-US microphones (Wildlife Acoustics, Maynard, Massachusetts, USA). The following recording settings were used; trigger level: 12kHz, min trigger frequency: 16 kHz, sample rate: 256kHz, gain: 12dB, min duration: 1.5ms, max duration: none and no compression. At the randomly selected site within the plot, the detector was attached to a tree with rope and the microphone held with bungee cords at a height of approximately 3m above the ground. The microphone in each case was positioned to gain optimal recordings within the understory and subcanopy space. The latitude and longitude settings on the SM4 recorders were left at zero due to the site location in relation to the equator. Recordings started 30 mins prior to sunset and continued until 30 mins after sunrise, recording 13 hours each day. Detectors remained in standby mode during the day to conserve batteries. The detectors were alternated between primary and secondary sites (following the 4 consecutive nights sampling across the 2 sites within each plot) when they were moved to avoid possible bias (Froidevaux et al. 2014). One detector failed in the second sample site in plot P4.

2.3 Acoustic analysis

Recordings were analysed with Kaleidoscope Pro Analysis Software (Wildlife Acoustics, USA). The files were processed and matched against auto ID Bats of the Neotropics 4.3.0, set to -1 More Sensitive (Liberal), Ecuadorian species list. A successful sequence, referred to as a ‘bat pass’ (Fenton, 1997), was included if it contained at least 5 echolocation calls, any bat passes with <5 echolocation calls were removed. Each bat pass was manually verified using both audio playback at 1/8 normal speed and visualisation via a spectrogram.

Recordings with multiple species within single files were marked ‘MultiBat’ and removed, so there was no evidence of conspecifics (Biscardi et al. 2004) only bat passes with <1 interspecific call were left in for analysis. Bat passes where call shape could not reliability be distinguished to species level or phonic group were marked ‘NoID’. There were issues distinguishing between the calls of *Eptesicus brasiliensis* and *Eptesicus furinalis* due to the low frequency and similar structure, so consequently they were classified as a phonic group, *Eptesicus* species (*Eptesicus* spp.). There were similar difficulties distinguishing the calls of *Molossus sinaloae* and *Molossus rufus* and these were grouped together into *Molossus* species (*Molossus* spp.). There were also a limited number of recordings which could only be identified into the group Molossidae species (Molossidae spp.): *Eumops glaucinus*, *Nyctinomops laticaudatus* and *Tadarida brasiliensis*. Bat pass identification was following methods of López-Baucells et al. (2016). There were also two groups of calls which could not be identified but the sound and call variables were similar in pattern and structure. These bat passes were grouped into unknown species 1 (Unknown sp.1) and unknown species 2 (Unknown sp.2). Twelve call parameters were extracted from the bat pass recordings automatically using Kaleidoscope software: number of calls (N), average duration of the calls, (Dur), time between calls (TBC), minimum frequency (F_{min}), maximum frequency (F_{max}), mean frequency (F_{mean}), characteristic frequency (F_c), characteristic slope (S_c) the frequency of the ‘knee’ of each call (F_k), time to the ‘knee’ (T_k), initial slope of the call (S_1), time to characteristic (T_c) and the quality of the call was also included (Qual %).

2.4 Statistical analysis

The recording of echolocation calls was an essential part of the experimental design which allows presence and absence and the level of bat activity to be monitored, facilitating comparison of community structure across forest types. It is not possible to generate a true count of individuals using acoustic monitoring, so activity was recorded based on number of bat passes (Rowse et al. 2016). All statistical and descriptive analyses were conducted using Microsoft Excel and R version 3.4.2 (R Core Team, 2015). In total 7412 bat passes were analysed.

It was important to validate the echolocation calls and so descriptive statistics (mean ± SD, coefficient of variation and minimum-maximum range) were calculated to facilitate future comparisons across literature. The 8 call variables (N, F_c, S_c, Dur, F_{max}, F_{min}, F_{mean}, TBC) were $\log_{10}$-transformed, standardised to a mean of zero and a standard deviation of one, and using the PCA function in base R, a Principal Component Analysis (PCA) enabled visualisation of the species and phonic groups. The number of bat passes recorded at each hour period, across the whole night was separated out by species / phonic group for each sampling night across every site and visualised via histograms in Excel (Appendix). The consolidated data for the two forest types were included in results. No statistical tests were run on this data, the activity level was used to provide context to the community structure analysis. Species richness and Shannon-Weiner diversity indices (Magurran 2003) were calculated for each of the plots (P2; P3; P4; P5; S1; S2; S3; S4) to compare relative abundance of bat species between forest types. The diversity indices were based on total bat passes for each species. To test for variation in species composition across the forest types, non-metric multi-dimensional scaling (NMDS) ordinations were calculated using the Bray-Curtis dissimilarity matrix. To assess the statistical significance of the observed differences across the forest sites, a nested ANOVA which uses pseudo-F values, was used to compare richness and diversity between forest types and within-site. Species community structure was compared between forest types using an Adonis test. Species richness, species diversity and Adonis test were calculated using the “vegan” package in R (Oksanen et al. 2015).

3. Results

A total of 25,8885 recordings collected by 2 detectors on 32 sample nights in July 2018 generated 18,101 recordings of which 7142 were analysed. Ten species, 3 phonic groups and 2 unknown species were identified; *Centronycteris centralis*, *Diclidurus ingens*, *Lasiurus blossevillii*, *Lasiurus cinereus*, *Lasiurus ega*, *Molossus molossus*, *Myotis nigricans*, *Myotis riparius*, *Saccopteryx bilineata*, *Saccopteryx leptura, Eptesicus spp., Molossus spp.*, Molossidae spp., Unknown Species 1 and Unknown Species 2. Three families were represented Emballonuridae, Molossidae and Vespertilionidae and the family calls as a percentage of total calls was 63%, 4%, and 31% respectively.

3.1 Echolocation calls

The visual checking of the calls revealed that some species consistently produced similar echolocation calls whilst others varied significantly (Table 1). *Centronycteris centralis* produced calls in a continuous stream around 40kHz which were easily identifiable (Fig. 2.a). The auto ID program identified all the *Diclidurus* species calls as *Diclidurus albus.* This species calls at around 26 – 30kHz. During manual verification it was found that the calls were much lower between 19 – 20 kHz, which is consistent with *Diclidurus ingens*. *Lasiurus blossevillii* and *Lasiurus ega* are both Vespertilionidae species. They have similar calls with a downward modulated frequency (FMd) and can be irregular and in alternating sequences. *L. blossevillii* call at higher frequencies (Fig. 2.b) than *L. ega* which is evident from the F_{max} ,F_{mim} and F_{mean} statistics. There was some uncertainty when verifying *Lasiurus cinereus* calls. These calls were all very low frequency, circa 15-16kHz, however the auto ID classifier grouped them together which was accepted due to the similarity of the call features and lack of credible alternative. *Molossus molossus* and *Molossus* spp. calls were easily identifiable with the pattern of 3 calls, scaled from lower, intermediate to a higher frequency call (Fig. 2.c). The calls are mainly quasi constant frequency and sometimes the third (highest frequency) call is missing. *Molossus molossus* could be distinguished from the *Molossus* spp. phonic group due to calls being higher in frequency. The start pulse would start at ~35kHz, compared to *Molossus* spp. which started ~25-30kHz. Species within *Molossus* spp. were undistinguishable from each other during manual verification. A third phonic group contained 3 Molossidae species (Molossidae spp; *Eumops glaucinus, Nyctinomops laticaudatus* and *Tadarida brasiliensis)* all with very low frequency calls which were again difficult to distinguish. *E. glaucinus* calls seem to be continuous low frequency calls with constant energy, displayed as red on the spectrogram. *Tadarida brasiliensis* calls were circa 20-27kHz and are responsible for the higher frequency statistics which are slightly out of the range of what is expected for this group (18-22kHz). Two *Myotis* species were identified. Most of the calls were verified to be *Myotis nigricans* (Fig. 2.d), however there were 2 calls which were too high in frequency to be that species (> 55kHz). These 2 calls were retained in the data set and identified as *Myotis riparius*. *Saccopteryx bilineata* and *Saccopteryx leptura* produce similar alternating calls, lower and higher and were quite easily identifiable. *S. bilineata* (Fig. 2.e) are lower in frequency (42-45kHz) compared to *S. leptura* (48-55kHz). The two unknown groups were low frequency calls, with no discernible call shape when visualised. However, the calls within the two groups were consistent with each other.

