What does resilience sound like? Coral reef and dry forest acoustic communities respond differently to Hurricane Maria

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ABSTRACT

Disturbance regimes and biodiversity—two factors that govern the stability of ecosystems—are changing rapidly due to anthropogenic forces including climate change. Determining whether ecosystems retain their structure and function through intensifying disturbance regimes is an urgent task. However, quantitatively assessing the resilience of natural systems is a complex and challenging endeavor, especially for animal communities, for which datasets around disturbance events are scarce. Here, we apply an emerging remote sensing technology—the recording and analysis of soundscapes—to quantify the resilience of Puerto Rican coral reef and dry forest animal communities in relation to Hurricane Maria, which struck the island in September 2017. Using recordings collected between March 2017 and January 2018 at three terrestrial and three marine sites, we measured three dimensions of resilience—the magnitude of the impacts (resistance), the spatial pattern of the impacts (heterogeneity), and the diversity and timeline of functional responses (recovery)—across eight sound types representing different broad taxonomic groups. While the coral reef communities exhibited high resistance to the storm, all sound types within the dry forest were significantly impacted, with two of the three insect choruses and bird vocalizations at dawn declining approximately 50% in the weeks following Hurricane Maria. The mid-frequency insect sound type returned to pre-storm levels after 56 days, while bird vocalizations returned after 67 days, though seasonal and lunar patterns underscored the importance of long-term data for accurately measuring trajectories of recovery. This study demonstrates that soundscape methodologies can help to quantify elusive dimensions of animal community resilience in order to better understand how biodiversity and ecosystem functioning will change under novel disturbance regimes.

1. Introduction

Patterns of disturbance and response shape ecosystem dynamics (Foley et al., 2005; Rockström et al., 2009; Turner, 2010), and ecosystems have developed high resilience to historical disturbance regimes—that is, they retain their essential structure and functioning after perturbation (Holling, 1973). Despite their remarkable natural resilience, the stability of ecosystems is increasingly being tested by

human activities, which are altering historical disturbance regimes and the capacity of ecosystems to recover (Johnstone et al., 2016). Increasing frequency and intensity of disturbances in combination with decreased response capacity can trigger enduring shifts into novel states that may fail to provide comparable ecosystem services (Folke et al., 2004). In this time of rapid environmental change, quantifying the resilience of ecosystems can improve our abilities to predict disturbance impacts, estimate the loss of ecosystem services, and conduct adaptive management. While resilience theories are becoming more refined, few practical methods exist to measure ecosystem resilience in real-world contexts (Bennett et al., 2005). Rigorous and replicable methods to measure ecological resilience are needed to better understand where, when, and how altered disturbance regimes will fundamentally transform ecosystems.

One measurable and important contributor to ecosystem resilience is biodiversity (Folke et al., 2004; Oliver, et al., 2015a; Oliver et al., 2015b; Peterson et al., 1998). Biodiversity-related mechanisms operating at the species, community, and landscape levels can bolster resistance to, and recovery from, perturbations (Oliver et al., 2015a). Species (and individuals within a species) vary in their ability to withstand perturbations, adapt to environmental changes, and maintain or expand populations following disturbance (Peterson et al., 1998). At the community level, resilience is strengthened when multiple species perform similar functional roles but exhibit a diversity of disturbance responses (Elmqvist et al., 2003). In this way, biodiversity has an insurance effect that has been demonstrated theoretically and empirically, whereby resilience improves with greater species richness and evenness across trait-response space (Chillo et al., 2011; Kissick et al., 2018; Mouillot et al., 2013). At the landscape level, higher environmental heterogeneity (and also beta diversity; see Mellin et al., 2014) increases the spatial heterogeneity of disturbance impacts, which bolsters resilience by creating refugia where organisms can persist through disturbance events (Oliver et al., 2010) and subsequently colonize more disturbed parts of the diverse landscape (Adger et al., 2005).

Biodiversity is often measurable, but traditional assessment techniques are typically limited in the taxa that are surveyed, are costly and impractical to conduct, especially over long durations and around unpredictable pulse disturbance events (Sueur et al., 2008). As a result, biodiversity datasets that contain pulse disturbances usually have low temporal resolution (i.e. monthly or seasonal surveys), which increases the risk of type I error when observed changes are caused by seasonality or longer-term stressors, as opposed to the disturbance of interest (the false snapshot effect; Adams, 2001). Low temporal resolution also fails to capture finer-scale changes in temporal variability that signal instability and approaching regime shifts (Carpenter and Brock, 2006). Furthermore, these survey efforts are usually short term (<2 years post-disturbance), precluding the capture of any longer-term response patterns. While human-led survey efforts will always constitute an essential part of biodiversity monitoring, especially to identify the processes and drivers linked with observed ecosystem changes, some of their shortcomings are being addressed through novel technological applications.

Remote sensing technologies that are automated and standardized can measure ecosystems at unprecedented temporal and spatial scales. Visual remote sensing (e.g., satellites, LiDAR, and drones) has emerged as an effective method for capturing changes in vegetation and habitat structure at fairly high temporal resolution (with measurements every few days), but it has limited applications for direct animal community monitoring (Gasc et al., 2018, but see Spaan et al., 2019). Audio recordings, however, are comparably effective at capturing changing patterns in wildlife presence or behavior (Gasc et al., 2018; Pijanowski et al., 2011a) and deliver data with millisecond-level temporal resolution. With recent advances in storage capacity and energy efficiency, acoustic recorders can now capture months or years of data between servicing periods (Gage and Axel, 2014; Gibb et al., 2019; Hill et al., 2018), making this technology highly useful for assessing the animal impacts of unpredictable pulse disturbances.

Soundscape recordings are increasingly being used to assess the impact of disturbance on animal communities (Indeck et al., 2015; Gasc et al., 2018; Lee et al., 2017). Because animal diversity and abundance have been shown to correlate with the complexity and amplitude of soundscapes (Buxton et al., 2018a, 2018b; Harris et al., 2016; Rowell et al., 2017; Sueur et al., 2014; Zhao et al., 2019), acoustic monitoring could potentially reveal the magnitude of environmental disturbances through the changes in soundscape characteristics after disturbance events. However, whether soundscape-disturbance relationships are generalizable across disturbance types and ecosystems is still unclear. Furthermore, identifying which soundscape components relate to different dimensions of disturbance ecology is critical to unlocking the potential of this emerging method.

We posit that soundscapes can be used to measure three components of ecological resilience: the magnitude of disturbance impacts (resistance), the spatial patterns of disturbance and recovery (heterogeneity), and the diversity and timeline of responses across species and functional groups (recovery). In ecosystems where animals from different taxonomic and functional groups produce sound, it is possible to acoustically assess the resistance and recovery of individual species, functional groups, and animal communities (Butler et al., 2016; Buxton et al., 2016; Coquereau et al., 2017). If multiple acoustic recorders are deployed within a habitat, analyzing the variability in acoustic responses across sites can also provide insight into the spatial heterogeneity of impacts (Browning et al., 2017). Overall system resilience can be evaluated by the degree of initial alteration (resistance) and the time it takes for post-disturbance soundscapes to regain similar composition and dynamics to pre-disturbance soundscapes (recovery) (Angeler et al., 2014).

Here, we analyzed soundscape resilience in two coastal ecosystems in Puerto Rico following Hurricane Maria (hereafter "Maria"), which swept across the island on September 20, 2017, just two weeks after Hurricane Irma, another major hurricane, passed by the island on September 6. While hurricanes are a natural, foundational disturbance in tropical coastal ecosystems, there is growing consensus that climate change is increasing the frequency of intense storms, especially in the Atlantic Ocean (Holland and Bruyère, 2014; Knutson et al., 2010, Pielke et al., 2003). Since at least 1995, we have experienced a multi-decade period of heightened storm activity in the Atlantic, with 2005 and 2017 as exceptionally hyperactive years (Chylek and Lesins, 2008). Maria was the strongest Atlantic storm in 2017 and the second most powerful storm to affect Puerto Rico in its documented history (Feng et al., 2018). The storm killed over 2000 people, caused $90 billion in damages, and drastically altered natural systems across the island (Halverson, 2018; Kishore et al., 2018; Van Beusekom et al., 2018). There was mass defoliation, with 23–31 million trees severely damaged or killed (Feng et al., 2018). Animal responses are still largely uncharacterized, though several studies have noted declines in granivorous, frugivorous, and nectivorous birds following Hurricane Maria and Hurricane Irma (Lloyd et al., 2019). Shallow coral reefs in Puerto Rico suffered severe damage during Maria, with wave-exposed sites receiving large swells that overturned, broke, or buried an estimated 11% of the island's corals (NOAA, 2018). Although the responses of plants, animals, and ecosystem structure to Caribbean hurricanes have been studied through traditional methods (Tanner et al., 1991), soundscape ecology could reveal other dimensions of ecosystem responses (Deichmann et al., 2017; Pijanowski et al., 2011a, 2011b).

