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Bat Species Diversity and Abundance of Trophic Guilds after a Major Hurricane along an Anthropic Disturbance Gradient

Luz María Sil-Berra [1], Cornelio Sánchez-Hernández [2,*], María de Lourdes Romero-Almaraz [3] and Víctor Hugo Reynoso [2]

1 Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México C.P. 04510, Mexico
2 Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México C.P. 04510, Mexico
3 Escuinapa No. 92 bis. Col. Pedregal de Santo Domingo, Ciudad de México C.P. 04369, Mexico
* Correspondence: cornelio@unam.mx

Abstract: The frequency and intensity of hurricanes have increased with climate change, and their effects on most taxa are not known. We analyzed a species diversity of bats in three locations with different regimes of anthropic disturbance. We assessed the effect of the season and post-hurricane time on the abundance of trophic guilds in coastal Jalisco, México, during the two years following Hurricane Patricia (category 4). During a sampling effort of 15,629.76 m^2 of netting, we captured 790 bats of 21 species. The species diversity was higher in the site with the highest proportion of primary tropical deciduous forest and was higher in 2016 than in 2017; the species composition did not differ greatly between the two years. The abundance of bats in various trophic guilds varied relative to the four climatic seasons. The general abundance of bats, frugivores-omnivores, and insectivores showed a significant increasing trend over time after the hurricane, which may indicate a recovery of the ecosystem or an abundance of early-successional fruiting plants. The results also confirm that species diversity recovers faster in a conserved forest. Thus, it is important to conserve natural areas to mitigate the effects of major disturbances.

Keywords: Chiroptera; climate change; disturbances; diversity; trophic guild; tropical deciduous forest

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1. Introduction

Hurricanes are tropical cyclones of great dimensions (300–340 km in diameter and with a 119 km/h minimum velocity) that occur in the North Atlantic Ocean, the Caribbean, and the Northeast Pacific Ocean. They contribute to the transport of the warm air mass of the tropics from low to high latitudes and change the "nutrients transport" [1]. Based on their intensity, hurricanes can influence in diverse ways the biodiversity and functioning of ecosystems [2–4]. In addition, the frequency and intensity of major hurricanes has increased in the last decades due to global climate change [5–7].

Several studies have focused on evaluating the direct and indirect effects of hurricanes on ecological and biological traits [8]. The direct effects are mostly due to the direct exposure to winds and rain, and can result in mortality or displacement of individuals and propagules [1]. The indirect effects are induced by changes in the physical environment, ecosystem productivity, and availability of resources, which can result in effects such as increased vulnerability due to the scarcity of resources or a high predation risk. These effects can occur during or immediately after the hurricane; for example, the change in the availability of resources can force changes in the diet, foraging, day-roosting habitat, or reproductive patterns. Meanwhile, the long-term effects can last from few years to centuries [8,9] and influence the recovery and ecological succession of ecosystems which include changes in the species composition, species diversity, and population sizes [10]. The level of the effect and recovery time vary in accordance with intensity, dimension, and time when hurricanes occur; the traits of the landscape; the structure of vegetation; topography; land use and management; and the natural susceptibility of species of plants and animals present to these events [4,9,11].

For terrestrial mammals, the exposure to extreme climate events, such as hurricanes and fires, has received some attention [12], as has their susceptibility as a result of their sensibility (vagility and territoriality) and their adaptive capacity (diet and habitat specialization) [13]. Previous studies indicate that Primates, Rodentia, and Chiroptera have the highest proportion of species affected by cyclones and fires worldwide [12].

Bats are an important group in ecosystems due to their wide ecological diversity and ecosystem services [14,15]. Their dispersion capacity provides a degree of resistance and resilience to disturbances in comparison with other terrestrial mammals [16,17]; however, some bat species have life-history traits or behaviors that make them vulnerable [18,19]. The effects of hurricanes on bats are multi-faceted and depend on habitat traits and their foraging, feeding, and roosting habits [20].

In October 2015, Hurricane Patricia (category 4, Saffir–Simpson scale) made landfall on the coast of Jalisco, Mexico, and affected the structure and phenology of vegetation [21–24], as well as the local distribution patterns, species diversity, and richness of various taxa (e.g., rodents and birds) [25,26]. In bats, an immediate effect was the decrease in the diversity of species and abundance of some functional groups, such as nectar-feeding bats. The effects were different among locations with distinct anthropogenic disturbance and hurricane impact regimes [20]. Understanding these assemblages is necessary to estimate the consequences of major natural events on the biodiversity and their interaction with anthropogenic disturbance in the longer term.

Land use can influence the effects, responses, and rate of recovery of ecosystems after hurricanes [8]. We evaluated the hurricane effects on bat assemblages in three locations with distinct vegetation traits, anthropogenic disturbance, and land use. Our purposes were: (1) to evaluate species diversity among locations and between two post-hurricane years; (2) to identify differences in seasonal abundance patterns among trophic guilds; and (3) to evaluate trends in abundance of each trophic guild during two years after Hurricane Patricia.

We expected to find a higher diversity in the second year after the hurricane in the most conserved areas and in locations less impacted by the hurricane. We also expected variation in bat abundance across seasons and an increasing trend of abundance of bats in general and in each trophic guild during the period after the hurricane. These changes would reflect the recovery in flowering and fructification phenology and in ecosystem functioning in general.

2. Materials and Methods

2.1. Study Sites

Our study was conducted in three locations in the coast of Jalisco, Mexico, in a heterogenous landscape conformed mainly by primary and secondary tropical deciduous forest, primary sub-deciduous forest, farming and grazing areas, and underdeveloped human settlements [27]. The region includes a Natural Protected Area, the Chamela-Cuixmala Biosphere Reserve, that subsumes 131,142 ha, mainly of tropical deciduous forest [28]. A pristine study location (Chamela) was found within this area. A moderately disturbed location (La Fortuna), 15 km N of Chamela, contained primary and secondary tropical deciduous forest in addition to farming and grazing areas. The most anthropically disturbed location (Zapata) is 15 km S of Chamela and included secondary tropical deciduous forest along with farming and grazing areas. More information about the study areas can be found in Bullock [20]. The eye of Hurricane Patricia passed through Chamela and Zapata, but not through La Fortuna.