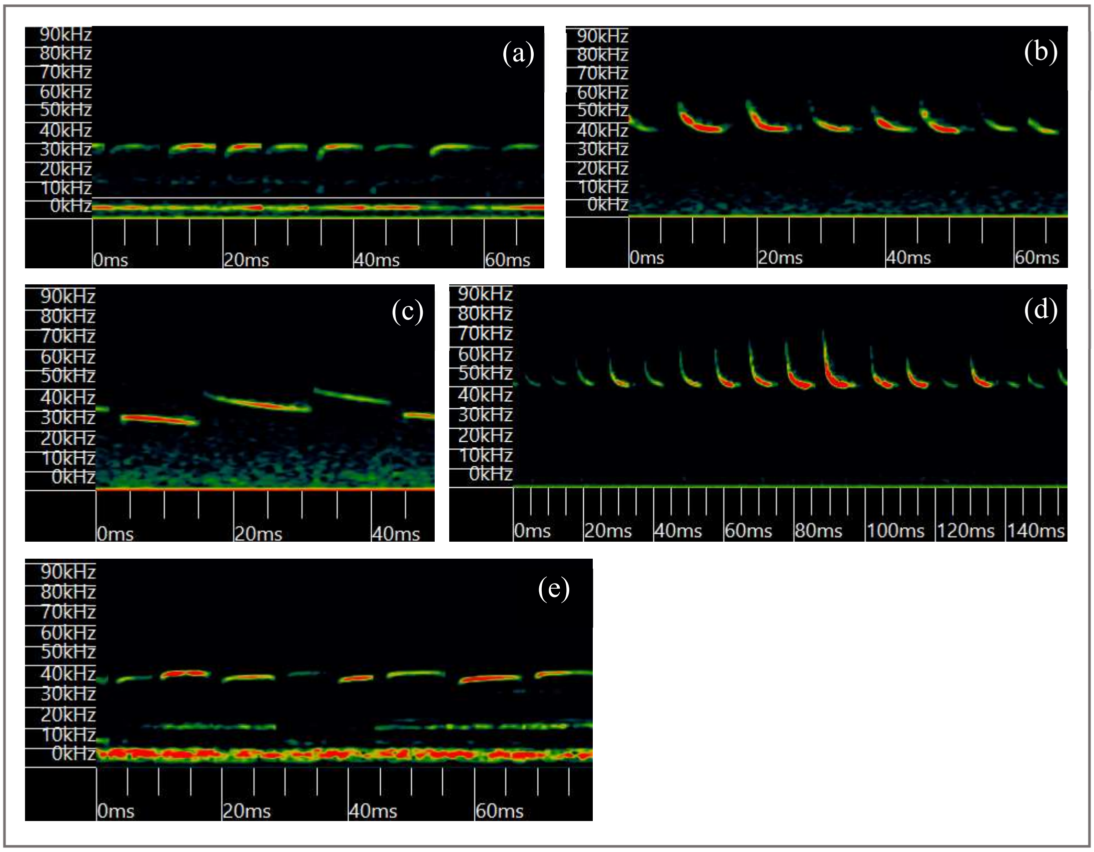

Fig. 2. Screen shots of spectrogram of echolocation calls from (a) *C. centralis*, (b) *L. blossevillii*, (c) *M. molossus* (d) *M. nigricans* (e) *S. bilineata*

Most of the call variation was explained by the first two components in the PCA (Fig.3). The first component explained the highest percentage of the variation (55.2%). The plot of these components displays a clear grouping of calls identified to species / phonic group which provides confidence that the auto ID and manual verification process has been successful. There is significant overlap of two species, *M. nigricans* and *L. blossevillii* which would be expected as their calls have significant overlap around the 45kHz frequency.

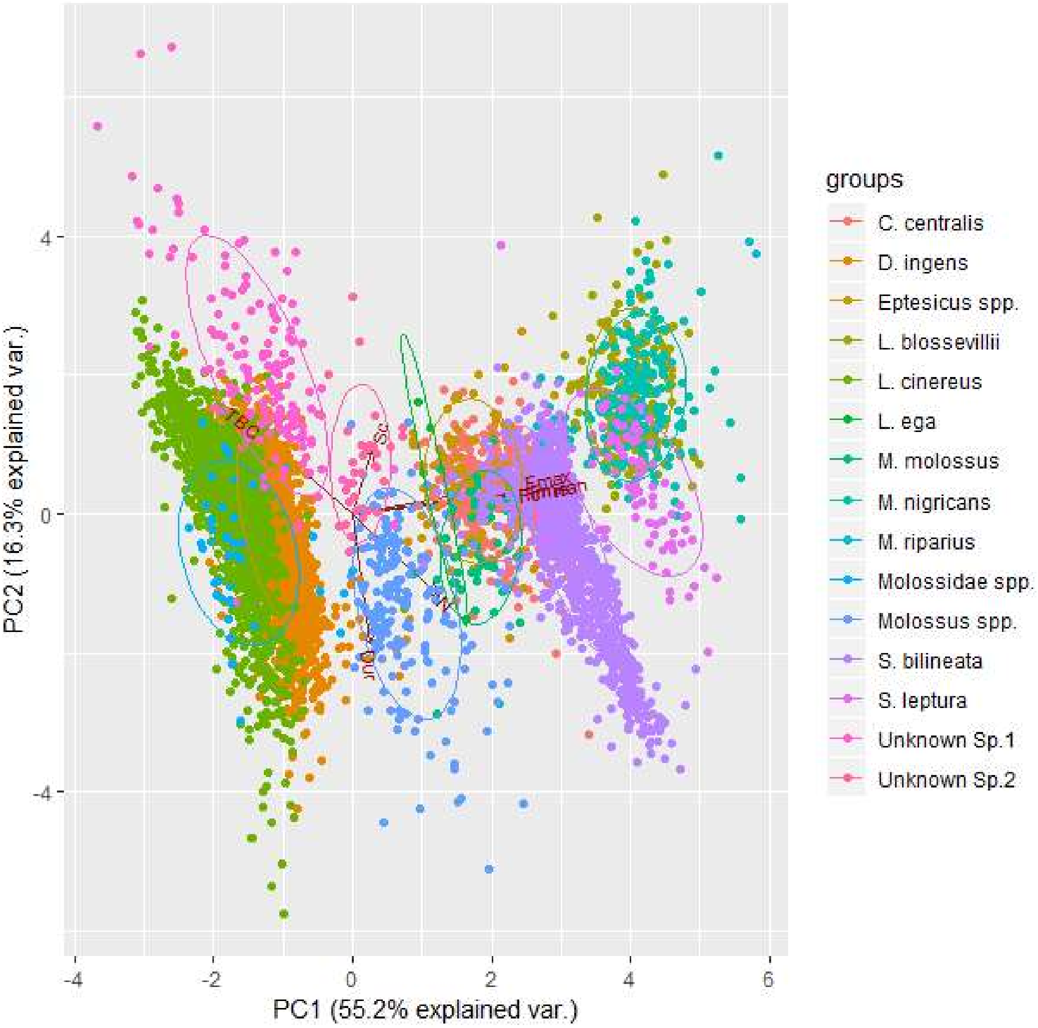

Fig. 3. Plot of the first and second principle component scores of a PCA based on 8 call variables (N/Fc/Sc/Dur/Fmax/Fmin/Fmean/TBC) which explain 71.5% of variation in calls.

