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Forest Structure and Composition Affect Bats in a Tropical Evergreen Broadleaf Forest

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Abstract: The lack of knowledge regarding many aerial insectivorous bats and their relationships with forest characteristics limits conservation decision-making for tropical rainforests and for this important bat group. Therefore, our objective was to understand the effects of forest structure and composition on these bats in the Neotropical evergreen broadleaf forest of Belize, Central America. We conducted bat monitoring and quantified 51 forest characteristics at 24 locations in the Chiquibul Forest Reserve (CFR) from May–July 2014. Simple linear and backward stepwise multiple regression analyses were used to examine relationships between bat richness and activity and forest characteristics. Bat genus richness and total activity were directly related to overstory canopy depth and inversely related to ≤ 4 structural characteristics. *Lasiurus*, *Myotis*, *Promops*, and *Pteronotus* spp. were affected by ≤ 7 forest characteristics; the responses were explained by preferences for less-cluttered, open space for flying and foraging and species-specific food and cover requirements. However, bat richness and activity were often unaffected by forest structure and composition in the CFR, suggesting that at this taxonomic level, bats may not be very sensitive to variation in forest characteristics, may not be very useful indicators of alteration, and may have some tolerance for disturbance and change.

Keywords: activity; bats; Belize; composition; forest; insectivorous; Neotropics; richness; structure

1. Introduction

In Neotropical rainforests, bats are one of the most species-rich mammal groups and can comprise more than 50% of all mammalian species present in lowland regions [1,2], but they are often threatened by changes to their habitat [3,4]. Their functional diversity [5–7] allows them to fulfill critical ecological roles as pollinators, seed dispersers, and arthropod predators, such that declines in bat populations could significantly affect ecosystem functions [8–12]. In addition, their often-predictable response to alterations in forest plant community structure and composition makes bats useful indicators of forest disturbance and change [7,13–15].

Most Neotropical rainforests are subject to natural and anthropogenic disturbances; this includes the Chiquibul Forest (CF) in Belize, Central America, a component of the Chiquibul-Maya Mountains Key Biodiversity Area, and a system known to support at least 46 bat species [16]. These dynamic forests, in part because of stand replacement disturbances such as episodic hurricanes and selective logging of a few valuable timber species, exhibit constant changes in their forest plant community

structure and composition [16–20]. These disturbances create canopy gaps of various sizes that often promote the growth of vines and pioneer tree species, and create regenerating stands characterized by dense undergrowth [17–20].

Changes in structure and composition of Neotropical rainforest plant communities can alter the availability of insectivorous bat food resources; number and type of bat roosts and refuges; vegetation structural complexity; degree of vegetation clutter; physical obstructions including foliage, branches, and stems that hinder bats' ability to fly and capture prey; and bat predation risk [21–27]. These alterations influence bat species occurrence and activity to differing degrees, depending on their wing morphology, which affects speed and maneuverability; their echolocation call characteristics, which affect the distance a call will travel; effects of vegetation; ecological requirements; and preferences for open (i.e., far away from obstacles, primarily vegetation), edge (i.e., close to, but not within, vegetation), or narrow (i.e., within vegetation) space [27–31].

Very few studies have examined bat–forest structure and composition relationships in areas subject to these various disturbances or have sought to understand specific forest characteristics influencing bat richness and activity [5,24,27,32–35]. In addition, the majority of studies examining bat–forest relationships in the Neotropics have focused on Phyllostomidae (i.e., leaf-nosed bats) [24,32–35], finding the aforementioned, species-specific responses to forest structure and composition. The response of non-Phyllostomid aerial insectivorous bats (e.g., members of the Emballonuridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Thyropteridae, and Vespertilionidae families) to forest structure and composition have been rarely studied [23].

The current lack of knowledge regarding non-Phyllostomid aerial insectivorous bats and their relationships with forest structure and composition currently limits management and conservation decision-making for Neotropical rainforests and for this important bat group (e.g., [3,4]). Therefore, our objective was to understand forest structure and composition effects on these bats in the Neotropical evergreen broadleaf forest of the Chiquibul Forest Reserve (CFR), Belize, Central America. We expected forest structural characteristics associated with clutter (e.g., shrub and tree density and canopy closure and depth) to be inversely related to overall bat richness and activity, as these areas would be avoided by open-space bat species.

