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Unexpected Diversity in Regenerating Sites Stresses the Importance of Baselines: A Case Study With Bats (Order Chiroptera) on the Osa Peninsula, Costa Rica

Elène Haave-Audet[1,2], Doris Audet[3], Michelle Monge-Velazquez[2], Eleanor Flatt[2], and Andrew Whitworth[2,4]

Abstract

Introduction: Background and Research Aims: Assessing biodiversity recovery is key to determine whether the objectives of habitat restoration for conservation are met. Many restoration initiatives use cross-sectional comparisons of wildlife communities to infer restoration impact instead of longitudinal assessments from a baseline state. Using an indicator of biodiversity in the neotropics— bats— we demonstrate how assessing community diversity and composition in an area targeted for restoration prior to implementation, and when compared to surrounding intact forest, provides the groundwork to track changes in the community post-restoration.

Methods: We assessed bat communities by 1) using mist-net surveys to identify species in the family Phyllostomidae (leaf-nosed bats), and 2) conducting acoustic surveys to identify non-phyllostomid species (aerial insectivores).

Results: For both groups, we found that areas targeted for restoration had similar diversity as the surrounding forest, but the two habitat types differed in community composition. Phyllostomids were captured at higher rates in forest, but aerial insectivores were detected at higher rates in restoration habitat.

Conclusion: Our baseline assessment revealed unexpected diversity in areas targeted for restoration. The presence of all trophic groups in restoration habitat suggests that bats provide key ecosystem services in the restoration process, such as through seed dispersal, pollination and insect pest control.

Implications for Conservation: Conducting a baseline survey of bats in areas targeted for restoration demonstrated that the community was not species poor at the baseline and was different from the surrounding forest, allowing us to better track restoration success and the effects of different restoration treatments.

Keywords

conservation, neotropics, bioacoustics, indicator species, rewilding, recovery

Monitoring indicator groups is essential to understand the efficacy of restoration approaches in re-establishing previous ecological communities (Carignan & Villard, 2002). Neotropical bats are often used as indicators of ecosystem health and management interventions because of their key roles within tropical ecosystems, yet sensitivity to habitat disturbance (Fenton et al., 1992; Medellín et al., 2000). In particular, the ability of bats to quickly disperse (compared with other less vagile groups), pollinate plants, and move seeds make them a

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group of interest to restoration ecologists (de la Peña-Domene et al., 2014; Kunz et al., 2011). Describing the bat community in areas targeted for restoration can be used as an indication of the current ecological state and inform which functional groups are present (e.g., Cole et al., 2010; de la Peña-Domene et al., 2014; Morrison & Lindell, 2012). If community assessments indicate that the species or functions of interest are absent, this information can be used to outline the restoration techniques required to attract target species. This is key for re-establishing plant-animal interactions critical to healthy ecosystem function (McAlpine et al., 2016).

In the neotropics, restoration is generally achieved through natural regeneration or tree planting (Lamb et al., 2005). Each method can impact plant and wildlife community compositions differently because of variation in structural complexity and conditions of the vegetation that emerge from different approaches. This can create variation in the resources available to animals as food and shelter. For example, J. L. Reid et al. (2015) found that the abundance of frugivorous bats was higher in areas that were restored through plantations compared to areas of natural regeneration—likely due to increased roosting habitat availability in plantations. The link between neotropical bat diversity, forest cover and successional stage suggests a general trend toward increasing diversity with increased forest cover and later stages of succession (e.g., de la Peña-Cuéllar et al., 2012; Farneda et al., 2018; García-Morales et al., 2016; Meyer et al., 2007). Furthermore, remnant forest patches and forest corridors, such as riparian strips within deforested landscapes, generally help to support diverse bat communities, despite being surrounded by resource poor habitat—provided that intact forests are present nearby (Carrasco-Rueda & Loiselle, 2019; de la Peña-Cuéllar et al., 2015; Galindo-González & Sosa, 2003).

Baseline assessments of the ecological community in areas targeted for restoration provide the ability to track changes post implementation of management programs (Gibbs et al., 1999). In the case of neotropical bats, Farneda et al. (2018) demonstrated that using historical data of an Amazonian bat community was useful to detect functional recovery of the assemblage following natural forest succession. Baseline assessments conducted in the context of a restoration initiative are key to understanding whether the management strategies in place are effective at restoring habitats to better support wildlife communities, re-establishing plant-animal interactions, and supporting diverse functional roles (Rocha et al., 2017b). In an experimental context, baselines address a potential confounding variable when comparing the outcome of different experimental treatments; this cannot be done from inferring initial stages via cross-sectional studies. Initial assemblages are key to the direction of early succession (in the context of different ecological roles) and are highly variable at the regional scale (Martínez-Ferreira et al., 2020).

Here we investigated the early stages of a restoration project in Costa Rica to: 1) test whether the baseline bat community in areas targeted for restoration differed from that of intact surrounding forest, in terms of diversity (richness, evenness, and composition), and 2) test for effects of small-scale landscape features (including restoration treatment) on bat abundance in restoration areas. We used two complementary methods, mist-netting and acoustic detection, to sample species from all trophic groups (MacSwiney et al., 2008), thereby accounting for all ecological roles bats might provide at the onset of restoration. To infer those ecological roles, we conducted our analyses at the whole assemblage level and by trophic group. Based on previously described patterns for bat assemblages, we expected that the diversity and evenness of the bat fauna would be higher in forest than in early-stage restoration sites (Castro-Luna et al., 2007; Meyer & Kalko, 2008). For the different trophic groups, we expected lower diversity and capture rate of seed dispersers (i.e., frugivores), pollinators (i.e., nectarivores) and gleaning animalivores in restoration sites (Avila-Cabadilla et al., 2014; Bobrowiec & Gribel, 2010; de la Peña-Cuéllar et al., 2012; Farneda et al., 2015). In contrast, we expected that aerial insectivores, particularly open space foragers, should already be using restoration sites (Bader et al., 2015; Estrada-Villegas et al., 2010).

Methods

Study Site

We conducted the study on the Osa Peninsula, in the southwest region of Costa Rica, at the Osa Biological Station (known locally as Piro Biological Station; 8.40388 N, 83.336618 W; Figure 1). Daily average temperatures at the field site range between 23.4 °C and 28.8 °C. Rainfall is seasonal (with a rainy season from June to November and a dry season from December to May). Annual rainfall ranges from 3,000 – 7,000 mm/year (Taylor et al., 2015).

