Influence of forest disturbance on bat community diversity in northeast Tobago, West Indies

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ABSTRACT

Bat assemblages were sampled at three habitats of varied disturbance within northeast Tobago over a 10-week period. Overall 995 individuals, representing 15 species, were caught through the use of mist nets. Community diversity, evenness, abundance, and feeding guild composition across sites were recorded. Our analysis showed lower species diversity and richness within the site experiencing ongoing disturbance. Results from the secondary forest suggest diversity can recover to natural levels if this disturbance ends. However, some species were only located within primary forest, which may be a result of specific ecological requirements.

Key words: Chiroptera, mist-netting, diversity

INTRODUCTION

Anthropogenic disturbance has reduced the quality, size, and number of forest habitats within the Neotropics, consequently impacting the animal species residing within them (Chapin III *et al.* 2000, Gibson *et al.* 2011). Different bat species show different levels of sensitivity to environmental change, in some cases leading to local extinctions and consequently shifts in community composition (Fenton *et al.* 1992, Medellín *et al.* 2000). This response to disturbance can differ between feeding guilds, for example gleaning animalivore numbers may decrease while frugivores benefit (Clarke *et al.* 2005). It is important to assess the effect of disturbance on bat communities within the tropics as they provide a variety of important ecosystem services such as pollination, seed dispersal, and pest control (Medellín *et al.* 2000).

The country of Trinidad and Tobago has recorded 68 species of bats, 24 of which are found in Tobago (Gomes and Reid 2015). While studies have previously been carried out in Tobago to assess the bat fauna present, there is currently no literature assessing the composition of habitat-specific bat communities on the island. Tobago's natural landscape supports a variety of forest habitats, containing lower montane, lowland and xerophytic rainforest, semi-evergreen and deciduous seasonal forest, dry evergreen forest and forested wetland. In recent history a fluctuating agricultural industry has left secondary forest covering the majority of the landscape, as sites have been left to recover and regenerate when plantations were abandoned (Helmer *et al.* 2012). Within the centre of the landmass, a smaller area of the primary montane forest remains, protected since 1776 as part of the Main Ridge Forest Reserve. Small towns surround the forested area, situated along the coastal road (Helmer *et al.* 2012, UNESCO).

The impact of landscape disturbance has been observed to affect multiple aspects of bat diversity and community structure within the Neotropics. Decreased species richness and diversity has been found within deforested areas of tropical forests (Brosset *et al.* 1996, Fenton *et al.* 1992). Selective logging in Trinidad was determined to have altered feeding guild abundance in comparison to primary forest (Clarke *et al.* 2005), while local-scale fragmentation of Neotropical forests was found to reduce species richness in Panama (Meyer *et al.* 2008). This paper presents the results of mist-net sampling of bat communities from three sites in northeast Tobago; an urban area, secondary forest and primary forest.

METHODS

Surveys were conducted over a ten week period from 21 June to 17 August 2016 using mist nets at ground and sub-canopy level. A total of 18 nights of sampling took place at three locations within northeast Tobago, six sample nights for each site. The sites consisted of an urban area experiencing frequent anthropogenic disturbance (Charlotteville Village, N11.32148, W060.55398) a secondary forest undergoing succession following previous disturbance (Dead Bay River, N11.29115, W060.63352), and a primary forest containing the mature climax vegetation of the island (Main Ridge Forest Reserve, N11.27832, W060.58253) (Fig.1). Detailed forest maps of Tobago allowed accurate identification of forest type and land cover (Helmer *et al.* 2012).

