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Habitat degradation homogenizes ecological responses to typhoons across a subtropical island

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Abstract

Climate change is increasing the frequency, intensity, and duration of extreme weather events across the globe. Understanding the capacity for ecological communities to withstand and recover from such events is critical. Typhoons are extreme weather events that are expected to broadly homogenise ecosystems through structural damage to vegetation and longer-term effects of salinization. Given their unpredictable nature, monitoring ecological responses to typhoons is challenging, particularly for mobile animals such as birds. Here, we report spatially variable ecological responses to typhoons across terrestrial landscapes. Using a high temporal resolution passive acoustic monitoring network across 24 sites on the subtropical island of Okinawa, Japan, we found that typhoons elicit divergent ecological responses among Okinawa's pristine forests, as indicated by increased spatial variability of biological sound production (biophony) among forested sites. However, no such post-typhoon shift in variability was observed among developed urban or agricultural sites. This indicates that natural forests have a diversity of pathways through which communities can respond to typhoons, whereas land use development produces communities more constrained in their disturbance responses. That is, spatial insurance effects among forest communities may provide resilience to typhoons at the landscape scale, but this spatial insurance was diminished by habitat degradation through land use development. Though site-level typhoon impacts on soundscapes and bird detections were not particularly strong, we nevertheless revealed spatial heterogeneity in typhoon responses, owing to the data resolution afforded to us by monitoring at scale (high temporal resolution, broad spatial extent). Our findings underscore the importance of natural forests in insuring ecosystems against disturbance, and demonstrate the potential of landscape-scale acoustic sensor networks for documenting the understudied ecological impacts of unpredictable extreme weather events.

Introduction

Climate change is increasing both the frequency and destructive potential of extreme weather events such as typhoons (Bhatia et al., 2019; Emanuel, 2005; Kossin et al., 2020; Li & Chakraborty, 2020). Typhoons bring exceptional winds and rainfall and can cause structural damage to terrestrial habitats through wind-damage (Everham & Brokaw, 1996), flooding (Gardner et al., 1991), and salinization by sea spray, particularly on islands (Elliott & Nino, 1960; Kerr, 2000). These destructive forces can impact the mortality, composition, and dynamics of trees (Lin et al., 2020; Morimoto et al., 2021), birds (Cely, 1991; Chevalier et al., 2019; Seki, 2005), bacteria (Ares et al., 2020), invertebrates (Azuma et al., 1997; Willig & Camilo, 1991), and other animals (Donihue et al., 2018; Pavelka et al., 2007; Testard et al., 2021).

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Land cover may affect exposure to—and hence the ecological consequences of—extreme weather events (Laurance, 1998). Several studies suggest that primary forest with a mix of vegetation types and life forms is most likely to resist and recover from typhoon disturbance (Abbas et al., 2020; Zampieri et al., 2020). Human activity and associated land use change has, therefore, considerable potential to modify the severity and reach of typhoons (Raymond et al., 2020). For example, land abandonment might be expected to dampen the effects of typhoons over time as intensively managed agricultural areas undergo natural succession to a more biologically and structurally diverse system, whereas deforestation through urbanisation or agricultural intensification should increase typhoon exposure (via loss of canopy structure) as well as subjecting ecological communities to the stressors and pollutants associated with these anthropogenic land uses (Daskalova et al., 2020; Senzaki et al., 2020; Sirami et al., 2008; Uchida & Ushimaru, 2014). Yet, despite the potential for land cover to moderate the impact of extreme events, the practical difficulties associated with ecological monitoring at scale have, to date, limited understanding of the extent of any differential impacts of typhoons across habitat types and of the consequences of such differences for landscape-scale biodiversity or spatial processes such as metacommunity dynamics and stability (Loreau et al., 2003; Wang et al., 2021).

Ecological stability is a central framework for considering disturbance impacts across spatial, temporal, and organisational scales, from populations to ecosystems (Hillebrand et al., 2018; Kéfi et al., 2019). Stability is a concept with multiple dimensions (Donohue et al., 2013; Hillebrand et al., 2018; Pimm, 1984), including components such as resistance to and recovery from disturbance (Baert et al., 2016; Yang et al., 2019), and the variability of ecological variables both in time and space (Tilman et al., 2006; Wang et al., 2017). Both disturbance events and ecological responses to such events vary across spatiotemporal scales (Clark et al., 2021; Ross et al., 2021b; Zelnik et al., 2018). This necessitates high-resolution and long-term monitoring of ecosystems to holistically capture the ecological impacts of infrequent extreme events such as typhoons. However, monitoring biodiversity over large spatial and temporal scales poses considerable logistical and financial challenges. Accordingly, most empirical studies of ecological stability are experimental (Kéfi et al., 2019), while observational studies of disturbance typically employ space-for-time substitutions (Butsic et al., 2017), or consider only single-time snapshots before and after disturbance (*e.g.*, Burivalova et al., 2014). In such cases, it is extremely challenging to isolate the relevant pathways through which disturbance events impact ecosystems in a holistic multidimensional way.

Recent advances in automation hold promise for understanding disturbance responses through large-scale continuous monitoring of biodiversity (Keitt & Abelson, 2021; Ross et al., 2023). Following developments in data acquisition, storage, and processing, passive acoustic monitoring of

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wildlife and soundscapes is growing in popularity (Burivalova et al., 2019; Gibb et al., 2019). As sensor networks are established to collect acoustic data autonomously (Keitt & Abelson, 2021; Sethi et al., 2020), a diverse range of ecological studies become tractable by leveraging high-resolution acoustic time series (*e.g.*, Deichmann et al., 2018; Lomolino et al., 2015; Rossi et al., 2017; Sueur et al., 2019; Ross et al., 2023). Studies of disturbance impacts on *soundscapes*—that is, all sound produced in an ecosystem (Pijanowski et al., 2011a, 2011b), including *biophony* (biotic sound), *geophony* (natural abiotic sound, such as rain), and *anthropophony* (human-related sound)—have recently emerged, though most commonly still make before-and-after or space-for-time comparisons (*e.g.*, Deichmann et al., 2017; Gasc et al., 2018). However, the high-resolution time series afforded by passive acoustic monitoring allows opportunistic measurement of soundscape responses to infrequent disturbance events, such as typhoons (*e.g.*, Gottesman et al., 2021), as well as documenting longer-term trends under climate change (Sueur et al., 2019). Acoustic monitoring thus provides an opportunity to overcome many of the challenges associated with studying extreme weather events, by allowing pre- and post-typhoon comparisons (Altwegg et al., 2017; Rajan et al., 2022), and capturing ecological responses to typhoons across scales in space and time (Lin et al., 2020) using a multidimensional stability framework (Donohue et al., 2013). Of the few studies that have used acoustic monitoring to capture storms or extreme events, most focused on marine soundscapes (Boyd et al., 2021; Locascio & Mann, 2005; Simmons et al., 2021), though Gottesman *et al*. (2021) recently showed that terrestrial soundscapes were less resistant than those of coral reefs to hurricane disturbance. Embedded within terrestrial soundscapes, bird vocalisations provide the opportunity to assess the impact of typhoons on critical indicator taxa (Gasc et al., 2017), while acoustic indices provide rapid information on a combination of biodiversity and other meaningful aspects of soundscape change (Bradfer-Lawrence et al., 2020; Harris et al., 2016; Rajan et al., 2022). There are, however, few studies that simultaneously assess both individual species vocalisations and acoustic indices explicitly (Ferreira et al., 2018; Ross et al., 2018).