Less than half of the original forested area in the Osa region is still covered by old growth forest (Weissenhofer et al., 2001). The Osa Biological Station is surrounded by 1,330-ha of privately protected land, encompassing a variety of habitat types, making it an ideal site for comparing bat assemblages in existing forest and deforested areas under restoration. Detailed description of the study site and land-use history can be found in Whitworth et al. (2018) and Sandor and Chazdon (2014). This study took place in an area of recently abandoned pasture (3 years; all cattle removed in 2014–2015) undergoing a large-scale restoration experiment,

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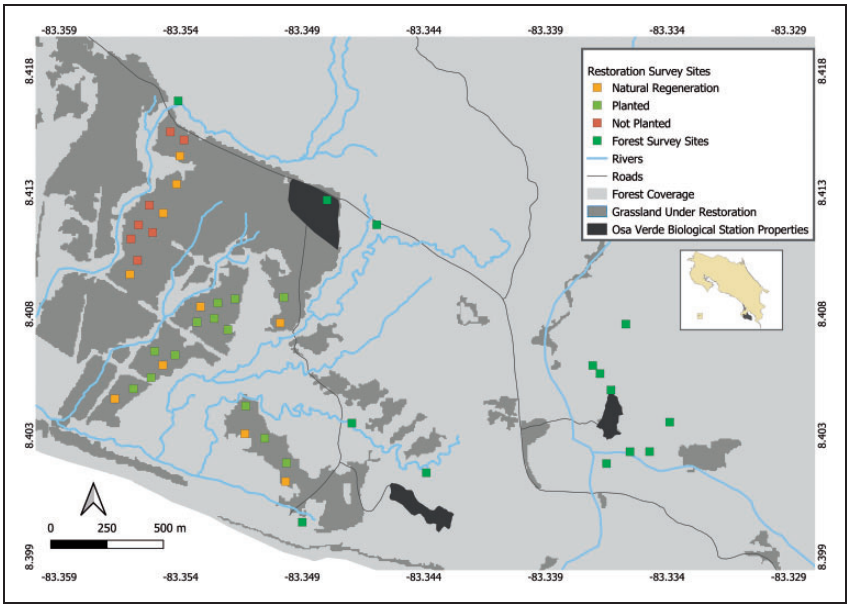


Figure 1. Map of the Osa Biological Station, Osa Peninsula Costa Rica, and Bat Survey Sites in Areas of Restoration and in the Surrounding Forest Matrix.

comprised of forty 0.5-ha experimental plots. The forty plots are divided into four restoration treatments: three planting regimes and a natural regeneration control. The restoration plots were completely cleared to soil prior to the start of the experiment and, except for natural regeneration plots, were subsequently maintained every six months to remove natural growth of grasses and vines around the planted trees. The altitude of area the under restoration ranged from 7–25 MSL.

Sampling Methods. We conducted bat surveys in 30 of the 40 experimental plots (Figure 1) at the onset of restoration, between May and December 2018. All 30 sites were sampled twice unless otherwise noted. The remaining ten plots were not surveyed due to logistical constraints (timeframe, personnel), and because the 30 plots that were sampled sufficiently represented the different planting strategies at the time of the study. Thirteen of these 30 plots were planted one year prior to sampling (hereafter referred to as *planted* sites), seven were planted in the year of sampling (immediately before or immediately after surveys, hereafter referred to as *not planted* sites), and ten were natural regeneration plots (Online Appendix 1, Figure 1.1). To provide the necessary context for the initial (baseline) community composition in areas to be restored, we also conducted bat surveys at 14 sites in the surrounding forested area, which included old growth and secondary forest in close proximity. We ensured that one of the two sampling rounds at each site took place in little to no moon visibility, since bat activity decreases in moonlit conditions (Saldaña-Vázquez & Munguía-Rosas, 2013).

Capture Surveys. In order to sample bats in the family Phyllostomidae, which includes all frugivorous (i.e., seed dispersers), nectivorous (i.e., pollinators) and gleaning animalivore species, we conducted mist-net surveys, which remains the most effective method for monitoring members of this family (Avila-Cabadilla et al., 2012). In the restoration sites, we set-up mist nets at the center of the 0.5-ha plot in a modified 'H' configuration, using two 12×2.5 m nets and one 9×5 m net (105 m^2 of mist-net per night, unless otherwise noted and accounted for in sampling effort; Online Appendix 1, Figure 1.1). In the forest sites, we used existing trails and clearings to block bat flyways: the area of mist-nets used at forest sites ranged from 75 m^2 to 105 m^2, depending on available space. Mist-nets were raised at sunset (between 17:45 and 18:00) and remained open for four hours. We interrupted netting during heavy rainfall. Once nets were open, we checked them for bats every 10 to 15 minutes. Once bats were removed from the net, they were kept in cloth holding bags until the end of the survey, to avoid recaptures. Bats were identified in the field, according to F. A. Reid (2009) and nomenclature followed York et al. (2019). Because of the difficulty of differentiating *Dermanura watsoni* and *D. phaeotis* based on dental characteristics, we identified captured individuals as *D. watsoni*, because of their greater likelihood of occurrence in the study region (F. A. Reid, 2009).

Acoustic Surveys. Acoustic sampling is most effective for the detection of aerial insectivores because most produce louder echolocation calls than phyllostomid species, but unlike the latter are less likely to be captured in mist-nets

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(Meyer et al., 2011). At the time of netting, we simultaneously recorded echolocation calls at the center of netting sites using full spectrum SM4bat detectors (Wildlife Acoustics, Maynard, MA, USA) placed ~1.5 m above ground. Calls were automatically recorded for one minute (recording interval) every 10 minutes for four hours at a sampling rate of 256 kHz, with trigger levels set at 16 kHz and 12 dB.

For species identification, spectrograms from the recordings were reviewed on screen by experienced observers (D. A. and E. H. A.) following the procedure described in Estrada-Villegas et al. (2010). The spectrograms were produced with either Kaleidoscope (v. 4.2.0) or SongScope software (v. 4.0, Wildlife Acoustics), selecting an FFT size of 256 and a 128 window size. Search phase calls were compared to a compilation of published call characteristics for species that are known to occur in the area and documented in a call library for the study site (see Online Appendix 2 for call identification criteria and sources).

Analyses

Bat Communities in Restoration and Forest Habitats. Given the different sampling methods, all analyses were conducted separately for phyllostomids (capture data) and aerial insectivores (acoustic sampling). The analysis of capture data excluded all non-phyllostomid bats (5% of bat captures, by individual). We conducted all analyses in R (v. 3.6.1) using RStudio (v. 1.2.1335; R Core Team, 2019; RStudio Team, 2018), and graphically depicted results using the package *ggplot2* (Wickham, 2016) and in SigmaPlot (v. 13). We quantified species richness for each of the two surveys at every sampling site. For each species or identified taxonomic unit (see Online Appendix 2), we also calculated a detection rate for each night of sampling. For phyllostomids, this was the capture rate per night (individuals/hr). For aerial insectivores, this was an activity index equal to the number of one-minute sampling intervals during which the species was detected per night. Such indices of activity based on occurrence counts are used as a proxy for abundance across habitat types and to compare the composition of aerial insectivore assemblages (Estrada-Villegas et al., 2010, 2012; Heer et al., 2015).

We assessed differences in species diversity across habitat types by calculating and plotting sample-size-based rarefaction and extrapolation (R/E) curves for Hill numbers using the package *iNEXT* (Hsieh et al., 2016). Species observations were pooled for the two sampling sessions and 'sites' were used as sampling units. We used species incidence (presence/absence) to calculate three Hill numbers—species richness, Shannon diversity, and Simpson diversity—with the function *iNEXT*, using the "incidence_raw" datatype. We plotted estimated values, sample coverage, and rarefied estimates, and assessed the overlap of the 95% confidence intervals to assign significance of differences in species diversity across habitat types (Chao et al., 2014).

