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Cloud Forest Bird Responses to Unusually Severe Storm Damage[1]

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ABSTRACT

In 1998, storms related to Hurricane Isis caused extensive gaps in the cloud forest of El Triunfo Biosphere Reserve in Chiapas, Mexico, where severe storms are infrequent. We examined how this disturbance affected bird species composition. Species richness and composition were similar both between pre- and post-disturbance forest and between newly created gaps and plots that remained forested after the hurricane. However, differences in response guilds were greater between pre- and post-disturbance plots than between forest plots with gaps after disturbance. Granivorous, omnivorous, and terrestrial species were more abundant before the hurricane, whereas insectivorous, midstory, and generalist foragers were more abundant after the hurricane. In addition, species with high sensitivity to disturbance were more abundant in the pre-disturbance forest, while low sensitivity species were more abundant after disturbance. In the post-disturbance forest, insectivorous species were most abundant in gaps and terrestrial-canopy foragers were most abundant in forest plots. Permanently open areas had significantly lower species richness, but had lowland generalist and second-growth species not present in the cloud forest. Results suggest that changes in species composition were not limited to the newly created gaps, but also affected the whole forest. The decline of high sensitivity species after disturbance supports the hypothesis that disturbance negatively affects specialists and benefits generalist species. Although there is evidence that natural communities tend to return to pre-disturbance conditions, changes in community structure could be aggravated if recurrent hurricanes occur before succession takes place.

RESUMEN

En 1998 tormentas asociadas al huracán Isis crearon huecos en el bosque de niebla de la Reserva de la Biosfera El Triunfo, Chiapas, México. Daños severos causados por tormentas son infrecuentes en esta área. La riqueza y composición de especies fueron similar antes y después de la perturbación, así como entre los huecos creados por la tormenta y el bosque. Sin embargo, las diferencias en los gremios de respuesta fueron mayores entre pre-y post-perturbación que entre huecos y bosque después de la perturbación. Especies granívoras, omnívoras, y terrestres fueron más abundantes antes del huracán. Mientras que especies insectivoras, de sotobosque, y generalistas de estrato fueron más abundantes después del huracán. Además, especies con alta sensibilidad a la perturbación fueron más abundantes antes de la perturbación, mientras que especies con baja sensibilidad incrementaron después de la perturbación. Después del huracán, especies insectívoras fueron más abundantes en los huecos y especies forrajeras de terrestre/dosel fueron más abundantes en el bosque. Áreas con perturbación permanente mostraron una riqueza menor que el bosque, pero tuvieron especies generalistas y de crecimiento secundario no presentes en el bosque. Concluimos que los cambios en la composición de especies no se limitan a los huecos creados, sino que también afectan al bosque circundante. El decremento de especies con alta sensibilidad después del huracán apoya la hipótesis de que las perturbaciones afectan a especies especialistas y beneficia a las generalistas. Este decremento podría agravarse si huracanes recurrentes ocurren antes que la sucesión ecológica natural tenga lugar.

Key words: *bird diversity; Chiapas; cloud forest; disturbance; Mexico.*

DISTURBANCE IS KNOWN TO BE IMPORTANT to maintain habitat heterogeneity in natural ecosystems. It was once viewed simply as a detrimental agent, but it is currently recognized that disturbance plays an important role in many ecosystems (Schemske & Brokaw 1981, White & Pickett 1985, Vandermeer 1996, Zimmerman *et al.* 1996, Brawn *et al.* 2001, Greenberg & Lanham 2001). White and Pickett (1985) define disturbance as "any relatively discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment." Connell (1978) summarized its ecological importance in the intermediate disturbance hypothesis. This hypothesis states that disturbance that is neither too severe, nor too minor, enhances species diversity by reducing competitive exclusion among species.

Species may differ in their response to disturbance depending upon their ecological niche, and disturbance size, frequency, and intensity (Miller 1982, Vandermeer *et al.* 2000, Platt & Connell 2003). Severe disturbance, such as large hurricanes, strip leaves, flowers, fruits, and seeds from plants (Reilly 1991, Wiley & Wunderle 1993, Zimmerman *et al.* 1994). This impact on food supplies may have an immediate negative impact on nectarivore, frugivore, and seed-eating bird species, whereas insectivores and omnivores may remain relatively unaffected (Waide 1991b, Wauer & Wunderle 1992, Wiley & Wunderle 1993). Hurricanes may also have a differential effect depending upon elevation. Montane bird populations have been reported to be affected more than lowland populations, probably because of the slow recovery rates from disturbance in montane forest in comparison to lowland forest (Wunderle *et al.* 1992). Less intense disturbance may also negatively affect specialists, but benefit generalists (McKinney 1997, McKinney & Lockwood 1999, Brawn *et al.* 2001), but see criticisms in Vazquez and Simberloff (2002). Nonsevere disturbance, such as treefall gaps, have been reported to play an important role in the maintenance of woody species diversity in forest ecosystems (Schnitzer & Carson 2001). Removal of old trees may allow rapid regrowth, so forest gaps have been reported to have higher levels of primary production, and consequently, higher vegetative structural complexity and fruit production (Blake & Hoppes 1986, Greenberg & Lanham 2001).

