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Rapid colonization and turnover of birds in a tropical forest treefall gap

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ABSTRACT. Ecological disturbance is an important factor that influences the abundance and distribution of species. Treefalls are a prominent source of disturbance in tropical forests, but robust characterization of community change after treefalls requires baseline data that are often not available. We capitalized on 25 yr of avian mark–recapture data from a lowland moist forest in central Panama to investigate the timescale of colonization and persistence of birds in a newly formed treefall gap. We compared bird species assemblages pre- and post-treefall to explore how the disturbance affected specific foraging guilds and overall assemblage structure (abundance and alpha diversity). We documented rapid colonization (i.e., within five months post-treefall) of the treefall gap by birds. Abundance and alpha diversity increased following the treefall, but both remained relatively constant in a nearby control plot. At the guild level, frugivores spiked in abundance and nectarivores (i.e., hummingbirds) increased in alpha diversity following the treefall. These results are in agreement with those of previous spatial studies of gap dynamics and suggest that certain tropical frugivores and nectarivores have a remarkable ability to rapidly find and exploit preferred resources and microhabitats embedded in a landscape matrix. Assemblage abundance and alpha diversity decreased back to pre-treefall levels within 1 and 4 yr of the treefall, respectively. Thus, even large gaps may provide only ephemeral benefits, highlighting the importance of periodic disturbance for landscape-level persistence of species that use gaps.

RESUMEN. **Colonización acelerada y recambio de especies de aves en un claro de bosque tropical producido por la caída de un árbol**

El disturbio ecológico es un factor importante que influencia la abundancia y distribución de especies. La caída de arboles es una fuente prominente de disturbio en bosques tropicales, pero caracterizaciones robustas del cambio en las comunidades después de la caída de un árbol requiere información base que no esta disponible con frecuencia. Utilizamos datos de marca recaptura colectados durante 25 años de un bosque húmedo tropical en Panamá central para investigar la escala de tiempo de la colonización y persistencia de aves en claros formados recientemente por caída de arboles. Comparamos la composición de especies de aves previo y posterior a la caída de un árbol con el fin de explorar como el disturbio afectaba gremios de forrajeo específicos y la estructura del ensamblaje en general (abundancia y diversidad alfa). Documentamos una colonización rápida (i.e., dentro de los primeros cinco meses posteriores a la caída del árbol) de los claros por aves. La abundancia y diversidad alfa incrementó luego de la caída del árbol, pero ambos permanecieron relativamente constantes en una parcela control cercana. Al nivel de los gremios, los frugívoros incrementaron en abundancia y los nectarívoros (i.e., colibríes) incrementaron en diversidad alfa posterior a la caída del árbol. Estos resultados coinciden con estudios espaciales previos de la dinámica de claros y sugieren que algunos frugívoros tropicales y nectarívoros tienen una capacidad asombrosa para encontrar rápidamente y explotar recursos preferidos y micro hábitats dentro de la matriz del paisaje. La abundancia y diversidad alfa del ensamblaje disminuyeron hasta niveles similares previos a la caída del árbol dentro de uno y cuatro años después de la caída de árbol respectivamente. Consecuentemente, inclusive claros de gran tamaño pueden proveer solamente beneficios efímeros, resaltando la importancia de los disturbios periódicos para la persistencia al nivel del paisaje de las especies que usan los claros.

Key words: Abundance, alpha diversity, disturbance, guild, treefall gap, tropical birds

Ecological disturbance, defined as any relatively discrete event that alters environmental conditions or causes changes to ecosystem, community, or population structure (*sensu*

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Pickett and White 1985), is widely recognized as playing a fundamental role in structuring biological communities across time and space (Levin and Paine 1974, Connell 1978, Sousa 1984, Levey 1988a, Brawn et al. 2001). In tropical forests, treefalls are a common form of disturbance that drive patterns of species diversity and turnover (Bongers et al. 2009, Dechnik-Vazquez et al. 2016). Spatially, treefalls provide environmental heterogeneity that allows coexistence of species with different habitat preferences, resource requirements, or competitive abilities (Dalling et al. 1998, Schnitzer and Carson 2001). Temporally, treefalls initiate the ecological process of succession, maintaining transitional habitat types and the species that depend on them (Whitmore 1978, Brokaw 1985, Schnitzer and Carson 2001). As a result, treefalls often contain unique assemblages of plants and animals (Schemske and Brokaw 1981, Dechnik-Vazquez et al. 2016) and can enhance local diversity in a variety of taxa (Denslow 1987, Fredericksen et al. 1999, Hill et al. 2001, Schnitzer and Carson 2001, Wunderle et al. 2005).