2. Materials and Methods

2.1. Study Area

The CFR, a component of the CF, is comprised of 61,288 ha in the Cayo District of western Belize, Central America. The CF forms an integral part of the Chiquibul-Maya Mountains Key Biodiversity Area and broader Maya Forest, the second-largest continuous area of moist tropical rainforest in the Americas. The CFR is a public reserve managed by the Belize Forest Department, and it is a tropical evergreen seasonal broadleaf forest comprised of hardwoods and palms, with almost no softwood component. Elevations range from 50 to 700 m and topography varies from rolling hills to steep slopes, with scattered rivers and streams. Soil types vary, but they are typically relatively fertile, thin, fine-grained clay- and silt-rich soils. Much of the CFR is underlain with limestone, leading to a vast network of caves. Mean daily temperatures range from 19 to 27 °C, and the area receives 2000 mm/year of rainfall over relatively distinct dry (February–May) and wet (June–January) seasons. The region is subject to regular hurricanes; the most recent major event was Hurricane Dean in 2007 (Category 5). Historically occupied by Mayans, the area currently has no permanent settlements [16]. In 2006, the Belize Forest Department issued a single long-term harvesting license for the CFR, where highly regulated, low-intensity polycyclic selective logging of hardwood species occurs [16,36]. The current land-use is primarily timber extraction, principally the single-tree selective cutting of mahogany (*Swietenia macrophylla*) and Spanish cedar (*Cedrela odorata*), with some nargusta (*Terminalia amazonia*) and sapodilla (*Manilkara chicle*). One large, North–South oriented logging road and several seasonal smaller roads provide limited access through the area. Illegal logging also occurs in the CFR, along

with gold mining, limited ecotourism, and non-timber forest product extraction [16]. The CF supports at least 46 bat species, 20 of which are non-Phyllostomid aerial insectivores [16].

2.2. Bat Monitoring

To examine the effect of forest structure and composition on bat richness (i.e., number of genera or families) and activity (i.e., number of bat passes), we conducted bat echolocation call monitoring [37] at 24 randomly located sites in the CFR (sites were determined by randomly generating locations, i.e., coordinates, from a CFR map, excluding extreme western, eastern, and southern borders because of access and safety concerns [36]) from May–July 2014. At each monitoring location, we used a Wildlife Acoustics SM2BAT+ (SM2) detector and associated SMX-US microphone (Wildlife Acoustics, Maynard, MA, USA) to passively detect, record, and store full-spectrum bat echolocation call sequences [38,39]. We secured detectors to trees, with microphones mounted at a 45° angle, at approximately 1.37 m above the ground, and programmed these to record from sunrise to sunset using the manufacturer's recommendations. We set the sampling rate to 192,000 Hz, which would have allowed the units to detect sounds of up to 96 kHz. However, the SMX-US microphone exhibits a drop in sensitivity above 60 kHz, resulting in the upper frequency detected being closer to 60–70 kHz [40]. In addition, we set detector gain to 48 dB; high-pass filter to 1/12th of sampling rate, or approximately 16 kHz, to help remove low-frequency noise files; trigger level to 12 signal-to-noise ratio (SNR), resulting in a recording being triggered if a sound was detected ≥ 12 dB above background levels; and recording format to WAC0, to reduce file size and to maximize file storage. We assumed that this microphone type and arrangement allowed us, in minimal clutter environments, to effectively sample bats to ~19.8 m above the ground (i.e., our mean canopy height) for species with call frequency ranges of <45 kHz [41]. At each location, we conducted bat echolocation call monitoring for five consecutive nights at four locations, beginning with the first 4 locations on 31 May 2014. We subsequently moved the detectors to four new locations, beginning on 6 June, 13 June, 19 June, 25 June, and 1 July 2014.

We stored digitally recorded bat call sequences on compact flash cards inside detectors, downloading them to a computer after each five day monitoring period, and then converted all recorded call sequences from WAC0 to WAV format using Kaleidoscope Pro 3 software [42]. During file conversion, we also used this software to scrub recordings from false detector triggers, including anthropogenic noise and non-biological sounds such as rain and wind. During classification, we defined a bat pass as a search-phase echolocation call sequence of ≥ 2 echolocation call pulses. To classify bat activity (i.e., passes) to family and genus post file-conversion and scrubbing, we used two methods: (1) automated identification using Kaleidoscope Pro 3 software and associated Neotropical and North American bat classifiers; and (2) visual identification of spectrograms [42–48] displayed in the Kaleidoscope Pro 3 Viewer. When classifying bat passes using automated and visual identification, differentiating among species' calls can be difficult; it is affected by the degree of clutter at sampling locations, direction the bat is pointing relative to the microphone when it emits a call, angle and direction of the detector microphone, call attenuation, Doppler shift, and similarity of call characteristics of different species [49–52]. Therefore, to avoid misidentification, we only classified recorded bat passes to family and genus. We used classified bat passes to examine richness by family and genus; bat activity, by family and genus; and relationship between forest structure and composition characteristics and bat richness and activity, for all bats' combined and common (>100 individual passes) families and genera.

2.3. Forest Characteristics

Within a week of conducting bat echolocation call monitoring at a location, we quantified 51 forest characteristics (Table 1) within a 0.1 ha nested circular plot centered on the bat detector (i.e., SM2; Figure 1). These forest characteristics were divided into seven strata: ground, shrub, ground-shrub, understory, midstory, overstory, and other. We also measured topographic characteristics at each location.