Catastrophic disturbances, usually in the form of large storms, are common in tropical regions (Whitmore 1998, Vandermeer *et al.* 2000). In particular, hurricane prone areas, namely the Bay of Bengal, northeastern Philippines, Queensland, Melanesia, and the Caribbean, have a

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higher probability of an extensive destruction event than other areas (Wiley & Wunderle 1993, Whitmore 1998). The ecological consequences of disturbance have been best documented for the Caribbean, where hurricanes are frequent (Wiley & Wunderle 1993, Vandermeer *et al.* 1996, Zimmerman *et al.* 1996). In other tropical areas, by contrast, severe natural disturbance events are not as frequent and the impacts could be different. Evidence suggests that organisms with broad ecological niches are favored in hurricane prone areas (Wunderle *et al.* 1987, 1992). In contrast, areas with relatively low disturbance regimes may harbor more specialized organisms, which may be negatively affected when severe disturbance events occur.

In 1998, El Triunfo Biosphere Reserve located on the Sierra Madre de Chiapas mountains in southern Mexico suffered massive storms as a consequence of the El Niño. Hurricane Isis hit the Pacific coast of Mexico in September 1998, causing heavy rains and severe floods. Cloud forest on the mountain peaks, although not directly affected by the hurricane, suffered considerable damage in the form of numerous gaps created by fallen trees, landslides, and floods. Landslides are relatively common on Chiapas highlands, but the magnitude of the damage produced by heavy rains in 1998 was exceptionally severe (Samaniego Herrera 2003). The last time damage of similar magnitude occurred on the upper cloud forest in the Sierra Madre of Chiapas was in 1940 (I. Gálvez, pers. comm.). We estimate that gaps increased from 4.8 percent of the forest area before the storms to 40.5 percent after 1998 (C. Tejeda-Cruz, unpublished data). Although this area is located in one of the six main tropical cyclone storm paths in the world, it has the lowest average yearly frequency of recorded tropical storms among them and very few storms have come inland during the period 1972–2000 (de Gouvenain & Silander 2003). The existence of pre-hurricane bird surveys in this area gave us the opportunity to assess the effects of natural disturbance on bird species diversity in this particular ecosystem. The presence of two permanent large grass-dominated open areas allowed us to make comparisons with a more drastic and permanent disturbance. These openings were made in around 1940 for cattle ranching and agriculture. When the reserve was decreed in 1990, original dwellers moved out but the clearings have been maintained opened for the two camp sites in the reserve's core zone I. Our objective was to study the consequences of large scale gap creation in an ecosystem where such phenomena are rare and document how hurricane damaged forest differs from pre-hurricane forest. We hypothesized that hurricanes would change biodiversity components such as species density, alpha diversity, and equitability at two different scales: (a) between pre-hurricane and post-hurricane forest and (b) among hurricane-created gaps, adjacent forest, and permanently open areas. Ecosystem structural changes between forest and gaps, and between pre- and post-disturbance forest, were also expected to affect bird species differentially depending upon preferred foraging strata. We also expected changes in species composition; in particular, we expected a decline in nectarivore, frugivore, and granivore species in post-hurricane forest and gaps, and an increase in insectivore and omnivorous species after storm damage.

METHODS

We conducted our study in El Triunfo Biosphere Reserve's core zone I, on the mountain range Sierra Madre de Chiapas in the state of Chiapas, southern Mexico (15°09′10″N, 15°57′02″N, and 92°34′04″W, 93°12′2″W). The natural vegetation above 1700 m is cloud forest (Leopold 1950) and the climate is temperate-humid with an average annual precipitation from 2400 to 4000 mm. Based on White and Pickett (1985), we defined gaps as any disruption on the forest canopy continuity of at least 10 m in length. Birds were sampled using point counts of 10 min duration and 25 m radius (Hutto *et al.* 1986). All samples were taken in the cloud forest between 1800 and 2200 m above sea level. Censuses were started 15 min after sunrise and continued until 1000 h, when bird activity decreased. To avoid pseudoreplication, points were placed at least 150 m apart, and were thus considered spatially independent. Points placed in gaps were no closer than 25 m from habitat edge. Raptors and aerial foragers were excluded from the analysis. A total of 41 point counts were conducted in May 1997. After the storm damaged the upper parts of the reserve in 1998 we realized the opportunities for this study, and the same points were resampled in May 2000. Seventeen of these points were transformed into gaps by the disturbance in 1998. In addition, we surveyed eight point counts in permanently open areas to allow comparisons with a more severe and lasting disturbance. Only birds actively using gaps and open areas were recorded for these habitats. All surveys were conducted by the first author.

In each gap, we measured the maximum length and width of the gap with a measuring tape to calculate gap area. From a point around the center of each gap, the area around each point was divided into four 90° quarters using a compass. Vegetation height of a randomly selected point in each of the quadrants was measured as well as the vegetation height at the center of the gap. We used these measurements to calculate mean gap vegetation height.

DATA ANALYSIS.—To compare species diversity, species accumulation curves derived from the means of 100 iterations were plotted (Colwell & Coddington 1997, Colwell 2000). A range of different community structure attributes were measured: species density ($\bar{S}$) (Gotelli & Colwell 2001), Shannon–Wiener diversity index ($H' = -\sum p_i(\log_e p_i)$), and Pielou's evenness index ($J' = H'(observed)/H'_{\max}$) and compared through one-way analysis of variance (ANOVA) or Kruskal–Wallis test, followed by multiple comparison *t*-test or Mann Whitney *U* test for individual pair of sites, test selection depending upon data normality (Clarke & Warwick 1994). To ensure that comparisons before and after disturbance were not confounded by differences in detectability associated with changes in vegetation structure, we used *G*-tests (Zar 1996) to assess if differences in the ratio of birds inside and beyond the 25 m radius were statistically significant (Fuller 2000).

