



Bat assemblages and their ectoparasites in a Honduran cloud forest: Effects of disturbance and altitude

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Abstract

The high diversity and endemism of cloud forests make them good models to explore the impacts of habitat disturbance on bat communities and their ectoparasites. Although bat responses to forest disturbance have been intensively studied, the response of their ectoparasites in cloud forests remains poorly known. We explore this knowledge gap by analyzing data gathered from 44 nights during a June-August field season in 2019 within Cusuco National Park, a protected cloud forest located in northwestern Honduras. Mist-netting was conducted at five recording stations between 1,300 and 1,925 m a.s.l., spanning a mix of closed-canopy forest and human-induced forest clearings. In total, 584 bats representing 36 species were identified. An overall ectoparasite prevalence of 41% was recorded from all bat captures. Prevalence was similar between males and females, although juveniles displayed a higher rate than adults, and some species were more prone to parasitism than others. Parasite prevalence was positively correlated with altitude. In lower montane forest, bat assemblages and parasite prevalence did not differ between closed-canopy forest and forest clearings. Conversely, in upper montane forest, bat diversity and parasite prevalence rates were higher in forest clearings. Overall, our results suggested that the effect of forest clearance varied with elevation and bat species. Forest

clearance in high-altitude forests may have severe impacts on bat communities, not only reducing their diversity, but also increasing susceptibility to parasite infection, with its associated debilitating effects.

Resumen extendido

Antecedentes: La alta diversidad y endemismos que presentan los bosques nubladados los hacen modelos perfectos para explorar los impactos que tiene la deforestación en el hábitat de las comunidades de murciélagos y de sus ectoparásitos. Aunque las respuestas de los murciélagos a la deforestación han sido ampliamente estudiadas, se sabe muy poco acerca de la respuesta de sus ectoparásitos. A menudo, la respuesta de los murciélagos a actividades antropogénicas depende de la especie y la estructura del paisaje. Por ese motivo, nuestro objetivo fue evaluar el efecto de la tala de bosques en los ensamblajes de murciélagos y en la prevalencia de ectoparásitos en las áreas de bosques montanos bajos y altos en el Parque Nacional Cusuco, un bosque de niebla protegido en el noroeste de Honduras.

Métodos: Entre los meses de junio y agosto del 2019 se realizaron muestreos con redes de niebla en cinco estaciones de investigación, localizados entre 1,300 y 1,925 m s. n. m., abarcando una mezcla de bosque con dosel cerrado y bosque con claros ocasionados por la tala. Por la noche se colocaron cinco redes en las estaciones de muestreo, se tomó la muestra de tres estaciones de manera simultánea, en promedio. Se procesó, marcó y recolectó ectoparásitos a cada murciélago capturado. Por otra parte, se analizó y comparó la composición y estructura de los ensamblajes de murciélagos mediante un análisis multidimensional no métrico (NMDS) y diversidad efectiva por números Hill. Así como también se comparó la prevalencia de los ectoparásitos influenciados por la fragmentación, a nivel de la comunidad y entre las especies más comunes mediante comparaciones múltiples y regresión múltiple binomial.

Resultados: Un total de 584 murciélagos fueron identificados satisfactoriamente, pertenecientes a 36 especies y cinco familias, siendo la familia *Phyllostomi-*

dae con mayor abundancia y riqueza. Se recolectaron ectoparásitos de 22 especies de murciélagos y se registró una prevalencia general de ectoparásitos del 46% de todas las capturas de murciélagos. La prevalencia fue similar entre machos y hembras, aunque los juveniles mostraron una tasa más alta que los adultos, y algunas especies fueron más propensas al parasitismo que otras. Además, se observó que la prevalencia del ectoparásito se correlacionó significativamente con la altitud. El ensamblaje de los murciélagos, en bosques de montaña baja no se encontraron diferencias significativas entre hábitats, en cuando a la diversidad y composición. Sin embargo, en los sitios de mayor altitud, los bosques con dosel cerrado presentaron una mayor diversidad en comparación con los sitios de bosque con claros ocasionados por la tala bosques. Este mismo patrón se observó en la prevalencia de ectoparásitos, pero las tasas de prevalencia fueron mayores en los claros ocasionados por la tala de bosque de montaña alta.

Discusión: El efecto de los sitios perturbados en los ensamblajes de los murciélagos varía entre elevaciones, provocando diferencias estructurales en las comunidades y en el dominio de las especies. Por otra parte, la prevalencia de ectoparásitos en individuos juveniles pudo deberse a la composición de refugios, hábitos sociales o de acicalamiento. La tala de árboles de los bosques montanos altos puede tener graves impactos en las comunidades de murciélagos, no solo reduciendo su diversidad, sino también aumentando la susceptibilidad a la infección por parásitos. Existe una creciente preocupación por la pérdida continua de biodiversidad en los bosques nubladados. Una mejor comprensión de estas funciones de respuesta a la presión podría proporcionar herramientas para integrar el desafío de adoptar los sistemas socio-ecológicos en los programas de conservación en Mesoamérica.

Introduction

A distinctive feature of the Mesoamerican biodiversity ‘hotspot’ (Myers, 2003; Myers *et al.*, 2000) is its cloud forest ecosystems, which occur from southern Mexico to Panama. Because of its geological history and varied topography, Central America and its cloud forests exhibit high biodiversity and endemism rates (CEPF, 2020; Powell & Palmlinteri, 2001). Cloud forests typically represent ‘islands in the sky’; patches of habitat with cooler, moister conditions compared with lower altitude forests. This distinctive habitat, coupled with their biogeographical isolation, has led to the evolution of many species unique to these forests (Helmer *et al.*, 2019), including within its bat communities. Cloud forest bat communities as a whole provide important ecosystem services, acting as seed dispersers, pollinators, and predators of pest species (Fleming, 1993; Kalko *et al.*, 1996; Medellín *et al.*, 2000). The diversity of bats in terms of both species and functional roles also contributes to the diversity of parasites that live on them.

Due, in part, to their ecological adaptations (specialist feeding guilds, flight, communal roosting), bats are parasitized by many groups of arthropods (Simmons & Conway, 2003), such as mites, ticks, fleas, bugs, and bat flies (Dick & Gracioli, 2013; Lourenço & Palmeirim, 2008; Marshall, 1982, reviewed in Haelewaters *et al.*, 2018, 2020). Of these, bat flies are the best known and best studied. Bat flies are highly specialized ectoparasites that are exclusively associated with bats. They live in the fur and on wing membranes and feed on the host’s blood. While bat flies are currently split into two families, Nycteribiidae and Streblidae, recent phylogenetic studies found that Streblidae is not a monophyletic group (Dittmar *et al.*, 2006). The nycteribiids, with about 276 described species in 11 genera, are most species-rich in the Eastern Hemisphere, whereas streblid bat flies (~240 species, 33 genera) are richer in the tropics and subtropics of the Western Hemisphere (Dick *et al.*, 2016; Gracioli & Dick, 2018; Haelewaters *et al.*, 2020).

The ecology of parasites remains poorly studied in most tropical regions and the effects of habitat loss and fragmentation on parasites are poorly understood. Stud-

ies that have explored this question have presented ambiguous patterns. Proximity to forest edges has been reported to lead to a reduction of ectoparasites in rats (Kiene *et al.*, 2020), which is consistent with the findings of Martínez-Mota *et al.* (2018), who studied parasite eggs in the stool of howler monkeys. On the other hand, Hiller *et al.* (2020), studying bat flies in Costa Rica, found that the direction of response to habitat types was host- as well as parasite-specific. Bat parasites such as bat flies can themselves be associated with numerous bacteria, viruses, blood parasites, and fungi (Liu *et al.*, 2020; Szentiványi *et al.*, 2019). Studies have shown their potential as vectors for disease agents such as Bartonella and Ledanteviruses (Dick & Dittmar, 2014; Goldberg *et al.*, 2017).

Mesoamerican cloud forests represent a good model for exploring the impacts of habitat disturbance on communities of bats and their parasites. Firstly, it is likely that many species found here are locally endemic, given high endemism in other taxa and the high levels of host-specificity displayed in many bat parasites. As such, these endemic species are likely to represent important conservation priorities for which novel data is particularly useful. Secondly, Mesoamerican cloud forests are heavily impacted by habitat destruction and degradation, experiencing some of the most severe rates of forest loss (relative to their overall area) of all Central American ecosystems (Cayuela *et al.*, 2006; Hansen *et al.*, 2020). Due to these pressures, it is necessary to conduct further research into their biodiversity, interactions, and responses to human disturbance.