Most previous studies of associations between treefalls and animals have focused on spatial patterns of diversity. For example, certain species of birds (Schemske and Brokaw 1981, Wunderle et al. 1987, 2005, Levey 1988a, b, Banks-Leite and Cintra 2008) and butterflies (Hill et al. 2001, Pardonnet et al. 2013) are more abundant in gaps, and gap assemblages differ relative to those of the forest interior. For tropical birds in particular, frugivores and nectarivores attain higher abundances and diversity in gaps, likely reflecting concurrent increases in resource availability, such as flowering/fruiting plant species (Levey 1988b, Wunderle et al. 2006).

Spatial studies are useful for inferring species' habitat preferences and community-level differences between gaps and the forest interior. However, they do not address the timescale of colonization, namely how rapidly species find and colonize treefall gaps and how long they subsequently persist in gaps. Wunderle et al. (2006) found that tropical birds responded to artificial gaps created by logging activities within 2 yr, suggesting that certain bird species can rapidly find and exploit treefall gaps on the landscape. However, succession can occur rapidly and gaps can close within as little as 4 to 5 yr (Fraver et al. 1998, Costa and Magnusson 2003), meaning that gaps may provide only ephemeral benefits to species prospecting for resources. Inferring such temporal patterns of gap use necessitates having baseline data prior to gap formation, which is challenging given the spatiotemporal unpredictability of treefalls. Indeed, the few longitudinal studies available in the literature have focused on large-scale anthropogenic disturbances, such as avian community responses to selective logging (Thiollay 1997, Wunderle et al. 2006) or habitat fragmentation (Stouffer and Bierregaard 1995), and the timescale of colonization and persistence by animals at smaller spatial scales, such as treefall gaps, remains poorly understood.

We leveraged a long-term mark–recapture study of tropical birds (Brawn et al. 2017) to investigate temporal dynamics (i.e., colonization and persistence) of avian responses to a large treefall gap in a lowland moist forest of central Panama. More specifically, we took advantage of a natural experiment—a 1-ha gap caused by multiple treefalls that occurred on a long-term study plot—to compare avian assemblages between the treefall plot and an adjacent plot that functioned as a control for disturbance. We characterized the assemblages pre- and post-treefall to explore potential treefall-induced changes in alpha diversity and abundance. We predicted that (1) alpha diversity and overall abundance would increase on the treefall plot, but remain relatively constant on the control plot, and (2) these increases would be underpinned by an influx of frugivores and nectarivores post-treefall (Schemske and Brokaw 1981, Levey 1988b, Wunderle et al. 2005, 2006). Additionally, we examined the timescale at which birds responded to and persisted in the treefall gap, with the goal of determining how long it took the treefall assemblage to revert back to its "original" state.

METHODS

We investigated the timescale of colonization and persistence of tropical forest birds in a large treefall gap in Soberanía National Park in the Republic of Panama. We leveraged 25 yr of mist-net data (1994–2019) from two 2-ha study plots, Hunt Club (hereafter, treefall plot) and Ridge (hereafter, control plot). The two plots were separated by ~ 500 m and embedded within the larger 104-ha Limbo Plot, a long-term research site consisting of older secondary and some primary tropical lowland moist forest (see Robinson et al. 2000 for more details). The plot is bisected by Pipeline Road, a one-lane gravel road surrounded by closed-canopy forest, and located at least 3.5 km from the nearest forest edge (Robinson et al. 2000). Panama is characterized by a distinct dry season (January–April) and rainy season (May–December), and 90% of annual precipitation ($\bar{x}$ = 2600 mm) at the study site occurs during the rainy season (Robinson et al. 2000). A large blowdown occurred on the treefall plot during the rainy season (October) of 2015. An emergent *Anacardium excelsum* was presumably uprooted in a storm and fell over, causing a chain reaction of other smaller treefalls that created a gap of ~ 1-ha, or nearly half of the treefall plot (Fig. S1).