We took advantage of three terrestrial and three marine automated recorders that we deployed in dry forest and coral reef habitats in coastal Puerto Rico that recorded soundscapes from March 2017 to January 2018, six months before to four months after Maria struck the island. To assess the impacts of the hurricane on the terrestrial and marine communities, we identified eight sound types representing different functional groups and measured 1) which sound types were significantly impacted by the storm and the magnitude of these impacts, 2) whether the marine and terrestrial acoustic communities were impacted by the storms, the magnitude of these impacts, and how these impacts differed

across sites, and 3) the recovery rates of sound types that were significantly impacted. We hypothesized that acoustic activity across all sound types would decline following Maria because of a combination of direct mortality, dispersal, and behavioral change (Waide, 1991a). We also hypothesized that the terrestrial impacts would be greater and more prolonged than the marine impacts, given post-storm field observations revealing greater physical modification of the dry forest sites, relative to the coral reef sites.

2. Materials and methods

2.1. Site descriptions

This study was conducted in coral reef and dry forest habitats in southwest Puerto Rico, the driest part of the island (Fig. 1a; Ewel and Whitmore, 1973). La Parguera Natural Reserve (LPNR), where we recorded coral reef soundscapes, is a marine protected area that covers all of the coastline of the Lajas municipality, extending 1 km inland and 9 nautical miles offshore from the shoreline (Fig. 1b). With respect to other reef systems around the island, it is large, has better-defined reef zonation (fore reef, reef crest, back reef, and lagoon), and contains extensive mangroves and seagrass beds that are nursery habitats for many reef fish species (Ballantine et al., 2008; Morelock et al., 1977). Approximately 20 km east of the sensors in LPNR, we recorded dry forest soundscapes at Guánica State Forest and Biosphere Reserve, which is considered the best preserved subtropical dry forest in the Caribbean (Fig. 1c; Ewel and Whitmore, 1973). Approximately half of Puerto Rico's bird species and 15 of its 17 endemic bird species inhabit Guánica State Forest (Arendt et al., 2015). It has four main forest types: upland deciduous, semi-evergreen, lowland scrub, and coastal mangroves (Lugo et al., 1978).

2.2. Acoustic data collection

From March 9, 2017 to January 1, 2018, we deployed three acoustic recorders in each of these two systems to capture and compare their annual soundscape dynamics (Table 1). At the coral reef sites in LPNR, three Wildlife Acoustics SM3M recorders equipped with HTI-96-MIN hydrophones were installed across an inshore to offshore gradient (near-shore, mid-reef, and shelf-edge). Each marine recorder was fastened to a rebar rod approximately 1 m above the substrate. Sensors recorded successive, hour-long recordings (sampling rate: 48 kHz; bit depth: 16 bits; gain: 18 dB). The arrival of the storm coincided with one of the recorder servicing periods, and as a result, data were not obtained in the 17 days immediately after the storm for the marine sites. Three Wildlife Acoustics SM4 terrestrial recorders were installed around the same time as the marine recorders across a coastal gradient in the Guánica Dry Forest (coastal, lowland, and upland). Each recorder was fastened to a tree at a height of 1.5 m. Sensors recorded 10 min every 30 min using built-in SM4 microphones (sampling rate: 48 kHz; bit depth: 16 bits; gain: 18 dB).

2.3. Soundscape analysis

Before analysis, recordings were screened, divided, and converted to mono. Marine recordings that were shorter than 59 min, captured during recorder servicing periods, or corrupted during data offloading, were removed from the dataset. Each hour-long recording was divided into 60 1-minute-long files. The percentage of days with incomplete or no data over the course of the study period was 23% at the near-shore site, 14% at the mid-reef site, and 20% at the shelf-edge site. Terrestrial recordings were converted to mono by selecting the audio channel with the greatest preservation of high frequency content following Maria. The percentage of days with incomplete or missing data for terrestrial sites was 22% at the coastal site, 25% at the lowland site, and 24% at the upland site.

2.3.1. Identifying biological components of the soundscape

Especially in a system with uncharacterized soundscapes, it is important to become familiar with the soundscape composition and dynamics prior to analysis (Gottesman et al., 2018). To identify the main biological sound types, BG listened to portions of over 200 recordings from each site (20 h) from different times of the day and different times of the year while reviewing their spectrograms. We also generated long-term power spectral density (Merchant et al., 2015) and false color spectrograms (Towsey et al., 2014a) to better understand soundscape dynamics over longer timeframes (Fig. 2; code and additional
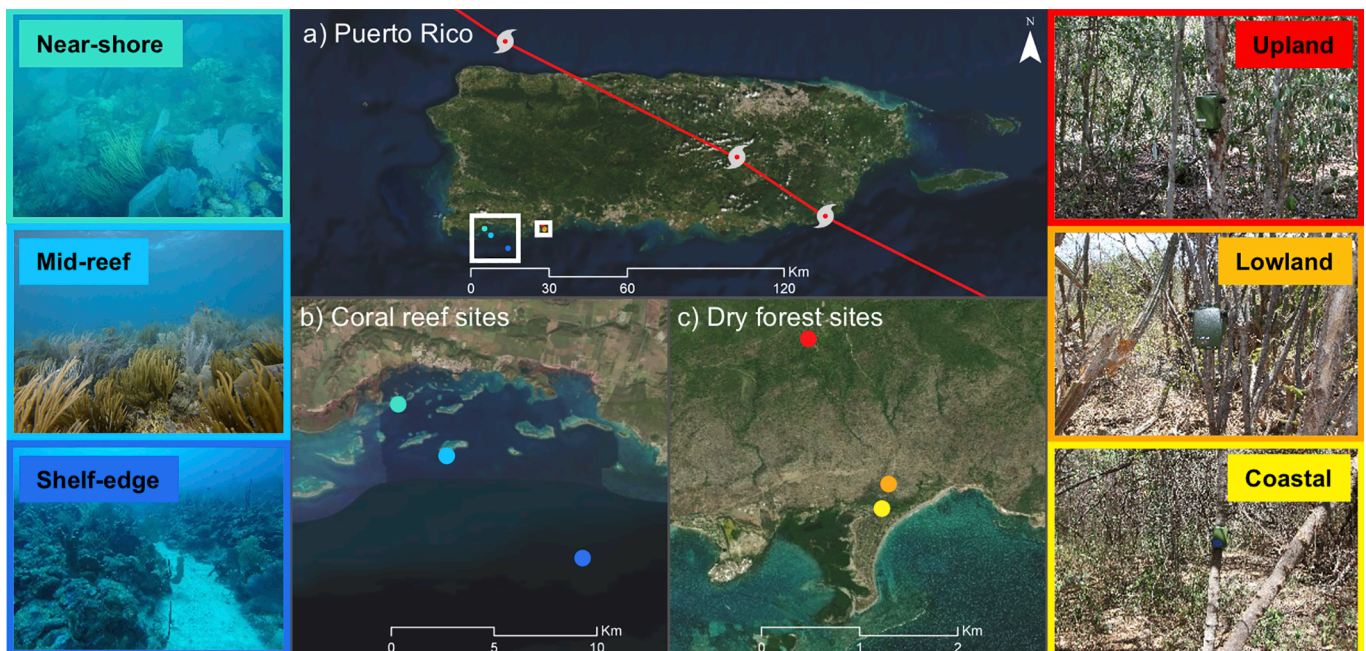

Fig. 1. Map of the study region including a) the island of Puerto Rico and the path of Hurricane Maria, b) the three marine recorder sites in La Parguera Reserve, and c) the three terrestrial recorder sites in Guánica Dry Forest. The six images on the left and right of the figure portray the six study sites. Frame colors of each site photo correspond to their points on the maps and are used to represent these sites in subsequent figures.

