

HUMAN DISTURBANCE IS NEGATIVELY AFFECTING BAT DIVERSITY IN NORTHERN TRINIDAD

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ABSTRACT

Tropical rainforests are becoming increasingly exposed to human activity and very few pristine or untouched environments remain. It is therefore important to understand how different species react to human disturbance in order to create effective conservation management plans. In the Neotropics, bats are incredibly diverse, partially due to the diversity of their feeding behaviours. However, this large dietary range also leaves specialised species vulnerable to extinction when threatened with human-mediated disturbance. Therefore, it is vital to understand the relationship between anthropogenic activity (such as deforestation and overexploitation), bat species diversity, and diet specialisation in order to protect the bat communities of the Neotropics.

From 7 June to 8 August 2017, 478 bats were caught over three sites in Northern Trinidad. Each site was analysed to understand the effects of differing levels of human disturbance on community composition, species diversity, abundance, richness, evenness, rarity, and feeding guild diversity. Bat species richness, diversity and evenness were all significantly and negatively affected by increasing levels of disturbance ($p < 0.05$ for all). Out of all the feeding guilds, the omnivores were the only group significantly affected by anthropogenic disturbance ($p < 0.001$).

These results suggest that continuous human disturbance negatively affects bat species diversity in Northern Trinidad. When disturbance is constant, only generalist species are able to cope with the continuous anthropogenic pressure as they are able to adjust their diets accordingly. Due to this quantitative and predictable reaction to anthropogenic activity, bats are ideal indicator species for monitoring disturbance in the Neotropics.

INTRODUCTION

Tropical rainforests cover less than 7% of the Earth's surface, yet they contain around 40% of all living species (Myers, 1992). For this reason, rainforests can be considered to be biodiversity hotspots with many rare or endangered species known to reside within them (Foley et al., 2007). However, these pristine ecosystems are disappearing at rapid rates as they are becoming increasingly exposed to human activity (Medellin et al., 2000).

Central America, the Caribbean and the Amazon are particularly vulnerable to rainforest loss and detrimental human activity, and it is thought that an estimated 37.9 million hectares of primary forest were removed from these areas from 1990-2015 (FAO (Food and Agriculture Organization of the United Nations), 2015). Forest clearance is believed to be the main cause of biodiversity declines as it affects species richness and can affect the productivity of ecosystems (Haddad et al., 2015).

Evaluating how disturbance is affecting local fauna and flora provides important information on which management plans and conservation decisions can be created (Medellin et al., 2000). Disturbance levels in an ecosystem can be estimated using indicator species as a surrogate measure. In order to be considered as an indicator, species need to be abundant, diverse and easy to sample (Mooney et al., 1995). In the Neotropics, bats fulfil all of these requirements and have been shown to respond to environmental changes in quantitative, predictable ways (Medellin et al., 2000).

As a general trend, species richness increases towards the equator, and bats are no exception to this pattern (López-Baucells et al., 2016). Bat diversity is particularly high in Trinidad as almost 70 species are present on the island (Gomes and Reid, 2015). Unfortunately, disturbance is a huge problem in the Caribbean, and forests are heavily influenced by the activities of man (Gomes and Reid, 2015). This is problematic as most species have specialised requirements in diet, roosting site or habitat preference (López-Baucells et al., 2016), which make them exceptionally vulnerable to disturbance. It is estimated that a quarter of all bat species are already threatened by anthropogenic (human-sourced) activity through loss of natural habitats, fragmentation, overexploitation, misguided persecution, climate change, and disease (López-Baucells et al., 2016).

A reduction in bat species diversity raises numerous environmental concerns as 80% of the plant species present in Neotropical rainforests rely on fruit-eating vertebrates to disperse their seeds (Gomes and Reid, 2015). In other words, 549 plant species would be negatively affected if human activity reduced the number of viable habitats available to bats or reduced bat population diversity (Lobova et al., 2009). However, the effects of human disturbance can be mitigated if environments are controlled and protected. Forests which have re-grown after disturbance have the potential to yield high levels of biodiversity similar to that of primary, undisturbed,

forest habitats if managed appropriately (Gomes and Reid, 2015).

