



Heightened extinction risk due to tropical cyclones in insular biodiversity hotspots

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ABSTRACT

Tropical Cyclones (TCs) represent a serious and potentially growing threat to global biodiversity, although spatial patterns in the severity of this threat are poorly explored. We provide the first global-scale analysis of TC-related extinction risk by examining both their frequency and the number of species they directly threaten in insular biodiversity hotspots; widely recognized spatial units representing both exceptional biodiversity and elevated threat. We first identified which insular hotspots possessed a theoretically high TC-related extinction risk by plotting 50 years of storm tracks for severe (category 4 and 5) TCs (STCs) and determined the frequency with which they occur within each insular hotspot. We then used IUCN Red List data to determine numbers of terrestrial vertebrates in each ‘high risk’ insular hotspot considered to be directly threatened with extinction by STCs. Five insular hotspots (Japan, Polynesia-Micronesia, Philippines, Madagascar and the Indian Ocean Islands, Caribbean Islands) were identified as being ‘high risk’, together accounting for >95 % of STCs falling within insular hotspots. However, the numbers of TC-threatened species in these hotspots varied greatly, from 128 in the Caribbean Islands (which encountered the fewest STCs of all ‘high risk’ hotspots) to eight in Japan (which received the most STCs). Results therefore indicate that TC-related extinction risk is not related to STC frequency, and other ecological and geographical factors are likely to be important drivers of risk. Regardless, our results show that several insular hotspots, particularly the Caribbean Islands, support many species at immediate risk of TC-driven extinction, and these require urgent conservation action. We advocate for the creation of an IUCN task force to oversee conservation strategies aimed at preventing extinctions of severely range-restricted storm-threatened species. We provide a watchlist of 60 such species with a particularly high risk of extinction which should be the initial focus for such a working group.

1. Introduction

Biodiversity loss is caused by a wide range of drivers that vary greatly in the rapidity with which they may push one or more species to extinction (Millennium Ecosystem Assessment, 2005). Due to the relatively slow speed inherent in some of these threats (e.g. climate change, Keith et al., 2014; or some diseases, Scheele et al., 2019), it can often be challenging to identify and assess signs of a species’ decline in a timely fashion. At the other end of the scale, catastrophic events striking small and/or isolated populations are arguably the most rapid and immediate

cause of extinction (Simberloff, 2000; Whittaker et al., 2023). Although such stochastic events are likely to have always been a cause of natural extinctions (Williamson, 1989), in the Anthropocene, the risk they pose to species is increasingly compounded by heightened levels of habitat fragmentation, introduction of invasive species, and other pressures, which in turn reduce population sizes and resilience (Dalsgaard and Temeles, 2024; Schoener et al., 2001; Turvey and Crees, 2019). This combination of longer-term pressures combined with a single catastrophic event has already led to species extinctions (e.g. del Hoyo et al., 2020; Olson, 1996; Galbreath, 2004).

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Amongst the most common catastrophic natural hazards threatening global biodiversity are tropical cyclones (henceforth 'TCs' - also variously named hurricanes or typhoons depending on the geographic region in which they occur). TCs can threaten biodiversity in several ways. In the short term, wind damage, flooding, and storm surges can damage and destroy habitats and cause heightened mortality (Fairbairn et al., 2022; Ross et al., 2009; Wiley and Wunderle, 1993; Wunderle et al., 1992). In the medium and long term, TC damage can alter ecosystem structure and ecological succession (Lugo, 2008; Wiley and Wunderle, 1993), facilitate the spread of invasive species (Bhattarai and Cronin, 2014) and alter species interactions and their evolutionary trajectories (Dalsgaard and Temeles, 2024). These risks are particularly acute in insular ecosystems, as the small spatial ranges and high habitat specificity inherent to many island endemics render them particularly vulnerable (Fordham and Brook, 2010; Simberloff, 1995; Trevino et al., 2007). Indeed, a large majority of recorded extinctions are of island endemics (Whittaker et al., 2023).

The risk TCs represent to global biodiversity is already recognised within the IUCN threat categorisation (IUCN, 2022). At present, 2705 species globally have storms and flooding listed as a threat, and these factors have been identified as important drivers in the extinction of 12 species (IUCN, 2023). TCs may also become an increasingly important driver of extinction in the future if climate change facilitates an increase in their frequency and intensity, as several studies have suggested (Goldenberg et al., 2001; Knutson et al., 2010; Moore et al., 2017; Sobel et al., 2016). However, while it is recognized that TCs represent a prevalent (and potentially growing) threat to global biodiversity, there has been no research published to date examining how this threat varies spatially or taxonomically. Also missing are prioritisation lists identifying species possessing a particularly high TC-related extinction risk. These constitute critical research gaps, given that a comprehensive understanding of the threat TCs pose to biodiversity and the identification of priority species are key to developing effective conservation mitigation strategies.

In this study, we make the first global assessment of how extinction risk posed by TCs varies geographically, focusing on insular biodiversity hotspots. The 34 global biodiversity hotspots (henceforth 'hotspots') - initially identified by Myers et al., 2000, and later expanded on by Brooks et al., 2006 - encompass just 1.4 % of Earth's land area, yet hold more than half of its species and are widely regarded as a cornerstone of 21st-century conservation prioritisation (Trew and Maclean, 2021). Because of this, hotspots were chosen as the focus of this study as they represent concentrations of both global diversity and threatened species (Myers et al., 2000), and because they are highly recognized, well-studied, spatially discrete areas that allow for meaningful quantitative comparison. We restricted our comparisons to insular hotspots specifically for two reasons. Firstly, the biogeographical characteristics of islands mean they possess intrinsically high extinction risk, even compared to the risks hotspots face generally (Loehle and Eschenbach, 2012; Matthews et al., 2022; Whittaker et al., 2023). Secondly, because even more so than hotspots generally, they represent discreet, clearly demarked geographical units that are relatively straightforward to obtain species-level data on, and as such lend themselves to comparative analysis. Amongst insular hotspots, we seek to (1) identify which possess a heightened theoretical risk of TC-driven extinctions (based on the frequency of severe TC events), (2) characterise how extinction risk varies spatially and taxonomically within these 'high risk' insular hotspots, and explore ecological and biogeographical factors which may drive differential risk, and (3) create a 'watchlist' of species within 'high risk' insular hotspots that are likely to be at immediate risk from TC-driven extinction (as well as a secondary list of species that fit the same criteria but occur outside of these insular hotspots).

2. Methods

2.1. Global distribution of severe TCs in biodiversity hotspots

We sourced spatial data for all 34 biodiversity hotspots from Hoffman et al. (2016). Historical TC linear track data (points tracking the centre of the TCs at 6-h intervals) of 0.1 degree spatial resolution (~10 km) was obtained from the International Best Track Archive for Climate Stewardship (version 4; Knapp et al., 2010). Given high variability in both the methods and the technology used to monitor TC's before the 1970s, we focussed our analysis on a 50-year period (1972–2022), excluding 2023 which was an incomplete year at the time of analysis.

Our examination of IUCN Red List accounts of TC-threatened species (see below) suggested that, historically, it has mainly been particularly severe storms that have adversely affected species' conservation status (93 % of named storms directly associated with a detrimental effect on a species' conservation status were of category 4 or category 5 on the Saffir-Simpson Hurricane Scale; Saffir, 1973; Simpson, 1974). Thus, for analysis, we only included TCs that reached a maximum category of 4 or 5 - henceforth 'STC's' (Severe Tropical Cyclones).

