Long-term assessment of resilience of avian assemblages following a major hurricane

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ABSTRACT

Strong tropical cyclones directly devastate forest habitats and indirectly affect forest-dependent animals. Many forecast models suggest cyclone intensity and size will increase as a result of climate change, and cyclone frequency also may increase. Short-term effects of strong cyclones on vertebrate assemblages are well documented, but we know little about longer-term effects. From 1997 to 2013 we monitored avian assemblages at tropical forest in southern Belize, a forest that was largely destroyed by category 4 Hurricane Iris in October 2001. We found little change in recruitment or species richness, but evenness dropped markedly the first two sampling efforts after the hurricane and species turnover (β diversity) did not stabilize until 6–9 years afterward. Body condition dropped immediately after the hurricane passed but recovered quickly. That population size of resident tropical, but not Neotropical migrant, bird species dropped across our 17-year study highlights the potential urgency of altered cyclonic activity: on average, a hurricane strikes Belize once per decade, yet an increase in frequency, to say nothing of destructive power, could serve to erode extant species associations, lead to local extirpation of forest-dependent species, and create novel, transitory assemblages whose chief characteristic is instability.

1. Introduction

It is axiomatic that cyclones inflict substantial ecological damage in the short term, especially to standing woody vegetation (Lugo, 2008). For vertebrate species, storm damage typically reduces population sizes and reshapes ecological communities at disturbed sites (Wunderle Jr, 1995; Tossas, 2006; García and Siliceo-Cantero, 2019; Marroquín-Páramo et al., 2021; Sil-Berra et al., 2021). Effects may be direct, such as mortality or displacement, or indirect, such as loss of food, roost sites, or nest sites (Wiley and Wunderle Jr, 1993).

In its broad outlines, assemblage recovery to pre-disturbance levels can occur relatively quickly (Johnson and Winker, 2010; Askins and Ewert, 2020), yet disturbance may induce humans to increase exploitation of forest ecosystems (Laurance et al., 2009; Kleinschroth and Healey, 2017), which delays or inhibits vertebrate population recovery (Goulding et al., 2016), and the cumulative effects of successive storms alter populations or communities more permanently (Marroquín-Páramo et al., 2021). Negative cumulative effects are a growing concern given that continued global warming is forecast to decrease the number of cyclones, including 'deep' cyclones, but increase both wind speed and rainfall amounts of these cyclones (Hawcroft et al., 2018; Patricola and Wehner, 2018; Esmaeili and Barbato, 2021; Pepler and Dowdy, 2021), thereby elevating their ecological impact.

The northern Central American isthmus (north of ~10°N) and adjacent Caribbean basin are cyclonic hotspots (Zhao et al., 2009; Lin et al., 2020)—locations across this region have a 5 % to at least 10 % probability of a hurricane strike in any given year (Pielke Jr et al., 2003), with Belize specifically hit, on average, once per decade over the past five millennia (McCloskey and Keller, 2009). Biodiversity is exceptionally high in the region—almost 8 % of the world's terrestrial species occur in an area that constitutes <1 % of Earth's land surface (Anderson et al., 2008)—setting the stage for a conservation crisis. Many populations of tropical species already face multiple threats to their persistence; addition of more destructive cyclones can do little but aggravate the threats.

Nevertheless, the considerable body of work conducted on ecological effects of cyclones is focused on response in the short term. Longer-term effects of cyclones, by contrast, are more difficult to elucidate, even