Traditionally, two climatic seasons are considered for this region: a rainy (July–October) and a dry season (November–June) [29]. However, based on the availability of bat resources and precipitation level, Stoner [30] proposed four climate seasons: (1) an early dry season from January to March, with some precipitation events [31] and when chiropterophilic flowering and canopy fruiting season is at their peak; (2) a late dry season from April to June, with few chiropterophilic flowering and fruits, but by the end of this season the first rains of the year start; (3) an early rainy season from July to September, when the peak of rainfall and chiropterophilic flowering occurs, but during which in general there are few fruits; (4) a late rainy season from October to December, with the last rains of the year, with some chiropterophilic flowering, and with a greater number of trees having fruits.

2.2. Bat Sampling

We sampled bats with mist-nets (Avinet, Inc., Portland, ME, USA; 75 denier, 2 ply, 38-mm mesh) set in three sampling stations in each location. Sampling occurred every three months during 2016 and 2017, covering the four seasons of the Chamela region [30]. In each sampling period, we placed eight mist-nets, five at ground level (three of 9 [height] $\times$ 2.68 m [length] and two of 12 $\times$ 2.68 m) and three at 3.0–5.68 m height (two of 9 $\times$ 2.68 m and one of 12 $\times$ 2.68 m). The distance between the adjacent nets varied from 20 to 50 m, and the nets remained open during five hours after sunset. The sampling effort of each sampling period was 217.08 m^2 net-nights (i.e., number of square meters of net set on a given night) with a total of 15,629.76 m^2 for the study.

We determined the identity of the bats using identification keys [32,33], following the classification proposed by Pavan and Marroig [34,35] for *Pteronotus*, by Baird et al. [36] for Lasiurini, and by Calahorra-Oliart et al. [37] for *Glossophaga*. We recorded biological and reproductive data, including forearm length (Truper® $\pm$ 0.05 mm) and mass (Pesola® $\pm$ 0.05 g). To avoid measuring the same individual twice and in case we had across-year recaptures, we marked small bats with numbered metal rings (Alloy Split Rings 2.9 mm, Porzana Ltd., East Sussex, UK) and the largest ones with plastic collars with colored beads. The bats were released at their capture sites.

2.3. Data Analysis

To compare the species diversity between years and locations, we built individual-based and sampled-coverage rarefaction curves in iNext [38]. The species diversity (order q = 0, 1, and 2) among locations was compared with the same number of individuals (n = 182) and the same coverage (0.98) throughout 1000 Bootstrap iterations and 95% CI.

To compare species composition between years and locations, we calculated similarity indices in SpadeR [39] with 1000 iterations in all cases. For comparison among locations in two years, we computed Bray–Curtis indices. This index is reliable when absolute abundances are compared under standardized sampling efforts across all of the communities. Additionally, we performed a paired comparison with Sørensen and Jaccard indices. For the comparison between years by location, we used the Chao–Jaccard and Chao–Sørensen indices. These indices consider the relative abundance of the species and are recommended when under-sampling is suspected and when it is likely that samples have many rare species [40], as occurs with bat assemblages.

To identify the drivers of differences in species diversity, we built rank-abundance curves for each location. We performed a Wilcoxon matched-pairs signed rank test on the number of individuals captured by species and by location, to identify the species with more changes in their abundance between years.

Bat species were classified into five trophic guilds: frugivore-omnivore, frugivore, nectarivore, insectivore, and hematophagous, according to relevant literature [33]. To evaluate the effect of the season and post-hurricane time on the abundance of bats by trophic guild, we used generalized linear models (GLM) with Poisson distribution. We performed two tests in each case: one with two classical seasons, dry and rainy (season1), and the other with the four seasons as described by Stoner [30] (season2). We evaluated four models that were compared with a null model with the anova function in R [41]:

Model 1: captures~season1 + post-hurricane time

Model 2: captures~season1

Model 3: captures~season2 + post-hurricane time
Model 4: captures~season2
Null model: captures~1

We selected the model with the lowest Akaike Information Criterion (AIC) and highest explained deviance that was significantly distinct from the null model.

Finally, to identify the trend direction in the abundance of bats, we transformed the data with $\sqrt{(x + 1)}$ to diminish the influence of extreme data due to seasonality. With these data, we performed Mann–Kendall trend tests [42–44] with all the data and by trophic guild in XLSTAT [45], and with the temporal series softened with the moving average model. The Mann–Kendall trend test or Kendall's τ (tau) is a non-parametric test that has been used to identify trends considering randomness and seasonality, mainly in climatological and hydrological analyzes (e.g., [46]).

3. Results

3.1. Species Diversity and Composition

We captured 790 bats from 21 species, 15 genera, and 6 families. The most frequently encountered species were the Jamaican fruit-eating bat, *Artibeus jamaicensis* (n = 190), common vampire bat, *Desmodus rotundus* (n = 167), Mexican mustached bat, *Pteronotus mexicanus* (n = 131), and great fruit-eating bat, *A. lituratus* (n = 122). The location with the most captures and the greatest number of species was Chamela (n = 316, 18 species), followed by La Fortuna (n = 292, 15 species) and finally Zapata (n = 182, 12 species; Table 1).

Table 1. Number of individuals captured at each study location.