In order to understand the effects of disturbance on bats, diet can be used as a correlate for rarity which helps to predict the probability of local species extinction (Laurance, 1991). Bats are known to eat fruit, pollen, nectar, invertebrates, vertebrates, and blood (Patterson et al., 2003). This high specialisation in diet means that bats have a substantial effect on forest dynamics by providing a variety of ecosystem services (López-Baucells et al., 2016). Bats contribute to rainforest plant diversity through pollination, seed dispersal, and insect control (Medellin and Gaona, 1999). Evidence has shown that bats scatter more seeds than birds in disturbed environments, as birds are rapidly becoming extinct due to human activity (Fleming, 1987; Medellin and Gaona, 1999). This is further increasing the importance of bats as dispersers for large-seeded fruits (Patterson et al., 2003).

In Trinidad and Tobago, bats represent over 70% of the local mammalian fauna (Gomes and Reid, 2015), and 25–30% of bats are frugivores (Lobova et al., 2009). By consuming the fruits of a plant, bats widely disperse seeds and help create and maintain seed banks on the forest floor (Fleming, 1987). In the presence of sunlight, bat-deposited seeds will germinate and begin the reforestation process (Gomes and Reid, 2015). Many pioneer tree species rely on this method of dispersal as they are specifically adapted to rapidly colonise gaps created by both natural and man-made disturbance (Gomes and Reid, 2015).

Additionally, insectivores are important for removing various pest species. An insectivorous bat can consume up to 25% of its body mass in potentially harmful insects every night, while a pregnant bat may ingest over three times that intake to over 100% of her body mass (Kunz et al., 2011). This ecosystem service protects crops from intense insect damage, and bats are also indirectly reducing the effects of several insect-borne diseases (Gomes and Reid, 2015).

Variety in diet maintains bat diversity at high levels, but also leaves species vulnerable to extinction when threatened with disturbance (Patterson et al., 2003). It is therefore vital to understand the relationship between anthropogenic activities, bat species diversity and diet specialisation so that conservation management plans can be created, and the incredible bat diversity of the Neotropics can be saved.

Study Aims

The main aim of this investigation was to net (catch) and record bat species at three sites in Northern Trinidad with differing levels of disturbance in order to understand how bat communities are being affected by human activity. This study focused on the differences in species composition, abundance, richness, diversity and evenness between sites. It was also investigated whether dietary guild diversity or rare species were affected by anthropogenic pressure. Locations were classified according to noise level, light pollution, and development of infrastructure.

METHODOLOGY

Study Locations

This study was carried out at three sites in Northern Trinidad (Figure 1). Sites were classified according to previously published criteria (Helmer et al., 2012). Site 1 was a highly disturbed urban area, Site 2 was a moderately disturbed secondary forest, and Site 3 was a protected, mature,

secondary forest with little human disturbance. The secondary forest sites contained vegetation that had completely or partially re-grown after historical disturbance (Medellin et al., 2000).

The urban site was located at the University of the West Indies St Augustine Campus (UWI). This site was highly disturbed as roads, pavements and footpaths were present on every side of the sampling area. When sampling, there was a high level of noise (79.55 dB), and the light pollution came from the university buildings and passing traffic.

The moderately disturbed secondary forest site was located at the William Beebe Tropical Research Station (WBTRS), in the Arima Valley of Trinidad's Northern Range. The vegetation surrounding the research station was in various stages of succession (William Beebe Tropical Research Station, 2004). While still considered to be moderately disturbed due to the close proximity of a quarry, human presence was limited compared to UWI. Noise pollution averaged at 55.4 dB, and any light pollution was created by the quarry and lamps on the WBTRS premises.

The least disturbed site, located within mature, protected, secondary forest, was situated on the grounds of the Asa Wright Nature Centre (AW). Asa Wright's main buildings were located on a former plantation (Asa Wright Nature Centre, n.d.) but the estate has now been largely reclaimed by secondary forest vegetation and lower montane rainforest (Asa Wright Nature Centre, n.d.). An average noise disturbance of 62 dB was recorded for Asa Wright, and the only source of light was the moon.