To determine the community composition at each site, individuals were caught and identified to species level through the use of field keys (Gomes and Reid 2015, Reid 2009). Three nylon mist nets were placed at ground level (2 x 12m, 1 x 9m) (monofilament 0.08mm , height 2.4m) and two nets at sub-canopy level (2 x 9m) to intercept potential flight paths along natural corridors. Nets were opened at sunset for four hours each night, typically from 1830h to 2230h, and checked every 15 minutes. Upon capture, each individual was weighed using Pesola Spring Balances

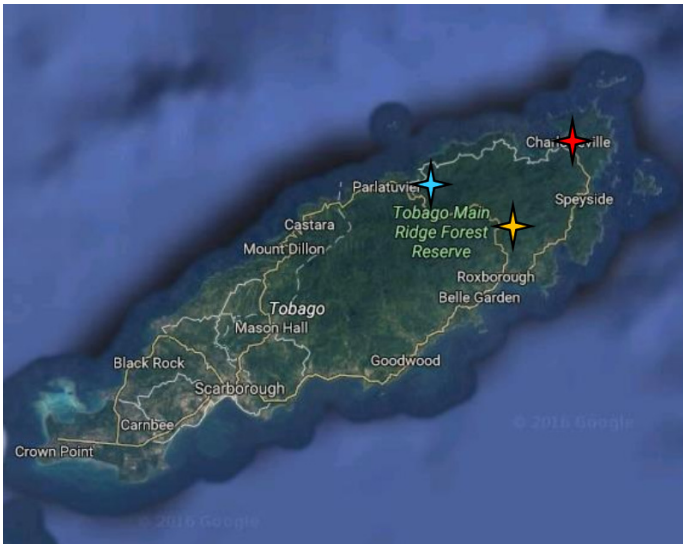

Fig. 1. Map of Tobago showing location of study sites (Urban Site: red, Secondary Site: blue, Primary Site: yellow) T

and forearm size was measured using 0-150mm Dialmax Vernier Dial Callipers (to the nearest 0.1mm) to assist in species identification (Gomes and Reid 2015, Reid 2009).

Data were analysed using programme R and package "vegan" (Oksanen *et al*. 2018). Calculation of mist net hours (MNH) assessed the capture rates between sites, and Pearson's Chi-square Test was used to evaluate statistical significance. The number of individuals caught of each species was recorded (abundance). Whittaker's Rank Abundance Plots were applied to represent the relative abundances per site against species rank. This allowed comparison between sites, despite differences in size and species composition (Magurran and McGill 2011). To allow improved comparison of species richness between sites, sample based accumulation curves were fitted for species richness at each site. An asymptote for abundance data was estimated using first order Jackknife estimators. Macgurran and McGill (2011), found that non-parametric measures (Chao 1, Chao 2, Jackknife) performed better in comparison to parametric measures as more precise, efficient, and less biased. In this study Jackknife was chosen against Chao 1 and Chao 2, as both Chao estimators calculated species richness to be lower than our observed species richness. Beta diversity was calculated using the Whittaker Index (βw), assessed pairwise over the three sites (Whittaker 1960). Whittaker's index of beta diversity was used as it is an effective index of species turnover (Koleff *et al.* 2003). Simpson's Reciprocal Index and Simpson's Evenness were used to evaluate the species diversity and species dominance respectively within each test site (Simpson 1949). Simpsons Index (1/D) was divided by species richness (S) to find Simpsons Evenness. One-way analysis of variance (ANOVA, F) was conducted on these two measures to determine if the differences across habitats was statistically significant. Power analysis of this ANOVA calculation (f=1.6, p= 0.01, power = 0.9) recommended a minimum of 4.013 samples nights per site, which confirmed our six sample nights per site as adequate. Where statistical significance was detected, additional post hoc Tukey Tests were carried out to assess the sites pairwise. Analysis of individual abundance per feeding guild were compared between sites using Pearson's Chi-Squared Test.

RESULTS

Sampling Effort: A total of 375.5 mist net hours were carried out over 18 sample nights. The overall capture rate was found to be 2.8 bats net^{-1} h^{-1}. Capture rate was 1.9 bats net^{-1} h^{-1} at the urban site and 2.4 bats net^{-1} h^{-1} at the secondary site. The most successful capture rate was found at the primary site at 4.1 bats net^{-1} h^{-1} (Table 1). This difference in individuals caught was shown to be statistically significant ($\chi 2$= 116.14, p<0.005).