Our aim was to classify theoretically 'high risk' insular hotspots by identifying those with the highest frequency of STC events across the study period. To do this, firstly, we superimposed historical TC track data onto our global hotspots map using ArcMap version 10.8.1 and tallied the number of STCs with at least part of their pathway falling within the boundary of each hotspot (i.e., insular and non-insular). We focused on any STCs occurring within the hotspot boundary (rather than just those that made landfall) as we were interested in identifying 'high risk' regions rather than assessing the impacts of individual past STCs. Secondly, we identified how many of the affected hotspots were 'insular hotspots' (those comprised entirely of islands - $n = 9$). Finally, in order to provide further validation of our list of 'high risk' insular hotspots we also tallied the number of STCs that made landfall on islands within insular hotspot boundaries. To do so, we obtained landmass data for each insular hotspot using world country data version 4.1 (sourced from OpenStreetMap geographic information system database <https://osmda.ta.openstreetmap.de/data/land-polygons.html>), removed landmasses with $<0.01 \text{ km}^2$ in area (the size of the smallest island to which a storm-threatened species is endemic - see below), and tallied STC tracks fitted with a very conservative 10 km buffer that intersected with islands within insular hotspots. We used this approach as TC radius can vary greatly over time due to atmospheric conditions, sea surface temperatures, and storm strength (Emanuel, 1999), thus sourcing a unique radius measurement per TC is not possible.

2.2. Hotspot biodiversity and threat metrics

We first tallied the number of terrestrial vertebrate species (amphibians, reptiles, birds, and mammals) present within each 'high risk' insular hotspot using the advanced search function on the IUCN Red List (IUCN, 2023), filtering for land regions (at a country/territory level) as appropriate for each hotspot. Appendix S1 provides a list of constituent countries/territories for each insular hotspot. We focussed on terrestrial vertebrates given that these represent the best-studied taxa with near-comprehensive coverage on the IUCN Red List and high availability of species-level ecological data (Martin et al., 2023), and hence are suitable for global scale comparative analyses. Note that our definition of 'terrestrial vertebrates' included species that spend part of their lifecycle on land (e.g. Sea Turtles) and species that frequently inhabit inland waterways and shallow coastal waters (e.g. Sirenia). We then calculated the total number of threatened species in these taxa (i.e. Data Deficient, Vulnerable, Endangered, and Critically Endangered) per 'high risk' insular hotspot (with numbers of Critically Endangered species being given special emphasis in our results). These species, along with their associated metadata, are presented in Appendix S2. We classed Data Deficient species as 'threatened' given that numerous studies have

shown that the majority of such species are likely to be at risk of extinction (e.g. Bland et al., 2015; Borgelt et al., 2022; Howard and Bickford, 2014; Jetz and Freckleton, 2015, but see González-del-Pliego et al., 2019) and there is established precedence for taking this approach in the experimental design of many other studies (e.g. Biega et al., 2017; Martin et al., 2014a). Nevertheless, numbers of Data Deficient species in our dataset are clearly reported in our results. Finally, for each ‘high risk’ insular hotspot we tallied the total number of species explicitly threatened under IUCN Red List threat category ‘11.4 Storms & flooding’ (henceforth ‘storm-threatened species’). This analysis only included extant, native species resident or seasonally breeding in each insular hotspot, with introduced species ($n = 1$), vagrants ($n = 5$), non-breeding species ($n = 7$), or locally extinct species ($n = 1$) being excluded (14 species excluded in total – Appendix S2). For all threatened species in our dataset, we also sourced three other variables related to their potential vulnerability to TCs: i) the number of islands a species is restricted to (based on distribution maps and species account text in IUCN, 2023), ii) the number of locations a species occurs in (following IUCN, 2023 – median values were calculated when a range of values was presented, with a random selection where median values could be one of two numbers), and iii) the spatial range of each species. For mammals and birds, spatial range data were sourced from the PanTHERIA (Jones et al., 2009) and AVONET (Tobias et al., 2022) trait databases, respectively. For amphibians and reptiles (which lack global trait databases with geographical variables) we used the coarser ‘estimated extent of occurrence’ value provided for each species in their most recent IUCN Red List account (IUCN, 2023; IUCN Standards and Petitions Committee, 2024). We also calculated average values for each of these three variables for storm-threatened species in each ‘high risk’ insular hotspot. Any of these variables that could not be scored for a given species were excluded from further analyses. To provide additional information regarding the specifics of storm-related threats for each species in our dataset, we also recorded data from three further variables provided in each IUCN Red List account: i) threat timing (e.g. if a threat is ongoing, predicted in the future), ii) threat scope (relating to how much of a species range the threat applies to), and iii) threat severity (relating to the speed in which the threat could drive species declines) (IUCN, 2023; IUCN Standards and Petitions Committee, 2024). Finally, we noted all named TCs explicitly mentioned as having a detrimental effect on a species’ conservation status in the Red List accounts for storm-threatened species, and cross-referenced these with the Knapp et al. (2010) database to determine their strength. This information was used to inform our choice of focusing on category 4 & 5 storms in our analysis (see above).

2.3. Geographic and ecological traits of ‘high risk’ insular hotspots

We wanted to characterise the geography and ecology of ‘high risk’ insular hotspots, with an emphasis on those traits that may exacerbate species’ vulnerability. Given that extinction risk is often linked to range size (Newsome et al., 2020; Pimm et al., 1988), and that species endemic to small islands will typically have smaller ranges than those endemic to large islands, we obtained landmass data for each insular hotspot, extracting the number of landmass polygons within the borders of each ‘high risk’ insular hotspot. From these data, we tallied the total number of individual landmass polygons (i.e. islands) per hotspot. We excluded those $<0.01 \text{ km}^2$ in area, this being the size of the smallest island where storm-threatened species in our dataset occur (Carrot Rock in the British Virgin Islands, home to Carrot Rock Skink *Spondylurus macleani* and Carrot Rock’s Anole *Anolis ernestwilliamsi*). We used these data to calculate an ‘insularity index’ (i.e. total number of landmass polygons divided by the total land area of each hotspot) to indicate how heavily each insular hotspot is dominated by large landmasses. We then looked at the relationship between this insularity index, STC frequency and the number of storm-threatened species. To explore any potential links between habitat loss and the numbers of storm-threatened species, we also

noted the estimated percentage of natural vegetation cover left within each insular hotspot, following Sloan et al. (2014). These estimates were obtained via a combination of automated and visual satellite-image analyses of land-cover classes and conditions as well as the mapping of major landscape disturbances. Finally, given that extinction risks are particularly elevated on oceanic islands (those that have never been connected to continental landmasses) compared to continental islands (those that were connected to continental landmasses during glacial periods) (Paulay, 1994), we determined whether each insular hotspot is comprised predominantly of oceanic or continental islands using maps in Sayol et al. (2020).

2.4. Creation of a watchlist of highest priority storm-threatened species

Finally, we created a ‘watchlist’ of storm-threatened species restricted to our ‘high risk’ insular hotspots, highlighting species of particularly high conservation concern (those with very small spatial ranges, meaning they could theoretically be wiped out by a single future STC event). To do this, we identified all storm-threatened species in our dataset that are both found only on a single island and inhabit just one location (following IUCN, 2023). We also included single island endemics scored as inhabiting an ambiguous number of locations if they were classified as ‘Critically Endangered (Possibly Extinct)’ by the IUCN (2023), given the likelihood that, if these species persist, they only inhabit a very small spatial area. Species on this watchlist were ranked in ascending order of spatial range size on the assumption that watchlist species with smaller ranges will be correspondingly more vulnerable to TC-driven extinction. To highlight the extent to which species on our watchlist are already receiving conservation attention, we indicated whether each of these has any active in-situ conservation actions listed on their IUCN (2023) account, excluding those simply occurring in protected areas, given that many tropical protected areas are ineffective in preventing biodiversity loss (e.g. Laurance et al., 2012). We also identified whether each species has insurance populations in captive breeding programs, following information on their IUCN (2023) accounts, and in the Species 360 database (Species 360, 2024), as well as noting species for which a breeding program has been attempted in the past. Given that the overall area of some insular hotspots is very large (e.g. Polynesia-Micronesia), with some parts being potentially less impacted by STCs than others, we also indicate species that occur in areas shown by our map of storm tracks to be less prone to STCs (and hence may represent a lower conservation priority). As an additional resource, we created an appendix (S3) highlighting all other species globally that fulfil the criteria for the watchlist, but do not occur in ‘high-risk’ insular hotspots (with the same additional notations described above).