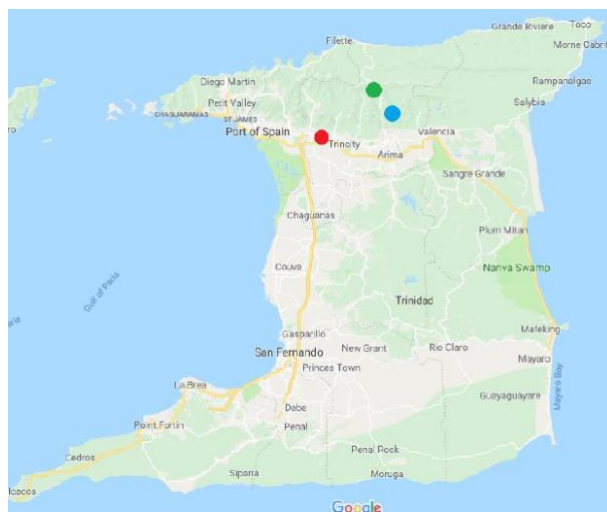


Figure 1: Map of Trinidad showing the three site locations. The University of the West Indies (Red), the William Beebe Tropical Research Station (Blue) and the Asa Wright Nature Centre (Green), (Google Maps, 2017).

Data Collection

Bats were captured using mist nets. At each site, two 12m mist nets were set up at ground level while a 'Triple High' was used to sample the canopy. This system had three 9m nets stacked on top of each other and was operated by a pulley system. Nets were strategically placed to intercept natural flight corridors, between forest banks or on man-made paths. A processing station was set up nearby so bats were handled and released as quickly as possible. The mist nets were erected and opened by sunset each sampling night and kept open for 4 hours, typically from 19:00 to 23:00, and were checked every 15 minutes. Once

a bat was caught, it was removed from the net as quickly as possible and placed in a cotton bag. The bat was then taken to the processing station. If the bat was visibly stressed, cold, injured, or pregnant, data were not collected and it was released immediately. During times of high capture rates, all nets were closed and cotton bags containing bats were hung up on a washing line in the order they were caught and what net they were removed from. This allowed for a rapid processing of individuals and kept handling time to a minimum. During times of heavy rainfall, nets were closed temporarily then shaken to remove excess water when reopened.

At the processing station, the time at which the bat was caught, the net it was removed from and the handler of the bat was recorded. Individuals were then weighed, and to help with species identification, forearm length was also measured. Age, sex and reproductive status were also noted. Individuals were then identified down to species level through the use of field keys on site (Gomes and Reid, 2015; Reid, 2017). If bats were showing signs of stress or energy depletion, a 1:3 sugar to water solution was fed to them via a syringe or, in the case of fruit-eating bats, banana or mango were cut up and offered.

Off-site, species were separated into their feeding guilds, such as omnivore, nectarivore, and frugivore, using several guides (Bonaccorso, 1975; Wilson et al., 1996; Gomes and Reid, 2015). Rarity was defined as how common the species is across the island of Trinidad rather than the number of individuals of that species caught within this study (Gomes and Reid, 2015). Brief descriptions of each site were also recorded, including: distances between nets and the processing station; the estimate measurement of the canopy height; noise and light disturbance; and the position of any clearings and the GPS co-ordinates.

Statistical Analysis

Data from 18 nights of sampling were analysed using R version 3.3.2. Differences between sites in all variables were analysed using one-way analysis of variance (ANOVA, F). Additional Post-hoc Tukey Tests were carried out if differences between sites were considered significant ($p < 0.05$).

RESULTS

Species Composition

Over 18 nights of data collection, 478 bats were recorded, representing 22 species from 6 families (Appendix 1). The vast majority of individuals belonged to the Phyllostomidae family (98.1%), followed by the Mormoopidae (0.6%), Molossidae and Emballonuridae (both 0.4%), and the Vespertilionidae and Natalidae (both 0.2%). *Artibeus jamaicensis* was the most common species, accounting for 49.6% of total captures. This was followed by *Carollia perspicillata* at 14.6% and *Phyllostomus discolor* at 13.6%. *Artibeus jamaicensis* was the most common species caught at UWI and the WBTRS, while *Carollia perspicillata* was the most abundant species at Asa Wright.

Only three species were sampled in all habitats: *Artibeus lituratus*, *Artibeus jamaicensis* and *Glossophaga soricina*. There were no species found to be unique to the disturbed UWI site, while two species were found exclusively at the WBTRS. Another nine species were found exclusively at the least-disturbed Asa Wright site.

Abundance and Capture Rate

The average capture rate for all sites was found to be 1.6 bats $\text{net}^{-1}\text{h}^{-1}$ (i.e. per net, per hour). The WBTRS had the highest number of individuals and the highest capture rate of 1.7 bats $\text{net}^{-1}\text{h}^{-1}$. However, this difference in individuals was not

statistically significant ($p > 0.05$). However, the capture rate for the triple high net was 0.6 bats $\text{net}^{-1}\text{h}^{-1}$ higher than the ground net and was considered significant ($p < 0.001$).