Family/Species	Trophic Guild [a]	Chamela	La Fortuna	Zapata	Total
Mormoopidae					
Pteronotus mexicanus	IN	40	76	15	131
Pteronotus psilotis	IN	1	3		4
Mormoops megalophylla	IN	1			1
Pteronotus davyi	IN	1			1
Natalidae					
Natalus mexicanus	IN	1			1
Noctilionidae					
Noctilio leporinus	PI		1		1
Phyllostomidae					
Artibeus jamaicensis	FO	111	52	27	190
Desmodus rotundus	HE	89	50	28	167
Artibeus lituratus	FO	25	52	45	122
Sturnira parvidens	FO	1	10	41	52
Glossophaga soricina	NE	14	10	15	39
Dermanura phaeotis	FO	19	8	1	28
Dermanura tolteca	FR	2	13	4	19
Leptoncteris yerbabuenae	NE	4	12		16
Centurio senex	FR	1	2	3	6
Glossophaga commissarisi	NE	2	1		3
Glossophaga morenoi	NE	1	1	1	3
Vespertilionidae					
Rhogeessa parvula	IN	2		1	3
Lasiurus frantzii	IN	1			1
Dasypterus intermedius	IN		1		1
Molossidae					
Nyctinomops aurispinosus	IN			1	1
Total species		18	15	12	21
Total individuals		316	292	182	790

[a] FO, frugivore-omnivore; FR, frugivore; NE, nectarivore; IN, insectivore; HE, hematophage; PI, piscivore.

Individual-based rarefaction analyses did not show significant differences in species richness (q = 0) among locations (Figure 1a). However, coverage-based rarefaction (Figure 1d) indicated a higher richness in Chamela than in other locations. In contrast, order 2 diversity showed that the number of effective species was lower in Chamela (Figure 1c,f); the abundance among the most frequently encountered species was more uneven in Chamela. In the comparison between years, no significant difference was demonstrated in overall species diversity. By location, diversity was higher in 2016 than 2017 only in Chamela for order 0 and 1 species diversity (Figure 2).

The similarity of species composition among locations varied from 0.60 to 0.68 (Bray–Curtis index). In paired comparisons, the similarity was highest between Chamela and Zapata and lowest between La Fortuna and Zapata. However, the differences were not significant (95% CI; Table 2), and high values in the indices reflect the few changes in species compositions between years for the three locations (Table 3).

The rank–abundance curve for Chamela showed a higher richness in 2016 than 2017, with the abundance distribution for 2016 being more homogeneous among species and there being a greater number of rare species. The most frequently netted species in 2016 were *A. jamaicensis*, *D. rotundus*, and *A. lituratus*, while in 2017 they were *A. jamaicensis*, *D. rotundus*, and *P. mexicanus* (Figure 3). The Wilcoxon pair tests were not significant when considering the number of individuals (p = 0.88) or relative abundance (p = 0.14), which indicated that there were differences between the two years in the abundance rank of the species, showing an increase in 2017 of *D. rotundus* and *P. mexicanus*, and a decrease of *A. lituratus* (Figure 4).

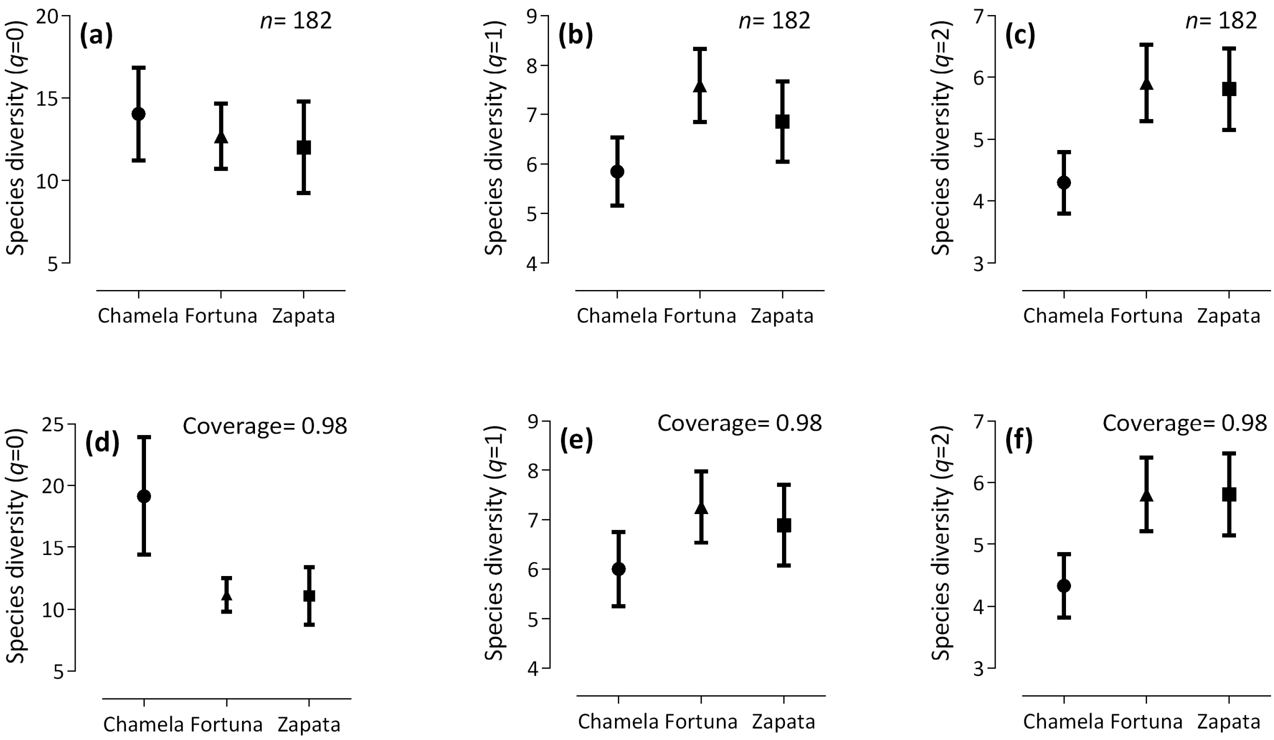

Figure 1. Diversity orders q = 0, 1, and 2 based in number of individuals (**a**–**c**) and sampling coverage (**d**–**f**) for three locations during two years of fieldwork.