3. Results

3.1. ‘High risk’ insular hotspots

We identified 427 occurrences of STCs with tracks falling within hotspots between 1972 and 2022, of which 327 (76.6 %) occurred in insular hotspots (Fig. 1). Based on the frequency of these events, five insular hotspots clearly show an elevated theoretical STC risk (together they experienced 93 % of all STCs over the last 50 years): Japan, Polynesia-Micronesia, Philippines, the Caribbean Islands (henceforth ‘the Caribbean’), and Madagascar and the Indian Ocean Islands (henceforth ‘Madagascar’) (Figs. 1 & 2). These hotspots together constituted $>95\%$ of cases where STC tracks overlapped with the area of an insular hotspot, and 72 % of all cases of STCs occurring in hotspots overall (insular or otherwise) (Figs. 1 & 2). When taking into account only those STCs which had made landfall, the list of ‘high risk’ insular hotspots remains the same although their ranking changes (Appendix S4).

Of these five insular hotspots, Japan experienced the most STCs ($n =$

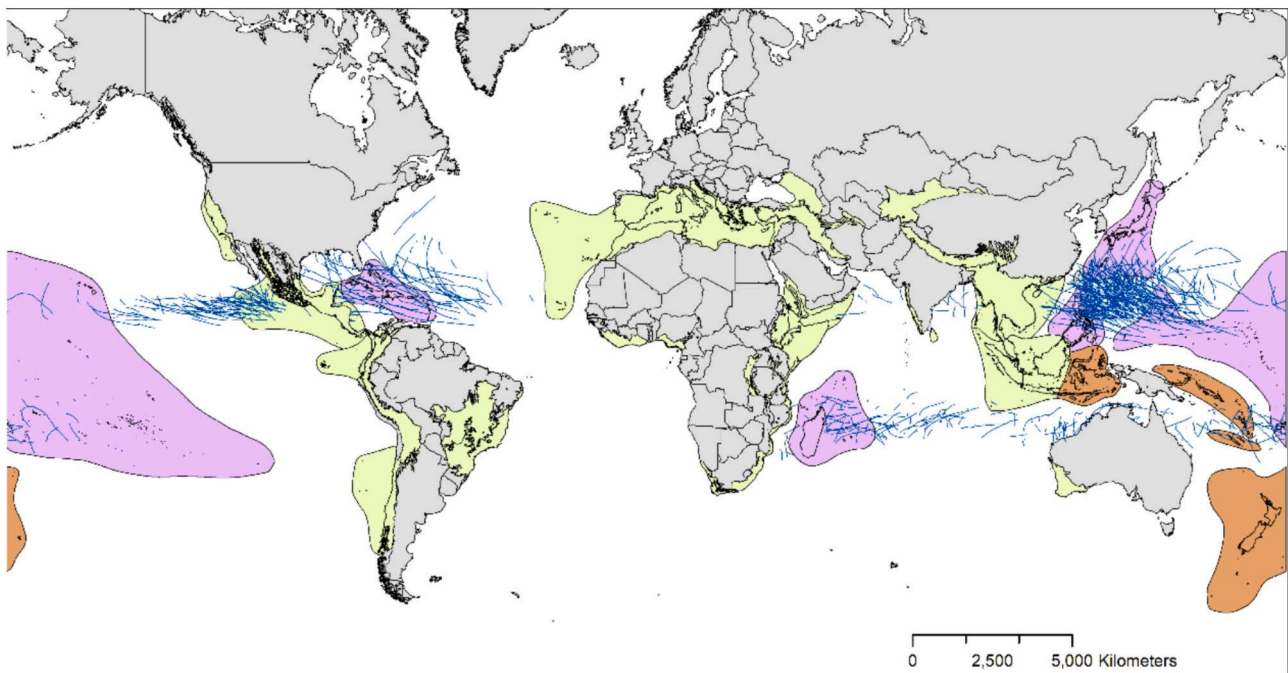


Fig. 1. Global frequency of severe (Category 4 and Category 5) tropical cyclones (STCs) impacting biodiversity hotspots (following Mittermeier et al. 2005). Blue lines indicate STC tracks logged on the International Best Track Archive for Climate Stewardship database over a 50-year period (1972–2022). Purple-shaded areas indicate insular hotspots identified in our analysis to be ‘high risk’ insular biodiversity hotspots (together being crossed by STC tracks of >95 % of all STCs logged as occurring within the borders of insular biodiversity hotspots). Orange shaded areas show the remaining insular biodiversity hotspots i.e., those which were not identified to be ‘high risk’. Green shaded areas indicate all other (non-insular) hotspots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

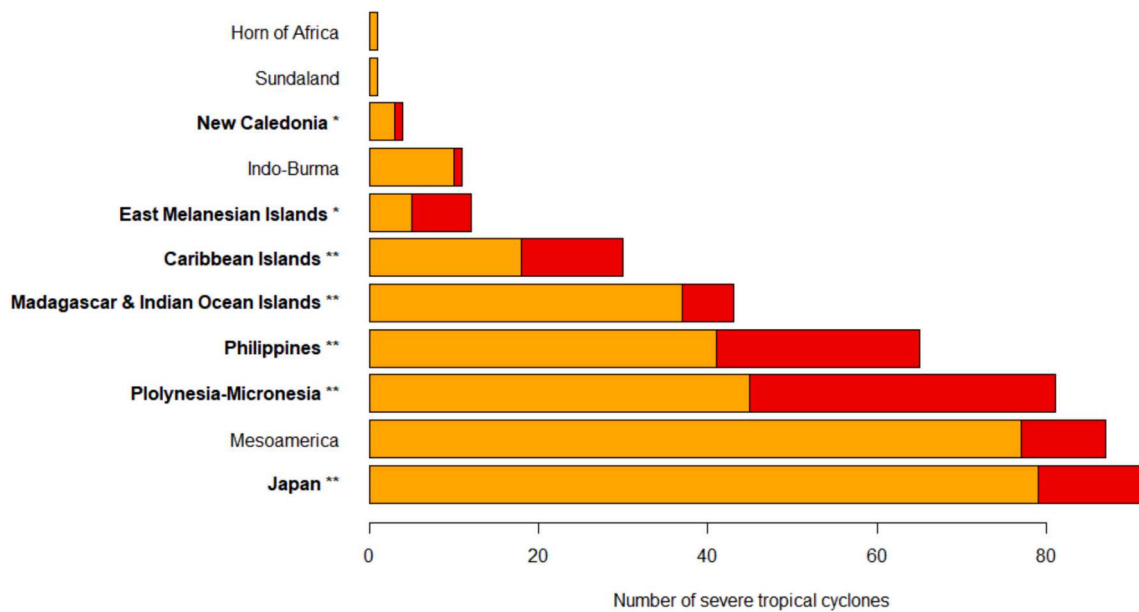


Fig. 2. Number of severe (Category 4 and Category 5) tropical cyclones (STCs) occurring within the borders of biodiversity hotspots (following Mittermeier et al. 2005) over a 50-year period (1972–2022). Insular hotspots are labelled in **bold**. Data were obtained from the Best Track Archive for Climate Stewardship database. Orange bars and red bars indicate the number of Category 4 and Category 5 STCs, respectively. ** = ‘high risk’ insular hotspots (together constituting >95 % of all records of STCs in insular hotspots). * = other insular hotspots. A total of 23 biodiversity hotspots experienced zero STCs during our study period and are not shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