Here, we exploit a dataset that is, to our knowledge, the highest-resolution dataset recording biological responses to an extreme weather event to date, capturing daily bird vocalisations and half-hourly acoustic indices in response to two large typhoons across 24 field sites on the island of Okinawa, Japan. We measure multiple dimensions of ecological stability for both soundscapes and individual bird species in response to a super-typhoon in September 2018, which was followed five days later by an extratropical cyclone. Our study spans Okinawa's full range of terrestrial habitats, allowing us to examine how land use can shape ecological responses to extreme events. Given that organisms are differently vulnerable to mortality and mechanical damage resulting from typhoons

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(Abbas et al., 2020; Zampieri et al., 2020), we expect land use to influence typhoon responses (Raymond et al., 2020).

Specifically, we test the hypotheses that typhoons (1) temporarily reduce soundscape richness and (2) bird vocalisation rates, and (3) homogenise soundscapes across sites. We also predict that (4) natural forest habitats should have soundscapes that are more resistant to typhoons owing to their closed canopy structure (Abbas et al., 2020; Nimmo et al., 2016). We expect to find differences in bird species responses to typhoons, perhaps as a function of their traits (Wiley & Wunderle, 1993). Closed canopy specialists, frugivores, granivores, and nectarivores should be most vulnerable to food resource losses following typhoons (Chevalier et al., 2019; Wiley & Wunderle, 1993; Zhang et al., 2016), while insectivores may benefit from increased access to prey in canopy gaps (Cely, 1991; Seki, 2005), and large-bodied or predatory birds may be especially vulnerable to typhoon-induced habitat alteration, owing to their dependence on prey availability and habitat area (*e.g.*, Ross et al., 2019) and their slow reproductive rates (Cely, 1991; Cohen et al., 2021; Wiley & Wunderle, 1993). These hypotheses draw on the idea that forest loss is a key catalyst of biodiversity change (Daskalova et al., 2020; Gibson et al., 2011). This is especially pertinent given the high richness and rates of endemicity and specialism among Okinawa's forest taxa (Inoue et al., 2019; Itô et al., 2000). Okinawa island is subject to rapid and ongoing land use change, particularly through deforestation for urbanisation and agricultural intensification (Ross et al., 2018; Takeuchi et al., 1981). Such land use change necessitates an explicit focus on habitat degradation as a driver of the ecological outcomes of intensifying natural disturbance regimes under climate change, including an increase in the frequency and destructive potential of typhoons and extreme storms around Okinawa (A. Iwasaki, unpublished data).

Methods

Study sites and typhoon impact

This study uses data from the OKEON (Okinawa Environmental Observation Network) Churamori Project (OKEON 美ら森プロジェクト; https://okeon.unit.oist.jp/) in Okinawa, Japan. We use data from OKEON's 24 field sites across the island of Okinawa, representing Okinawa's full range of land cover types (Figure 1). Elsewhere, we describe the geographic variation among the sites (Ross *et al*., 2018), which were assessed using reflectance estimates from Landsat 8 images to estimate proportional land cover for various land cover classes within a 1,000 m circular buffer surrounding each site, an appropriate scale for detecting land cover effects on highly mobile taxa such as birds. We classified land cover into the following categories: dense closed-canopy forest; grassland and scrubland (that is, low-medium growth coastal and disturbed vegetation, and managed grasses); agricultural land (primarily for sugarcane); urban areas characterised by materials such as asphalt and

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concrete with limited vegetation; sand and dirt with limited vegetation; freshwater bodies; and miscellaneous land cover not described in the above categories. To deal with the challenge of multicollinearity among land cover classes, we used an unsupervised learning approach to identify clusters of sites with similar land cover. We used k-means clustering (optimal k = 2 clusters) to identify sites that clearly differentiated in Principal Component Analysis (PCA) space, where the first PCA axis captured Okinawa's primary land use gradient and explained 81.2% of the variance among our sites (Supplementary Figure S1). The PCA loadings show that the two clusters identified represent a distinction between sites that are primarily forested and those that are either agricultural or urban (Figures 1b and S1), hereafter together referred to as 'developed' sites.

Acoustic data has been collected at each OKEON site since February 2017, but here we focus on a 66-day period in 2018 surrounding the landfall of two large typhoons, Trami and Kong-Rey. Trami passed closest to Okinawa on 29 September 2018 and was followed closely by Kong-Rey on 4 October 2018 (Japan Meteorological Agency [JMA] 2018; Figure 1a). We isolated recordings from the 30-day periods before (*pre-disturbance* period: 30 August – 28 September 2018) and after (*post-disturbance* period: 06 Oct – 04 Nov 2018) the typhoons made landfall, comprising a total of 771,840 minutes of data (Figure 1). Okinawa and the Ryukyu archipelago are increasingly exposed to more frequent and intense typhoons (A. Iwasaki, unpublished data), with annual typhoon seasons bringing disturbance events of varying magnitude (Elliott & Nino, 1960). Typhoon Trami was the largest typhoon (tropical cyclone) to hit Okinawa since OKEON acoustic recording began, with windspeeds reaching 183 km h^{-1} on 29 September 2018 (JMA 2018). Trami was followed shortly after by Kong-Rey, which was less severe, striking Okinawa as an extratropical cyclone (JMA 2018). The chosen acoustic recordings therefore include a well-characterised pre-disturbance state (Ross et al., 2018, 2021a), followed by an extreme weather event and post-disturbance period during which soundscapes could potentially recover to their pre-disturbance state (Figures 1c and 1d).