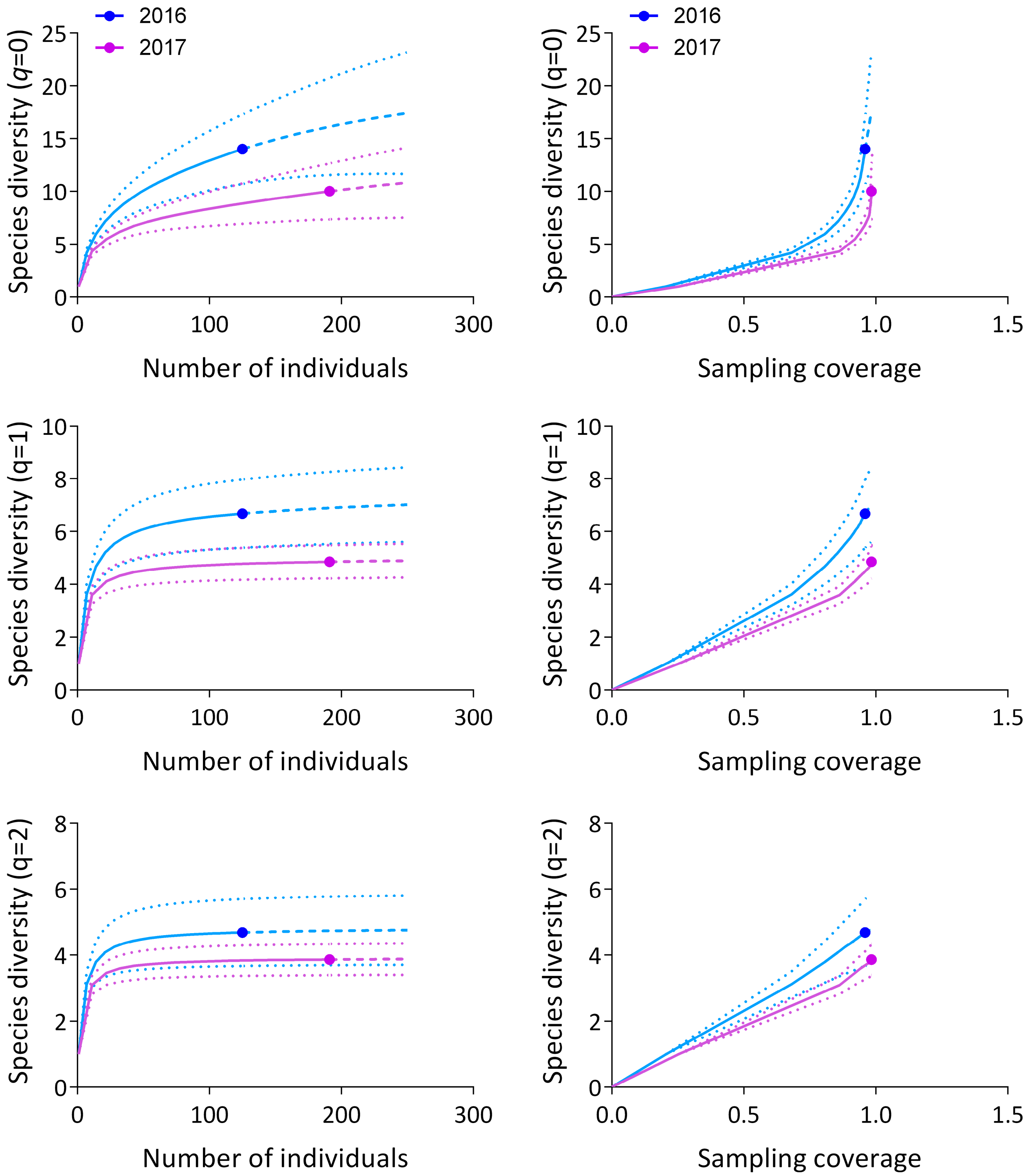

Figure 2. Interpolation (continuous lines) and extrapolation curves (discontinuous lines) of species diversity orders q = 0, 1 and 2, based in number of individuals (**left panel**) and sampling coverage (**right panel**) for Chamela in 2016 (blue line) and 2017 (purple line).

Table 2. Bat species composition similarity among locations after two years of Hurricane Patricia and CI (95%).

Locations	Jaccard's Index	Sørensen's Index
Fortuna-Chamela	0.429 (0.214–0.644)	0.600 (0.361–0.840)
Fortuna-Zapata	0.367 (0.171–0.564)	0.537 (0.323–0.751)
Chamela-Zapata	0.474 (0.222–0.725)	0.643 (0.376–0.910)

Table 3. Bat species composition similarity by location between two post-hurricane years (2016 vs. 2017) and CI (95%).

Location	Chao-Jaccard's Index	Chao-Sørensen's Index
Fortuna	0.968 (0.899–1.040)	0.983 (0.957–1.010)
Chamela	0.875 (0.869–0.881)	0.933 (0.930–0.936)
Zapata	0.957 (0.765–1.150)	0.978 (0.847–1.110)

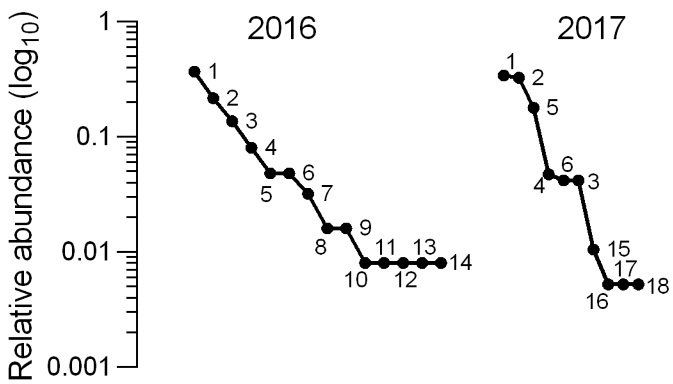

Figure 3. Rank-abundance curves of bat species captured in 2016 and 2017 in Chamela, Jalisco. 1: *Artibeus jamaicensis*, 2: *Desmodus rotundus*, 3: *A. lituratus*, 4: *Dermanura phaeotis*, 5: *Pteronotus mexicanus*, 6: *Glossophaga mutica*, 7: *Leptonycteris yerbabuenae*, 8: *G. commissarisi*, 9: D. *tolteca*, 10: *Mormoops megalophylla*, 11: *P. psilotis*, 12: *P. fulvus*, 13: *G. morenoi*, 14: *Sturnira parvidens*, 15: *Rhogeessa parvula*, 16: *Natalus mexicanus*, 17: *Centurio senex*, 18: *Lasiurus frantzii*.