Although bat responses to forest disturbance have been intensively studied, the influence of deforestation on bat ectoparasite prevalence in cloud forests remains poorly known. Moreover, these bat responses are often species-specific, as well as sensitive to spatial scale, degree of deforestation, and landscape matrix (Meyer *et al.*, 2016). At the population level, studies suggest that abundance responses to fragmentation are highly species- and guild-specific. Where abundances in frugivorous and nectivorous bat species often increase with disturbance, gleaners and carnivorous and insectivorous species typically decrease in abundance (Meyer & Kalko, 2008; Sampaio *et al.*, 2003). On the other hand, at

the assemblage level, a positive or negative response depends on the structure, type of fragmentation, and habitat (Faria *et al.*, 2006; Farneda *et al.*, 2015). Bat assemblages vary along elevation gradients, and it is highly likely that they also vary along disturbance gradients in cloud forest ecosystems as well. However, the relative importance of these two variables for driving composition of bat communities and their ectoparasites remains poorly explored in Mesoamerican cloud forests. Therefore, our primary aim was to assess the effect of altitude and human-induced forest clearance on bat assemblages and their ectoparasites in lower and upper montane forests, as a first step to understanding the impact of these environmental gradients. While the ectoparasites have not yet been identified, we were also interested in parasite prevalence on different bat species, and how prevalence is affected by age of the bat host, reproductive status, altitude, and anthropogenic forest clearance. In this study, we present the results of our mist-netting surveys during field season 2019 at Cusuco National Park (CNP), a protected cloud forest in northwestern Honduras, where deforestation has rapidly accelerated in recent years, especially in the western side of the park (Martin *et al.*, 2021).

Methods

Study area

Cusuco National Park (CNP, located at 15°32'31"N 88°15'49"W) is a 23,440-ha protected area of montane cloud forest located in the Sierra de Omoa, part of the Merendón mountain range in northwestern Honduras. The park spans an altitudinal range of 500–2,242 m a.s.l. and is divided into 7,690 ha of core zone and 15,750 ha of buffer zone, where some limited agriculture and other land use is permitted (Martin & Blackburn, 2009). The area receives an average of 2,788 mm of rain annually (Fundación Ecologista, 1994) and has a mean summer day time temperature (June–July) ranging from 21 °C at 1,150 m a.s.l. (range: 18–23.5 °C) to 15 °C at 2,200 m a.s.l. (13–16.5 °C) (Jones *et al.*, 2020). The park represents a mosaic landscape with four categories of forest: tropical lowland dry forest, tropical moist forest, montane (cloud) forest, and

‘bosque enano’ or dwarf forest found above 2,000 m a.s.l. (Hoskins *et al.*, 2018), although only small fragments of the first two categories remain in the buffer zone of the park.

Mist-netting

As part of the long-term biodiversity monitoring efforts by Operation Wallacea (Gilroy *et al.*, 2017), we conducted mist-netting surveys at five camps (recording stations) from June 8th to August 1st, 2019, located between 1,300 m and 1,925 m a.s.l. inside the core zone of CNP. Within each camp, depending on the local topography, we established three to five fixed-location mist-netting sites between 300 and 600 m apart (a total of 19 mist-netting sites). Three camps were sampled per night for six nights per week. For each survey session at each site, we used five nets (four 6 m × 2.6 m, one 12 m × 2.6 m nets, all with 36-mm mesh and five shelves) placed along trails and streams that acted as natural corridors. Mist nets were opened before sunset and checked every 15–30 minutes for six hours. Once a mist-netting site was sampled, it was not surveyed again for at least three days. We did not survey during nights with heavy rainfall. Sampling effort was calculated by summarizing the total meters of net and multiplying this by the number of hours nets deployed per night and presented as m²h (Straube & Bianconi, 2002).

We processed, marked, and released bats at the location of capture following previously described protocols (Sikes, 2016). Processing included species identification, determination of the sex, relative age (juvenile or adult), determined by the degree of ossification of the metacarpal-phalangeal joints (Baagøe, 1977), and reproductive status (female: non-reproductive, pregnant, lactating, post-lactating; male: scrotal, non-scrotal). We also measured the forearm length (mm) and body mass (g) and marked captured bats by clipping a small patch of dorsal fur. This temporary marking procedure is a useful and harmless technique for identifying recaptured individuals. We identified individuals to species-level using taxonomic keys (Medellín *et al.*, 2007; Mora, 2016; Timm & Laval, 1998). Bat taxonomy follows

Tejedor (2005) (for *Natalus lanatus*), Velazco & Simmons (2011) (for *Sturnira parvidens*), Mantilla-Meluk & Muñoz-Garay (2014) (for *Myotis pilosatibialis*), and IUCN (IUCN, 2020) (for all other bat species).

Ectoparasite collection

Collection of ectoparasites (bat flies and mites) was conducted following methods described by Walker *et al.* (2018). In order to collect fast-moving bat flies from their bat hosts, we first applied 96% ethanol with a paintbrush to slow them down. We removed ectoparasites using rigid Swiss Style Forceps #5 with superfine tip (BioQuip #4535, Rancho Dominguez, CA, USA) or Featherweight Forceps with narrow tip (BioQuip #4748). Some ectoparasites were collected by hand. Upon collection, ectoparasites were immediately transferred to 1.5 mL Eppendorf tubes or 0.2 mL PCR tubes (one tube per bat host) filled with 96% ethanol for preservation and long-term storage.

Data analysis

We constructed species accumulation curves with 1000 randomizations for observed and estimated species richness (Jackknife 2 and Bootstrap) for CNP by considering each night as an independent sampling occasion. Then we evaluated the efficiency of the sampling effort and the representation of bat communities in the different camps by the estimation of Hill numbers. With this approach, by providing estimators for inter- and extrapolation, it is possible to compare different sample sizes. This extrapolates the smallest samples and compares species richness estimates at equal sampling completeness (Chao *et al.*, 2014). To compare the proportions of parasite prevalence between sexes and ages we applied Chi-squared tests.

To compare the bat community and ectoparasite prevalence between closed-canopy and anthropogenic forest clearing sites, we took three main approaches: 1) first, we performed a Nonmetric Multidimensional Scaling (NMDS) using Bray–Curtis dissimilarity; 2) then we estimated the diversity via Hill numbers; 3) finally, we compared the relative abundance and parasite prevalence at assemblage level and for the most commonly captured species. We determined the rela-

tive abundance for each species in each site using the following equation: $RA_{spi} = \text{Total captures} \div \text{mnh} \times 100$.

RA_{spi} = relative abundance for a species “i”; total captures = number of captures per species in a site; mnh = total number of hours that the nets remained open (Medellín *et al.*, 2000). The results were multiplied by 100 to correct for small values (de Carvalho *et al.*, 2019).

Because bat assemblages differ significantly with respect to elevation (Medina-van Berkum *et al.*, 2020), we conducted two separate analyses, one considering the camps in lower montane forest (1,200–1,400 m a.s.l., Guanales and El Cortecito) and another considering the camps in upper montane forest (1,500–1,700 m a.s.l., Base Camp and El Danto). We estimated Hill numbers using individual-based abundance rarefaction and extrapolation (Hsieh *et al.*, 2016). The following diversity measures were calculated: q_0 (species richness), which is insensitive to species abundance; q_1 (the exponential of Shannon entropy, referred here as Shannon diversity), which measures the number of common species in a community, (Chao *et al.*, 2014). Species diversity profiles were compared through overlapping confidence intervals (5–95%). To test for differences in species composition between closed-canopy forest and forest clearing sites, we used an Analysis of Similarity (ANOSIM), based on Bray–Curtis dissimilarity distances of species relative abundance. ANOSIM provides a r value between 0 (minimum similarity) and 1 (maximum similarity). A p -value < 0.05 indicates that the results of the analysis are significant.

Finally, to test whether relative abundance and parasite prevalence was influenced by human-induced clearings at assemblage level and at species-specific level, Mann–Whitney U-tests were conducted. Additionally, a GLM with a binomial distribution was performed, where presence of ectoparasites was the binomial dependent variable (1 = parasites, 0 = no parasites) and disturbance degree, age, and sex were the independent variables. To correct for the unequal sampling effort per site, a variable log (effort) as offset was included in the formula (Hosmer *et al.*, 2013).

For all analysis we excluded all recaptured bats, and all statistical analyses were performed using R software version 3.6.1 (R Core Team, 2020) and the packages “vegan” (Oksanen *et al.*, 2019) and “iNext” (Hsieh *et al.*, 2016). To assess the Nonmetric Multidimensional Scaling, we used PAleontological STatistics (PAST) 2.17c software (Hammer *et al.*, 2001).