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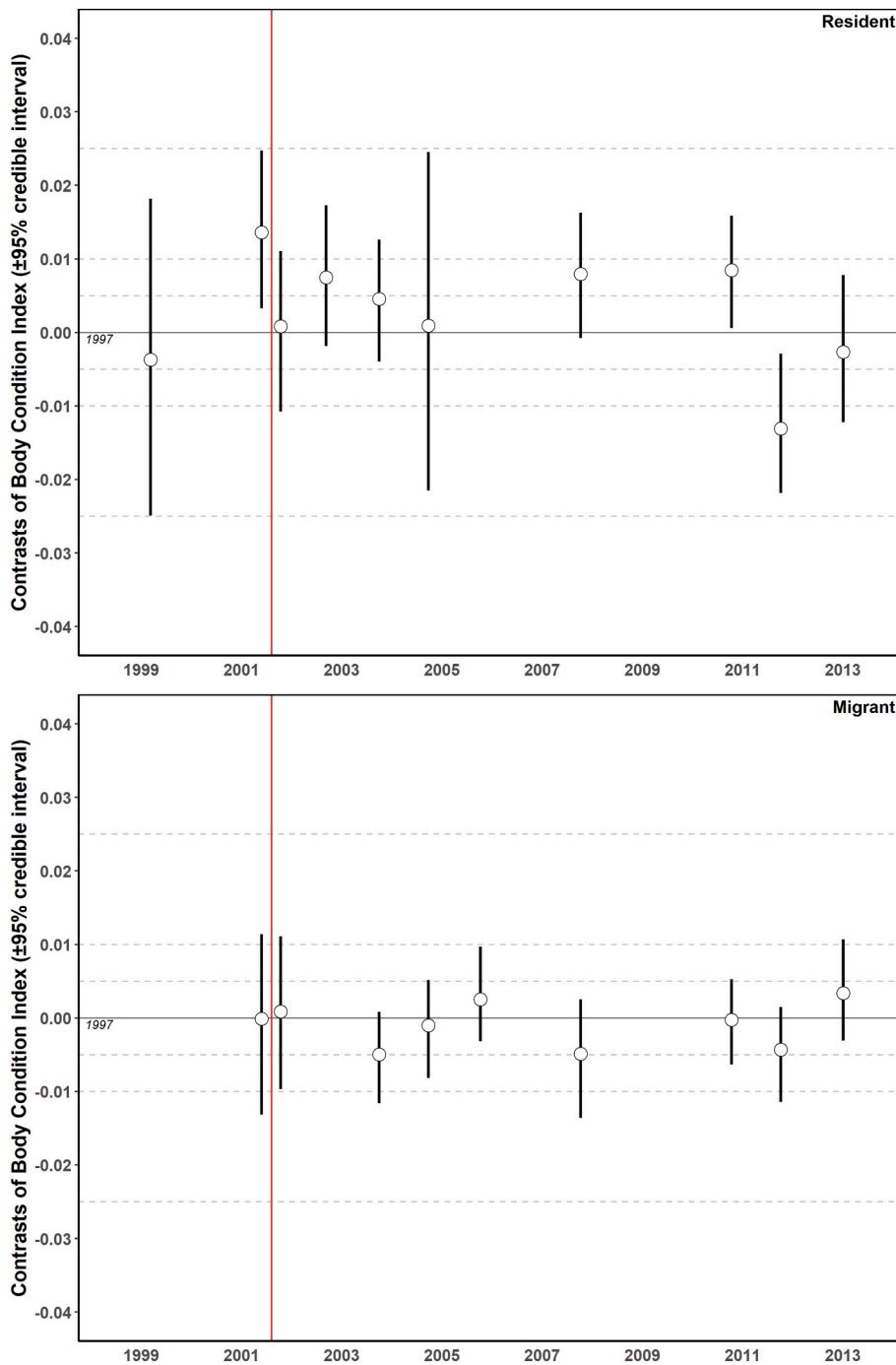
Fig. 1. Body condition index across years for resident breeders (top) and Neotropical migrants (bottom) captured near Big Falls, Belize, 1997–2013. Results are contrasts ±95 % highest density credible interval of a Bayesian mixed-effects model with species as the random factor. Contrasts are against the baseline of 1997. Note that body condition estimates for migrants are effectively stable across years—credible intervals of all contrasts overlap the 1997 standard—whereas body condition of residents fluctuated, with upward spikes in 2001 pre-hurricane (the red vertical line), in late 2007, and in late 2010 but a dip in late 2011. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

though our understanding of ecological resilience rests on longer-term data (Nikinmaa et al., 2020). Hence, it is imperative to determine the extent to which populations recover after a cataclysmic event and equally important to begin to understand the ways in which recovery is or is not achieved.