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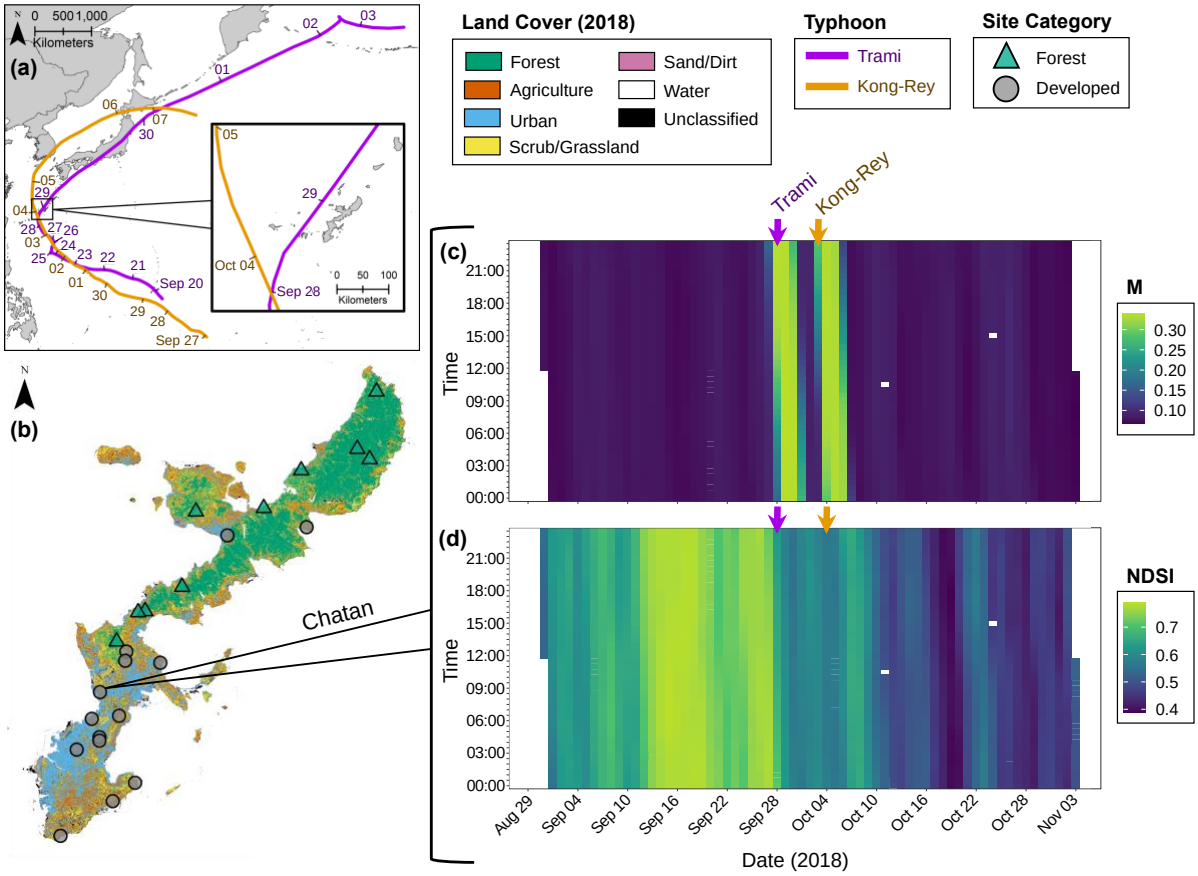

Figure 1. Field sites, timeline, and typhoon impact. (a) Map showing the tracks (coloured lines) of two large typhoons that hit Okinawa: super typhoon Trami in orange (20 Sep-03 Oct 2018; closest pass on 29 Sep 2018) and extratropical cyclone Kong-Rey in purple (27 Sep-07 Oct 2018; closest pass on 04 Oct 2018). (b) Map of Okinawa, including different land cover classifications based on a Landsat 8 image from 2018 (see Ross *et al.*, 2018 for details). 24 Field sites with acoustic recorders are marked with coloured points; green triangles are sites grouped in the forested site cluster (n = 10), and grey circles those in the developed cluster (n = 14) based on unsupervised k-means clustering of land cover variables (see *Methods*). (c-d) illustrative example time series of the study period at the developed Chatan field site (see b), showing the dates of the typhoon arrival (marked with coloured arrows) and the 30-day periods preceding and following typhoon impact. Dates along the X-axes span the full study period (30 Aug-04 Nov), and times along the Y-axes span 00:00-23:30 in half-hour intervals). Each grid cell then represents the value of a detrended and normalised acoustic index for the 10-minute recording corresponding to each time-by-date combination. To illustrate the potential for acoustic indices to reveal typhoon impacts, we show c) the median of the amplitude envelope (M; see Ross et al., 2021a), where higher values (lighter colours) represent louder soundscapes across all frequency bands (Depraetere et al., 2012), and (d) the normalised difference soundscape index (NDSI), where higher values (lighter colours) represent a dominance of biophony in the soundscape, while lower values (darker colours) comprise mostly anthropophony (Kasten et al., 2012). Note the signal of the typhoons on the soundscape, clear in (c) as an increase in total soundscape volume as the typhoons pass Okinawa, and in (d) as a decline in the relative contribution of biophony (lighter colours) to the soundscape following the typhoons, suggesting changes to

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vocalisation behaviour and possible mortality in the wake of typhoon impact. Geophony such as the heavy wind and rain caused by typhoons typically produces broadband sound, so does not produce a clear signal in (d), unlike in (c).

Acoustic monitoring and data processing

Song Meter SM4 recorders (Wildlife Acoustics Inc., Concord, MA, USA) are installed at approximately breast height (~1.3m) at each field site and are programmed to record at default gain settings (+16 dB) via two omnidirectional microphones on a schedule of 10-minutes recording, 20-minutes standby, with recording starting on every hour and half hour. Data are saved to an SD card in stereo .WAV format at a sampling rate of 48-kHz. All audio data collected as part of the OKEON Churamori Project are archived with the Okinawa Institute of Science and Technology's high-performance computing centre.

For each 10-minute audio file, we computed three commonly used acoustic indices in R (version 4.2.1; R Core Team 2022) using the *soundecology* package (version 1.3.3; Villanueva-Rivera & Pijanowski 2018). We calculated the normalised difference soundscape index (NDSI) and its two component indices, biophony ($NDSI_{Bio}$) and anthropophony ($NDSI_{Anthro}$), by first generating a spectrogram via fast Fourier transformation (Hanning window size = 256) and splitting it into 1-kHz frequency bands. Biophony and anthropophony are then calculated as the sum of the amplitude of all 1-kHz bands in, respectively, the 2-11-kHz and 1-2-kHz frequency ranges (Kasten et al., 2012). NDSI is calculated as the ratio between these two components, such that higher values indicate a larger proportion of biophony in the soundscape relative to anthropophony; NDSI scales -1 to +1, where -1 indicates complete dominance of anthropophony (low-frequency sound) whereas +1 indicates total biophony (Kasten et al., 2012). This approach is preferable in our case over the original suggestion to compare anthropophony with the highest amplitude frequency band from the biophony range (Kasten et al., 2012), since it provides less weight to anthropophony and a greater focus on biophony (S. Gage, pers. Comm.), which is important when considering biotic responses to typhoons. Choice of acoustic indices was determined by previous work in this system showing that our focal indices generally covary with biodiversity across the range of sonic conditions experienced in Okinawa (Ross et al., 2021a). To facilitate comparisons among indices across studies, we normalised acoustic index values before analysis, producing relative proportions by dividing $NDSI_{Bio}$ and $NDSI_{Anthro}$ each by their site-specific maximum (Bradfer-Lawrence et al., 2020), and normalising NDSI as (NDSI + 1)/2, since it ranges -1 and +1 and so cannot be scaled by its maximum to normalise values (Fairbrass et al., 2017).

We also used machine learning methods (see Ross et al., 2018) to identify and count detections of three key focal bird species from our recordings. We used Kaleidoscope Pro (version 5.3.0; Wildlife Acoustics Inc., Concord, MA, USA) to train software recognisers for the large-billed

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crow (*Corvus macrorhynchos*, ハシブトガラス in Japanese), the Japanese bush warbler (*Horornis diphone*, ウグイス), and the Ryukyu scops-owl (*Otus elegans*, リュウキュウコノハズク). Together, these species exhibit a range of life histories, habitat affinities, vocal repertoires, and conservation statuses (Hamao, 2013; Inoue et al., 2019; Itô et al., 2000; McWhirter et al., 1996; Ross et al., 2018), including a small-ranged forest habitat specialist (*O. elegans*), and are therefore expected to vary in their sensitivity to typhoons and land cover. Species detection algorithms often transfer poorly across sites as a result of site-specific differences in background sonic conditions (Ross et al., 2018, 2021a), but we developed reliable detectors (≤15% false positives on visual inspection) at 21 sites for *C. macrorhynchos*, 17 sites for *H. diphone*, and 7 of the 10 forest sites for *O. elegans* (Table S1). Kaleidoscope Pro uses a supervised clustering approach based on Hidden Markov Models to separate sound types. Local experts cross-checked automated clustering of sound sources and reclassified sound clusters where necessary to refine species recognisers. Owing to the volume of data used in this study, we did not calculate exact false positive rates for species detections. Instead, we used Kaleidoscope Pro's 'distance-from-cluster-centroid' measure to estimate identity confidence; larger distance values represent detections that are less likely to be the target species. Filtering by distance-from-centroid then allows rapid removal of low certainty detections. We chose a conservative distance filter of 0.5, though our results were qualitatively similar under less conservative filters (Figure S2).