92), followed by Polynesia-Micronesia ($n = 81$), the Philippines ($n = 65$) Madagascar ($n = 43$) and the Caribbean ($n = 30$) (Fig. 2). However, in terms of frequency of the most powerful (category 5) STCs, Polynesia-Micronesia received the highest number ($n = 36$), followed by the Philippines ($n = 24$), Japan ($n = 13$), the Caribbean ($n = 12$) and

Madagascar ($n = 6$) (Fig. 2). Mesoamerica was the only continental hotspot experiencing a significant number of STCs (20.3 % of the total occurring in all hotspots). The remaining 7 % of analysed STCs were distributed in five hotspots (three continental [Indo-Burma, Horn of Africa and Sundaland], two insular [East Melanesian Islands and New

Caledonia]), with 23 hotspots not experiencing any STCs between 1972 and 2022 (Fig. 1, Appendix S4).

3.2. Threatened vertebrate diversity in ‘high risk’ insular hotspots

Amongst the identified ‘high risk’ insular hotspots, the Caribbean supports the largest number of terrestrial vertebrate species ($n = 2024$),

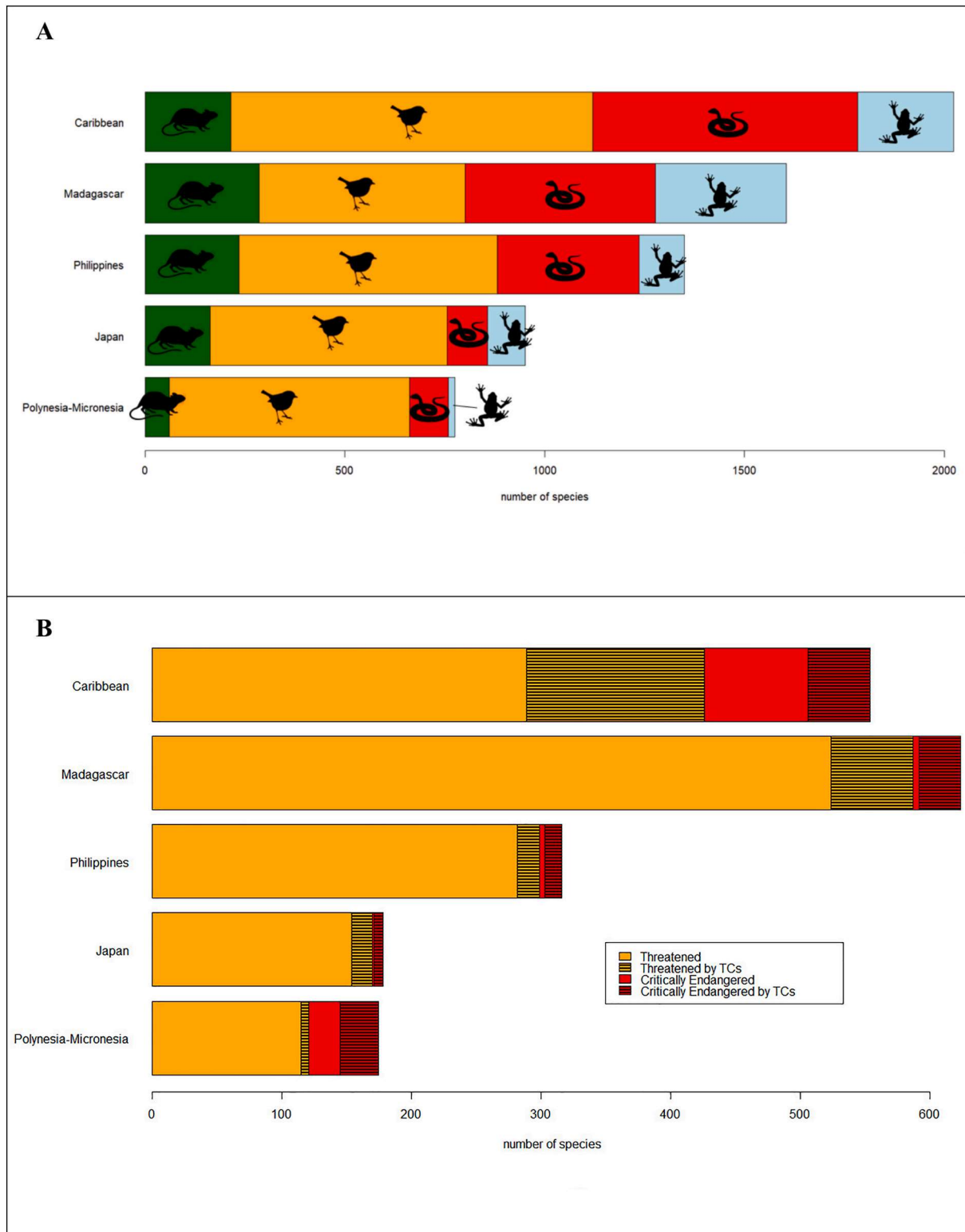


Fig. 3. A) number of terrestrial vertebrate species (amphibians, reptiles, birds, mammals) in each of our ‘high risk’ insular biodiversity hotspots, B) number of threatened (DD, VU, & EN; orange) and Critically Endangered (red) terrestrial vertebrate species per ‘high risk’ insular hotspot. Hatching represents the proportion that is explicitly threatened by TCs (threat 11.4). All data sourced from IUCN (2023). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

followed by Madagascar ($n = 1605$), Philippines ($n = 1350$), Japan ($n = 951$), and with Polynesia-Micronesia harbouring the lowest number of species ($n = 776$) (Fig. 3A). A similar pattern can be seen in the number of threatened terrestrial vertebrate species per insular hotspot (Fig. 3B), with Madagascar having the greater number of threatened species overall ($n = 624$), the Caribbean having the most Critically Endangered species ($n = 181$), and with the other insular hotspots having considerably fewer threatened terrestrial vertebrate species. However, when it comes to the number of storm-threatened taxa (total $n = 244$, of which nine (3.7 %) are classified as Data Deficient) (Fig. 3B), the Caribbean has by far the most species ($n = 128$, of which 48 are Critically Endangered), followed by Polynesia-Micronesia ($n = 54$, of which 30 are Critically Endangered), with the remaining insular hotspots having considerably fewer storm-threatened species (Fig. 3B). Of the 244 storm-threatened taxa, birds were the most heavily represented (81 species) followed by reptiles (69 species), amphibians (56 species) and mammals (37 species) (Appendix 2).

3.3. Geographic and ecological traits of 'high risk' insular hotspots

Insularity index scores were fairly similar between insular hotspots, except for the outlier of Polynesia-Micronesia (index score of 0.109; nearly five times greater than the next highest index score) (Fig. 4). The remaining natural vegetation cover was fairly similar between insular hotspots, ranging from 4.4 % in Madagascar (the lowest) to 8.2 % in Japan (the highest) (Table 1). Japan is the only insular hotspot comprised predominantly of continental islands, with all other insular hotspots being oceanic (Table 1).