To detect differences in capture/detection rate of phyllostomids and aerial insectivores between forest and restoration habitats, we used mixed effects models using the package *lme4* (Bates et al., 2015). We modelled phyllostomid capture rate (individuals/hr; log transformed) and aerial insectivore detection rate (ratio of the number of sampling intervals in which each species was detected in a night, summed across detected species; log transformed) using mixed-effect linear models, with sampling site as a random effect. Because bat activity can be affected by moonlight (Saldaña-Vázquez & Munguía-Rosas, 2013), we also included the percent luminosity during the sampling period as an explanatory factor in analyses. Luminosity data was obtained from timeanddate.com (Thorsen, 2019); if the moon was not visible at the time of sampling (i.e., not risen), percent luminosity was set to zero.

Prior to analyzing differences in community composition across habitat types, we conducted a Mantel test on the species-site dissimilarity matrices for each of the four assemblage-habitat combinations and found no spatial autocorrelation in patterns of community composition; dissimilarity matrices were calculated using the function *vegdist* in the R package *vegan* (Oksanen et al., 2019), and Mantel tests were conducted using the *vegan* function *mantel* (phyllostomid-forest: $r = .02$, $p = .38$; phyllostomid-restoration: $r = .12$, $p = .11$; aerial insectivore-forest: $r = .20$, $p = .09$; aerial insectivore-restoration: $r = .07$, $p = .12$). We then took a three-parted approach to explore differences in community composition across habitat types and identified species' trophic groups to explore emergent patterns across ecological roles of bats. Phyllostomid species were assigned to the following foraging groups, based on the primary component of their diet (F. A. Reid, 2009): frugivore, nectarivore, animalivore, and sanguivore (see Online Appendix 3, Table 3.1). Aerial insectivores were assigned to the following foraging groups: open-space foragers and forest/edge foragers (Online Appendix 3, Table 3.2), based on functional traits and habitat use (Estrada-Villegas et al., 2010; Heer et al., 2015; Jung et al., 2007). First, to describe and visually compare the characteristics of the bat assemblages (species composition and relative abundance) across habitats, we plotted rank abundance graphs (Feinsinger, 2001). We used the proportion of individuals (p_i) captured (phyllostomids) or proportion of detections (aerial insectivores) of a given species relative to the total captures/detections, plotted on a logarithmic scale to facilitate comparisons between plots with different sample sizes. Second, to

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quantify differences in community composition, we used permutational multivariate analysis of variance (PerMANOVA) using the *adonis* function in the R package *vegan* (Oksanen et al., 2019), to determine whether habitat type affected the community composition of phyllostomid and aerial insectivore assemblages. We visualized patterns of community composition using non-metric multidimensional scaling (NMDS), using Bray-Curtis distances, using the *vegan* function *metaMDS* (Oksanen et al., 2019). To construct the phyllostomid species matrix, we combined species incidences over the two sampling nights at each site and used the total number of individuals of each species detected at a site as an index of abundance. There was one restoration site at which we did not capture any phyllostomids in either sampling night, thus it was omitted from analysis. To construct the aerial insectivore species matrix, we used the combined species presence/absence over each of the sampling nights at a site. There were two forest sites at which no aerial insectivores were detected in either of the two sampling nights, thus they were omitted from analysis. Third, to quantify habitat type associations across species and trophic groups, we calculated the group-equalized phi correlation coefficient between species' incidence (presence/absence) and habitat type and the associated 95% confidence intervals using the function *strassoc* in the R package *indicspecies* (De Cáceres & Legendre, 2009). Associated *p*-values were calculated using the function *multipatt*.

Effect of Landscape Characteristics on Detection Rate in Restoration Habitat. To evaluate potential landscape correlates of bat abundance in restoration habitat, we modelled the effect of landscape characteristics and early differences in habitat structure due to restoration treatment on phyllostomid and aerial insectivore detection rate. We included the following landscape characteristics: the distance to the forest edge (from the center of each restoration plot to the nearest forest edge, measured in the field), the distance to streams (from the center of each restoration plot, extracted using GIS software), the amount of forest coverage within 200 m of the sampling location, and the presence of vegetation islands (identified in the field as vegetation clusters containing more than three trees). We included the percent forest cover within 200 m of sampling sites as a predictor variable to account for the heterogeneity of forest coverage surrounding each restoration category. We set our buffer size to 200 m based on previous findings from J. L. Reid et al. (2015) that demonstrated that forest structure had the greatest impact on fruit bat activity at this scale. At our study site, this scale is appropriate to reflect between-site variation in nearby forest cover (see Figure 1) while minimizing excessive overlap between sampling points. Percent forest cover within the buffer zone was calculated from aerial imagery in QGIS (v. 3.4; QGIS Development Team, 2019). Because we were only interested in small-scale landscape characteristics, we combined the detection data from the two sampling nights at each restoration site. None of the continuous predictors were strongly correlated, and there were no differences in the mean values of the continuous predictors across restoration treatments, as determined using Kruskal-Wallis tests (Online Appendix 5; Figure 5.1), thus they were all included in the models. We modelled the responses without the intercept, to assess the effect size of each predictor on detection rate. For each sampling technique, we first ran models for the entire assemblage. For phyllostomid capture rate (individuals/hr), we used a linear model; we omitted one outlier to meet model assumptions (see Online Appendix 5, Table 5.1 for details). For aerial insectivore detection rate (activity index) we ran a Gamma generalized linear model (GLM) with a log-link function. To investigate the effect of landscape characteristics on different trophic groups, we then conducted the same analysis on each trophic group separately. Trophic groups with few species and/or detections, which included nectarivores, animalivores, and sanguivores, were modelled using logistic regression (binomial GLM). Frugivores were modelled using a linear model, and forest foragers were modelled with a linear model after detection rate was square root transformed. Open space foragers were modelled using a Gamma GLM with a log-link function.

Results

Capture and Acoustic Sampling Outcomes

The two mist-netting sessions in 30 restoration sites and 14 forest sites amounted to a total capture effort of 22,791.6 m^2•hr in restoration sites and 9,321.4 m^2•hr in forest sites (overall effort: 32,113 m^2•hr). In total, we captured 611 bats (347 in restoration habitat and 264 in forest habitat), representing 29 species from six families (Online Appendix 3, Table 3.1). Of those captures, 582 (95%) were phyllostomids, from each of the five subfamilies known to occur in the region (F. A. Reid, 2009). Bats were caught during each sampling session in all forest sites, whereas in six of the restoration sites, no bats were captured in at least one of the two sampling nights. Moon luminosity ranged from 0–99.9% and was on average 45.4% (±41.15% s.d.) over the 88 sampling nights.

Acoustic sampling took place in each of the same restoration and forest sites as mist-netting (Figure 1). All sites were surveyed twice, except for one forest site, which was only acoustically surveyed once (due to a logistical error). We collected 2,155 minutes of recordings, including 1,470 minutes in restoration habitat and

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685 minutes in the forest habitat leading to 887 detection counts for aerial insectivores (702 in restoration and 185 in forest). We identified 14 species from five different families based on their distinct call characteristics (Online Appendix 3, Table 3.2).