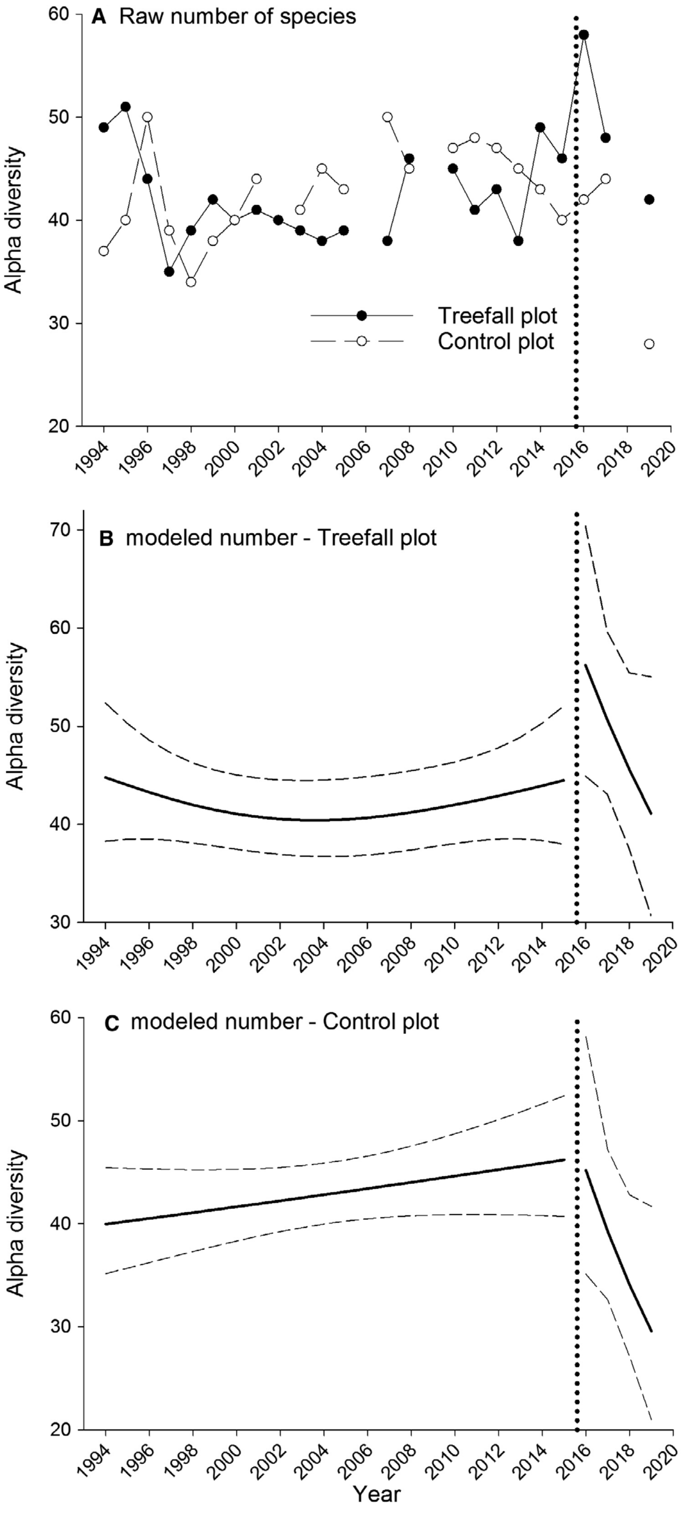
Bird capture and sampling protocol. From 1994 to 2019, we set up 20 mist-nets (3 × 12-m, 36-mm mesh) and sampled birds twice per year at each study plot, once in the dry season and once in the rainy season. Nets were set at ground level and opened from 06:00 to 18:00 each day until 600 total net-hours of sampling time were accumulated. Nets were temporarily closed, and sampling was paused during heavy rains or other inclement weather until conditions improved. Following the treefall in October 2015, seven of the 20 net lines at the treefall plot were located within or immediately adjacent to the treefall gap.

Upon capture, we transported birds back to a banding station, where we banded individuals of most species with uniquely numbered aluminum bands. For kingfishers (Family Alcedinidae) and hummingbirds (Family Trochilidae), we clipped the distal end of one or two rectrices in unique combinations to identify individuals recaptured during the same sampling period. To examine how variation in ecology and life-history traits across the species assemblage influenced responses to the treefall disturbance, we categorized species into guilds. We used a guild classification system modified from Stotz et al. (1996) that incorporated information on diet, habitat use, and forest stratum (Table S1). Overall, we classified species into 10 guilds, including ant-follower, canopy/second-growth, granivore, mixed-flock, nectarivore, omnivore, piscivore, raptor, understory frugivore, and understory insectivore. We excluded temperate latitude migrants from analyses due to low capture rates and because they were only present during dry season sampling.