We present analyses of data from mist-net capture and recapture of resident breeders and Neotropical migrants across a 17-year span (1997–2013) during which a major (category 4) hurricane struck our study site in Belize. We explored how recruitment, population size, species richness, species evenness, and body condition changed over this span. We hypothesized that resident species would exhibit greater variation in recruitment and condition relative to migrants, which served as 'controls' because their condition or recruitment we affected by off-site factors. We further hypothesized that richness, evenness, and population size of residents would decline immediately after the 2001 hurricane before each returned slowly to pre-hurricane estimates, and that temporal β diversity—species turnover or dissimilarity between sampling periods—would not reach limits of sampling error until years later, after vegetation recovered sufficiently from cyclonic damage.
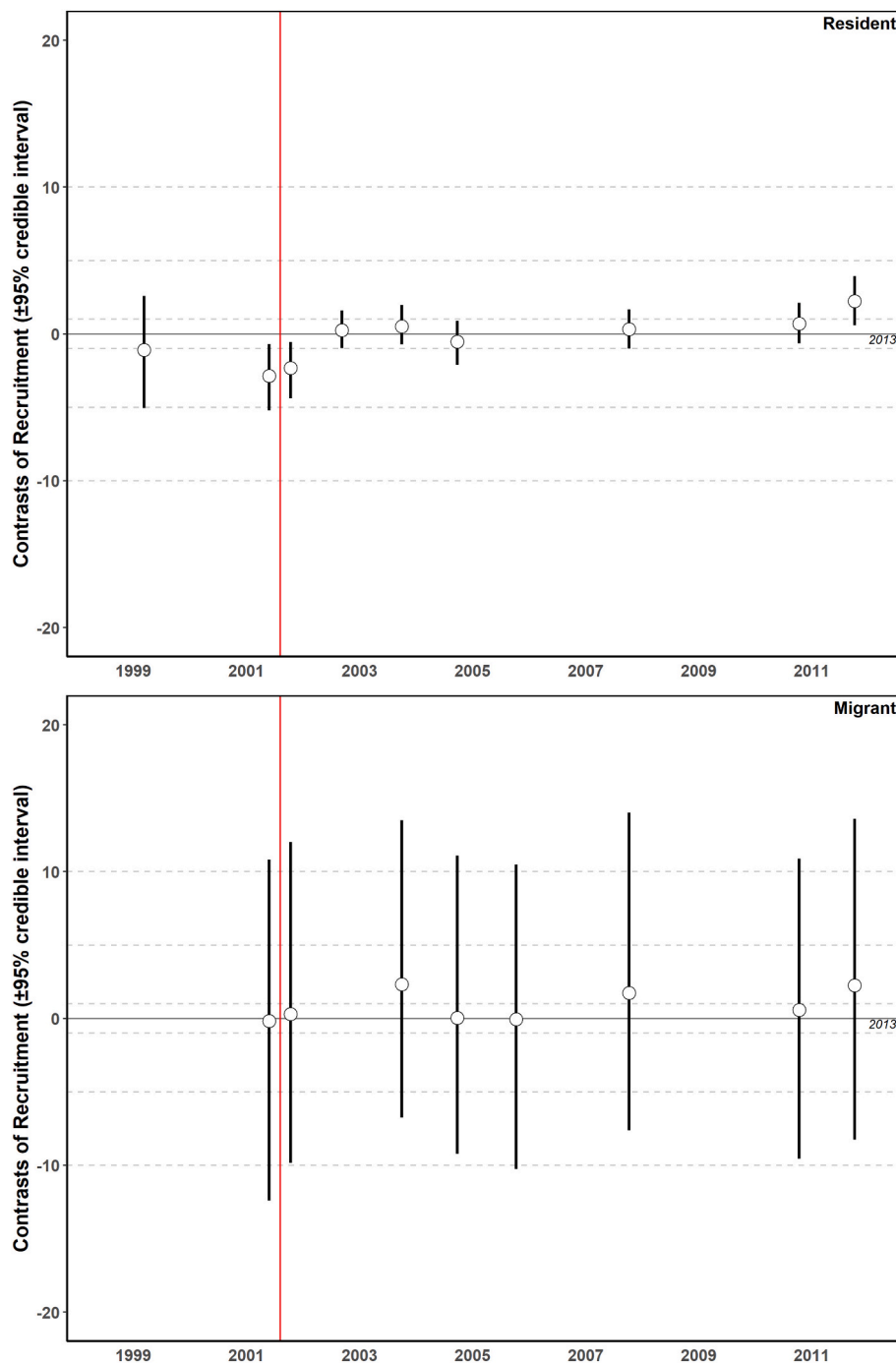
Fig. 2. Recruitment, estimated as the proportion of hatch-year/s-year (HY/SY) birds captured, across years for resident breeders (top) and Neotropical migrants (bottom) near Big Falls, Belize, 1999–2013. Results are contrasts ±95 % highest density credible interval of a Bayesian mixed-effects model with species as the random factor. Contrasts are against the baseline of 2013 because recruitment data for 1997 were insufficient [$n = 5$] to establish it as the baseline. Recruitment of migrants was unchanged across years and was relatively stable for residents excepting in 2001, the year of Hurricane Iris (the vertical red line), when the number of hatch-year birds dropped sharply. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Methods

2.1. Study site and field protocol

The study site was a 1.3-ha remnant primary (i.e., unlogged) forest adjacent to a quarter-century-old second-growth forest, itself bordering a dilapidated but partly active citrus orchard, all of it located in the floodplain of the Rio Grande (~300 m away) near Big Falls, Toledo District, Belize (16°15.89′N, 88°52.49′W; elevation 20 m). Citrus orchards have proliferated somewhat in the immediate area since the study was initiated, but the site nevertheless remains within tens or hundreds of meters of mature secondary forest or other remnant patches of primary forest. Climate is typified by a dry and relatively cool winter and spring and wet and relatively warm summer and autumn.