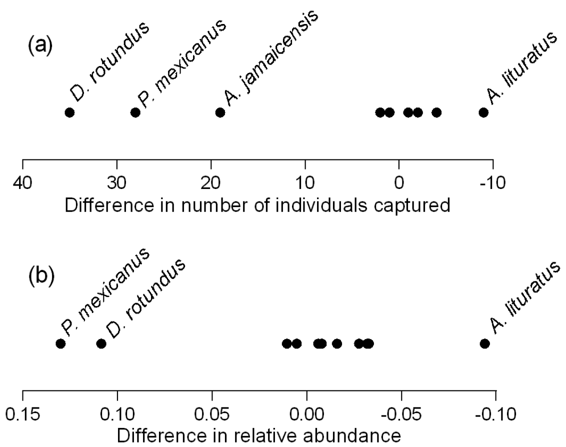

Figure 4. Differences in number of captures and relative abundance between 2016 and 2017 of captured species in Chamela. Only names of species with the greatest changes are included. Some of the dots in the cluster of points around zero represent multiple species.

3.2. Seasonal and Post-Hurricane Abundance Trends

GLM analyses considering the three locations showed that the number of bats captured was influenced by the season and the post-hurricane time. All evaluated models showed significant differences among the seasons. The best model was model 3, which included the four seasons and the post-hurricane time. This indicated that in the early rainy season more bats were captured, and in the early dry and late rainy seasons fewer bats were caught (Figure 5a).

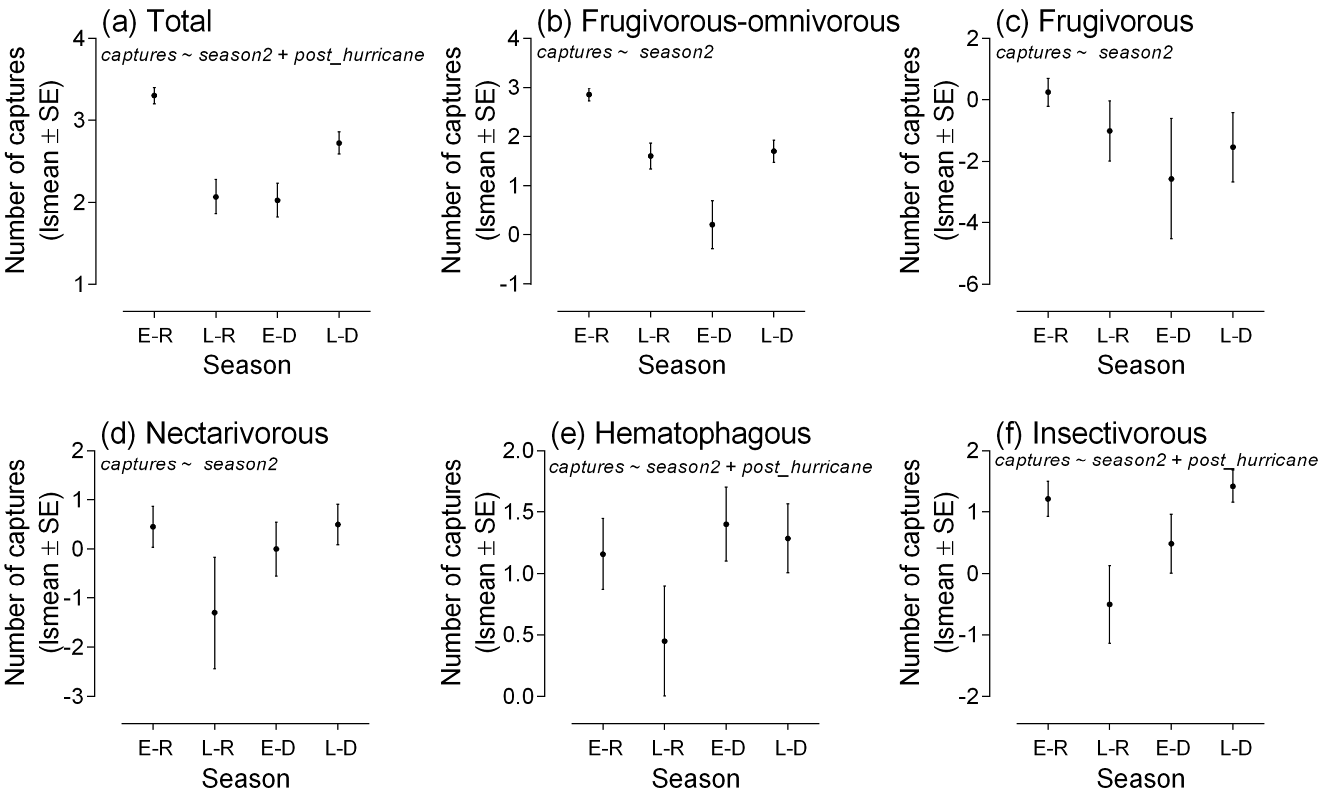

Figure 5. Seasonal variation in abundance of bats (number of captures), total (**a**) and by trophic guilds (**b**–**f**), in accordance with selected models throughout GLMs. E-R: Early rainy, L-R: Late rainy, E-D: Early dry, L-D: Late dry. Details are shown in Table S1 of Supplementary Materials.

For the frugivore-omnivore and frugivore bats, models 3 and 4 were the best. According to these models, more frugivore-omnivore and frugivore bats were captured in the early rainy season, fewer frugivore-omnivore bats in the late rainy and late dry seasons, and fewer frugivore bats in the early and late dry seasons (Figure 5b,c).