Statistical analysis. We conducted all analyses in program R 3.6.1 (R Core Team 2019). For the analyses of alpha diversity, or total number of species captured, we used the "mcgv" package (Wood and Wood 2015) to construct a generalized additive model (GAM) with a Poisson error distribution and a log-link function to allow for non-linear patterns over time. We tested for temporal autocorrelation and found none. We modeled pre-treefall diversity (1994–2015) and post-treefall diversity (2016–2019) separately, with alpha diversity as the response variable and a smoothed term of sampling year (allowing it to vary non-linearly) and an interaction between sampling year and plot (control vs. treefall) as fixed effects.

As an index of total abundance, we used capture rates of birds in mist-nets. Although this method has been criticized in the literature (Remsen and Good 1996), mist-nets can still capture a large proportion of the surrounding bird community (Blake and Loiselle 2001) and capture rates are still frequently used as a proxy for abundance (Freeman 2019, Şekercioğlu et al. 2019). We initially used a GAM with a Poisson error distribution and a log-link function to model abundances. We observed strong temporal autocorrelation between successive years and when we attempted to add an autocorrelation structure

Fig. 1. Alpha diversity per year at Hunt Club (treefall plot) and Ridge (control plot) using (A) raw counts of unique species for both plots, (B) modeled counts from GAMs for pre- and post-treefall years for the treefall plot, and (C) modeled counts from GAMs for pre- and post-treefall years for the control plot. Dotted line indicates the occurrence of the treefall gap (October 2015).


A Raw number of species
Alpha diversity
Treefall plot
Control plot
B modeled number - Treefall plot
C modeled number - Control plot
Year

to the data (i.e., auto-regressive model of order 1, auto-regressive model average with different parameters), we were still unable to adequately control for temporal autocorrelation. Therefore, we opted for an alternative approach and instead modeled the response variable as the difference in abundance between a given year and average annual abundance over the entire study, using a GAM with a Gaussian distribution. Using this approach, we no longer detected temporal autocorrelation, and our models retained the same fixed effects and the two model approach (pre- and post-treefall) that we used for alpha diversity. For guild-specific comparisons, we compared the distributions of diversity and abundance in the pre-treefall years to the distributions of diversity and abundance in the post-treefall years using Kolmogorov–Smirnov tests for each guild.

RESULTS

Alpha diversity. Although we observed fluctuations in alpha diversity based on raw data (Fig. 1A), we found no evidence of temporal variation in alpha diversity during either the pre-treefall (1994–2015) or post-treefall (2016–2019) years for either the treefall plot (pre-treefall: effective degrees of freedom [edf] = 1.74, $P = 0.46$; post-treefall: edf = 1.00, $P = 0.13$) or control plot (pre-treefall: edf = 1.0, $P = 0.19$; post-treefall: edf = 1.0, $P = 0.07$), although both plots were undergoing downward trends in diversity during the post-treefall years (Fig. 1B,C).

Prior to the treefall, the highest raw annual alpha diversity observed on the treefall plot was 51 species (1995) and median diversity (50th percentile) was 41 species (Fig. 1A). In the year after the treefall (2016), alpha diversity was 58, outside the maximum diversity observed during the previous 21 yr. However, raw alpha diversity quickly returned to pre-treefall levels, dropping to 48 by 2017 and 42 by 2019, close to the long-term median of the treefall plot (Fig. 1A).

Results based on modeled data (based on predicted output from the GAM) are similar to the observations from the raw data. When comparing changes in alpha diversity over time, the 2016 predicted value of 56.2 species is outside the pre-treefall 95% confidence interval (36.7–52.4), although the pre- and post-treefall confidence intervals did overlap (2016: 95% CI: 44.9–70.4; Fig. 1B). One year after the treefall (2017), modeled alpha diversity dropped to 50.7 species, back within the 95% CI of the pre-treefall distribution, and continued to decline to average pre-treefall levels. Thus, alpha diversity on the treefall plot returned to pre-treefall levels within 1 yr.