Species Composition & Abundance: A total of 995 bats were sampled, representing 15 species from four families (Table 2). The Phyllostomidae accounted for the majority of bats caught (94.7%), followed by Vespertilionidae (3.3%), then Molossidae (1.5%) and Emballonuridae (0.5%). Individual species counts were dominated by species from the Phyllostomidae family

Table 1. Summary of total number of individuals sampled (n), mist net hours, and rate of capture per net per hour, as defined by the different nets used for each site.

Site	Ground Nets			Triple High Nets			Total		
	n	MNH	Bats net^{-1} h^{-1}	n	MNH	Bats net^{-1} h^{-1}	n	MNH	Bats net^{-1} h^{-1}
Urban	64	48.5	0.8	158	72	2.2	223	120.5	1.9
Secondary	138	47	2.9	146	72	2	284	119	2.4
Primary	221	44.5	5	267	73.5	3.6	488	118	4.1
Total	424	140	3	572	217.5	2.6	995	357.5	2.8

- *Artibeus jamaicensis* (60.3%), *Carollia perspicillata* (15.6%), and *Artibeus cinereus* (11.8%). All other species were present at relatively low numbers (2.6% - 0.2%). The urban site contained 46.7% of the total species caught, the secondary site contained 86.7%, and the primary site contained 93.3%. Six species were shared among all habitats sampled (*C. perspicillata, Glossophaga longirostris, Artibeus lituratus, A. jamaicensis, A. cinerus and Myotis attenboroughi*). Three species were found exclusively within the primary site (*Saccopteryx leptura, Micronycteris megalotis, and Centurio senex*). One individual of the species *Anoura geoffroyi* was captured at the secondary site, and one individual at the primary site. Whittaker rank abundance plots (Fig. 2) depict the relative abundance of species within each sample site. At all three sample sites, the majority of species are found to be rare while a small number of species are abundant in high numbers, indicating a low species evenness.

Species Richness & Diversity: Species accumulation curves achieved a near asymptote for both the urban and primary site. A slightly lower rate of accumulation is present for the secondary site and while the curve levels out slightly, no clear asymptote was reached (Fig. 3). Regression analysis for total species richness (Fig. 4) estimated the asymptote would occur at 8.1 for the urban site, 15.5 for the secondary site, and 14.8 for the primary site. This indicates sampling detected close to the total estimated species for the urban and primary site, while at the secondary site 3 - 4 species remained unrecorded.

The beta diversity across all sites was 0.36. The lowest beta diversity value was found between the secondary and primary site ($\beta w = 0.15$), followed by the urban and secondary site ($\beta w=0.26$). The highest beta diversity value was found between the urban and primary site ($\beta w =0.42$). Bat species diversity as calculated through Simpsons Index (1/D) showed a significant difference between the study sites (one-way ANOVA, $F(2, 15) =15.52$, $p=0.0002$). The urban site showed statistically significant differences from both secondary and primary sites ($p=0.0001$, $p=0.005$ respectively). As $p>0.05$ between the secondary site and the primary site, there was no significance difference between bat species diversity at the two sites. No significant difference was present for Simpson's Evenness between any of the survey sites (Table 3).

Table 2. Bat species captured within the study, along with their respective family and sub-family, feeding guild, total sample abundance and sample abundance found within each Site. See table 4 for feeding guilds.

Taxon			Guild	Site			Total
Family	**Subfamily**	**Species**		**Urban**	**Secondary**	**Primary**	
Emballonuridae		*Saccopteryx leptura*	AI	0	0	5	5
Molossidae		*Molossus molossus*	AI	13	2	0	15
Phyllostomidae	Carolliinae	*Carollia perpicillata*	F	14	52	79	145
	Glossophaginae	*Anoura geoffroyi*	N	0	1	1	2
		Glossophaga longirostris	N	1	4	2	7
	Phyllostomianae	*Micronycteris megalotis*	GA	0	0	2	2
		Phyllostomus hastatus	O	0	3	6	9
	Stenodermatinae	*Artibeus lituratus*	F	3	11	8	22
		Artibeus jamaicensis	F	185	131	284	600
		Artibeus cinereus	F	6	44	66	116
		Chiroderma villosum	F	0	9	2	11
		Centurio senex	F	0	0	2	2
		Sturnira lilium	F	0	9	17	26
Vespertilionidae		*Eptesicus brasiliensis*	AI	0	11	11	22
		Myotis nigricans	AI	1	7	3	11
			Total	223	284	488	995