Species Richness

By the end of data collection, 19 species had been recorded at Asa Wright, 11 were recorded at the WBTRS, and only 6 were recorded at UWI. Sampling within the separate habitats found that 86.4% of species were caught at Asa Wright, 50.0% were caught at the WBTRS, and 27.3% were caught at UWI. The number of species caught was significantly different between sites ($p = 0.017$). Post-hoc Tukey Tests confirmed that differences in species richness were significant between UWI and Asa Wright ($p = 0.014$). All other pairwise tests between sites were non-significant ($p > 0.05$).

Using species accumulation curves (Figure 2), only UWI's rate of species accumulation began to level out, suggesting all species present at that site were recorded. However, the WBTRS and Asa Wright rates were continuing to increase which indicated that there were more species to be discovered at those sites. The estimated total number of species at each site was 6.5 for UWI, 19 for the WBTRS, and 23 for Asa Wright. The total number of species caught at each site was 6 for UWI, 11 for the WBTRS, and 19 for Asa Wright. Therefore, sampling detected close to the total estimated species for UWI, whereas around 8 species were unrecorded at the WBTRS, and approximately 4 species remained to be recorded at Asa Wright.

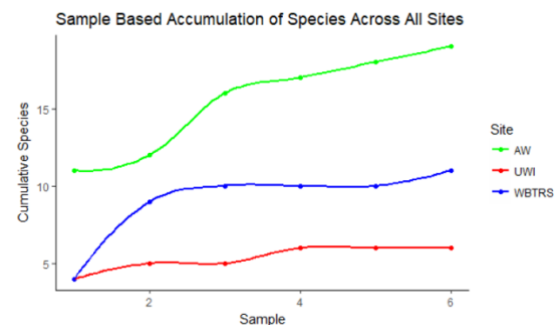


Figure 2: Accumulation of species over 6 nights of data collection at each site. The rate at which new species are added to the inventory provides estimates about the total species richness of an assemblage.

Species Diversity

Differences in diversity as calculated using the Simpson's Index were significant between the study sites ($p < 0.001$). Further statistical tests confirmed that the differences in species diversity between UWI and the WBTRS to the Asa Wright site were statistically significant ($p < 0.001$); whereas a comparison of UWI to the WBTRS was non-significant ($p > 0.05$). According to the Simpson's Index, bat species diversity was the highest at Asa Wright and the lowest at the WBTRS. However, when plotted in a k-dominance curve (Figure 3), UWI was the least diverse assemblage.

Beta diversity was recorded using Whittaker's measure (BW). The greatest difference in species composition was between Asa Wright and UWI (0.6), followed by the WBTRS and UWI (0.529). The WBTRS and Asa Wright were considered to have the most similar species composition (0.467).

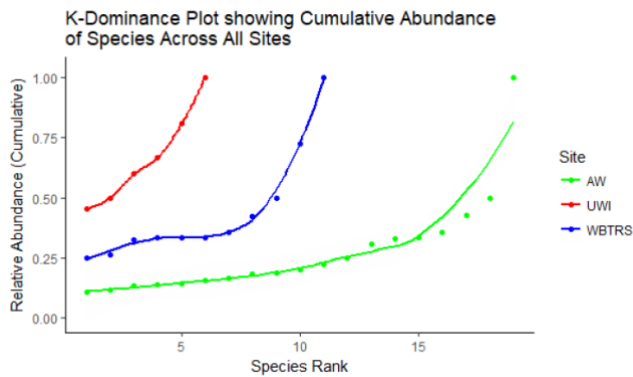


Figure 3: K-dominance plot for bat assemblages caught across the three different sites. More elevated curves represent less diverse assemblages. In this case, UWI (red) is considered the least diverse.

Species Evenness

Differences in evenness as calculated using Simpson's Evenness were significant between sites ($p = 0.026$). UWI had the highest evenness, whereas the WBTRS had the lowest. Differences in species evenness between the WBTRS and Asa Wright were significant ($p = 0.035$); whereas, differences between UWI and Asa Wright and between UWI and the WBTRS were not ($p > 0.05$ for both).