Species were assigned to functional groups. Foraging strata preferences were defined following Parker *et al.* (1996) and dietary guilds were based on Stiles and Skutch (1989), Terborgh *et al.* (1990), Howell & Webb (1995), and Greenberg *et al.* (1997). To make a better match with dietary preferences and improve the response resolution, we simplified foraging strata use criteria proposed by Parker *et al.* (1996) into four categories: (1) upper (incorporates Parker's canopy and midstory/canopy species); (2) middle (includes Parker's midstory and understory/midstory species); lower (comprises Parker's understory/terrestrial and terrestrial/understory species); and (4) generalist (includes Parker's terrestrial/canopy, terrestrial/midstory, and understory/canopy species). Species response to disturbance was categorized by their sensitivity to disturbance according to an independent assessment (Parker *et al.* 1996). The change in the abundance of disturbance sensitive species can be used as an indicator of disturbance severity (Barlow *et al.* 2002, Petit & Petit 2003, Tejeda-Cruz & Sutherland 2004).

Responses to changes in habitat structure due to disturbance for the plots sampled in 2000 and changes over time at resampled plots were analyzed graphically using nonmetric multi-dimensional scaling (MDS) methods (Clarke & Warwick 1994). MDS visually summarize similarity between samples, so that the distance between points represents their similarity. This method was selected because of its lack of assumptions about the distribution or type of data and because it addresses some of the major problems of other ordination techniques (Clarke & Warwick 1994). Analysis was performed using PRIMER v.5 software (Clarke & Warwick 1994). Similarity matrices for bird species were built using Bray–Curtis similarity index from untransformed data. Differences in species composition were examined using the analysis of similitude test (ANOSIM), and similarity percentage analysis (SIMPER) was used to examine the contribution of each species to the average Bray–Curtis dissimilarity between years and habitats and to determine their contribution to similarity within groups (Clarke & Warwick 1994). A probability of 0.05 or less was accepted as significant and P values shown are two-tailed.

RESULTS

DETECTABILITY BEFORE AND AFTER DISTURBANCE.—For all species combined, the ratio of individuals recorded inside and beyond the 25 m radius before disturbance was 3.1 and after disturbance was 3.0 ($G = 0.09$, $P = 0.77$). This calculation was also made for 21 species with adequate sample sizes. Four species ($P < 0.05$) were more detectable before the hurricane—Collared Trogon [*Trogon collaris*], Gray-breasted Wood-Wren [*Henycorina leucophrys*], Spotted Nightingale-Trush [*Catharus dryas*], Ruddy-capped Nightingale-Trush [*Catharus frantzi*], and Yellow Grosbeak [*Pheucticus chrysopeplus*]. None of these 21 species was significantly more detectable in post-disturbance forest. However, we did not find a clear relationship between changes in species' detectability ratio and changes in the average number of individuals per survey after the hurricane. Therefore, changes in detectability were not a significant confounding factor in this study.

PRE- AND POST-DISTURBANCE COMPARISONS.—We found a total of 79 bird species. When comparing all point counts, including gaps, no significant differences were found in species richness and bird species densities between pre- and post-disturbance treatments. Species richness (S) was slightly higher before (49 species) than after disturbance (44 species) (Fig. 1a), but mean species density ($Z = -3.651$, $P < 0.001$) and Shannon–Wiener diversity ($t = -3.731$, $P < 0.001$) were higher after disturbance (Fig. 2a). Pre-disturbance plots averaged 9.6 species per sample compared to 11.5 species per sample found in post-disturbance forest (Wilcoxon Test, $Z = -3.651$, $P < 0.001$). Similarly, mean Shannon–Wiener diversity was 2.08 in pre-disturbance versus 2.30 in post-disturbance ($t = -3.731$, $P < 0.001$).

For the 17 plots that became gaps after the storm, pre-disturbance plots had 35 species and post-disturbance had 36 species. But again,

