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How wildlife respond to tropical cyclones: short-term tactics and long-term impacts

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ABSTRACT

From butterflies to lizards and from sharks to seabirds, wildlife exhibit tactics to survive the impacts of tropical cyclones, also known as hurricanes, cyclones, or typhoons depending on where they occur. Some species seek refuge during the storm by moving, some remain in place and ride it out, and others move longer distances, avoiding the main impacts of the storm altogether. Tropical cyclones can have direct impacts on wildlife (e.g. mortality) but can also have indirect effects by altering resources and habitat, with downstream impacts on abundance and recruitment. Using examples from across taxa and ecosystems, we explore the pathways by which tropical cyclones can influence wildlife populations and communities. We describe tactics demonstrated by wildlife that enable them to survive the immediate impacts of the storm, as well as the longer-term impacts after the storm. We give examples of tropical cyclones as a selective pressure and as a facilitator for the introduction of invasive species. We also describe how tropical cyclones may provide a net benefit to some native species. The ecological and evolutionary impacts of tropical cyclones on wildlife can be complex, as they are often intertwined with concurrent pressures from land-use change, human development, and climate change. As the frequency of intense tropical cyclones is predicted to increase globally, identifying the mechanisms by which wildlife cope with such disturbances can aid in understanding and mitigating the impacts of climate change on wildlife.

Key words: behaviour, hurricane, natural selection, mortality, tropical cyclone, typhoon, wildlife.

CONTENTS

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I. INTRODUCTION

The year 2023 was the first year on record in which all seven tropical cyclone formation basins developed a category 5 tropical cyclone in the same year (Livingston & Samenow, 2023). Major tropical cyclones have been making landfall in the same region in quick succession (e.g. Hurricanes Irma and Maria devastated Puerto Rico within 2 weeks in 2017), and tropical cyclones are devastating the West Pacific even more frequently (Marler, 2014). Tropical cyclones have made landfall in places where the risk was previously low – in 2004, Hurricane Catarina was the first and thus far, the only reported tropical cyclone in the south Atlantic Ocean (Pezza & Simmonds, 2005). In 2024, Hurricane Beryl became the earliest category 4 hurricane that has ever been recorded in the Atlantic basin and Hurricane Milton rapidly intensified from a tropical storm to a category 5 hurricane in less than 24 h (Beven, Alaka & Fritz, 2025). The intensification of extreme weather events, such as tropical cyclones (a term that includes hurricanes, cyclones, and typhoons) is one of numerous consequences of climate change (IPCC, 2014; Stott, 2016; Herring *et al.*, 2021; Wehner & Kossin, 2024), and experts anticipate that rising sea levels and warming sea surface temperatures will intensify future tropical cyclones (Goldenburg *et al.*, 2001; Saunders & Lea, 2008; Coumou & Rahmstorf, 2012; Knutson *et al.*, 2020). Tropical cyclone intensity, intensification rate, and associated rainfall rate have been increasing (Elsner, Kossin & Jagger, 2008; Bhatia *et al.*, 2019; Guzman & Jiang, 2021; Garner, 2023), so much so that Wehner & Kossin (2024) proposed the addition of a hypothetical 'category 6' to the Saffir–Simpson hurricane wind scale. Indeed, models predict an increased frequency of intense tropical cyclones in the future (Christensen *et al.*, 2013; Knutson *et al.*, 2020).

Both the immediate impacts of tropical cyclones, as well as the aftermath, can be catastrophic on the natural environment. Intense winds can topple forests over vast areas (Lugo, 2008; Barrow *et al.*, 2007), storm surge can inundate both coastal freshwater wetlands and otherwise dry areas with salt water (Needham & Keim, 2012; Zachry *et al.*, 2015; Walls *et al.*, 2019), and extreme precipitation can cause both coastal and inland flooding with impacts that last long after the storm has passed (Maymandi, Hummel & Zhang, 2022; Walker *et al.*, 2023). Even entire islands have washed away during tropical cyclones (e.g. a small Hawaiian island mostly disappeared during Hurricane Walaka in 2018; Young *et al.*, 2024). Tropical cyclones can deposit thick layers of sediment in aquatic environments and cause conditions that sap dissolved oxygen from these ecosystems (Tilmant *et al.*, 1994; Lovelace & McPherson, 1998). These relatively local, yet ecosystem-level disturbances change the ecological space available to organisms (Lugo, 2008), and in some cases, are enough to drive evolutionary change (Newton, 2007; Grant *et al.*, 2017). However, not all impacts are negative for wildlife: some ecosystems benefit from the sediment and nutrient pulses that result from tropical cyclones (Conner *et al.*, 1989).

Studies on the ecological impacts of tropical cyclones are often serendipitous because the timing and location of tropical cyclones is unpredictable, making it difficult to design before-and-after studies or identify adequate controls. Further, even if resources are in place to study extreme weather events, the ability of researchers to safely observe wildlife behaviour during severe weather is limited. To help fill some of these knowledge gaps, researchers have suggested global collaboration of tropical cyclone research for proactive extreme-event ecological research (Lugo, 2008; Pruitt *et al.*, 2019; Patrick *et al.*, 2022*a*) and proposed research frameworks to integrate cross-ecosystem responses to tropical cyclones (Hogan *et al.*, 2020). Previous reviews have summarized overall tendencies in the demographic impacts of extreme weather events on wildlife populations (refer to Maxwell *et al.*, 2019; Parmesan, Root & Willig, 2000; Walker *et al.*, 2023), but to our knowledge, none has synthesized trends in wildlife responses to the immediate and lasting disturbances caused by tropical cyclones. Synthesis of the growing number of seemingly unique empirical studies could reveal commonalities within and among taxa.

The question of how natural communities respond to climate change remains a key fundamental question in ecology and conservation biology (Sutherland *et al.*, 2013; Román-Palacios & Wiens, 2020; Patrick *et al.*, 2022*b*). In this narrative review, we capture the breadth of our current knowledge of the ecological and evolutionary impacts of tropical cyclones on wildlife, both negative and positive. We selected papers from the literature that describe the diversity of behaviours, across taxa and ecosystems, that wildlife exhibit immediately before and during the storm itself, as well as the direct and indirect impacts of tropical cyclones on wildlife after the storm. We discuss examples of how tropical cyclones impact populations and communities by acting as selective evolutionary forces and by facilitating the spread of invasive species. We describe how anthropogenic pressures and the timing of the storm can influence the magnitude of a tropical storms' impact on wildlife, and how human actions can help mitigate the impacts. We show that many of these patterns span taxa and ecosystems. Finally, we draw this knowledge together to explore why some populations or species are more vulnerable to the impacts of tropical cyclones.

II. METHODS

We focused our review on short-term tactics exhibited by wildlife species that enable them to survive tropical cyclones, as well as longer-term direct and indirect impacts on populations, species, and communities after the storm (Fig. 1). First, eight of us (Z. B. H., E. D., A. F., P. E. N., S. N., K. P., N. R., and B. R.) independently performed unstructured searches of the literature to frame our research question. We then used forward and backward citation searches of relevant studies to identify additional studies to consider. We did not consider papers that simulated population viability and extinction

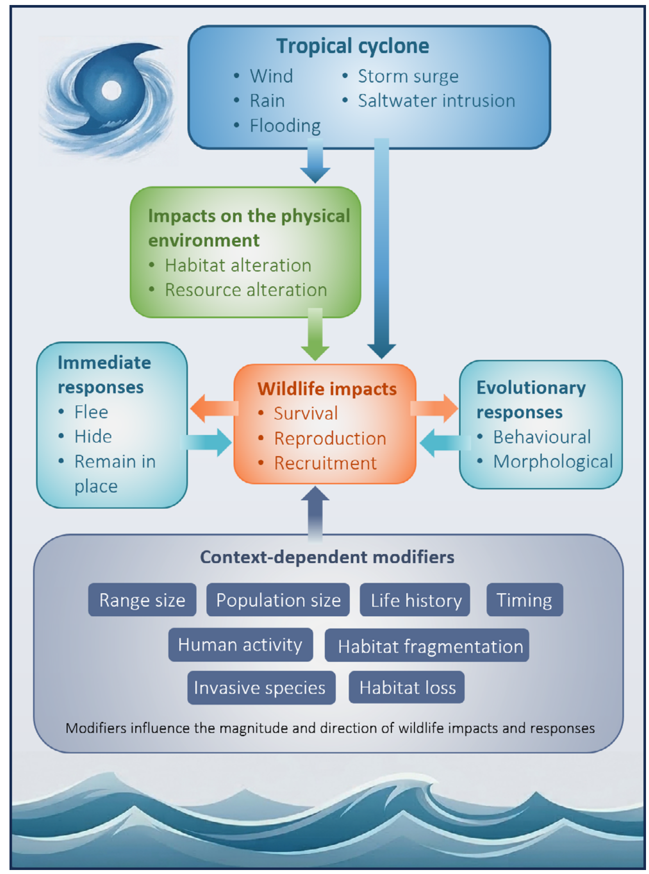

Fig. 1. Conceptualization of the pathways by which tropical cyclones can influence wildlife. Tropical cyclones impact wildlife survival, reproduction, and recruitment both directly and indirectly by affecting wildlife habitat and resources. The impacts to wildlife can be negative or positive, affecting wildlife at individual, population, species, and community levels. Wildlife have evolved strategies to survive tropical cyclones, and in some cases, tropical cyclones act as selective pressures that shape behaviour and morphology. The degree of impact to wildlife is modified by extrinsic factors such as the timing of the storm relative to life-history stage, habitat loss and fragmentation, and through the introduction of invasive species. Factors such as range size, population size, and life-history traits can make some species more vulnerable. Human activity further influences the magnitude of a tropical cyclone's impact *via* changes to landscape structure and wildlife population size, and *via* climate change that alters the timing and frequency of tropical cyclones. Conservation actions, such as habitat restoration and conservation breeding, can help to alleviate the impacts of tropical cyclones on wildlife.