Table 1. Forest structure and composition of the Chiquibul Forest Reserve (CFR), Belize, Central America, in summer 2014.

Strata	Characteristic	Abbreviation	Mean \pm SE ^a
Topography	Elevation (m)	Elev	636.5 \pm 10.9
	Slope (%)	Slope	12.4 \pm 3.4
Ground ^b	Total cover (%)	GTotCov	97.6 \pm 0.7
	Hardwood cover (%)	GHdCov	5.7 \pm 0.7
	Palm cover (%)	GPaCov	4.3 \pm 0.8
	Graminoid cover (%)	GGrCov	0.6 \pm 0.4
	Forb cover (%)	GFoCov	5.4 \pm 0.8
	Litter cover (%)	GLiCov	84.5 \pm 2.5
	Litter depth (mm)	GLd	31.1 \pm 2.8
	Bare soil (%)	GBs	1.8 \pm 0.6
Shrub ^c	Exposed rock (%)	GEr	0.6 \pm 0.3
	Canopy cover (%)	SCc	10.6 \pm 0.9
Ground-shrub ^d	Vertical obstruction from 5.6 m (%)	Vo56	64.2 \pm 3.9
	Vertical obstruction from 17.8 m (%)	Vo178	95.3 \pm 1.0
Understory ^e	Total density (no./ha)	UTotDen	4729.2 \pm 374.3
	Hardwood density (no./ha)	UVarTotDen	4016.7 \pm 349.9
	Palm density (no./ha)	UPaDen	2841.7 \pm 304.4
	Vine density (no./ha)	UViDen	1325 \pm 167.2
	Total dbh (cm)	UTotDbh	3.1 \pm 0.1
	Hardwood dbh (cm)	UHdDbh	2.8 \pm 0.1
	Palm dbh (cm)	UPaDbh	4.2 \pm 0.5
	Palm height (m)	UPaHt	1.4 \pm 0.1
Midstory ^f	Vine basal diameter (cm)	UViBd	2.9 \pm 0.1
	Total density (no./ha)	MTotDen	575.8 \pm 44.1
	Hardwood density (no./ha)	MHdDen	557.5 \pm 44.6
	Palm density (no./ha)	MPaDen	18.3 \pm 5.4
	Total dbh (cm)	MTotDbh	19.1 \pm 0.4
	Hardwood dbh (cm)	MHdDbh	19.1 \pm 0.4
Overstory ^g	Palm dbh (cm)	MPaDbh	19.0 \pm 1.5
	Total density (no./ha)	OTotDen	31.3 \pm 3.3
	Hardwood density (no./ha)	OHdDen	30.8 \pm 3.2
	Palm density (no./ha)	OPaDen	0.4 \pm 0.4
	Total dbh (cm)	OTotDbh	56.1 \pm 3.0
	Hardwood dbh (cm)	OHdDbh	56.1 \pm 3.0
	Palm dbh (cm)	OPaDbh	43.5 \pm 0.0
	Total canopy cover (%)	OTotCc	93.4 \pm 1.0
	Hardwood canopy cover (%)	OHdCc	64.3 \pm 3.3
	Palm canopy cover (%)	OPaCc	29.4 \pm 3.6
	Canopy height (m)	OCanHt	19.8 \pm 0.7
	Canopy base (m)	OCanBa	10.6 \pm 0.4
	Canopy depth (m)	OCanDp	9.2 \pm 0.4
Other	Log density (no./ha)	LogDen	72.0 \pm 10.0
	Log midpoint diameter (cm)	LogDia	21.6 \pm 1.3
	Log length (m)	LogLen	7.2 \pm 0.8
	Stump density (no./ha)	StumpDen	17.1 \pm 3.2
	Stump basal diameter (cm)	StumpBd	30.0 \pm 4.1
	Stump height (m)	StumpHt	0.7 \pm 0.1
	Snag density (no./ha)	SnagDen	34.6 \pm 5.5
	Snag dbh (cm)	SnagDbh	20.7 \pm 1.6
	Snag height (m)	SnagHt	6.6 \pm 0.4
	Snag decay class (1–4)	SnagDecC	3.0 \pm 0.2

^a Standard error of the mean. ^b Woody (including vines) and herbaceous vegetation ≤ 0.5 m in height with $\geq 50\%$ of the stem area in the plot, litter, bare soil, and exposed rock. ^c Horizontal canopy cover of woody vegetation ≤ 2.0 m in height. ^d Vertical obstruction/cover of all living and dead vegetation, rocks, etc. ≤ 2.0 m above the ground.

^e Living woody vegetation ≥ 1.37 m tall and < 10 cm diameter at breast height (dbh). ^f Living woody vegetation ≥ 1.37 m tall and ≥ 10 to < 40 cm dbh. ^g Living woody vegetation ≥ 1.37 m tall and ≥ 40 cm dbh.