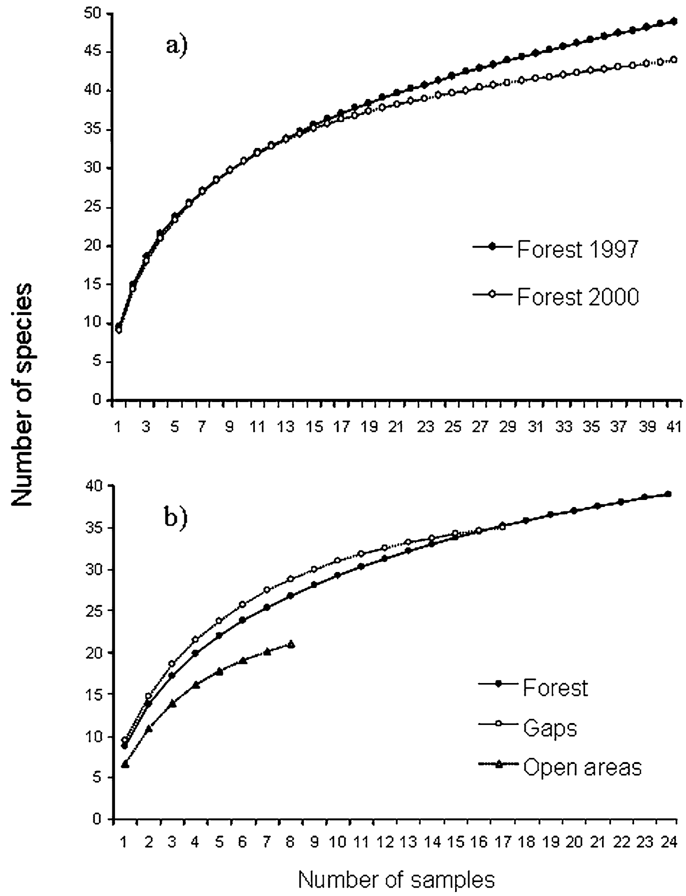

FIGURE 1. Species accumulation curves based on 100 iterations for all species in the cloud forest of El Triunfo Biosphere Reserve, Chiapas, Mexico. (a) Comparison of forest before and after disturbance and, (b) comparison among gaps, forest, and permanently open areas after disturbance.

species density and Shannon–Wiener diversity were higher in post-disturbance plots ($\bar{S} = 10.71$; $t = -2.96$, $P < 0.05$; $H' = 2.24$; $t = -3.14$, $P < 0.05$) than in pre-disturbance plots ($\bar{S} = 8.76$, $H' = 2.01$). Evenness (J') did not differ before and after disturbance (Mann Whitney test, NS).

Bird community structure changed over time when comparing all plots before and after disturbance. Differences between the two sampling periods on the MDS ordination were found for gap samples only. In this case, pre-disturbance plots clustered apart from post-disturbance plots (Fig. 3a). In contrast, no clear pattern was found for plots that remained forested. Results from the analysis of similarity tests indicate significant differences in the avian community structure among plots that remained forested after disturbance (global $R = 0.098$, $P < 0.002$, average dissimilarity = 64.53%) and among samples transformed into gaps (global $R = 0.266$, $P < 0.001$, average dissimilarity = 68.62%).

WITHIN YEAR COMPARISONS.—In the post-disturbance forest, we found that gaps had 35 species, whereas plots that remained forested had 39 species. Forest and gaps differed only in evenness ($Z = -2.33$, $P < 0.05$)

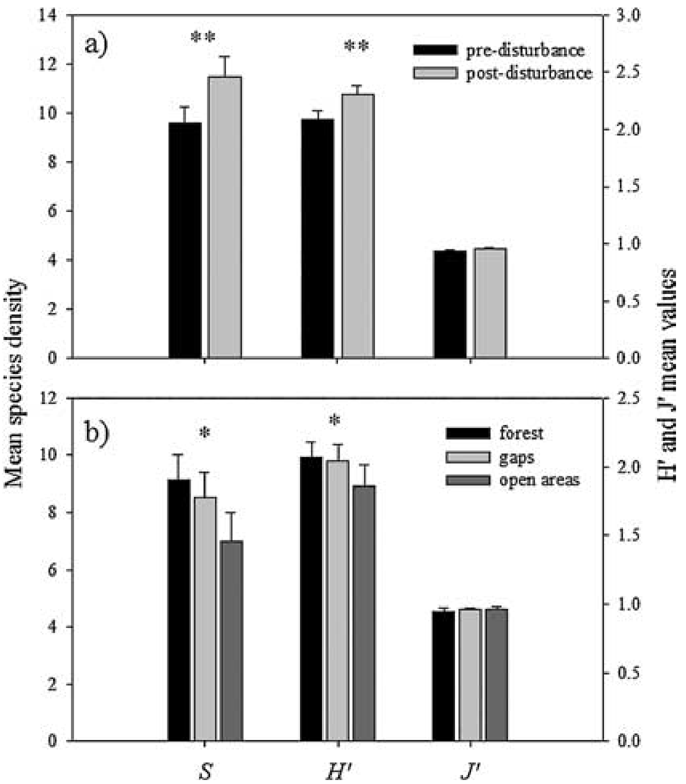

FIGURE 2. Differences in species density (S), Shannon–Wiener diversity (H′), and evenness (J') between pre- and post-disturbance treatments (a), and among habitats in post-disturbance treatments (b) in the cloud forest of El Triunfo Biosphere Reserve, Chiapas, Mexico. Asterisk (∗) indicates $P \leq 0.05$, double asterisk (∗∗) indicates $P \leq 0.001$. Error bars represent 95 percent confidence intervals.

