Chapter

More Urbanization, Fewer Bats: The Importance of Forest Conservation in Honduras

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Abstract

Urbanization is a phenomenon that results in fragmentation and eventual destruction of forests. Suburbanization is a subset of that same phenomenon in which fragmentation has resulted in the retention of small patches of the original forest and surviving old growth trees. Alternatively, the area surrounding the central city had been cleared for agricultural use and the suburban residents have planted many trees in parks and private property. This fragmentation will of course affect many species of bats, including species of the family Phyllostomidae. In this work, we estimate and compare the diversity of phyllostomid bats in three landscapes in Honduras: forests, suburban, and urban areas, from 2015 to 2018. Concurrently, we compared bat activity patterns based on the hour and percentage of moonlight at the time they were captured, and we compared external measurements, forearm and ear length. Urban areas are the least diverse and exhibited the lowest abundance. The forearm and ear length were significantly different only between forests and urban areas. The degree of lunar phobia also differed among those landscapes, but the time of capture did not differ. This is the first attempt to describe the activity patterns of phyllostomids in these studied areas and the effect of urbanization on Honduran bats. As expected, we found that from forests to cities, the diversity and abundance of phyllostomids decreased. However, there are many gaps in our knowledge of how totally or partially urbanized areas are affecting phyllostomid bats in Honduras.

Keywords: Chiroptera, CU-UNAH, Honduras, phyllostomid bats, Río Plátano Biosphere Reserve, Sabanagrande, suburbanization, taxonomic diversity

1. Introduction

1.1 Urbanization, suburbanization, and bats

It is generally agreed that urbanization has had a major negative effect on populations and diversity of native plants and animals. Nevertheless, humans plant a wide variety of vegetation in their urban and suburban areas, thus initiating the food chain on which most animals depend. Although diversity is clearly greatly reduced in the urban setting, at the population level the effect has been extremely heterogeneous across the animal kingdom. Bats (Chiroptera) are an extremely diverse group, with more than 1400 species worldwide, living in almost all habitats. The reaction of bats to urban environments was recently reviewed [1]. Jung and Caragh [1] determined that the behavioral and/or morphological traits at the level of individual species determine species' adaptability to urban areas. Further, they determined that the driving factors for species adaptability to urban areas may be regionally divergent.

As Jung and Caragh [1] point out, bats are found in all cities over the world. Of the approximately 20 families of bats, only two tend to avoid cities entirely, the Rhinolophidae and Mormoopidae, whereas a heterogeneous reaction at the species level is typical of the other families.

Urban habitats have both potential disadvantages and advantages from the perspective of bats. Clearly cities are high in noise, light, and chemical pollution compared to natural habitats. Light pollution may be an especially difficult factor to which bats must adapt. Depending on roosting requirements, cities may provide abundant roost sites, such as buildings, or not, for example for bats that roost in vegetation. Often drinking water and food supplies are enhanced by the human residents of the city, again depending on the bats' specific requirements. Since tree cover in cities averages less than 30% [2], bats adapted to forests may not do well, whereas in grassland and savannah areas, bats may find the tree cover advantageous [3].

Although there have been many studies of urban bats, these have been concentrated in temperate North America and Europe, and focus mainly on bats of the family Vespertilionidae, e.g., Dixon [4], Hale et al. [5], Pearce and Walters [6]. Bat activity and diversity seem to be highest in older suburban areas and parks and decrease towards the center of cities where there is little vegetation. It is clear to us that the change from urban to suburban to rural is a continuum; therefore, it is not productive to divide this continuum into discrete units except very generally as we are doing here for comparative purposes. The differences between urban and suburban can, for example be exemplified by such physical differences as tree density, percent paved area, building size and density, etc. These variables change in a predictable way as we pass through the continuum. Thus, when we approach 0% paved area, very low building density, and/or 100% tree density, we have reached the end of the continuum and are in forest or agricultural zones.

Although a few species do very well in cities, as for example, the huge colony of *Tadarida brasiliensis* in downtown Austin, Texas, U.S.A. [7], the majority of species that occur in a given area are rare or absent from urban areas [1]. Norberg and Rayner [8], pointed out that bat species with high wing loadings and aspect ratios, and thus presumed to forage in open areas, seem to be the most abundant and diverse in cities. Several studies [9–11] show that in general, foraging activity of bats seems to be higher in rural and forested areas than in urban areas.

A threat to bat populations, clearly related to urbanization, is mortality on highways. This problem has been but rarely studied, mostly in the temperate zone (e.g., [12]) but clearly exists. Recently a study in Brazil demonstrated that significant bat mortality is occurring on Brazilian highways as well [13].

There are relatively few studies of bats in urban areas of the Neotropics. Jung and Kalko [14] in Panama, using audio recordings, report decreased diversity and abundance in the urban setting, compared to the high diversity in forests in that country. They also note that in the city, most of the bats are high flying species, primarily of the Molossidae. In Costa Rica one of us [15] found the same trend with audio recordings in a large metropolis and in a smaller provincial capital. Jung and Kalko [16], recording in a small city adjacent to forest, found higher diversity than in large urban centers, but noted that some species that were abundant in the nearby forest were never recorded in town. For our purposes, we may think of this town as a suburban area. In Costa Rica, in a large urban center, but recording only in city parks, the number of bat passes was much greater in the larger parks than in the smaller parks [17]. Overall, those authors found considerably less activity than we consistently found in non-suburban settings [14]. The urban bats identified from the calls were all from the families Vespertilionidae and Molossidae. In another Costa Rican study the author mist-netted in parks in the city, finding a relatively small number (for the netting effort) of bats of the family Phyllostomidae, all of which were very common species that eat fruit and/or nectar [18].