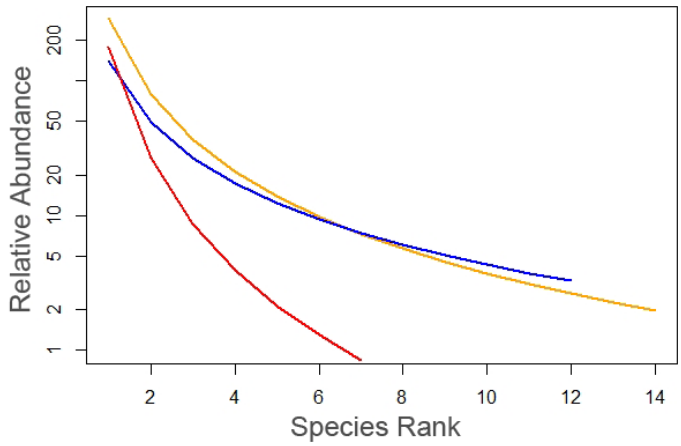

Fig. 2. Log relative species abundance for a) urban site, b) secondary site, c) primary site

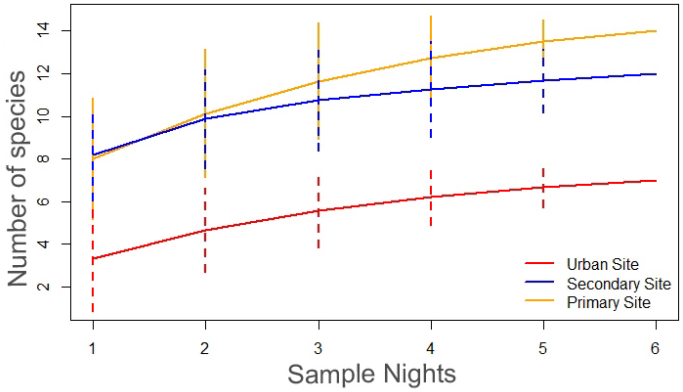

Fig. 3. Sample-based species accumulation curve for each site sampled.

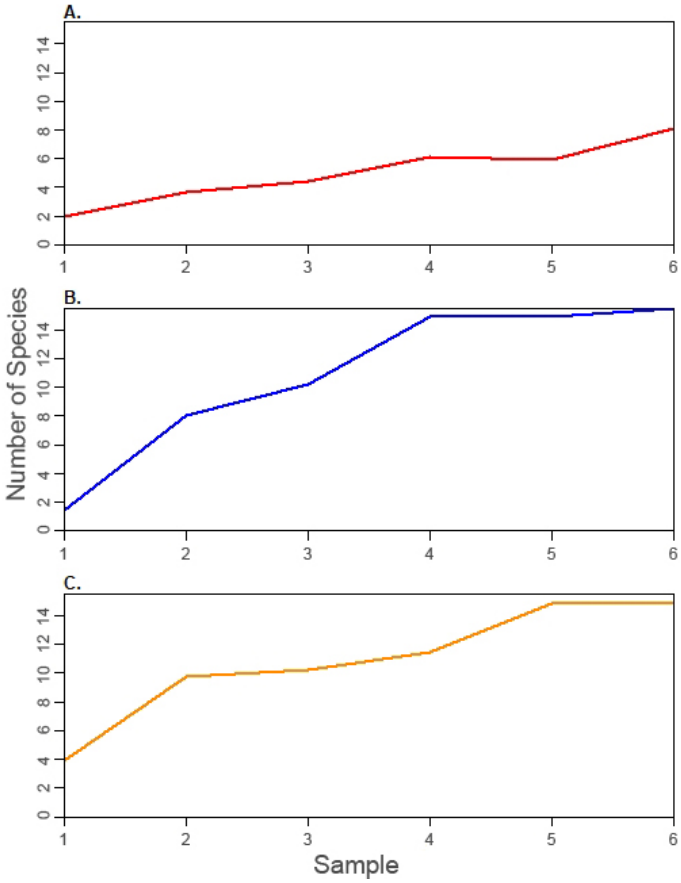

Fig. 4. Estimated species richness using first-order jackknife for A. urban site, B. secondary forest site, C. primary forest site.