Table 1

Site information for coral reef and dry forest recording locations, including latitude, longitude, depth or elevation, distance from shore, and notes about the habitat.

|	Site	Latitude	Longitude	Depth or Elevation (m)	Distance from Shore (km)	Notes
Coral reef	Near-shore	17.957367	−67.0696	14	1.8	steeply sloping linear reef
	Mid-reef	17.934883	−67.0489	18	4.5	octocoral-dominated forereef
	Shelf-edge	17.890483	−66.9887	22	5.8	spur and groove coral
Dry forest	Coastal	17.95451	−66.8630	3	0.2	mangrove/scrub interface
	Lowland	17.95676	−66.8623	12	0.4	scrub
	Upland	17.97004	−66.8697	148	1.9	deciduous
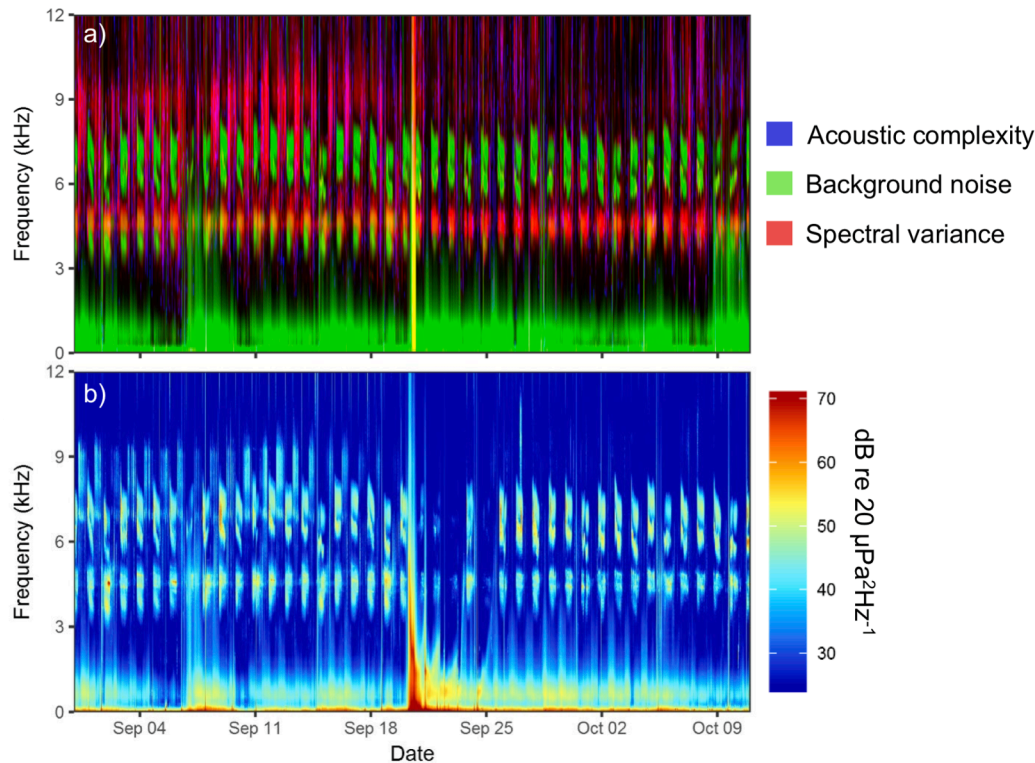
Fig. 2. Long-term false color (a) and power spectral density (b) spectrograms for the coastal dry forest site. In the false color spectrogram, the multiple insect sound types are shaded in different colors. After the storm, the low-frequency insect chorus (shaded green between 3 and 4 kHz) is mostly absent. Similarly, the red streaking between 5 and 10 kHz, which represents diurnal bird vocalizations, is greatly diminished after Maria. Acoustic complexity sums the sequential changes in intensity for each frequency band (Pieretti et al., 2011). The second index, background noise, corresponds to the mode of the decibel intensity values for each frequency bin in the spectrogram (Towsey, 2017). The third index, spectral variance, was developed for this study and is the standard deviation of intensity values within a frequency bin. The power spectral density spectrogram was created by stitching together power spectral density values calculated for the first minute of each recording. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

spectrograms available through GitHub; see Supplementary Information for details). In the marine soundscapes, fish and snapping shrimp were the primary sound producers, and their sounds were easily distinguishable in the time–frequency domain. In the terrestrial environment, insects and birds were the primary sound producers, and their sounds were distinguishable as well. For the fish and insects, we identified different frequency bands containing their sounds when spectrograms were viewed with a window length of 8192 samples. On the basis of these taxonomic and frequency distinctions, we defined distinct sound types.

Across all sites, we identified eight broad biological sound types, four for the coral reef and four for the dry forest, and quantified their

frequency ranges and temporal dynamics (Table 2). In the marine system, sound types included a low-frequency fish (LFF) chorus that occurred around dusk, a high-frequency fish (HFF) chorus that occurred at night, sporadic fish pulses (FP) that generally peaked at dawn and dusk, and broadband snaps from snapping shrimp (SS) that were ever-present but exhibited peaks at dawn and dusk. In the terrestrial system, sound types included bird vocalizations (BV) that peaked at dawn, and low-, mid-, and high-frequency insect (LFI, MFI, and HFI) choruses that peaked at night. We sought to measure the acoustic activity of each sound type that we identified for each day of the study period. For sound types that dominated their respective frequency bands (fish choruses, shrimp snaps, and insect choruses), we measured sound pressure levels

Table 2

Information for the eight sound types including their frequency ranges, active hours, and measurement methods as well as references to studies that employed similar methods.

Habitat	Sound type	Symbol	Frequency range (Hz)	Active hours	Measurement method	Reference(s)
Coral Reef	Low-frequency fish chorus	LFF	150–450	18:00–22:00	Peak SPL	Rowell et al., 2017; Kaplan et al., 2018
	High-frequency fish chorus	HFF	900–2000	22:00–05:00	Peak SPL	Rowell et al., 2017; Kaplan et al., 2018
	Fish pulses	FP	50–650	All hours	Band-limited energy detector	Luczkovich et al., 2016
	Snapping shrimp	SS	3000–24,000	All hours	Median SPL	Lillis et al., 2014; Rossi et al., 2017
Dry forest	Low-frequency insect chorus	LFI	2500–4300	18:00–05:00	Median SPL	Staaterman et al., 2017
	Mid-frequency insect chorus	MFI	4300–5250	18:00–05:00	Median SPL	Staaterman et al., 2017
	High-frequency insect chorus	HFI	5500–10,000	18:00–05:00	Median SPL	Staaterman et al., 2017
	Bird vocalizations	BV	1000–10,000	06:00–08:00	Spectral saturation	Towsey, 2017; Burivalova et al. 2018

(SPLs) in those frequency bands. For sound types that did not dominate their frequency bands (bird vocalizations and fish pulses), we calculated other acoustic metrics that better measured these sounds (described in Section 2.3.3). We consulted experts in Puerto Rican taxa and bioacoustics (Michelle Umpierre, David Mann, and RA for fish sounds, OAC for birds, and OAC and Carl Strang for insects) to identify the producers of these sound types when possible.

2.3.2. Dominant sound type analysis

To measure the six dominant sound types (two fish choruses, snapping shrimp, and three insect choruses), we first calculated SPLs in R (R Core Team, 2012) using "PAMGuide" (Merchant et al., 2015). Audio files were converted into the time–frequency domain with a short-term Fourier transform (STFT) using a Hann window, a window length of 0.5 s, and zero overlap. For each sound type, the output of the STFT (12,000 frequency bins by 120 time windows) was cropped to the upper and lower bounds of the sound type's frequency range, summed within each time window, and then converted into calibrated dB values using the hydrophone sensitivities calculated for each marine unit (NS: −164.3; MR: −164.6; SE: −164.4 (dB re 1 V/μPa)) or the default microphone sensitivity for SM4 units (−35 dB re 1 V/Pa) that was provided in the Wildlife Acoustics SM4 documentation. This analysis yielded 120 SPL values per sound type per recording. We calculated the median SPL to obtain one SPL measurement per recording.

To then obtain a measurement of daily acoustic activity for each of these sound types, we applied a 1-hour moving average and then calculated either the peak or median value across each daily activity period, depending on the sound production dynamics of each sound type. For the low- and high-frequency fish choruses, we calculated the peak value of each activity period (LFF and HFF) since peak levels have been shown to correlate with fish abundance (Rowell et al., 2017) and also because these choruses did not always span the entire nighttime period. For the shrimp-dominated frequency band, in which snaps were always present, we calculated the median daily SPL value (SS). For the low-, mid-, and high-frequency insect bands, which typically spanned nighttime chorusing periods, we also utilized the median value (LFI, MFI, and HFI).

2.3.3. Non-dominant sound type analysis

2.3.3.1. Bird vocalizations.
To measure the acoustic activity of birds, we calculated the saturation of soundscapes at dawn (06:00–08:00; sunrise times ranged from 06:12 on August 22 to 06:59 on December 31). Since a diverse assemblage of bird species produced sound during this period with minimal masking from insects or other sources, we followed previous work that showed that measuring the saturation of dawn soundscapes positively correlates with bird community diversity (Burivalova et al., 2018; Depraetere et al., 2012; Towsey et al., 2014b). Soundscape saturation refers to the percentage of frequency bins that are acoustically "active" within a recording. Our methods followed those of Burivalova et al. (2018) and are detailed in S1.