In contrast to the treefall plot, diversity in the control plot did not change between pre- and post-treefall years. The maximum diversity observed on the control plot from 1994 to 2015 was 50 species, and the median was 43 species (Fig. 1A). The diversity observed in 2016 was 42 species, comparable to the average diversity during all previous years. Likewise, modeled results indicated that the alpha diversity in 2016 (45.2, 95% CI: 35.1–58.1) was within the pre-treefall distribution (35.1–52.4).

To examine treefall-induced changes in alpha diversity at the guild level, we compared annual guild diversity in pre-treefall years to that of the post-treefall years on the treefall plot. Only nectarivores significantly changed in alpha diversity following the treefall, and they more than doubled in diversity, increasing from an average of 3.3 species/yr to 7.3 species/yr (Table 1). In 2016, 11 species of nectarivores were captured, whereas the maximum captured in all previous years was seven (Table S2). In the first sample following the treefall (dry season 2016, five months after the treefall), we captured five species of hummingbirds that were rarely or never captured at our study site prior to the treefall, including the first records of three species, Garden Emerald (*Chlorostilbon assimilis*), Rufous-breasted Hermit (*Glaucis hirsutus*), and Snowy-bellied Hummingbird (*Amazilia edward*), the second capture of Rufous-tailed Hummingbirds (*Amazilia tzacatl*), and the sixth and seventh captures of Band-tailed Barbthroats (*Threnetes ruckeri*).

ABUNDANCE

Although there was some temporal variation in total bird abundance based on raw data (Fig. 2A, Table S3), model results indicated no temporal trend in bird abundance during the pre-treefall years for the treefall plot (edf = 2.10, $P = 0.30$; Fig. 2B), but an increasing trend in abundance during the pre-

Table 1. Comparison of pre-treefall (1994–2015) and post-treefall (2016–2019) average annual alpha diversity (based on raw alpha diversity) for the 10 foraging guilds at the treefall plot using Kolmogorov–Smirnov tests.

Foraging guild	Pre-treefall diversity	Post-treefall diversity	P
Ant-follower	4.80	4.67	0.91
Canopy	0.50	0.67	1.0
Granivore	0.20	0.67	0.93
Mixed-flock	6.25	6.67	0.93
Nectarivore	**3.25**	**7.33**	**0.02**
Omnivore	3.15	4.33	0.22
Piscivore	0.80	1.0	0.97
Raptor	0.50	0.33	1.0
Understory frugivore	5.25	5.33	1.0
Understory insectivore	15.90	16.67	0.37

Bold values indicate a significant change between pre- and post-treefall diversity

treefall years (1994–2015) for the control plot (edf = 2.0, $P < 0.01$, Fig. 2C). However, we observed no significant temporal trends in abundance during the post-treefall years (2016–2019) for either the treefall plot (edf = 1.23, $P = 0.11$) or the control plot (edf = 1.7, $P = 0.26$), although both plots were undergoing declines in bird abundance (Fig. 2).

Prior to the treefall, the highest raw annual abundance observed on the treefall plot was 238 birds and median abundance was 173.5 (Fig. 2A). Abundance in the year after the treefall (2016) was 307, far above the maximum abundance observed in the previous 21 yr. Following this peak in abundance, abundance dropped to 244 individuals by 2017, but still remained above pre-treefall levels until 2019, when it returned to close to its average annual level (177 individuals; Fig. 2A).

Similar to observations based on the raw data, when comparing the modeled results of differences in abundance between the current year and the average abundance across all years, the mean values and 95% CIs for 2016 (118.4 individuals, 94.4–142.3) and 2017 (71.6 individuals, 52.4–90.9) were both well above the 95% CI for the pre-treefall years (−35.7–25.4). By 2018, the mean value of 29.9 individuals was still just above the upper limit of the pre-treefall 95% CI. In 2019, the mean value (−8.4) had returned to within the pre-treefall 95% CI. Thus, abundance returned to pre-treefall levels in 4 yr, indicating a greater lagged effect of individual bird abundance than for alpha diversity.

On the control plot, the highest raw annual abundance observed from 1994 to 2015 was 209, and the median was 162 (Fig. 2A). The abundance in 2016 was 180 individuals, higher than average, but within the previously observed distribution. Likewise, when examining model results, 95% CIs for pre-treefall years ranged from −69.2–50.9, and 2016 was within that range (22.7, 95% CI: −3.2–48.5).