Feeding Guilds: Trophic analysis for number of individuals captured showed frugivores dominated all habitats, representing over 90% of individuals at any site sampled. Aerial insectivores were the next most common guild, averaging over 5% of total number captured. Nectarivores, omnivores and gleaning animalivores all fell beneath 1% of captures. (Table 4). Gleaning animalivores and omnivores were represented by just one species each, *Micronycteris megalotis* and *Phyllostomus hastatus* respectively (Table 1). In addition, the gleaning animalivorous guild was only present within the primary site. No statistical significance was found for differences in feeding guild abundance between sample sites.

DISCUSSION

The three bat communities sampled were found to differ in terms of species abundance, species diversity, and species richness. Both diversity and richness were significantly lower in the urban site, which suffers from continuous anthropogenic disturbance. The secondary site was indicated to contain the highest species diversity and estimated richness. The highest abundance of individuals was recorded at the primary site, which was also home to three species not detected in either of the other two habitats. Higher bat species turnover occurs between the urban site and the primary site, where habitat variation lowers the proportion of species shared between two sites (Estrada and Coates-Estrada 2002). Both the beta diversity and alpha diversity values agree with our assumption of a disturbance gradient affecting the habitats, from the urban to secondary site then primary site.

One trait that appears to be shared by all bat assemblages sampled in Tobago is domination of community composition by a small number of species, as seen in the Whittaker rank abundance plots and species evenness calculations. This is a typical characteristic of island habitats and tropical rainforest communities (Meyer and Kalko 2008, Stevens and Willig 2002). In this study, *A. jamaicensis* is the predominant species found at all sites. As a generalist frugivore capable of undertaking prolonged flights, *A. jamaicensis* is able to exploit human modified landscapes avoided by more sensitive species (Ortega and Castro-Arellano 2001).

The urban site used within our study suffers from light pollution, sound pollution, human activity and reduced vegetation, and subsequently provides fewer ecological

niches (Brosset *et al.* 1996, Hourigan *et al*. 2006). The low species diversity and richness recorded at this site corresponds with other studies noting lower diversity in deforested habitats (Clarke *et al.* 2005, Fenton *et al.* 1992). Four out of the seven species caught within the urban area had previously been identified as the first species to colonise a disturbed area (*A. jamaicensis*, *A. cinereus*, *C. perspicillata*, *M. molossus)* (Brosset *et al.* 1996). The disturbances affecting this habitat may prevent reforestation from occurring, thus reducing the ability of other, less resilient, bat species to persist here.

The Phyllostominae sub-family of bats, represented here by *M. megalotis* and *P. hastatus*, show sensitivity to disturbance and are often only present in pristine landscapes (Bobrowiec and Gribel 2010, Medellín *et al.* 2000). *M. megalotis* was located solely within the primary site. This habitat restriction may be a consequence of dietary specialisation as a gleaning animalivore, hunting arthropods and vertebrates from surfaces in narrow space, rendering the species unable to adapt to anthropogenic disturbance (Clarke *et al.* 2005). *P. hastatus* is a large omnivorous predator that avoids areas where habitat modification is present (Schulze *et al.* 2000). The presence of *P. hastatus*within the secondary site indicates the site has recovered to a significant degree from previous disturbance.