To validate the bird vocalization index, we manually surveyed the calling activity of different avian species in 45 recordings. We randomly selected five 1-minute recordings from dawn for (Blake, 2021) each of the three sites at three time phases: before Maria (August 30–September 15, excluding September 6–September 7 due to the passage of Hurricane Irma), soon after the storm (September 25–October 11), and 8–10 weeks after the storm (November 20–December 11). All surveys were conducted by a single observer (OAC) who is an experienced ornithologist proficient in acoustic bird identification and familiar with Puerto Rican avifuana. Recordings were randomly ordered and files renamed with generic labels prior to analysis to avoid potential reviewer bias. OAC identified species by consulting multimedia sound libraries (xeno-canto and the Macaulay Library), and then counted the number of calls and the number of songs produced per species in each spectrogram as in an avian

point count survey (Blake, 2021; Brinley Buckley et al., 2018). We did not correct for potential double counting in these tallies because oftentimes the individual producer was unclear and because we reasoned that a greater abundance of songs and calls would still be a valid index of the avian community diversity. We then used R and *rmcorr* (Bakdash and Marusich, 2017) to conduct a repeated measures correlation analysis on the relationship between the dawn saturation index and 1) the total number of songs and calls and 2) the species richness of vocalizing species, including site as a random effect. We validated model assumptions by performing a Shapiro-Wilk test to check for normality of residuals and a Levene's test to check for homogeneity of variance. We also confirmed that relationships between the dependent and independent variables were linear and parallel across conditions. This analysis revealed a significant correlation between the dawn saturation index and the total number of songs and calls per recording ($r = 0.48$, $p = 0.001$) and the species richness of calling species ($r = 0.31$, $p = 0.040$), indicating that soundscape saturation was an adequate index of bird species diversity in this context. We present additional results on changes in species-specific and community-wide acoustic activity following Maria in S2.

2.3.3.2. Fish pulses.
We detected sounds produced by fish using the band-limited energy detector (BLED) in Raven 1.6. Within a defined frequency band, the BLED detects acoustic events that exceed background noise by a user-defined signal-to-noise threshold. To determine settings for the BLED algorithm, we generated a training dataset of sixty recordings in a randomized block design, with 10 recordings for each site/period combination (periods are defined in Section 2.4). Raven 1.6 has an "interactive" mode where users can tweak BLED parameters and observe real-time changes in detection accuracy, and we used this mode to select suitable parameters based on visual evaluation of detections in spectrograms. To speed up the analysis, we only applied the BLED algorithm to every tenth file, starting on the hour, and then computed daily averages. Parameters for the BLED models are detailed in S.4.

We assessed the true positive rate of the BLED algorithms by evaluating the presence/absence of fish sounds in 400 randomly selected clips with detections present (200 clips for each detector). BG aurally and visually reviewed clips in "review" mode in Raven 1.6, which depicted sounds in an 8-by-8 grid of spectrograms with window lengths of 4096 samples. To improve the accuracy of the manual review, we applied a time pad of 1.0 s and a frequency pad of 500 Hz. A detection was considered positive if a fish sound was seen or heard during the clip (not including the padded portion). We did not quantitatively assess the false negative rate due to the difficulty in creating a manually scored dataset, as there were numerous types of fish pulses with varying signal-to-noise ratios in these recordings. However, from the interactive mode, we are confident that the detectors captured the majority of sounds produced by fish within these frequency bands and therefore provided a sufficient overall index of fish calling activity (example spectrograms showing detections are in Supplementary Information). The low-frequency detector had a true positive rate of 91% (near-shore: 93%; mid-reef: 86%; shelf-edge: 96%). The high-frequency detector had a true positive rate of 94.5% (near-shore: 88%; mid-reef: 95%; shelf-edge: 100%).

2.4. Statistical analysis

We first defined pre-storm and post-storm periods of 15 or 20 days depending on data availability (Fig. 3). The lengths of these periods were chosen in order to include inherent short-term variation due to diel and lunar periods and minor weather events, while minimizing seasonal variation or long-term trends that could potentially confound the measurement of hurricane impacts. In the marine environment, the pre-storm period spanned from August 17 to September 5 (20 days) and the post-storm period spanned from October 7 to October 26 (20 days). In the terrestrial environment, the pre-storm period spanned from
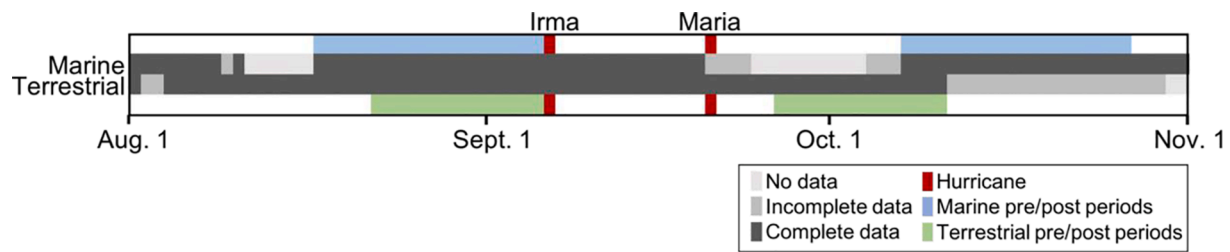
Fig. 3. Timeline showing data availability, storm occurrences, and pre-storm and post-storm periods for the terrestrial and marine sites.

August 22 to September 5 (15 days) and the post-storm period spanned from September 26 to October 10 (15 days). We assumed that sound production patterns across these time periods were relatively consistent and that acoustic differences between periods were due to the storm. We elaborate on and provide justification for these assumptions in the Discussion.

2.4.1. Assessment of impacts—sound type level

We performed linear mixed effects analyses in R using *lme4* (Bates et al., 2018) to determine if Maria significantly impacted the daily acoustic activity of each sound type. In these models, period (pre- or post-storm) was considered as a fixed effect and site was considered as a random effect to account for the repeated daily measurements at each site. For marine sound types, since sound production in shrimp and fish can vary in accordance with the lunar phase, we also included daily lunar luminosity as a fixed effect, which was estimated in R using *lunar* (Lazaridis, 2014). For all sound types, we validated model assumptions using methods described in Section 2.3.3.1. We performed a $\log_{10}$ transform on LFI to meet the normality assumption. We also rank transformed MFI, LFF, and HFF because they failed to meet the normality assumption, making it impossible to obtain model coefficients for these three sound types. We obtained *p* values by analysis of deviance that compared each of the eight models to a null model that lacked period as a fixed effect. We considered the period coefficient to be indicative of the magnitude and direction of the impact.

2.4.2. Assessment of impacts—community level

To visualize community level impacts, we plotted marine and terrestrial acoustic communities in ordination space. For each system, we conducted a principal coordinates analysis (PCoA) based on the Bray-Curtis distance matrix of daily sound type values using the *vegan* package in R (Oksanen et al., 2017). Since LFI and MFI were highly correlated ($r(88) = 0.86$, $p < 0.001$), we summed them prior to community analyses (LMFI). Prior to the ordination, to standardize the magnitudes of the different acoustic metrics, we rescaled values for each sound type between 0 and 1 using the "rescale" function in the *scales* package. We measured two dimensions of community-level impacts. We assessed the magnitude of community alteration by calculating the distance between pre- and post-storm site centroids. To measure the relative influences of period and site on the PCoA values, we conducted an analysis of variance using distance matrices with the "adonis" function in *vegan*. To obtain another index of soundscape disturbance, we assessed changes in average daily soundscape variability by calculating the dispersion of points around their respective site-period centroid. To determine whether there were significant changes in variability, we conducted pairwise comparisons of pre- and post-storm dispersions for each site using the "permutest" function in *vegan*.

2.4.3. Quantification of recovery

We also sought to estimate the response trajectories of impacted sound types, so we employed a logistic curve that has been broadly applied for modeling population growth (Lambert et al., 2014; Pitcher et al., 2000):

$$Z(t) = \frac{Z_o Z_K}{Z_o + (Z_K - Z_o)\exp(-rt)} \tag{1}$$

where $Z(t)$ is the estimated value for a single acoustic index Z at a date t, Z_0 is the initial value of Z at the initial date ($t = 0$), Z_K is the equilibrium Z targeted as the converging value as t approaches infinity, and r is the recovery per day. Only the coastal terrestrial site had sufficient data for this temporal analysis of LFI, MFI, and BV, as the marine sites had temporal gaps following the storm and the lowland and upland units did not record from mid-October to early November. Furthermore, at the coastal site, HFI did not decline after the storm, so there was no recovery to assess for this sound type.