For guild-specific changes in abundance on the treefall plot, we compared annual guild abundance in pre-treefall years to abundance in the post-treefall years. Only understory frugivores significantly changed in abundance after the treefall, increasing from 58.0 unique individuals/yr in the pre-treefall years to 103 unique individuals/yr in the post-treefall years (Table 2). These increases were due almost exclusively to increased capture rates of Red-capped Manakins (*Ceratopipra mentalis*), an understory frugivore, with 62 unique captures in 2016 compared to a pre-treefall median of 19 captures/yr. Nectarivore abundance also increased from 12.6 unique individuals/yr to 29.3 individuals/yr post-treefall, but this difference was not significant ($P = 0.16$; Table 2). These increases were largely driven by 16 unique captures of Snowy-bellied Hummingbirds (*Amazilia edward*) in 2016, the first and only year that they were captured across the 25-yr sample.

Fig. 2. Abundance of unique individuals per year across all species at Hunt Club (treefall plot) and Ridge (control plot) using (A) raw abundance of all unique individuals for both plots, (B) modeled abundance from GAMs for pre- and post-treefall years for the treefall plot, and (C) modeled abundance from GAMs for pre- and post-treefall years for the control plot. Dotted line indicates the occurrence of the treefall gap (October 2015).

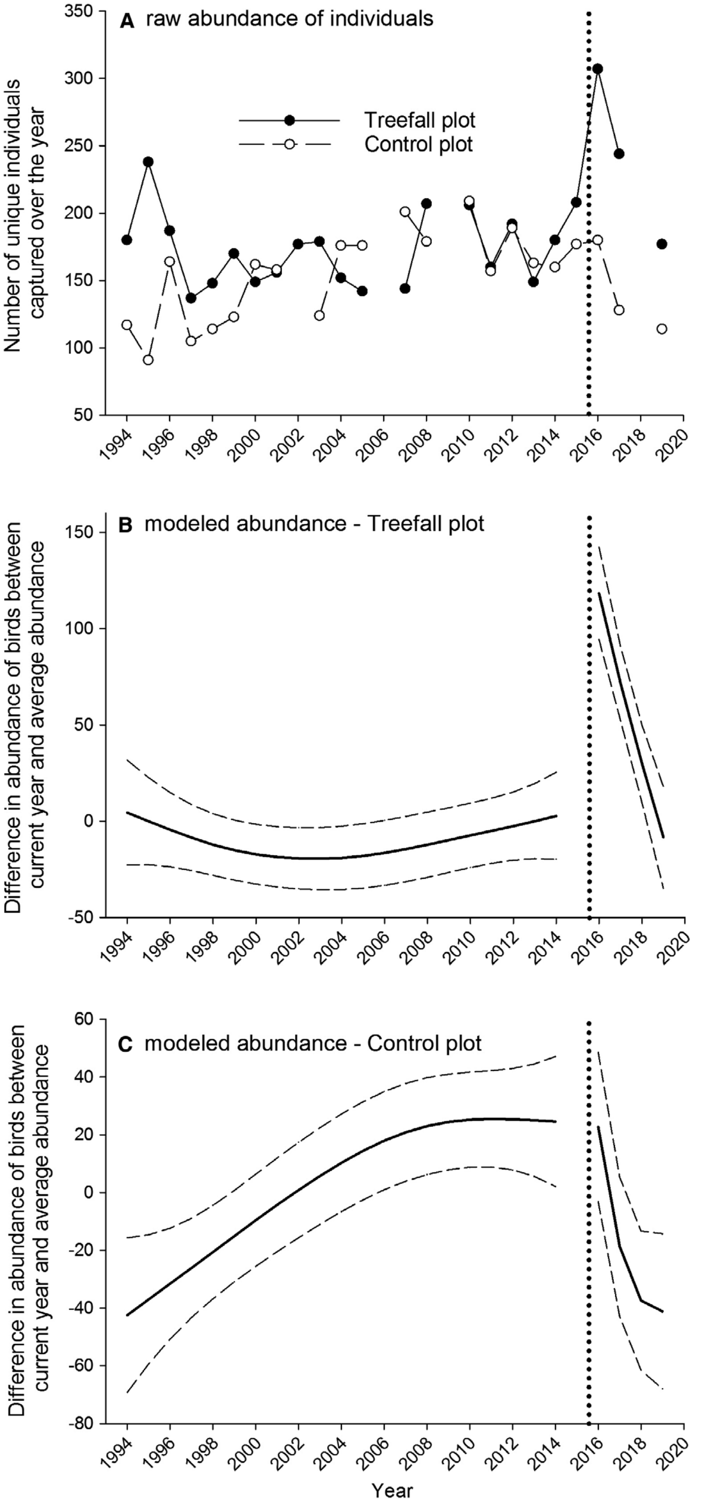

A raw abundance of individuals
Number of unique individuals captured over the year
Treefall plot
Control plot
B modeled abundance - Treefall plot
Difference in abundance of birds between current year and average abundance
C modeled abundance - Control plot
Difference in abundance of birds between current year and average abundance
Year