For the nectarivore guild, the differences among models were minimal and there was no post-hurricane effect. According to model 4, which is the simplest with a higher explained deviance and a lower AIC, more nectivore bats were captured in the early rainy and late dry seasons and fewer in the late rainy season (Figure 5d). For hematophage bats, the explained deviance in all models was low. Model 3 showed an effect of the season, with fewer captures in the late rainy season and the post-hurricane time (Figure 5e).

For the insectivore guild, the explained deviance did not exceed 31% in all the models. Model 3 showed the highest deviance (31%) and the lowest AIC (274.2). This model showed that more insectivore bats were captured in the late dry and early rainy seasons ($p = 0.71$), and there was a post-hurricane effect (Figure 5f).

The Mann–Kendall trend test showed that the number of captures of all bats increased after the hurricane (Figure 6). By guilds, the abundance of frugivore-omnivore and insectivore guilds increased ($p < 0.01$). Nectivore bats showed a decrease, but it was not significant ($p = 0.07$). Frugivore and hematophage bats did not show any trend (Figure 6).

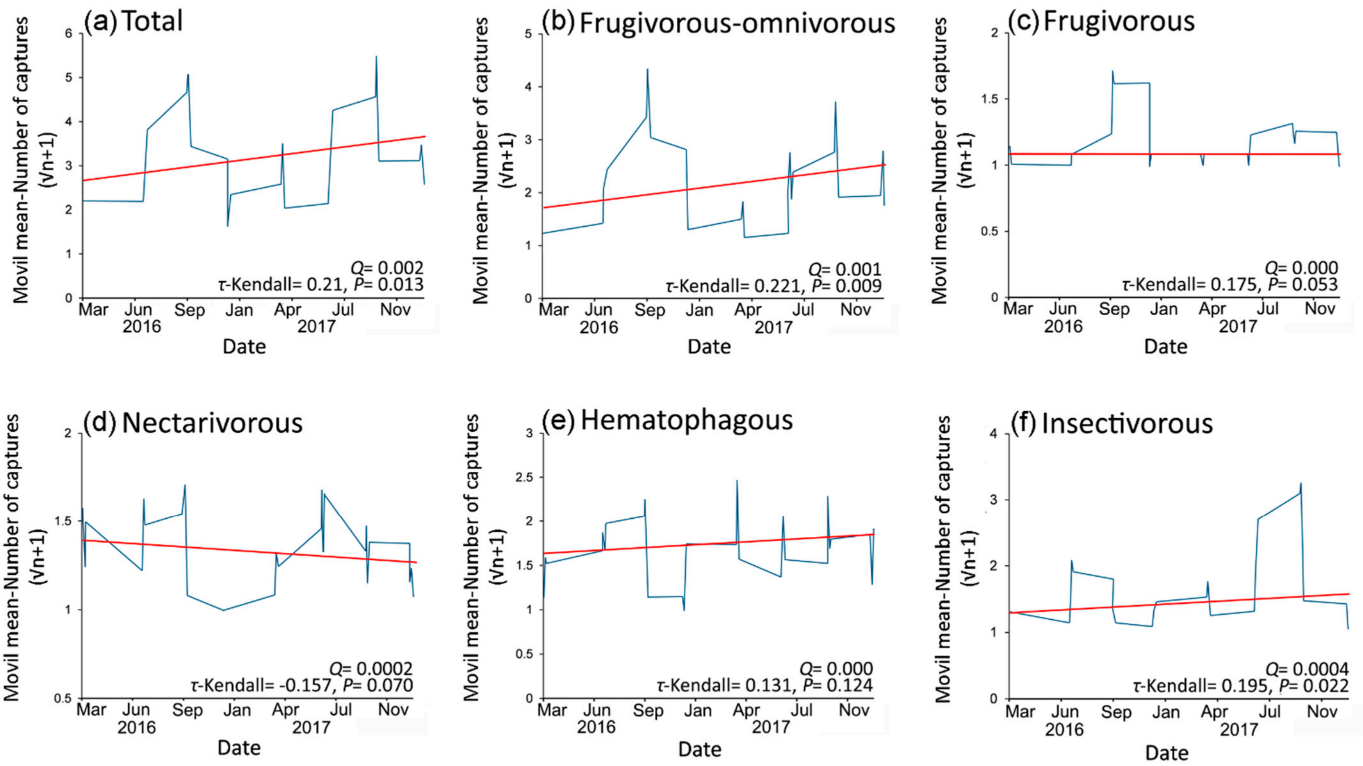

Figure 6. Post-hurricane trends in the abundance of bats, total (**a**) and by trophic guilds (**b**–**f**), from March 2016 to December 2017. Sen's slope (red line) adjusted to smoothed curve (blue line).

4. Discussion

As expected, two years after Hurricane Patricia, bat species richness was higher in Chamela than in the other locations, but it had a lower evenness among the most common species (lower diversity order 2). Previous reports indicated that eight months after Hurricane Patricia, the dominance and evenness were lower in Chamela and Zapata compared with pre-hurricane samplings, and the species richness was not different among locations [20]. These results suggest that areas with a high quantity and diversity of native vegetation such as Chamela, which contains primary deciduous and semideciduous forest, are more resilient when facing natural disturbances. This may indicate that there was a greater availability of resources, despite the disturbance, in a shorter amount of time with the end result being a higher bat species richness.