Species Rarity

50% of the species caught in this study were classified as uncommon or rare using the field guide by Gomes and Reid (2015) (Appendix 1). 36.4% of all rare species were found at Asa Wright, 18.2% were at the WBTRS, and only 4.5% were at UWI. Out of the 9 species that were exclusively found at the Asa Wright site, all but 2 were considered uncommon or rare (Appendix 1). However, the number of rare species at each site was not statistically significant ($p = 0.055$).

Feeding Guilds

82.4% of all individuals were frugivores. Omnivores were the next most common feeding guild accounting for 13.8%, followed by aerial insectivores (1.9%), nectarivores (1.5%) and foliage gleaners (0.4%).

Within-site analysis for feeding guilds showed that at UWI, 53.1% of individuals were frugivores, followed by omnivores at 44.1%. 98.3% and 91.1% of individuals caught at the WBTRS and Asa Wright respectively were frugivores. The only significant difference between sites and feeding guilds was the omnivorous guild ($p = < 0.001$).

DISCUSSION

The results of this investigation have shown that continuous anthropogenic disturbance negatively affects bat species diversity, evenness, richness and feeding guild diversity in Northern Trinidad. However, only the highly disturbed site was significantly lower in these variables, which suggested that disturbance was only detrimental to bats if persistent. This suggests that if given the correct protection and management, secondary forest sites recovering from disturbance can still reach high levels of diversity, similar to undisturbed areas.

The majority of bats recorded within this study belonged to the Phyllostomidae (Appendix 1). This group feeds almost exclusively on fruit and they help introduce seeds into previously disturbed habitats, assisting with forest regeneration (López-Baucells et al., 2016). Phyllostomidae were most abundant at the WBTRS and Asa Wright which suggests that they were helping these areas recover from historical anthropogenic disturbance by maintaining seed banks and assisting with the process of reforestation (Gomes and Reid, 2015).

According to Fenton et al. (1992) and Wilson et al. (1996), Emballonuridae, insectivorous Phyllostominae and Vespertilionidae are more abundant in undisturbed environments. In this study, Emballonuridae were indeed only found at the less-disturbed WBTRS and Asa Wright sites, and Vespertilionidae were only found at Asa Wright (Appendix 1). However, insectivorous Phyllostominae were captured mainly at the highly disturbed site. The only insectivorous Phyllostominae caught at UWI was *Phyllostomus discolor*, and its abundance was very high (Appendix 1). *P. discolor* is associated with agriculturally developed areas and eats plants belonging to the banana family (Kwiecinski, 2006). Banana plants were abundant at UWI, and this possibly explains *P. discolor*'s high abundance.

Artibeus jamaicensis was the most abundant species in this study (Appendix 1). A frugivore generalist but fig specialist (Medellin et al., 2000), *A. jamaicensis* has been widely reported to be common in a variety of habitats including human-modified areas (Ortega and Castro-Arellano, 2001). *A. jamaicensis* was the most common species at UWI and the WBTRS (Appendix 1) which suggests that it is highly tolerant of human activity. Considering it is a dominant species in the frugivorous bat community and adjusts well to disturbance, it is no surprise that this species has successfully adapted to anthropogenic activity across the island of Trinidad.

The second most abundant species, *Carollia perspicillata*, is reported to be present in light or moderately disturbed areas (Wilson, Ascorra and Solari, 1996) as long as the forest composition remains relatively intact (Patterson, Willig and Stevens, 2003). This study had the same result as *C. perspicillata* was only caught at Asa Wright and the WBTRS (Appendix 1). Although Asa Wright was considered a relatively undisturbed site in this study, the centre conducted tours through the area we sampled which could possibly have contributed to some light disturbance. Furthermore, *C. perspicillata* is an understorey species, feeding heavily on pioneer and secondary plants (Medellin et al., 2000); both the WBTRS and Asa Wright are located within secondary forests. Clarke and Downie (2001) suggest that *Carollia* abundance may be correlated with this local density of pioneer plants rather than be restricted by a modified habitat.

Artibeus lituratus, *Artibeus jamaicensis* and *Glossophaga soricina* were found at all sites (Appendix 1). All three are abundant in Trinidad (Gomes and Reid, 2015) and they are all considered to be generalists (Garcia, Rezende and Aguiar, 2000; Gomes and Reid, 2015). *A. jamaicensis* and *A. lituratus* are both widespread and are able to exploit different kinds of food. This means they easily adapt to several habitats, including forests and areas of disturbance (Garcia et al., 2000). Despite being classified as a nectarivore in this study, *G. soricina* is known to eat fruit pulp (Gomes and Reid, 2015) and is considered to be tolerant of disturbed environments (Fenton et al., 1992). These three species seem to have adapted well to anthropogenic activity due to their generalist diets.