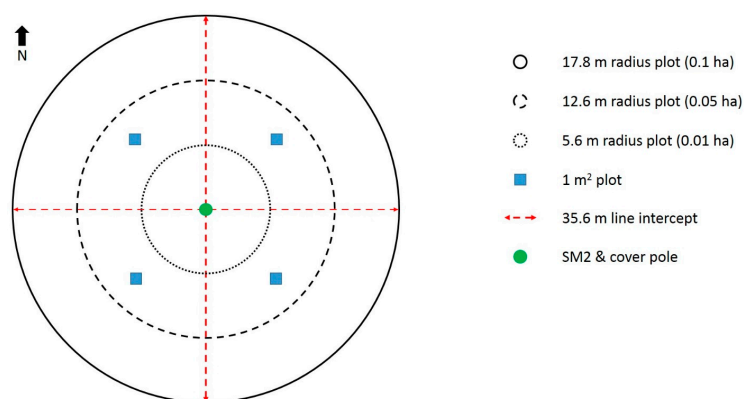


Figure 1. A 0.1 ha circular nested plot design used to study forest composition and structure effects on Neotropical aerial insectivorous bats in the Chiquibul Forest Reserve (CFR), Belize, Central America, in summer 2014. Plots, lines, and poles sampled different strata and types of cover, and SM2s sampled bat richness and activity.

2.3.1. Ground Strata

We estimated cover (%) (ocular estimate) of forbs, graminoids, palms, and hardwoods measuring <0.5 m in height, as well as litter, bare soil, and exposed rock, in four 1 m² quadrats, one located 9 m from the center in each of the quadrants (i.e., NE, NW, SE, and SW) of our 0.1 ha circular plot (Figure 1). We recorded all cover estimates on a scale: 1 = 0–5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–95%; 6 = 96–100% [53]. The cover estimates for litter, forbs, graminoids, palms, and hardwoods were not mutually exclusive (i.e., each could add to 100%). At the center of each 1 m² quadrat, we measured litter depth (cm; Table 1; Figure 1).

2.3.2. Shrub Strata

We assessed shrub cover (%) 1 m above the ground, along two perpendicular 35.6 m transecting lines centered on our 0.1 ha circular plot using the line intercept method [54] (Table 1; Figure 1).

2.3.3. Ground-Shrub Strata

We determined vertical vegetation obstruction (%) by viewing, from 1 m above the ground, a 2 m tall cover pole [55] centered on our 0.1 ha circular plot. We obtained measurements in each of the four cardinal directions at distances of 5.6 and 17.8 m (Table 1; Figure 1).

2.3.4. Understory Strata

We counted (no.) and measured diameter at breast height (dbh; cm) of all understory hardwood stems and palms (i.e., stems ≥ 2 m tall and, for hardwoods, with a dbh of <10 cm) within a 0.01 ha circular quadrat centered on the 0.1 ha circular plot. Because palms of this stratum often lack a dbh, we measured palm height (to the highest leaf) as an index of volume using a Suunto PM-5 clinometer [54] (Suunto, Vantaa, Finland). We also counted (no.) and measured basal diameter (bd; cm) of vines at ground level, regardless of their size. We used the counts, dbh, and bd measurements to determine total understory density (no./ha) and mean understory dbh and bd (cm), as well as density and mean dbh and bd, of midstory hardwoods, palms, and vines (Table 1; Figure 1).

2.3.5. Midstory Strata

We counted (no.) and measured dbh (cm) of all midstory stems (i.e., stems ≥ 2 m tall and with a dbh of ≥ 10 cm and <40 cm) within a 0.05 ha circular quadrat centered on the 0.1 ha circular plot, in order to determine total midstory density (no./ha) and mean midstory dbh (cm), as well as density and mean dbh of midstory hardwoods and palms (Table 1; Figure 1).

2.3.6. Overstory Strata

We counted (no.) and measured dbh (cm) of all overstory stems (i.e., stems ≥ 2 m tall and with a dbh of ≥ 40 cm) within the 0.1 ha circular plot, in order to determine total overstory density (no./ha) and mean overstory dbh (cm), as well as density and mean dbh of overstory hardwoods and palms (Figure 1). We used a GRS densitometer (Geographic Resource Solutions, Arcata, CA, USA) to measure total overstory canopy cover (%) and canopy cover of overstory hardwoods and palms, at 2 m intervals along two perpendicular 35.6 m transecting lines centered on the 0.1 ha circular plot, for a total of 35 subsamples (Figure 1). Finally, we assessed overstory canopy height (m; i.e., top of overstory canopy), base (m; i.e., height of the lowest overstory canopy limb), and depth (m; i.e., overstory canopy height minus overstory canopy base) using a Suunto PM-5 clinometer [54] at the center of the 0.1 ha circular plot and at the ends of the 35.6 m transecting lines, for a total of five subsamples (Table 1; Figure 1).