Analysis of acoustic indices

Before measuring the stability of acoustic indices through time, we detrended the normalised acoustic index time series using a centred moving average with a three-day window size in the *R* package *forecast* (version 8.14; Hyndman & Khandakar, 2008). We chose a three-day moving average because increasing the temporal window size of the moving average function to five or seven days produced qualitatively similar results at the expense of time series length and dampened soundscape dynamics (Figure S3). We then measured four components of stability at each site for normalised and detrended acoustic time series: temporal stability, resistance, recovery time, and spatial variability (Table S2; Donohue et al., 2013). Temporal stability was calculated as 1 minus the coefficient of variation (that is, the standard deviation divided by the mean) of the 30-day pre-typhoon period and the 30-day post-typhoon period, separately. Resistance was the maximum absolute change between the mean pre-typhoon baseline state and the maximum point of deviation from that state within 48 hours of the second typhoon passing (Hillebrand et al., 2018). Recovery time was 1 minus the time (in hours) between the point of maximum deviation from baseline (from which resistance was measured) and the point at which values returned to the pre-typhoon baseline (mean ± 95% confidence interval)

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and stayed within them for 24 hours (White et al., 2020), though results were generally robust to alternative window sizes (Figure S4).

We calculated spatial variability from mean values across sites per time point (Table S3). Higher values of spatial variability among sites represent a greater diversity of potential responses through asynchronous biomass fluxes within or among species, providing spatial insurance through patch dynamics (Leibold et al., 2004; Loreau et al., 2003; Wang et al., 2021). To test for potential land cover effects on spatial variability, we also calculated spatial variability among only those sites characterised as either forested or developed (Figure S1). To aid comparison, stability components were normalised by their maximum (0-1) and defined such that larger values represent greater stability (see Table S2 for detailed explanation of stability components and their interpretation).

All analyses were done in *R* (version 4.2.1, R Core Team 2022), using the packages *brms* and *segmented* (Bürkner, 2017; Muggeo, 2008). We tested for interactive effects of typhoons and land use on mean acoustic index states and temporal stability of indices, and for land use effects on acoustic index resistance and recovery time. For these analyses, we fitted generalised linear mixed effects models, with field site included as a random effect, using Stan (Stan development team 2020), implemented via the *brm* function in *brms* (Bürkner, 2017). For all four response variables, the modelled fixed effects included land use category (forest or developed) and typhoon state (pre- or post-typhoon). Given their nature, resistance and recovery time were not modelled as a function of typhoon impact. Default Hamiltonian Monte Carlo was used for the MCMC algorithm and all priors were uninformative. As our response variables fell on the [0,1] scale, we used the Beta model family with logit link. Model comparisons were made with leave-one-out cross validation (LOOIC) implemented in *brms* calculated via Pareto-smoothed importance sampling (Vehtari et al., 2017). We chose models with lowest LOOIC as best performing models (excepting cases where ΔLOOIC < 4.0, where model selection favoured the model with fewer parameters), since lower LOOIC indicates higher predictive accuracy. Four independent MCMC chains were run, each with a warmup phase of 5,000 iterations and sampling phase of 45,000 iterations. We inspected trace plots and density plots visually for chain mixture and verified convergence using the Gelman-Rubin $\hat{R} < 1.01$ and effective sampling size statistics (Gelman & Hill, 2006). We also tested for spatial autocorrelation of model residuals using the Moran's *I* test statistic for each fitted model (Gittleman & Kot, 1990). Moran's *I* results were always non-significant (that is, we did not detect significant spatial autocorrelation in any models), so we report results of the nonspatial models. Results of these models are presented as 95% highest density intervals (credible intervals) of all chains' posterior parameter draws after the burn-in period.

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For models of spatial variability responses, we fitted break-point models of spatial variability as a function of land use category (forest versus developed) using the *R* package *segmented* (Muggeo, 2008). Break-point models fit segmented relationships between predictor and response variables to determine whether the form of the relationship changes as a function of the predictor variable. In our case, we modelled spatial variability as a function of land use category and time, with two fixed break points specified at the onset of the first typhoon (00:00, 29 Sep 2018), and immediately following the second typhoon (00:00, 6 Oct 2018), allowing intercepts, but not slopes, to vary. To prevent overfitting, we constrained models to these two *a priori* break-points. We selected best fitting models using likelihood ratio tests, where significant ($p < 0.05$) tests indicated a model with break point parameters and an additional intercept was a significant improvement over one without such parameters. In all cases where break-point models were selected, we compared spatial variability values before the first break-point (pre-typhoon) and after the second break-point (post-typhoon) by comparing the 95% confidence intervals of the pre- and post-typhoon periods; nonoverlapping confidence intervals suggest a change in spatial variability at the $p < 0.05$ confidence level.

Analysis of automated species detections

Given the lower temporal resolution of daily summed time series of bird species detections (*i.e.*, one value per day rather than 48), we did not estimate resistance or recovery time for bird species detections. Rather, we focused our analyses on the temporal stability of bird detections for each species across the 30-day pre- and post-typhoon periods and the spatial variability of detections per day across all sites, and across sites falling into each land use category (forested versus developed). Note that the forest specialist *Otus elegans* was not detected in any developed sites (Table S1), so for this species there is no data subset to compare between land cover types. As automated species detections produced count data, we did not normalise raw values of bird species detections.

As for acoustic indices, we tested for interactions between land use and typhoon effects on the mean number of daily detections (mean state) and the temporal stability of daily detections. We compared species effects by fitting a three-way interaction between species identity, land use, and typhoon period (two levels: before versus after the typhoons). We specified *brms* models as described previously, but with lognormal error distributions, which outperformed other error structures based on LOOIC. To aid convergence, we additionally set weakly informative priors of $N(0,2)$ for all predictor variables in both models, but otherwise opted for uninformative priors. For spatial variability, we fit break-point models of a three-way interaction between species identity, land use, and typhoon effects, with two fixed break points delineating the typhoon period as described

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above. We evaluated the suitability of fitting break-point models by comparing break-point models with linear models via likelihood ratio tests. Pairwise contrasts were made using 95% confidence intervals of the pre- and post-typhoon break points for each species and land use data subset.

Results

Acoustic index results

We found that NDSI was significantly lower at many sites after the typhoons (Fig. 2a). This overall pattern seemed not to be driven by an underlying change in the biophony component of NDSI (Fig. 2b), but rather by an increase in anthropophony following the typhoons (Fig. 2c). There was no land use or typhoon effect on the temporal stability, resistance, or recovery of NDSI, $NDSI_{Bio}$, or $NDSI_{Anthro}$. However, in some cases we found differences in acoustic index values following the typhoons (Table S3).