risk, although simulation papers do suggest that tropical cyclones have the potential to increase extinction risk (e.g. Breininger, Brugman & Stith, 1999; Falcy & Danielson, 2014). We did not report on studies that showed an absence of response, unless there was a link to a strategy for survival, because of the difficulty in identifying and omitting cases where no observed response was a function of low relative threat (i.e. storm path and strength in relation to the location of the population under study) or small monitored sample size. Our non-exhaustive review of the literature was not geographically or taxonomically limited, although it was weighted toward locales and taxa for which there were published studies [refer to Marler (2014) for a review of the disproportionate number of studies in the Atlantic basin]. Our liberal use of the term 'wildlife' encompassed all undomesticated, non-captive animal populations. Our narrative review was not a systematic review of the literature; Maxwell *et al.* (2019) and Neilson *et al.* (2020) have published recent systematic reviews and quantified trends in wildlife responses to extreme weather events. Rather, our aim was to give a qualitative context to these previous reviews by presenting the diversity of responses described across the literature in a variety of wildlife taxa and revealing trends within them. Rotating, organized storms with sustained wind speeds exceeding 119 km/h are called 'typhoons' when they originate in the north-western Pacific Ocean, 'cyclones' when they originate in the south Pacific and Indian Oceans, or 'hurricanes' when they originate in the Atlantic and north-eastern Pacific Oceans (NOAA, 2024). In our review, we use the more general term 'tropical cyclone' unless describing a specific, named storm.

III. TACTICS: SHORT-TERM BEHAVIOURS TO SURVIVE THE STORM

When a tropical cyclone is approaching, wildlife can either move outside of the path of the storm, seek short-term refuge nearby and avoid the brunt of the impact, or remain in place and ride out the storm (Fig. 1). Here, we give examples across taxa and ecosystems of behaviours exhibited by wildlife that enable them to survive the immediate impacts of tropical cyclones.

(1) Avoid the storm's path

Some mobile species can avoid the impacts of a tropical cyclone by moving out of the storm's path. These behaviours are difficult to observe in nature and, thus, examples are rare. One example comes from the Mozambique Channel of the Indian Ocean. While flying at sea, adult great frigatebirds (*Fregata minor*) may perceive strong winds ahead of the cyclone's arrival. In response, they were observed flying at higher altitudes above the storm, thus avoiding the storm's negative impacts (Weimerskirch & Prudor, 2019). In another example, several species of shark have been observed leaving shallow, coastal nursery waters and heading to deeper ocean water as major cyclonic storms approach, in some cases moving 80 km away (e.g. Strickland *et al.*, 2020). On the coast of Florida, USA, juvenile blacktip sharks (*Carcharhinus limbatus*) evacuated a nursery bay within hours of Hurricane Gabrielle making landfall in 2001; presumably the drop in barometric pressure as the storm approached was the cue for direct, synchronous movement to deeper water that is less turbulent than shallow, near-shore areas (Heupel, Simpfendorfer & Hueter, 2003). Even juveniles with no previous experience with tropical cyclones evacuated the shallow waters as the hurricane approached, suggesting that this behavioural response, at least in some shark species, is innate (Heupel *et al.*, 2003; Udyawer *et al.*, 2013). Some larger-bodied sharks, however, show a different response to approaching tropical cyclones: tiger sharks (*Galeocerdo cuvier*) remained in shallow coastal waters, perhaps to capitalize on a potential increase in prey accessibility near the coast following the storm (Gutowsky *et al.*, 2021).

Moving to avoid the path of a storm may not always be possible, such as when birds encounter a tropical cyclone while migrating over the ocean (Butler, 2000; Newton, 2007). It is not uncommon for migrating birds to be blown off course by tropical cyclones, sometimes being carried hundreds of kilometres away (e.g. Fussell & Allen-Grimes, 1980; LeGrand, 1990; Dinsmore & Farnsworth, 2006). Birds caught in tropical cyclones tend to be in constant flight and may be unable to feed, leaving them in poor physical condition after the storm, as well as relocated to a place that may not have the seasonal resources necessary to refuel and restart migration (Dionne *et al.*, 2008). For example, as Hurricane Wilma moved northward along the eastern coast of North America in 2005, southbound migrating birds were caught in the hurricane's path (Dionne *et al.*, 2008). Chimney swifts (*Chaetura pelagica*) were reported thousands of kilometres outside of their range after the storm, as far away as England, Ireland, Portugal, and Spain (Dionne *et al.*, 2008). Similarly, Hurricane Idalia moved northeast from the Caribbean region in 2023, making landfall in Florida before tracking across Georgia and South Carolina, USA. In its wake, American flamingos (*Phoenicopterus ruber*) were observed in at least 13 US states and as far north as Wisconsin and Ohio, USA (eBird, 2023), in regions where the species does not typically occur (Torres-Cristiani *et al.*, 2020; Fig. 2). These individuals originated from the Yucatán region of Mexico and blew northward with Hurricane Idalia (Davis, 2023).

Birds are not the only taxon to be transported by tropical cyclones to places where they do not typically occur. The Central American snapping turtle (*Chelydra rossignonii*) is a freshwater species that is considered globally vulnerable (van Dijk *et al.*, 2007). Days after Hurricane Eta impacted the mainland coast of Honduras in 2020, one adult Central American snapping turtle was found washed ashore on Utila Island, Honduras, which is approximately 39 km off the coast of Honduras, presumably transported in the water by the hurricane (Brown *et al.*, 2021). Similarly, green iguanas (*Iguana iguana*) have been transported

Fig. 2. American flamingos (*Phoenicopterus ruber*) observed in Franklin County, Pennsylvania, USA on 9 September 2023, likely transported there by Hurricane Idalia. Hurricane Idalia made landfall in Florida, USA on 30 August 2023, more than 1,300 km south of Pennsylvania. American Flamingos have been spotted in at least 13 states in the USA since the hurricane (eBird, 2023). Photograph credit: R. (CC-BY-NC).

to new islands during tropical cyclones by floating across open ocean on rafts of debris (refer to Section V; Censky, Hodge & Dudley, 1998).

(2) Seek refuge

Some species avoid the immediate effects of tropical cyclones by moving shorter distances to seek refuge. A striking example of this behaviour was documented in central Mozambique in the wake of significant flooding from Tropical Cyclone Idai. Walker *et al.* (2023) showed that several herbivores, such as bushbuck (*Tragelaphus sylvaticus*), greater kudu (*T. strepsiceros*), and African elephant (*Loxodonta africana*), moved from low-elevation floodplains to higher-elevation woodland habitat. Lions (*Panthera leo*), too, moved to higher elevations (Walker *et al.*, 2023). While moving upslope, bushbucks perched on top of termite (*Macrotermes* spp.) mounds that had become islands in the floodwaters; they moved from mound to mound, *en route* to higher elevation, thus finding refuge at both the macro- and microhabitat levels (Walker *et al.*, 2023). White-tailed deer (*Odocoileus virginianus*) moved outside of seasonal home ranges to find refuge at higher elevations, thereby avoiding low-lying, flooded marshes (Samuel & Glazener, 1970; Abernathy *et al.*, 2019). Some anurans also demonstrate avoidance of flooding that accompanies tropical cyclones: anecdotal observations of the endemic Baja California treefrog (*Pseudacris hypochondriaca*) suggest that during tropical cyclones, individuals find refuge in rock crevices in canyon walls 1.5 m above their normal pond habitat and above the mean height of floodwaters (Luja & Rodríguez-Estrella, 2010).

Seeking refuge during tropical cyclones is not limited to terrestrial wildlife. Sea kraits (*Laticauda* spp.) temporarily leave littoral habitats prior to tropical cyclones, taking refuge in cavernous spaces beneath volcanic rocks of the seacoast, which provides protection from turbulent shallow waters during the storm (Liu, Lillywhite & Tu, 2010). It is thought that sea kraits sense the low barometric pressure that precedes a storm, allowing them to escape otherwise risky locations (Liu *et al.*, 2010). Moving to find refuge during a tropical cyclone has also been observed in riverine fish. Adult common snook (*Centropomus undecimalis*), a euryhaline species, in the Shark River in Florida, USA, moved downstream to the safety of deeper water along the coast just hours before Hurricane Irma made landfall in 2017 (Massie *et al.*, 2020). This rapid downstream movement was presumably cued by a combination of dropping barometric pressure and rainfall-driven water levels in the upper river system where the riverine fish typically reside (Massie *et al.*, 2020).

Some pelagic seabirds have a seemingly counterintuitive behaviour to avoid strong cyclonic winds: they seek refuge by flying into the eye of the storm. Atlantic yellow-nosed albatrosses (*Thalassarche chlororhynchos*) and wandering albatrosses (*Diomedea exulans*) were tracked flying into the eye of a storm, where wind speeds were lower (Nourani *et al.*, 2023).

Red imported fire ants (*Solenopsis invicta*) have a unique behaviour that allows them to survive flood events – they create their own refuge by forming living, floating rafts that consist of hundreds of thousands of individuals (Morrill, 1974; Mlot, Tovey & Hu, 2011, 2012; Fig. 3). Individual ants cooperate to link their bodies together, trapping pockets of air between them. These rafts may stay intact on the water's surface for days to weeks (Morrill, 1974; Adams *et al.*, 2011; Mlot *et al.*, 2011). Floating rafts of invasive fire ants were observed across the southern and southeastern USA in floodwaters following Hurricane Harvey (Zhang, 2017), Hurricane Florence (O'Neill, 2018), and Hurricane Ian (Fox 35 Orlando News Staff, 2022), for example.