1.2 Bat diversity in Honduras

Because of its location on the relatively narrow isthmus of Central America, connecting North and South America, Honduras is home to species typical of South America, others typical of temperate North America, and some that are endemic to Central America and southern Mexico. According to a recent review, [19] there are 113 species of bats currently known from Honduras, and we expect several more species will be added in the future. In Central America, only Costa Rica has more species, with 120 listed [20]. As detailed in the paper cited [19], the bats belong to seven different families, the Emballonuridae (9 species), the Phyllostomidae (59 species), the Mormoopidae (5 species), the Noctilionidae (2 species), The Thyropteridae (1 species), the Natalidae (2 species), the Molossidae (17 species), and the Vespertilionidae (18 species).

These species include frugivores, nectarivores, insectivores, sanguinivores, carnivores, and omnivores, and occupy many essential ecological niches in Honduras, dispersing seeds, pollinating flowers, and controlling insect numbers, among others.

1.3 Objectives and hypothesis

We lack information demonstrating how urbanization is affecting the diversity of bats in Honduras, Central America. We hypothesize that, on a continuum from forests to cities, the diversity of New World leaf-nosed bats (Phyllostomidae) will be significantly reduced. Therefore, this works aims to estimate and compare the diversity of phyllostomid bats in three landscapes in Honduras: forests, suburban, and urban areas; to determine if the forearm and ear length has any significant effect on species composition of bat assemblages in the three landscapes; and to describe the activity patterns of those assemblages.

2. Materials and methods

2.1 Concepts

When defining "urbanization" and "suburbanization", which are processes that are closely related and linked along a continuum, we follow Tammaru et al. [21]. We will consider suburbanization as the expansion of suburbs by the increase of its population from the migration of residents of the central city [21, 22]. Thereby, we will refer to the Ciudad-Universitaria of the Universidad Nacional Autónoma de Honduras (CU-UNAH) as the "urban area" in this manuscript. The same authors described suburbanization is the redistribution of a population away from central cities and into suburbs. In this work, we are referring to Sabanagrande as the "suburban area". All other studied areas in this work are considered as "forests" located in the Río Plátano Biosphere Reserve. See below for the description of each studied area.

2.2 Studied areas

All the coordinates are given in **Table 1** and represented in **Figure 1**, and each site is described below:

2.2.1 CU-UNAH

Surveys were carried out at the National University Campus' Botanical Garden in Tegucigalpa, capital city of Honduras, in the Department of Francisco Morazán (**Table 1**). The ecosystem is a tropical dry forest [23]. The species of Fabaceae, Myrtaceae, and Asteraceae are the most common, including *Muntingia calabura*, *Byrsonima crassifolia*, *Lonchocarpus sanctuarii* and cultivated plants, such as *Hibiscus rosa-sinensis*, *Russelia equisetiformis* and *Psidium guajava* [24].

2.2.2 Sabanagrande

We studied a tropical moist forest [23] located in the central region of Honduras in the Department of Francisco Morazán, municipality of Sabanagrande (**Table 1**). The vegetation included *Pinus oocarpa*, *P. maximinoi*, *Quercus oleoides*, and plants of the genus *Miconia* (Melastomataceae), *Curatella* (Dilleniaceae), *Psidium* (Myrtaceae), *Calliandra* (Fabaceae), and *Ficus* (Moraceae). Extensive livestock and crops of *Zea mays* (Poaceae) can also be found near the studied areas [25].

2.2.3 RPBR

The RPBR, including La Moskitia, is located within the departments of Gracias a Dios, Olancho, and Colón. Based on Holdridge [23], the life zone represented is tropical wet forest. The RPBR is the only site in Honduras declared as world Heritage. Some plant species associated with the study area are *Swietenia macrophylla* (Meliaceae), *Cedrela odorata* (Meliaceae), *Cordia alliodora* (Meliaceae), *Chamaedorea tepejilote* (Arecaceae), *Geonoma congesta* (Arecaceae), *Cecropia obtusifolia* (Urticaceae), *Psychotria poeppigiana* (Rubiaceae), and *Sloanea picapica* (Eleocarpaceae) [26].

2.3 Taxonomy, mist-netting, and ethical guidelines

We followed the most recent taxonomic checklist of the bats that occur in Honduras [19]. All the bats were captured using mist-nets of 12.5 x 2.5 m with a mesh of 35 mm. We followed Kunz and Kurta [27] for positioning the mist nets according to the vegetation, landscape, bodies and water and phenophases (fruits and flowers) of the plants. Bats were identified and measured (FA = forearm length; E = ear length; BH = body height) using taxonomic keys of Timm, LaVal and Rodriguez [28] Medina-Fitoria [29], and Mora [30]. We quantified the sampling effort by multiplying the area of all of the mist-nets that were opened during each night by the number of hours that remained open [31] in which a total of 47,686.8 m^{2}*h was accumulated. All the bats were handled according to the guidelines for the use of wild mammals in research and education [32].