Table 1. Descriptive statistics of call variables, where *n* = sample size (number of bat passes), N = number of calls, F_c = characteristic frequency, S_c = characteristic slope, Dur = duration of call (ms), F_{max} = maximum frequency, F_{min} = minimum frequency, F_{mean} = mean frequency, TBC = time between calls (ms). Means ± SD are included, followed by CV (coefficient of variation) and min-max (the range).

Species/ phonic group	*n*	Call Variables							
		N	F_c	S_c	Dur	F_{max}	F_{min}	F_{mean}	TBC
C. centralis	386	24.3 ± 18.7	39.6 ± 2.3	-4.6 ± 8.8	3.8 ± 0.5	40.2 ± 2.3	37.1 ± 2.4	39.3 ± 2.3	273.1 ± 116.3
		76.7	5.7	-190.6	12.5	5.7	6.3	5.8	42.6
		5-157	31.1-94.9	-34.2-31.6	2.4-5.8	31.6-45.8	29.2-43.6	30.9-44.7	73.7-778.8
D. ingens	2940	13.7 ± 9.9	20.3 ± 0.9	0.3 ± 8.3	4.2 ± 1.2	20.8 ± 0.9	19.9 ± 0.9	20.3 ± 0.85	511.8 ± 349.1
		72.2	4.2	2544.9	27.5	4.1	4.3	4.2	68.2
		5-95	18.1-29.3	-49.6-41.2	2.2-10.7	18.4-29.7	17.7-28.6	18.1-29.1	15.6-2747.7
Eptesicus spp.	83	23.0 ± 19.4	34.5 ± 1.6	23.1 ± 9.7	4.8 ± 0.8	41.9 ± 3.8	33.9 ± 1.5	36.3 ± 2.0	291.8 ± 118.8
		84.5	4.6	42.1	16.2	9.1	4.5	5.4	40.7
		5-87	30.6-38.6	-3.9-50.7	2.7-6.8	35.0-58.7	30.2-38.3	32.4-43.4	111.9-619.1
L. blossevillii	194	19.7 ± 14.9	47.4 ± 0.9	25.8 ± 15.2	3.6 ± 0.7	59.6 ± 6.1	46.7 ± 0.9	49.9 ± 1.4	175.1 ± 119.7
		75.2	1.8	59.0	18.8	10.3	1.8	2.9	68.4
		3-94	42.0-49.5	-20.1-96.3	2.4-5.8	46.6-73.8	41.5-48.7	43.0-54.2	56.5-1043.7

L. cinereus	1689	14.4 ± 10.1 70.5 5-93	18.0 ± 1.2 6.6 14.3-28.9	1.5 ± 7.2 476.9 -27.2-36.0	4.0 ± 1.3 32.4 2.2-13.3	18.4 ± 1.2 6.7 14.5-29.3	17.7 ± 1.1 6.4 14.1-28.0	18.0 ± 1.2 6.6 14.3-28.8	832.6 ± 497.5 59.7 42.5-3404.5
L. ega	4	17.0 ± 18.1 106.3 6-44	32.7 ± 0.5 1.5 32.1-33.1	20.3 ± 1.4 7.1 -19.1-22.3	4.6 ± 1.7 37.3 3.4-7.1	36.3 ± 1.7 4.6 35.1-38.8	32.2 ± 0.6 1.7 31.7-32.9	33.6 ± 0.3 0.9 33.2-33.9	327.3 ± 162.1 49.5 198.1-564.5
M. molossus	54	16.9 ± 10.2 60.4 6-49	37.6 ± 1.9 5.0 32.7-42.1	7.0 ± 5.7 82.1 -13.6-27.3	5.8 ± 1.2 21.3 3.1-10.0	38.8 ± 2.1 5.3 33.8-44.0	36.6 ± 2.1 5.7 30.8-41.4	37.7 ± 2.0 5.3 32.9-42.2	253.6 ± 115.0 45.3 83.5-692.2
M. nigricans	212	22.6 ± 10.2 80.5 4-122	48.3 ± 1.7 3.5 39.9-52.6	24.7 ± 16.2 65.8 -46.3-107.5	3.7 ± 0.7 18.2 2.5-5.3	58.7 ± 5.6 9.6 46.3-75.1	47.6 ± 1.7 3.5 39.5-51.2	50.5 ± 2.0 4.0 41.6-55.8	193.4 ± 107.4 55.5 54.7-629.8
M. riparius	2	6.5 ± 3.6 54.4 4-9	60.0 ± 0.1 0.2 59.9-60.1	41.4 ± 1.3 3.2 40.5-42.3	2.5 ± 0.1 2.7 2.4-2.5	71.4 ± 1.3 1.7 70.5-72.3	59.5 ± 0.5 0.7 59.2-59.8	62.6 ± 0.4 0.6 62.4-62.9	402.8 ± 6.34 1.6 398.3-407.3
Molossidae *spp.*	42	13.6 ± 7.6 55.4 5-37	16.9 ± 3.5 20.6 13.6-26.0	2.4 ± 7.6 319.7 -11.3-23.1	4.5 ± 1.4 30.6 2.6-8.4	17.5 ± 4.2 24.2 13.8-29.0	16.5 ± 3.3 20.1 13.5-24.4	16.9 ± 3.7 21.5 13.6-26.1	357.3 ± 366.9 102.7 22.2-1464.0

Molossus spp.	181	26.2 ± 21.6 82.4 5-118	30.4 ± 2.3 7.4 26.0-39.2	4.4 ± 9.5 217.3 -25.1-35.0	6.3 ± 1.8 29.3 3.0-12.0	31.6 ± 2.6 8.3 26.5-40.2	29.4 ± 2.2 7.5 25.1-38.2	30.4 ± 2.3 7.6 25.8-39.2	271.6 ± 117.1 43.1 77.0-717.1
S. bilineata	1078	45.1 ± 40.3 89.2 4-169	44.6 ± 1.6 3.5 32.0-51.1	-5.3 ± 6.4 -121.7 -46.0-36.0	4.5 ± 0.8 18.2 2.5-8.7	45.2 ± 1.6 3.5 32.5-51.8	42.8 ± 1.6 3.7 31.0-49.1	44.3 ± 1.6 3.5 31.8-47.6	215.2 ± 120.2 55.9 56.9-1272.8
S. leptura	89	35.4 ± 27.6 78.2 5-117	51.7 ± 3.0 5.7 32.3-54.2	-6.5 ± 7.7 -119.7 -27.7-15.8	3.9 ± 0.7 17.5 2.5-5.6	52.4 ± 3.0 5.6 33.3-54.8	49.5 ± 2.9 5.8 31.7-52.8	51.3 ± 2.9 5.7 32.4-53.9	314.1 ± 331.2 105.4 82.4-2710.7
Unknown Sp.1	151	7.0 ± 3.6 51.9 3-21	24.7 ± 0.9 3.5 22.5-29.7	0.1 ± 21.9 18445.3 -103.3-71.1	2.7 ± 0.4 16.5 2.1-5.0	25.6 ± 1.0 3.7 23.3-30.8	23.9 ± 0.8 3.5 22.0-29.0	24.6 ± 1.0 3.9 18.7-29.6	1954.6 ± 1188.3 60.8 19.8-6222.5
Unknown Sp.2	37	15.8 ± 7.2 45.5 6-27	28.4 ± 1.2 4.3 25.6-30.3	8.5 ± 20.6 244.0 -23.2-71.8	3.6 ± 0.5 13.4 2.9-5.0	29.3 ± 1.1 3.7 26.7-31.4	27.6 ± 1.3 4.5 25.0-29.3	28.5 ± 1.2 4.0 25.8-30.2	563.6 ± 332.7 59.0 15.7-1456.0

3.2 Activity patterns

The activity patterns between the primary forest and secondary forest are distinct (Fig. 4.). Within primary forest there is a peak around 6pm followed by a sharp decline and then a slow increase in activity up to midnight which again drops slightly around 2am only to increase and peak at between 3am and 4am before declining again before dawn. *Diclidurus ingens* and *L. cinereus* dominate the primary forest with *C. centralis* and *S. bilineata* also having a significant presence, however these species have increased activity early in the evening (6-7pm) and then just before dawn (5-6am). In the secondary forest there are a significant number of species present and active between 6-7pm, however bat passes numbers are low during this period. This trend continues throughout the night with different species present but with low bat pass activity. *Diclidurus ingens* appears to dominate the secondary forest type also, with significant activity up to midnight, a reduction around 1am before increasing again, although not to the previous peak activity level, and maintaining activity until 5am. *Lasiurus cinereus* and *S. bilineata* also have a significant presence in the secondary forest type.