2.3.7. Other

We assessed density of logs (i.e., dead woody vegetation ≥ 10 cm in diameter at midpoint, and with the majority of the stem laying horizontally on the ground), stumps (i.e., dead woody vegetation < 1.37 m tall and ≥ 10 cm in diameter), and snags (i.e., dead woody vegetation ≥ 1.37 m tall and ≥ 10 cm dbh) by counting each within the 0.1 ha circular plot. We measured stump and snag heights using a Suunto PM-5 clinometer [54] and assigned all snags to one of four decay classes (i.e., 1 = branches: 80–100% remaining, bark: 80–100% remaining, height: fully broken top; 2 = branches: few to none, bark: 30–80%, height: broken top; 3 = branches: limb studs—none, bark: $\leq 30\%$ with $\geq 50\%$ of the height and $> 80\%$ with $< 50\%$ of the height, height: broken top (50%); and 4 = branches: none, bark: $< 80\%$, height: $< 50\%$; Table 1; Figure 1) [56].

2.3.8. Topography

At the center of the 0.1 ha circular plot, we determined elevation (m) using a Garmin GPS 72 (Garmin, Olathe, KS, USA) and slope (%) using a Suunto PM-5 clinometer [54] (Table 1; Figure 1).

2.4. Data Analysis

Bat richness and activity may vary through time [37]. Therefore, to justify combining data from different sampling periods in the analyses, we used an analysis of variance to determine if bat richness and activity varied among sampling periods [57]. Bat family richness, genus richness, and activity did not vary by sampling period ($p \geq 0.329$). Therefore, we combined data across periods to examine how forest characteristics affected bat richness and activity.

We used simple linear regression [57] to examine univariate relationships between the dependent bat richness and activity variables (i.e., family richness, genus richness, total bat activity, and activity of common genera and families) and independent forest characteristics (Table 1). We then used backward stepwise multiple regression (F -to-enter = 0.15; F -to-remove = 0.15; tolerance = 0.30) to examine relationships between the same dependent bat richness and activity variables and independent forest characteristics [57,58]. To reduce the number of potential independent forest characteristics in the analyses, we first eliminated those with $p > 0.200$ in the univariate analyses [59], and we then eliminated one variable from any highly correlated pairs ($r \geq 0.70$). The variable retained was that with the greatest F -ratio derived from the univariate analyses [58,60]. Standardized coefficients (SC) were used to evaluate the relative contributions of independent forest characteristics in the final multiple regression models [61]. As a post hoc analysis, we used correlation analyses [57] to examine the univariate relationships between canopy depth and other forest characteristics (Table 1).

We rank-transformed all data prior to analyses to meet normality and homogeneity of variance assumptions [57,61,62] and concluded statistical significance for all tests at $p \leq 0.05$ level [57]. We performed all analyses using SYSTAT 13 [61]. For clarity and brevity, we only present statistically significant results.

3. Results

We monitored bat richness and activity at 24 randomly selected locations for 120 nights (5 nights/location) from May–July 2014, for a total of approximately 1440 monitoring hours (12 h/night). During this time, we recorded 13,420 bat passes and classified 73% ($n = 9791$) as belonging to one of 5 families and 16 genera of aerial insectivorous bat (Table 2). Molossidae and *Eumops* spp. were the most active family and genus, respectively. A large number of Vespertilionidae, in particular *Myotis* spp. and *Lasiurus* spp., were also recorded (Table 2).

Table 2. Bat activity in the Chiquibul Forest Reserve (CFR), Belize, Central America, in summer 2014.

Group	Bat Activity (No. of passes)	Relative Bat Activity
Emballonuridae	108	0.011
<i>Balantiopteryx</i> spp.	30	0.003
<i>Diclidurus</i> spp.	70	0.007
<i>Peropteryx</i> spp.	2	0.000
<i>Rhynchonycteris</i> spp.	1	0.000
<i>Saccopteryx</i> spp.	5	0.000
Molossidae	5071	0.518
<i>Cynomops</i> spp.	35	0.004
<i>Eumops</i> spp.	4655	0.475
<i>Molossus</i> spp.	20	0.002
<i>Promops</i> spp.	361	0.037
Mormoopidae	1203	0.123
<i>Mormoops</i> spp.	49	0.005
<i>Pteronotus</i> spp.	1154	0.118
Noctilionidae	53	0.005
<i>Noctilio</i> spp.	53	0.005
Vespertilionidae	3356	0.343
<i>Eptesicus</i> spp.	3	0.000
<i>Lasiurus</i> spp.	1286	0.131
<i>Myotis</i> spp.	2053	0.210
<i>Perimyotis</i> spp.	14	0.001

Bat family richness was not affected by any individual forest characteristics ($p \geq 0.080$). No combination of forest characteristics sufficiently explained bat family richness ($p = 0.841$). Bat genus richness was affected by three individual forest characteristics (Table 3). The combined effects of four structural characteristics best explained bat genus richness ($p = 0.023$; $R^2 = 0.861$), where canopy depth (OCaDp) ($SC = 0.948$) was of greatest importance, followed by hardwood density (OHdDen) ($SC = -0.458$), palm dbh (MPaDbh) ($SC = 0.376$), and palm cover (GPaCov) ($SC = 0.375$).