Results

Bat assemblages. We captured a total of 590 bats (40,912 m²h), of which 584 could be reliably identified. The remaining 1% escaped before they could be fully identified. The rate of recapture was 7.7% (42 bats) and varied among sites (Table 1). Our study sample of bats represented 36 species in 26 genera, belonging to five families. Species accumulation curves did not show a stabilizing trend, indicating that the number of species would have increased if we had sampled more nights (Figure 1). Phyllostomidae was the most abundant and speciose family, with 81% of the total captures representing 27 species; followed by Vespertilionidae (16%), Mormoopidae (3%), and Natalidae and Molossidae, which each represented < 1% of total captures. *Sturnira hondurensis* (n = 106) was the most commonly captured species, followed by *Artibeus jamaicensis* (102), *Myotis pilosatibialis* (74), *Dermanura tolteca* (70), and *Glossophaga soricina* (29), together comprising 72% of total captures. Ten species (28% of all species) were captured once during the entire 2019 field season (Table 1).

Overall, the proportion of captured males and females was similar. Adults accounted for 77% of the captures. For those species with more than five captures (n = 15), the adult sex ratio (male: female) ranged from 3:1 (*Bauerus dubiaquercus*) to 1:3 (*G. soricina*). Palpably pregnant individuals were recorded 88 times for 20 species (71% of the species recorded) and evidence of lactation was recorded in 35 females of 12 species (Table 1). The proportion of pregnant females captured varied among species. Among the commonly captured bats, 68% of adult females of *G. soricina* were pregnant in the surveyed period, 59% of *A. jamaicensis*, but only 33% of *S. hondurensis* and 4% of *M. pilosatibialis*.

Bat ectoparasites. Excluding bats that represented recaptures and bats that escaped or were released before processing for a variety of reasons, ectoparasites were recorded on 240 out of 521 screened bats (overall prevalence 46%), representing 22 bat host species (Table 1). Parasite prevalence by bat species ranged from 8% in both *Glossophaga commisarisi* and *Hylonycteris underwoodi* to 91% in *Pteronotus mesoamericanus*. In general, the parasite prevalence between female and male bats was similar (females 48%, males 43%). However, males of *G. soricina* and *D. tolteca* had a higher parasite prevalence compared to females (Chi-squared test, *G. soricina*: $\chi^2 = 10.15$, $p = 0.001$; *D. tolteca*: $\chi^2 = 3.18$, $p = 0.007$), whereas *A. jamaicensis* females had a higher prevalence than males (Chi-squared test, $\chi^2 = 4.61$, $p = 0.032$). Taking into account the age of the bats, juveniles had higher parasite prevalence compared to adults (juveniles 57%, adults 42%; Chi-squared test, $\chi^2 = 4.891$, $p = 0.027$). The relationship between parasite prevalence and reproductive status was marginally significant (Chi-squared test, $\chi^2 = 5.95$, $p = 0.051$), with reproductive adults having a decreased parasite prevalence (Bonferroni post hoc, $p = 0.015$) compared to non-reproductive juvenile and adult individuals.

Effect of human-induced forest clearings on bat assemblage and ectoparasite prevalence.

The comparison of bat assemblages between closed-canopy and human-induced forest clearing sites showed different patterns for lower versus upper montane forest sites. For sites in lower montane forest, the bat assemblages did not differ significantly between habitat types ($R^2_{\text{ANOSIM}} = 0.18$, $p = 0.153$). The lower r value suggests that dissimilarities in mist-netting sites within recording stations were greater than between habitats. On the other hand, for upper montane forest sites, bat assemblages differed between closed-canopy and human-induced forest clearings ($R^2_{\text{ANOSIM}} = 0.8$, $p = 0.002$; Figure 3a–b).

In terms of species diversity, the effect of human-induced forest clearings also showed different patterns between lower and upper montane forest

(Figure 3). The comparison of species richness (q_0) showed that lower montane forest sites did not differ significantly between disturbance types. However, in upper montane forest, closed-canopy forest sites had significantly higher richness compared to sites with human-induced forest clearings (Figure 3c–d). Taking into account the relative abundance values of all species (Shannon diversity (q_1)), species diversity showed similar patterns. However, once the dominant species was accounted for (Simpson diversity (q_2)), species diversity indices showed different patterns (Figure 3e–f). Bat assemblages were dominated by a smaller number of species in closed-canopy forest sites. Conversely, in upper montane forest sites, closed-canopy sites harbored a higher diversity of bats compared to forest clearings. Of the five most commonly captured bats at lower montane forest sites, *S. hondurensis* was significantly more abundant in human-induced clearings, whereas *A. jamaicensis* and *D. tolteca* were more abundant in closed-canopy forest. On the other hand, in upper montane sites, *D. tolteca* was only present in closed-canopy forest, whereas *C. sowellii* was more abundant in human-induced forest clearings habitats (Figure 2).

In general, upper montane sites had higher parasite prevalence compared to lower montane sites (MANN-WHITNEY U TEST, $U = 58$, $p = 0.016$, FIGURE 4). Parasite prevalence did not differ between closed-canopy and human-induced forest clearings habitats in lower montane forest sites (Mann-Whitney U Test, $U = 6$, $p = 0.685$); but it did at upper montane forest sites, where human-induced forest clearings habitats had higher prevalence rates compared to those in closed canopy forest (Mann-Whitney U Test, $U = 17$, $p = 0.047$), although this varied among bat species (Table 2). For example, prevalence of ectoparasites on *M. pilosatibialis* was higher in forest clearings (GLM, $p = 0.018$). On the other hand, parasite prevalence for *S. hondurensis* (GLM, $p = 0.265$) did not differ among habitats but did differ between ages (GLM, $p = 0.024$), where juveniles had higher parasitism rate compared to adults. In lower montane sites, parasite prevalence in *S. hondurensis* was higher in closed-canopy forest habitats (GLM, $p = 0.038$), but no such difference was observed for other common species such as *A. jamaicensis* or *G. soricina* (GLM, $p = 0.72$ and $p = 0.06$, respectively).

Discussion

Cusuco National Park has been listed as the 123rd most irreplaceable protected area in the world (Le Saout *et al.*, 2013). However, in recent years illegal logging within the park has intensified, impacting species populations and overall community composition (Hoskins *et al.*, 2018; Martin *et al.*, 2021). In a period of 44 survey nights, we recorded 61% of the known bat species in CNP (Medina-van Berckum *et al.*, 2020) and our results showed that bat assemblages were affected by anthropogenic forest clearance, particularly in upper montane forest sites. This pattern was also correlated with ectoparasite prevalence; sites within anthropogenic forest clearings had higher ectoparasite prevalence than closed-canopy forest sites, however the effect was also largely species-specific.

Overall, parasite prevalence did not differ between sexes and among reproductive statuses. Prevalence did, however, vary among bat species, suggesting species-specific preferences of ectoparasites (Hiller *et al.*, 2020; Pilosof *et al.*, 2012). We found variation in ectoparasite prevalence between sexes of three bat species: *A. jamaicensis*, *D. tolteca*, and *G. soricina*. High prevalence in female hosts (*G. soricina* and *D. tolteca*) might be due to the longer time that they tend to spend in their roost to provide maternal care (Esbérard *et al.*, 2012; Patterson *et al.*, 2008a), whereas high prevalence in males might be an ectoparasite dispersion strategy, as male bats will disperse to form new colonies (Bertola *et al.*, 2005). Prevalence may also be influenced by social behavior patterns and roosting habits of individual bat species. Patterson *et al.* (2007) found that bats roosting in more permanent structures had increased measures of parasitism (parasite prevalence, number of bat fly species per bat).

Moreover, our results showed that juvenile individuals had higher prevalence of ectoparasites compared to adults. This is consistent with the results of a preliminary study on bat ectoparasites in CNP (Stars, 2017), which found that 78% of the captured juveniles had ectoparasites compared to only 50% of adults. Higher parasite prevalence in juveniles is

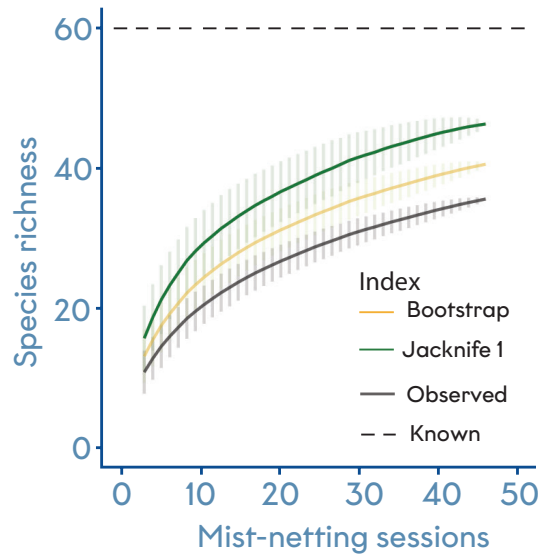


Figure 1. Species accumulation curve of bats captured in Cusuco National Park, north-western Honduras, between June and August 2019. The black curve indicates observed richness. Non-parametric species richness estimator values are shown in the green curve (Jackknife1) and yellow curve (Bootstrap) with 95% of confidence intervals. The black broken line represents the total number of bats species known for the park based on 15 years of survey effort (Medina-van Berkum *et al.*, 2020).