We captured birds in a series of thirty paired 12-m mist nets, half of which had a mesh size of 30 mm and half a mesh size of 36 mm. Captured birds were identified to species, aged, measured, and weighed; afterward, they were released from a makeshift banding station located centrally on site. Data were obtained 25 December 1997–4 January 1998, 12–19 March 1999, 10–17 March and 11 August–15 November
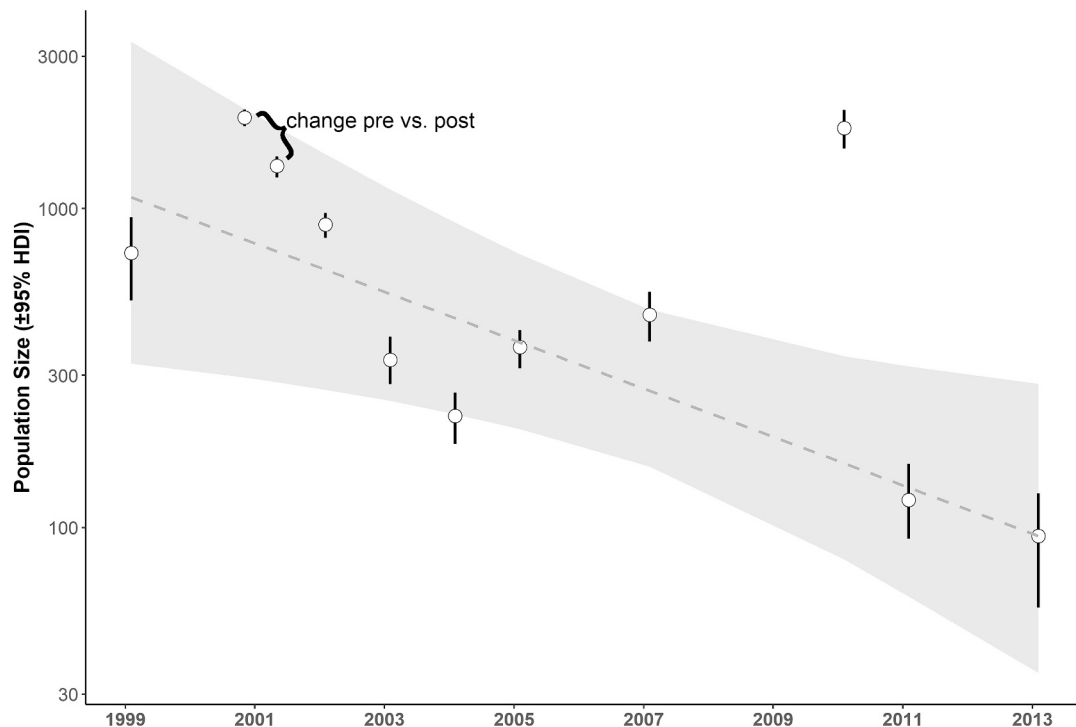
Fig. 3. Population size (on a $\log_{10}$ scale) of resident breeding birds near Big Falls, Belize, 1999–2013 (no recaptures were recorded in 1997). Results are estimates from a Bayesian implementation of the Schnabel index ±95 % highest density credible intervals, to which was fit a Bayesian linear regression (the fit line and shaded 95 % credible band). Population size of residents dropped markedly immediately after Hurricane Iris passed and has dropped steadily since (>99.1 % of posterior estimates of the slope were negative). Population size from 2010 was anomalously high because within-year recaptures ceased to be recorded midway through the banding effort, inflating the population size estimate.

2001, 8 September–15 November 2002, 29 September–18 October 2003, 22 September–17 October 2004, 9 October–3 November 2005, 8–20 October 2007, 12–24 October 2010, 4–13 October 2011, and 2–8 January 2013. Netting in 2001 was interrupted by Hurricane Iris, a category 4 tropical cyclone that passed through the study site on 9 October 2001—see Johnson and Winker (2010) for details about the storm's effects and about sampling protocol. Netting data for 2001 are therefore divided into pre-cyclone (on or before 7 October) and post-cyclone (on or after 11 October).

2.2. Statistical analyses

We estimated annual body condition (mass [g] divided by wing chord [mm]) and recruitment (proportion of hatch-year/second-year captures) across species. For comparative purposes, we separately analysed resident species and Neotropical migrant species. Estimates were obtained by means of a Bayesian mixed effects model, with species as the random factor and year as the fixed factor (in these and all other analyses, year 1997 included data obtained in the first few days of 1998). Data likelihood was normal with priors flat but constrained to be >0 (neither body condition nor recruitment can be negative).

Other analyses focussed solely on resident breeders. We estimated species richness with a Bayesian implementation of the Chao2 estimator (Chao et al., 2009). Incidences were counted annually—i.e., the number of species captured just once or just twice, counts needed for the Chao2 estimator, were calculated for each calendar year. Likelihood for count data was negative binomial; again, priors were flat. Species evenness was estimated as Pielou's *J* (Pielou, 1966), a ratio of the commonly used Shannon index and the raw (not estimated) species richness. As with the Chao2 estimator, our Bayesian implementation employed a negative binomial likelihood for the data. We estimated annual population size, taken across all resident breeders, via a Bayesian implementation of the Schnabel index (Schnabel, 1938), with likelihood in this case Poisson

rather than negative binomial because values were larger and were not overdispersed. Data for 2010 were problematic because many within-year recaptures were not recorded, which inflates estimates of population size. In an effort to reduce inflation, we removed from the 2010 dataset all captured individuals, mostly hummingbirds, that were not banded. Lastly, we estimated β diversity—change in species composition between our sampling efforts—as absolute turnover: $(S_1 - c) + (S_2 - c)$, where S_1 is species richness in the first effort, S_2 species richness in the second effort, and *c* the number of shared species across the two efforts. We restricted estimates of β diversity to consecutive survey efforts during which sampling was conducted in autumn (i.e., 1997, 1999, and 2013 were excluded) to avoid introducing seasonal bias.

Bayesian models were custom built in JAGS and run via the 'rjags' package (Plummer, 2019) in the R statistical environment. We used standard diagnostics to ensure good mixing and no autocorrelation in MCMC chains and sound, unimodal posterior distributions.