Bat Communities in Restoration and Forest Habitats. In the restoration habitat, we captured 18 species of phyllostomid bats, including 10 frugivores, 5 gleaning animalivores, 1 nectarivore and 1 sanguivore (Online Appendix 3, Table 3.1), whereas in the forest habitat, we captured 19 phyllostomid species, including 9 frugivores, 6 gleaning animalivores, 3 nectarivores and 1 sanguivore. The completeness of the inventory, estimated from the rarefaction, was 97% in restoration and 96% in forest (Online Appendix 4, Figure 4.1a). Based on the 95% confidence intervals of the estimated species richness, Shannon diversity and Simpson diversity indices, there were no significant differences between estimated richness, entropy, and evenness between restoration and forest habitat types, although the mean estimates were lower in restoration than in forest habitats (Figure 2A and B). Based on the linear mixed effect model, capture rate was significantly lower in restoration habitat than forest habitat, and luminosity had a small but significant negative effect on capture rate (Table 1).

For aerial insectivores, we detected 14 species in restoration sites, 10 of which were also present in forest sites (Online Appendix 3, Table 3.2). The completeness of the inventory was 100% in restoration habitat and 97% in forest habitat (Online Appendix 4, Figure 4.1b). While there was no significant difference between habitat types on estimated species richness based on overlapping 95% confidence intervals, entropy and evenness, as calculated using the Shannon and Simpson diversity indices, were lower in forest than in

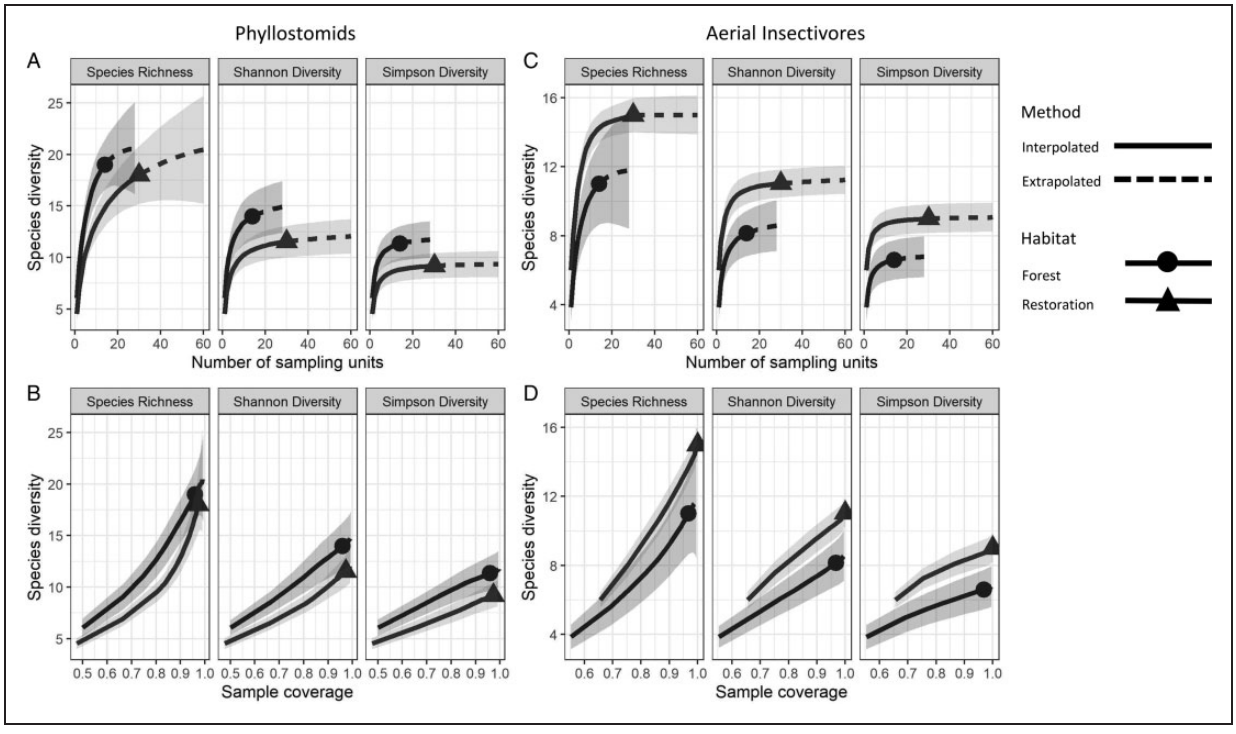


Figure 2. Rarefied Diversity Estimates. Estimated species richness, Shannon diversity and Simpson diversity indices with 95% confidence intervals in forest and restoration habitats for (A and B) phyllostomids and (C and D) aerial insectivores. Top panels depict estimated values accumulated by sampling units (sites) and bottom panels depict estimates corrected for sample coverage (survey completeness).

Table 1. Effect of Habitat Type and Luminosity on Bat Detection Rates.

	Intercept (forest)	Habitat (restoration)	Luminosity
Phyllostomids	1.21 (0.17 SE)	−0.52 (0.19 SE) ***	−0.003 (0.002 SE) **
Aerial Insectivores	−0.31 (0.08 SE)	0.29 (0.08 SE) ***	−0.001 (0.001 SE)

The response variables for phyllostomids (individuals/hr; log transformed) and aerial insectivores (activity index; square root transformed) were modelled using mixed-effects linear models. Sampling sites were included as a random effect (not shown). Full model outputs are provided in Online Appendix 4.
*$p < .1$. **$p < .05$. ***$p < .01$.

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restoration habitat (Figure 2C and D). Further, the detection rate of aerial insectivores was significantly lower in forest than in restoration habitat, but there was no effect of luminosity (Table 1).

For phyllostomid community composition, both habitats presented similar shapes of the rank abundance graphs (Figure 3), but the occurrence and relative abundance of species varied between habitats. Some species were only detected in one of the two habitat types, with four species unique to the forest habitat (*Chrotopterus auritus, Lophostoma silvicolum, L. brasiliense,* and *Lichonycteris obscura*), and three unique to the restoration habitat (*Micronycteris hirsuta, M. minuta,* and *Chiroderma villosum*). In their overall abundance, frugivores represented 77% of all captures in restoration habitat and 85% of forest captures, while nectarivores' relative abundance was 12% in restoration and 6% in forest. Gleaning animalivores represented 8% and 7% of captures in restoration and forest habitats, respectively. The relative abundance of the only sanguivore, *Desmodus rotundus*, was similar in both habitat types (2.6% of captures in restoration and 2.3% of captures in forest). Phyllostomid community composition was significantly affected by habitat type (restoration vs forest), based on PerMANOVA ($R^2 = 0.14$, $p = .001$; Figure 4A). At the species level, there were two species that showed a significant association with restoration sites, both frugivores: *Uroderma convexum* and *Sturnira parvidens* (Figure 5A). There were three species that showed a significant association with forest sites, also frugivores: *Dermanura watsoni, Carollia sowelli,* and *Artibeus jamaicensis* (Figure 5A).