(3) Shelter in place

For some species, sheltering in place may be the best option to maximize survival during a tropical cyclone. When tropical cyclones impacted Florida's coastal waters, the federally

Fig. 3. Thousands of red imported fire ants (*Solenopsis invicta*) form a floating raft, enabling them to survive the flooded Choctawhatchee River, Florida, USA. Photograph: W. Jamie Barichivich, with permission.

endangered Florida manatee (*Trichechus manatus latirostris*) showed no movement inland or further offshore to deeper water and instead sheltered in place during storm activity (Langtimm *et al.*, 2006), likely benefiting from the protection of barrier islands and mangrove forests (Tilmant *et al.*, 1994; Meyers *et al.*, 2006). Similarly, during Hurricane Michael, a category 5 storm that made landfall in Florida in 2018, Lamont, Johnson & Catizone (2021) did not detect any movement of four species of turtles [loggerhead (*Caretta caretta*), Kemp's ridley (*Lepidochelys kempii*), green sea turtle (*Chelonia mydas*), and diamondback terrapin (*Malaclemys terrapin*)] even though the hurricane made landfall less than 30 km from the bay where the turtles were located. Unlike other mobile seabird species, brown pelicans (*Pelecanus occidentalis*) are less active during the passage of a tropical cyclone, sheltering among nearby barrier islands and estuarine systems (Wilkinson *et al.*, 2019). Sheltering in place may be less risky for this relatively large-bodied coastal seabird than moving to avoid the storm entirely and may be cued by increasing wind velocity and decreasing barometric pressure (Wilkinson *et al.*, 2019). Adult spotted seatrout (*Cynoscion nebulosus*) did not move from an estuary off the coast of Texas, USA during a nearly direct hit by Hurricane Harvey in 2017, and their spawning activity was largely unaffected (Biggs, Lowerre-Barbieri & Erisman, 2018).

Whether an individual shelters in place may be dictated by life stage. While adult pelagic seabirds are generally less vulnerable to the effects of tropical cyclones when they are out at sea (Hennicke & Flachsbarth 2009; Section III.1), juveniles tend to ride out tropical cyclones by remaining at their onshore colonies (Weimerskirch & Prudor, 2019). For the relatively inexperienced fledgling and juvenile seabirds that lack the flight and foraging capability of adults, this behaviour is thought to be a trade-off between the risk of staying onshore and the potentially greater risk of heading out to sea during a storm (Nicoll *et al.*, 2017; Weimerskirch & Prudor, 2019).

IV. IMPACTS: LONG-TERM IMPACTS AFTER THE STORM

Tropical cyclones can have lasting impacts on wildlife after the storm passes. These impacts can be direct, by causing mortality or reducing recruitment, but also indirect, by altering, destroying, or enhancing habitat and resources. Here, we give examples, across wildlife taxa and ecosystems, of the direct and indirect impacts of tropical cyclones at multiple levels of organization, from individuals to species to communities.

(1) Direct and indirect mortality

There are many examples of tropical cyclones causing mortality of wildlife, and it is likely that the magnitude is underestimated because post-storm conditions make surveying difficult (e.g. Marsh & Wilkinson, 1991). In 2004, Hurricane Catarina, the only reported hurricane in the south Atlantic Ocean, displaced seabirds inland and at least 354 Atlantic petrels (*Pterodroma incerta*) were reported dead (Bugoni, Sander & Costa, 2007). Marsh & Wilkinson (1991) estimated that at least 400 adult American oystercatchers (*Haematopus palliatus*) died when Hurricane Hugo hit the coast of South Carolina in 1989. Hurricane Hugo also killed 200–400 brown pelicans (Cely, 1991) and caused high mortality of red-cockaded woodpeckers (*Leuconotopicus borealis*; Section VIII.2*a*). In addition to direct mortality, during prolonged periods of heavy rain associated with early-season tropical cyclones, adult red-cockaded woodpeckers were unable to forage and provision nestlings, resulting in nestling mortality (Neal *et al.*, 1993; Conner *et al.*, 2005). American alligators (*Alligator mississippiensis*) have been found dead or under severe hyperosmotic stress from storm surge water inundating their freshwater habitat after a tropical cyclone (Lance *et al.*, 2010). Population density of queen conch (*Aliger gigas*), a federally threatened marine gastropod in the Florida Keys, USA, declined following Hurricane Irma in 2017, when conchs died after being buried in sand and rubble; populations had barely recovered when the same area was impacted 5 years later by Hurricane Ian (Vos *et al.*, 2024).

Tropical cyclones can be particularly severe for sea turtle populations because the nesting season tends to overlap with the tropical cyclone season in the Caribbean Sea and northwest Atlantic Ocean (Pike & Stiner, 2007; Dewald & Pike, 2014). Sea turtle eggs incubating under the sand can be washed away (Mishra *et al.*, 2023) or drowned by storm surge and extreme rainfall (Milton *et al.*, 1994; Limpus, Miller & Pfaller, 2020). Hatchling emergence can be hindered by beach sand erosion and accretion caused by the storm (Milton *et al.*, 1994) and indeed, complete nest loss has been reported (e.g. Cely, 1991; Milton *et al.*, 1994). Sea turtle life history, however, may help buffer populations from these extreme weather events. Individual adult female sea turtles do not nest every year; rather, in nesting years, individual females deposit multiple clutches of eggs every few weeks over the course of the relatively long reproductive season, thereby reducing the probability that any one storm will destroy all her eggs (Miller, 1997; Dewald & Pike, 2014; Cassill, 2021). Freshwater turtle eggs are also vulnerable to flooding from tropical cyclones (Ernst, 1974), and preliminary surveys after Hurricane Ian hit the west coast of Florida in 2022 suggest high mortality of several freshwater turtle species (Lechowicz, 2022).

(*a*) *Water quality*

One mechanism by which tropical cyclones cause wildlife mortality is through altered water quality. Hypoxic water conditions produced by the suspension of anaerobic sediments and the decomposition of large amounts of organic debris caused mass mortality of over 280 million inland freshwater fish in Louisiana, USA following Hurricane Ida in 2021 (Louisiana Department of Wildlife and Fisheries, 2022). Similarly, over 29,000 American paddlefish (*Polyodon spathula*) and at least 50–100 adult Gulf sturgeon (*Acipenser oxyrinchus desotoi*) were found dead in hypoxic water following tropical cyclones (Lovelace & McPherson, 1998; Dula *et al.*, 2022). Over 9.4 million saltwater fish also perished off the coast of Louisiana after Hurricane Andrew in 1992 (Lovelace & McPherson, 1998). In addition to hypoxic conditions, tropical cyclones produce immense rainfall that reduces salinity in coastal ocean water. As a result, a major eastern oyster (*Crassostrea virginica*) die-off occurred off the coast of Texas after Hurricane Harvey in 2017 due to prolonged exposure to low-salinity sea water in the estuary (Du *et al.*, 2021). The loss of critical species like eastern oysters, which play an essential role in filtering water and providing habitat for other marine life, can lead to cascading effects on the ecosystem, impacting both biodiversity and the overall health of coastal ecosystems (Ruesink *et al.*, 2005; zu Ermgassen *et al.*, 2013).

(*b*) *Strandings*

Storm surge associated with tropical cyclones causes wildlife mortality by carrying marine wildlife inland, leaving them stranded when the surge water recedes. At least two mass strandings and subsequent deaths of pygmy killer whales (*Feresa attenuata*) have been associated with tropical cyclones (Mignucci-Giannoni *et al.*, 2000; Clua, Manire & Garrigue, 2014). Common bottlenose dolphins (*Tursiops truncatus*), dugongs (*Dugong dugon*), Florida manatees, and green sea turtles have been found stranded in floodwater and on mudflats several kilometres inland, likely carried in by storm surge water (Marsh, 1989; Langtimm *et al.*, 2007; Rosel & Watts, 2008).

(*c*) *Disease*

Tropical cyclones contribute to wildlife mortality by increasing disease risk. Mass mortality of green sea urchins (*Strongylocentrotus droebachiensis*) occurred within weeks of two separate hurricanes (Juan in 2003 and Bill in 2009) that hit the Atlantic coast of Nova Scotia, Canada (Scheibling, Feehan & Lauzon-Guay, 2010). The mortalities were not directly caused by the hurricane itself, but by the hurricane-mediated introduction of a non-native, pathogenic amoeba (*Paramoeba invadens*) into coastal waters that infected and killed the urchins (Scheibling *et al.*, 2010; Scheibling & Lauzon-Guay, 2010). Similarly, Paerl *et al.* (2001) noted a rise in systemic bacterial infection in several species of fish after three tropical cyclones hit the coast of North Carolina, USA. Conversely, tropical cyclones can lead to lower disease risk in some systems. For example, Cyclone Yasi caused reduced rainforest canopy cover when it hit northeastern Queensland, Australia in 2011 (Roznik *et al.*, 2015). This reduction in canopy cover caused an increase in temperature and evaporative water loss in the microhabitat of the common mistfrog (*Mosleyia rheocola*), thereby reducing the frogs' infection risk by the chytrid fungus (*Batrachochytrium dendrobatidis*) (Roznik *et al.*, 2015).

(2) Impacts on wildlife habitat and resources

The alteration and destruction of natural areas that provide shelter, resources, and suitable habitat for reproduction can have a variety of impacts on wildlife. High winds during a tropical cyclone that denude trees of flowers, fruit, leaves, and branches are particularly devastating for frugivores and nectarivores. Decreases in abundance of frugivorous bats [e.g. Jamaican fruit-eating bat *Artibeus jamaicensis* in Montserrat and Dominica (Pedersen, Genoways & Freeman, 1996; Sims, 2022)] and obligate frugivorous birds (e.g. Puerto Rican bullfinch *Melopyrrha portoricensis*; Lloyd, Rimmer & Salguero-Faría, 2019) have been documented following tropical cyclones; individuals of these species may have dispersed in search of resources, or populations may truly have declined from mortality. Some generalist species switch their diet if their preferred food is unavailable after a tropical cyclone, giving diet generalists an advantage over obligate frugivores and nectarivores. After Hurricane Iris hit the coast of Belize in 2001, destroying the canopy and uprooting trees, arboreal Central American black howlers (*Alouatta pigra*) that survived the storm opportunistically consumed fruit from deadfall trees and then shifted their diet to leaves when surviving trees failed to produce fruit (Pavelka *et al.*, 2003; Behie & Pavelka, 2005). After Tropical Cyclone Idai hit Mozambique in 2019, small-bodied antelope were forced to switch to a lower-quality diet, resulting in reduced nutritional condition 3 months after landfall; larger-bodied species were more robust (Walker *et al.*, 2023).