	Departament	Locality	Municipality	Latitude	Longitude	Elevation (m asl)	Landscape
1	Francisco Morazán	Carboneras	Sabanagrande	13.794	−87.248	985	Suburban
2	Gracias a Dios	Ciudad Blanca 1	Brus Laguna	15.246	−84.969	250	Forest
3	Gracias a Dios	Ciudad Blanca 2	Brus Laguna	15.246	−84.972	214	Forest
4	Gracias a Dios	Ciudad Blanca 3	Brus Laguna	15.245	−84.96	245	Forest
5	Gracias a Dios	Ciudad Blanca 4	Brus Laguna	15.245	−84.969	225	Forest
6	Gracias a Dios	Ciudad Blanca 5	Brus Laguna	15.248	−84.968	223	Forest
7	Gracias a Dios	Ciudad Blanca 6	Brus Laguna	15.245	−84.965	204	Forest
8	Gracias a Dios	Ciudad Blanca 7	Brus Laguna	15.251	−84.974	239	Forest
9	Gracias a Dios	Ciudad Blanca 8	Brus Laguna	15.244	−84.966	233	Forest
10	Gracias a Dios	Ciudad Blanca 9	Brus Laguna	15.241	−84.969	206	Forest
11	Francisco Morazán	El Ocotal	Sabanagrande	13.791	−87.314	976	Suburban
12	Francisco Morazán	La Finca “Divisadero”	Sabanagrande	14.561	−87.801	1105	Suburban
13	Francisco Morazán	La Tigra	Sabanagrande	13.800	−87.313	790	Suburban
14	Gracias a Dios	Las Marías Pesh 1	Juan Francisco Bulnes	15.680	−84.838	33	Forest
15	Gracias a Dios	Las Marías Pesh 2	Juan Francisco Bulnes	15.679	−84.846	50	Forest
16	Gracias a Dios	Las Marías Pesh 3	Juan Francisco Bulnes	15.676	−84.851	28	Forest
17	Gracias a Dios	Las Marías Pesh 4	Juan Francisco Bulnes	15.676	−84.843	33	Forest
18	Gracias a Dios	Pico Dama 1	Juan Francisco Bulnes	15.695	−84.915	373	Forest
19	Gracias a Dios	Pico Dama 2	Juan Francisco Bulnes	15.695	−84.915	360	Forest
20	Gracias a Dios	Pico Dama 3	Juan Francisco Bulnes	15.692	−84.915	394	Forest
21	Gracias a Dios	Pico Dama 4	Juan Francisco Bulnes	15.695	−84.917	433	Forest
22	Gracias a Dios	Pico Dama 5	Juan Francisco Bulnes	15.694	−84.915	383	Forest
23	Francisco Morazán	UNAH (CC)	Distrito Central	14.008	−87.165	1073	Urban
24	Francisco Morazán	UNAH (JB)	Distrito Central	14.087	−87.166	1050	Urban

	Departament	Locality	Municipality	Latitude	Longitude	Elevation (m asl)	Landscape
25	Francisco Morazán	UNAH (Lagunas)	Distrito Central	14.086	−87.160	1050	Urban
26	Francisco Morazán	UNAH (Polideportivo)	Distrito Central	14.086	−87.169	1062	Urban
27	Gracias a Dios	Waikna Tara	Juan Francisco Bulnes	15.660	−84.893	44	Forest

Table 1.
Description of all the 27 localities that were studied and were classified among urban, suburban, and forests.

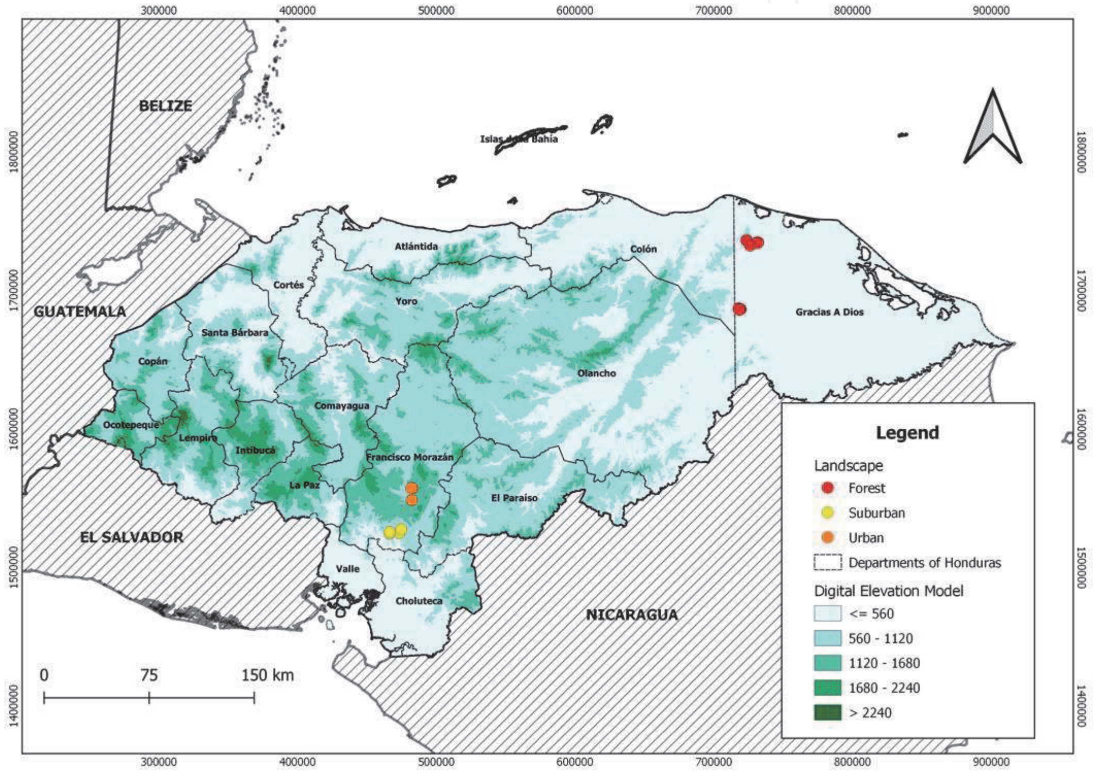

Figure 1.
Forest, suburban, and urban areas used in this study.