3. Results

Over the course of the study we captured 112 resident species and 40 migrant species. Mist nets are known to be biased: some species are more easily caught than others (Remsen Jr and Good, 1996). On the basis of field notes of all species noted at Big Falls during our mist-netting efforts (M. A. Patten pers. obs.), we captured almost all (~93 %) of Neotropical migrant species. By contrast, we captured nearer to ¾ (76.2 %) of resident species, although nearly all uncaptured species were those one would not expect to catch in mist nets at a forested site, including large raptors (e.g., *Spizaetus tyrannus*, the Black Hawk-Eagle), nocturnal hunters (e.g., *Ciccaba nigrolineata*, the Black-and-white Owl), scavengers (e.g., *Sarcoramphus papa*, the King Vulture), strictly terrestrial birds (e.g., *Crypturellus soui*, the Little Tinamou), canopy dwellers (e.g., *Amazona albifrons*, the White-fronted Parrot), aerial insectivores (e.g., *Chaetura vauxi*, Vaux's Swift), strictly aquatic birds (e.g., *Cairina moschata*, the
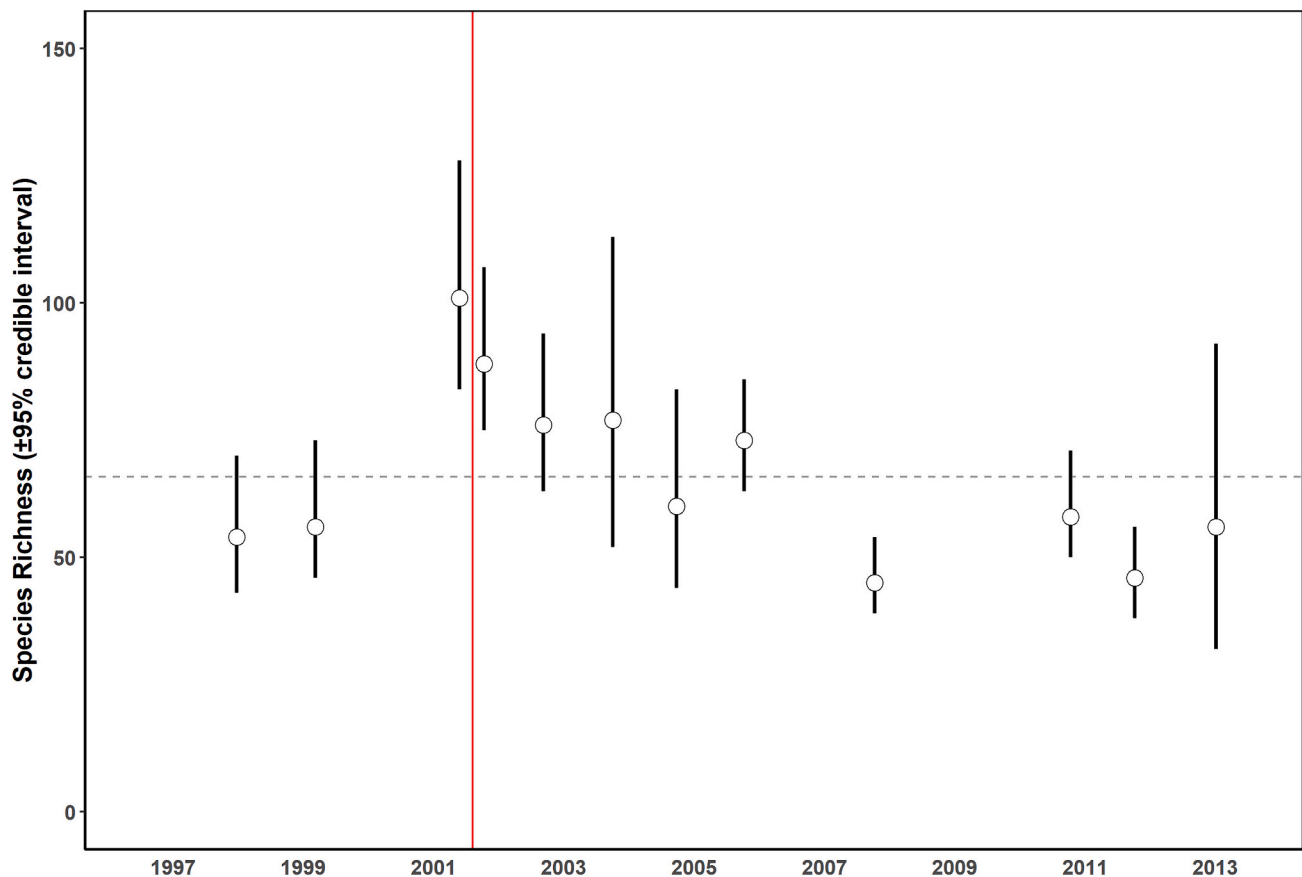
Fig. 4. Species richness (*S*) of resident breeding birds near Big Falls, Belize, 1997–2013. Results are estimates from a Bayesian implementation of the Chao2 estimator ±95 % highest density credible intervals. The horizontal line marks long-term mean *S*. Richness has varied markedly but in general was highest at and immediately after the passage of Hurricane Iris (the vertical red line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Muscovy Duck), and human commensals (e.g., *Quiscalus mexicanus*, the Great-tailed Grackle). Only three species reasonably could be classified as 'missed', in that they inhabit tropical forest and were noted on or near the study site: *Momotus lessonii* (Lesson's Motmot), *Rhytipterna holerythra* (the Rufous Mourner), and *Myiodynastes luteiventris* (the Sulphur-bellied Flycatcher).