Species that depend on tree canopies are particularly vulnerable to tropical cyclones, as evidenced by two endemic arboreal frogs in Puerto Rico. The tree-hole coqui (*Eleutherodactylus hedricki*) and the cricket coqui (*E. gryllus*), considered endangered and critically endangered, respectively (IUCN SSC Amphibian Specialist Group, 2021a,b), lay eggs in tree cavities and in bromeliad plants on tree trunks in the forest canopy. Both species experienced population declines following habitat destruction from Hurricanes Irma and Maria in

2017 (Campos-Cerqueira & Aide, 2021). This contrasts with some amphibians that breed in ephemeral freshwater wetlands (e.g. eastern spadefoot *Scaphiopus holbrookii*) that may encounter an increase in freshwater breeding habitat after significant rainfall associated with tropical cyclones (Johnson & Furhmann, 2020; Section IX.1).

Tropical cyclones can limit availability of freshwater when storm surge and saltwater intrusion make water holes unsuitable. Such is the case for endangered Key deer (*Odocoileus virginianus clavium*), a subspecies of white-tailed deer endemic to the Florida Keys. After Hurricanes Georges in 1998 and Irene in 1999 hit the Florida Keys, more than 25% of monitored water holes were unsuitable for deer because of high salinity, with the salinity remaining high for several weeks (Lopez *et al.*, 2003).

(3) Population extirpation and species extinction

Perhaps the largest impact that a tropical cyclone could have at the species level is to facilitate extirpation or extinction, whether directly or indirectly. For example, the endangered Miami blue butterfly (*Cyclargus thomasi bethunebakeri*), once common throughout southern coastal Florida, was thought extinct after Hurricane Andrew in 1992 wiped out the last known population on an island in the Florida Keys (Carroll & Loye, 2006). The species has since been rediscovered on other remote islands and the Florida Museum of Natural History now has a conservation breeding facility with butterflies for reintroduction (Florida Museum, 2021). Similarly, in 1996 Hurricane Lili caused the extirpation of web-spider populations on small islands in the Bahamas (Spiller, Losos & Schoener, 1998). The islands were, however, quickly recolonized by web-spiders, in part because of the spiders' over-water dispersal abilities (Spiller *et al.*, 1998). Small mammal populations have also been temporarily extirpated because of tropical cyclones, such as isolated populations of the endangered Perdido Key beach mouse (*Peromyscus polionotus trissyllepsis*) on the coast of Florida (Austin *et al.*, 2015; Section VIII.2*b*).

There are several island-endemic bird species that have teetered on extinction, in part due to the direct and indirect effects of tropical cyclones. The Cozumel thrasher (*Toxostoma guttatum*) and the Bahama nuthatch (*Sitta insularis*) are both critically endangered island-endemic birds. For both species, habitat destruction caused by successive tropical cyclones is thought to be a main factor in their decline; the last known sighting of the Cozumel thrasher was in 2004, and the Bahama nuthatch was last seen in 2019 (BirdLife International, 2020; Gardner *et al.*, 2024). Similarly, habitat destruction caused by Hurricane Hugo in 1989 reduced the already-imperilled Puerto Rican parrot (*Amazona vittata*) to just 26 surviving individuals (Waide, 1991b); fruiting trees in the last known refuge for the Puerto Rican parrot were knocked down or severely defoliated (Wunderle, 1999). The pre-hurricane cyclic fruiting pattern was disrupted for more than 2 years after the hurricane, adding a further stressor for the Puerto Rican parrot, whose reproductive phenology is timed to these typically cyclical fruiting patterns (Wunderle, 1999). Although Puerto Rican parrots raised in conservation breeding facilities are helping to augment the wild population (White, Collazo & Vilella, 2005), Hurricanes Irma and Maria in 2017 were detrimental to ongoing recovery efforts for the species, which remains critically endangered (BirdLife International, 2023). The Kauaʻi ʻŌʻō (*Moho braccatus*) and the Kāmaʻo (*Myadestes myadestinus*), once relatively common forest birds on the Hawaiian island of Kauaʻi, were in severe decline when Hurricane Iwa in 1982 and Hurricane Iniki in 1992 damaged the habitat of their last remaining refuge; both species are now extinct (Van Riper & Scott, 2001; Foster *et al.*, 2004).

Tropical cyclones increase extinction risk, but the relationship can be complex (Turvey *et al.*, 2021). For example, the presence of predator species can impact extinction risk of native species after tropical cyclones (Schoener, Spiller & Losos, 2001). The interaction of population size and tropical cyclone intensity can also influence extinction risk: Spiller *et al.* (1998) showed empirically that small populations of lizards and spiders are more likely to go extinct after a tropical cyclone, but for catastrophic storms, even relatively large populations went extinct. Land-use change also plays a role – habitat fragmentation caused by coastal development impeded recolonization after tropical cyclones extirpated populations of beach mice (Pries, Branch & Miller, 2009).

(4) Community-level impacts

Tropical cyclone impacts on individuals and populations, as well as on their resources, have the potential to scale up to influence community structure (Dalsgaard & Temeles, 2024). Changes in vegetative structure from tropical cyclones have impacted the diversity and composition of bird and bat communities (Gannon & Willig, 1994; Perdomo-Velázquez *et al.*, 2017; Jones *et al.*, 2001; Sims, 2022). These changes in community structure may be local and temporary, as some individuals simply moved to nearby refuges with habitat that received less storm damage (Gannon & Willig, 1994; Rittenhouse *et al.*, 2010). This highlights the role of intact, connected habitat in facilitating movement and recolonization of wildlife after the storm (Rittenhouse *et al.*, 2010).

Community structure of freshwater wetland fauna can also be altered by tropical cyclones when storm surge and saltwater over-wash increase salinity (Gunzburger *et al.*, 2010; Walls *et al.*, 2019). Schriever *et al.* (2009) found that herpetofauna abundance and diversity decreased after three tropical cyclones in Louisiana altered wetland salinity. Davis *et al.* (2023) showed that amphibian species richness in freshwater wetlands declined after tropical storm-related flooding facilitated the introduction of fish into wetlands that were previously fishless, altering amphibian communities through predation and competition. By contrast, despite sustained salinity in coastal freshwater wetlands in Florida's St. Marks National Wildlife Refuge following Hurricane Dennis in 2005, there was no detectable change in anuran species richness or community structure, even 1 year after the storm

(Gunzburger *et al.*, 2010). These amphibian communities, having evolved under a regime of reoccurring extreme weather events and exposure to brackish water, may be locally adapted to elevated salinity levels, suggesting variability among wetland-breeding communities in their tolerance of acute or sustained changes in wetland salinity (Gunzburger *et al.*, 2010; Brown & Walls, 2013).

The causes and consequences of community structure change following extreme weather events are functions of interacting and cascading direct and indirect impacts on species and their ecosystems (Jiguet, Brotons & Devictor, 2011). The variety of positive, negative, and ambiguous responses of wildlife to extreme weather, across taxa and environments, and at all levels of organization (Maxwell *et al.*, 2019), make it especially difficult both to measure and predict impacts at the community and ecosystem levels and as such, this area is ripe for future research.

V. TROPICAL CYCLONES AND NON-NATIVE SPECIES SPREAD

Tropical cyclones can facilitate the introduction and spread of invasive non-native flora and fauna (Bilger, 2001; Searcy *et al.*, 2023), which can have lasting community-level effects (Bellingham, Tanner & Healey, 2005; Goulding, Moss & McAlpine, 2016). One of the most notorious invasive species in Florida, the Burmese python (*Python bivittatus*), now occurs throughout much of southern Florida (Guzy *et al.*, 2023). In 1992, Hurricane Andrew purportedly damaged a facility in southern Florida that housed Burmese pythons for the pet trade, causing the release of hundreds of pythons into the wild. Although not the cause of the initial invasion (Willson, Dorcas & Snow, 2011), this event may have augmented the population. Hurricane Andrew was also implicated in the accidental introduction of both the African sacred ibis (*Threskiornis aethiopicus*) and the western swamphen (*Porphyrio porphyrio*) in Florida, when hurricane-force winds destroyed buildings housing these species (Pranty *et al.*, 2000; Herring, Call & Johnston, 2006; Johnson & McGarrity 2009a,b). Similarly, the introduction of the Australian redclaw crayfish (*Cherax quadricarinatus*) from illegally stocked earthen ponds into Puerto Rico's natural environment was likely facilitated by Hurricane Georges in 1998 (Williams *et al.*, 2001). The introduction of non-native tunicates at harbours on the coast of North Carolina in 2018 was associated with Hurricane Florence (Hutchings *et al.*, 2023). Tropical cyclones have been implicated in the invasion of lionfish (*Pterois volitans/miles*) from their non-native range in Florida to the Bahamas (Johnston & Purkis, 2015; Fig. 4). Hurricanes Irma and Maria facilitated the re-invasion of black rats (*Rattus rattus*) to Green Cay, a small island near Saint Croix, United States Virgin Islands in 2017 (Shiels *et al.*, 2020). Green Cay is one of two islands where the endangered St. Croix ground lizard (*Pholidoscelis polops*) still naturally occurs, and black rats are a threat to the persistence of this species (Fitzgerald *et al.*, 2015). Similarly, 15 green iguanas colonized the island of Anguilla by floating on a raft of uprooted trees following two hurricanes in 1995 (Censky *et al.*, 1998). Since then, the native and critically endangered Lesser Antillean iguana (*Iguana delicatissima*) on Anguilla has faced competition and hybridization with the thriving, non-native green iguana (van den Burg, Breuil & Knapp, 2018; Pounder *et al.*, 2020).