3.3 Community structure

Secondary forest plots had slightly higher richness with 14 species / phonic groups in total detected, compared to 12 in primary forest plots. Secondary plot 1 had the highest mean richness (9 spp.) followed closely by secondary plot 3 (8 spp.). Primary plot 4 had the highest mean richness (7 spp.). Secondary plot 2, primary plot 3 and primary plot 5 had low mean species richness with all 3 plots recording < 3 species (Fig.5.). For all sites within forest types, a two-dimensional NMDS ordination adequately shows community variation. There was no significant community structural differences between forest types (ADONIS, *F* = 1.30 p = 0.219), however there was a significant difference among sites within forest types (ADONIS, *F* = 3.23 p < 0.0001).

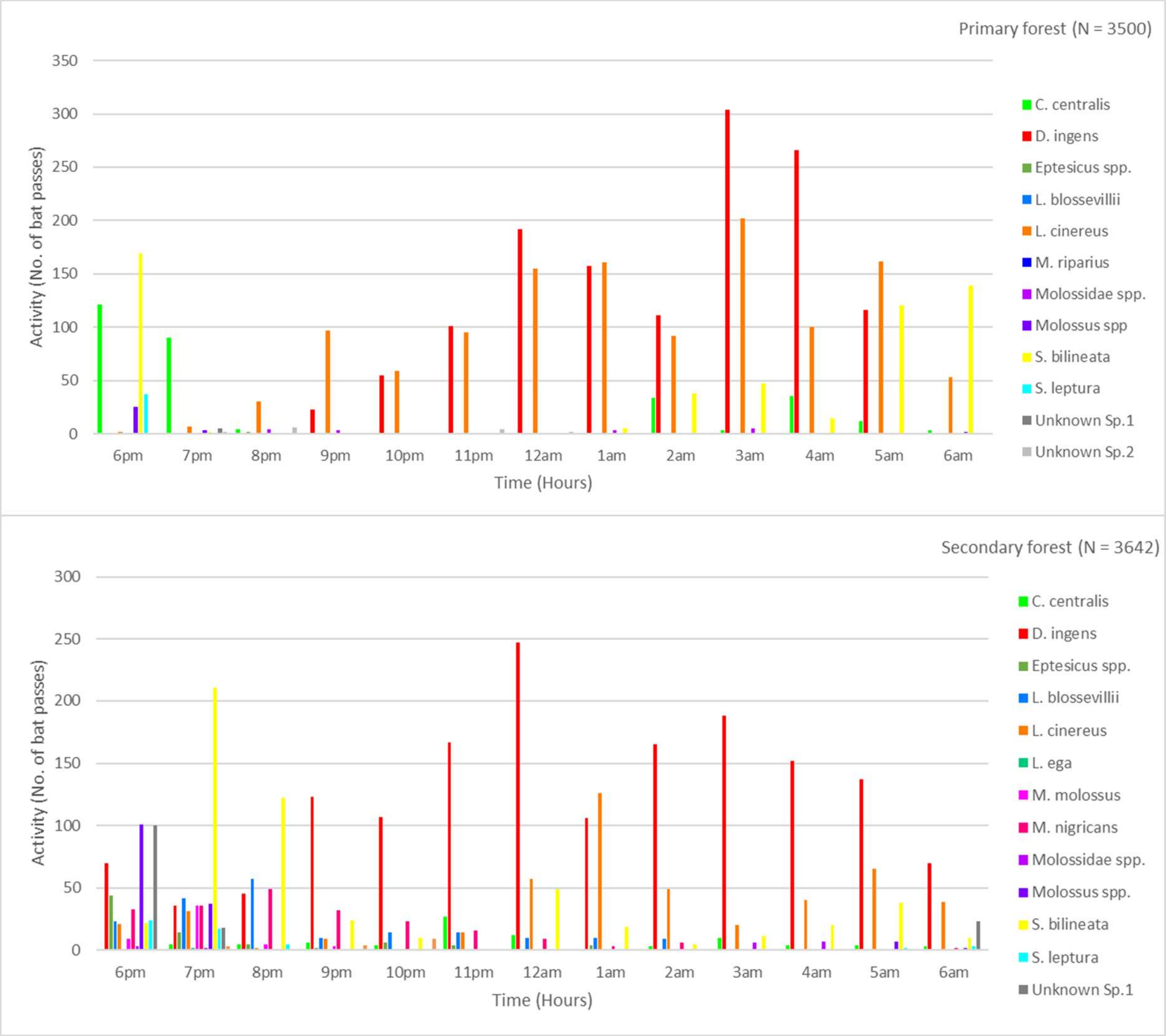

Fig. 4. Consolidated overview of total call activity patterns for all species present in primary and secondary forest types.

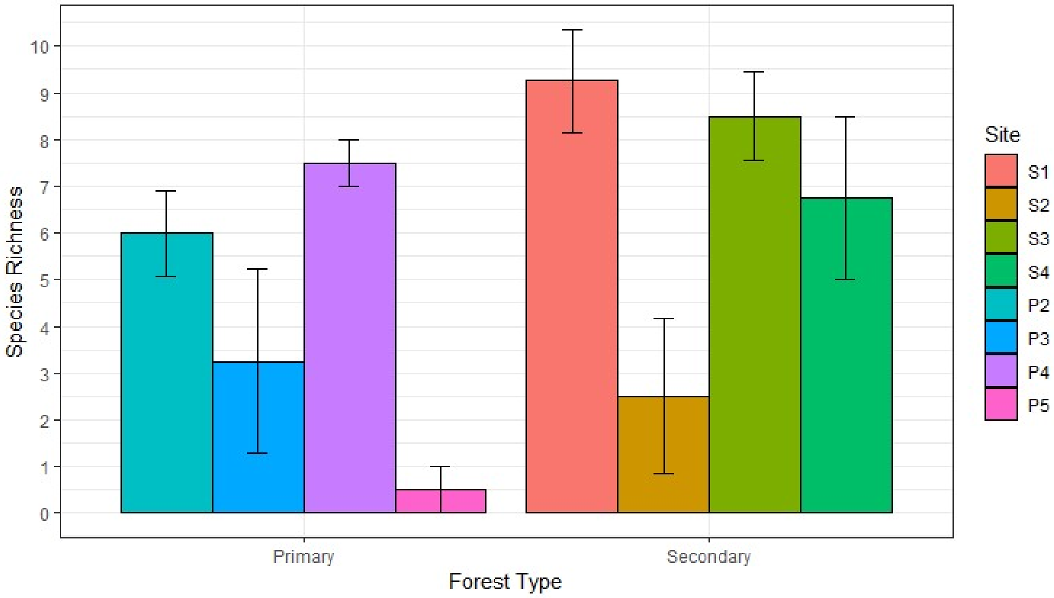

Fig. 5. Average species richness across the 8 different plots within locally defined primary and secondary forest.