To minimize the effect of seasonal soundscape changes, we restricted our analysis from an initial date (t_0) to December 31, 2017. The three sound types we evaluated had lagged declines in the days following Maria, so we defined t_0 for each sound type as the date with the minimum value during the post-storm period (October 9 for LFI, October 1 for MFI, and October 2 for BV). For LFI, we observed a strong lunar cycle with approximately 8 dB of variation. To better measure impacts caused by the hurricane, we removed this lunar component by decomposing the time series using the "decompose" function in *stats*. We considered recovery time to be when the sound type reached pre-storm levels (Z_K), which we defined as the median of pre-storm values. The recovery growth rate (r) was calculated through *nlinfit* in MATLAB, which aims to minimize the sum of the square of the residuals for Equation (1) over a defined time period (t_0–December 31, 2017). Required recovery time to reach quasi-equilibrium status ($t*$) was calculated through the analytical expression inversely derived from Eq. (1) as:

$$t^* = \frac{1}{r}\ln\left(\frac{\alpha(Z_K - Z_o)}{(1-\alpha)Z_o}\right) \tag{2}$$

where α is the threshold ratio for determining the quasi-equilibrium status. α values theoretically range from 0 to 1, and we employed $\alpha = 0.99$ for $t*$ estimation.

3. Results

3.1. Assessment of impacts—sound type level

In the marine environment, sound types exhibited mixed responses to Maria (Fig. 4a). SS exhibited a small but significant increase of 0.5 dB ($\chi^2 = 32.53$, $p < 0.001$) that was driven by the two more inland sites, near-shore and mid-reef, where SS increased by 1.1 dB and 0.8 dB, respectively. This increase at the two inland sites was sizeable with respect to the full study period SS range, which was approximately 3 dB (including the increase after Maria). The LFF significantly increased ($\chi^2 = 4.28$, $p = 0.039$), mainly because it intensified at the shelf-edge following Maria. FP decreased by 6.27 detections per minute ($\chi^2 = 45.91$, $p < 0.001$). There was no statistical difference in HFF, though there was a 3.4 dB increase at the near-shore site, minimal change at the mid-reef site, and a 4.8 dB decrease at the shelf-edge site ($\chi^2 = 0.39$, $p = 0.531$; Fig. 5a).

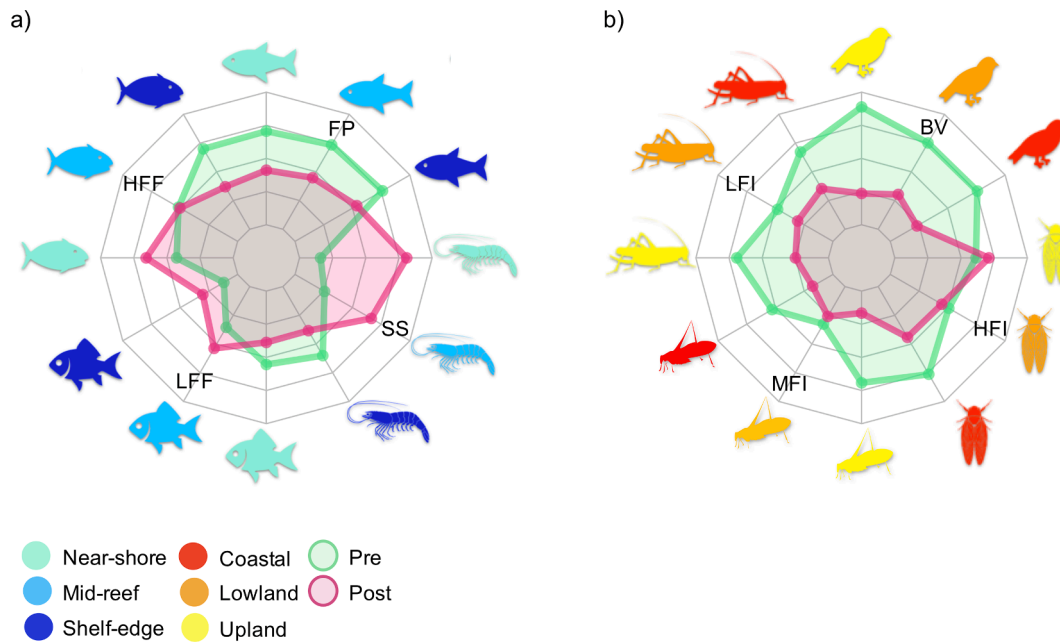All four of the terrestrial sound type occurrences declined

Fig. 4. Soundscape change between the 15- to 20-day periods before and after Hurricane Maria in a) the three coral reef sites in La Parguera and b) the three dry forest sites of Guánica. To create the radar plots, we first scaled values for each sound type between 0 and 1. Then, we computed the means of the pre- and post-storm periods for each sound type for each site. The outer ring is equal to the highest value recorded for each sound type and the inner ring is equal to the lowest. In a) SS = snapping shrimp; LFF = low-frequency fish chorus; HFF = high-frequency fish chorus; FP = fish pulses. In b) LMFI = low- and medium-frequency insect choruses; HFI = high-frequency insect chorus; BV = bird vocalizations.

significantly following Maria (Fig. 5b). BV declined from 57% to 22% ($\chi^2 = 120.81$, $p < 0.001$). LFI declined from 63.2 dB to 57.4 dB, which represents almost a halving of sound pressure levels ($\chi^2 = 42.88$, $p < 0.001$). MFI declined significantly ($\chi^2 = 27.71$, $p < 0.001$) from 58.2 to 53.0. HFI declined 1.9 dB, from 82.9 dB to 81.0 dB ($\chi^2 = 6.80$, $p = 0.009$), though this difference was driven primarily by the decrease at the lowland site (Fig. 5b).

3.2. Assessment of impacts—community level

The PCoA plots illustrate divergent community responses in the coral reef and dry forest ecosystems (Fig. 6). In the marine realm, site-specific differences exceeded the effect of the storm (period: $R^2 = 0.04$, $p = 0.001$; site: $R^2 = 0.67$, $p = 0.001$), while the reverse appears true in the dry forest (period: $R^2 = 0.33$, $p = 0.001$; site: $R^2 = 0.26$, $p = 0.001$). In the coral reef PCoA plot, points were primarily clustered by site, with the near-shore site clusters located on the right side of the plot towards the FP eigenvector, the mid-reef clusters located towards the bottom-left of the plot near the SS and HFF eigenvectors, and the shelf-edge clusters located toward the upper left of the plot near the LFF eigenvector, though there was substantial overlap between the near-shore and mid-reef sites. There also appeared to be a secondary clustering effect of the storm, evidenced by the partial separation between pre and post points within the three larger site clusters. In the dry forest PCoA plot, the six site-period clusters divided into clear pre- and post-storm regions, with pre-storm points appearing toward the upper-left quadrant of the plot (towards the BV eigenvector) and post-storm points appearing toward the right side of the plot (away from sound type eigenvectors). While the upland and lowland sites were similar to each other prior to the storm, they became more distinct after the storm, mainly due to the increased dispersion of lowland points, which shows the greater variation in post-storm soundscapes.

In both marine and terrestrial systems, the distances between pre- and post-storm site centroids in the PCoA plots were generally higher for sites closer to the coastline. In the marine environment, the largest difference was near-shore (Bray-Curtis distance = 0.24), followed by shelf-

edge (0.17), followed by mid-reef (0.12). In the terrestrial environment, the largest difference was coastal (0.33), followed by lowland (0.32), and then by upland (0.22). Soundscape variability increased at all sites following the storms. In the marine environment, mean soundscape variability increased 20% (0.10–0.12 in median distance to centroid). In the terrestrial environment, mean soundscape variability increased 119% (0.07–0.16). Unlike impact magnitude, changes in variability did not generally increase with proximity to the coast. In the marine environment, the near-shore site had the greatest change in variability (+0.06; 69% increase; $p = 0.006$), followed by the shelf-edge (+0.04; 48% increase; $p = 0.006$). The mid-reef increased moderately (+0.02; 17% increase; $p = 0.078$), though the change was not significant. In the terrestrial environment, the lowland habitat exhibited the greatest change in variability (+0.16 in median distance to centroid; 168% increase; $p < 0.001$), followed by the coastal (+0.06; 110% increase; $p < 0.001$) and upland sites (+0.05; 67% increase; $p < 0.001$).

3.3. Assessment of recovery

At the coastal site, LFI (with the lunar component removed) reached pre-storm levels ($Z_K = 69.6$) after 34 days (confidence interval = 25–51; Fig. 7). MFI reached pre-storm levels ($Z_K = 68.7$) after 56 days (confidence interval = 41–85). BV reached pre-storm levels ($Z_K = 0.61$) after approximately 67 days (confidence interval = 55–85). In the Discussion, we consider how lunar and seasonal soundscape changes impact estimating the trajectories of recovery, and we highlight the importance of long-term data in evaluating soundscape impact and recovery patterns.