Acoustic detections were dominated by two species in restoration sites: *Saccopteryx bilineata* representing 39% of all detections and *Molossus* sp with 37%: both were detected at all sites. In forest, *S. bilineata* was the single dominant species representing 56% of all detections and recorded at 11 of the 14 sites. The 11 species classified as forest foragers also occurred in restoration sites (Figure 3C and D). Two of them, *Pteronotus personatus* and *P. gymnonotus* were commonly encountered in restoration sites, but were acoustically undetected in forests. In contrast, of the three species classified as open-space foragers, only *Molossus* sp was detected in forest (10% of detections in that habitat). For the aerial insectivore community composition, the PerMANOVA also

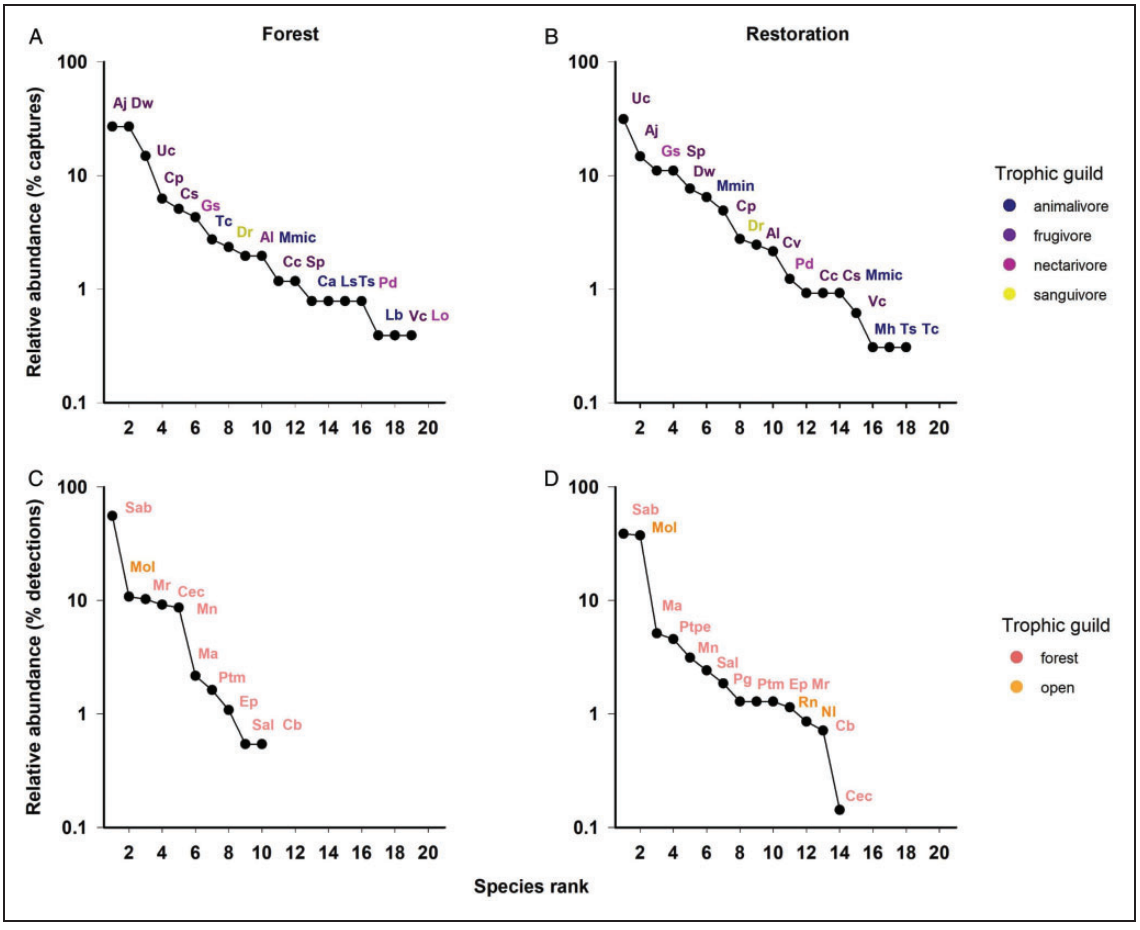


Figure 3. Rank-abundance Curves of Bat Species by Habitat. Phyllostomid species captured in (A) forest and (B) restoration sites and aerial insectivores detected acoustically in (C) forest and (D) restoration. Labels adjacent to data points represent species ID (list of codes can be found in Online Appendix 3).

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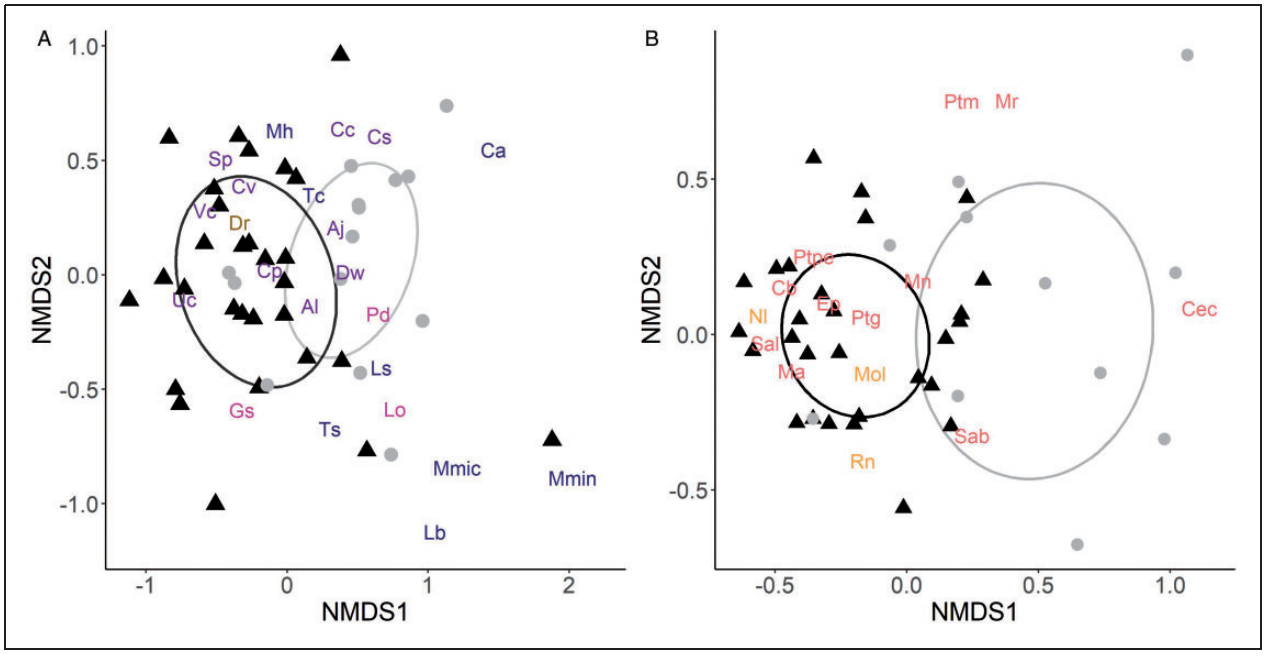


Figure 4. Bat Assemblages Across Restoration (Triangles) and Forest (Circles) Habitats. Ellipses represent the 95% CI of site scores (black = restoration, gray = forest). A: Ordination plot of the phyllostomid assemblage (k = 3, stress= 0.14), with species scores represented by species codes (see Online Appendix 3 for definitions). Species' trophic groups are denoted by colour: Frugivores in purple, nectarivores in magenta, animalivores in blue, and sanguivores in yellow. B: Ordination plots of aerial insectivore assemblages (k = 3, stress= 0.15) with open-space foragers represented in yellow and forest/edge foragers in orange.