Body condition varied considerably more for resident breeders than it did for Neotropical migrants captured on the site—for residents, condition was higher in pre-hurricane 2001, perhaps in 2002, and in 2007 and 2010, but it was markedly lower in 2011 (Fig. 1). Recruitment for both resident and migrant species was fairly constant across years with the exception of 2001, the year of the hurricane, in which it was markedly lower for residents (Fig. 2).

Estimated population size of resident breeding birds has dropped steadily across the 17 years of sampling, including a marked drop with the passage of Hurricane Iris in 2001 (Fig. 3). (Population size of Neotropical migrants has not changed: β = −0.10, HDI = [−0.21, 0.02].) By contrast, species richness may have declined across the 17-year study, although the trend is weak, and the estimate for the most recent sampling period, 2013, cannot be distinguished from the long-term mean (Fig. 4). Species evenness dropped markedly immediately after Hurricane Iris passed and did not recover to the long-term mean until two years later (Fig. 5), although altered species composition belied evenness estimates: β diversity did not drop to a lower, steadier level until between six and nine years post-hurricane (Fig. 6).

4. Discussion

In general we can conclude that assemblages of tropical birds are

resilient to strong cyclonic storms. We observed immediate drops, in resident species, in population size and species evenness, but no discernible change in body condition, recruitment, or species richness. We had not expected to see the steady drop in breeding resident birds, *N*, but only a sharp drop immediately after Hurricane Iris (Fig. 3), comparable to population drops in other post-hurricane studies (Wiley and Wunderle Jr, 1993; Rittenhouse et al., 2010; Askins and Ewert, 2020). In our dataset, the steady drop was even higher given that the seeming outlier in 2010 likely was artificially high because within-season recaptures were not recorded consistently on banding sheets. Nonetheless, Winker noted contemporaneously in his field notes that the number of between-year recaptures that year was high relative to rates in 2007. It might be hypothesized that sharp drops after cyclonic damage to habitat result from disproportionate mortality of young birds, but recruitment estimates (Fig. 2) do not support such a hypothesis, implying that cyclone mortality is indiscriminate with respect to age.