TABLE 1. List of bats species captured in Cusuco National Park, north-west Honduras

Species	Recording stations at Cusuco National Park						Total	EC
	GU	CO	BC	DA	CA			
Phyllostomidae								
<i>Anoura geoffroyi</i> (N) ⁺	0	0	4	0	0	4	Yes	
<i>Artibeus jamaicensis</i> (F)*	88	14	5	1	0	108	Yes	
<i>Carollia sowelli</i> (F) ⁺	7	7	6	5	0	25	Yes	
<i>Carollia subrufa</i> (F)	1	0	1	0	0	2	Yes	
<i>Centurio senex</i> (F) ⁺	1	0	0	0	0	1	No	
<i>Chiroderma salvini</i> (F)*	2	0	0	0	0	2	Yes	
<i>Choeroniscus godmani</i> (F)	0	0	1	0	0	1	No	
<i>Dermanura azteca</i> (F)	3	0	2	0	0	5	Yes	
<i>Dermanura phaeotis</i> (F) ⁺	2	0	2	0	0	4	No	
<i>Dermanura tolteca</i> (F)* ⁺	31	5	29	0	1	72	Yes	
<i>Dermanura watsoni</i> (F)* ⁺	3	1	3	0	1	8	Yes	

<i>Desmodus rotundus</i> (S)	2	0	5	0	0	7	Yes
<i>Diphylla ecaudata</i> (S)	0	0	1	0	1	2	No
<i>Enchisthenes hartii</i> (F)* ⁺	3	3	1	0	0	7	Yes
<i>Glossophaga commissarisi</i> (N)*	6	2	3	2	0	13	Yes
<i>Glossophaga leachii</i> (N)*	3	0	1	0	0	4	Yes
<i>Glossophaga soricina</i> (N)*	14	12	3	0	0	29	Yes
<i>Hylonycteris underwoodi</i> (N)* ⁺	0	6	6	0	0	12	Yes
<i>Micronycteris minuta</i> (I)	0	1	0	0	0	1	No
<i>Micronycteris schmidtorum</i> (I)	0	0	1	0	0	1	No
<i>Phyllostomus hastatus</i> (O)* ⁺	0	0	2	0	0	2	No
<i>Platyrrhinus helleri</i> (F)*	1	0	0	0	0	1	No
<i>Sturnira hondurensis</i> (F)* ⁺	4	18	58	19	8	107	Yes
<i>Sturnira parvidens</i> (F)*	0	0	0	0	2	2	No
<i>Trachops cirrhosus</i> (C)*	0	1	0	1	0	2	Yes
<i>Vampyressa thylene</i> (F)	1	0	0	0	0	1	No
<i>Vampyrodes major</i> (F)*	7	0	5	0	0	12	Yes
Vespertilionidae							
<i>Bauerus dubiaquercus</i> (I)*	3	0	5	0	0	8	Yes
<i>Eptesicus brasiliensis</i> (I)*	0	2	3	0	0	5	Yes
<i>Eptesicus furinalis</i> (I)	0	0	1	0	0	1	No
<i>Lasiurus frantzii</i> (I)	0	0	1	0	0	1	No
<i>Myotis pilosatibialis</i> (I)* ⁺	1	1	52	12	9	75	Yes
Molossidae							
<i>Molossus rufus</i> (I)*	1	0	0	0	0	1	No

Mormoopidae							
<i>Pteronotus davyi</i> (I) ⁺	2	0	3	0	0	5	No
<i>Pteronotus mesoamericanus</i> (I)*	0	1	6	5	0	12	Yes
Natalidae							
<i>Natalus lanatus</i> (I)	0	0	1	0	0	1	Yes
Summary							
Captures	191	74	210	45	22	542	
Species	21	14	28	7	6	36	
Elevation m a.s.l.	1287	1400	1572	1591	1825		
Unique species	5	1	0	8	1		
Effort m ² h	8,872	5,692	16,912	4,185	5,25	40,912	
Capture rate	0.022	0.013	0.012	0.010	0.004	0.013	
Recapture rate	13 (6.8%)	3 (4.1%)	21 (10%)	2 (4.4%)	3 (13.6%)	42 (7.7%)	
Individuals with ectoparasites	80	27	96	27	10	240	

Table 1. List of bats species captured in Cusuco National Park, Honduras in June-July 2019, with information on captures per bat species (recaptures removed), camp elevation, survey effort, and recapture and parasitism rates per camp (GU = Guanales, CO = El Cortecito, BC = Base Camp, DA = El Danto, CA = Cantiles). EC indicates species from which ectoparasites were collected. Letters in parenthesis after each name indicates primary dietary guild as defined by Kalko *et al.* (1996) and Soriano (2000): C = carnivorous, F= frugivorous, I = insectivorous, N= nectivorous, S= sanguivorous. Underlined names represent species listed as Threatened (Hernández 2015, IUCN 2020). An asterisk (*) indicates that pregnant females were captured and plus (+) indicates that lactating females were captured.

also reported in Mexican, Panamanian, and Venezuelan sites (Hiller *et al.*, 2020; Patterson *et al.*, 2008b; Tlapaya-Romero *et al.*, 2015). This may be linked to several factors, such as stable roosts and a close relationship between mother and offspring allowing for ample opportunities for parasite transmission events. In addition, young individuals have thinner skin, their immune system is still underdeveloped, and they are deficient in their grooming skills (Bertola *et al.*, 2005; Dick & Patterson, 2007; Hiller *et al.*, 2020).

The effect of small human-induced forest clearings on bat assemblages varied between elevations and this effect was species-specific. Whereas some studies have shown that deforestation has little or no effect on species richness (Meyer & Kalko, 2008; Ochoa, 2000), others have reported structural differences in the community and shifts in species dominance and ranks distribution (Clarke *et al.*, 2005; Peters *et al.*, 2006). Our results showed that in lower montane forest, species richness and Shannon diversity did not differ between habitats. However, Simpson diversity was significantly lower in closed-canopy forest, indicating that the bat assemblage was composed by one or a few dominant species. On the other hand, the effects of forest clearance were significantly stronger in upper montane forest, where human-induced forest clearings harbored few bat species and the assemblage was dominated by one or a few species, compared to closed-canopy forest. This negative effect on bat diversity at higher elevations might be related to food availability constraints (Castaño *et al.*, 2018; Soriano, 2000).

In lower montane forest, our results showed an opposite trend compared to previous studies, which found that fragmented areas tend to harbor few species of bat with assemblages being characterized by a small number of dominant species (e.g.: Meyer & Kalko, 2008; Sampaio *et al.*, 2003). The opposite pattern found in CNP might be related to the large number of *A. jamaicensis* captures in closed-canopy sites. Despite being known as a species tolerant of human disturbance, in this study, *A. jamaicensis* was less abundant in forest clearings than in closed-canopy sites. This may be due to the fact that the forest clearings are still at an early successional stage, where transformation of the land has not yet provided enough fruiting resources. In comparison, a higher number of captures of *A. jamaicensis* has been reported in Buenos Aires, a village located at

the buffer zone of the park (Estrada-Villegas *et al.*, 2007; Thompson & Vulinec, 2017), particularly in shaded coffee plantations.

In addition to varied impacts on bat species resulting from human-induced forest clearing, the effect on ectoparasites was similarly variable. While, in general, upper montane forest sites had higher parasite prevalence rates compared to low montane forest sites, there was considerable variability in parasitism among bat host species and disturbance category within these altitude zones. In lower montane forests, overall parasite prevalence did not vary between habitat types, although individual species showed differing prevalence rates. While other common species showed no difference in parasite prevalence, *S. hondurensis* showed a high prevalence in closed-canopy forest habitat. Conversely, in upper montane forest, higher overall prevalence was recorded in human-induced forest clearings, especially for *M. pilosaticubialis*. Bat behavior, availability of resources, and micro-climatic conditions of bat roosts are the fundamental factors that influence the changes in parasite prevalence and intensity (Hiller *et al.*, 2020). Habitat alterations, such as forest clearance, affect both roosting availability and resources and may have a positive effect on parasite prevalence by increasing roost crowding. The highly variable levels of parasite prevalence among habitat types, species, and altitudes at CNP reflects the findings of Brearley *et al.* (2013), who found that the relationships between wildlife diseases and human-modified landscapes are rarely consistent, and particularly so in rural agricultural landscapes.