Table 3. Bat genus richness and total bat activity relationships with forest structure and composition in the Chiquibul Forest Reserve (CFR), Belize, Central America, in summer 2014.

Dependent Variable	Independent Variable (Forest Characteristic ^b)	Relationship ^a		
		β	p	r^2
Genus richness (No. of species)	GPaCov	0.424	0.037	0.182
	OTotDen	−0.489	0.017	0.232
	OHdDen	−0.534	0.009	0.271
Total bat activity ^c (No. of bat passes)	GFoCov	−0.522	0.016	0.235

^a Simple linear regression of rank-transformed data for significant ($p \leq 0.05$) relationships. ^b See Table 1 for variable descriptions. ^c All bat species' passes combined.

Total bat activity was affected by one individual forest characteristic (Table 3). The combined effects of three structural characteristics best explained overall bat activity ($p = 0.019$; $R^2 = 0.385$), where

forb cover (GFoCov) (SC = −0.407) was of greatest importance, followed by snag density (SnagDen) (SC = −0.308), and OCanDp (SC = 0.296).

Emballonuridae activity was not affected by any individual forest characteristics ($p = 0.068$). No combination of forest characteristics sufficiently explained Emballonuridae activity ($p = 1.000$).

Molossidae activity was not affected by any individual forest characteristics ($p \geq 0.070$). No combination of forest characteristics sufficiently explained Molossidae activity ($p = 1.000$). *Eumops* spp. activity was not affected by any individual forest characteristics ($p \geq 0.076$). No combinations of forest characteristics sufficiently explained *Eumops* spp. activity ($p = 1.000$). *Promops* spp. activity was affected by seven individual forest characteristics (Table 4). The combined effects of three structural characteristics best explained *Promops* spp. activity ($p = 0.001$; $R^2 = 0.539$), where total dbh (UTotDbh) (SC = −0.409) was of greatest importance, followed by GPaCov (SC = 0.357) and OCanDp (SC = 0.340).

Table 4. Bat activity relationships with forest structure and composition for common families and genera (>100 passes) in the Chiquibul Forest Reserve (CFR), Belize, Central America, in summer 2014.

Dependent Variable	Independent Variable (Forest Characteristic ^b)	Relationship ^a		
		β	p	r^2
Molossidae				
<i>Promops</i> spp.	GTotCov	−0.523	0.012	0.253
	GPaCov	0.479	0.019	0.226
	GLiCov	0.412	0.047	0.167
	UTotDbh	−0.485	0.016	0.236
	MTotDen	−0.423	0.039	0.179
	MHdDen	−0.474	0.019	0.225
	OCanDp	0.504	0.012	0.253
Mormoopidae	GHdCov	0.438	0.041	0.176
	Vo178	−0.445	0.032	0.192
	SnagDbh	0.603	0.011	0.294
<i>Pteronotus</i> spp.	Vo178	−0.472	0.022	0.217
	SnagDbh	0.541	0.030	0.226
	StumpHt	0.790	0.045	0.258
Vespertilionidae				
<i>Lasiurus</i> spp.	UPaHt	0.564	0.004	0.318
	OTotDen	−0.497	0.017	0.232
	OHdDen	−0.484	0.022	0.216
	StumpBd	−0.681	0.023	0.301
<i>Myotis</i> spp.	Vo56	−0.407	0.048	0.166
	Vo178	−0.469	0.023	0.213
	MTotDbh	0.421	0.041	0.177
	SnagDbh	0.613	0.012	0.288

^a Simple linear regression of rank-transformed data for significant ($p \leq 0.05$) relationships. ^b See Table 1 for variable descriptions.

Mormoopidae activity was affected by three individual forest characteristics (Table 4). The combined effects of two structural characteristics best explained Mormoopidae activity ($p = 0.006$; $R^2 = 0.438$), where snag dbh (SnagDbh) (SC = 0.509) was of greatest importance, followed by vertical obstruction from 17.8 m (Vo178) (SC = −0.380). *Pteronotus* spp. activity was affected by three individual forest characteristics (Table 4). The combined effects of two structural characteristics best explained *Pteronotus* spp. activity ($p = 0.012$; $R^2 = 0.389$), where SnagDbh (SC = 0.440) was of greatest importance, followed by Vo178 (SC = −0.405).