Species richness is expected to be less sensitive to disturbance than is species evenness (Mackey and Currie, 2000). That we saw no pattern in species richness but detected a sharp drop in species evenness immediately after Hurricane Iris and in the subsequent year is consistent with this expectation. Our data showed that evenness returned to its long-term mean in just two years (Fig. 5), despite catastrophic damage to the study site's forest habitats (Johnson and Winker, 2010). Ultimately, it may be that predictions derived from ecological theory "are sufficiently broad that essentially any relationship between diversity and disturbance is consistent with them" (Mackey and Currie, 2000), yet empirical data suggest that evenness increases after cyclonic damage (Schriever et al., 2009; Martínez-Ruiz and Renton, 2018; Marroquín-Páramo et al., 2021). Such results imply that disturbance disrupts
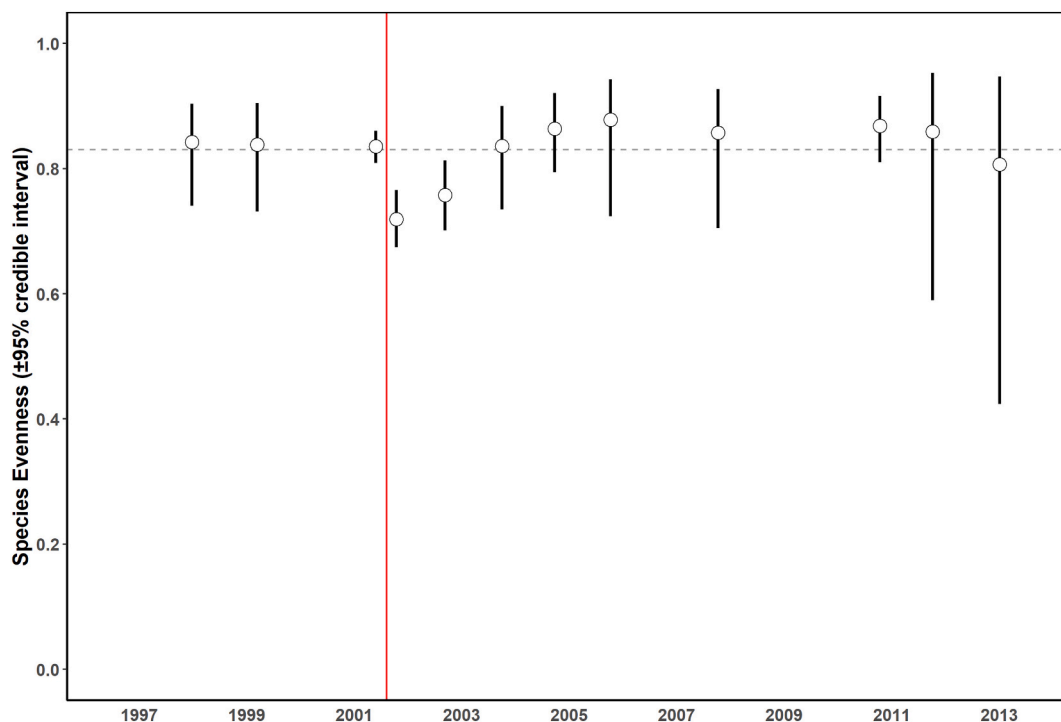
Fig. 5. Species evenness of resident breeding birds near Big Falls, Belize, 1997–2013. Results are estimates from a Bayesian implementation of Pielou's *J* ± 95 % highest density credible intervals. The horizontal line marks long-term mean *J*. Evenness of residents dropped markedly immediately after Hurricane Iris passed (the vertical red line) and remained low for a year until it reached pre-cyclone levels, where it has remained. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
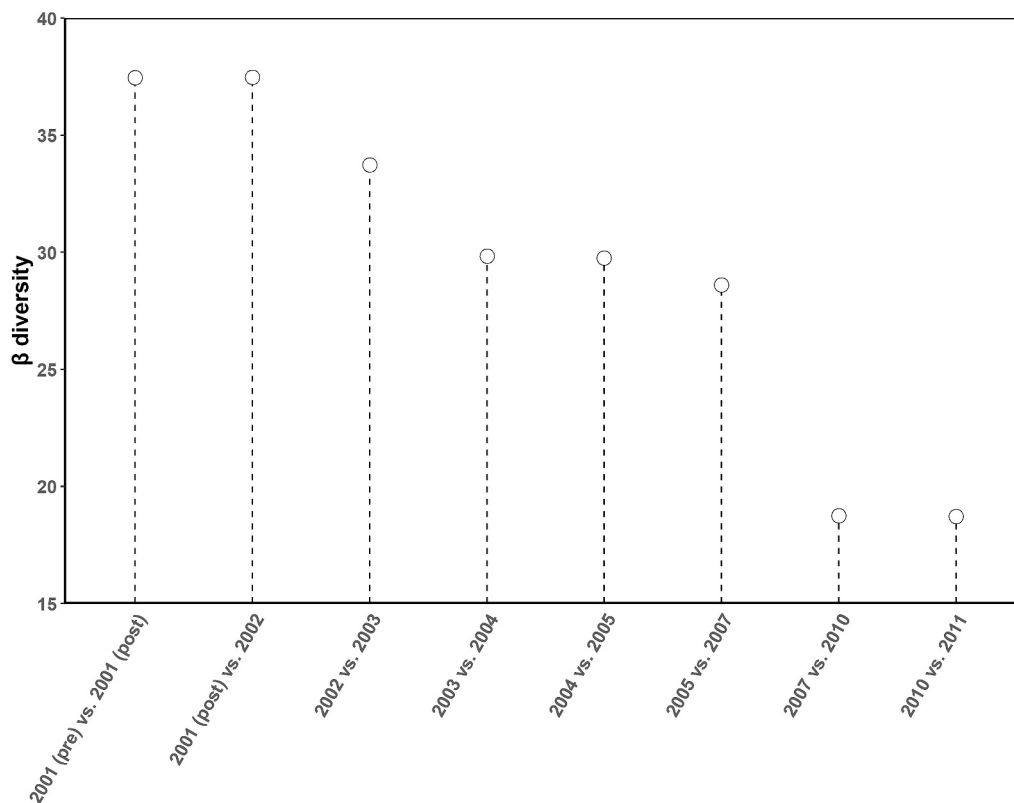

Fig. 6. Estimated β diversity of breeding resident species between autumn sampling periods near Big Falls, Belize, 2001 (pre-hurricane) to 2010. Results are estimates from a Bayesian implementation of absolute species turnover (see text). Note the relatively high turnover before and after Hurricane Iris, when forest cover changed considerably (Johnson and Winker, 2010), and between the first post-hurricane sampling and the subsequent year, when forest recovery was underway. β diversity steadily dropped as the forest returned to second growth and open areas disappeared.

assemblages in a way that previously numerically dominant species are no longer dominant. Our result implies the opposite: certain species were more dominant immediately after Hurricane Iris passed. A species-by-species examination of capture histories points to an expected pattern of increase in open-habitat species at the expense of forest species, a pattern that has played out across the northern Neotropics (Patten and Smith-Patten, 2011; Levey et al., 2023).

Evenness rebounded quickly, but β diversity—species turnover or dissimilarity between sampling periods—took much longer, at least six years as opposed to just two (Fig. 6). A review of post-hurricane effects of avian assemblages across a broad spatial area (Rittenhouse et al., 2010) found that post-disturbance assemblages remained unlike pre-disturbance assemblages for at least five years after cyclonic damage was sustained. Such a pattern has logical appeal in that tropical plant communities are substantially defoliated during the first several years after cyclonic damage, and return to pre-disturbance levels of both canopy cover and species composition may take up to two decades (Lugo, 2008). Fruit load also drops drastically post-hurricane and does not return to pre-hurricane levels for several years (Renton et al., 2018). Hence, the pattern in β diversity 2001–2011 at our study area likely represented both within- and among-species temporal response to vegetation (and associated forage) recovery, which ultimately will vary with hurricane intensity (Lugo, 2000; Renton et al., 2018).