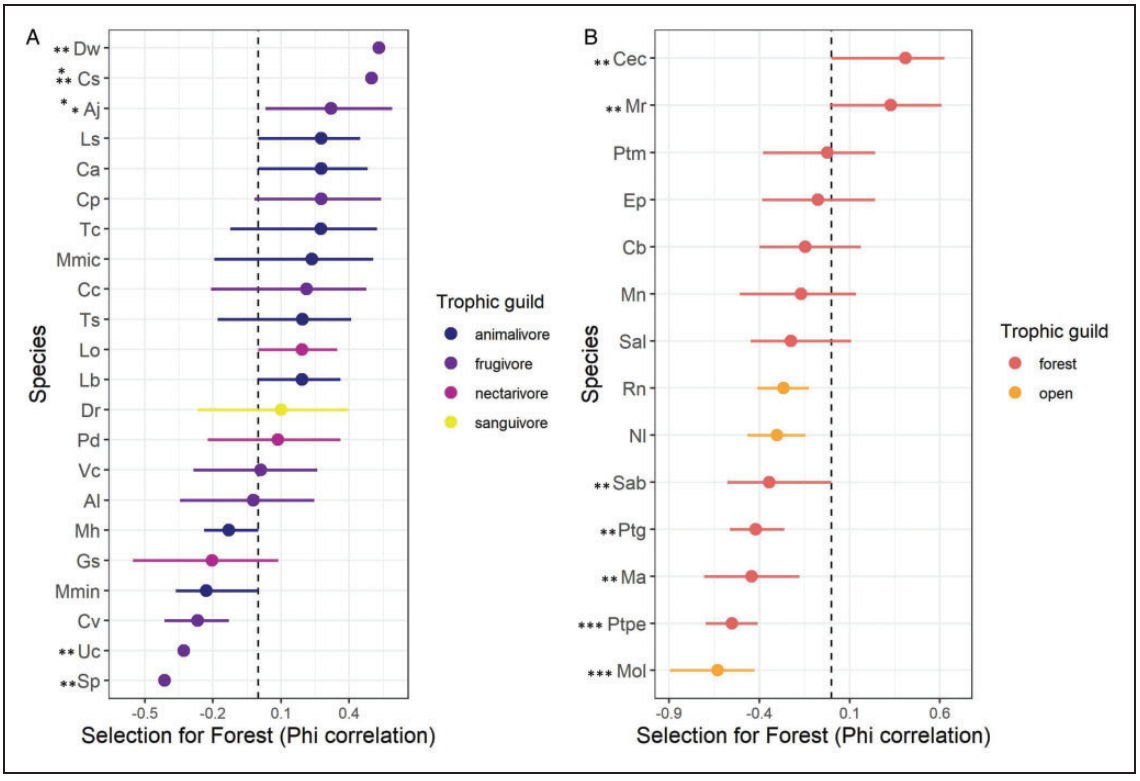


Figure 5. Habitat Associations by Species. Species selection coefficient for forest habitat (with 95% bootstrapped confidence intervals) for (A) phyllostomids and (B) aerial insectivores. The strength of selection was measured using the group-equalized phi correlation coefficient. Positive values indicate an association with forest, and negative values indicate association with restoration habitat. Species codes are defined in Online Appendix 3. Colors depict trophic group. Significance at alpha = 0.1*, alpha = 0.05**, alpha = 0.01*** calculated by permutation tests.

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revealed a significant effect of habitat type ($R^2 = 0.22$, $p = .001$; Figure 4B). At the species level, five species displayed a significant association with restoration sites: only one was an open space forager (*Molossus* sp), and the remaining four were forest species (*Pteronotus personatus, Myotis albescens, P. gymnonotus,* and *Saccopteryx bilineata*; Figure 5B). Two species displayed a significant association with forest sites, both forest foragers (*Centronycteris centralis* and *Myotis riparius*; Figure 5B).

Effect of Landscape Characteristics on Detection Rate in Restoration Habitat. Among the 30 restoration sites, 10 were natural regeneration, 13 had been planted within the last 1.5 years, and 7 had not yet been planted or had been planted no more than four months prior to sampling. Of the 30 sites, only 10 had vegetation islands. The mean distance to the forest edge was 61.38 m (±29.91 m s.d.) and ranged from 22.1 m to 130 m. The mean distance to the nearest stream was 100.24 m (±31.42 m s.d.) and ranged from 49.08 m to 160.38 m. The mean percent forest cover within 200 m of the site was 25% (±21% s.d.), and ranged from 0% to 71%. Phyllostomid capture rate was significantly higher in natural regeneration sites and in sites with at least one vegetation island (Figure 6; Table 2). Frugivore capture rate was also significantly higher in sites with at least one vegetation island, while nectarivore presence was significantly positively affected by percentage of forest coverage (Table 2). The presence of animalivores and sanguivores was not significantly