In some areas, bat diversity may be so high that sampling all groups becomes impractical. This problem is prominent in tropical studies where whole segments of faunas often escape detection (Patterson et al., 2003). While mist net techniques can be easily standardised and have been used widely for bat surveys, they only seem to be efficient at sampling the Phyllostomidae family (LaVal and Fitch, 1977). In order to record species previously undetected, it would be useful to use other methods, such as acoustic sampling or harp traps (Ochoa et al., 2000). However, the families potentially underrepresented by the sampling method do not typically respond to disturbance in quantifiable ways, so their presence may not have had a significant effect on the results (Fenton et al., 1992; Castro-Luna et al., 2007).

Tropical bats are expected to respond to habitat conversion with reductions in both species richness and abundance (Patterson et al., 2003). In this study, species richness was the highest at the least-disturbed site and the lowest at the most-disturbed site, which indicates that species richness decreases with increasing disturbance. Due to the high levels of human activity at UWI, reforestation is prevented from occurring, which means that plant diversity is reduced and specialist bats fail to adapt to that environment.

The estimates for total species richness suggest that the WBTRS and Asa Wright were more similar than originally expected. It was estimated that UWI only had 6.5 species, while the WBTRS and AW had similar total richnesses of 19 and 23. The WBTRS and Asa Wright were also considered the most similar sites in terms of species composition using Beta diversity. Even though the forests around Asa Wright and the WBTRS have not reached maturity, they both had a considerably high level of biodiversity. Forests with patches of secondary vegetation provide more niches for bats than unharmed forest, which allows them to support a higher number of species than expected (Castro-Luna, Sosa and Castillo-Campos, 2007).

Bat species diversity was significantly different between sites with the highest diversity at Asa Wright but, rather unexpectedly, the WBTRS was considered the least diverse. However, when visualised in a k-dominance plot, UWI had the most elevated curve, which suggested that it was the least diverse assemblage (Figure 2). Magurran (2004) suggested that the Simpson's Index was heavily weighted towards the most abundant species in the sample while being less sensitive to species richness. *Artibeus jamaicensis* dominated captures at the WBTRS, which accounted for 72.5% of individuals and may have contributed to this result.

The highly disturbed site had the highest evenness whereas the moderately disturbed site had the lowest. High abundances of the generalists *Artibeus jamaicensis* and *Phyllostomus discolor* at UWI had likely contributed to this result. Each site was dominated by one or two species which increased the species evenness. *Artibeus jamaicensis* dominated UWI and the WBTRS, while *Carollia perspicillata* dominated Asa Wright.

Overall, 36.4% of total rare species were caught at Asa Wright, and out of the nine species exclusively caught there, only two were not considered rare or uncommon. Despite species rarity not being considered significant in this study, it is important to note that the least-disturbed site hosted the largest number of uncommon species. Asa Wright's protective strategies seem to be working as 42.1% of species caught on their grounds were considered rare. Primary or older secondary forests need to be protected to save these more specialised groups of bats, as no unique rare species were present at UWI.

Frugivores dominated captures, representing 82.4% of all individuals. This was followed by the omnivorous guild at 13.8%. It is common for frugivorous bats to dominate assemblages in Neotropical forests (Patterson et al., 2003) as fruit resources are abundant throughout the year (Patterson et al., 2003). On the other hand, insectivores are especially sensitive to deforestation and other forms of habitat disturbance (Patterson et al., 2003). They are likely to be more abundant in less-disturbed areas due to a higher plant diversity, which supports higher insect diversity (Wilson et al., 1996). This was reflected in the results, as the majority of aerial insectivores and foliage gleaners were found at Asa Wright. Aerial insectivores may contribute to 30-50% of species in local assemblages in the Neotropics (Patterson et al., 2003), but they are hard to capture in mist nets, and are often underrepresented as they fly high in the canopy and can easily evade capture due to their sophisticated echolocation systems (Patterson et al., 2003). Despite using a triple-high net at all sites, there was still a large amount of space between the nets and the canopy in which several species of bat had most likely evaded capture.