Deforestation in CNP has accelerated rapidly in recent years (Martin *et al.*, 2021), which puts its bat communities in danger (Hernández, 2015). This is especially so at higher elevations, where species are more limited in their food resources (Castaño *et al.*, 2018). While the presence of a certain species does not necessarily imply population stability, it does suggest some tolerance of anthropogenic forest clearance. However, this is strongly influenced by the landscape matrix (Silva *et al.*, 2020). All forest clearing sites surveyed in this study were surrounded by closed-canopy forest, creating an edge effect, where bats could still use the resources of this forest. However, declines in species richness in forest

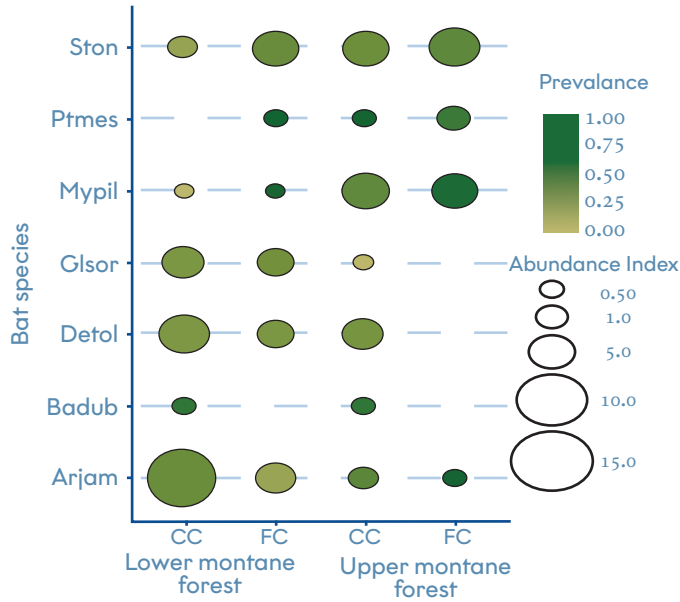


Figure 2 Relative abundance and proportion of parasitism prevalence in the eight most abundant bat species captured in Cusuco National Park during the summer of 2019. CC indicates closed canopy sites, and FC indicates human-induced forest clearings. Empty spaces indicate that the species was not captured in the specific camp during the surveyed period. Bat species: Arjam: *Artibeus jamaicensis*, Badub: *Bauerus dubiaquercus*, Casow: *Carollia sowelli*, Detol: *Dermanura tolteca*, Glsor: *Glossophaga soricina*, Mypil: *Myotis pilosatibialis*, Ptmes: *Pteronotus mesoamericanus* and Sthon: *Sturnira hondurensis*.

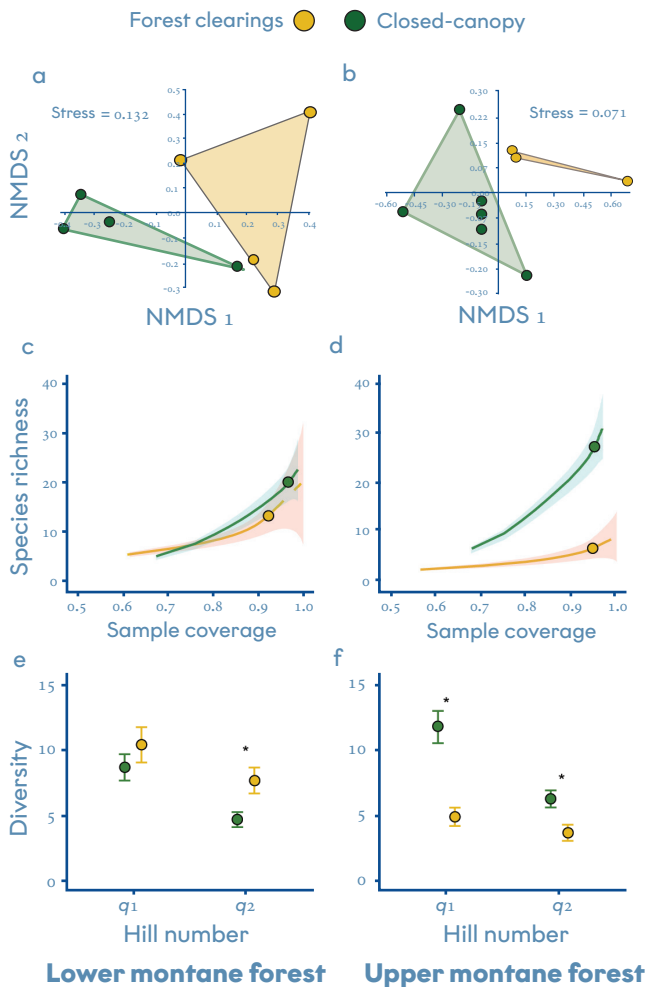


Figure 3 Results of Nonmetric Multidimensional Scaling analyses using Bray–Curtis similarity, sample coverage and Hill numbers diversity (q_1 and q_2) comparing bat assemblages within Cusuco National Park, north-western Honduras. Bat assemblages at lower montane (left) and upper montane forest (right) were compared in closed-canopy (green symbols) and human-induced forest clearings (yellow symbols) sites. Stress numbers indicate the match between inter object distance (sites) and dissimilarity. The lower the stress value, the better the match. All extrapolation curves of the Hill numbers were plotted to a doubling in sample size, and 500 bootstrap replicates were used to estimate 95% confidence intervals.

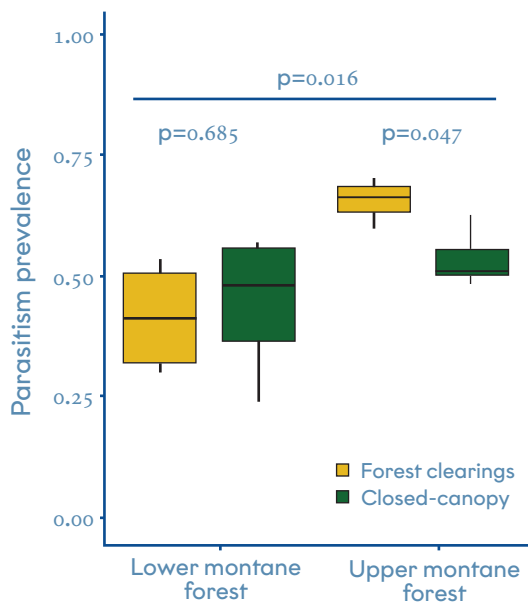


Figure 4 Parasitism proportion in closed canopy and human-induced forest clearing habitats in Cusuco National Park, north-western Honduras. Proportion (Median, 1st and 3rd quartiles, SD) of bats with ectoparasites in lower and upper montane forest. Differences between habitat and vegetation type were tested with Mann-Whitney U test. P values < 0.05 indicate significant differences.

TABLE 2. Summary of generalized linear models with binomial logistic regression of parasitism prevalence within the five most common bat species captured in Cusuco National Park, Honduras

LMF	<i>Artibeus jamaicensis</i>			<i>Sturnira hondurensis</i>			<i>Glossophaga soricina</i>		
Predictors	OR	Z	p	OR	Z	p	OR	Z	p
Habitat	1.30	0.36	0.720	0.05	-2.07	0.038[≠]	0.17	-1.83	0.067
Sex	0.33	-2.02	0.043[♀]	0.73	-0.31	0.755	2.05	0.67	0.504
Age	2.03	1.05	0.293	3.44	0.96	0.337	5.35	1.42	0.155
UMF	<i>Myotis pilosatibialis</i>			<i>Sturnira hondurensis</i>			<i>Carollia sowelli</i>		
Predictors	OR	Z	p	OR	Z	p	OR	Z	p
Habitat	0.08	-2.36	0.018[≠]	0.53	-1.12	0.265	1.13	0.07	0.941
Sex	0.62	-0.92	0.357	0.51	-1.40	0.163	N/A ^a		
Age	0.62	-0.61	0.543	3.35	2.25	0.024[¥]	0.84	-0.10	0.921

^aOnly male *C. sowelli* individuals were captured.