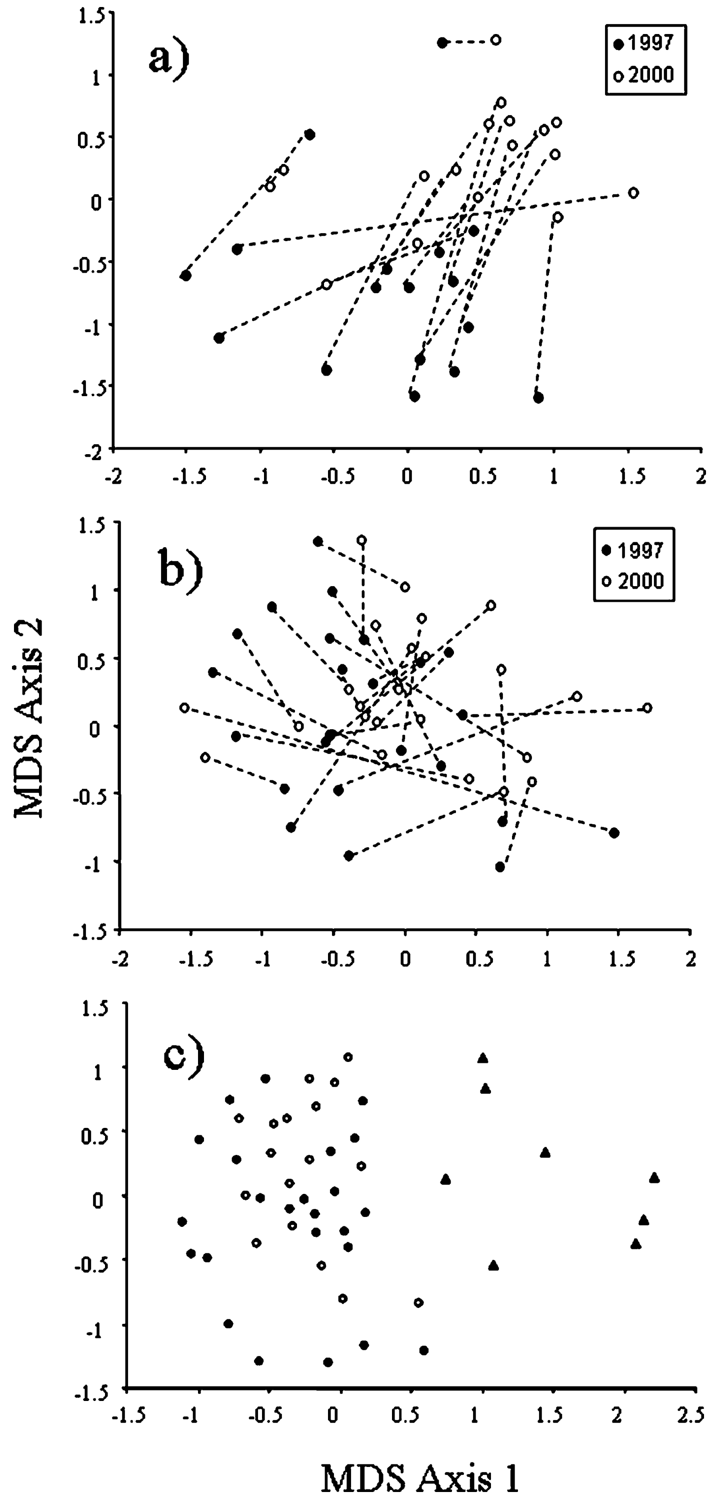

FIGURE 3. Plots of the first two MDS dimensions showing changes in the avian community after storm damage in El Triunfo Biosphere Reserve, Chiapas, Mexico. Chart (a) shows forest sites that were transformed into gaps; chart (b) shows points that remained forested. Dark circles indicate 1997 plots and clear circles are 2000 plots. Dotted lines link same plot. Chart (c) shows differences among forest (dark circles), gaps (clear circles), and open areas (dark triangles) for 2000 data only.

(Fig. 2b). Mean species richness and Shannon–Wiener diversity were not significantly different among forest and gaps. Permanently open areas had a much lower accumulation curve (Fig. 1b). Mean species richness ($F = 3.862$, $P < 0.05$) and Shannon–Wiener diversity ($\chi^2 = 6.066$, $P < 0.05$) were significantly different among forest, gaps, and open areas. Pair-wise tests showed that permanently open areas were significantly different to both gaps and forest. Mean species richness was higher in both gaps ($Z = -2.691$, $P < 0.01$) and forest ($Z = -2.335$, $P < 0.05$). Shannon–Wiener diversity was also higher in gaps ($Z = -2.390$, $P < 0.05$) and forest ($Z = -2.176$, $P < 0.05$).

In contrast, MDS ordination did not show a clear cluster for plots that remained forested. Permanently open areas clearly showed a different species composition (Fig. 3c). Differences were also significant among gaps, forest, and open areas in the post-disturbance forest (global $R = 0.418$, $P < 0.001$, average dissimilarity = 56.8%). Pair-wise tests showed significant differences in species composition in all possible habitat pair combinations (Table 1).

Changes in the abundances among habitats of Common Bush-Tanager (*Chlorospingus ophtalmicus*) and Gray-breasted Wood-Wren, the two most common species in the forest, had a great contribution in the similarity between disturbance treatments (Table 2). In permanently open areas, some forest species disappeared (*e.g.*, Gray-breasted

TABLE 1. *Results from analysis of similarity (ANOSIM) and similarity percentage analysis (SIMPER) of the bird communities before and after the disturbance, among forest, gaps, and open areas in the post-disturbance forest in the cloud forest of El Triunfo Biosphere Reserve, Chiapas, Mexico.*

	R	*P*	Average dissimilarity (%)
Before, after disturbance			
Forest 1997, 2000	0.098	0.002	64.5
Gaps 1997, 2000	0.266	0.001	68.6
All 1997, 2000	0.15	0.001	66.6
After disturbance			
Forest, gaps	0.142	0.04	65.1
Forest, open areas	0.771	0.001	83.3
Gaps, open areas	0.784	0.001	84.5
Global	0.418	0.001	

Wood-Wren) or declined in abundance (*e.g.,* Common Bush-Tanager, Brown-backed Solitaire [*Myadestes occidentalis*], Slate-throated Redstart [*Myioborus miniatus*]). The latter group of species, although still present in the permanently open areas, persisted only in association with edges (Tejeda-Cruz, pers. obs.). Generalists and edge species were important elements in the permanently open areas (*e.g.,* Rufous-collared Sparrow [*Zonotrichia capensis*], Clay-colored Thrush [*Turdus grayi*], Southern House Wren [*Troglodytes musculus*]).