Fig. 4. Tropical cyclones have likely facilitated the spread of invasive lionfish (*Pterois volitans/miles*) across parts of their non-native range (Johnston & Purkis, 2015). Photograph credit: Robin White (CC BY-NC 4.0).

VI. TROPICAL CYCLONES AS SELECTIVE EVOLUTIONARY FORCES

Extreme weather events can be a driver of evolutionary change, even over contemporary timescales (Parmesan *et al.*, 2000; Grant *et al.*, 2017; Dalsgaard & Temeles, 2024). These changes can be behavioural or morphological, and in some cases can leave a population maladapted to the changed environment.

(1) Behavioural trait responses

Some behavioural traits exhibited by wildlife may be shaped by exposure to tropical cyclones. Dalsgaard & Temeles (2024) posited that dietary generalism in tropical island-dwelling species may have evolved, at least in part, in response to tropical cyclones, as individuals of species with specialized diets may not survive after a storm. The geographic location of sea turtle nesting is another example of a behavioural trait that has likely been shaped by past tropical cyclone activity. Female sea turtles lay eggs in nests under beach sand, making the eggs particularly vulnerable to the impacts of tropical cyclones. Females show natal philopatry to nesting beaches, returning to nest at the same beach where they hatched (Limpus *et al.*, 1992). Fuentes, Bateman &

Hamann (2011) found that four species of sea turtles nesting on the beaches of eastern Queensland, Australia were more likely to select beaches with low tropical cyclone activity. Fuentes *et al.* (2011) suggested that past tropical cyclone activity has shaped the distribution of sea turtle nesting sites through natural selection: sites with a high incidence of cyclonic activity likely have reduced nesting and hatching success over time (e.g. Milton *et al.*, 1994), reducing the number of turtles that later return to those risky sites to nest (Fuentes *et al.*, 2011).

(2) Morphological responses

Tropical cyclones have the potential to cause morphological changes in some wildlife populations. Perhaps one of the strongest examples to date is in neotropical anoles (*Anolis* spp.) that occur on islands in the Caribbean Sea (Huey & Grant, 2020). Some *Anolis* species cling to vegetation to withstand the extreme wind associated with tropical cyclones (Donihue *et al.*, 2018). Anoles that survived tropical cyclones had larger toe pads and longer forelimb bones (Donihue *et al.*, 2018, 2020; Rabe *et al.*, 2020), physical traits that increase the clinging ability of anoles during high winds (Crandell *et al.*, 2014; Kolbe, 2015; Donihue *et al.*, 2018; Dufour *et al.*, 2019). Individuals with weaker clinging ability were likely blown from their perches into the ocean where they perished (Donihue *et al.*, 2018). This phenotypic response held true across anole species and across regions (Donihue *et al.*, 2020). Further, the next generation of anoles also had larger toepads and in fact, anole populations that have experienced more tropical cyclones over the last 70 years tended to have larger toepads (Donihue *et al.*, 2020).

Interestingly, the phenotypic response to a tropical cyclone's selective pressure on clinging capacity in *Anolis* is mediated by the environment in which they reside. The toepads and forefeet of the crested anole (*Anolis cristatellus*) were longer and narrower in forest-dwelling individuals but were wider in urban populations of the same species after Hurricanes Irma and Maria devastated Puerto Rico in 2017 (Michaud *et al.*, 2023). Seemingly, different toe pad shapes are beneficial for clinging to different surfaces. Acevedo *et al.* (2022) did not find evidence of selection for increased clinging ability in the yellow-chinned anole (*A. gundlachi*) in Puerto Rico's interior forests. Anoles exposed to hurricane-force winds in inland forests of large islands are less likely to be blown into the ocean, and instead might survive by finding refuge in the forest understory (Acevedo *et al.*, 2022).

The mangrove tree crab (*Aratus pisonii*; Fig. 5) responds to rising tides by climbing structures such as mangrove trees. The northward range expansion of the mangrove tree crab in the southeastern USA has outpaced range shifts of its native mangrove habitat, and instead, mangrove tree crabs have colonized saltmarsh ecosystems at the species' leading range edge (Cannizzo & Griffen, 2018). Cannizzo & Griffen (2018) found that after Hurricane Matthew impacted the southeast coast of the USA in 2016, the body size of

Fig. 5. A mangrove tree crab (*Aratus pisonii*) observed in 2019 on Leffis Key, Florida, USA. Hurricanes may cause selection for smaller body size in mangrove tree crabs at the northern extent of their range, where tall, woody structures for climbing to seek refuge are relatively rare (Cannizzo & Griffen, 2018). Photograph: Art Nadelman, with permission.

mangrove tree crabs that inhabit saltmarshes was smaller than that of tree crabs inhabiting mangrove swamps. Presumably, where there were fewer tall or woody structures to climb in the saltmarsh habitat, the larger-bodied mangrove tree crabs were unable to survive the impacts of the hurricane compared to smaller-bodied crabs (Cannizzo & Griffen, 2018).

(3) Maladaptation

Tropical cyclones have the potential to disrupt coevolutionary relationships, leaving one or both species maladapted. For the red-shouldered soapberry bug (*Jadera haematoloma*) in southeastern Texas, prolonged flooding following Hurricane Harvey in 2017 led to rapid evolutionary change, and specifically maladaptation to local host plants (Comerford *et al.*, 2023). The length of the soapberry bugs' mouthparts is adapted to the shape of their local food source. Comerford *et al.* (2023) showed that after hurricane flooding caused local extinction of soapberry bug populations, it was the long-winged dispersal forms that recolonized from nearby. Wing length is genetically correlated with mouthpart length, meaning that recolonized populations had significantly longer mouthparts relative to pre-flood populations, and this persisted for at least three generations. The consequence was that populations in the recolonized habitats were maladapted to feeding on two of the three local host plants because their mouthparts were too long. Thus, flooding from the hurricane eroded over 60 years of adaptive divergence in mouthpart length (Comerford *et al.*, 2023).

Similarly, damage to plants from tropical cyclones has resulted in the disruption of a tightly coadapted plant–hummingbird mutualism. In 2017, Hurricane Maria significantly reduced flowering of a native *Heliconia* plant species on the island of Dominica. By contrast, non-native *Heliconia wagneriana* plants, which have longer flowers than the native *Heliconia*, remained relatively abundant after the storm. Male purple-throated caribs (*Anthracothorax jugularis*), which have relatively short bills to match the native *Heliconia* plant, were not as well adapted to the long-flowered shape of the non-native *Heliconia wagneriana* (Temeles & Bishop, 2019). Follow-up surveys after the hurricane revealed that male purple-throated caribs had longer bills, on average, than before the hurricane, and the non-native *Heliconia wagneriana* had shorter flowers. This suggests that the hurricane caused directional selection on both plant and pollinator, at least in the short term (Temeles & Bishop, 2019; Schrøder *et al.*, 2024).

VII. THE MAGNITUDE OF IMPACT CAN DEPEND ON TIMING

The timing of a tropical cyclone in relation to a species' annual life cycle can determine the magnitude of the storm's impact on the population. Hurricane Laura, for example, made landfall in the breeding range of Louisiana's coastal population of mottled duck (*Anas fulvigula*) in 2020. Hurricane Laura was a late-season storm that hit when waterfowl were moulting their flight feathers and were therefore unable to fly out of the hurricane's path, causing ~40% mortality of adult females (Ringelman *et al.*, 2021). In general, the breeding season of many shorebird and seabird species occurs outside of the cyclone season, thus minimizing the potential for direct nest failure during an active storm. For seabirds whose breeding season overlaps with the tropical cyclone season, however, these extreme storms have the potential to affect survival and recruitment negatively. When Tropical Cyclone Rosie crossed the Indian Ocean in 2008, high winds and large ocean swells hit the shores of Christmas Island, Australia. Christmas Island supports a large breeding colony of the red-tailed tropicbird (*Phaethon rubricauda*), a long-lived seabird that breeds year-round (Hennicke & Flachsbarth, 2009). The cyclone destroyed over 34% of the red-tailed tropicbird nest sites, 41% of the active nests, and 61% of the eggs on Christmas Island (Hennicke & Flachsbarth, 2009). No adult red-tailed tropicbirds were thought to have died from the cyclone, leading Hennicke & Flachsbarth (2009) to surmise that despite the drastic impact on reproduction that year, the effect of Tropical Cyclone Rosie on overall population dynamics might not have been severe. Like many long-lived species with delayed maturity (e.g. Heppell, 1998; Hyslop *et al.*, 2012; Ancona *et al.*, 2017), adult survival of the red-tailed tropicbird has a greater influence on population growth rate than does juvenile survival or recruitment (Sæther & Bakke, 2000). Similarly, Cyclone Isla hit Bedout Island off the coast of northwestern Australia in 2023 during the peak breeding season for many seabirds. However, in this event, the cyclone killed 80–90% of adult seabirds [lesser frigatebird (*Fregata ariel*), brown booby (*Sula leucogaster*), and the endemic masked booby subspecies (*S. dactylatra bedouti*)] on the island (Lavers *et al.*, 2024). As seabirds typically have long generation times and low fecundity, the loss of so many breeding adults means that population recovery will be slow and future tropical cyclones in this region could be devastating (Lavers *et al.*, 2024).

For some species, certain life stages are better able to withstand the impacts of tropical cyclones. Storm surges from tropical cyclones have wiped out entire island populations of adult and juvenile brown anoles (*Anolis sagrei*; Spiller *et al.*, 1998) but the eggs can survive the storm surge, at least temporarily (Losos, Schoener & Spiller, 2003; Schoener, Spiller & Losos, 2004). Indeed, the timing of a tropical cyclone can have a larger impact on anole populations than its severity. Brown anole populations recovered after Hurricane Floyd, a strong, early-season hurricane in 1999, solely from the eggs; all anoles that had hatched prior to the storm perished in the storm surge (Schoener *et al.*, 2004). The storm surge from a relatively weak, late-season tropical cyclone, however, wiped out anole populations because it occurred after the egg stage was complete (Schoener *et al.*, 2004).