4. Discussion

Our study provides evidence that soundscapes can reflect three dimensions of ecological resilience: the magnitude of disturbance impacts (resistance), the spatial patterns of impacts (heterogeneity), and the diversity and timing of responses among species and functional groups (recovery). We hypothesized that the activity of all sound types would decline following Maria due to a combination of direct mortality from
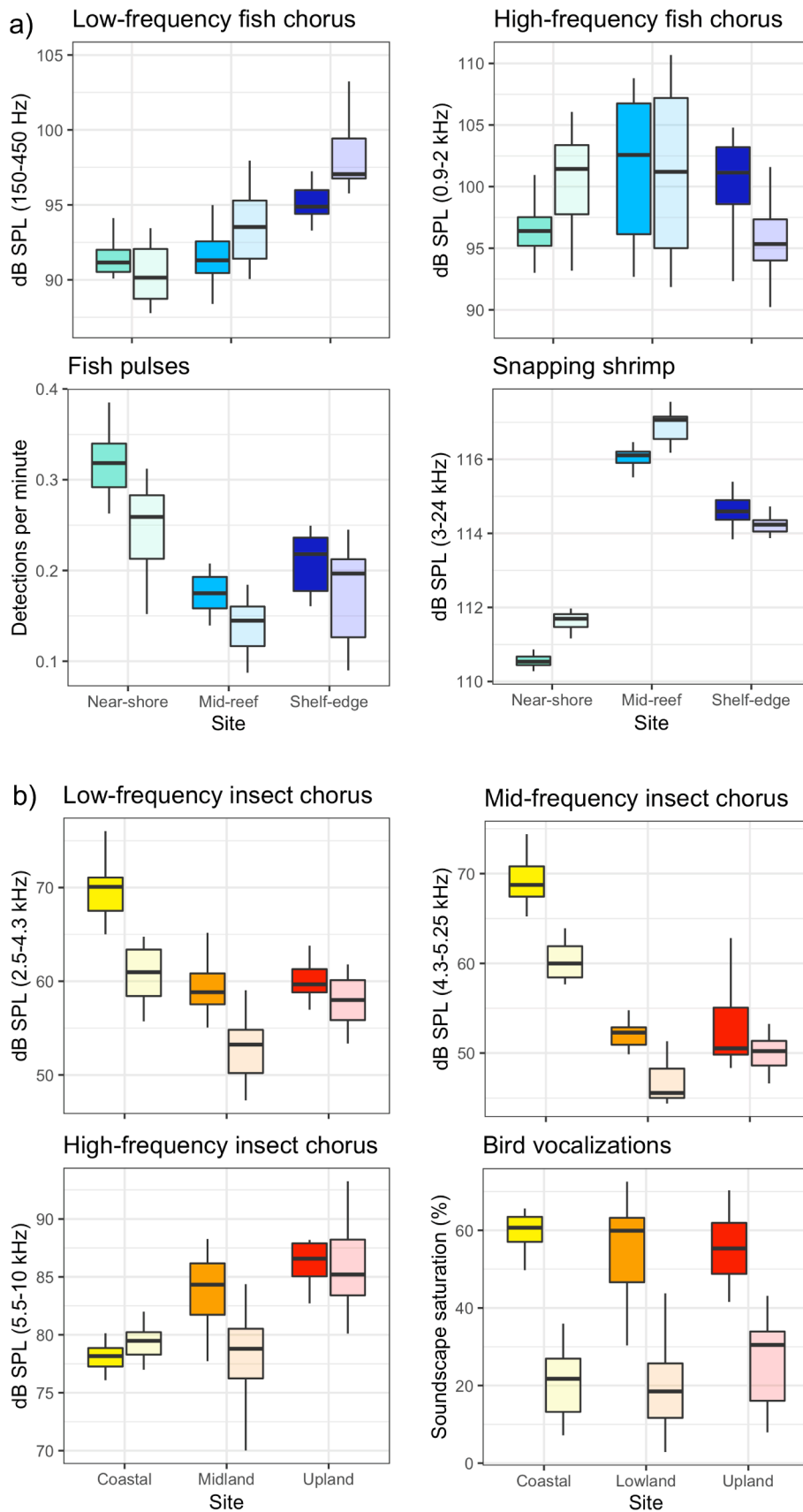
Fig. 5. Boxplots of sound types before (opaque boxes) and after (translucent boxes) Hurricane Maria at the coral reef (a) and dry forest (b) sites. The middle band of each box represents the median value. The upper and lower hinges represent the upper and lower quartiles, respectively. The upper and lower whiskers extend to the largest and smallest values no further than 1.5 times the inter-quartile range.
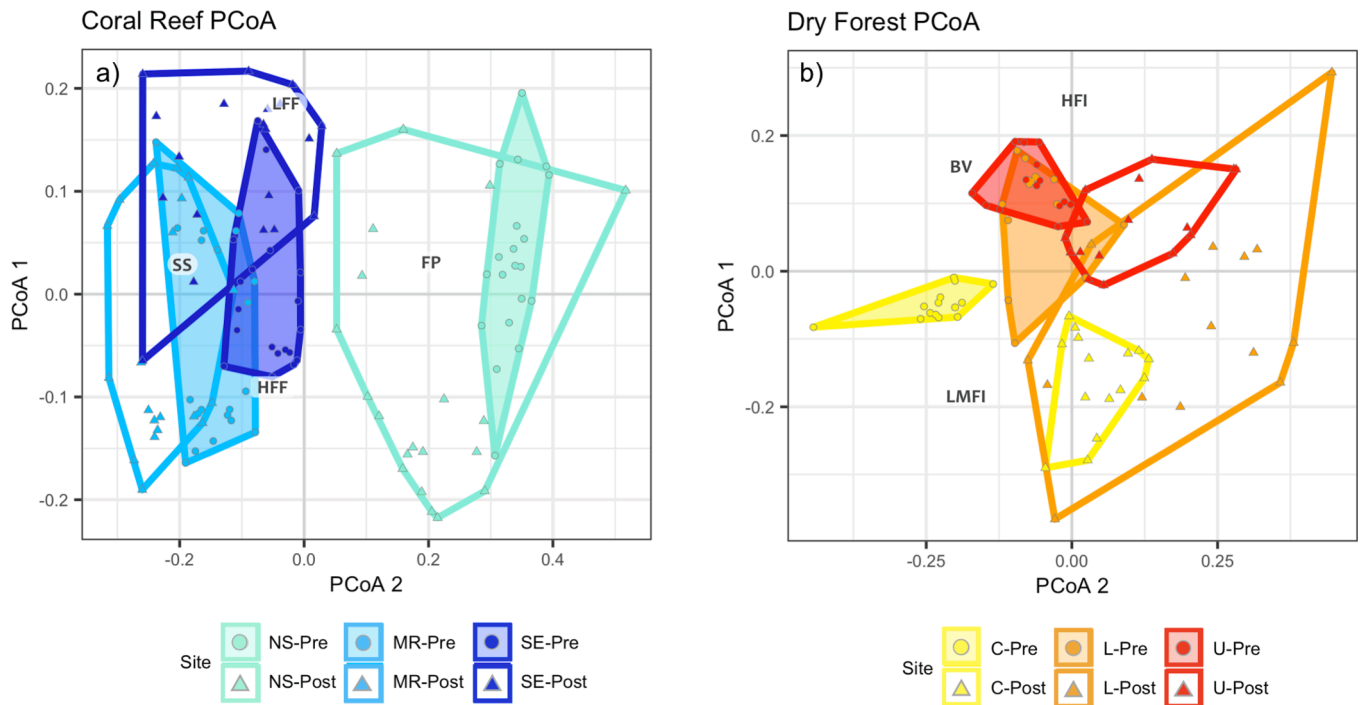
Fig. 6. Principle coordinates analysis plots illustrating the acoustic communities in the a) coral reef and b) dry forest sites. Pre-storm days are circles and post-storm days are triangles. Pre-storm clusters are shaded polygons and post-storm clusters are outlined polygons. In (a), NS = near-shore, MR = mid-reef, and SE = shelf-edge. In (b) U = upland; L = lowland; C = coastal. Sound type text labels are located at the termini of their respective eigenvectors. In (a) SS = snapping shrimp; LFF = low-frequency fish chorus; HFF = high-frequency fish chorus; FP = fish pulses. In (b) LMFI = low- and mid-frequency insect choruses; HFI = high-frequency insect chorus; BV = bird vocalizations.

the storm, altered behavior, and post-storm movement that resulted in less acoustic activity. Our findings partially supported this hypothesis. In the terrestrial sites, we observed significant declines in the four sound types and in eight of the twelve sound type-site pairs. Contrastingly, in the marine realm, only FP significantly declined following the storms, and two sound types, LFF and SS, significantly increased. We also predicted that the magnitude of soundscape alteration would correlate with the degree of environmental alteration, which was greater in the terrestrial system compared with the nearby marine environment. This prediction was validated, at least with respect to short-term impacts (<2 months), both for individual sound types and acoustic communities. Distances between pre- and post-storm cluster centroids were 64% greater in the dry forest than in the coral reef. Below we explain the implications of our results for understanding the effects of Maria on species, habitats, and ecosystems. Additionally, we offer suggestions for the future application of soundscape research to evaluate ecological resilience, and we present some caveats about our study.