Polynesia-Micronesia, Madagascar, and the Caribbean each have very high percentage values of hotspot endemic species amongst their storm-threatened species (range 90.7 % - 95.3 %, Table 2), with such

percentage being the lowest for the Philippines (58.8 %) and Japan (37.5 %). Storm-threatened species in the Caribbean are, on average, found on the smallest number of islands (1.6 islands), while those in Madagascar are found in the least number of locations (3 locations). Storm-threatened species in the Philippines have the largest spatial ranges on average (583,697 km²) with Polynesia-Micronesian storm-threatened species having the smallest spatial ranges on average (420 km²).

3.4. Watchlist of TC-threatened species at greatest risk

We identified 60 species which met the criteria for inclusion on our watchlist of priority TC-threatened species: 23 birds, 19 reptiles, 14 amphibians, and three mammals (Table 3). Four of these species (6.6 %) are classified as DD. The greatest number of these species occur in the Caribbean (32 species) while the Philippines supports the least (zero species). The spatial range size of these species ranges from 0.01 km² to 1488.84 km². A total of 26 species (43.3 %) within this watchlist receive some form of active in-situ conservation action, while just six species (10 %) possess an ex-situ conservation breeding program; five with and one without in-situ conservation action. Five species; four in Polynesia-Micronesia and one in Madagascar (8 % of all watchlist species), occur in parts of their respective insular hotspots that may, based on past STC track data, be less likely to experience STC events. For 52 % of species in the watchlist, the threat posed by TCs is considered to be ongoing, with TCs being considered a serious future threat for an additional 43 % (Appendix S2). Data on the scope of TC threat are available for 58 % of the watchlist species and for all of them, they are estimated to affect the majority (>50 %) of their global populations (Appendix S2). Severity of TC threats were assessed for only 38 % of the watchlist species; for the majority of these they are predicted to drive rapid to very rapid declines

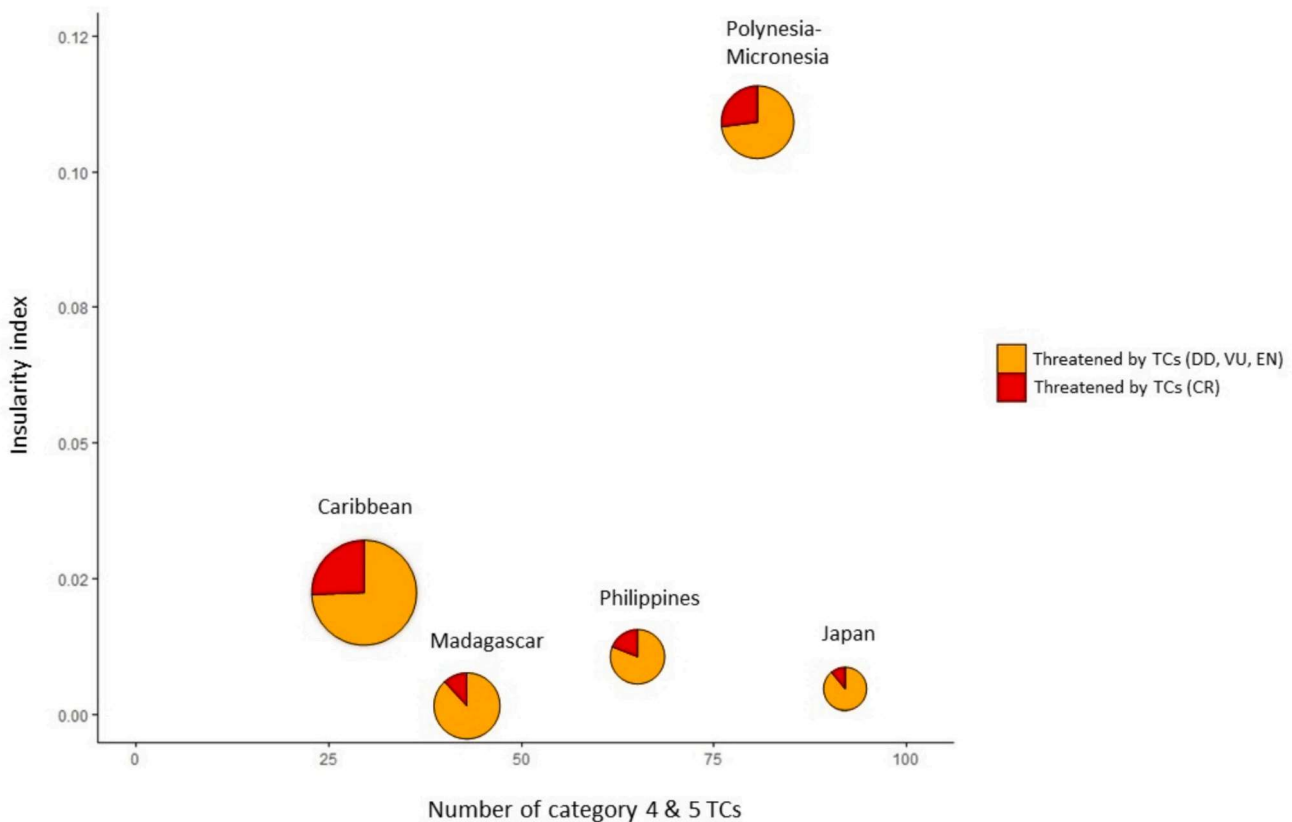


Fig. 4. Frequency of category 4 and category 5 tropical cyclones and insularity index scores in five 'high risk' insular biodiversity hotspots. Insularity index scores are the number of landmasses in each hotspot divided by the total land area of each hotspot (km). Bubble size indicates the number of storm-threatened species per hotspot (with a proportional breakdown of Critically Endangered storm-threatened species and all other storm-threatened species).

Table 1

Summary of geographical data for five ‘high risk’ insular biodiversity hotspots. Landmass count is the number of individual islands in each hotspot. Insularity index (landmass count divided by total land area) is an indicator of the dominance of large landmasses within each hotspot. Remaining natural vegetation values were derived from Sloan et al. (2014). Archipelago type indicates whether islands in each insular hotspot are predominantly continental or oceanic (following Sayol et al., 2020).

Hotspot name	Landmass count	Total land area (km ²)	Insularity index	Remaining natural vegetation (%)	Archipelago type
Japan	3143	369,048	0.009	8.2	Continental
Polynesia-Micronesia	6678	44,267	0.151	5.2	Oceanic
Philippines	3546	292,331	0.012	8.0	Oceanic
Madagascar	713	596,819	0.001	4.4	Oceanic
Caribbean	6473	222,585	0.029	5.8	Oceanic

Table 2

Summary of geographical characteristics of storm-threatened species within ‘high risk’ insular biodiversity hotspots. ‘Hotspot endemics’ indicates the number of storm-threatened species in each hotspot which are endemic to that hotspot (with the percentage value these represent all storm-threatened species in parentheses). Values for average number of islands and average number of locations are based on data sourced from the IUCN Red List (2023). Average spatial range data are derived from AVONET (Tobias 2022) and PanTHERIA (2009) for birds and mammals, respectively, and IUCN extent of occurrence values (2023) for amphibians and reptiles.