Many amphibians rely on aquatic environments for reproduction, and thus the timing of tropical cyclones can have a large impact on their reproductive success (Walls, Barichivich & Brown, 2013). The marbled salamander (*Ambystoma opacum*; Fig. 6), distributed in the southeastern USA, has a unique reproductive strategy that depends on predictable, seasonal rainfall events. In autumn, female marbled salamanders migrate to nesting grounds to breed and lay eggs in dry, low-elevation areas that will eventually flood. Females guard the eggs on the dry ground for several weeks while the embryos develop. Then, when heavy winter rains flood the wetland, the well-developed larvae hatch. Early-season flooding from tropical cyclones can thus cause near-complete reproductive failure (Walls *et al.*, 2013; Hall, 2022). In Alabama, USA for example, heavy rain and

Fig. 6. A marbled salamander (*Ambystoma opacum*) observed in Florida, USA in 2021. Heavy rainfall and flooding from hurricanes can cause near-complete nest failure (Walls *et al.*, 2013; Hall, 2022). Photograph: Susan Walls, with permission.

flooding from successive Hurricanes Sally, Zeta, and Delta in 2020 caused marbled salamander nests to become inundated after eggs were laid but well before the larvae had developed, resulting in premature hatching and nest failure (Hall, 2022). Early-season flooding that occurs before adult marbled salamanders arrive at the dry ephemeral pool basins prevents breeding (Wojnowski, 2000). If a female does successfully deposit eggs along the dry margins of a prematurely filled pond basin, those eggs will not hatch unless the nest site receives more water later in the season (Wojnowski, 2000).

Storm surge from tropical cyclones can also impact reproductive success of amphibians that breed in coastal freshwater ponds. After Hurricane Michael hit the coast of Florida in 2018, storm surge pushed sea water into ephemeral coastal wetlands. These same coastal wetlands were essential breeding ponds for the federally threatened frosted flatwoods salamander (*Ambystoma cingulatum*), and the combined effects of increased early-summer rainfall and high salinity after the hurricane may have caused reduced juvenile recruitment (Walls *et al.*, 2019).

Fig. 7. Pacific flying fox (*Pteropus tonganus*) observed in 2018 on an island in the south Pacific Ocean near Fiji. The frugivorous flying fox is particularly vulnerable to tropical cyclones when the post-storm lack of food forces individuals to seek food in villages, making them vulnerable to hunting and predation (Pierson *et al.*, 1996). Photograph by Cheryl Rosenfeld (CC BY-NC).

VIII. ANTHROPOGENIC INTERACTIONS

Human actions can significantly influence wildlife following tropical cyclones in both negative and positive ways. These actions can hinder ecological recovery if the interaction leads to further pressure on wildlife populations, or it can have a positive effect if conservation efforts lead to restored habitat or increased population abundance.

(1) Synergistic effects of tropical cyclones and anthropogenic pressures

In some ecosystems, the negative impacts of tropical cyclones on wildlife have been amplified by human interactions. For example, in 1990 and 1991, Cyclones Ofa and Val hit the South Pacific islands of Samoa, destroying roosting habitat and food resources for the Pacific flying fox (*Pteropus tonganus*; Fig. 7) and the endemic Samoan flying fox (*P. samoensis*). The abundance of both species declined after Cyclone Ofa, especially the Pacific flying fox with a 90–99% population decline (Craig, Trail & Morrell, 1994; Pierson *et al.*, 1996). The high mortality rate was not directly related to the storm, however. The cyclones damaged trees that provided food (nectar, flowers, and fruit) for the Pacific flying fox, forcing weak and starving individuals to travel outside of reserves and into villages to feed on fallen cultivated fruit, where they became vulnerable to predation by domestic animals and hunting by humans; predation and hunting are suspected as the main cause of the severe post-storm population declines (Pierson *et al.*, 1996). Observations suggest nearly 100% mortality of young Pacific flying foxes after the cyclones (Pierson *et al.*, 1996). The post-storm diet of the Samoan flying fox, however, consisted of leaves, allowing it to remain relatively safe in the protected reserves (Pierson *et al.*, 1996).

Cyclone Ernest hit southern Madagascar in 2005, reducing forest food availability for the ring-tailed lemur (*Lemur catta*) in the Beza Mahafaly Special Reserve (LaFleur & Gould, 2009). After the cyclone, lemurs left the reserve to feed on cultivated crops in nearby farm fields. While humans in the Beza Mahafaly area do not generally harm crop-raiding lemurs, lemurs outside of the forest reserve were vulnerable to predation by predatory birds and feral dogs and cats (LaFleur & Gould, 2009). Similarly, Hurricane Ivan struck Grand Cayman as a Category 5 storm in 2004. After the storm, Cayman parrots (*Amazona leucocephala caymanensis*) approached human settlements in search of food, where some were vulnerable to persecution (Bradley, as reported in Wunderle, 2005).

(2) Conservation efforts to mitigate impacts to imperilled species

Human actions can help mitigate the impacts of tropical cyclones on wildlife when habitat is damaged or populations have declined. Actions such as habitat restoration and translocation of captive-bred individuals after population extirpation have been used successfully in some systems.

(a) *Restoration and creation of habitat and resources*

Creation of habitat may help mitigate damage to wildlife resources caused by tropical cyclones. For example, damage to the tree canopy in Puerto Rico caused by Hurricane Maria in 2017 reduced availability of arboreal habitat for the common coqui (*Eleutherodactylus coqui*). After the hurricane, researchers deployed artificial 'coqui houses' (Stewart & Pough, 1983) that provided arboreal retreats and nesting sites when environmental conditions were most stressful for the frogs (Burrowes *et al.*, 2021).

Similarly, habitat creation helped recovery of the federally threatened red-cockaded woodpecker (Fig. 8), a species that requires excavated cavities in mature, living longleaf pine (*Pinus palustris*) trees for nesting (Jackson, Lennhartz & Hooper, 1979; Hooper, 1988). Due to extensive habitat loss across its range over the last two centuries, the red-cockaded woodpecker now exists in isolated populations, several of which have been negatively impacted by tropical cyclones [e.g. in Georgia and Texas (Engstrom & Evans, 1990; Bainbridge *et al.*, 2011)]. In 1989, the eye of Hurricane Hugo passed over the Francis Marion National Forest in South Carolina, home to one of the largest remaining populations of red-cockaded woodpecker, and one of the only populations that was known to be increasing at that time (Hooper, Krusac & Carlson, 1991; Watson *et al.*, 1995). Hurricane Hugo destroyed 87% of the active cavity trees and 60% of forage trees (Watson *et al.*, 1995; Hooper, Watson & Escano, 1996). An estimated 63% of the woodpeckers in the forest were killed or missing (Watson *et al.*, 1995; Hooper *et al.*, 1996). Soon after, U.S. Forest Service staff began creating artificial nest cavities for this species, a new and mostly untested endeavour at the time (Watson *et al.*, 1995; Koches, 2023). Watson *et al.* (1995) reported that 540 artificial nest cavities were constructed in the forest prior to the 1990 nesting season, and the woodpeckers were using them. Even more encouraging was that woodpeckers successfully fledged from the artificial nest cavities (Watson *et al.*, 1995). Within 3 years after Hurricane Hugo, the number of adult red-cockaded woodpeckers in the Francis Marion National Forest increased by 33%, and more than 60% of the nests were in artificial cavities (Watson *et al.*, 1995). Now, the recovered red-cockaded woodpecker population in the Francis Marion National Forest is used as a source for translocation of birds to other parts of their historic range (Warren & Nairn, 2011; Koches, 2023), and artificial cavities are a common reintroduction and conservation tool for this species (Martin, Gigliotti & Ferguson, 2021).

Fig. 8. A red-cockaded woodpecker (*Leuconotopicus borealis*) observed in 2023 in Alabama, USA. Hurricane Hugo destroyed most of the mature pine trees on the coast of South Carolina that red-cockaded woodpeckers require for cavity nesting (Watson *et al.*, 1995; Hooper *et al.*, 1996). Photograph: Julie C. (CC-BY-NC).

Conservation efforts have also helped the recovery of endangered Key deer in the Florida Keys. After Hurricane Irma in 2017 caused salinization of the limited freshwater on the islands, it became difficult for Key deer to find fresh water (Section IV.2). In response, staff from the National Key Deer Refuge deployed small plastic swimming pools and other receptacles full of fresh water as a temporary supplement for Key deer that survived the storm (Nobel, 2017).

(*b*) *Translocation and captive breeding*

Despite the devastating impacts that tropical cyclones can have on coastal ecosystems, back-up plans to restart recently extirpated populations are in place for some at-risk species. The federally endangered Perdido Key beach mouse, for example, lives in three isolated populations in the dunes of one barrier island along the coast of Florida and Alabama. All three populations have independently become extirpated following tropical cyclones, and all have been recolonized by multiple human-mediated translocation events of wild Perdido Key beach mice or, in one instance, likely by natural recolonization from a nearby population (Holier *et al.*, 1989; Austin *et al.*, 2015; Greene, Gore & Stoddard, 2016). In September 2004, Hurricane Ivan made landfall about 40 km west of Perdido Key as a category 3 storm. Just before landfall, Florida Fish and Wildlife Conservation Commission staff collected eight Perdido Key beach mice as a precaution (Austin *et al.*, 2015; Greene *et al.*, 2016). Since then, captively bred individuals from the original eight have been distributed to several facilities, who cooperatively maintain and breed the mice in conservation breeding facilities. In 2010, 48 captive-born beach mice were reintroduced to the Gulf State Park population that had been extirpated since 1997 following Hurricane Opal (Oli, Holler & Wooten, 2001; Greene *et al.*, 2016). After five years, the population of Perdido Key beach mice in Gulf State Park had increased to ∼206 individuals (Greene *et al.*, 2016). Captive breeding at the facilities continues (Brevard Zoo, 2022; Fig. 9). Captive breeding has also been used to augment wild populations of the Puerto Rican parrot and the Miami blue butterfly; both species are vulnerable to the interacting effects of habitat loss and tropical cyclones (Section IV.3).