COMPARISONS OF ECOLOGICAL ATTRIBUTES.—Differences in ecological attributes (feeding guilds, foraging strata, and sensitivity to disturbance, Table 3) were much more evident for changes over time (significant differences in 13 categories) than between forest and gaps (significant in only two categories).

There were differences between pre- and post-disturbance forest and between forest and gaps in the post-disturbance forest (Table 3). Granivorous ($U = 483$, $P < 0.001$) and terrestrial ($U = 466$, $P < 0.001$) birds were more abundant before disturbance. In particular, granivorous species with a preference for low levels, particularly the White-faced Quail-Dove [*Geotrygon albifacies*], were more abundant before the hurricane ($U = 501$, $P = 0.001$) (Table 2). Omnivorous birds were more abundant before disturbance only for points that were transformed into gaps ($t = 2.146$, df $= 32$, $P < 0.05$), whereas omnivorous birds with no preference for a foraging stratum were more abundant after disturbance ($U = 634.5$, $P < 0.05$). Insectivorous birds ($t = -3.738$, df $= 80$, $P < 0.001$), in particular in the upper ($U = 626.5$, $P < 0.05$) and middle ($U = 430$, $P < 0.001$) strata, were more abundant in post-disturbance forest. Birds with preference for terrestrial canopy ($U = 680.5$, $P < 0.05$) and midstory strata (U $= 503$, $P = 0.001$) and birds with no preference for any strata were also more abundant after disturbance ($U = 640.5$, $P = 0.01$).

Insectivorous birds were more abundant in gaps in the post-disturbance forest ($U = 131$, $P < 0.05$), in particular at midstory ($U = 120$, $P < 0.05$). Yellowish Flycatcher [*Empidonax flavescens*], a midstory insectivorous species, in part accounts for differences in the number of insectivores (Table 2). Birds foraging in terrestrial to canopy levels were the only foraging guild that was more abundant in the forest samples ($U = 147.5$, $P < 0.05$).

TABLE 2. *Contributions from the first ten species to the average dissimilarity between years, between forest and gaps, and between forest and permanently open areas in El Triunfo Biosphere Reserve, Chiapas, Mexico. Last column shows P values from Wilcoxon signed rank test for the between years comparison or Mann Whitney* U *exact test for the post-disturbance comparisons. H denotes species with high sensitivity to disturbance.*

Species	Abundance		Average dissimilarity	Cumulative % of dissimilarity	*P*
Between years (gaps only)	1997	2000			
Chlorospingus ophthalmicus	3.00	2.29	9.5	13.8	0.812
Henicorina leucophrys	1.47	2.35	4.5	20.6	0.031
Turdus infuscatus (H)	1.41	0.47	4.3	26.7	0.049
Myadestes occidentalis (H)	0.65	1.47	3.7	32.1	0.025
Catharus dryas (H)	1.18	1.29	3.5	37.2	0.719
Atlapetes brunneinucha	0.88	0.71	3.0	41.6	0.448
Geotrygon albifacies (H)	1.18	0.41	3.0	46.0	0.005
Catharus frantzi	0.82	0.24	2.7	49.9	0.058
Chlorophonia occipitalis	0.53	0.53	2.5	53.5	0.877
Lampornis viridipallens	0.71	0.47	2.3	56.9	0.214
After disturbance	Forest	Gaps			
Chlorospingus ophthalmicus	2.33	2.41	6.7	10.3	0.61
Henicorina leucophrys	1.13	2.12	5.4	18.6	0.01
Myadestes occidentalis (H)	0.63	1.12	3.5	23.9	0.06
Basileuterus belli	0.92	0.18	3.5	29.3	0.003
Catharus dryas (H)	0.63	1.00	3.4	34.5	0.305
Atlapetes brunneinucha	0.50	0.76	3.0	39.1	0.561
Myioborus miniatus	1.00	0.59	2.8	43.4	0.059
Empidonax flavescens	0.25	0.65	2.5	47.4	0.028
Lampornis viridipallens	0.71	0.47	2.5	51.3	0.251
Vermivora superciliosa	0.46	0.41	2.5	55.0	0.892
Permanent disturbance	Forest	Open areas			
Chlorospingus ophthalmicus	2.37	1.25	8.0	9.49	0.070
Henicorina leucophrys	1.54	0.00	6.3	16.96	0.0001
Zonotrichia capensis	0.00	1.25	5.6	23.62	0.0001
Pheucticus chrysopeplus	0.17	1.00	4.3	28.76	0.003
Catharus dryas	0.78	0.50	4.0	33.35	0.163
Turdus grayi	0.00	0.88	3.7	37.93	0.0001
Myadestes occidentalis	0.83	0.25	3.4	41.97	0.078
Myioborus miniatus	0.83	0.38	3.1	45.70	0.093
Piranga bidentata	0.10	0.63	2.9	49.22	0.009
Troglodytes musculus	0.00	0.63	2.8	52.53	0.003