4.1. Influence of habitat

Our study demonstrates that habitat type can mediate species disturbance responses. Apart from BV, where declines were relatively consistent across sites, the direction and/or magnitude of sound type alteration appeared to be influenced by habitat type, especially for the three insect choruses, LFF, and SS. For example, the LFI chorus exhibited steeper declines at the coastal (9.6 dB) and upland sites (6.4 dB; the two sites with greater vegetation density) than at the lowland scrub site (3.1 dB). The two vegetation-dense sites likely had more diverse insect communities prior to the storm and also suffered greater defoliation and more downed trees that could have damaged insect habitats and resulted in insect mortality. In the marine realm, the drastic increase in the LFF chorus that we observed around Maria only occurred two other times during the study period: after Hurricane Irma, and on one occasion in

mid-November. The intensification of the LFF chorus around the storms could have been due to the movement of larger fish species that relocate during disturbance events (Bacheler et al., 2019). The location of this chorus at the shelf-edge site offered anecdotal support for the hypothesis that deep-water reefs are less susceptible to hurricane damage than shallow-water reefs and therefore can serve as refugia for coral and fish species (Walsh, 1983). In our study, the shelf-edge was the most stable site with respect to differences between pre- and post-storm soundscapes. This pattern has been observed previously for fish species after Hurricane Allen in Jamaica (Kaufman, 1983). In both the marine and terrestrial systems, the magnitude of soundscape alteration generally increased toward the coast, likely reflecting more extreme effects of the hurricane closer to the coast. Wave impacts can be expected to be greater in shallow water, and coastal vegetation is highly exposed to untempered winds from the ocean.

4.2. Influence of taxon

Resistance levels and response trajectories also differed by sound type, likely reflecting underlying taxonomic differences. For example, the HFI chorus exhibited minimal change at two of the three terrestrial sites, indicating high resistance among the taxa that produced sound within this frequency band, including Tettigoniidae (7.4–8.2 kHz), Gryllidae (5.5–6.0 kHz and 6.8–7.4 kHz), and *Hemiptera cicadomorpha* (6.0–6.6 kHz). In contrast, LMFI and BV experienced sizeable alterations across sites (50% to 60% declines), but also showed signs of recovery in the weeks following the storm. The insect choruses reached pre-storm levels sooner than the bird vocalizations, though there were rather large and overlapping confidence intervals around these estimates. One hypothesis to explain this difference is that taxonomic groups that are less mobile (e.g., arthropods) would need to adapt traits that enhance their short-term *in situ* resistance to perturbations, while mobile species (e.g., birds) could adapt traits that exploit their dispersal abilities. For
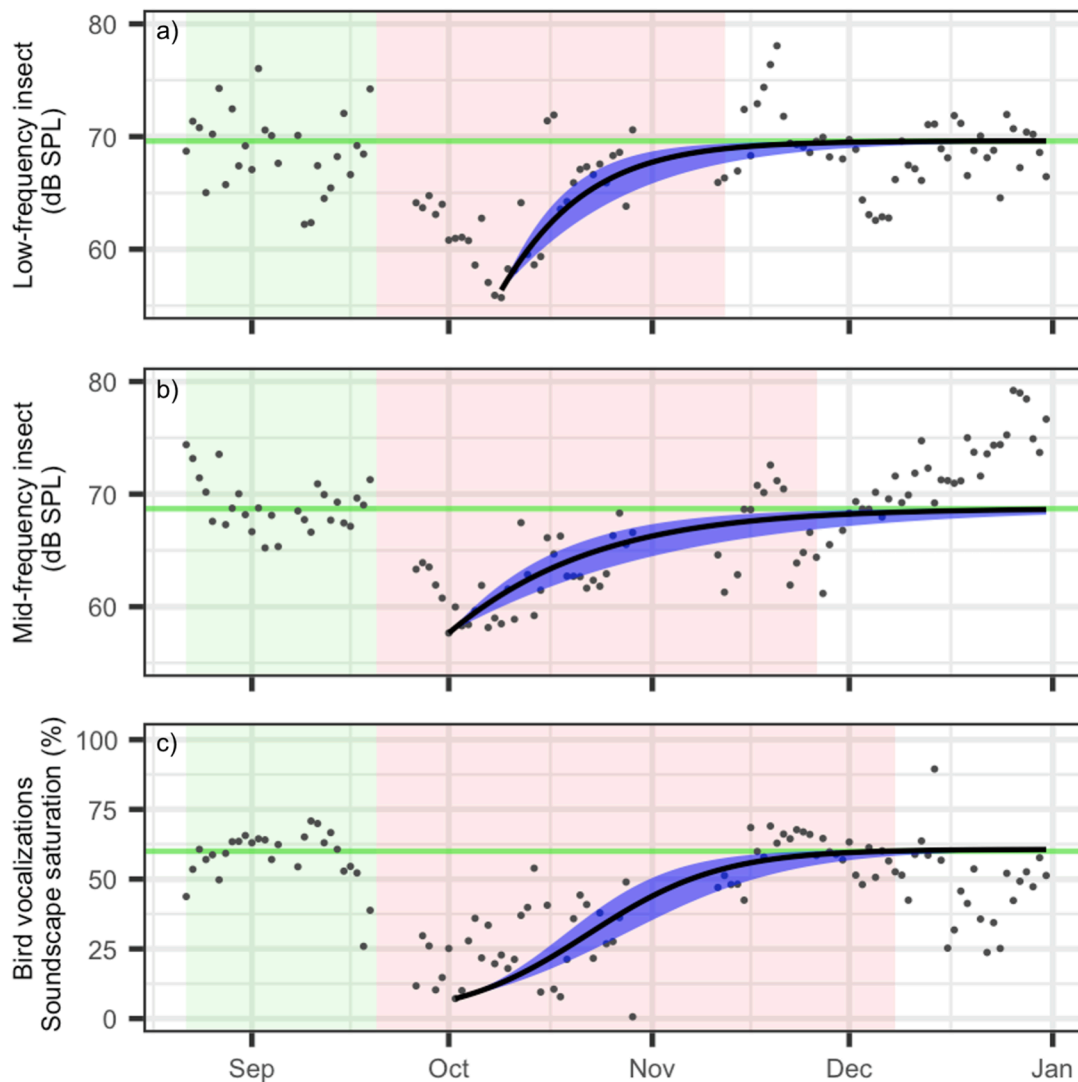
Fig. 7. Recovery dynamics of the a) low-frequency insect chorus (with lunar component removed) b) mid-frequency insect chorus, and c) bird vocalizations at the coastal dry forest site from August 2017 to January 2018. Gray circles represent daily index values. The green horizontal line indicates the equilibrium threshold, the black line represents the logistic curve, and the blue shading indicates the 95% confidence interval around the curve. The green shaded area encompasses the pre-storm period, and the red shaded area represents the period after Maria until the system "recovered". (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

example, hurricane-induced natural selection resulted in changes to morphological traits that enhanced clinging capacity in a small-bodied lizard, *Anolis scriptus*, following Hurricanes Irma and Maria in the Turks and Caicos Islands (Donihue et al., 2018). Conversely, it has recently been shown that some bird species like the golden-winged warbler (*Vermivora chrysoptera*) can detect large storm events several days before their arrival in order to pre-emptively avoid them (Streby et al., 2015). Here, we observed a decrease in BV in the two days before Maria struck on September 20. From September 8 to 17, BV ranged from 64% to 73%. It decreased to 26% on September 18 and 39% on September 19. Whether or not this decrease was caused by the storm remains unclear.

Our results are consistent with previous studies that investigated hurricane responses across the following taxonomic groups.

4.2.1. Fishes

The response of fishes to hurricanes is dependent on storm magnitude, habitat type, and species. Changes can include decreased species richness, decreased abundance, shifts in population and community composition, and altered behavior. These short-term impacts can persist

for several weeks (Paperno et al., 2006) or longer than one year (Kaufman, 1983). For fish that produce sound, their acoustic activity can provide an index of their resilience to hurricanes. Three recent studies have shown that fish continued chorusing directly after the passage of Category 4 hurricanes: one recorded sand seatrout (Cynoscion arenarius) around Hurricane Charley (2004) off the coast of Florida (Locascio and Mann, 2005), one recorded spotted seatrout (Cynoscion nebulosus) after Hurricane Harvey (2017) in Aransas Bay in Texas (Biggs et al., 2018), and one recorded two fish choruses after Hurricane Irma (2017) in the Florida Keys (Simmons et al., 2021). While data were unavailable directly after Maria, in the 3–4 days after Hurricane Irma, the high-frequency fish chorus reached its highest measured levels. While FP did drop after the storm, this decline could have resulted from elevated background noise during several days in mid-October instead of a reduction in fish calling activity. Following the hurricane, there was an increase in suspended particulate material deposited into Guánica Bay, which collected there due to lower than usual wave action following the storm. The elevated background noise coincided with the first large wave action after Maria around October 17, 2017 (Cheriton et al., 2019), which increased turbidity and possibly impacted background

noise levels and/or fish calling behavior.