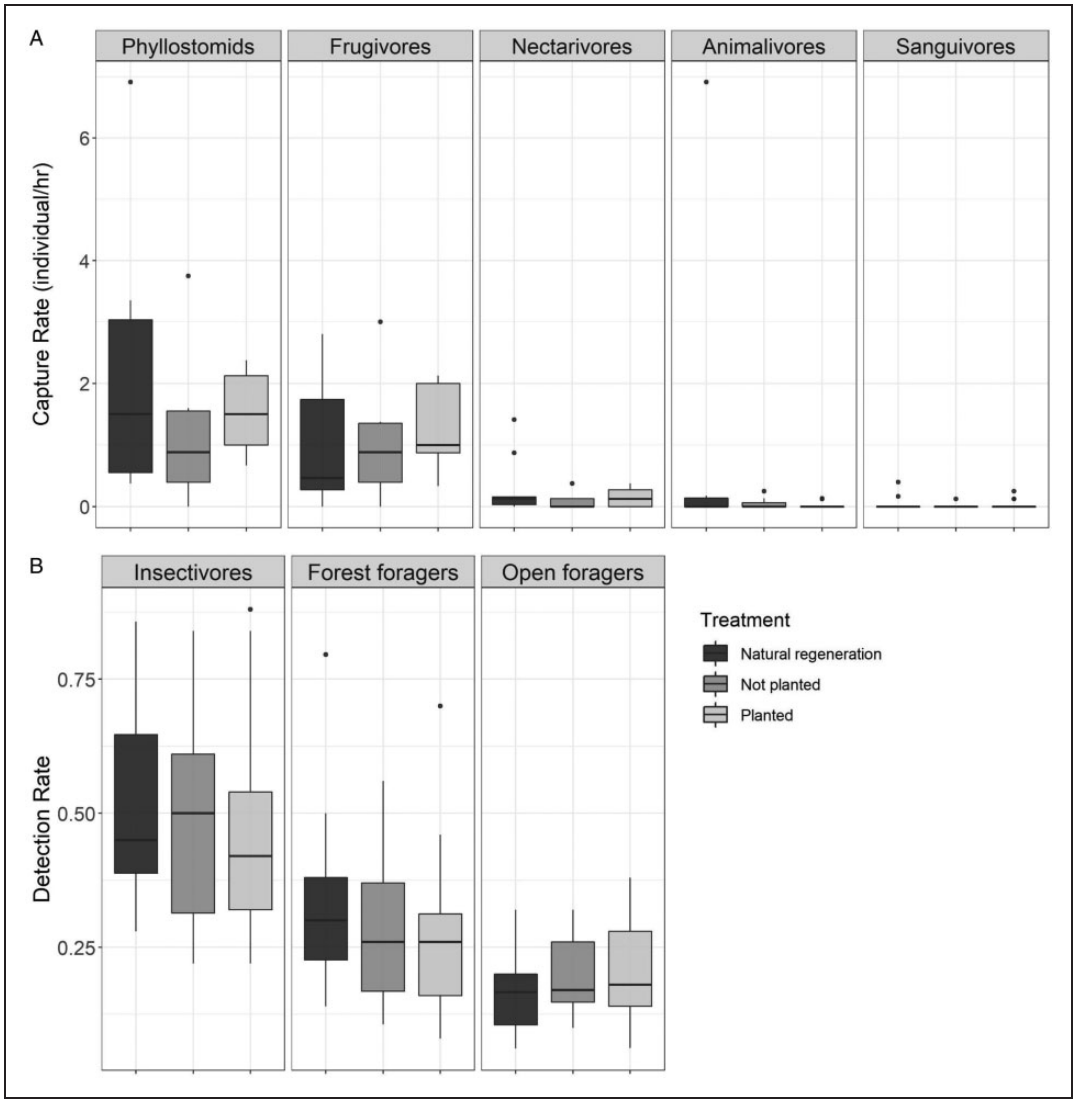


Figure 6. Detection Rates in Restoration Habitat by Treatment Category. (A) Phyllostomid detection rate (individuals/hr) and (B) aerial insectivore detection rate (activity index). The left-most panel depicts detection rate of the entire assemblage, and subsequent panels depict detection by trophic group.

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Table 2. Effect of Landscape Characteristics And Restoration Treatment On Bat Detection Rate Or Presence/Absence In Restoration Habitat.

	Natural regeneration	Not planted	Planted	Distance forest edge	Distance streams	Forest coverage	Islands
[1]**Phyllostomids**	1.71 (0.87 SE)*	ns	ns	ns	ns	ns	1.17 (0.42 SE)**
[1]Frugivores	ns	ns	ns	ns	ns	ns	0.77 (0.37 SE)**
[2]Nectarivores	ns	ns	ns	ns	ns	7.51 (4.253 SE)*	
[2]Sanguivores	ns	ns	ns	ns	ns	ns	ns
[2]Animalivores	ns	ns	ns	ns	ns	ns	ns
[3]**Aerial Insectivores**	ns	ns	ns	ns	ns	ns	ns
[3]Open spp	−1.41 (0.45 SE)**	−1.18 (0.47 SE)*	−1.17 (0.49 SE)*	ns	ns	ns	ns
[1]Forest spp	0.54 (1.45 SE)***	0.49 (0.15 SE)***	0.467 (0.16 SE)***	ns	ns	ns	ns

Effect sizes and standard errors of significant predictors are included. Non-significant predictors are depicted by *ns*. Full model outputs provided in Online Appendix 5. Footnotes indicate type of model. Response variable modelled using [1]linear model, [2]binomial GLM, [3]Gamma glm (log-link).
*$p < .1$. **$p < .05$. ***$p < .01$.

affected by any of the landscape characteristics (Table 2). The combined detection rate of aerial insectivores was also not significantly affected by any landscape characteristics (Figure 6). However, both forest foragers and open space foragers were independently affected by the restoration treatment; detection rate was highest in natural regeneration sites for forest foragers, but was highest in the planted sites for open space foragers (Figure 6; Table 2).

Discussion

Our case study assessing bat biodiversity in areas designated for restoration compared to surrounding intact forest highlights the importance of baseline biodiversity assessments as a tool to monitor restoration efficacy, revealing unexpected patterns of species diversity. Overall, we found that the bat community was different in very early-stage restoration sites compared to surrounding mature forest sites. However, contrary to our predictions, restoration sites were not impoverished subsets of the forest community. Further, the presence of bats from all trophic groups in early stages of restoration demonstrates that bats are potentially important ecological agents of rainforest regeneration at our study site.

Studies of bat communities in and in response to early successional stages are generally lacking (Martínez-Ferreira et al., 2020), and assessing baseline biodiversity of the bat community refuted the assumption that restoration sites are initially species poor prior to the implementation of restoration. Whereas previous studies have found that abandoned pastures and sites in early stages of recovery are characterized by few species with high relative abundance (Avila-Cabadilla et al., 2009; de la Peña-Cuéllar et al., 2015; Medellín et al., 2000), we found that the phyllostomid (leaf-nosed) bat assemblage was not different in terms of species richness, entropy, nor evenness across forest and restoration sites. Although we found that phyllostomid bats were less abundant in restoration sites compared to surrounding intact forest, abundance based on capture rates was likely underestimated in open areas (i.e., in restoration habitat). This is because there is a lower probability that bats will encounter mist nests in open areas compared to forest areas, where bat flyways are restricted by denser vegetation (increasing the probability of capture in forest trails; Palmeirim & Etheridge, 1985). Consistent with our predictions and the findings of Estrada-Villegas et al. (2010), we found that the aerial insectivore community was more diverse and abundant in restoration sites than in forest sites. In forest, the effect of acoustic attenuation (due to vegetation clutter) on the detection of different aerial insectivores may be more pronounced for the forest species, which emit calls of higher frequency and lower intensity than open space foragers (Schnitzler & Kalko, 2001), especially if their movements are constrained by the vegetation (Heer et al., 2015). Furthermore, most forest insectivores tend to be active in the higher forest strata and just above the canopy (Marqués et al., 2016). Together, this could explain the absence of some of the forest insectivores in the forest samples; in future studies, lower detection rates in forest habitat could be resolved by adding recording devices in the canopy. What is noteworthy, however, is the high detection of those forest specialist species in the restoration sites, a phenomenon that has been observed in other open habitats (banana and pineapple plantations; Alpízar et al., 2019). Assessing community composition of the aerial insectivore assemblage demonstrated that more species were associated with restoration habitat than expected, including those species that are forest foragers.