Species with low sensitivity to disturbance were more abundant in the post-disturbance forest ($U = 494$, $P < 0.001$), whereas the abundance of species with high sensitivity to disturbance was higher only in the plots not disturbed after the hurricane ($U = 82.5$, $P < 0.05$)

TABLE 3. *Bird ecological attributes that showed significant differences in the mean number of individuals between years and habitats at El Triunfo Biosphere Reserve, Chiapas, Mexico. Mean number of individuals (±SD) is shown. Differences were tested using Mann-Whitney* U *test and, when data have a normal distribution,* t*-test.*

	Year					Habitat				
Attributes	1997 ($N = 41$)		2000 ($N = 41$)		P	Forest ($N = 24$)		Gaps ($N = 17$)		P
Dietary guilds										
Granivorous	1.46	(1.40)	0.61	(0.77)	<0.001	0.21	(0.66)	0.18	(0.39)	ns
Insectivorous	3.98	(4.27)	5.56	(1.76)	<0.001	4.04	(1.6)	5.23	(2.01)	<0.05
Omnivorous	10.35	(5.29)	7.35	(2.29)	<0.05[†]	5.37	(2.87)	5.82	(2.37)	ns
Foraging strata										
Terrestrial	1.54	(1.34)	0.61	(0.77)	<0.001	0.21	(0.66)	0.17	(0.39)	ns
Terrestrial/canopy	0.10	(0.37)	0.29	(0.51)	<0.05	0.37	(0.57)	0.06	(0.24)	<0.05
Midstory	0.37	(0.62)	1.00	(0.92)	<0.001	0.79	(0.88)	1.00	(1.00)	ns
Generalist	0.12	(0.4)	0.37	(0.53)	<0.05	0.37	(0.57)	0.11	(0.91)	ns
Diet/strata										
Upper insectivorous	0.95	(1.22)	1.41	(1.20)	<0.05	1.46	(1.14)	1.00	(0.86)	ns
Midstory insectivorous	0.59	(0.85)	1.59	(1.2)	<0.001	1.13	(1.03)	2.00	(1.27)	<0.05
Low granivorous	1.39	(1.28)	0.61	(0.77)	<0.001	0.21	(0.66)	0.18	(0.39)	ns
Generalist omnivorous	0.05	(0.22)	0.32	(0.52)	<0.05	0.38	(0.57)	0.12	(0.33)	ns
Sensitivity to disturbance										
High	5.59	(1.54)	4.00	(2.03)	<0.05[†]	2.33	(1.43)	3.06	(1.78)	ns
Low	1.59	(0.99)	2.49	(1.21)	<0.001	2.00	(1.21)	2.71	(1.53)	ns

[†]Indicates differences were significant for gaps only when $N = 17$ for each treatment. Nonsignificant results are denoted by ns.

(Table 3). Black Thrush (*Turdus infuscatus*) and White-faced Quail-Dove were the two high sensitivity species that contributed most to the differences between years (Table 2). Blue-throated Motmot (*Aspatha gularis*), although contributing only with 1.6 percent of the dissimilarity between groups, was significantly more abundant before disturbance ($Z = -2.236$, $P = 0.025$). Although other high sensitivity species were more abundant before disturbance, differences were only significant when they were grouped (Table 3). These species include Highland Guan (*Penelopina nigra*), Black-throated Jay (*Cyanolica pumilo*), and Tawny-throated Leaftosser (*Sclerurus mexicanus*). Only one high sensitivity species, Brown-backed Solitaire, was significantly more abundant in 2000. For low sensitivity species, the Chestnut-capped Bushfinch (*Atlapetes brunneinucha*) contributed most to the dissimilarity between years (4.4%), but was not significant. Slate-throated Redstart and Yellowish Flycatcher were the two species that next contributed most to differences between years; together they accounted for 6.4 percent of the difference, although differences were not statistically significant for individual species. Abundances of high and low sensitivity species were similar in forest and gaps in the post-disturbance forest (Table 3).

ENVIRONMENTAL VARIABLES.—Neither mean vegetation height nor gap size was significantly related to species richness nor the number of individuals (vegetation height: $R^2 = 0.0084$ for species density and $R^2 = 0.0074$ for number of individuals; gap size: $R^2 = 0.0337$ for number of species and $R^2 = 0.0031$ for number of individuals). Gaps averaged 880.11 m^2 (684.28 SD).

DISCUSSION

Changes in community structure were more distinct between years than between habitats in the disturbed forest. This suggests that changes in the bird community after disturbance were not limited to the newly created gaps, but also affected species composition in the entire forest. Although we found that total species richness remained at similar levels in the disturbed and undisturbed forest, mean species density and mean Shannon–Wiener diversity per sample were significantly higher in disturbed forest. For small scales, these results are consistent with the generally accepted idea that disturbance plays an important role in maintaining ecological diversity (Brawn *et al.* 2001). However, the fact that there were no differences in species richness in pre- and post-disturbance forest suggests an absence of disturbance effects at larger scales (Wiley & Wunderle 1993).