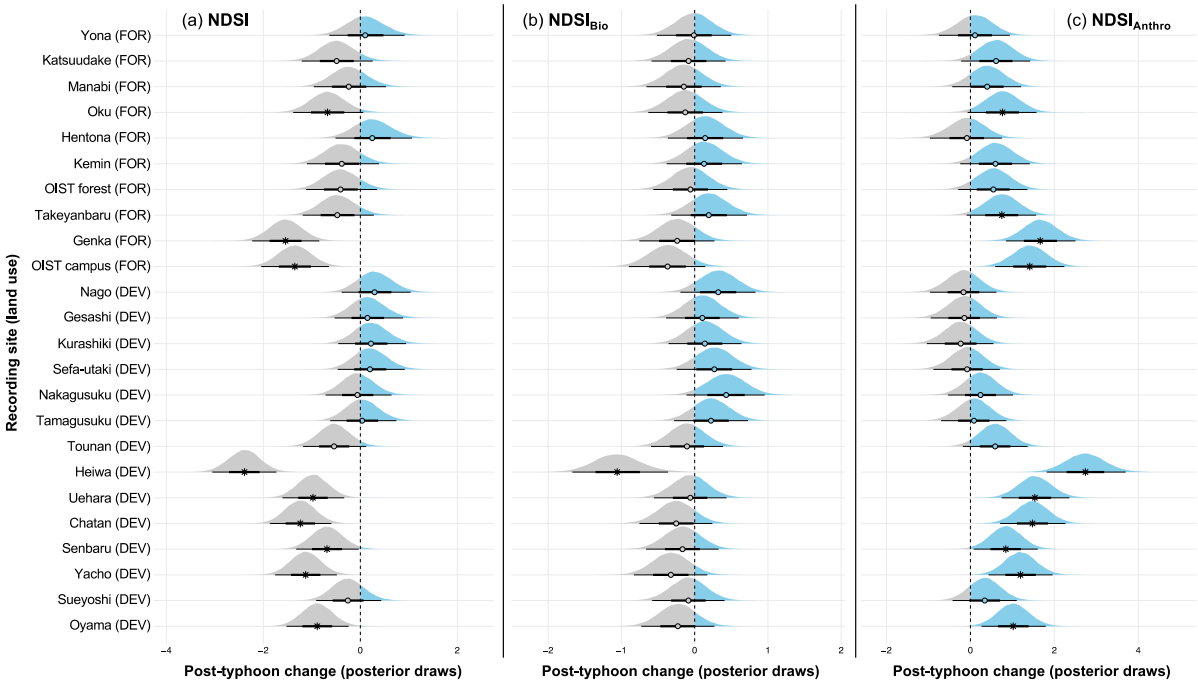

Figure 2. Comparison of acoustic index mean state values before and after the typhoons. Posterior distributions represent 90,000 post-convergence MCMC draws of the change from pre- to post-typhoon periods, where values below zero (grey) indicate a post-typhoon decline, and values above zero (blue) a post-typhoon increase in mean state value. Non-zero-spanning credible intervals are marked with *, while circles indicate zero-spanning credible intervals (no change based on the posterior distribution). Draws are shown per site, ordered from most forested (top) to most developed (bottom) based on principle component axis 1 of the land use dimensionality reduction (PCA; see Fig. S1). Panels represent changes in mean state values for three acoustic indices: the normalised difference soundscape index [NDSI] (a), biophony [$NDSI_{Bio}$] (b), and anthropophony [$NDSI_{Anthro}$] (c).

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When modelling the effects of typhoons and land use on spatial variability of acoustic indices through time, break-point models outperformed linear models in all cases (likelihood ratio tests: $p < 0.05$). Following the typhoons, the spatial variability of NDSI increased (Fig. S5). This post-typhoon spatial divergence in NDSI was underlain by an increase in biophony, but not anthropophony (Fig. 3). Moreover, spatial variability in biophony increased among forested sites but not among developed ones following the typhoons (Fig. 3b). $NDSI_{Anthro}$ did not differ significantly through time (Fig. 3c) or between land use classes (Fig. 3d).

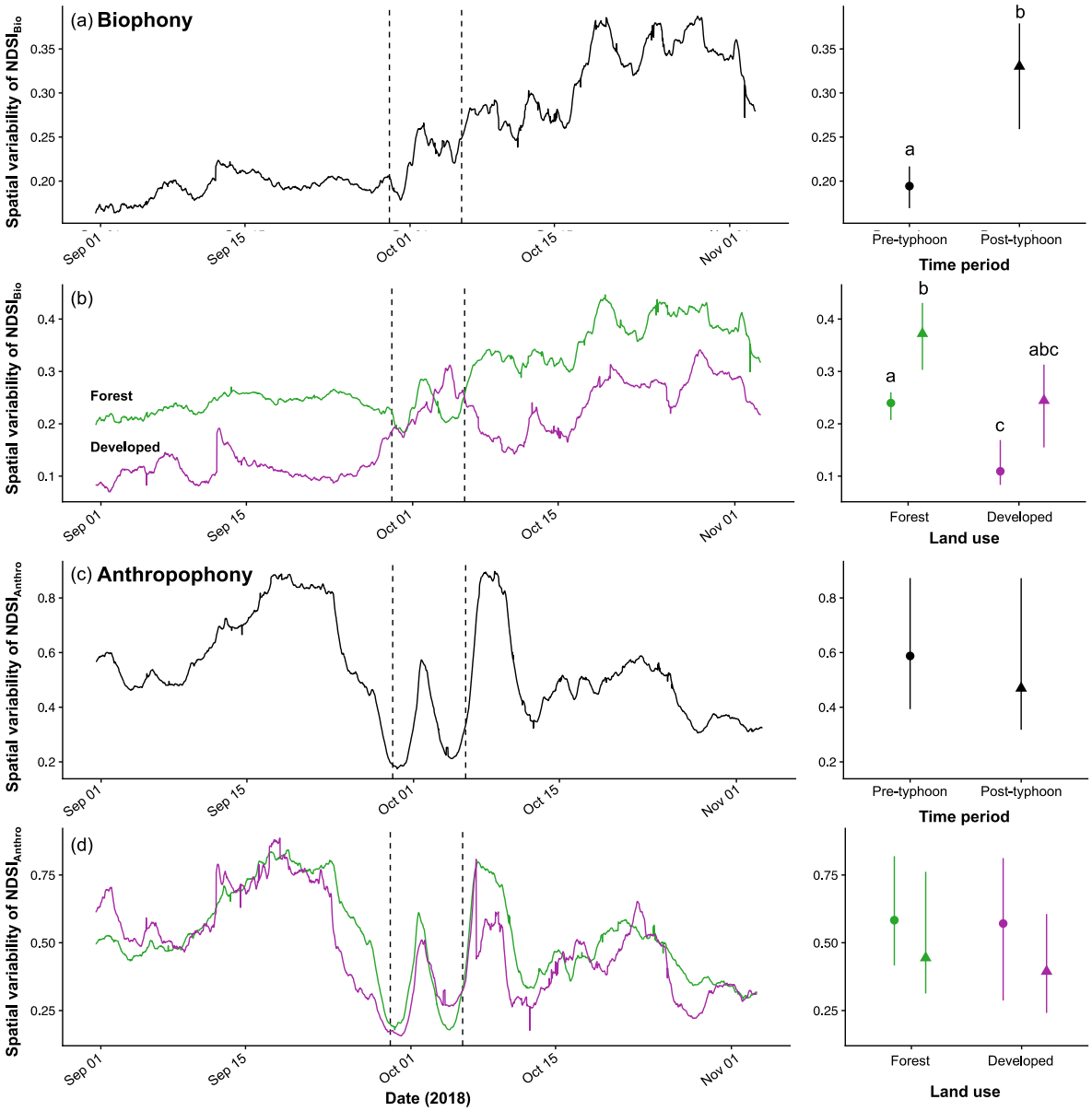

Figure 3. Spatial variability of biophony [$NDSI_{Bio}$] and Anthropophony [$NDSI_{Anthro}$] through time. Left panels show time series of $NDSI_{Bio}$ (a,b) and $NDSI_{Anthro}$ (c,d) spatial variability across all sites (a,c), and across forest (green)