2.4 Diversity, landscape, and activity patterns analyses

The diversity of each landscape was measured using the Alpha Diversity Index (following Jost [33] and Moreno et al. [34]), and species richness was estimated with Chao 1. These analyses were based in the sampling effort of each site and the abundances of each species using EstimateSMac 910 with 100 randomizations [35, 36].

For the activity patterns analyses we used the abundances of all the species [37] and correlated them with the time and the percentage of the moon illumination in which bats were captured from each type of landscape. Moon illumination was taken for each date from the following website: https://www.moongiant.com/ [38]. We used the Shapiro–Wilk test to test for the normal distribution and Levene's test to test for the homogeneity of variances of the data. Considering that data was normally distributed, means of the forearm length, ear length, body height, time, and moon percentage were represented by the ANOVA (Analysis of Variance) analyses in **Table 2**. To compare means we performed posthoc Tukey tests at a

Landscape	Individuals	Species	Sampling effort (m^2*h)	Chao 1 estimator	Alpha diversity index	Individuals per m^2*h	Species per m^2*h	FA (mm)	E (mm)	BH (mm)	Moon illumination (%)	Time
Forests	376	24	14,567.4	28.97	5.72	0.03	0.0016	74.68 (29.00–91.35)	30.75 (9.48–42.54)	53.29 (36.8–69.78)	65.26 (15.5–99.52)	5:30 PM – 5:20 AM
Suburban	169	17	18,839.4	19.24	4.71	0.01	0.0009	67.74 (33.01–69.46)	16.59 (7.67–17.83)	57.60 (45.9–69.30)	47.46 (0.24–94.43)	6:00 PM – 2:00 AM
Urban	143	7	14,280.0	7.5	1.54	0.01	0.0005	67.71 (31.10–72.00)	23.99 (9.82–28.34)	68.73 (55.96–81.50)	50.06 (0.06–100)	5:30 PM – 2:20 AM

Table 2.
Diversity data and means of the morphometrics and ecological data of the 688 bats studied.

confidence level of 95%. For all the analyses we considered significant differences when p ≤ 0.05. Except for time, in which we use the Spearman's correlation coefficient to determine any relation between the landscapes and the time activity.

To determine taxonomic similarities between the landscapes (urban and suburban areas and forest) we performed multiple regressions of distance matrices [39]. In addition, to represent graphically the taxonomic composition in the distinct habitat types, we performed a NMDS (non-metric multi-dimensional scaling) analysis with two dimensions and plotted the NMDS axes against landscapes [40]. All analyses were performed in R Core Team [41] version 3.4.2, using the vegan [42] and ecodist [43].

3. Results

3.1 Alpha diversity in three landscapes

According to Chao 1 (**Table 2**), urban areas (percentage of how many species According to Chao 1, urban areas (percentage of how many species were recorded in parentheses) are the least diverse, as expected, because only 7.5 species are expected (93.3%) followed by suburban areas (87.2%) with 19.24, and then by forests with 28.97 (82.2%). Supporting Chao 1, the Alpha diversity index was highest in forests with 5.72, followed by suburban and urban areas (**Table 2**), in that order. Considering the sampling effort, urban areas are not only the least diverse but also the least abundant based on number of bats captured, followed by suburban areas and forests (**Table 2**). Even though we found three different assemblages (**Figure 2**) we found no significant correlation between taxonomical α-diversity and the type of landscape (R^2 = 0.04; DF = 1,24; P = 0.24). However, we found species such as *Artibeus jamaicensis*, *A. lituratus*, *Glossophaga soricina* and *Sturnira parvidens* that were recorded in all three landscapes. But there were certain species that were recorded only in certain landscapes, for example, *Glossophaga leachii* in urban areas, *Lonchorhina aurita* in suburban areas, and *Tonatia bakeri* and *Vampyressa thyone* on forests (**Table 3**; **Figure 3**).