Frugivores accounted for over 90% of individuals captured within the study, and the resulting seed dispersal carried out by various species allows multiple stages of succession to occur. Bats are responsible for the dispersal of pioneer flora species following habitat disturbance. Upon maturing, this initial vegetation provides more favourable conditions for specialised bat species that frequent later stages of succession, until the seeds of climax flora can be dispersed (Gomes and Reid 2015). However, as is the case with *M. megalotis*, the absence of *C. senex* within the secondary site may show conditions are still not suitable for rarer species that require climax vegetation. *C. senex* has adapted to feed upon mature canopy fruits, and so is less involved in the reforestation of disturbed areas than species such as *C. perspicillata* and *A. jamaicensis* (Gomes and Reid 2015).

The interaction of multiple frugivorous species with their environment can create a more heterogeneous habitat. Species diversity was highest in the secondary site, and our analysis estimates that this site contains the highest number of species. The species accumulation curve (Fig. 3) indicates there may still be a small number of species to be discovered given further sampling effort. The primary site contained more of the specialist species, but with increased disturbance in the secondary forest, the secondary site may be able to support a wider range of species. Both forest specialists and generalists, and edge and open ecosystem species can find suitable habitat here

Table 3. Diversity analysis. Species richness (S), total number of individuals caught, Simpsons Index (1/D, and Simpsons evenness index (1/D/S) between each sample site.

Site	Number of Species (S)	Number of Individuals	Simpson Index (1/D)	Simpsons Eveness Index 1/D/S)
Urban	7	223	1.435	0.205
Secondary	12	285	3.623	0.302
Primary	14	488	1.592	0.185

Table 4. Feedings guilds present at each site, by individuals captured and percentage of total sample

Site	Urban		Secondary		Primary		Total	
Feeding Guild	**Number Captured**	**Percent**	**Number Captured**	**Percent**	**Number Captured**	**Percent**	**Number Captured**	**Percent**
Frugivore	208	93.27%	256	90.14%	458	93.85%	922	92.66%
Nectarivore	1	0.45%	5	1.76%	3	0.61%	9	0.90%
Aerial Insectivore	14	6.28%	20	7.04%	19	3.89%	53	5.33%
Gleaning Animalivore	0	0.00%	0	0.00%	2	0.41%	2	0.20%
Omnivore	0	0.00%	3	1.07%	6	1.23%	9	0.90%

(Castro-Luna *et al.* 2007a, Connell 1978).

The primary site showed the highest capture rate, contrasting with results from Trinidad (Clarke *et al.* 2005), French Guiana (Brosset *et al.* 1996), and Mexico (Medellín *et al.* 2000). Tobago's primary forest has been protected since 1776 when the Main Ridge was established as a Forest Reserve, preventing rainforest fragmentation, which has affected abundance in other Neotropical sites (Meyer *et al.* 2008). The importance of maintaining conservation efforts and protecting areas such as the Main Ridge Forest Reserve is evident, as it allows the persistence of specialised species and guilds sensitive to disturbance while supporting high numbers of individuals.

The use of mist nets within this study may have potentially under-sampled aerial insectivores. Families such as Molossidae and Vespertilionidae include species that possess the ability to detect and avoid mist nets while feeding, although these families do not typically show significant responses to disturbance (Castro-Luna *et al.* 2007b). Mist nets are extremely efficient for sampling the Phyllostomidae family, which is the most species-rich bat family present in the Neotropics. However, additional sampling methods such as acoustic sampling or harp traps could identify previously undetected species (Ochoa *et al.* 2000) and build a more complete community inventory for Tobago. The secondary site has an elevation of around 600m, double the height of both the urban and primary sites. Previous publications in the tropics have found bat species diversity to typically decrease with increasing elevation, and a peak richness occurs at around 300m elevation (McCain 2007). We can therefore exclude this factor as an alternative explanation to our results. Future studies may still benefit from sampling multiple forest sites at differing levels of elevation to identify any relationship between elevation and species diversity within Tobago. Tobago has large expanses of secondary forest, and the ability of the forest to recover from previous disturbance has allowed bat community diversity to recover. As the majority of bat species within our study are frugivores, a suggestion for further research would be to assess the role of bats in forest regeneration on the island.

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