Omnivores were a substantial guild only at the disturbed site. Omnivorous bats are usually more abundant in areas that have been subjected to continuous disturbance (Wilson et al., 1996; Garcia-Morales, Badano and Moreno, 2013) and are often considered to be impartial to human activity. Garcia-Morales et al. (2013) described omnivores as having 'broad ecological plasticity' as they are generalists in their diets and can adapt their feeding habits when under stress.

CONCLUSION

In summary, continuous anthropogenic disturbance negatively affects bat species diversity, evenness, richness, and feeding guild diversity in Northern Trinidad. When disturbance is continuous, specialised bat species cannot cope and often disappear from that environment. Only generalist species are able to adapt to continuous anthropogenic pressure as they are able to adjust their diets accordingly.

A quarter of bat species are already threatened by anthropogenic activity, and to prevent this catastrophe, we must do more to protect bat diversity 'hot spots' such as Trinidad. The Asa Wright Nature Centre has already shown that with proper management and care, disturbed areas can reach levels of diversity close to primary forest. Although bats are great indicator species, more research needs to be done on the other fauna in the area before management plans can be acted upon.

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APPENDIX 1

TAXON			SITE				TOTAL
FAMILY	SUBFAMILY	SPECIES	GUILD	UWI	WBTRS	ASA WRIGHT	
Emballonuridae		<i>Saccopteryx billineata</i>	AI	0	0	1	1
		<i>Saccopteryx leptura</i> *	AI	0	1	0	1
Molossidae		<i>Molossus molossus</i> *	AI	1	1	0	2
Mormoopidae		<i>Pteronotus parnellii</i>	AI	0	0	2	2
		<i>Pteronotus personatus</i> *	AI	0	0	1	1
Natalidae		<i>Natalus tumidirostris</i> *	AI	0	0	1	1
Phyllostomidae	Carolliinae	<i>Carollia perspicillata</i>	F	0	14	56	70
	Glossophaginae	<i>Anoura geoffroyi</i> *	N	0	0	2	2
		<i>Glossophaga soricina</i>	N	3	1	1	5
	Phyllostominae	<i>Phyllostomus discolor</i>	O	63	0	2	65
		<i>Tonatia saurophilia</i> *	FG	0	0	2	2
		<i>Trinycteris nicefori</i> *	O	0	0	1	1
	Stenodermatinae	<i>Artibeus cinereus</i>	F	0	1	5	6
		<i>Artibeus jamaicensis</i>	F	65	129	43	237
		<i>Artibeus lituratus</i>	F	9	5	3	17
		<i>Centurio senex</i> *	F	0	2	0	2
		<i>Chiroderma villosum</i> *	F	0	3	2	5
		<i>Platyrrhinus fusciventris</i>	F	0	5	12	17
		<i>Sturnira lilium</i>	F	2	0	2	4
<i>Uroderma bilobatum</i>		F	0	16	19	35	
<i>Vampyrodes carraccioli</i> *	F	0	0	1	1		
Vespertilionidae		<i>Eptesicus brasiliensis</i> *	AI	0	0	1	1
			Total	143	178	157	478