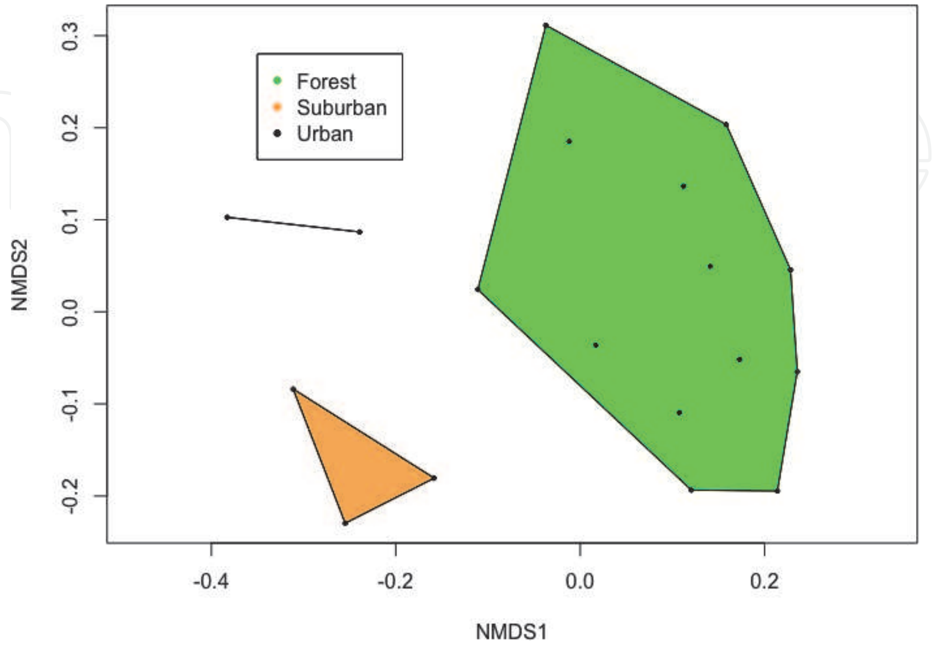

Figure 2.
Non-metric multi-dimensional scaling (NMDS) of three landscapes which represents three different bat assemblages.

	Species	Forest	Suburban	Urban	Total
1	*Artibeus inopinatus*		23		23
2	*Artibeus jamaicensis*	92	48	56	196
3	*Artibeus lituratus*	71	10	62	143
4	*Carollia castanea*	20			20
5	*Carollia perspicillata*	85	23		108
6	*Carollia sowelli*	29			29
7	*Centurio senex*		1	1	2
8	*Chiroderma gorgasi*	2			2
9	*Chiroderma salvini*		3		3
10	*Chiroderma villosum*		9		9
11	*Choeroniscus godmani*		3		3
12	*Chrotopterus auritus*	2			2
13	*Dermanura phaeotis*	8	1		9
14	*Dermanura tolteca*		2		2
15	*Dermanura watsoni*	5			5
16	*Desmodus rotundus*	5	6		11
17	*Diphylla ecaudata*		2		2
18	*Glossophaga commissarisi*	9		2	11
19	*Glossophaga leachii*			1	1
20	*Glossophaga soricina*	3	18	18	39
21	*Hylonycteris underwoodi*	1			1
22	*Lonchorhina aurita*		5		5
23	*Lophostoma brasiliense*	2			2
24	*Micronycteris hirsuta*	2			2
25	*Micronycteris microtis*	4	1		5
26	*Phylloderma stenops*	1			1
27	*Phyllostomus discolor*	4	7		11
28	*Phyllostomus hastatus*	1			1
29	*Platyrrhinus helleri*	6			6
30	*Sturnira parvidens*	1	7	3	11
31	*Tonatia bakeri*	1			1
32	*Uroderma convexum*	18			18
33	*Vampyressa thyone*	4			4
	Total	**376**	**169**	**143**	**688**

Table 3.
Description of the occurrence of the landscapes in which the 33 phyllostomid bats were recorded.

3.2 Activity patterns vs. morphological traits

Considering time (**Figure 4**), we found no significant correlations in any type of landscape: forests and suburban areas (R^2 = 0.00; DF = 1,154; P = 0.23), forests and

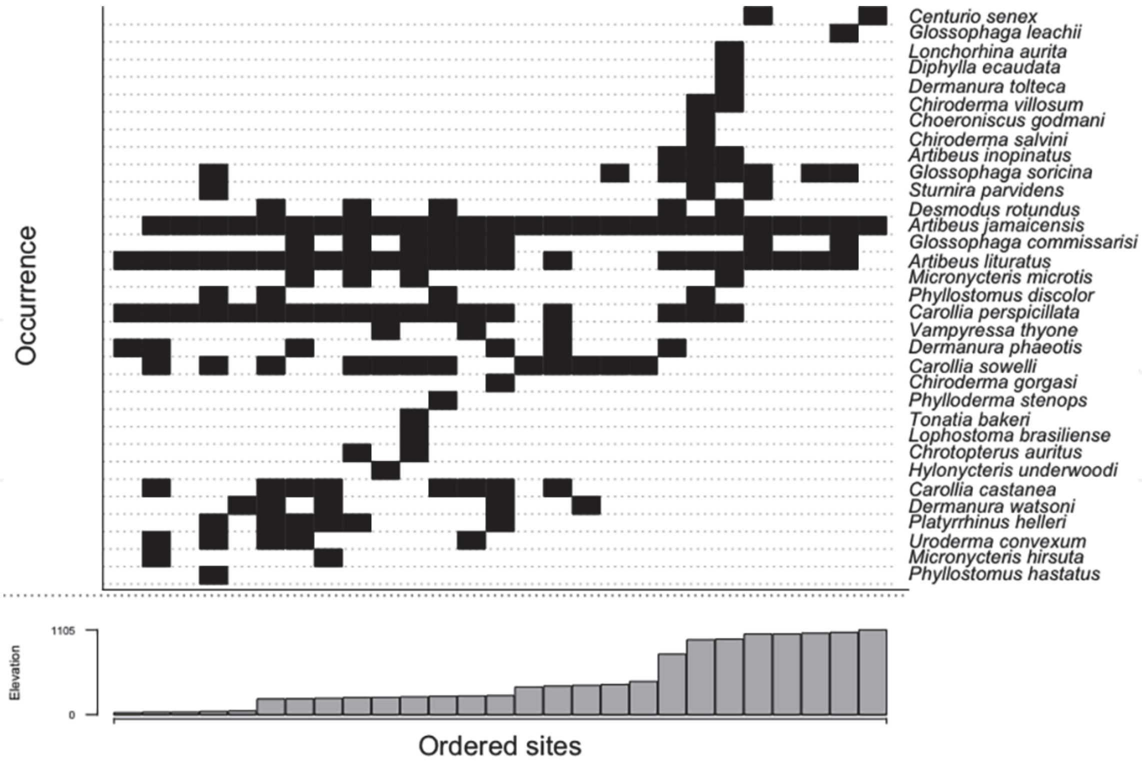

Figure 3.
Occurrence of phyllostomid bats based on the elevation of the studied areas.