IX. NOT ALL IMPACTS ARE NEGATIVE

Previous reviews have revealed wildlife responses to extreme weather events are not necessarily negative (Maxwell *et al.*, 2019; Neilson *et al.*, 2020). In fact, in some systems, tropical cyclones have contributed to increased survival and

Fig. 9. A Perdido Key beach mouse (*Peromyscus polionotus trissyllepsis*) at the Brevard Zoo's conservation breeding facility in Florida, USA. The Brevard Zoo is one of several institutions breeding this endangered species for potential reintroduction into the wild. Photograph: Brevard Zoo, with permission.

recruitment through enhanced habitat, increased food resources, or by having negative impacts on predator abundance.

(1) Enhanced habitat and food resources

For some wildlife populations in some ecosystems, tropical cyclones result in the generation of additional habitat, which can have a net positive effect on the population. For example, although snowy plovers (*Charadrius nivosus*) nest on sandy ocean beaches in areas prone to tropical cyclones, juveniles have typically fledged by the time the autumn tropical cyclone season occurs. When tropical cyclones redistribute sand along the coast, sand accumulation can increase the amount of potential breeding and brood-rearing habitat for snowy plovers. Convertino *et al.* (2011) found that snowy plovers along the coast of Florida were seven times more likely to nest on a beach that had been impacted by a tropical cyclone the previous autumn. Similarly, populations of the federally threatened piping plover (*C. melodus*) increased along the coast of New York, USA after Hurricane Sandy in 2012 (Robinson *et al.*, 2020). The number of black skimmer (*Rynchops niger*) nests also increased in the breeding season following tropical cyclones on the coast of Louisiana, presumably because of an increase in nesting habitat on the beach (Raynor *et al.*, 2013). This may not be the case for all beach-nesting species in all areas, as tropical cyclones can also cause significant beach erosion (Fearnley *et al.*, 2009). Further inland, downed woody debris caused by Hurricane Hugo in 1989 had a positive impact on shrew (*Blarina carolinensis* and *Sorex longirostris*) abundance one decade later by creating rich habitat for the species (Cromer *et al.*, 2007).

In aquatic ecosystems, heavy rainfall that accompanies a tropical cyclone can fill ephemeral ponds and facilitate amphibian breeding after the storm. For example, peaks in gopher frog (*Lithobates capito*) breeding activity are associated with high rainfall events from tropical cyclones in southeastern USA (Crawford *et al.*, 2022). Similarly, the eastern spadefoot toad spends much of its life underground, but is stimulated to emerge, migrate, and lay eggs in ephemeral ponds following heavy rainfall events (Pearson, 1955; Greenberg & Tanner, 2004). In fact, the eastern spadefoot has been coined the "hurricane toad" because hurricanes and tropical storms can trigger explosive breeding events (Johnson & Furhmann, 2020). The diverse life histories across Amphibia means that tropical cyclones do not necessarily have a positive impact on population growth. In marked contrast to the eastern spadefoot, the nexus of storm timing and reproductive timing can, in some systems, result in near-complete reproductive failure for amphibians (Walls *et al.*, 2013; Section VII).

Strong winds and changing sea surface temperatures associated with tropical cyclones can enhance ocean productivity, which can have positive impacts on piscivorous species. Blue-footed boobies (*Sula nebouxii*), for example, breed colonially on islands in the eastern Pacific Ocean and plunge-dive for small pelagic fishes near their colonies (Ancona *et al.*, 2017). The eastern Pacific tropical cyclone season overlaps with the last 10 weeks of the breeding season for blue-footed boobies on Isla Isabel, Mexico. Interestingly, both adult survival rate and recruitment of blue-footed boobies tend to increase after the passage of a tropical cyclone (Ancona *et al.*, 2017). Ancona *et al.* (2017) proposed that tropical cyclones may cause an increase in the ocean's primary productivity, causing fish populations to thrive, which, in turn, has a positive effect on piscivorous seabird populations. Similarly, juvenile Trindade petrel (*Pterodroma arminjoniana*) survival tends to be higher in areas with increased tropical cyclone activity, presumably due to improved foraging opportunities at sea caused by the storms (Nicoll *et al.*, 2017). Desertas petrels (*Pterodroma deserta*) followed tropical cyclone wakes for thousands of kilometres to capitalize on higher prey abundance (Ventura *et al.*, 2024).

Tropical cyclones may indirectly impact reproduction of herbivorous mammals if vegetation growth increases after a storm. Fawn production of endangered Key deer was higher after strong winds associated with Hurricane Georges in 1998 reduced the forest overstory (Lopez *et al.*, 2003). Lopez *et al.* (2003) surmised that female Key deer capitalized on the new understory growth after the hurricane, which may have improved female body condition and positively impacted herd productivity. This is not a ubiquitous finding, however; fawn production of white-tailed deer in the Everglades region of Florida was markedly reduced after Hurricane Andrew struck the region in 1992 (Labisky, Miller & Hartless, 1999).

(2) Fewer predators

Tropical cyclones can have net positive impacts on native prey species by having negative impacts on their predators.

The small Indian mongoose (*Urva auropunctata*) is an invasive species on many islands in the Caribbean Sea and is a major predator of sea turtle nests and hatchlings on these islands (Leighton, Horrocks & Kramer, 2011). Mongoose populations on Saint Croix Island declined following Hurricanes Irma and Maria in 2017; it is speculated that decreased abundance of this predator could relieve pressure on sea turtle populations (Shiels *et al.*, 2020). After Hurricane Isabel hit the coast of North Carolina in 2003, there was a marked increase in American oystercatcher nest survival, in part because nest predation by raccoons (*Procyon lotor*) was relatively low after the hurricane (Schulte & Simons, 2016). Similarly, Leumas (2010) found increased nest success of least terns (*Sternula antillarum*) following tropical cyclones on Louisiana's barrier islands, presumably a result of the storms' negative impact on nest predator abundance.

X. WHY ARE SOME SPECIES MORE VULNERABLE?

A species' viability is, in part, shaped by local and landscape-scale processes that drive its resiliency, redundancy, and representation, known in conservation biology as the three Rs (U.S. Fish and Wildlife Service, 2016; Smith *et al.*, 2018). These three Rs are cornerstones of the Species Status Assessment framework that uses science to inform decisions under the Endangered Species Act in the USA (U.S. Fish and Wildlife Service, 2024); extinction risk due to catastrophic events is minimized when the three Rs are high (U.S. Fish and Wildlife Service, 2016; Smith *et al.*, 2018). As such, understanding differing vulnerabilities of wildlife species to tropical cyclones can inform development of conservation strategies (Walls *et al.*, 2019; Johnson, 2021). Based on our review, we propose three characteristics that, by influencing resiliency, redundancy, and representation, make some wildlife populations more vulnerable to the impacts of tropical cyclones: range size, life history, and compounding factors.

(1) Restricted range

Small populations tend to have higher extinction risk (Pimm, Jones & Diamond, 1988; Purvis *et al.*, 2000), and indeed, species with small geographic distributions are some of the most vulnerable to the impacts of tropical cyclones (Simberloff, 2000). In fact, globally, the species predicted to be most at risk of extinction due to tropical cyclones occur on islands in the tropics (Gonçalves *et al.*, 2024). Island populations tend to be small in both abundance and range size, contributing to their elevated extinction risk (Spatz *et al.*, 2017; Dalsgaard & Temeles, 2024). Species with restricted ranges have fewer options for taking refuge during a storm relative to widespread, continental species; they have inherently low redundancy and thus few, if any, options for natural recolonization after a large-scale disturbance (Simberloff, 2000). Further, island populations tend to be faced with additional, simultaneous threats from habitat conversion, species introductions, disease, and overexploitation – pressures that contribute to their vulnerability to catastrophic disturbances (Spatz *et al.*, 2017; Leclerc, Courchamp & Bellard, 2018). In our review, every example of a species extirpation or extinction that was facilitated by a tropical cyclone involved an island population with a restricted range and exposure to at least one other pressure (Section IV.3). In many cases, the population was already in decline (e.g. the Kaua'i 'Ō'ō and the Kāma'o) and the compounding impact of a tropical cyclone accelerated extinction.

(2) Life history

Some life-history traits contribute to a species' vulnerability to the impacts of tropical cyclones. Sessile and slow-moving benthic organisms may be vulnerable because they are unable to move to seek refuge (e.g. queen conch; Section IV.1). Species with specific habitat requirements, such as tree canopies, for part of their life cycle are likely to be negatively impacted by tropical cyclones when trees are knocked down (e.g. cavity-nesting birds and arboreal frogs; Section IV.2). Obligate frugivorous and nectarivorous species are also vulnerable, whereas species that switch forage if their main food source is not available after the storm tend to be less impacted (e.g. Central American black howlers; Section IV.2). Species with high dispersal ability and high redundancy are, theoretically, able to rapidly recolonize parts of their range where they were extirpated after a tropical cyclone, making them less vulnerable at a landscape scale (e.g. web-spiders; Section IV.3). Species that reproduce during the tropical cyclone season but that spread out their reproductive effort spatially and temporally might be less vulnerable (e.g. sea turtles; Section IV.1). Species with shorter generation times, resulting in a higher propensity for the evolution of physical traits that increase survival during a storm, might be less vulnerable in the long term (e.g. *Anolis* spp.; Section VI.2). On the other hand, long-lived species with low fecundity will be slow to recover if the adult segment of the population is impacted (e.g. seabirds; Section VII). Large-bodied, mobile species might be more able to seek refuge and endure post-storm reductions in forage quality and quantity, provided that sufficient connected habitat exists (Section IV.4).