Table 2. Summary of generalized linear models with binomial logistic regression of parasitism prevalence within the five most common bat species captured in Cusuco National Park, Honduras. Effect of degree of deforestation, sex, and age on parasite prevalence in lower montane forest (LMF) and at upper montane forest (UPM). Odd ratios (OR), z and p values per species and predictors are shown. Symbols indicate a higher prevalence in human-induced forest clearing (≠), females (♀), and juveniles (¥).

edge habitats have been linked to habitat avoidance by animalivorous bats, because of flight constraints or increase of predation risk (Meyer & Kalko, 2008; Rocha *et al.*, 2017). Moreover, the effect of forest clearings largely depends on their size and successional stage. In this study, the studied forest clearings were less than five years old, and the response of bat assemblages and their relationship with ectoparasites to deforestation might change over time, depending on the land use or the regeneration rate of these habitats. Longer-term studies of logging impacts are therefore necessary to determine these impacts more thoroughly. Although the analyses were corrected by sampling effort, it is worth mentioning that the biases of sampling effort might still have affected the results of bat diversity estimates, increasing the potential of a type III error. Increasing survey effort not only increases the capture rate, but also the possibility of capturing rare species. Moreover, sites with human-induced clearings might reduce the efficiency of mist-nettings, since mist nets are more effective in locations with dense vegetation-containing corridors (Duffy *et al.*, 2000; Hourigan *et al.*, 2008).

In summary, the results of this study suggest that the effect of forest clearance varies with elevation and bat species. Forest clearings in high-altitude forests may have severe impacts on bat communities, not only reducing their diversity, but also increasing susceptibility to parasite infection. In order to gain a better understanding of the complex underlying mechanisms involved in the responses of bat assemblages and their ectoparasites to deforestation, long-term studies are required. Further research into this system should use complementary sampling methods and include environmental and disturbance variables across spatial and temporal changes (Rocha *et al.*, 2018), as well as include effects of food resources and physiological constraints on bat communities and their parasites (Meyer *et al.*, 2016). Moreover, further research needs to employ quantitative and multi-parameter approaches to evaluate the effect of human-induced forest clearings on taxonomic diversity, functional guild, behavior, immune systems, interactions with other organisms, and ecosystem services. There is an increasing concern about the ongoing loss of biodiversity in cloud forests and a better understanding of these pressure-response functions might provide tools to

integrate the challenge of embracing socio-ecological systems in conservation programs in Mesoamerica.

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References

- BAAGØE, H. J. (1977). Age determination in bats (Chiroptera). *Videnskabelige Meddelelser Dansk Naturhistorisk Forening*, 140, 53–92.
- BERTOLA, P. B., AIRES, C. C., FAVORITO, S. E., GRACIOLLI, G., AMAKU, M., & PINTO-DA-ROCHA, R. (2005). Bat flies (Diptera: Streblidae, Nycteribiidae) parasitic on bats (Mammalia: Chiroptera) at Parque Estadual da Cantareira, São Paulo, Brazil: Parasitism rates and host-parasite associations. *Memorias Do Instituto Oswaldo Cruz*, 100(1), 25–32. <https://doi.org/10.1590/S0074-02762005000100005>
- BREARLEY, G., RHODES, J., BRADLEY, A., BAXTER, G., SEABROOK, L., LUNNEY, D., LIU, Y., & McALPINE, C. (2013). Wildlife disease prevalence in human-modified landscapes. *Biological Reviews*, 88(2), 427–442. <https://doi.org/10.1111/brv.12009>
- CASTAÑO, J. H., CARRANZA, J. A., PÉREZ-TORRES, J., CASTANO, J., & PEREZ-TORRES, J. (2018). Diet and trophic structure in assem-

- blages of montane frugivorous phyllostomid bats. *Acta Oecologica*, 91(May), 81–90. <https://doi.org/10.1016/j.actao.2018.06.005>
- CAYUELA, L., GOLICHER, D. J., BENAYAS, J. M. R., GONZÁLEZ-ESPINOSA, M., & RAMÍREZ-MARCIAL, N. (2006). Fragmentation, disturbance and tree diversity conservation in tropical montane forests. *Journal of Applied Ecology*, 43(6), 1172–1181. <https://doi.org/10.1111/j.1365-2664.2006.01217.x>
- CEPF. (2020). *CEPF.net - Mesoamerica. Critical Ecosystem Partnership Fund*. <https://www.cepf.net/our-work/biodiversity-hotspots/mesoamerica>
- CHAO, A., GOTELLI, N. J., HSIEH, T. C., SANDER, E. L., MA, K. H., COLWELL, R. K., & ELLISON, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1), 45–67. <https://doi.org/10.1890/13-0133.1>
- CLARKE, F. M., ROSTANT, L. V., & RACEY, P. A. (2005). Life after logging: Post-logging recovery of a neotropical bat community. *Journal of Applied Ecology*, 42(2), 409–420. <https://doi.org/10.1111/j.1365-2664.2005.01024.x>
- de Carvalho, W. D., Martins, M. A., Esbérard, C. E. L. E. L., & Palmeirim, J. M. (2019). Traits that allow bats of tropical lowland origin to conquer mountains: Bat assemblages along elevational gradients in the South American Atlantic Forest. *Journal of Biogeography*, 46(2), 316–331. <https://doi.org/10.1111/jbi.13506>
- DICK, C. W., & DITTMAR, K. (2014). Parasitic bat flies (Diptera: Streblidae and Nycteribiidae): Host specificity and potential as vectors. In S. Klimpel & H. Melhorn (Eds.), *Parasitology Research Monographs (Vol. 5): Bats (Chiroptera) as vectors of diseases and parasites* (pp. 131–155). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-39333-4_6
- DICK, C. W., & GRACIOLLI, G. (2013). Checklist of world streblidae (Diptera: Hippochoidea). *Field Museum of Natural History*.
- DICK, C. W., GRACIOLLI, G., & GUERRERO, R. (2016). Family Streblidae. *Zootaxa*, 4122(1), 784. <https://doi.org/10.11646/zootaxa.4122.1.67>
- DICK, C. W., & PATTERSON, B. D. (2007). Against all odds: Explaining high host specificity in dispersal-prone parasites. *International Journal for Parasitology*, 37(8–9), 871–876. <https://doi.org/10.1016/j.ijpara.2007.02.004>
- DITTMAR, K., PORTER, M. L., MURRAY, S., & WHITING, M. F. (2006). Molecular phylogenetic analysis of nycteribiid and streblid bat flies (Diptera: Brachycera, Calyptratae): Implications for host associations and phylogeographic origins. *Molecular Phylogenetics and Evolution*, 38(1), 155–170. <https://doi.org/10.1016/j.ympev.2005.06.008>
- DUFFY, A. M., LUMSDEN, L. F., CADDLE, C. R., CHICK, R. R., & NEWELL, G. R. (2000). The efficacy of Anabat ultrasonic detectors and harp traps for surveying microchiropterans in south-eastern Australia. *Acta Chiropterologica*, 02(2).
- ESBÉRARD, C. E. L., ASTÚA, D., GEISE, L., COSTA, L. M., & PEREIRA, L. G. (2012). Do young *Carollia perspicillata* (Chiroptera: Phyllostomidae) present higher infestation rates of Streblidae (Diptera)? *Brazilian Journal of Biology*, 72(3), 617–621. <http://www.ncbi.nlm.nih.gov/pubmed/22990835>
- ESTRADA-VILLEGAS, S., ALLEN, L., GARCÍA, M., HOFMANN, M. J., & MUNROE, M. L. (2007). Bat assemblage composition and diversity of the Cusuco National Park. Report. In *Operation Wallacea*.
- FARIA, D., LAPS, R. R., BAUMGARTEN, J., & CETRA, M. (2006). Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. *Biodiversity and Conservation*, 15(2), 587–612. <https://doi.org/10.1007/s10531-005-2089-1>
- FARNEDA, F. Z., ROCHA, R., LÓPEZ-BAUCELLS, A., GROENENBERG, M., SILVA, I., PALMEIRIM, J. M., BOBROWIEC, P. E. D., & MEYER, C. F. J. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, 52(5), 1381–1391. <https://doi.org/10.1111/1365-2664.12490>
- FLEMING, T. H. (1993). Plant-visiting bats. *American Scientist*, 81(September-October), 460–467.
- FUNDACIÓN ECOLOGISTA. (1994). *Evaluación Ecológica Rápida (EER). Parque Nacional 'El*

Cusuco' y Cordillera del Merendon. *The Nature Conservancy and PACA (Proyecto Ambiental para Centro América)*.