Species turnover includes apparent extirpation from the site of six species recorded in 1997, 1999, or 2001 that were not recorded after the passage of Hurricane Iris. Two of these species, *Leptopogon amaurocephalus*, the Sepia-capped Flycatcher, and *Lanio aurantius*, the Black-throated Shrike-Tanager, inhabit primary humid forest. If either species returns to the study site it may be decades in the future, assuming no further deforestation (from whatever cause). Of particular concern is the shrike-tanager, as species in the genus *Lanio* play important sentinel or nuclear roles in mixed-species flocks (Ridgely and Tudor, 1989; Howell and Webb, 1995; Mangini et al., 2023). Absence of *Lanio aurantius* could inhibit formation or cohesion of mixed-species flocks. Two missing species were *Campylopterus curvipennis* (the Wedge-tailed Sabrewing) and *C. hemileucurus* (the Violet Sabrewing), both forest-dwelling hummingbirds, and another was *Myiodynastes maculatus* (the Streaked Flycatcher), a species found most often at edges of primary or mature secondary forest. The final missing species was *Myiozetetes similis* (the Social Flycatcher), a common species of edges and disturbed (e.g., populated) areas whose post-hurricane absence we cannot explain.

Just over 10 % (12 of 112) resident species were captured on-site only in Iris's immediate aftermath, likely as a result of temporary displacement (Johnson and Winker, 2010). Three of these species—*Polioptila bilineata* (the White-browed Gnatcatcher), *Chlorophanes spiza* (the Green Honeycreeper), *Stilpnia larvata* (the Golden-hooded Tanager)—are canopy dwellers. An additional fourteen resident species captured only in the first four years post-hurricane (through 2005) included several additional canopy dwellers, such as *Notharchus hyperrhynchus* (the White-necked Puffbird), *Tityra semifasciata* (the Masked Tityra), and *Euphonia hirundinacea* (the Yellow-throated Euphonia). Felling of large trees evidently forced down-storey displacement post-hurricane (Wunderle Jr, 1995), increasing probability of capture. That nearly one-fourth (26 of 112) of resident species were captured only immediately after Iris or within the subsequent four years, before substantial forest recovery, highlights the potential magnitude of species turnover in disturbed tropical systems.

Within genus turnover is instructive. *Sporophila corvina*, the Variable Seedeater, a forest species partial to edges or treefall gaps, was captured every sampling period across the 17-year study, but captures dropped initially in the wake of Hurricane Iris. Captures rates of *Sporophila funerea*, the Thick-billed Seed-Finch, a forest species partial to forest interior, dropped markedly after Hurricane Iris but rebounded with the forest recovery. *Sporophila morelleti*, Morelet's Seedeater, a species of open habitats, disturbed areas, and scrub, was captured in by far the highest numbers in the two sampling periods immediately after

Hurricane Iris but not captured at all in the last three sampling periods, when the site supported mostly tall second growth forest. In a similar vein, of the three *Leptotila* doves captured, *L. cassini*, the Gray-chested Dove, is strictly a forest denizen, most often primary forest but also more mature secondary forest; captures of it dropped in the first two post-hurricane sampling periods. By contrast, *L. plumbeiceps*, the Gray-headed Dove, favors second-growth; it was captured only post-Iris, from immediately after passage through 2011. We note that each of these species is primarily granivorous. Granivores may be more numerous following a major hurricane (Levey and MacGregor-Fors, 2021), although species turnover within foraging guild is less well documented.

Taken together, our three clear findings—an immediate drop but quick (< 2 y) recovery of evenness, a longer-term decline in population size, and the lengthy (> 6 y) return time for species turnover—make possible certain predictions for a world in which tropical cyclones are likely to become more intense (Hawcroft et al., 2018; Patricola and Wehner, 2018; Esmaeili and Barbato, 2021) and may become more frequent (Lugo, 2000; Balaguru et al., 2023). First, patterns of numerical dominance in avian assemblages may be permanently disrupted if recovery time is insufficiently long. Loss of species, especially those sensitive to disturbance of the light environment (Patten and Smith-Patten, 2012; Rutt et al., 2023), may lead to stable evenness at reduced species richness. Second, population size may be permanently lowered—especially for forest-dependent species, a pattern documented elsewhere in the northern Neotropics (Levey et al., 2023)—and could be exacerbated by permanent changes in tree species composition (Zhang et al., 2022). Third, avian assemblages may never be stable because species composition will fluctuate dynamically at a much more rapid pace than baseline expectations, until after a period over which more-frequent disturbance—including, importantly, synergy between destructive hurricanes and steady deforestation from industrial agriculture (Arevalo et al., 2016), including orchards and plantations—establishes early successional second-growth forest of a more "permanent" nature.

CRediT authorship contribution statement

Michael A. Patten: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Andrew B. Johnson:** Writing – review & editing, Validation, Resources, Methodology, Investigation. **Kevin Winker:** Writing – review & editing, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

We have no conflicts of interest to declare. Further, none of the authors has any financial interests at stake or any intellectual property disputes. Funding for this work was piecemeal and often from carryover or research incentives and thus cannot be reported at the level of individual grants.

Data availability

Data will be made available on request.

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