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and developed (purple) sites separately (b,d). Dashed lines delineate the pre- and post-typhoon periods. Right panels show the 95% confidence intervals of spatial variability across all sites (a,c), and separated by land use (b,d), for the pre-typhoon (circles) and post-typhoon (triangles) periods. Significant ($p < 0.05$) pairwise contrasts are denoted with different subscript/superscript letters (*e.g.*, "a" differs from "b" but not "ab").

Automated species detection results

Species identity interacted with the typhoons, producing species-specific typhoon responses (Table S3). Detections of *C. macrorhynchos* and *O. elegans* were similar preceding and following the typhoons (Fig. 4a and 4c), whereas *H. diphone* was detected less often after the typhoons (Fig. 4b). We also found that, following the typhoons, species detections were more stable (less variable) through time, regardless of the species considered (Fig. 5; Table S3). We found no effect of land use on the mean number of daily species detections or the temporal stability of daily detections (Table S3).

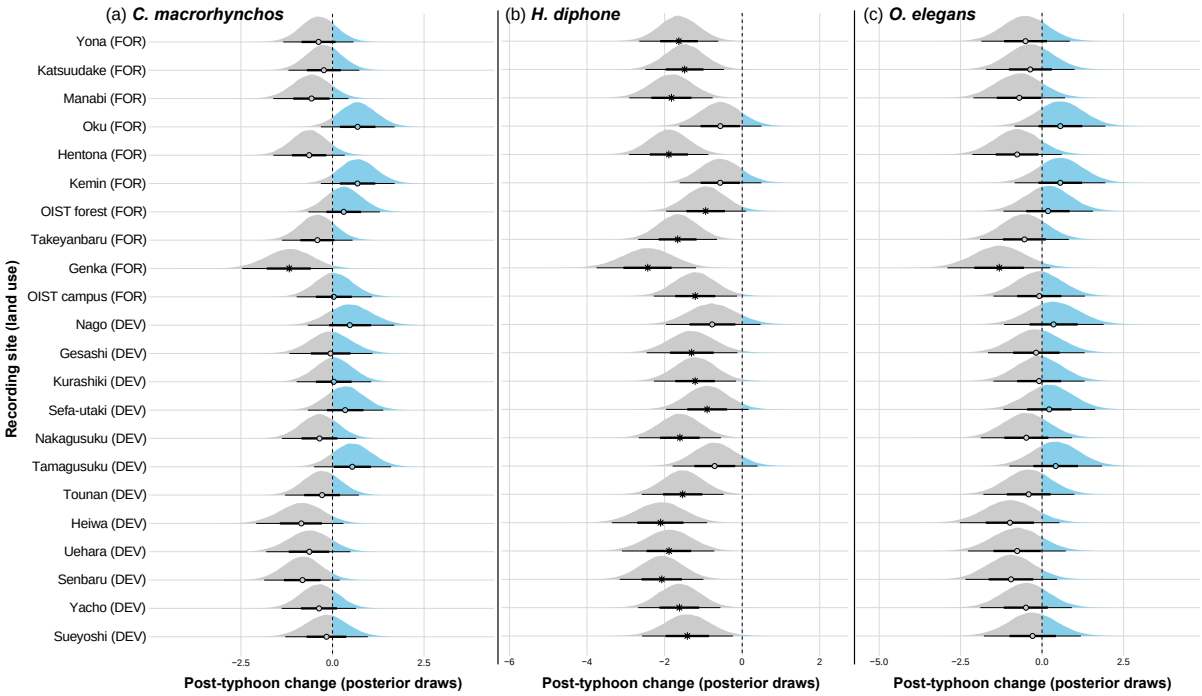

Figure 4. Comparison of mean daily species detections before and after the typhoons. Posterior distributions representing 90,000 post-convergence MCMC draws of the change from pre- to post-typhoon periods, where values below zero (grey) indicate a post-typhoon decline, and values above zero (blue) a post-typhoon increase in mean daily automated species vocalisation detections. Non-zero-spanning credible intervals are marked with *, while circles indicate zero-spanning credible intervals (no change based on the posterior distribution). Draws are shown per site, ordered from most forested (top) to most developed (bottom) based on principle component axis 1 of the land use dimensionality reduction (PCA; see Fig. S1). Panels represent changes in mean daily species detections for our three focal species: *Corvus macrorhynchos* (a), *Horornis diphone* (b), and *Otus*

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elegans (c). Inferred posterior draws (automatically computed through the site random effect term) extrapolated to field sites where species were not present (Table S1) are shown as faded distributions.

Figure 5. Comparison of temporal stability of species detections before and after the typhoons. Posterior distributions represent 90,000 post-convergence MCMC draws of the change from pre- to post-typhoon periods, where values below zero (grey) indicate a post-typhoon decline, and values above zero (blue) a post-typhoon increase in the temporal stability of automated species vocalisation detections (all species). Non-zero-spanning credible intervals are marked with *, while circles indicate zero-spanning credible intervals (no change based on the posterior distribution). Draws are shown per site, ordered from most forested (top) to most developed (bottom) based on principle component axis 1 of the land use dimensionality reduction (Fig. S1). See Figure S6 for posterior draws of individual species.

When modelling the effects of typhoons, land use, and species identity on spatial variability of bird detections through time, break-point models did not perform significantly better than models without break point terms based on likelihood ratio tests (Spatial variability across all sites: $L.Ratio_{13,7} = 6.98$, $p = 0.32$; within land use categories: $L.Ratio_{20,10} = 16.2$, $p = 0.093$). Accordingly, there was no significant post-typhoon change in spatial variability of species detections either overall or when broken down by land use (Fig. 6). Before the typhoons, *Otus elegans* had highest spatial variability in detections, and after the typhoons its spatial variability remained higher than that of *Corvus*

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macrorhynchos, but not of *Horornis diphone* (Fig. 6a). When further broken down by land use, species did not vary in their land use-specific spatial variability before the typhoons. However, after the typhoons, *O. elegans* had higher spatial variability in detections among forested sites than did *C. macrorhynchos* (Fig. 6b).