* Rare/Uncommon

REFERENCES

- Asa Wright Nature Centre, n.d. *About the Asa Wright Nature Centre*. [Online] Available at: <<http://asawright.org/about-the-centre/>> [Accessed 10/10/2017].
- Bonaccorso, F.J., 1975. *Foraging and Reproductive Ecology in a Community of Bats in Panama*. PhD. University of Florida.
- Castro-Luna, A.A., Sosa, V.J. and Castillo-Campos, G., 2007. Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. *Animal Conservation*, 10(2), pp. 219-228.
- Clarke, F.M. and Downie, J.R., 2001. A Bat (Chiroptera) Survey of Mora Rainforest in Trinidad's Victoria-Mayaro Forest Reserve. *Biodiversity and Conservation*, 10, pp. 725-736.
- FAO (Food and Agriculture Organization of the United Nations), 2015. *FRA 2015 and the State of the Forest Sector in the Region*. Lima, Peru: Latin American and Caribbean Forestry Commission.
- Fenton, M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, K. and Syme, D. M., 1992. Phyllostomid Bats (Chiroptera: Phyllostomidae) as Indicators of Habitat Disruption in the Neotropics. *Biotropica*, 24(3), pp. 440-446.
- Fleming, T.H., 1987. Fruit bats: prime movers of tropical seeds. *Bats*, 5, pp. 3-8.
- Fleming, T.H., 1988. *The Short-tailed Fruit Bat: A Study in Plant-Animal Interactions*. 2nd Ed. Chicago, Illinois: University of Chicago Press.
- Foley, J.A., Asner, G.P., Heil Costa, M., Coe, M.T., Defries, R., Gibbs, H.K., Howard, E.A., Olson, S., Patz, J., Ramankutty, N. and Snyder, P., 2007. Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment*, 5(1), pp. 25-32.
- Garcia, Q.S., Rezende, J.L.P. and Aguiar, L.M.S., 2000. Seed dispersal by bats in a disturbed area of Southeastern Brazil. *Revista de Biologia Tropical*, 48, pp. 125-128.
- Garcia-Morales, R., Badano, E.I. and Moreno, C.E., 2013. Response of Neotropical Bat Assemblages to Human Land Use. *Conservation Biology*, 27(5), pp. 1096-1106.
- Gomes, G.A. and Reid, F.A., 2015. *Bats of Trinidad and Tobago: A Field Guide and Natural History*. Trinidad and Tobago: Trinibats.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D. and Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2), p. 9.
- Helmer, E.H., Ruzycki, T.S., Benner, J., Voggesser, S.M., Scobie, B.P., Park, C., Fanning, D.W. and Ramnarine, S., 2012. Detailed maps of tropical forest types are within reach: Forest tree communities for Trinidad and Tobago mapped with multiseason Landsat and multiseason fine-resolution imagery. *Forest Ecology and Management*, 279, pp. 147-166.
- Kunz, T.H., De Torre, B., Bauer, E., Lobova, D. and Fleming, T.H., 2011. Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, 1223, pp. 1-3.
- Kwiecinski, G.G., 2006. *Phyllostomus discolor*. *American Society of Mammalogists*, 801, pp. 1-11.
- Laurance, W.F., 1991. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conservation Biology*, 5, pp. 79-89.
- Laval, R.K. and Fitch, H.S., 1977. Structure, movements and reproduction in three Costa Rican bat communities. *Occasional Papers of the Museum of Natural History, the University of Kansas*, 69, pp. 1-28.
- Lobova, T.A., Geiselman, C.K. and Mori, S.A., 2009. *Seed Dispersal by Bats in the Neotropics*. New York City: Botanical Garden, New York City.
- López-Baucells, A., Rocha, R., Bobrowiec, P., Bernard, E., Palmeirim, J. and Meyer, C., 2016. *Field Guide to Amazonian Bats*. Manaus, Brazil: Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.
- Medellin, R.A. and Gaona, O., 1999. Seed dispersal by bats and birds in forest and disturbed habitats in Chiapas, Mexico. *Biotropica*, 31, pp. 432-441.
- Medellin, R.A., Equihua, M. and Amin, M.A., 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Conservation Biology*, 14, pp. 1666-1675.
- Mooney, H.A., Lubchenco, J., Dirzo, R. and Sala, O.E., 1995. Biodiversity and Ecosystem Functioning: Basic Principles. In: V.H. Heywood, ed. *Global Biodiversity Assessment United Nations Environmental Programmes*. Cambridge, United Kingdom: Cambridge University Press, pp. 275-325.
- Myers, N., 1992. *The Primary Source: Tropical Forests and Our Future*. London: W.W. Norton Ltd.
- Ortega, J. and Castro-Arellano, I., 2001. *Artibeus jamaicensis*. *Mammalian Species*, 662, pp. 1-9.
- Patterson, B.D., Willig, M.R. and Stevens, R.D., 2003. Trophic strategies, niche partitioning, and patterns of ecological organisation. In: T. H. Kunz and M.B. Fenton, eds. *Bat Ecology*. London: University of Chicago Press, pp. 536-579.
- Reid, F.A., 2017. *Bats of Trinidad; An Identification Guide* [Field Key Booklet]. June 2017.
- William Beebe Tropical Research Station, 2004. *Background: History, Location and Research*. [Online] Available at: <<http://www.wbtrs.org/history.html>> [Accessed 11/10/2017].
- Wilson, D.E., Ascorra, C.F. and Solari, S., 1996. Bats as Indicators of Habitat Disturbance. In: D.E. Wilson and A. Sandoval, eds. *The Biodiversity of South-eastern Peru*. Smithsonian Institution, pp. 613-625.