(3) Compounding factors

The strategies exhibited by wildlife that enhance survival during and after tropical cyclones may be becoming increasingly ineffective in the face of human development, land conversion, and climate change (Cely, 1991; Parmesan *et al.*, 2000). Prior to extensive human settlement, the effects of tropical cyclones on wildlife might have been localized and populations might have had a high likelihood of recolonizing and recovering. With extensive land-use change and human development, especially in coastal regions, many wildlife populations are now fragmented, isolated, and often restricted to the small pockets of habitat that remain, making them inherently more vulnerable to extreme weather events (Cely, 1991; Parmesan *et al.*, 2000). For example, beach mouse recolonization after tropical cyclones can be hindered by coastal development (Section VIII.2*b*; Pries *et al.*, 2009). Similarly, loss of habitat connectivity may limit post-storm recolonization by birds and bats (Section IV.4). Restoring connectivity among isolated populations and conserving remaining intact habitats can only increase ecosystem resilience to extreme weather events (Maxwell *et al.*, 2019); large tracts of intact, connected habitat support higher population abundance, facilitate movement to parts of the range that were not impacted by a tropical cyclone, and provide an avenue for recolonization of decimated portions of the range. Small populations tend to be more vulnerable to stochastic events such as tropical cyclones, and indeed, population declines prior to tropical cyclones have contributed to the extinction of several bird species (Section IV.3). The synergistic effects of declining population size and small or fragmented distributions, coupled with an increasing frequency of the most catastrophic storms, calls into question the ability of wildlife populations to rebound from these catastrophic events in the future (e.g. West Indian woodpecker *Melanerpes superciliaris*; Akresh *et al.*, 2021).

XI. STUDY LIMITATIONS

Research focused on the complex, interacting, and cascading effects of tropical cyclones on wildlife is still growing, and there are likely many species in a variety of ecosystems with tactics and responses to tropical cyclones that we, as scientists, have not yet observed. There are many studies that we have not included here because of the sheer number of published examples (refer to Maxwell *et al.*, 2019). Thorough reviews of avian responses to tropical cyclones can be found in Waide (1991a) and Wiley & Wunderle (1993), and a review of the effects of tropical cyclones on forest and mangrove ecosystems is provided by Lugo (2008) and Krauss & Osland (2020), respectively. The impacts of tropical cyclones on coastal and marine ecosystems were reviewed by Correia & Smee (2022) and Feehan *et al.* (2024). Wunderle & Wiley (1996), Cely (1991), Sergio, Blas & Hiraldo (2018), Parmesan *et al.* (2000), Maxwell *et al.* (2019), and Neilson *et al.* (2020) reviewed the impacts of extreme weather events and disturbance on wildlife more generally; Maxwell *et al.* (2019) performed a systematic review of the tropical cyclone literature. Our review complements these quantitative or systematic reviews by showcasing the diversity of responses exhibited by wildlife to tropical cyclones and by exploring commonalities, across taxa and ecosystems, in how tropical cyclones shape wildlife populations and communities. A limitation of our study, and in the tropical cyclone literature as a whole, is the general bias towards tropical cyclone research in the Atlantic basin (Marler, 2014). As Marler (2014) argued, more research focus in the western Pacific Ocean, where tropical cyclone frequency and accumulated cyclone energy is higher, could increase our understanding of ecosystem resilience and resistance. Finally, comparing the magnitude of tropical cyclone impacts across ecosystems is difficult because of the wide variety of disturbances and responses observed. Hogan *et al.* (2020) proposed a research framework to evaluate quantitatively ecosystem responses to tropical cyclones. This standardized approach, which quantifies the magnitude of change and recovery time and links these to a standardized measure of tropical cyclone disturbance, can help facilitate meta-analyses and predictions of future impacts.

XII. A LOOK TO THE FUTURE

The activity of intense tropical cyclones has been shifting earlier in the season in both the Northern and Southern Hemispheres (Truchelut *et al.*, 2022; Shan *et al.*, 2023). In the North Atlantic basin, where research effort has been greatest, a longer active tropical cyclone season has also been detected in recent decades (Kossin, 2008; Patricola, Hansen & Sena, 2024). The timing of animal reproduction is a function of a multitude of trade-offs to maximize reproductive success (Bronson, 2009). Thus, significant changes to the historical timing of tropical cyclone activity could have consequential impacts on survival, recruitment, and life history if storm activity starts to coincide with vulnerable life stages when historically it did not (Moreno & Møller, 2011). Further, poleward shifts in the latitude at which tropical cyclones reach their maximum intensity have been documented (Kossin, Emanuel & Vecchi, 2014). Thus, coastal ecosystems that did not evolve under the periodic disturbance of tropical cyclones could be exposed to extreme weather events more often.

The seven tropical cyclone formation basins around the globe are predominantly within the tropics, regions that are also remarkably biodiverse (Michener *et al.*, 1997; Gaston, 2000; Gonçalves *et al.*, 2024). Climate change is predicted to contribute to an increase in the frequency of intense tropical cyclones (Christensen *et al.*, 2013; Knutson *et al.*, 2020), a pressure that could eventually overwhelm the adaptive capacity and resiliency of wildlife in some of the most biodiverse places on Earth. Interestingly, there appears to be a repeated pattern of trade-offs between ecosystem resistance and resilience to tropical cyclones, a relationship that spans ecosystem type (Patrick *et al.*, 2022b). This means that ecosystems that are better able to withstand change (i.e. resistant) tend to be slower to recover (i.e. resilient) after a storm (Patrick *et al.*, 2022b). The ability of wildlife populations to bounce back from the impacts of more frequent, high-intensity tropical cyclones, particularly as land-use change further degrades and fragments habitat and as many species continue to face additional threats, remains an important and yet unanswered question. Research and conservation actions that increase ecosystem resistance and resiliency to extreme weather events in all basins can help to alleviate the impacts of tropical cyclones on wildlife (Patrick *et al.*, 2022a,b), especially in this era of unprecedented global change.

XIII. CONCLUSIONS

(1) Alteration of wildlife habitat and resources because of tropical cyclones can impact wildlife survival, reproduction, and recruitment, which affects wildlife at the individual, population, species, and community levels and across a diversity of taxa and ecosystems (Fig. 1).
(2) In both aerial and aquatic ecosystems, wildlife respond to tropical cyclones by moving outside the path of an active storm (e.g. adult great frigatebirds flying above the storm and some sharks swimming to deeper waters), by seeking refuge (e.g. Baja California treefrogs find crevices in canyon walls above floodwaters), or by sheltering in place. A diversity of species may be able to detect dropping barometric pressure, giving them advanced warning of an approaching storm (e.g. sharks, sea kraits, common snook, and brown pelicans).
(3) Wildlife mortality events during and after a tropical cyclone have various proximate causes. In addition to direct mortality during the storm (e.g. drowned turtle eggs and marine mammal strandings), tropical cyclones alter water quality (e.g. hypoxia causing mass mortality of riverine fish) and escalate disease risk (e.g. in green sea urchins). Tropical cyclones can facilitate population extirpations and species extinctions.
(4) Tropical cyclones can be a driver of evolutionary change, even over contemporary timescales, by acting on behaviour (e.g. sea turtle nest site selection) and morphology (the size of anole toe pads).
(5) Human actions, such as habitat restoration after the storm and conservation breeding programs to support reintroduction, have helped the recovery of wildlife populations after tropical cyclones (e.g. red-cockaded woodpeckers and Perdido Island beach mice). Alternatively, human actions have hindered wildlife population recovery (e.g. Pacific flying foxes).
(6) Tropical cyclones can facilitate the introduction and spread of non-native species, which can have lasting ecosystem-level impacts.
(7) The timing of tropical cyclones can make the difference between minor and catastrophic effects on wildlife populations, depending on the reproductive phase of the population when the storm hits (e.g. marbled salamanders and red-tailed tropicbirds).
(8) Some species may benefit from tropical cyclones if the extent of their habitat increases (e.g. beach-nesting snowy plovers), if their food resources increase (e.g. blue-footed boobies benefit from increased ocean productivity after a storm), or if the abundance of their predator declines.
(9) Wildlife vulnerability to tropical cyclones is a function of range size, life history, and other compounding factors. Diet- and habitat-specialists are particularly vulnerable. Habitat loss and fragmentation means that coastal wildlife populations may be less resilient to future tropical cyclones.
(10) The frequency of the most intense tropical cyclones is predicted to increase with climate change. Concurrent pressures from land-use change, human development, and climate change mean that the impacts of tropical cyclones on wildlife could increase.

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XV. AUTHOR CONTRIBUTIONS

E. L. K.: Conceptualization (equal); Writing – original draft (lead); Investigation (equal); Writing – review & editing (equal). M. K. M.: Writing – review & editing (equal). Z. B. H.: Investigation (supporting); Writing – review & editing (supporting). K. E. M.: Conceptualization (equal); Investigation (supporting); Writing – review & editing (supporting). W. J. B.: Writing – review & editing (supporting). E. D.: Investigation (supporting). A. F.: Investigation (supporting); Writing – review & editing (supporting). M. I.: Writing – review & editing (supporting). P. E. N.: Investigation (supporting); Writing – review & editing (supporting). S. N.: Investigation (supporting); Writing – review & editing (supporting). K. P.: Writing – review & editing (supporting). N. R.: Investigation (supporting); Writing – review & editing (supporting). B. R.: Investigation (supporting); Writing – review & editing (supporting). D. S.: Writing – review & editing (supporting). S. C. W.: Writing – review & editing (supporting). E. H. E.: Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Project administration (lead); Supervision (lead); Writing – original draft (supporting); Writing – review & editing (supporting).

XVI. DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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