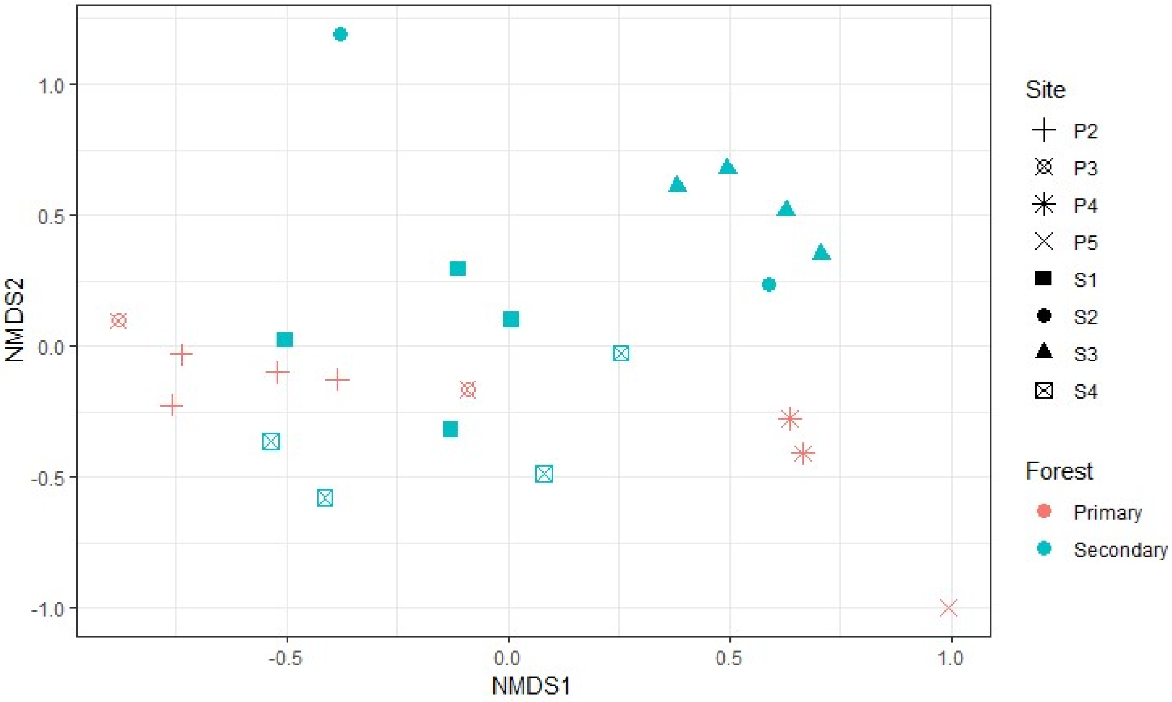

Fig. 6. Arrangement of 23 sampling nights (9 nights yielded no recordings following analysis) along the axes of non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity.

4. Discussion

The echolocation calls show clear grouping on a species / phonic group basis providing validation that the identification method is consistent. There were distinct patterns of activity found between forest types but the individual site variation highlights the complexities of species-specific behavioural ecology. The community structure was not significantly different between forest types but there was evidence of significant differences among sites within forest types, suggesting that aerial insectivorous bat responses to forests are linked to a multitude of ecological factors (diet, morphological traits, home range) that can not be mapped onto simple forest type categories.

4.1 Echolocation calls

Echolocation calls of aerial insectivorous bats were analysed and quantified. PCA analysis showed clear grouping of calls indicating variation across the species / phonic groups. Whilst the clustering was pronounced it is also evident that there is variation in calls within species / phonic groups which agrees with Biscardi et al. (2004). The calls of the Molossidae family species account for just 4% of the total calls which is low compared to the other families. This could be due to sampling technique as Molossidae bats are fast flyers found in the open space above the canopy (Moras et al. 2018). Given the low placement of acoustic recorders in this study, the calls could represent a limited percentage of high intensity calls which passed through the canopy story and were picked up by the detectors (Marques et al. 2015). Findings from Surlykke & Kalko (2008) also found that *M. Molossus* recordings were limited due to their hunting height being further than 10 m from the microphone. All species identified in this study are present in Ecuador apart from *D. ingens*. According to the IUCN (Lim et al. 2016) and

Ecuadorian list of mammals (Ecuadorian Ministry of the Environment, 2015) *D. ingens* has not yet been confirmed present in Ecuador. A review paper (The Emballonuridae family in Ecuador: A geographical and collections records catalogue by Tirira and Arévalo in Tirira & Burneo 2012) gave reason to believe that *D. ingens* might be found in the North West of the country as a natural progression from the Colombian population. These results provide evidence to support this claim. The echolocation call data provides a starting point for building up an Ecuadorian specific acoustic call library.

4.2 Activity patterns

The analysis provides a cumulative overview of the activity patterns across the San Jose de Payamino landscape but the site specific information shows the extent of variation in responses to local site dependent habitat attributes (Kunz 1973; Presley et al. 2009). There was a significant period of rain over the two days of sampling in primary plot 3 site 1 and secondary plot 2 site 1 (Appendix). It is likely that the significant rain fall reduced bat activity over those days, as found by Fenton (1970) and Erickson & West (2013), but not by Scanlon & Petit (2008) who observed no significant difference in activity between rain and no rain fall nights. One consistent theme across most sites was early emergence and activity levels directly after sunset. Although not tested here, this is likely to correlate with increased prey availability and is supported by Jones & Rydell (1994) who found that tropical bats emerge early, in particular, aerial hawkers that need to balance foraging and predator avoidance in open space. These results reinforce the necessity for sampling over the whole night in order to assess the behavioural ecology on a species-specific basis (Skalak et al. 2012; Froidevaux et al. 2014; Zeppelini et al. 2017).

4.3 Community structure

These results document a rich and diverse community structure that, contrary to expectations, isn’t significantly different between forest types but is significantly different amongst sites within forests types. These bat species-specific responses to local habitat features are not unusual and have been found across different forest and urbanised landscapes (Furlonger et al. 1987; Estrada-Villegas et al. 2010; Jung & Kalko 2011; Dawson et al. 2012). Secondary forest plots had slightly higher species richness compared to primary plots (14:12). Seven species were present in the locally described primary forest and 9 species in secondary forest, all three phonic groups and unknown species 1 were represented in both forests, and unknown species 2 was only found in primary forest. There was only one species, *M. riparius*, which was detected in primary forest and not detected in secondary forest plots but only 2 calls were identified for this species leaving it ambiguous over whether this is a correct identification. The 3 species detected in secondary plots that were not present in primary forest were *L. ega*, *M. molossus* and *M. nigricans. Lasiurus ega* is better adapted to foraging around forest edges whilst the other two species are well adapted to open space foraging (Siemers & Kalko 2001; Rydell et al. 2002; Sampaio et al. 2003) and would not be expected to be found in cluttered forest habitat. The species found present across both forests were *C. centralis, D. ingens, L. blossevillii, L. cinereus, S. bilineata and S. leptura. Centronycteris centralis* are predominantly found foraging in small opening within dense forest (Jung et al. 2007), *D.ingens* have been detected foraging at canopy and subcanopy level (Marques et al. 2015)*, L. blossevillii* forage in large gaps or along forest edges (Denzinger et al. 2017), *L. cinereus* prefers canopy cover but will also forage around forest edges (Furlonger et al. 1987) and *Saccopteryx spp*. can be found foraging in the understory and beneath the canopy and the two species often overlap in the same habitat (Kalko & Handley 2001). Plot 4 had the highest species richness of the primary plots, the two sampling sites were located within a patch of undisturbed primary forest between a secondary regrowth patch and a cleared area which was being used for farming. The detectors failed to record for the 2 nights in the second site location, yet this area of forest detected the highest number of different species for primary plots. It also had low levels of bat activity (bat passes (N) = 100). Aerial insectivorous bats can easily take advantage of different areas of the forest due to their powered flight (Marques et al. 2015). This plot might be used as a flyway to connect foraging patches (Rocha, López-Baucells, et al. 2017) which would positively affect the species richness in this plot without the high level of foraging activity (bat passes). High activity levels were observed in primary plot 2 (N = 3056) This pot was dominated by call *D.ingens* and *L. cinereus* which could indicate a preferential foraging area. The bat pass duration length was untested in this study but Kerbiriou et al. (2018) found that bat passes were longer in preferred foraging habitat or sites as the bat was either circling around or meandering through the habitat creating longer recordings. This was compared to relatively short passes by the microphone which might indicate a bat is commuting or passing through the space using it as a 'flyway'. Plot 1 had the highest species richness of the secondary plots, however there wasn't a lot of variance between the number of species present across plot; 1, 3 and 4. As previously discussed, it is presumed that activity in secondary plot 2 was heavily depressed due to the significant rain fall over the two days. All secondary plots had some level of human disturbance including; walk ways, forest edges, selectively logged clearings. However, secondary plot 4 had particularly dense vegetation and canopy cover with very limited human disturbance. It was arguably more similar to primary forest type and the comparable species richness would support this.