Vespertilionidae activity was not affected by any individual forest characteristics ($p \geq 0.064$). No combination of forest characteristics sufficiently explained Vespertilionidae activity ($p = 0.142$). *Lasiurus* spp. activity was affected by four individual forest characteristics (Table 4). The combined effects of three structural characteristics best explained *Lasiurus* spp. activity ($p = 0.036$; $R^2 = 0.387$), where palm height (UPaHt) (SC = 0.476) was of greatest importance, followed by log length (LogLen) (SC = −0.287) and snag height (SnagHt) (SC = −0.072). *Myotis* spp. activity was affected by four

individual forest characteristics (Table 4). The combined effects of four structural characteristics best explained *Myotis* spp. activity ($p \leq 0.001$; $R^2 = 0.764$), where total dbh (MTotDbh) (SC = 0.467) was of greatest importance, followed by litter cover (GLiCov) (SC = 0.376), Vertical obstruction from 5.6 m (Vo56) (SC = −0.364), and SnagDbh (SC = 0.353).

Canopy depth was correlated with palm canopy cover ($p = 0.038$; $r = -0.427$), midstory total density ($p = 0.025$; $r = -0.456$), midstory hardwood density ($p = 0.014$; $r = -0.497$), and canopy height ($p \leq 0.001$; $r = 0.712$). There were no other relationships between canopy depth and other forest characteristics ($p \geq 0.091$).

4. Discussion

We recorded the majority (90%) of the genera of non-Phyllostomid aerial insectivorous bats known to occur in the CFR [16], and three genera, *Noctilio* (Noctilionidae), *Eumops*, and *Promops* (both Molossidae) spp., not previously reported to occur in the reserve, although they are known to occur in other regions of Belize [63,64]. Despite not previously having been known to occur in the CFR, *Eumops* spp. was the most frequently recorded bat genus. *Rhynchonycteris* and *Molossus* spp. were infrequently detected, likely because their call frequency ranges fell outside of our effective sampling heights in the forest, which may also have been the case for previously documented genera (i.e., *Natalus* and *Rhogeessa* spp.) that went undetected [16,41,42,63,64].

Genus richness and total activity of detected aerial insectivorous bats and activity of a number of individual genera responded to forest structure and composition. Genus richness and total bat activity were directly related to overstory canopy depth. Some bats—Mormoopidae (*Pteronotus* spp.), Noctilionidae (*Noctilio* spp.), and Vespertilionidae (*Eptesicus* spp., *Lasiurus* spp., *Myotis* spp., and *Perimyotis* spp.)—came from narrow- or edge-space families and genera [8,23,64,65]. These bats fly more slowly but are much more maneuverable and able to fly easily in areas of high structural complexity and clutter [66,67]; as a result, they tend to prefer edge or narrow space typically found in less disturbed areas, often with denser overstories, midstories, understories, and ground layers [30]. Their echolocation calls are also higher in frequency and of shorter duration, as insects are typically being detected over shorter distances [31]. The greater activity of edge-space *Lasiurus* spp. with increasing understory palm density supported this conclusion. In addition, a deeper canopy, often associated with greater clutter, may have led to a reduced predation risk [68,69].

However, the majority of bats detected, which contributed to genus richness and total bat activity, came from open-space families and genera that typically prefer to fly and forage in areas with little clutter (i.e., Molossidae (*Promops* and *Eumops* spp.), Emballonuridae (*Balantiopteryx*, *Diclidurus*, and *Peropteryx* spp.), and Mormoopidae (*Mormoops* spp.) [23,28]). The mobility of open-space bats is thought to be an important trait in determining their habitat preferences [70] and responses to forest structure and composition. These species are built for speed rather than for maneuverability, and they fly best in open areas with little clutter, where they can move quickly and cover long distances; these conditions are often associated with newly disturbed areas [23,30,71]. These bats are not adept at flying in cluttered, obstacle-rich environments [29,67]. In addition, they emit low-frequency, narrowband echolocation calls that allow for the long-range detection of insects across large, open areas [31]. Greater bat genus richness with lower overstory total and hardwood density, and greater bat activity with lower snag density further supported the conclusion that such bats prefer areas with less clutter; as does the increased activity of open-space *Promops* spp. with a reduced midstory total and hardwood density.

Characteristics of many of the bat genera detected suggest total bat activity and, to some extent, richness are inversely related to canopy depth because of the increased clutter often created by a deeper canopy. It is possible that canopy clutter is below the threshold at which these open-space bats cease using the forests. Further, while it is deep, the canopy may be relatively clutter-free. This conclusion is supported by inverse relationships between canopy depth and palm canopy cover and midstory total and hardwood density, structural characteristics that would clutter the lower portion of the canopy; and by a lack of any relationship with other canopy characteristics, such as overstory density and

canopy cover. It may also be that the deeper canopy, often associated with greater clutter, allowed bats to avoid predators and continue foraging, particularly when light levels in more open areas would have increased their chances of predation [13,22,23,30,68,69].