- GILROY, D., JONES, S., VULINEC, K., THOMPSON, P., HOSKINS, H., CREEDY, T., JOCQUE, M., GREEN, S., LONSDALE, G., PHIPPS, C., BURDEKIN, O., & BROWN, T. (2017). Operation Wallacea Cusuco National Park, Honduras 2016 & 2017: End of Season Report. *Operation Wallacea: Old Bolingbroke, UK*, 1–81.
- GOLDBERG, T. L., BENNETT, A. J., KITYO, R., KUHN, J. H., & CHAPMAN, C. A. (2017). Kanyawara Virus: A novel Rhabdovirus infecting newly discovered Nycteribiid bat flies infesting previously unknown Pteropodid bats in Uganda. *Scientific Reports*, 7(1), 5287. <https://doi.org/10.1038/s41598-017-05236-w>
- GRACIOLLI, G., & DICK, C. W. (2018). Checklist of the world Nycteribiidae (Diptera: Hippoboscidae). *Field Museum of Natural History*.
- HAELEWATERS, D., DICK, C. W., COCHERÁN PITTÍ, K. P., DITTMAR, K., & PATTERSON, B. D. (2020). Bats, bat flies, and fungi: Exploring uncharted waters. In B. K. Lim, M. B. Fenton, R. M. Brigham, S. Mistry, A. Kurta, E. H. Gillam, A. Russell, & J. Ortega (Eds.), *50 years of bat research. Foundations and new frontiers: fascinating life sciences*. Springer Nature. <https://doi.org/In press>
- HAELEWATERS, D., HILLER, T., & DICK, C. W. (2018). Bats, bat flies, and fungi: A case of hyperparasitism. *Trends in Parasitology*, 34(9), 784–799. <https://doi.org/10.1016/j.pt.2018.06.006>
- HAMMER, Ø., HARPER, D. A. T., & RYAN, P. D. (2001). Past: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1), 1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm
- HANSEN, M. C., WANG, L., SONG, X. P., TYUKAVINA, A., TURUBANOVA, S., POTAPOV, P. V., & STEHMAN, S. V. (2020). The fate of tropical forest fragments. *Science Advances*, 6(11), 1–10. <https://doi.org/10.1126/sciadv.aax8574>
- HELMER, E. H., GERSON, E. A., SCOTT BAGGETT, L., BIRD, B. J., RUZYCKI, T. S., & VOGGESSER, S. M. (2019). Neotropical cloud forests and páramo to contract and dry from declines in cloud immersion and frost. In *PLoS ONE* (Vol. 14, Issue 4). <https://doi.org/10.1371/journal.pone.0213155>
- HERNÁNDEZ, D. J. (2015). PROGRAMA PARA LA CONSERVACION DE MURCIÉLAGOS DE HONDURAS (PCMH). In B. RODRÍGUEZ-HERRERA & R. SÁNCHEZ (Eds.), *Estrategia centroamericana para la conservación de murciélagos*. Universidad de Costa Rica, Escuela de Biología.
- HILLER, T., BRÄNDEL, S. D., HONNER, B., PAGE, R. A., & TSCHAPKA, M. (2020). Parasitization of bats by bat flies (Streblidae) in fragmented habitats. *Biotropica*, 52(3), 488–501. <https://doi.org/10.1111/btp.12757>
- HOSKINS, H. M. J., BURDEKIN, O. J., DICKS, K., SLATER, K. Y., MCCANN, N. P., JOCQUE, M., CASTAÑEDA, F. E., & REID, N. (2018). Non-volant mammal inventory of Cusuco National Park, northwest Honduras: Reporting the presence of Jaguar, *Panthera onca* (Linnaeus, 1758), and demonstrating the effects of zonal protection mammalian abundance. *Check List*, 14(5), 877–891. <https://doi.org/10.15560/14.5.877>
- HOSMER, D. W. J., LEMESHOW, S., & STURDIVANT, R. X. (2013). *Applied Logistic Regression* (3rd ed.). John Wiley & Sons.
- HOIRIGAN, C. L., CATTERALL, C. P., JONES, D., & RHODES, M. (2008). A comparison of the effectiveness of bat detectors and harp traps for surveying bats in an urban landscape. *Wildlife Research*, 35(8), 768–774. <https://doi.org/10.1071/WR07154>
- HSIEH, T. C., MA, K. H., & CHAO, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7(12), 1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- IUCN. (2020). *The IUCN Red List of Threatened Species. Version 2020-1*. Retrieved from <http://www.iucnredlist.org>.
- JONES, S. E. I., SUANJAK, M., TOBIAS, J. A., & FREEMAN, R. (2020). Comparative physiology of five tropical montane songbirds reveals differential seasonal acclimatisation and cold adaptation. *BioRxiv, Preprint*, 1–34. <https://doi.org/10.1101/2020.05.22.111328>

- KALKO, E. K. V., HANDLEY, C. O., & HANDLEY, D. (1996). Organization, diversity, and long-term dynamics of a neotropical bat community. In M. Cody & J. Smallwood (Eds.), *Long-Term Studies of Vertebrate Communities* (pp. 503–553). Academic Press.
- KIENE, F., ANDRIATSITOHAINA, B., RAMSAY, M. S., RAKOTONDAMANANA, H., RAKOTONDRAVONY, R., RADESPIEL, U., & STRUBE, C. (2020). Forest edges affect ectoparasite infestation patterns of small mammalian hosts in fragmented forests in Madagascar. *International Journal for Parasitology*, 50(4), 299–313. <https://doi.org/https://doi.org/10.1016/j.ijpara.2020.01.008>
- LE SAOUT, S., HOFFMANN, M., SHI, Y., HUGHES, A., BERNARD, C., BROOKS, T. M., BERTZKY, B., BUTCHART, S. H. M., STUART, S. N., BADMAN, T., & RODRIGUES, A. S. L. (2013). Protected areas and effective biodiversity conservation. *Science*, 342(6160), 803–805. <https://doi.org/10.1126/science.1239268>
- LIU, J., HAELEWATERS, D., PFLIEGLER, W. P., PAGE, R. A., DICK, C. W., & AIME, M. C. (2020). A new species of *Gloeandromyces* from Ecuador and Panama revealed by morphology and phylogenetic reconstruction, with a discussion of secondary barcodes in Laboulbeniomycetes taxonomy. *Mycologia*, 112(6), 1192–1202. <https://doi.org/10.1080/00275514.2020.1781496>
- LOURENÇO, S., & PALMEIRIM, J. M. (2008). Which factors regulate the reproduction of ectoparasites of temperate-zone cave-dwelling bats? *Parasitology Research*, 104(1), 127–134. <https://doi.org/10.1007/s00436-008-1170-6>
- MANTILLA-MELUK, H., & MUÑOZ-GARAY, J. (2014). Biogeography and taxonomic status of *Myotis keaysi pilosatibialis* LaVal 1973 (Chiroptera: Vespertilionidae). *Zootaxa*, 3793(1), 60. <https://doi.org/10.11646/zootaxa.3793.1.2>
- MARSHALL, A. G. (1982). Ecology of insects ectoparasitic on bats. In T. H. Kunz (Ed.), *Ecology of Bats* (1st ed., pp. 369–401). Springer US. https://doi.org/10.1007/978-1-4613-3421-7_10
- MARTIN, T. E., & BLACKBURN, G. A. (2009). The effectiveness of a Mesoamerican “paper park” in conserving cloud forest avifauna. *Biodiversity and Conservation*, 18(14), 3841–3859. <https://doi.org/10.1007/s10531-009-9683-6>
- MARTIN, T. E., JONES, S. E. I., CREEDY, T. J., HOSKINS, H. M., MCCANN, N. P., BATKE, S. P., KELLY, D. L., KOLBY, J., DOWNING, R., ZELAYA, S. M. S., GREEN, S. E. W., LONSDALE, G., BROWN, T., WATERS, S., RODRÍGUEZ, F., MCCRAVY, K. W., SOUZA, M. L., CRACE, D., NUÑEZ-MINO, J. M., J.M., HAELEWATERS, D., MEDINA-VAN BERKUM, P., PHIPPS, C.D., BARKER, R.J., CASTAÑEDA, F., REID, N., & JOCQUE, M (2021). A review of the ecological value of Cusuco National Park: an urgent call for conservation action in a highly threatened Mesoamerican cloud forest. *J Mesoam Biol., Special issue*, 1, 6–50.
- MARTÍNEZ-MOTA, R., POZO-MONTUY, G., BONILLA SÁNCHEZ, Y. M., & GILLESPIE, T. R. (2018). Effects of anthropogenic stress on the presence of parasites in a threatened population of black howler monkeys (*Alouatta pigra*). *Therya*, 9(2), 161–170. <https://doi.org/10.12933/therya-18-572>
- MEDELLÍN, R. A., ARITA, H. T., & SÁNCHEZ, Ó. (2007). *Identificación de los murciélagos de México* (Second). UNAM.
- MEDELLÍN, R. A., EQUIHUA, M., & AMIN, M. A. (2000). Bat diversity and abundance as indicators of disturbance in neotropical rainforests. *Conservation Biology*, 14(6), 1666–1675. <https://doi.org/10.1111/j.1523-1739.2000.99068.x>
- MEDINA-VAN BERKUM, P., VULINEC, K., CRACE, D., LÓPEZ-GALLEGO, Z., & MARTIN, T. E. (2020). Community composition of bats in Cusuco National Park, Honduras, a mesoamerican cloud park, including new regional and altitudinal records. *Neotropical Naturalist*, 3, 1–24. <https://www.eaglehill.us/neononline/access-pages/003-MedinaVanBerkum-accesspage.shtml>
- MEYER, C. F. J., & KALKO, E. K. V. (2008). Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: Land-bridge islands as a model system. *Journal of Biogeography*, 35(9), 1711–1726. <https://doi.org/10.1111/j.1365-2699.2008.01916.x>