It is evident that complex local-scale habitat features, which were not measured in this project including flyways, edge effects, canopy cover, open spaces and dense vegetation (Gorresen & Willig 2004; Ferreira et al. 2017; Rocha, López-Baucells, et al. 2017) are likely to have had a significant effect on activity levels and species richness. Between forest types there was no significant difference between the species richness and overall activity levels. The question must then be asked, how different were the locally defined primary and secondary plots? The forest types in this study were identified by the local community and may represent low levels of differentiation in this area or reflect a discriminating factor important to local humans but that is not relevant to bat activity. Bat responses to habitat disturbance are varied and species-specific (Medellín et al. 2000) (Bernard & Fenton 2007)(Castro-Luna et al. 2007)(Klingbeil & Willig 2009). Some species are more tolerant, others more sensitive but forest cover has been suggested to be the best predictor of species richness (Rocha, López-Baucells, et al. (2017). There is evidence however to suggest that some small human disturbances and integrated forest types (primary and secondary) on a large scale is not detrimental as it can support a wider range of species than one forest type alone (Rocha, Ovaskainen, et al. 2017) (Willig et al. 2019).

5. Conclusions

In conclusion, the aerial insectivorous bat community structure of San Jose de Payamino was diverse and not significantly different between the two locally defined forest types. Across the plots there were complex and species-specific responses in terms of activity levels and species presence/dominance. These acoustic surveys have provided valuable information about the aerial insectivorous species of bats in the buffer zone of the Sumaco Galeras National Park in Ecuador and support the conservation efforts to limit human disturbance which on a small scale does not seem to be having a detrimental effect on the bat fauna.

6. Future work

This study would recommend further investigation into the presence of *Diclidurus ingens*. Visual verification might be possible as the 'Greater ghost bat' is usually distinct in flight given its white fur. However, catching and measuring would confirm the presence of this species. This could be achieved via mist net surveys which would also allow the Phyllostomidae family to be sampling which are not detectable via acoustic surveying. To gain a complete understanding of the bat fauna of San Jose de Payamino a combination of mist netting and echolocation survey will create a much more complete picture of the local species richness and community structure.

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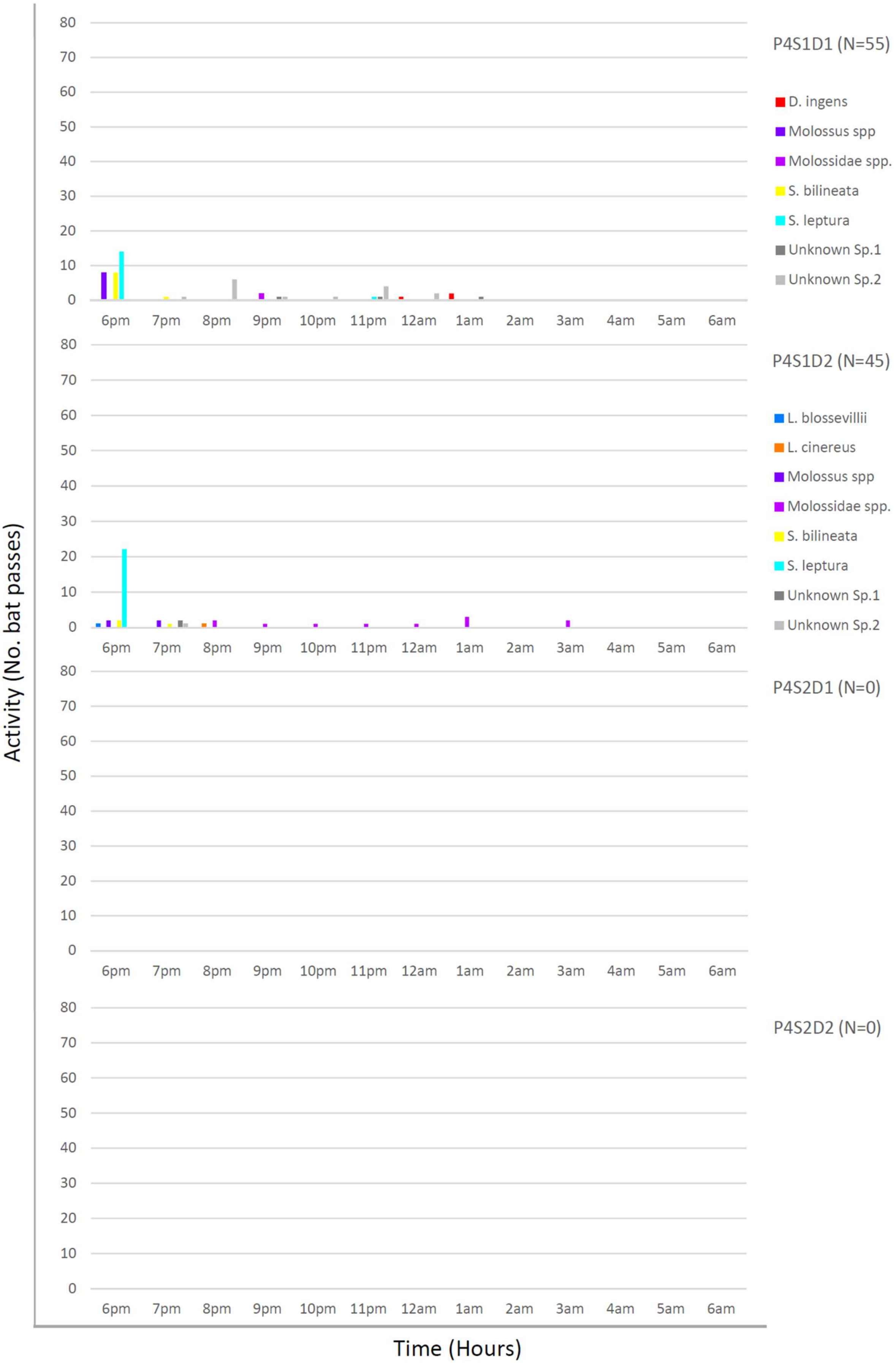
Appendix