Our results are consistent with previous studies that have shown declines in nectarivore and granivore bird species after disturbance. Our study is also consistent with the notion that insectivores and omnivores may benefit from disturbance. Insectivorous birds contributed considerably to differences between treatments; insectivores in the upper and middle strata preferred disturbed forest. Other studies reported that immediately after Hurricane Hugo hit Puerto Rico abundance of insectivorous birds increased, but after a few months, insectivore abundance returned to original levels (Waide 1991a, Wunderle 1995). This may suggest that in our study insectivorous birds would be more abundant shortly after disturbance, since differences were still detectable 20 mo after the hurricane. Montane cloud forest has the slowest recovery rate of all tropical forests (Byer & Weaver 1977). Thus, the persistence of this difference over time may be related to the relatively slow growth rate of cloud forest trees (Wunderle *et al.* 1992, Wiley & Wunderle 1993, Foster 2001). Insectivore abundance may also be related to the high diversity and turnover rate of insects reported for hurricane-affected areas. Insectivorous birds may be more resilient to disturbance because their food supply has a high level of resiliency, diversity, and turnover (Waide 1991a, Wunderle *et al.* 1992, Wiley & Wunderle 1993). This is also true for food supply in treefall gaps. In mainland Panama, Schemske and Brokaw (1981) found that all gap species in lowland forest were insectivorous.

Our failure to detect an increase in frugivorous birds may also be related to the 20-mo interval after storm damage. Successional processes may have increased fruiting plant abundance to pre-disturbance levels. In some forests, gaps created by tree falls have more frugivorous species because understory plants produce more fruits in gaps (Blake & Hoppes 1986, Levey 1988). Studies on the short-term effects of hurricanes have found, however, that avian frugivores and nectarivores decline after hurricanes (Askins & Ewert 1991, Waide 1991a). The difference between these studies and our findings may be related to the intensity of the disturbance and time elapsed after disturbance.

We found a decline of terrestrial-granivore species after the hurricane, in particular the White-faced Quail-Dove. A decline of quail-doves after hurricanes has been reported also for Puerto Rico (Waide 1991a) and St. Croix (Wauer & Wunderle 1992). These studies suggest that quail-doves are sensitive to hurricane-mediated reductions in seeds on the forest floor. We believe that disturbance effects on quail-doves in our study area are temporary because the extensive remaining intact forest may provide refuge for this species as observed for quail-doves after Hurricane Hugo in Puerto Rico (Wunderle 1995). Additionally, seed stocks in gaps were probably returning to pre-hurricane levels. Loss of food supplies is considered a major cause of short-term population changes in hurricane-affected areas (see review in Wiley and Wunderle 1993). Given sufficient time, however, biological communities have a tendency to return to pre-disturbance conditions if successional processes are allowed to take place.

The absence of differences in numbers of canopy species between forest and gaps may be related to what Wunderle (1995) describes as a "downward shift" by canopy species. This is a displacement of canopy dwellers to lower levels in disturbed areas where the canopy layer has been severely damaged. This means that canopy species might be present in the gaps, but feeding at lower levels. Wunderle (1995) suggests that this may create a strong selective pressure for species that are foraging height generalists.

Birds in tropical forest often show narrow habitat preferences (Schemske & Brokaw 1981). We found a slight, but significant, decline in species with a high sensitivity to habitat transformation after disturbance. In contrast, low sensitivity species were more abundant in disturbed forest. This suggests that disturbance may have an impact on both forest interior specialists and generalist species. In the Caribbean, where hurricanes are frequent, habitat structure may be more heterogeneous because of recurrent disturbance; thus, the existence of many generalist species may be an adaptive strategy (Waide 1991b, Wunderle *et al.* 1992, Wunderle 1995, Whitman *et al.* 1998). But in areas where disturbance events are infrequent, the number of generalists would be expected to be low. This may the case for our study area, where disturbance was beneficial for generalist species, in particular feeding at middle levels. If we consider the degree of sensitivity as a measure of habitat specialization, then we can assume that the results support in part the notion that disturbance negatively affects specialists and benefits generalist species, although not all specialists were negatively affected. The definition of specialist species is still debated, however (Vazquez & Simberloff 2002).

The small differences between gaps and forest after disturbance might be related to the fact that gaps were on average small and that storm-damage in our area was not of the severity reported for hurricanes in the Caribbean. The gaps we studied could be comparable to the natural treefall gaps in the area. Previous studies suggest that high-altitude bird populations could emigrate to relatively less-damaged lowland habitats when highlands are severely damaged (Wunderle *et al.* 1992, Wiley & Wunderle 1993). We cannot state whether or not this is the case for our area because we did not survey lowland habitats. However, if emigration took place, bird populations are expected to return to upland habitats as the vegetation recovers. When natural ecological succession is allowed to occur, it is likely that disturbance would have a short-term effect. Nevertheless, initial gaps may allow wind disturbance and increased desiccation in the forests, creating much larger gaps if recurrent hurricanes occur before the re-establishment of the canopy. Differences between forest and permanently open areas suggest that a more severe and lasting disturbance event benefits secondary growth species and generalist species, some of which are more common at lower elevations, whereas several forest interior species are absent from such disturbed sites.

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