	Japan	Polynesia-Micronesia	Philippines	Madagascar	Caribbean
Hotspot endemics	3 (37.5 %)	49 (90.7 %)	10 (58.8 %)	34 (91.9 %)	122 (95.3 %)
Average number of islands (±SD)	5.4 ± 4.7	5.1 ± 13.0	3.8 ± 3.0	1.9 ± 1.5	1.6 ± 1.6
Average number of locations (±SD)	5.3 ± 5.1	5.9 ± 13.9	36.8 ± 25.7	3.0 ± 2.2	5.2 ± 11
Average spatial range in km ² (±SD)	38,301 ± 73,518	419 ± 980	583,697 ± 1,182,935	16,319 ± 63,738	19,006 ± 165,949

(Appendix S2). Appendix S3 provides details of an additional 31 species occurring worldwide that fulfil the *same* criteria of those on our watchlist (are restricted to a single island, have only a single location listed on their IUCN Red List account, are globally threatened, and have storms and flooding listed as a specific threat), but do not occur in our ‘high risk’ insular hotspots (i.e. they occur anywhere else globally).

4. Discussion

This study highlights not only that the majority of STCs occur in insular biodiversity hotspots, but also that >95 % of these affect only five ‘high risk’ insular hotspots, regardless of their size. This is true whether taking into account all STCs which occur in insular hotspots or only those which made landfall, although distribution of risk amongst those five hotspots is expected to vary depending on a number of factors including chance and size of individual STCs. The emergence of clear ‘high risk’ areas is not necessarily surprising, given that some other insular hotspots (e.g. Wallacea, New Zealand) are at latitudes where TCs are rare or absent (Ramsay, 2017). Importantly, however, our results also show that extinction risk posed by TCs is not uniform even within ‘high risk’ insular hotspots. Madagascar, Polynesia-Micronesia and, especially, the Caribbean have notably high numbers of storm-threatened species, whereas Japan and the Philippines have relatively few.

The reasons why such substantial differences occur in TC-related extinction risk between ‘high risk’ insular hotspots remain challenging to prove. It does not appear, however, to be directly linked to STC frequency. For instance, our results show that Japan, despite experiencing the highest number of STCs, has the fewest storm-threatened species, whilst the Caribbean, which experiences the lowest number of STCs, has the highest number of such species. The extent of remaining original vegetation also does not seem to be a driver of our observed differences, as all insular hotspots have <10 % of original vegetation cover (Sloan et al., 2014). While it is true that the insular hotspots with the least storm-threatened species (Japan and the Philippines) have the most remaining original vegetation, the differences are small compared to the most deforested insular hotspot (e.g. the difference between Japan and Madagascar is just 3.8 %). The Caribbean (which has the most storm-threatened species) also has more original habitat remaining than either Polynesia-Micronesia or Madagascar. Numbers of threatened species overall also do not seem to predict numbers of storm-threatened species – while the Caribbean has the most Critically Endangered

species, Madagascar has the most threatened species overall, yet substantially fewer storm-threatened species than the Caribbean.

Physical geography, and in particular island size, may have an important influence on observed threat levels in each insular hotspot. Our results show that the two insular hotspots with the greatest number of storm-threatened species (Caribbean and Polynesia-Micronesia) also have the highest insularity index scores (although very different STC occurrence rates). It is unsurprising that where insular hotspots are fragmented into larger number of smaller islands, species are most susceptible to local extirpation or extinction due to the core principles of island biogeography (Whittaker et al., 2023). The geological history of the insular hotspot is also likely to be important. The fact that Japan has the fewest storm-threatened species and is the only predominantly continental island group is notable. It is equally notable that the Philippines (with the second-fewest number of storm-threatened species) is the only oceanic insular hotspot in which most of its constituent islands become connected during glacial periods (Robles et al., 2015). Additionally, the islands of Japan and the Philippines are generally clustered together and are located relatively close to continental landmasses compared to some other ‘high risk’ insular hotspots (e.g. Madagascar and Polynesia-Micronesia). A consideration of both these factors, and the tenants of the theory of island biogeography (MacArthur and Wilson, 1967), could help explain why storm-threatened species here have, on average, much larger ranges than species in other ‘high risk’ insular hotspots. This may also be why these insular hotspots have comparably few storm-threatened species overall.

Geological history may also help explain patterns of previous extinctions in insular hotspots. It is noteworthy that known prehistoric and historic extinctions in the Caribbean, Polynesia-Micronesia, and Madagascar (the insular hotspots with the most TC-threatened species and with little inter- or intra-hotspot landmass connectivity during glacial periods) are high compared to those in the Philippines and Japan (the insular hotspots with the fewest TC-threatened species and the greatest glacial landmass connectivity; e.g. Turvey et al., 2021; Matthews et al., 2022; Sayol et al., 2024). Indeed, not a single bird species is known to have gone extinct from the Philippines in the last 130,000 years (Sayol et al., 2020, 2024), and low extinction rates have been reported on other oceanic islands with similar ‘continental’ characteristics (Meijer et al., 2015). While it cannot be proved that this is exclusively due to this archipelago’s geological origins, a broader point can be made that insular hotspots of previous extinctions may be good predictors of present-day storm-related threats.

Table 3

Watchlist of 60 species with a particularly high risk of tropical cyclone-driven extinction. All are restricted to a single island and have only a single location listed on their IUCN (2023) account (with the exception of three CR (PE) species (†)), are globally threatened (classified as DD, VU, EN or CR), and have storms and flooding (IUCN Red List threat category 11.4) listed as a specific threat. Species are ranked in ascending order by spatial range. Species with an unknown spatial range size are ranked last. Species indicated by a = are jointly ranked (as they share the same spatial range as the species immediately above/below). Spatial range data for birds and mammals are derived from AVONET (Tobias et al., 2022) and PanTHERIA (2009), respectively, and from IUCN (2023) for amphibians and reptiles. * = Species which have evidence of active in-situ conservation actions (following IUCN, 2023), § = species which have a captive breeding program (following IUCN, 2023 and Species 360, 2024), and ‡ = species where previous attempts at captive breeding have failed. Species marked with ¶ occur in parts of their hotspot that may be less likely to experience severe tropical cyclones (as indicated by storm tracks in Fig. 1).