Previous research has indicated that the dry forest in Chamela has low resistance to hurricanes, but is highly resilient due to the quantity of moisture left. The recovery rate depends on wind magnitude, post-disturbance climate variations, and vegetation traits [22,47]. These factors, in addition to landscape traits and anthropic degradation regimen, may influence the recovery of populations and bat assemblages after hurricanes [48]. Hurricane Patricia caused more damage to tree structure in primary vegetation than in secondary vegetation, but primary vegetation was more resilient in terms of lower mortality and higher density of leaf outbreaks [22]. This may have been the result because primary vegetation has a greater height, diameter, and age [22], which in turn provide a greater ability for vegetation to obtain resources, and leads to a faster recovery of the bat assemblages in the most conserved locations such as Chamela. Previous reports have documented changes in the roosting habits after hurricanes, such as there being more roosts inside reserves than outside, and displacement to more permanent roosts such as caves [48]. Though tree damage can create new roosts in broken tops and cavities, usually bats are more often found in older trees where they find an optimal microclimate [49]. Also, changes in the diet of frugivorous species occurred in that they consumed more leaves than fruits after hurricanes [48]. Leaf outbreaks and roosts in primary vegetation after the hurricane could have provided resources exploited by frugivorous bats in Chamela.

Lower order-2 diversity in Chamela suggests a low evenness in the abundance of the most frequently encountered species, *Artibeus jamaicensis* and *D. rotundus*. The recovery of resources may have been exploited mainly by frugivorous-omnivorous species, or by those that do not rely heavily on vegetation. Similarly, in avian assemblages, an increase in the capture rates of omnivores and open-area foragers has been documented after hurricanes [50].

Chamela also had the greatest differences in diversity and species composition between years. Contrary to expectation, diversity was higher in 2016 than in 2017 (n = 14 vs. 10 in species richness and n = 5 vs. 3 in rare species) in Chamela. Additionally, there was a greater evenness in the abundance among species in 2016, and the species-composition similarity decreased to a greater extent between years in comparison with the other locations. These changes could have been the result of several factors. First, the higher vegetation cover in Chamela compared with other locations may have functioned as a shelter area for generalists (e.g., *A. lituratus* and the pygmy fruit-eating bat, *Dermanura phaeotis*), specialists (e.g., the Commissaris's long-tongued bat, *Glossophaga commissarisi*, and the Toltec fruit-eating bat, *Dermanura tolteca*), common species (e.g., *A. jamaicensis* and *D. rotundus*), and rare species (e.g., the Thomas's naked-backed bat, *Peronotus fulvus*, and the western long-tongued bat, *Glossophaga morenoi*) in 2016 immediately after the hurricane. According to the intermediate-disturbance hypothesis and the recovery process, the most resistant species and those not so resistant that colonize new niches after disturbances were able to share the same area, thus increasing diversity.

Second, climate variation between years can influence diversity. The Chamela Weather Station, UNAM, indicated that 2016 was drier than 2017, which would possibly result in lower diversity in 2016. However, humidity favors the vegetation of the entire region and due to a more humid condition in 2017, some species of bats may have dispersed to other areas searching for food or habitat (e.g., *A. lituratus*), thus reducing the local diversity in this year. The greater difference in species composition between years was the result of an increase in 2017 in the abundance of *A. jamaicensis* and *D. rotundus*, and a decrease of *A. lituratus*; the number of the rare species also was lower in 2017. Although *A. jamaicensis* and *A. lituratus* are related species and have similar diets [51], *A. lituratus* feeds on a higher quantity of pioneer plants [52,53] (which should be more abundant after a storm), it has a larger body size and a larger home range, and forages in canopy and understory, as well as different successional stages [54]. Consequently, in 2017, *A. lituratus* could have extended its home range or moved to other locations with earlier successional stages.

The fact that the species composition between La Fortuna and Zapata was less similar than between Chamela and Zapata may be an effect of the decline in similarity by distance [55]. La Fortuna and Zapata are the furthest apart, and greater differences in composition could be expected with respect to the impact of Hurricane Patricia.

Despite the negative effects of the hurricane on the abundance of some bat functional groups [20], there was a seasonal variation in the abundance of trophic guilds, as suggested by Stoner [30]. This abundance was higher during the early rainy season (July to September) and lower in the late rainy season (October to December) and early dry season (January to March). During the early rainy season, there is a higher precipitation, greater abundance of chiropterophilic flowers (e.g., the orange flame vine, *Combretum fruticosum*, the morrito, *Crescentia alata*, the pochote, *Ceiba aesculifolia*, columnar cactus, *Stenocereus chrysocarpus*), and some fruits are more readily available, which benefits all trophic guilds. The decrease in abundance of bats in the late rainy season may result from a decrease in the rains and in chiropterophilic flowering (although many trees would still have fruits), which would explain the smaller decrease in the abundance of frugivore guilds. In the early dry season, the second peak of chiropterophilic flowering (e.g., *C. fruticosum*, *Ceiba aesculifolia*, the morning glories, *Ipomoea ampullacea*, the orchidtree, *Bauhinia ungulata*, the agave, *Agave ortgiesiana*) and canopy fruiting occur [30,56]. The increase in the abundance of members of the nectarivore guild coincides with that, but not with the decrease in the abundance of species in the frugivore-omnivore guild. This could be the result of the impact of Hurricane Patricia on the phenology of plants [57], but more information is needed.

The representative species of the frugivore-omnivore guild were *A. jamaicensis*, *A. lituratus*, and *D. phaeotis*, so it would be important to research the response to disturbances of some plants that are an important part of their diet, such as figs (*Ficus* ssp.), mombins (*Spondias* ssp.), columnar cactus (*Stenocereus* ssp.), guava (*Psidium* ssp.), cecropias (*Cecropia* ssp.), and nightshade (*Solanum* ssp.) [33,51,58–61]. For example, it has been reported that some *Ficus* species are medium-low resistant to winds by hurricanes [62] which in Chamela is one of the genus with more resprouting capacity [22]; in contrast, columnar cactus are more vulnerable to these winds for their trunk shape and structure [63].

Another factor influencing variation in abundance of bats is reproduction patterns. The greater abundance of frugivore bats in the early wet season may be associated with our high capture rates of juvenile individuals ($n = 67$ for *A. jamaicensis* and $n = 26$ for *A. lituratus*) compared to other seasons all together ($n = 5$ for *A. jamaicensis* and $n = 0$ for *A. lituratus*). This may indicate that, although these bats have a continuous polyestrous reproductive pattern, they have a birth peak that coincides with the beginning of the fruiting peak. This may reflect a strategy to ensure the survival success of future adults, in which the fruiting peak (October to December) concurs with the time when the young reach postnatal development. Additionally, foraging time or distance also may change in accordance with the availability of resources or reproduction conditions [64–66], modifying the capture rate in mist-nets.