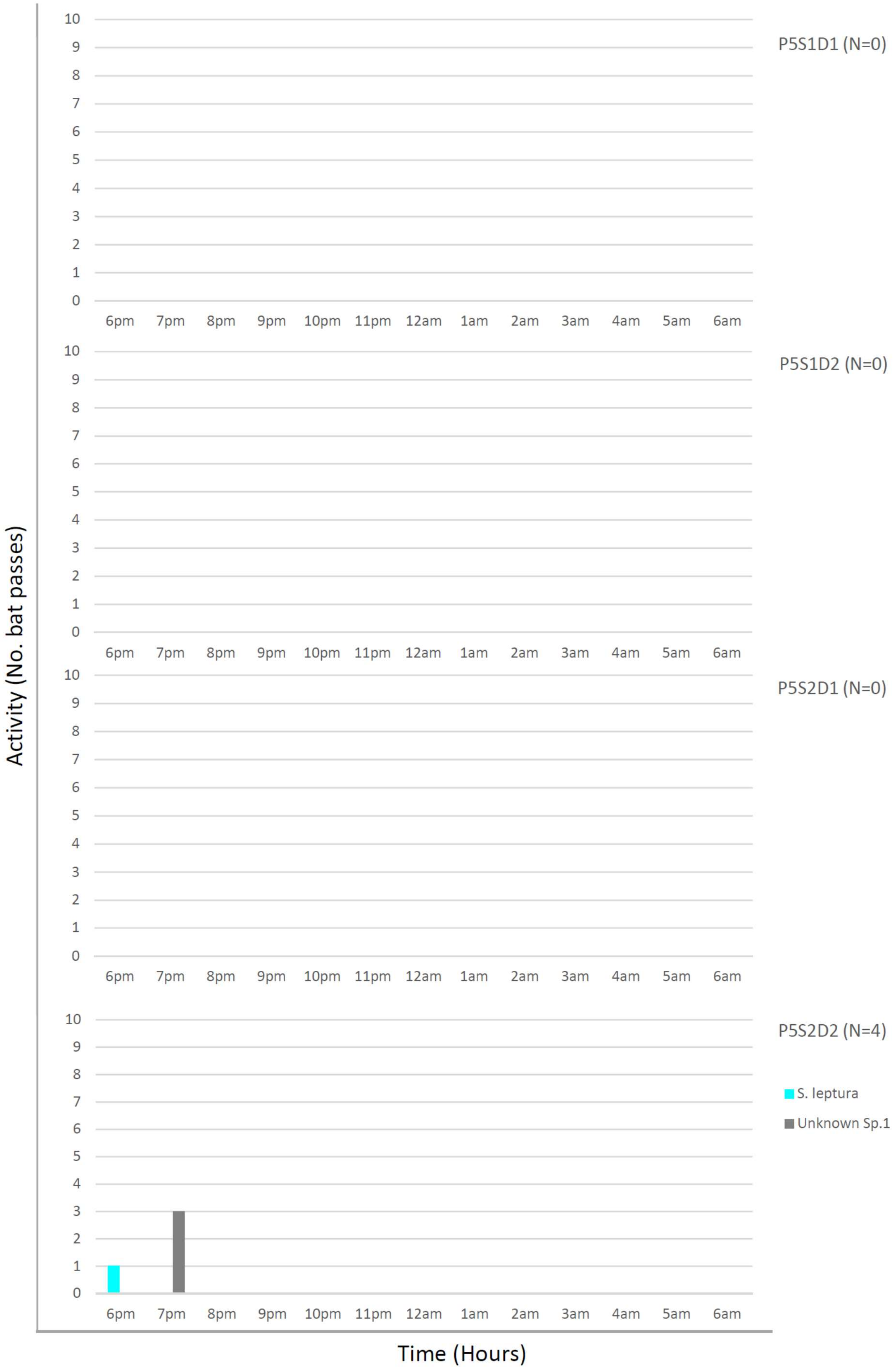
Primary Plot 2 (Total Bat Passes = 3056)

Primary Plot 3 (Total Bat Passes = 340)

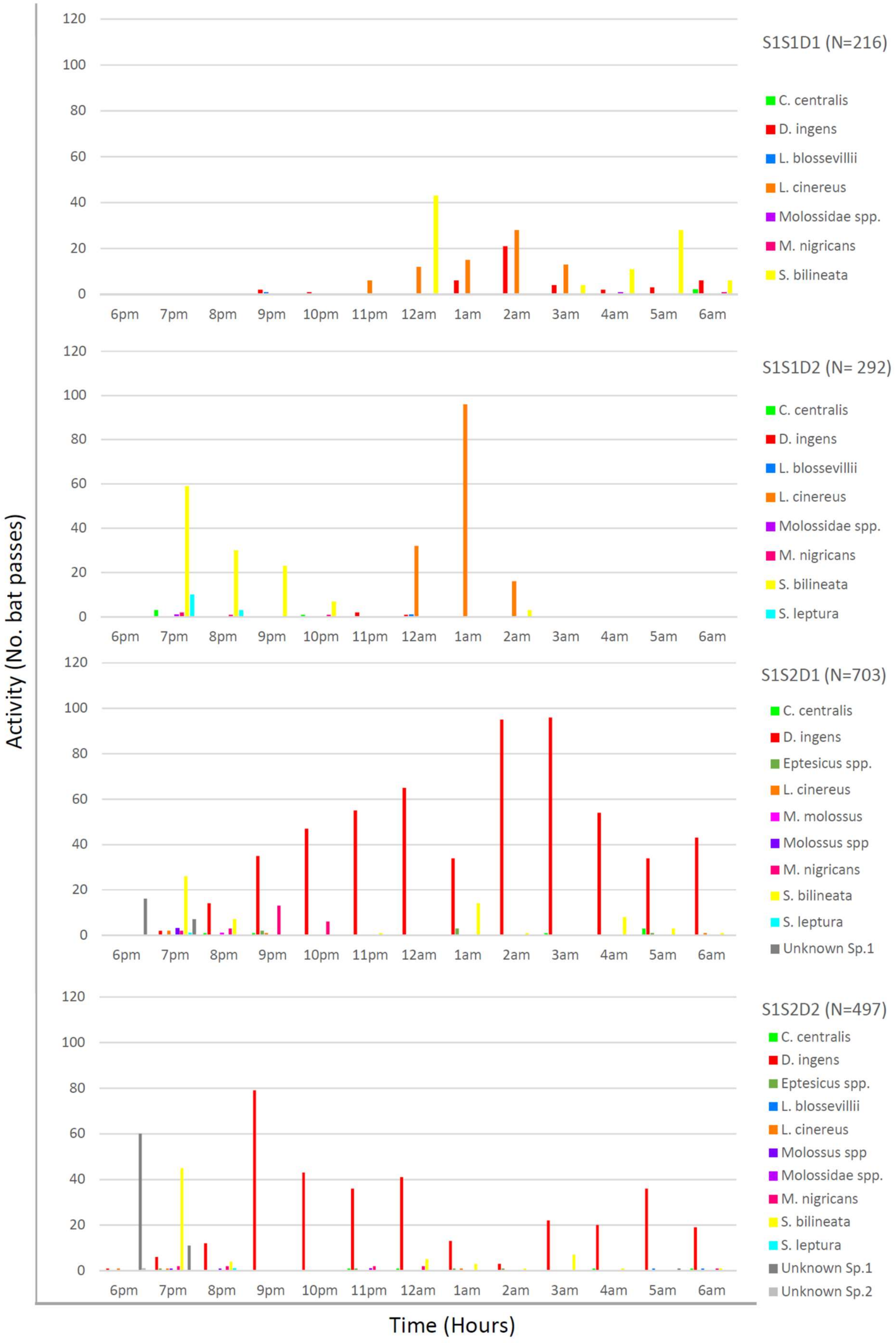
Primary Plot 4 (Total Bat Passes = 100)