Additionally, open-space bats may favor a deeper overstory canopy because of its association with plant species they use as resources (e.g., food, roosts, perching sites [32]). Certainly, a high insect abundance (i.e., bat food) has been associated with the canopy of Neotropical rainforests [72–74], as food resources for phytophagous insects (e.g., foliage, flowers, fruits) are more abundant in the canopy [75], and there is a greater diversity of niches than in the midstory or understory [76].

Open-space *Promops* spp. activity increased with reduced midstory total and hardwood density, and edge-space *Lasiurus* spp. activity increased with lower overstory total and hardwood density and snag height. The majority of these species prefer to fly and forage in areas with little clutter (e.g., reduced tree density [23,28]). In temperate regions, increases in activity of open-space aerial insectivorous bat species, similar to *Promops* and *Lasiurus* spp., are associated with reduced tree density that occurs following thinning. The structural changes resulting from reduced tree density benefit these bats by creating a habitat structure they are able to use more effectively [27,50,77,78].

Myotis, *Promops*, and *Pteronotus* spp. activity were inversely related to several ground cover and vertical obstruction (i.e., shrub cover) characteristics, including forb cover, total ground cover, and vertical obstruction at 5.6 and 17.8 m. These forest characteristics provide a measure of ground-level clutter. In Neotropical rainforests, vegetation is typically denser because of an abundance of herbaceous plants, shrubs, and tree saplings, resulting in greater clutter at or near the ground, compared to the midstory and overstory [23]. This is even more pronounced in disturbed forests, where gaps allow increased light penetration that favors the development of dense undergrowth [17–19]. This dense ground cover does not provide the obstacle-free environment needed for many aerial insectivorous bats to fly and capture prey [23], including open-space bats such as *Promops* spp. and more maneuverable edge-space species in the Emballonuridae family (e.g., *Saccopteryx*, *Cormura* spp. [67]), which are similar to many *Myotis* spp. Marques et al. [23] observed a far greater abundance of aerial insectivorous bats, many of which were open-space species, foraging at overstory and midstory canopy levels, apparently to avoid the clutter of the ground and understory layers. It was surprising that activity of *Pteronotus* spp., a species that typically prefers narrow spaces and is adapted to flying in clutter [67], was inversely related to vertical obstruction, a measure of vegetation density. However, a similar response was observed for temperate bat species that favor narrow spaces [77,79–81]. Narrow-space species may be better able to exploit forest habitats regardless of clutter, and may forage in areas that are most profitable [82].

We found *Myotis* spp., *Pteronotus* spp., and Mormoopidae activity to be directly related to snag dbh and height and stump height. *Myotis* spp. are primarily snag roosters [64] and should be influenced by the size and abundance of roost locations. Effects of roost site size have not been addressed quantitatively in the Neotropics. However, roost site availability (i.e., number and types of roosts) influences bat community composition and structure on Caribbean islands [83] and in North America [6]. Members of the Mormoopidae family, including *Pteronotus* spp., are primarily cave roosters [64], and their relationship with snag dbh and stump height is not easily explained. We also observed an inverse relationship between *Lasiurus* spp. activity and snag height, log length, and stump basal diameter. Most members of the *Lasiurus* genus roost in foliage and under the bark of live trees [64]. Thus, this inverse relationship with snag, log, and stump characteristics is unclear, but it is possibly related to reduced clutter in the lower strata.

Family and genus richness and total-, family-, and genus-specific activity exhibited a lack of response to changes in many forest characteristics; there was no response in richness for some families (Emballonuridae, Molossidae, and Vespertilionidae) and genera (*Eumops* spp.) examined, suggesting that these bats may not be very sensitive to changes in forest structure or composition. It is also possible that combining species and examining relationships at genus and family levels masks some relationships.

5. Conclusions

Most forest structure and composition characteristics in the CFR did not affect family and genus richness or total activity of aerial insectivorous bats, or activity of individual bat families and genera. Genera affected included *Lasiurus*, *Myotis*, *Promops*, and *Pteronotus* spp. and, of these, *Promops* spp. exhibited the greatest response; this was likely explained by preferences for less-cluttered, open space, and by species-specific food and cover requirements. The lack of response to many forest characteristics suggests that non-Phyllostomid aerial insectivorous bats in this study may be less sensitive to changes in forest structure and composition than Phyllostomids [24,32–35], or that the relationships need to be examined at finer taxonomic levels, and that, at this level, they may not be as useful as indicators of alteration [13–15]. Further, these species may have some tolerance for disturbance and change, such as the hurricanes and selective logging experienced in the CFR and possibly to changes in forest structure and composition associated with climate change.

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