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Although we only detected differences in diversity in the aerial insectivore assemblage, we detected differences in community composition (species' presence and relative abundance) between habitat types in both aerial insectivores and phyllostomids. Contrary to our expectations for phyllostomids, which are generally sensitive to fragmentation (Rocha et al., 2017b), we detected representative species in each trophic group with associations in forest and in restoration habitat. The strong association of *Uroderma convexum* (a canopy frugivore) and *Sturnira parvidens* (understory frugivore, exploiting pioneer plants) with restoration sites is likely explained by the availability of roosting habitat in the surrounding vegetation. Both species readily roost in secondary growth. *U. convexum* construct tents in a wide range of palm and broad-leaved plants (Kunz et al., 1994; Rodríguez-Durán, 2020), which were abundant in forest islands and edges surrounding the restoration habitat, and *S. parvidens* use several roost types, including cavities, vine tangles and foliage (Fenton et al., 2000, 2001; Rodríguez-Durán, 2020). Only two frugivorous species, *Dermanura watsoni* (canopy forager) and *Carollia sowelli* (understory forager) were strongly associated with forest habitat. We expected the gleaning animalivores (phyllostomines) to show the strongest association with forest, or further still, to be completely absent from the restoration sites, since they are the trophic group most affected by habitat disturbance and fragmentation (Farneda et al., 2020), and many of them are old growth specialists (Rocha et al., 2017a). While fewer animalivore species were associated with restoration habitat than forest habitat, we did not expect to observe them with comparable relative abundances across habitats. For the aerial insectivores, our results of habitat association indicated that some forest foraging species (*Centronycteris centralis* and *Myotis riparius*) actively avoided open spaces, even though they are not constrained by manoeuvrability. Among the Emballonuridae (sac-winged bats), *C. centralis*' echolocation calls are the most specialized for detection in confined spaces (Jung et al., 2007), limiting their effectiveness in open spaces due to their short detection range. In the Amazonian rainforest, *M. riparius* also preferentially foraged in the understory, while other aerial insectivores, including other *Myotis* species, were more active in the higher strata and above the canopy (Marqués et al., 2016), suggesting a behavioral specialization for forest foraging. Together, our results on community composition and species habitat association support the idea that the responses of particular species to habitat disturbance is context specific (reviewed in Carballo-Morales et al., 2021; Farneda et al., 2020) and that members of each trophic group can be present at the onset of restoration.

The contributions of bats to recovering ecosystems depend on the functional traits of the species present and on their abundance. Our second objective was to assess the potential landscape drivers of bat abundance for the different foraging groups, including the effect of the different restoration treatments (natural regeneration, planted, not planted) in the early stages of restoration. For the phyllostomid assemblage as a whole, the most important characteristic was the presence of remnant vegetation islands in restoration sites; such islands may be providing bats with nocturnal and diurnal roosting sites (Bernard & Fenton, 2003; Evelyn & Stiles, 2003). Since most frugivores captured in restoration sites were *S. parvidens* and *U. convexum*, these results are consistent with their roosting behaviour. For the nectarivores (*Glossophaga soricina*) specifically, the proportion of forest coverage within 200 m of the sampling site was positively associated with incidence. Because *G. soricina* roost in cavities (Rodríguez-Durán, 2020), it is plausible that these small bats were roosting in larger trees within the forest matrix, taking advantage of cover in their commuting flights, or were commuting through restoration areas to reach foraging areas at the forest edges. Nectarivores have been documented to benefit from edge habitats where their food resources might be abundant (García-Morales et al., 2013; Rocha et al., 2017a). Surprisingly, we did not find the same association for gleaning animalivores, the group most dependent on forest for persistence (Farneda et al., 2020; Voss et al., 2016). However, none of the restoration sites in our study were more than 130 m away from forest edge. Studies on the movements of individual phyllostomines are limited (Bernard & Fenton, 2003; Jones et al., 2017; Vleut et al., 2019), and none have attempted to measure their movement at such a small scale. For the aerial insectivores, the type of restoration treatment significantly affected detection rate. Natural regeneration was associated with higher detection rates of forest species and open space species. Since natural regeneration sites were not maintained by manual cutting at the time of the baseline survey in contrast to planted and not planted sites, these sites were overgrown with tall grasses and shrubs, potentially attracting a high number of insects and other arthropods, which may in turn be attractive to aerial insectivores. However, this does not explain the slight but significantly higher relative abundance of open space foragers in sites that were not planted compared to planted sites, as it is unlikely for structural clutter to have an effect at that stage of forest regeneration.

Because we did not track bat movements across the survey area in our study, there are some limitations to the conclusions we can draw about how bats are using the different habitats. Since we captured bats without marking them or following their movements, beyond

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presence/absence, we cannot tell whether the bats we detected were actively using restoration sites (e.g., for foraging and roosting), or just passing through on their way to a suitable foraging site (Bernard & Fenton, 2003; Ripperger et al., 2015). Nevertheless, it is reasonable to assume that bats at this study site contribute to seed dispersal (Cole et al., 2010; Galindo-Gonzalez et al., 2000), and that bats prey on phytophagous insects, as demonstrated in other localities (M. B. Kalka et al., 2008; M. Kalka & Kalko, 2006; McCracken et al., 2012; Morrison & Lindell, 2012). Another limitation of our study is that we cannot know the effect of seasonality and phenology on community composition because we conducted surveys over seven consecutive months. Changing insect abundances over the course of rainy and dry seasons could affect gleaning animalivore and aerial insectivore communities (Hagen & Sabo, 2012), while forest phenology may drive regional differences in nectivorous and frugivorous bat diversity, as suggested by Ferreira et al. (2017).

Although our baseline assessment of bat communities in restoration sites uncovered surprising diversity, the surrounding forest at our study site is largely intact and contains a significant proportion of old growth forest, making this system a best-case scenario with a healthy source population (Whitworth et al., 2016, 2021). Had our restoration site been in an isolated abandoned pasture, a long distance from any old-growth forest, we might expect to see far more impoverished levels of bat diversity; however, some 85% of secondary forests have been shown to occur within 1 km of old growth forest (Sloan et al., 2016), thus our study location seems typical for where many restoration or regeneration efforts are occurring. In a study with different restoration treatments, such as this one, conducting a baseline assessment at the onset of restoration allows restoration practitioners to control for initial within-treatment differences in diversity (Rocha et al., 2018). As restoration progresses at our study site, we expect to see an increasing effect of restoration treatment on bat communities, as natural regeneration sites and active planting sites begin to structurally diverge; with a baseline of the bat communities, it is now possible to track at what point those differences become important to bat community diversity and composition, which, in turn, will inform future restoration initiatives.

Implications for Conservation

This case study demonstrates the importance of establishing baselines to determine ongoing success of rainforest restoration for biodiversity and ecosystem function recovery. Two commonly used measures of assessing restoration success are to: 1) quantify the time to recovery of a disturbed or degraded area (Rydgren et al., 2020), and 2) assess the connectivity of the restored habitat to surrounding intact sites (Volk et al., 2018). Baseline assessments of wildlife populations are key to best understanding both measures, since baselines provide an explicit initial snapshot of the state of the focal area. Without a temporal baseline in place, assessments must be made between spatially separated study sites where differences can often be harder to disentangle from underlying differences between study locations. Establishing animal biodiversity baselines is relevant to the broader goals of ecological restoration and conservation, since the re-establishment of ecological interactions is critical for rebuilding resilient systems (Block et al., 2001). A comprehensive assessment of key wildlife communities at the onset of restoration can serve to accomplish one of two outcomes: 1) baselines can highlight areas where the source population holds potential for re-establishing ecological interactions in regenerating areas, and 2) baselines can be used to target the recovery of key missing functional groups that could contribute to ongoing rainforest recovery, both of which can strengthen the outcomes of restoration and improve success.

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Author Contributions

E. H. A., D. A., M. M. V., and A. W. conceived the idea. E. H. A. and D. A. conducted fieldwork and analyses. All authors contributed to writing and editing the manuscript.

Declaration of Conflicting Interests

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Supplemental material

Supplemental material for this article is available online.

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