Rank	Class	Common name	Scientific name	Hotspot	IUCN category	Spatial range (km ²)
1 =	Reptilia	Carrot Rock Skink	<i>Spondylurus macleani</i>	Caribbean	CR	0.01
1 =	Reptilia	Carrot Rock's Anole	<i>Anolis ernestwilliamsi</i>	Caribbean	CR	0.01
3	Reptilia	Censky's Ameiva	<i>Pholidoscelis corax</i>	Caribbean	E	0.049
4	Reptilia	Ornate Ground Snake*	<i>Erythrolamprus ornatus</i>	Caribbean	CR	0.09
5	Reptilia	Sombrero Ameiva	<i>Pholidoscelis corvinus</i>	Caribbean	CR	0.366
6 =	Aves	St. Kitts Bullfinch	<i>Melopyrrha grandis</i>	Caribbean	CR	1
6 =	Reptilia	Mortlock Islands Scaly-toed Gecko	<i>Lepidodactylus oligoporus</i>	Polynesia-Micronesia	CR	1
6 =	Reptilia	Noble's Anole	<i>Anolis altavelensis</i>	Caribbean	CR	1
9	Aves	Nihoa Finch*	<i>Telespiza ultima</i>	Polynesia-Micronesia	CR	1.55
10	Reptilia	Durrell's Night Gecko*	<i>Nactus durrellorum</i>	Madagascar	Vu	2.38
11 =	Reptilia	Curly-tailed Lizard sp.	<i>Leiocephalus altavelensis</i>	Caribbean	CR	4
11 =	Amphibia	Haitian Marshfrog‡	<i>Eleutherodactylus caribe</i>	Caribbean	CR	4
13	Reptilia	Conception Bank Silver Boa	<i>Chilabothrus argentum</i>	Caribbean	CR	7
14	Aves	Rota White-eye*‡	<i>Zosterops rotensis</i>	Polynesia-Micronesia	CR	8.18
15	Reptilia	Redonda Anole*	<i>Anolis nubilus</i>	Caribbean	CR	10
16	Amphibia	Haitian Ventriiloquial Frog	<i>Eleutherodactylus dolomedes</i>	Caribbean	CR	11.4
17	Reptilia	East Plana Curlytail	<i>Leiocephalus greenwayi</i>	Caribbean	Vu	13
18	Amphibia	Rock Pocket Frog	<i>Eleutherodactylus junori</i>	Caribbean	CR	18.2
19 =	Aves	Maui Nukupuu*	<i>Hemignathus affinis</i>	Polynesia-Micronesia	CR (PE)	22
19 =	Aves	Kauai Nukupuu*	<i>Hemignathus hanapepe</i>	Polynesia-Micronesia	CR (PE)	22
21	Aves	Makatea Fruit-dove¶	<i>Ptilinopus chalcurus</i>	Polynesia-Micronesia	Vu	25.1
22	Aves	Tuamotu Kingfisher*	<i>Todiramphus gambieri</i>	Polynesia-Micronesia	CR	25.36
23	Aves	Tahiti Monarch*¶	<i>Pomarea nigra</i>	Polynesia-Micronesia	CR	27.52
24	Aves	Reunion Cuckooshrike*	<i>Lalage newtoni</i>	Madagascar	CR	28.71
25	Aves	Puaiohi*	<i>Myadestes palmeri</i>	Polynesia-Micronesia	CR	32.06
26	Aves	Seychelles Scops-owl	<i>Otus insularis</i>	Madagascar	CR	38.38
27 =	Amphibia	Maisi Frog	<i>Eleutherodactylus bresslerae</i>	Caribbean	CR	45.6
27 =	Amphibia	Hispaniolan Crowned Frog	<i>Eleutherodactylus corona</i>	Caribbean	CR	46.6
29	Amphibia	Mona Coqui*§	<i>Eleutherodactylus monensis</i>	Caribbean	Vu	54.7
30	Amphibia	Leaf Mimic Frog	<i>Eleutherodactylus sisypodemus</i>	Caribbean	CR	55.17
31	Aves	Akohekohe*‡	<i>Palmeria dolei</i>	Polynesia-Micronesia	CR	57.85
32	Reptilia	Aneгада Blindsnake	<i>Antillotyphlops catapontus</i>	Caribbean	DD	60
33	Amphibia	Jamaican Peak Frog	<i>Eleutherodactylus alticola</i>	Caribbean	CR	60.98
34	Aves	Imperial Amazon*	<i>Amazona imperialis</i>	Caribbean	CR	61.28
35	Reptilia	Finca Ceres Anole	<i>Anolis juangundlachi</i>	Caribbean	CR	70
36	Reptilia	Mona Rhinoceros Iguana*‡	<i>Cyclura stejnegeri</i>	Caribbean	CR	80
37	Aves	Iphis Monarch*¶	<i>Pomarea iphis</i>	Polynesia-Micronesia	CR	81.42
38	Aves	Bahama Nuthatch	<i>Sitta insularis</i>	Caribbean	CR	83.64
39	Aves	Akikiki*§	<i>Oreomystis bairdi</i>	Polynesia-Micronesia	CR	85.6
40	Reptilia	Cuban Short-nosed Blindsnake	<i>Cubatyphlops contorhinus</i>	Caribbean	DD	86.3
41	Amphibia	Frog sp.¶	<i>Anodonthyla theoi</i>	Madagascar	CR	88.61
42	Aves	Mariana Crow*§	<i>Corvus kubaryi</i>	Polynesia-Micronesia	CR	92.35
43	Amphibia	Cricketer Coqui	<i>Eleutherodactylus gryllus</i>	Caribbean	CR	99
44	Mammalia	Kosrae Flying Fox¶	<i>Pteropus ualanus</i>	Polynesia-Micronesia	E	103.24
45	Mammalia	Rodrigues Flying Fox*§	<i>Pteropus rodricensis</i>	Madagascar	E	111.5
46	Aves	Palila*§	<i>Loxioides bailleui</i>	Polynesia-Micronesia	CR	134.59
47	Reptilia	Gau Banded Iguana§	<i>Brachylophus gau</i>	Polynesia-Micronesia	E	220
48	Aves	Maui Alauahio*‡	<i>Paroreomyza montana</i>	Polynesia-Micronesia	E	255.12
49	Aves	Anjouan Scops-owl*	<i>Otus capnodes</i>	Madagascar	E	271.7
50	Reptilia	Sea Krait sp.‡	<i>Laticauda schistorhynchus</i>	Polynesia-Micronesia	Vu	300
51	Aves	Anianiau*	<i>Magnuma parva</i>	Polynesia-Micronesia	Vu	318.21
52	Mammalia	Fijian Monkey-faced Bat	<i>Mirimiri acrodonta</i>	Polynesia-Micronesia	CR	440.14
53	Reptilia	Imias Blindsnake	<i>Cubatyphlops notorachius</i>	Caribbean	DD	445.9
54	Aves	Okinawa Woodpecker*	<i>Dendrocopos noguchii</i>	Japan	CR	585.25
55	Aves	Reunion Marsh-harrier*	<i>Circus maillardi</i>	Madagascar	E	1488.84
56	Reptilia	Cuban Pallid Blindsnake	<i>Cubatyphlops anousius</i>	Caribbean	DD	Unknown
57	Amphibia	Zapata Toad*	<i>Peltophyne florentinoi</i>	Caribbean	E	Unknown
58	Amphibia	Arntully Robber Frog†	<i>Eleutherodactylus orcutti</i>	Caribbean	CR (PE)	Unknown
59	Amphibia	Eneida's Coqui†	<i>Eleutherodactylus eneidae</i>	Caribbean	CR (PE)	Unknown
60	Amphibia	Webbed-footed Coqui†	<i>Eleutherodactylus karlschmidti</i>	Caribbean	CR (PE)	Unknown

Interestingly, taxonomic breakdowns of both storm-threatened species generally and species in our watchlist show the same pattern; birds being the most numerous storm-threatened taxa, followed by reptiles, amphibians, and finally mammals. This is likely due to the former two groups having a better ability to disperse to small island ecosystems than

the latter two groups (Matthews and Triantis, 2021; Vences et al., 2003), and with these small island endemics being especially susceptible to TC-related threats. The large numbers of TC-threatened birds may also, however, represent a conservation opportunity. Birds are a particularly well-studied group (Clark and May, 2002; Ducatez and Lefebvre, 2014)

and are often successful in attracting conservation interventions (e.g. Seddon et al., 2005). This may indicate strong precedence for implementing successful conservation projects for the numerous bird species highlighted in our lists.