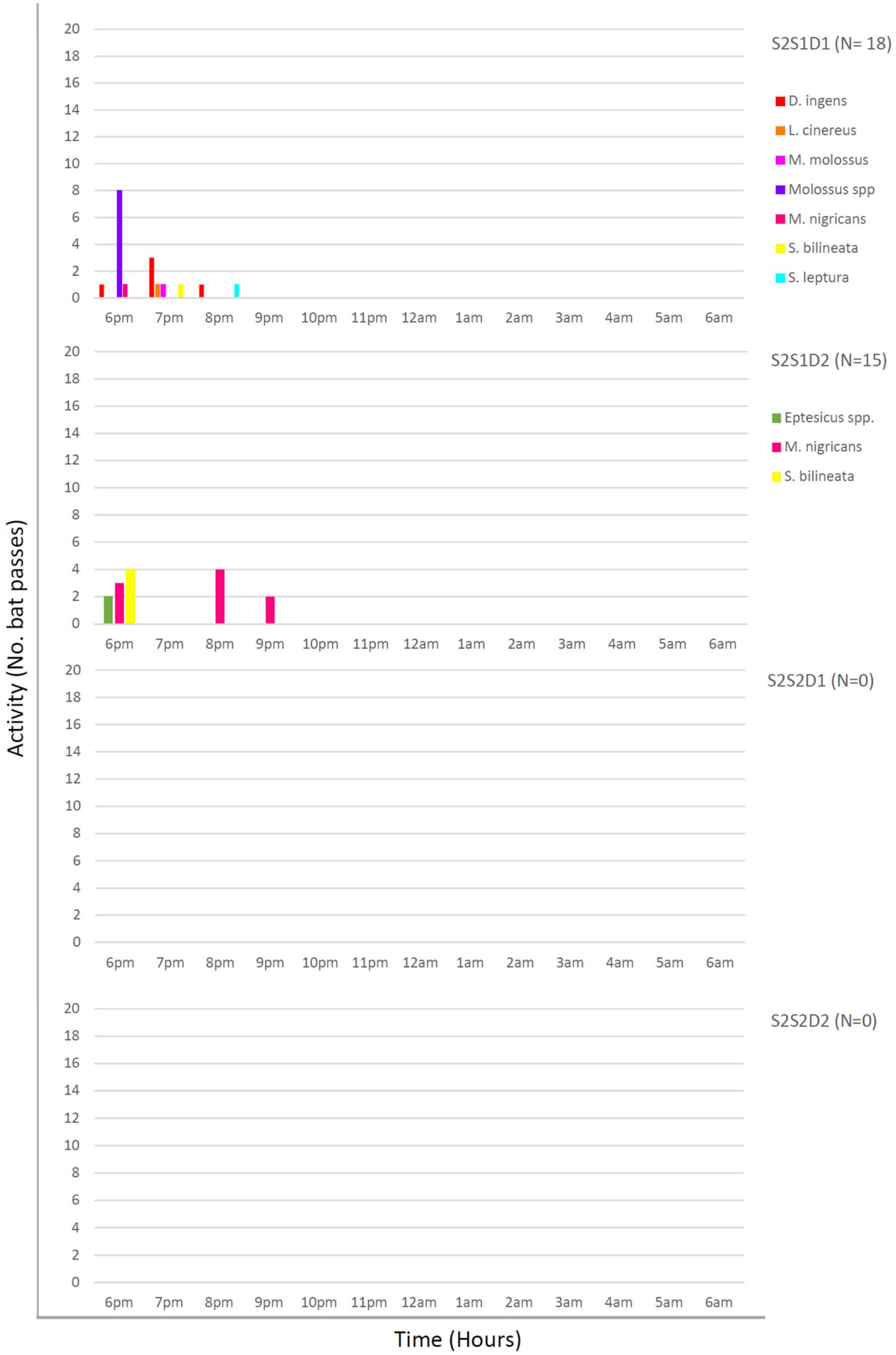
Primary Plot 5 (Total Bat Passes = 4)



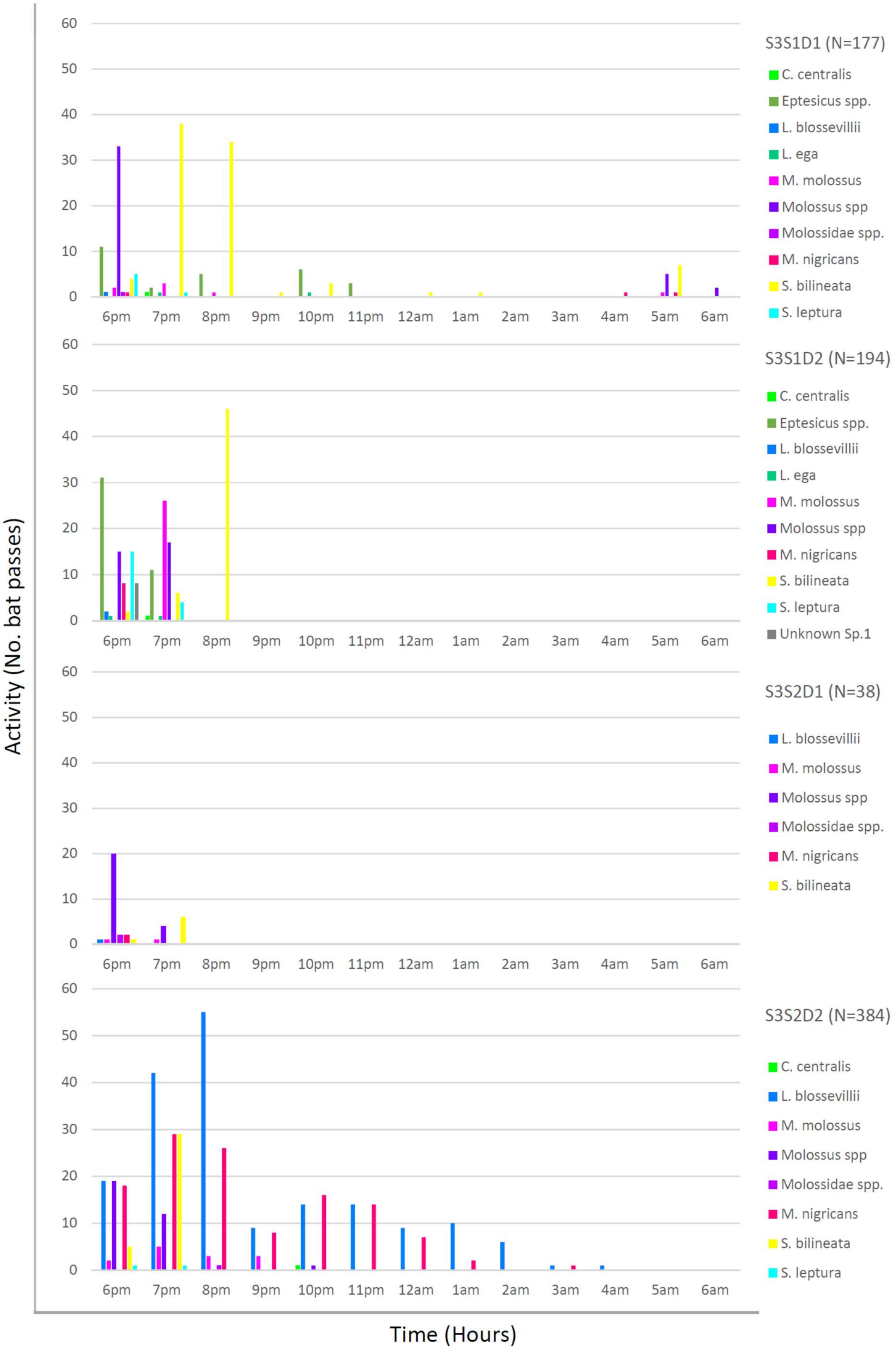
Secondary Plot 1 (Total Bat Passes = 1708)



Secondary Plot 2 (Total Bat Passes = 33)



Secondary Plot 3 (Total Bat Passes = 793)



Secondary Plot 4 (Total Bat Passes = 1108)