urban areas ($R^2 = -0.01$; DF = 1,139; P = 0.62), and urban and suburban areas ($R^2 = -0.00$; DF = 1,139; P = 0.99). In the case of body height means, only the suburban areas and forests have no significant differences ($F_{(2,203)} = 2.3$, p = 0.21; **Figure 5A**), and were divided into two groups urban areas (a) and forests and subruban areas (b). See **Table 4** to see the other p values of this and other analyses. The ear length means were only significant different in suburban and forests landscapes ($F_{(2,165)} = 4.57$, p = 0.05; **Figure 5B**), however, all the landscapes were assigned to the same group (a). When comparing forearm length means with posthoc Tukey tests, landscapes were classified into two groups urban (a) and suburban and forests (a) and only the comparison between suburban areas and forests was not significant ($F_{(2,431)} = 21.41$, p = 0.99; **Figure 5C**). Finally, the moon

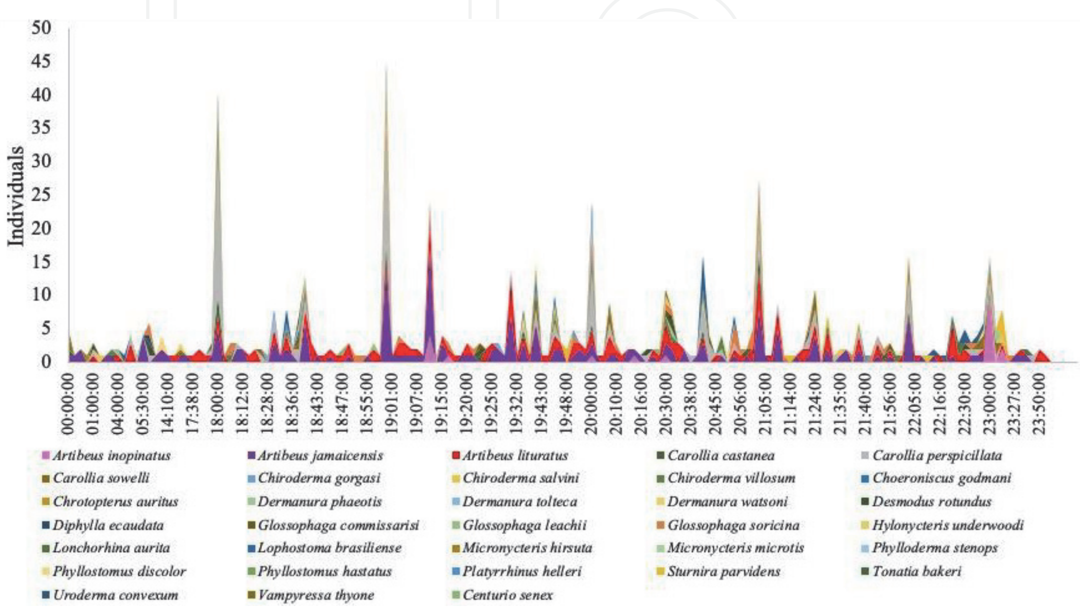

Figure 4.
Time activity patterns of the 33 phyllostomid species recorded.