- MEYER, C. F. J., STRUEBIG, M. J., & WILLIG, M. R. (2016). Responses of tropical bats to habitat fragmentation, logging, and deforestation. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 63–103). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_4
- MORA, J. M. (2016). Clave para la identificación de las especies de murciélagos de Honduras. *Ceiba*, 54(2), 93. <https://doi.org/10.5377/ceiba.v54i2.3283>
- MYERS, N. (2003). Biodiversity hotspots revisited. *BioScience*, 53(10), 916. [https://doi.org/https://doi.org/10.1641/0006-3568\(2003\)053\[0916:HR\]2.0.CO;2](https://doi.org/https://doi.org/10.1641/0006-3568(2003)053[0916:HR]2.0.CO;2)
- MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., FONSECA, G. A. B., KENT, J., DA FONSECA, G. A., & KENT, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <http://www.ncbi.nlm.nih.gov/pubmed/10706275>
- OCHOA, J. G. (2000). Efectos de la extracción de maderas sobre la diversidad de mamíferos pequeños en bosques de tierras bajas de la guayana venezolana. *Biotropica*, 32(1), 146–164. <https://doi.org/10.1111/j.1744-7429.2000.tb00457.x>
- OKSANEN, J., F. GUILLAUME BLANCHET, M. F., KINDT, R., LEGENDRE, P., MCGLINN, D., MINCHIN, P. R., R. B. O'HARA, G., SIMPSON, L., SOLYOS, P., STEVENS, M. H. H., SZOEC, E., & WAGNER, H. (2019). vegan: Community Ecology Package. In *R package version 2.5-6*. <https://cran.r-project.org/package=vegan>
- PATTERSON, B. D., DICK, C. W., & DITTMAR, K. (2007). Roosting habits of bats affect their parasitism by bat flies (Diptera: Streblidae). *Journal of Tropical Ecology*, 23(2), 177–189. <https://doi.org/10.1017/S0266467406003816>
- PATTERSON, B. D., DICK, C. W., & DITTMAR, K. (2008a). Sex biases in parasitism of neotropical bats by bat flies (Diptera: Streblidae). *Journal of Tropical Ecology*, 24(4), 387–396. <https://doi.org/10.1017/S0266467408005117>
- PATTERSON, B. D., DICK, C. W., & DITTMAR, K. (2008b). Parasitism by bat flies (Diptera: Streblidae) on neotropical bats: effects of host body size, distribution, and abundance. *Parasitology Research*, 103(5), 1091–1100. <https://doi.org/10.1007/s00436-008-1097-y>
- PETERS, S. L., MALCOLM, J. R., & ZIMMERMAN, B. L. (2006). Effects of selective logging on bat communities in the southeastern Amazon. *Conservation Biology*, 20(5), 1410–1421. <https://doi.org/10.1111/j.1523-1739.2006.00526.x>
- PILOSOFF, S., DICK, C. W., KORINE, C., PATTERSON, B. D., & KRASNOV, B. R. (2012). Effects of anthropogenic disturbance and climate on patterns of bat fly parasitism. *PLoS ONE*, 7(7), e41487. <https://doi.org/10.1371/journal.pone.0041487>
- POWELL, G., & PALMINTERI, S. (2001). *Central America: Southern Mexico, southern Guatemala, into Honduras, El Salvador, and Nicaragua*. <https://www.worldwildlife.org/ecoregions/nt0303>
- R CORE TEAM (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>
- ROCHA, R., LÓPEZ-BAUCELLS, A., FARNEDA, F. Z., GROENENBERG, M., BOBROWIEC, P. E. D., CABEZA, M., PALMEIRIM, J. M., & MEYER, C. F. J. (2017). Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects. *Landscape Ecology*, 32(1), 31–45. <https://doi.org/10.1007/s10980-016-0425-3>
- ROCHA, R., OVASKAINEN, O., LÓPEZ-BAUCELLS, A., FARNEDA, F. Z., SAMPAIO, E. M., BOBROWIEC, P. E. D., CABEZA, M., PALMEIRIM, J. M., & MEYER, C. F. J. (2018). Secondary forest regeneration benefits old-growth specialist bats in a fragmented tropical landscape. *Scientific Reports*, 8(1), 3819. <https://doi.org/10.1038/s41598-018-21999-2>
- SAMPAIO, E. M., KALKO, E. K. V., BERNARD, E., RODRÍGUEZ-HERRERA, B., & HANDLEY, C. O. J. (2003). A biodiversity assessment of bats (Chiroptera) in a tropical lowland rainforest of central Amazonia, including methodological and conservation considerations. *Studies on Neotropical Fauna and Environment*, 38(1), 17–31.

- SIKES, R. S. (2016). Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663–688. <https://doi.org/10.1093/jmammal/gyw078>
- SILVA, I., ROCHA, R., LÓPEZ-BAUCELLS, A., FARNEDA, F. Z., & MEYER, C. F. J. (2020). Effects of forest fragmentation on the vertical stratification of neotropical bats. *Diversity*, 12(2). <https://doi.org/10.3390/d12020067>
- SIMMONS, N. B., & CONWAY, T. M. (2003). Evolution of ecological diversity in bats. In T. H. Kunz & M. B. Fenton (Eds.), *Bat ecology* (pp. 493–535). University of Chicago Press.
- SORIANO, P. J. (2000). Functional structure of bat communities in tropical rainforests and andean cloud forests. *Ecotropicos*, 13(1), 1–20.
- STARS, E. (2017). *Assessing parasite load within the bat population of Cusuco National Park, Honduras*. MSc thesis. The University of Nottingham.
- STRAUBE, F., & BIANCONI, G. (2002). Sobre a grandeza e a unidade utilizada para estimar esforço de captura com utilização de redes-de-neblina. *Chiroptera Neotropical*, 8(1/2), 150–152.
- SZENTIVÁNYI, T., CHRISTE, P., & GLAIZOT, O. (2019). Bat Flies and Their Microparasites: Current Knowledge and Distribution. *Frontiers in Veterinary Science*, 6(April), 1–12. <https://doi.org/10.3389/fvets.2019.00115>
- TEJEDOR, A. (2005). A new species of funnel eared bat (Natalidae: *Natalus*) from Mexico. *Journal of Mammalogy*, 1542(October). [https://doi.org/10.1644/1545-1542\(2005\)86\[1109:ANSOFB\]2.0.CO;2](https://doi.org/10.1644/1545-1542(2005)86[1109:ANSOFB]2.0.CO;2)
- THOMPSON, P., & VULINEC, K. (2017). BATS OF CUSUCO NATIONAL PARK. IN T. GILROY, D., JONES, S., VULINEC, K., THOMPSON, P., HOSKINS, H., CREEDY, T., JOCQUE, M., GREEN, S., LONSDALE, G., PHIPPS, C., BURDEKIN, O. & BROWN (Ed.), *Operation Wallacea Cusuco National Park, Honduras 2016 & 2017: End of Season Report*. Operation Wallacea: Old Bolingbroke, UK.
- TIMM, R. M., & LAVAL, R. K. (1998). A field key to the bats of Costa Rica. *Occasional Publication Series*, 22, 1–30.
- TLAPAYA-ROMERO, L., HORVÁTH, A., GALLINA-TESSARO, S., NARANJO, E. J., & GÓMEZ, B. (2015). Prevalencia y abundancia de moscas parásitas asociadas a una comunidad de murciélagos cavernícolas en La Trinitaria, Chiapas, México. *Revista Mexicana de Biodiversidad*, 86(2), 377–385. <https://doi.org/10.1016/j.rmb.2015.04.012>
- VELAZCO, P. M., & SIMMONS, N. B. (2011). Systematics and taxonomy of Great striped-faced bats of the Genus *Vampyroides* Thomas, 1900 (Chiroptera: Phyllostomidae). *American Museum Novitates*, 3710, 1–36.
- WALKER, M. J., DORRESTEIN, A., CAMACHO, J. J., MECKLER, L. A., SILAS, K. A., HILLER, T., & HAELEWATERS, D. (2018). A tripartite survey of hyperparasitic fungi associated with ectoparasitic flies on bats (Mammalia: Chiroptera) in a neotropical cloud forest in Panama. *Parasite*, 25(April), 19. <https://doi.org/10.1051/parasite/2018017>