4.2.2. Shrimps

There was a small but significant increase in SPL in the high-frequency band dominated by shrimp snaps due to elevated levels over the five weeks that followed Maria at the two more shoreward sites. Though this increase has questionable biological significance, it was statistically significant in part due to the negligible variation within both the pre- and post-storm periods. This pattern did not correspond with changes in water temperature during this time period, so explanations for this change likely stem from other biological, environmental, or equipment-related factors.

4.2.3. Insects

The low-, mid-, and high-frequency insect choruses declined for several weeks following Maria at some or all of the sites. These impact and response dynamics likely reflect taxa- and guild-level traits that mediate hurricane responses (Schowalter et al., 2017). Hurricanes trigger a rapid restructuring of resources (i.e., foliage to litter) that can benefit detritivores and negatively impact arboreal herbivores (Schowalter et al., 2017).

4.2.4. Birds

Bird vocalizations, measured by dawn chorus saturation, declined 59% in the weeks following Maria. This reduced saturation likely reflects a combination of dispersal from the coast and mortality following the storm due to a lack of resources. Frugivore and nectivorous birds declined by 30–70% in the months after hurricanes in Mexico (1988), St. John (1989), and Puerto Rico (1989), while insectivorous and omnivorous birds lacked similar guild-wide patterns (Askins and Ewert, 1991; Lynch, 1991; Waide, 1991a, 1991b). This pattern suggests that the effects of hurricanes could be mediated by resource availability and dispersal from affected sites instead of direct mortality (Waide et al., 1991b). Hurricanes remove flowers, fruits, and seeds, so additional stress could come after the storm when resources are scarce. Supporting this hypothesis, the bird with the greatest number of sounds detected at our sites, the bananaquit (*Coereba flaveola*; n = 235), is a nectivorous bird. It probably was greatly impacted by the defoliation caused by the storm. The Puerto Rican tanager (*Nesospingus speculiferus*; n = 203), the bird with the second-highest number of detections, is an omnivore that feeds mainly on invertebrates (Pérez-Rivera 1997), but understory fruit gleaning accounted for 63% in its foraging behavior at a study site in Rio Chiquito, Luquillo Experimental Forest in Puerto Rico (Cruz 1987), so it also could have declined after the storm. Of the eight species with more than 10 detections, seven fed at least partially on fruits and nectar. Therefore, it would be reasonable to expect these species to endure consequences from the storm (Waide et al., 1991b). An alternative explanation for sparser dawn choruses is behavioral changes, rather than changes in abundance. For example, birds' nests and territories may have been destroyed by the storm, rendering vocal territorial displays worthless. This hypothesis could explain a pre- to post-storm shift from mostly songs to mostly calls in our annotated dataset.

4.3. Influence of ecosystem

Dry forest sites were more impacted than coral reef sites. While we observed sizeable short-term effects on the dry forest animal community, several studies have recently demonstrated the remarkable resiliency of dry forest ecosystems to disturbance, including the intensifying hurricane regimes that are plausible toward the end of the 21st century (Álvarez-Yépiz et al., 2018; Bhaskar et al., 2018; Holm et al., 2017; Imbert and Portecop, 2008). However, these studies have mainly focused on the resilience of vegetation and soil, as opposed to animal communities. Given the functional roles of animals in maintaining ecosystem structure and function (e.g., seed dispersal and herbivory; Carlo and Morales, 2016), assessing the resiliency of animals to

changing disturbance regimes is necessary to predict overall ecosystem resiliency. Similarly to dry forests, Caribbean coral reefs can be highly resilient to hurricanes, though large storm events can cause major damage to coral reefs (NOAA, 2018). The capacity of coral reefs to recover stems in part from the resilience of resident fish and mobile invertebrates, which maintain critical reef-sustaining functions that facilitate reef recovery after disturbance events (Gordon et al., 2018). The relatively small change in the marine soundscapes at these sites indicated such community resistance.

5. Study limitations

The first main challenge of our study was separating hurricane-related soundscape impacts from seasonal and lunar dynamics that also could have contributed to soundscape changes (see Section 3 in Supplementary Information for more information). In the coral reefs, there were both annual and lunar cycles. Fish chorusing activity and snapping shrimp sound levels generally increased during the summer months, which is consistent with other studies (Staaterman et al., 2014). The high-frequency chorus also peaked around new moons and hit minima around full moons. Despite these annual and lunar cycles, the soundscape changes following Maria appeared distinct from these patterns. In the dry forest habitat, there were long-term phenological patterns including increased dry season (December–March) activity for some insect sound types, which we determined from additional recordings collected in the months after the study period. Post-storm changes in the dry forest were relatively sudden and followed by a return to the prior state over a time period that did not correspond to seasonal trends. Unlike typical lunar variation, the post-storm nadirs in activity were steeper (for the LFI and MFI) or longer (for BV) than those observed in typical lunar cycles. Still, evaluating short-term recovery was complicated by the prevalence of lunar and seasonal soundscape changes, particularly for the LFI chorus, which peaked around new moons and was lowest around full moons (see Supplementary Information); lunar patterns in insect sound production are still not well documented (but see Lang et al., 2006). Reference data spanning previous years would enable the direct comparison of post-disturbance soundscapes with baseline conditions and facilitate the detangling of disturbance-related impacts from lunar or annual cycles. Such comparisons should become more feasible as passive acoustic monitoring is incorporated into environmental monitoring platforms, open-access soundscape databases proliferate, and acoustic phenologies for different habitat types are described in the scientific literature (e.g., Aide et al. 2013). Increased knowledge of the acoustic composition and dynamics of different ecosystems will enable researchers to understand inherent sources of soundscape variability in order to better measure the magnitude of disturbance impacts.

Our second challenge involved data lapses at key time periods, including directly after Maria at the three marine sites. These holes in the acoustic record prevented anecdotal descriptions of community responses immediately after Maria, and also reduced our ability to build recovery models for most of the sites. Despite this challenge, we were able to evaluate the short-term impacts (15–20 days) and responses (4 months) that enabled us to measure resilience to the hurricane.

The third challenge we faced can also be viewed as an opportunity. Some of the broad sound types measured in this study could be split into more distinct sound types that each likely represent different soniferous genera or species, each with their own recovery dynamics and ecological significance. Most soundscape studies still employ broad measurement types like band-level measurements or acoustic indices (Sugai et al., 2019). These methods are relatively easy to employ and suitable for characterizing large community shifts, but they are likely only accessing a fraction of the informational content encoded in soundscape recordings. Developing automated sound-type based analyses will propel this field towards a better understanding of ecosystem dynamics and disturbance response (Lin et al., 2017). As more sound types are ascribed

to taxa, particularly in the marine realm, we can complement existing knowledge of functional roles and community structure with information on species-level contributions to soundscape dynamics.

Regarding soundscape metrics, one contribution of this study is the suggestion that increased soundscape variability may be an indicator of a disturbed landscape. Thus far, soundscape studies have mainly focused on measuring complexity or amplitude within a single recording, and from these values comparing sites or temporal periods (but see Francomano et al., 2020). Changes in the variability of soundscape components across different temporal scales appears to be a meaningful indication of disturbance. Direct comparison of soundscape variability with measures of physical habitat alteration would help corroborate this hypothesis. Of course, some systems are inherently more variable than others. The coral reef sites contained sound types that were influenced by the lunar phase and therefore these soundscapes contained more short-term (inter-day) variability than the dry forest soundscapes, where soundscape patterns were mainly driven by daily and annual phenologies. That said, time-series modeling can assist in detangling temporal soundscape patterns by separating natural sources of variation from ones that signify disturbance and potentially anticipate regime shifts.

6. Conclusions

This study illustrates the ways in which Hurricane Maria impacted dry forest animal communities and to a lesser extent those of nearby coral reefs. Furthermore, it serves as a proof of the concept that soundscape recording and analysis can be used to quantify different aspects of ecological disturbance and resilience. In this time of rapid environmental change, soundscapes can signal the ways in which altered disturbance regimes are transforming ecosystems.

Author contributions

BG, FM, RA, DM, EW, BP conceptualized the study; FM, RA, DM, EW, and BP provided funding and resources to conduct the study; JO collected and curated the data; BG, DF, SY, BP developed methods for the study; BG, SY, OAC, and DF analyzed the data; BG wrote the original draft; all authors reviewed and edited subsequent drafts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107635.

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