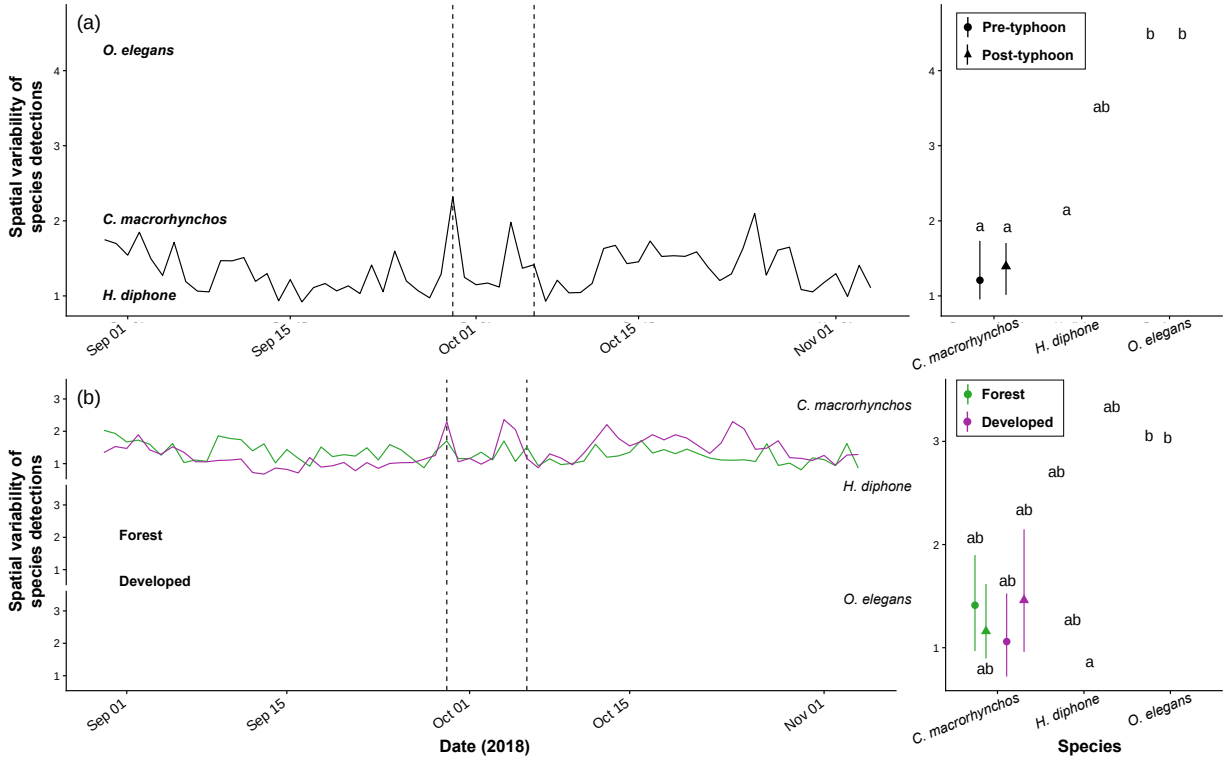

Figure 6. Spatial variability of automated daily species detections through time. Left panels show time series of spatial variability of daily species detections across all sites (a), and across forest (green) and developed (purple) sites separately (b), for each of *Corvus macrorhynchos* (darkest), *Horornis diphone*, and *Otus elegans* (lightest). Dashed lines delineate the pre- and post-typhoon periods. Right panels show the 95% confidence intervals of spatial variability of daily species detections across all sites (a) or separated by land use (b) for the pre-typhoon (circles) and post-typhoon (triangles) periods. Significant ($p < 0.05$) pairwise contrasts are denoted with different subscript/superscript letters (*e.g.*, "a" differs from "b" but not "ab").

Discussion

This study leverages high-resolution acoustic monitoring data from an island-wide sensor array to record ecological responses to extreme weather events in the form of two large typhoons. We found no land use effects on most dimensions of stability measured. However, we found post-typhoon increases in the spatial variability of biophony ($NDSI_{Bio}$) and the normalised difference soundscape index (NDSI) among forested sites, indicating that the typhoons elicited divergent ecological responses among Okinawa's forests. Moreover, we detected no such change in spatial

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variability in response to the typhoons among Okinawa's developed urban and agricultural sites. The observed divergence in biophony responses to typhoons among forest sites, but not developed urban or agricultural sites, suggests that land use and habitat change can hinder the reactive capacity of ecological communities and their associated soundscapes. The observed variation in typhoon responses among forest community soundscapes may indicate a greater variety of pathways through which biotic communities in forests can respond to disturbance (Vogel et al., 2019). Such *response diversity* is increasingly recognised as a potentially key driver of stability and statistical portfolio effects, owing to its effects on asynchrony and spatial community dynamics (Mori et al., 2013; Ross et al., 2022). In contrast, those communities in developed urban or agricultural sites showed more homogenous responses to the typhoons, perhaps as a direct consequence of land use change *per se*, or of its effect on local biodiversity. We did not directly measure local biodiversity in this study, instead estimating the activity of some key focal bird species using automated species detections. However, previous work in this system provided evidence for a loss of rare and endemic birds under land use development, producing communities that are a nested subset of forest bird communities in Okinawa's developed south (Ross et al., 2018). Despite generally aligning well with acoustic index results for other response measures, the species surveyed here did not exhibit responses that diverged in space following the typhoons, as might have been expected based on biophony results. This suggests that the spatial divergence in the biotic component of soundscapes recorded here may be better explained by other species (of birds or other taxa) not targeted in this study. Future work expanding on these analyses to provide a more holistic view of the Okinawan biota should therefore prove fruitful for identifying individual species contributions to typhoon responses. If our biophony results are indeed a product of biotic responses to typhoons as would be expected from theory (Kasten et al., 2012), then a post-typhoon increase in spatial variability may reflect changes to species' patchiness. For example, Willig and Camilo (1991) described an increase in spatial patchiness of the snail *Caracolus caracol* following Hurricane Hugo in Puerto Rico, caused by a thinning of populations due to post-hurricane mortality.

Soundscape composition after the typhoons saw an increase in anthropophony, but not a decline in biophony as might be expected were populations impacted negatively by typhoon disturbance (*e.g.*, Cely, 1991; Pavelka et al., 2007). In contrast, the observed post-typhoon increase in spatial variability in NDSI was driven by biophony rather than anthrophony. This suggests that, while biophony may not have been affected substantially by typhoon disturbance at the individual site level, variation in biotic responses at larger scales across field sites nonetheless manifested as changes in the spatial variability of biophony after the typhoons. That we did not detect particularly strong site-level typhoon impacts, but rather saw spatial divergence in ecological responses to typhoons across

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multiple sites, underscores the necessity of monitoring at scale. Multi-site acoustic sensor arrays such as ours thus provide opportunity to monitor both local and regional biodiversity change, in turn providing critical new insight for conservation management (Roe et al., 2021; Sethi et al., 2020a; Van Parijs et al., 2015). The observed post-typhoon increase in anthropophony on the other hand, likely reflects a change in sound propagation driven by vegetative structural damage and thinning of previously dense habitats, as is often documented following large storms (Abbas et al., 2020; Elliott & Nino, 1960). We did not measure habitat structure directly, and so the causes of increases to anthropophony following typhoons Trami and Kong-Rey cannot be demonstrated empirically. We did, however, observe significant damage and alterations to habitat structure of forested field sites (T. Yoshida & M. Yoshimura, pers. obs.). Automated bird species detections were, conversely, more stable through time after the typhoons, suggesting disturbance may affect the consistency of species vocalisations in Okinawa (see also Fraterrigo & Rusak, 2008), or perhaps that typhoon-induced changes to habitat structure allow vocalisations to travel further without attenuation, and hence be more reliably detected by our sensors.