Nectarivorous and insectivorous bats have two peaks of abundance during the early rainy and late dry seasons. In contrast, Stoner [30] reported a higher abundance of nectarivorous bats in the early rainy and early dry seasons at Chamela. It could be that the peak abundance of chiropterophilic flowers during the early dry season (January to March) in 2016 was affected by Hurricane Patricia, which would have resulted in a delay in the peak abundance of nectarivorous bats. Other probable causes may be related with interannual climatic variation, for example winter rains influenced by El Niño Southern Oscillation (ENSO) [67], that could promote changes in the abundance pattern of bats.

The beginning of chiropterophilic flowering can occur during the late dry season, continuing until the early rainy season [30]. Important plants for the most frequently encountered nectarivore species (Merriam's long-tongued bat, *Glossophaga mutica,* and lesser long-nosed bat, *Leptonycteris yerbabuenae*) are manjack (*Cordia alliodora*), white silk-cotton tree (*Ceiba pentandra*), *C. alata*, shavingbrush tree (*Pseudobombax ellipticum*), morning glory (*Ipomoea* sp.), and columnar cactus (*Stenocereus* sp.) [33,56,68]. For the genus *Cordia*, the main damages resulting from Hurricane Patricia were broken and inclined trunks. For *Crescentia*, it was secondary broken branches. Damages for *Ipomoea wolcottiana* were the most severe, with uprooted trees [22]. As mentioned earlier, columnar cacti were severely damaged [63].

The greater abundance of insectivorous bats during the late dry and early rainy seasons can be explained by the timing of the first rains, which increases the abundance and diversity of insects. The most abundant insectivore was *P. mexicanus*, a generalist species in terms of diet and habitat. The variation in its abundance paralleled insect availability [69,70]. In Chamela, *P. mexicanus* feeds mainly on Lepidoptera and Diptera. It does not show changes in dietary breadth with the season, and their diet overlaps with that of Dobson's lesser mustached bat, *P. psilotis* [71], although this latter species is scarce in the region.

Vampire bats were less abundant in the late rainy season. Temporal variations in *Desmodus rotundus* are mainly related to livestock management practices [72] and, to a lesser extent, to variation in the abundance of other prey [73] and to temperature variation due to seasonality [74,75]. The management of cattle by villagers varied seasonally and with respect to the availability of resources. When resources are limited, villagers confine cattle or let them graze in smaller areas, which can influence the capture rate of hematophagous bats. In Chamela, the nights are colder from December to February than during the rest of the year [76], which may influence the activity of vampire bats. Variation in abundance of vampire bats is also related to reproduction. Although they exhibit a continuous asynchronous polyestrous reproduction pattern, births have been reported to peak in the rainy season [77–79]. More detailed studies could provide additional information on local variation in activity, local movements, foraging patterns, and population dynamics, as well as the association of these with climatic seasonality.

The increasing trend in abundance of bats may indicate recovery of the forest and ecosystem in general two years after the hurricane. However, by trophic guilds, this trend was found only in the frugivore-omnivore and insectivore bats. In addition, an analysis of both before and after the hurricane indicated that the abundance of nectarivore bats decreased after this event [20]. Altogether, results may indicate that this guild had not recovered by the end of our sampling in December 2017. This agrees with findings by Renton et al. [57], who reported that phenological patterns of flowering and fructification in general had not recovered from the impact of Hurricane Patricia a year later, but specific studies on chiropterofilic plants are needed. Similarly, in avian assemblages, frugivore and nectarivore guilds were the most affected two years after Hurricane Iris (category 4) in Belize [50]. *Glossophaga mutica* appears to be one of the most affected bats in that region. This bat was consistently the most frequently captured species in samplings prior to Hurricanes Jova (category 2; October 2011) and Patricia [30,61,80–82]. However, it was not in the most recent studies [26] and not even in our study, in which it represented only 6% of the abundance of all phyllostomid bats.

Among the recommendations for future studies, we urge that long-term data be gathered so that it would be possible to analyze the relationship among interannual climate variations and the effects of hurricanes and bat diversity. This would also allow analysis of long-term data to predict population-size changes and to distinguish variation in populations, due to the effects of hurricanes from natural patterns as a result of to stochastic events or natural population dynamics. These studies are particularly needed for vulnerable species such as nectarivores, in order to decipher their ecological interactions and discover what factors are affecting the populations of these species.

5. Conclusions

Based on our findings, we conclude that: (1) the species diversity of bats recovered faster in areas with more primary forest; (2) despite the impact of the hurricane on forest phenology, the abundance of trophic guilds maintained seasonality, mainly for frugivore and nectarivore guilds; (3) an increasing trend in the abundance of frugivore-omnivore and insectivore bats may indicate a recovery of their resources; and (4) nectarivore bats were the most severely impacted by Hurricane Patricia, and it is likely that their resources had not yet recovered two years after the impact. The resilience of tropical deciduous and semideciduous forests facing extreme climate events such as hurricanes, promotes recovery of biodiversity at a higher rate. The high vagility of bats compared to other taxa may confer advantages after certain disturbances, allowing faster recovery of assemblages; however, basic resources required by bats must be available. Hence, it is important to conserve natural protected areas for their function as shelter areas and to increase the complexity in agricultural or abandoned areas, in order to mitigate the effects of extreme events such as hurricanes. Understanding the effects of seasons and storms on local assemblages may serve as a place-holder for making inferences about climate change as we accumulate more years and more data.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14100818/s1. Table S1: Models (GLM's with Poisson distribution) to assess the effect of seasonality and post-hurricane time on the number of bats captured from March 2016 to December 2017.

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