Historically, global analyses like the one presented here have been instrumental in the geographical prioritisation of conservation resources (Mittermeier et al., 2011). However, this is only the first step and further processes are necessary to identify conservation priorities at much finer scales, given the uneven distribution of species and threats (Brooks et al., 2006; Whittaker et al., 2005). The exploratory analyses we present here provide some indication of which characteristics may or may not influence TC extinction risk, but this remains an area requiring further quantitative research. For instance, further exploration of variables considered in this study would be important, as would investigation into how factors such as ecological traits, which are known to effect a species' extinction risk generally (Chichorro et al., 2019; Munstermann et al., 2022) influence susceptibility to TC-related threats specifically. However, regardless of the underlying reasons driving TC-related threats, the fact remains that many species in insular biodiversity hotspots – particularly but not exclusively in the Caribbean, Polynesia-Micronesia, and Madagascar – are highly threatened by TCs. Although any of the 60 species we present in our watchlist could be driven to extinction by a single future STC event, data on the timing, scope and severity of such threat for each species may offer some basis for prioritisation of research and conservation efforts (Appendix S2). The 31 additional species presented in our supplementary appendix (those fulfilling the same criteria as those on our watchlist but occurring outside our 'high risk' insular hotspots; Appendix S3) generally represent lesser conservation priorities. This is indicated by a majority (71 %) being shown to occur in areas that do not regularly experience STC events. This is an inverse pattern to species in our watchlist, where only 8 % occur in parts of our 'high risk' insular hotspots that may experience lower STC risk. Indeed, even ignoring this, the fact that there are almost twice as many species fulfilling our watchlist criteria in our 'high risk' insular hotspots, as in the rest of the world combined, strongly indicates that these species are of the highest conservation priority. All the same, the additional species in our appendix still possess an inherent vulnerability that is worth highlighting to conservation planners, and some species on the list (especially those occurring in the Mesoamerican biodiversity hotspot) undoubtedly face high TC-related extinction risks (e.g. Cozumel Raccoon *Procyon pygmaeus*; Willcox, 2020).

It should also be noted that species on both lists are a conservative representation of those meeting our criteria. Firstly, to ensure a robust experimental design, our analysis focused on terrestrial vertebrates only; our watchlist would be much longer if all taxonomic groups were included. Even when focussing exclusively on terrestrial vertebrates, data for some species are lacking, and more species would likely qualify for our watchlist if their IUCN Red List accounts were more comprehensive. For instance, the Cuban Pallid Blindsnake *Cubatyphlops anousius* is a storm-threatened species occurring on a single island and almost certainly occurs in just a single location (Fong, 2017), although it does not meet our criteria due to the number of locations it occurs in being given as 'N/A' in its Red List account. The confounding effect of incomplete IUCN Red List accounts on conservation prioritisation research has previously been reported elsewhere (Martin et al., 2023). As a further example, taxa which are terrestrial only for part of their life cycle, such as sea turtles, appear to be more resilient to TCs, but further research is needed to understand whether the frequency of large storms can affect long-term population viability (Dewald and Pike, 2014). Additionally, it is possible that various endemic species restricted to small islands which are currently not listed as threatened by the IUCN (2023) could still suffer a sharp change in their conservation status following a powerful TC event - e.g. Saint Lucia Warbler *Setophaga delicata*, or Guadeloupe Woodpecker *Melanerpes herminieri*. Future STC events may also drive extirpations of wider-ranging species from specific islands, as has likely occurred recently with the Bahama Warbler

Setophaga flavescens (Pereira et al., 2023; Pereira and Pyle, 2025). Thus, it is important to emphasize that, while species on our watchlist represent important conservation priorities, a wider analysis and future updates to the Red List accounts would likely lead to more species being included, as of course would expanding the list to include taxa beyond terrestrial vertebrates. This is only a first attempt to compile such a list, in the hope that a broader discussion can ensue amongst conservationists, as inevitably many more species may currently face similarly severe TC-related risks.

TCs have already been identified as key drivers in several modern extinction events (e.g. Laysan Honeycreeper *Himatione fraithii*; Olson, 1996) and have resulted in other species becoming 'lost' (Martin et al., 2023) and possibly extinct e.g. Cozumel Thrasher *Toxostoma guttatum* (Perdomo-Velázquez et al., 2017). We show here that many other species could potentially join the ranks of these storm-driven extinctions after just a single future STC event. Indeed, it may already be too late for some species on our watchlist – there is a high chance that the Bahama Nuthatch *Sitta insularis*, for example, has already become extinct following the impacts of Hurricane Dorian in 2019 (Gardner et al., 2024; Mlodinow et al., 2021).

Given the importance placed on our global responsibility to prevent extinctions (Hughes and Grumbine, 2023), all species on our watchlist (and to a lesser extent others with a lower, yet still substantial, storm-derived extinction risk, such as those in Appendix S3), should be considered important conservation priorities. However, presently this often does not appear to be the case. Less than half of the species on our watchlist have any active conservation action, and just 10 % have insurance populations held by captive breeding programs. As such, if averting TC-driven extinctions is to be achieved, a greater allocation of conservation resources towards the most 'at risk' species is required, as is a greater sense of urgency.

There are several ways in which conservation actions may effectively mitigate TC extinction threats. Given that the most urgently threatened species are single-island endemics, it may be prudent to establish more ex-situ conservation and translocation projects for these species, in line with the IUCN-endorsed 'One Plan Approach' (Byers et al., 2013; IUCN – SSC Species Conservation Planning Sub-Committee, 2017; Traylor-Holzer et al., 2019). This is, of course, easier said than done, given that both these intervention types are generally expensive, subject to political barriers, and are not always successful (Berger-Tal et al., 2020; Bowkett, 2014; Martin et al., 2014b). Several species on our watchlist have indeed been the subject of previous failed captive breeding attempts (e.g. Akohekohe *Palmeria dolei*; USFWS, 2011) or unsuccessful translocation efforts (e.g. Durrell's Night Gecko *Nactus durrellorum*; Cole et al., 2009). On the other hand, other species would almost certainly be on our watchlist if it were not for successful captive breeding and/or translocation programs e.g. Millerbird *Acrocephalus familiaris* (Pyle and Pyle, 2017), Cabrera's Hutia *Mesocapromys angelcabrerai* (Turvey et al., 2017), and numerous amphibians, which are being increasingly successfully bred in ex-situ conservation facilities (Biega et al., 2017). Given that successful translocations and ex-situ breeding would substantially reduce the extinction risk for the species on our watchlist, we advocate for the planning and implementation of these wherever possible and appropriate, especially where a high chance of success is likely (Traylor-Holzer et al., 2019). Certain effective in-situ conservation actions to mitigate TC risk for bird species are identified in Wunderle (2005), which include community outreach, considering TC impacts when planning protected areas, and the construction of physical structures (such as nest boxes for cavity-nesting birds).

Regrettably, the timing involved in these kinds of conservation interventions may often be too long for the urgency of the task at hand. Moreover, given that most insular hotspots consist of several countries, each with a variable amount of resources at their disposal, conservation efforts are likely to be hindered by regional geopolitical complexities (Vallès et al., 2021). International differences are likely to lead to diverging views on whether or how action is taken, but interaction and

dialogue can be key to resolving these differences (e.g. Cummins, 2004). On the other hand, species with a very restricted distribution, such as those on our watchlist, may have the advantage of falling under the jurisdiction of one national or regional administration. Ultimately, the scale of management should match the scale of the conservation issue (Dallimer and Strange, 2015). Thus, we would argue that some *super partes* leadership is needed to guide further conservation at a regional level due to the urgency of the threat. We suggest that this could be the focus of a to-be-created specialist group ('task force') under the auspices of the IUCN Species Survival Commission, which could allow for the identification of conclusive criteria for the compilation of a definitive watchlist (e.g. see similar efforts with different criteria by Ameça y Juárez et al., 2013), as well as the redistribution of expertise and funds while committing to consistent and effective principles of conservation planning (Byers et al., 2022; Lees et al., 2021). If the conservation community does not step up their efforts in areas with high TC extinction risk, for many species the next cyclone season could well be their last.

CRedit authorship contribution statement

Simon Valle: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Data curation, Conceptualization. **David J. Pereira:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Thomas J. Matthews:** Writing – review & editing, Validation. **Thomas E. Martin:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111184>.

Data availability

The data used are of public dominion and all sources have been acknowledged in the manuscript

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