Table 2. Comparison of pre-treefall (1994–2015) and post-treefall (2016–2019) average annual abundances (based on raw abundances) for the 10 foraging guilds at the treefall plot using Kolmogorov–Smirnov tests.

Foraging guild	Pre-treefall abundance	Post-treefall abundance	*P*
Ant-follower	26.00	18.33	0.67
Canopy	0.75	1.00	1.00
Granivore	0.20	0.67	0.62
Mixed-flock	20.20	22.67	0.49
Nectarivore	12.55	29.33	0.16
Omnivore	7.70	10.33	0.62
Piscivore	1.35	2.33	0.22
Raptor	0.55	0.33	1.00
Understory frugivore	**57.95**	**103**	**0.02**
Understory insectivore	43.50	51.33	0.62

Bold values indicate a significant change between pre- and post-treefall abundance.

DISCUSSION

In the year after the treefall, we found that alpha diversity and abundance increased dramatically on the treefall plot, but both remained relatively stable on the control plot. These rapid changes in alpha diversity and abundance in the treefall plot assemblage were primarily due to the presence of nectarivorous hummingbirds and understory frugivores. Assemblage alpha diversity and abundance returned to pre-treefall levels within ~ 1 and 4 yr of gap formation, respectively, suggesting that treefall gaps are ephemeral resources and demonstrating the importance of periodic disturbance for maintaining local diversity in tropical forests.

Long-term monitoring allowed us to track a “natural” experiment and provide one of the first temporal characterizations of gap colonization in tropical birds. Most previous studies have compared gap assemblages to forest interior assemblages and used space-for-time substitutions to infer temporal gap dynamics (Schemske and Brokaw 1981, Wunderle et al. 1987, Levey 1988b, Banks-Leite and Cintra 2008). In one of the few temporal studies of gap use by tropical birds, Wunderle et al. (2006) found increased bird abundance in early successional gaps after selective logging, although they were artificial gaps and sampling did not begin until 20 mo post-logging.

We found that alpha diversity of nectarivores and abundances of nectarivores and frugivores began increasing markedly within five months after gap formation, confirming the results of previous spatial studies (Levey 1988b, Wunderle et al. 2005, 2006, Banks-Leite and Cintra 2008) and providing novel temporal evidence of the ability of birds in these guilds to rapidly find gaps on the landscape. Such rapid colonization of gaps suggests that birds in these guilds may move considerable distances while prospecting for certain habitats/resources on a landscape level. For example, forest nectarivores can travel hundreds of meters in continuous forest (Hadley and Betts 2009, Volpe et al. 2014), and experimental dispersal challenges have shown that both frugivores and nectarivores have greater mobility across gaps than birds in other guilds (Moore et al. 2008).

Although we did not collect data pre- and post-treefall on the plant community, we consider it likely that these two guilds were responding to an increased abundance of flowering and fleshy-fruited plants that colonize early successional gaps (Levey 1988a, b, Loiselle and Blake 1991). Indeed, tropical frugivores have been shown to track food resources (Saracco et al. 2004), spend disproportionately more time in gaps (Levey 1988b), and deposit seeds of their food plants preferentially in gaps (Levey 1988b). Tropical nectarivores, such as hummingbirds, also track food resources and can become hyperabundant in areas where resource availability is high (Cotton 2007), such as gaps or fragmented forests (Stouffer and Bierregaard 1995). Of the eight hummingbird species captured during our first sampling period (March 2016) after the treefall, five had rarely or never been captured before the treefall. We expect that the high mobility of hummingbirds (Stouffer and Bierregaard 1995, Moore et al. 2008) and ability to track patchy floral resources concentrated in gaps (Cotton 2007) contributed to their influx, although studies where food resources pre- and post-treefall were quantified would be needed to test this hypothesis.