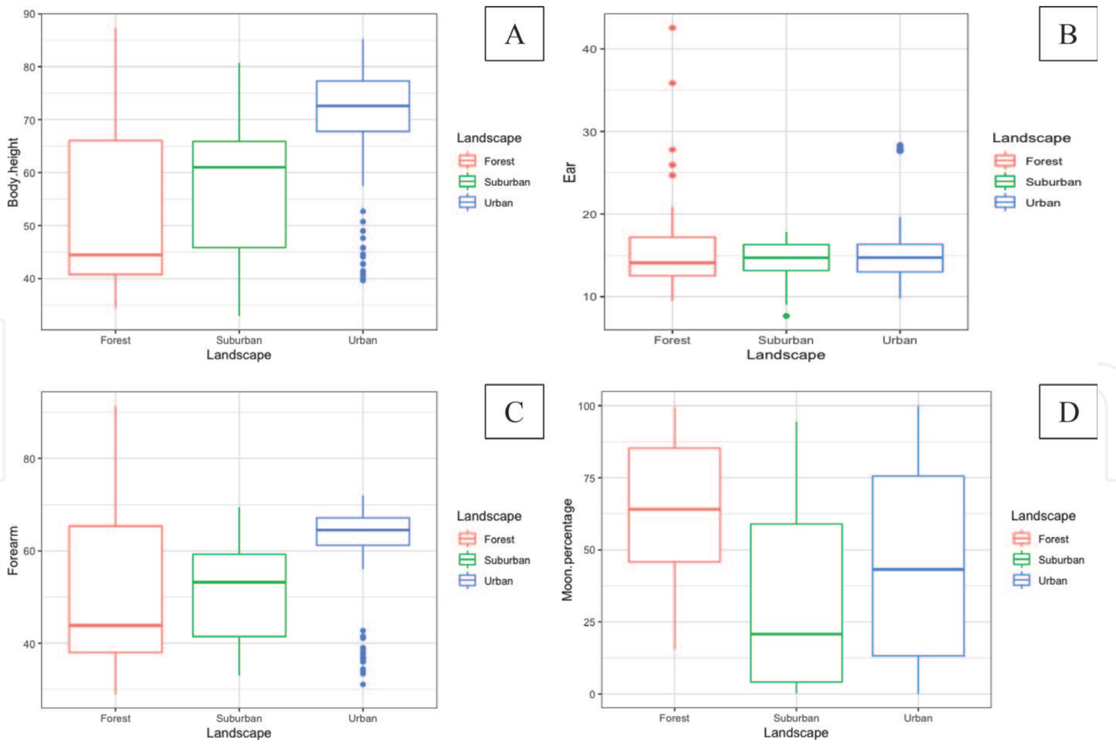

Figure 5.
ANOVA analyses of the body height (A), ear length (B), forearm length (C), and moon percentage (D) time in which phyllostomids were captured.

Landscape	Forests	Suburban	Urban
Forests - FA	—	0.99	<0.01
Suburban - FA	0.99	—	<0.01
Urban - FA	<0.01	<0.01	—
Forests – E	—	0.05	0.17
Suburban - E	0.05	—	0.61
Urban - E	0.17	0.61	—
Forests - BH	—	0.21	<0.01
Suburban - BH	0.21	—	<0.01
Urban - BH	<0.01	<0.01	—
Forests - moon	—	<0.01	<0.01
Suburban – moon	<0.01	—	<0.01
Urban - moon	<0.01	<0.01	—

Table 4.
Statistical results from the comparison of the posthoc Tukey analyses. Abbreviations are as follow: FA = forearm length; E = ear length; BH = body height; moon = moon percentage.

percentage mean in which bats were captured was significant different among all the landscapes (**Figure 5D**), categorized into three different groups a (forest), b (urban areas), and c (suburban areas).

4. Discussion

As expected in Honduras, there is a consistent decrease of phyllostomid bat diversity and abundance from forests to cities. As anticipated, we found that the diversity is less in urban areas (cities) and suburban areas in comparison to forests. However, these remnants of forest are important for bat conservation in urban areas. For example, the high abundance of *Artibeus* and *Glossophaga* in CU-UNAH are, hopefully, helping in the regeneration of trees by seed dispersal and pollination [44] in this small remnant of forest in the capital city of Honduras. On the other hand, suburban areas may also have important species. For instance, Sabanagrande may be the most important area for the conservation of *Artibeus inopinatus* [25, 45], which is considered to be Data Deficient (DD) by the IUCN (International Union for the Conservation of Nature) [46]. That suburb also houses species such as *Micronycteris microtis* which is more typical of forest remnants [47]. In contrast to urban and suburban areas, forests clearly have the highest diversity and abundance of phyllostomid bats. Unfortunately, except in protected areas, these forests are being constantly fragmented and with time, they tend to become agricultural or urban landscapes. Species that cannot acclimatize or adapt to these anthropogenically modified landscapes will disappear. Those that occupy very limited geographic distributions likely will become extinct. Olivier et al. [48] point out that two major drivers of habit degradation are urbanization and agricultural intensification which decrease community stability, including bats.

4.1 How urbanization is affecting bat diversity

Urbanization is the second most detrimental anthropogenic agent of landscape change [49], since bat diversity and species abundance are comparatively lower in cities than in primary forests or rural areas [3]. This is the case not only for Honduras, but worldwide. For example, in Poland, urbanization pressure is a common phenomenon in several protected areas due to the dispersion of buildings and the expansion of summer construction [49]. Additionally, artificial lighting and sound pollution can alter commuting processes in foraging bats, especially sound which has a more deterrent effect for bats than light as some insectivorous bats feed on the insects that are attracted to streetlights [50–52]. Interestingly, habitat degradation affects the diversity of bat communities in more complex ways than simply population stability [48].

Bat response and sensitivity to urbanization varies among species assemblages in urbanized landscapes. In this way species with high tolerance become more abundant and dominant. However, the low diversity and abundance of urban bat fauna can be attributed, at least partially, to a shortage of roosting sites [53]. For a better understanding of bats that do not fly below canopy in urban areas, acoustic monitoring can provide data for species that are rarely captured in mist nets ([17], and see introduction, this chapter). Unfortunately, we have little such data for Honduras as of now.

The fact that forearm length was only significantly different between forests and urban areas and the ear length between suburban areas and forests can be explained from two points of view. First, we found that Sabanagrande has a mixture of the other two assemblages, and even has species that were found only there (e.g., *L. aurita*). Additionally, Sabanagrande has a mixture of ecological characters, and even though it is becoming urbanized, there are still important forest remnants. Similar to Mexico [47], we found that in suburban areas (referred to as intermediate disturbance sites), the predominant species was *Carollia perspicillata,* (subfamily Carollinae*).* Our results support the hypothesis of Medellín et al. [47] in which phyllostomines (subfamily Phyllostominae) disappear from disturbed areas because of their specific requirements (e.g., foraging activity; [54]) because all the phyllostomines recorded in this study were in forest remnants.