The focal bird species considered here generally differed in their responses to typhoons. Automated vocalisation detections of the Japanese bush warbler (*Horornis diphone*) declined after the typhoons, while those of the large-billed crow (*Corvus macrorhynchos*) and Ryukyu scops owl (*Otus elegans*) did not. Given that acoustic surveys cannot differentiate between cases where a species is not producing sound and those where that species is not present (Toth et al., 2022), we cannot say with certainty that *H. diphone* populations declined following the typhoons. Regardless, our detected post-typhoon declines in *H. diphone* vocalisations—either through behavioural changes, distributional shifts, or local mortality—were consistent across >80% of the field sites in which this species was detected. Habitat specialism may explain the observed species-specific differences in vocalisation changes following the typhoons; *H. diphone* relies on undergrowth and bushes for foraging (Haneda & Okabe, 1970) and typhoon disturbance has the potential to alter the structure of this habitat (Abbas et al., 2020; Elliott & Nino, 1960), in turn affecting the invertebrate communities on which *H. diphone* feeds (Azuma et al., 1997). In contrast, the forest specialist *O. elegans* was not detected less frequently after the typhoons, suggesting that its habitat and/or foraging were unaffected by the typhoons, or perhaps that cavity nesting reduced typhoon impact by reducing exposure to extreme weather (Inoue et al., 2019). Such species-specific responses to disturbance may more generally reflect differences in life history and other functional response traits (Suding et al., 2008), which can be useful predictors of community dynamics, disassembly, and stability in birds (*e.g.*, Ausprey et al., 2022; Burivalova et al., 2015; Hordley et al., 2021; Zhang et al., 2016). Similarly, different vocalisation typhoon responses among field sites may reflect differences in underlying

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vegetative changes as determined by plant functional response traits. For example, Craven *et al*. (2016) found that functionally diverse Canadian forests were dominated by trees with response traits that promoted resilience to recurrent anthropogenic disturbance through rapid regrowth, rather than resistance to projected climate change through drought or flood tolerance. The response traits of plants may then, in turn, determine the structural habitat change experienced by birds and other vocalising animals (*e.g.*, Abbas et al., 2020), as well as directly influencing sound propagation (Morton, 1975).

Though we and others have demonstrated the capacity for passive acoustic monitoring methods to capture unpredictable extreme weather events (Gottesman et al., 2021; Simmons et al., 2021), such methods are often limited in their ability to accurately reflect biodiversity patterns. A recent meta-analysis reports a generally positive link between acoustic indices and biodiversity (Alcocer et al., 2022), but one with diminishing effect sizes over time as studies increasingly forego appropriate validation, and as study designs incorporate yet wider varieties of non-target sounds, which can hinder the interpretability of those acoustic indices aiming to reflect biodiversity (Ross et al., 2021a). Though our acoustic indices and automated species vocalisation results were not a perfect match, their joint use provides two separate lines of evidence for typhoon-induced soundscape change; such species and soundscape methods are still rarely used in combination despite their clear potential to provide complementary information on ecological dynamics (*e.g.*, Ferreira et al., 2018; Ross et al., 2018). That said, building reliable vocalisation recognition algorithms remains a challenge, particularly when aiming for transferability to different habitats or seasons, which provide a range of non-target sounds beyond those on which algorithms may have been trained. Increasing application of deep learning to such problems will likely help provide a solution (*e.g.*, Sethi et al., 2020b) as will continued efforts to build labelled sound libraries from which automated species detection algorithms can be trained (Deichmann et al., 2018). Moreover, soundscape dynamics are frequently characterised by strong seasonal cycles (*e.g.*, Vokurková et al., 2018), presenting a challenge when attempting to disentangle disturbance responses from seasonal soundscape change (Ross et al., 2023). For example, our focal species differ in their seasonality and phenology, meaning that natural phenological differences may in part be responsible for the differences in species' typhoon responses we observed here. Our moving average detrend aimed to remove as much seasonal signal as possible, though longer time series are needed for more sophisticated approaches to deseasonalisation (*e.g.*, wavelet decomposition) to be effective (Cazelles et al., 2008). Our *k*-means clustering approach to distinguish field sites by their dominant land use identified an optimal split of two clusters, separating primarily forested sites from those dominated by developed urban or agricultural land use. However, these developed land uses can act on ecological dynamics and stability in different ways. For example,

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Olivier *et al*. (2020) used citizen science data from across France to show that agricultural intensification directly affected population, and, in turn, community stability of birds, while urbanisation acted only indirectly on community stability through changes to diversity and population asynchrony. Our study design, which was based on unsupervised (*k*-means) site clustering by dominant land use consequently did not allow us to directly compare urban and agricultural field sites, despite their potential for contrasting effects on ecological stability.

Our study tested the capacity for land use and climate change in the form of extreme weather events to jointly shape ecological stability. Using passive acoustic monitoring data from a landscape-scale sensor network across Okinawa Island, we found that land use rarely modified ecological responses to typhoons. However, soundscapes diverged across the landscape following the typhoons, contrary to the expected typhoon-induced soundscape homogenisation. This post-typhoon spatial divergence occurred among forested but not developed urban and agricultural field sites, suggesting that forest sites exhibited a wider variety of pathways through which soundscapes could respond to typhoon disturbance. That is, land use intensification may produce ecological communities that are more homogeneous in how they respond to disturbance (Vogel et al., 2019), while forest sites harbour communities with greater potential for collective resilience to future disturbance through patch dynamics and rescue effects among different local forest communities (Leibold et al., 2004). Such spatial insurance effects have the potential to contribute to landscape-scale stability and spatial portfolio effects by affecting population and community asynchrony (Loreau et al., 2003; Wang et al., 2021), and our results suggest that land use development can degrade the natural insurance capacity of Okinawa's forests. This study draws on prior knowledge of Okinawan biodiversity (Inoue et al., 2019; Itô et al., 2000; McWhirter et al., 1996), the performance of passive acoustic methods in this system (Ross et al., 2018, 2021a), and the characteristics of typhoons and land use intensification across Okinawa Island (Elliott & Nino, 1960; Takeuchi et al., 1981). Such baseline data provides a critical backdrop against which our results stand, allowing us to infer species and soundscape responses to the joint threats of climate change and land use intensification from acoustic recordings of typhoons (Altwegg et al., 2017). As longer and higher-resolution acoustic data is amassed through multi-site acoustic sensor arrays (*e.g.*, Roe et al., 2021; Sethi et al., 2020a; Van Parijs et al., 2015), the utility of passive acoustic monitoring to document ecological responses to extreme weather events across the globe will become ever clearer, particularly in light of the increasing frequency and destructive potential of extreme events in the Anthropocene.

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Conflict of Interest

The authors declare no conflict of interest.

Data availability statement

The data supporting the findings of this study and all R code are available via the Zenodo digital repository as Ross, S. R. P.-J., Friedman, N. R., Armitage, D. W., Dudley, K. L., Yoshimura, M., Yoshida, T., Economo, E. P., & Donohue, I. (2023). Habitat degradation homogenizes ecological responses to typhoons across a subtropical island (v0.2-review) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.7520062

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