In addition to improving our understanding of the timescale of colonization, our baseline data allowed us to characterize persistence in the treefall gap. We found that the alpha diversity on the treefall plot returned to its pre-treefall baseline within 1 yr post-treefall. Abundance on the treefall plot spiked post-treefall and declined more slowly, taking 4 yr to return to pre-treefall levels. Alpha diversity likely declined faster because many nectarivores were singleton captures during the first year post-treefall and were not present at high densities on the plot. This rapid return of diversity and abundance to pre-treefall levels is consistent with previous studies documenting total gap closure within as few as 4-5 yr after gap formation in tropical forests (Fraver et al. 1998, Costa and Magnusson 2003). In contrast, the few studies to examine temporal persistence in treefall gaps found steady increases in the abundance of birds in regenerating gaps up to 4 yr after gap formation (Wunderle et al. 2005, 2006). We posit that these differences in persistence are likely attributed to differences in the scale of disturbance between the studies. The gap created by the treefall on our plot was natural, whereas the few other studies to document temporal dynamics of gap usage were conducted at or adjacent to large-scale selective logging operations (Wunderle et al. 2005, 2006). Thus, directly comparing rates of succession and gap closure in a natural treefall gap and selectively logged forests may be inappropriate. Our findings uniquely demonstrate that natural gaps may only provide ephemeral, short-lived resource opportunities for tropical forest birds.

Based on island biogeography theory, the probability of colonization of a gap is expected to increase with gap size and proximity to second-growth habitats (Wolfe et al. 2015). Because the Limbo plot in our study is comprised largely of older secondary forest and some primary forest (Robinson et al. 2000) and is at least 6 km from second-growth habitats at the beginning of Pipeline Road, how second-growth species managed to colonize the gap in our study is unclear. For example, species such as Thick-billed Seed-finches (*Sporophila funerea*) prefer grassy areas or second-growth habitats and are uncommon in forest habitats (Rising 2020). One possibility is that these second-growth species took advantage of a number of other large treefalls that occurred in 2015, owing to the transition between a dry El Niño year and a wet La Niña year, along Pipeline Road (C. E. Tarwater, pers. obs.), to eventually arrive at the Limbo plot. Alternatively, gap specialists and second-growth species may move through the landscape matrix in search of productive gaps, and such a large gap (~ 1-ha) may make the probability of colonization high (Levey 1988b, Banks-Cintra and Leite 2008). As stated above, nectarivores may travel longer distances and some understory frugivores, such as manakins (Family Pipridae), may engage in short-distance migration, indicating that they can move long distances across the landscape (Boyle et al. 2010). Unfortunately, we are unable to test these hypotheses due to the lack of replication in our study.

In conclusion, we provide one of the first temporal characterizations of colonization and persistence of a treefall gap by tropical forest birds. Our results confirm the results of previous spatial studies comparing gap vs. forest interior bird assemblages and provide novel temporal evidence that certain guilds have a remarkable ability to rapidly find and colonize treefall gaps. The influx of nectarivores and frugivores following gap formation is consistent with the intermediate disturbance hypothesis (Connell 1978), with disturbances such as treefalls expected to introduce habitat heterogeneity, provide more available niche space, and promote local diversity. Given the ephemeral persistence by birds in the treefall gap at our study site, periodic disturbance (i.e., frequent treefalls) may be required for birds to reap the resource benefits they provide over longer temporal scales (Connell 1978, Petraitis et al. 1989, Brawn et al. 2001). Finally, our results suggest that with increasing forest fragmentation and secondary succession throughout the tropics (Powell et al., 2013, Taubert et al. 2018), certain species like nectarivores and frugivores may benefit from the expansion of gap-like habitats that support their food plants.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s website.

Fig. S1. Photo of the large *Anacardium excelsum* blowdown that caused the 1-ha treefall gap to occur on the Hunt Club study plot in October 2015.

Table S1. Bird species mist-netted on the two study plots (Hunt Club-treefall, Ridge-control) in Soberanía National Park in the Republic of Panama between 1994 and 2019, including common name, scientific name, the guild classification used in this study, the guild classification used in Stotz et al. (1996), and ecological traits (stratum, diet, and substrate).

Table S2. Alpha diversity of birds captured at Hunt Club (treefall plot) for each avian guild in Soberanía National Park in the Republic of Panama (1994 to 2019).

Table S3. Abundance of birds captured at Hunt Club (treefall plot) for each avian guild in Soberanía National Park in the Republic of Panama (1994 to 2019).