Secondly, the functional traits varied. For example, the well-conserved forests of the RPBR have larger species that were only recorded there (e.g., *T. bakeri*) but in less abundance. In these species their ear length and wingspan are relatively larger, in contrast to those of the large species *Artibeus lituratus*, found in CU-UNAH and Sabanagrande. Ramírez-Mejía et al. [55] demonstrated that the most dominant functional group of bats in their studies were those with intermediate values of body mass and wing morphology, which represents the phyllostomids' adaptive response to landscape degradation.

Species such as *Phyllostomus hastatus*, which is widespread in Honduras, have a larger forearm length and therefore a larger wingspan. Additionally, these species and others of the subfamily Micronycterinae, Lonchorhininae, and Glyphonycterinae, have larger ears because they are gleaners and thus ear length is related to their dietary habits, and these gleaners are more susceptible to the gradual degradation of remnant forests and effects of urbanization (e.g., sound and light pollution) [47]. In other words, phyllostomid gleaners (e.g., phyllostomines) and related subfamilies are indicators of relatively undisturbed rainforests [47, 56]. However, a few species, notably *Micronycteris microtis,* for example, may tolerate moderate levels of urbanization. More ecological data is needed to support this hypothesis.

4.2 From cities to forests: Activity patterns of phyllostomids in Honduras

We hypothesize that New World leaf-nosed bats in forests are more likely to be negatively affected by brightness of the moon because of safety concerns (hunting activities by visually oriented predators like owls) when the moon is brighter [15]. In contrast, urban and suburban areas have equally high light intensity every night (e.g., traffic lights, streetlights, shopping centers, etc.). Another feature that supports our hypothesis is that we found significant difference between all the areas. This is probably because the light intensity of suburban areas is increasing in the same way as in urban areas, and the bats that survive there are able to acclimatize quickly. However, the time patterns were not significantly different among the three landscapes due to the wide range and different foraging behaviors. In general, phyllostomids have an early activity peak and then declining activity through the night [57]. Habitat specialization, nutrient intake, and food procurement are features that are associated with bat success in transformed landscapes [55, 58].

There are two more works describing activity patterns in Honduras. The first one, Medina-Fitoria et al. [59] studied certain areas included in the RPBR, and determined that in the Caribbean slope of Nicaragua and Honduras, mature and intact primary forests are the most important habitats to conserve. They also determined that fragmentation due to extensive cattle farming and agriculture is perhaps the major threat to these forests. And the second study, in the northwestern region of Honduras, in Cusuco National Park, by Medina-Berkum et al. [60] indicated that the presence of *Chrotopterus auritus* and *Trachops cirrhosus* only in the core zone of the park is probably because the core zone still comprises intact and closed forest habitats that may provide a higher abundance of prey for them, and that these species are generally more abundant in undisturbed areas. Primary and pristine forests are clearly among the most important remaining habitats for bat conservation in Honduras, considering that many phyllostomids depend on this type of forest. For example, the core zone and areas nearby of the RPBR are the only ones left in which *Ectophylla alba* may be found in Honduras due to the requirements of the species [61]. (Even in 1967 that was the only habitat in which one of us, RKL, captured *Ectophylla alba*).

Although we predicted that from forests to cities, the diversity of phyllostomids will decrease, this is the first attempt to describe their activity patterns in these areas in Honduras. Considering the extension of forests, Duarte et al. [62] mentioned that 48% of the Honduran territory is covered by forests. With the high rate in which they are being diminished is approximately 23,303.56 hectares per year [63], the probability of losing bat species in Honduras is all too real. On the other hand, there are some species that have been adapting very well, as is the case of *A. jamaicensis* and *A. lituratus*. These are species that were recorded in all three landscapes we studied and were the most common in urban areas. And even if they are considered as tolerant species, they have an important role in urban and suburban area as seed dispersers [64], and probably they should be considered as the phyllostomid species most tolerant to urbanization in Honduras. It appears that species of *Sturnira* and *Glossophaga* are also adapting well to this phenomenon.

5. Conclusion

Undoubtedly, the RPBR is one of the most important regions in Honduras, and probably in Central America, for bat conservation due to the large extensions of pristine forests and the limited occurrence and abundance of certain species (e.g., *Chiroderma gorgasi*) in that region. Unfortunately, even this region will be subject to the effects of encroaching clearing for agriculture and urbanization, if inadequately protected. Indeed, some species become acclimatized to urbanization, and some species, most notably *A. jamaicensis* and *A. lituratus*, now tolerate higher levels of disturbance than many other species. More studies are needed to determine and explain their tolerance to urbanization. There are other species that have very specific requirements, including intact primary forest, for their survival. (e.g., *T. saurophila*). This is the first attempt to study how urbanization is affecting a mammalian group in Honduras and is also the first comparison of bat diversity among three different landscapes. Yet, there are many variables that should be analyzed, compared, and described. For example, we recommend measuring light and sound intensity in urbanized areas and comparing them with those of the forests, to determine more specifically how these characteristics are affecting the diversity and abundance of phyllostomid bats in Honduras. Finally, it is still unknown which morphometrical characteristics are important in explaining the adaption of some phyllostomid bat species to urbanized areas. Another factor is the relative amount of fragmentation in the various areas we studied. There are many gaps in our knowledge of how totally or partially urbanized areas are affecting phyllostomid bats in Honduras, and even though there are some similar activity patterns, we can conclude that their diversity and abundance is decreasing in urbanized areas. Considering the increase of urbanization in Honduras plus the high rate of deforestation (approximately 63.85 hectares per day), a conservation plan for Honduran bats is fundamental.

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Conflict of interest

The authors declare no potential conflict of interest.

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