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Ecosystem damage by increasing tropical cyclones

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Climate change is driving an ongoing increase in tropical cyclone (TC) activity. While global economic losses are projected to double by 2100, there are no comparable predictions for TC impacts to coastal ecosystems that protect and sustain human lives and livelihoods. Here, rising North Atlantic TC (NATC) activity from 1970 to 2019, influenced by anthropogenic and natural climate forcing, is used to study the ecosystem impacts of intensifying TCs, potentially indicative of broader future climate change scenarios. Analysis of 97 NATC landfalls revealed 891 immediate post-storm impacts on ecosystems, with particularly detrimental effects on mangrove forests. Specifically, NATCs reduced the performance of individual species. Additionally, they altered community structure and processes through impacts on foundation species and their associated organisms. The severity of impacts was directly correlated with NATC landfall intensity (wind speed) for mangroves, whereas changes to waves, surge, sediments, and salinity caused most impacts on coral reefs, salt marshes, seagrass meadows, and oyster reefs (respectively), indicating complex intensity-damage interactions for many ecosystems. The analyses also revealed a positive correlation between very intense NATC activity and ecosystem damages. The research highlights a concerning trend of escalating impacts on coastal ecosystems under rising storm intensities, with the potential to challenge ecosystem resilience.

Tropical cyclones (TCs) are intense storms that cause loss of human life and destruction of coastal infrastructure and habitats¹. These storms are referred to as typhoons in the Northwest Pacific, cyclones in the Indian Ocean and Southwest Pacific, and hurricanes in the Atlantic and Northeast Pacific. Often, they are classified on the Saffir-Simpson scale (category 1–5) based on maximum sustained wind speeds². Category 4–5 storms are considered “very intense” TCs³. The relative proportion of very intense TCs has increased globally in recent decades, and global models project likely additional increases in both the proportion and frequency of very intense TCs and individual TC lifetime maximum surface wind speeds at 2 °C of anthropogenic warming^{3,4}. Individual TCs can cause 10’s of billions (USD) in damages^{5–7}, they are the leading contributor to US billion-dollar disasters⁸, and total global economic damages are expected to double by the end of the century, potentially reaching 400% of current levels without climate change adaptation^{9,10}. Across a range of latitudes, individual TCs have damaged hundreds to thousands of hectares of coral reef, mangrove forest, salt marsh, and seagrass meadow habitats^{11–15}. These TC-induced ecosystem damages have cascading effects on humans, including the loss of

coastal protection, wildlife habitat, and carbon sequestration¹⁶. Despite these impacts, estimates for future trends in TC damages across coastal marine ecosystems are lacking, highlighting a significant gap in knowledge required for effective marine resource management and climate adaptation planning.

TCs affect all dominant coastal marine ecosystems, including those characterized by biogenic habitats such as reef-building marine animals (e.g., coral reefs and oyster reefs) and meadows and forests of submergent (e.g., seagrass and kelp) and emergent (e.g., salt marsh and mangrove) marine plants and macroalgae^{16–21}. The intense winds, waves, precipitation, and altered atmospheric pressure associated with TCs can cause physical damage to organisms^{14,16,20}. This includes breakage, abrasion, and dislodgment^{14,16,20}. Additionally, TCs can alter sediment dynamics resulting in habitat erosion or burial and degrade water quality^{21,22}. Yet, predicting the overall impact of rising TC activity on ecosystems is challenging due to the complex interactions between TCs and ecosystems, and limited understanding of general relationships between TC attributes and ecosystem damages²³. For example, while TC landfall intensity (i.e., wind speed) has been posited as a primary determinant of marine ecosystem damages (e.g.,

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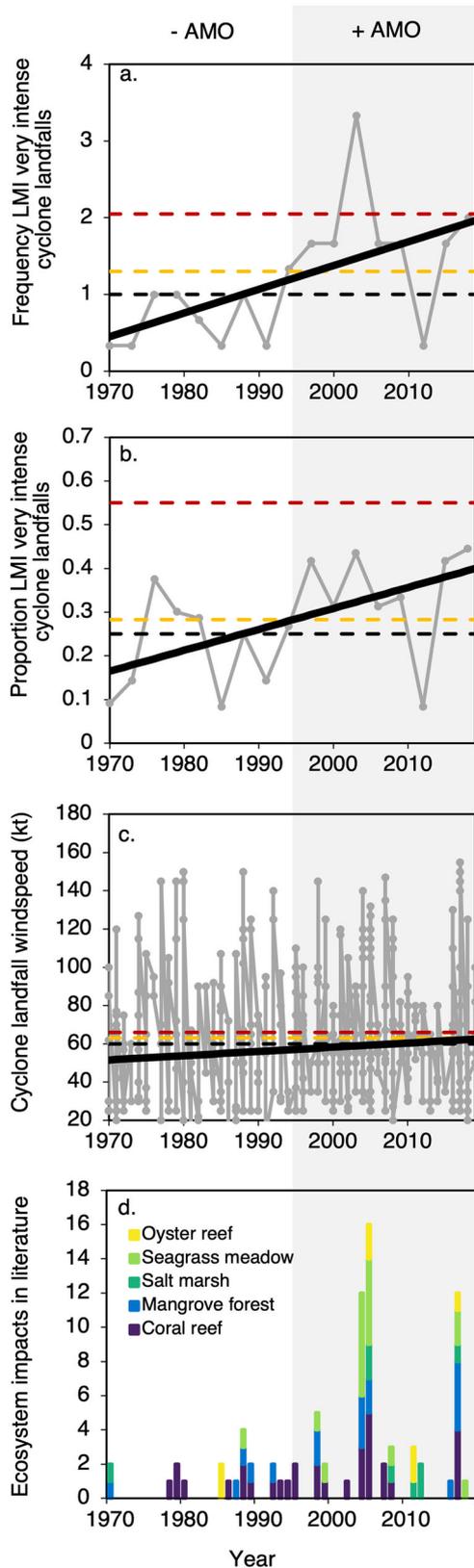


Fig. 1 | North Atlantic tropical cyclone (NATC) landfall activity (1970–2019). **a** Annual landfall frequency (count) of very intense NATCs (lifetime maximum intensity, “LMI”, category 4–5) (3-yr bins). **b** Proportion of landfalling very intense NATCs (LMI category 4–5 relative to all LMI category 1–5) (3-yr bins). **c** Wind speed at landfall of all LMI category 1–5 NATCs, and **(d)** Landfall NATCs with impacts reported in the literature across five coastal marine ecosystems. Dashed black lines in (a–c) indicate historical baselines for the North Atlantic (1986–2005 median); dashed orange and red lines are the median and maximum percent change (respectively) applied to the baseline taken from similar storm metrics in high-resolution global models at 2 °C of anthropogenic warming³. –/+AMO indicate negative and positive phases of the Atlantic Multidecadal Oscillation (more recently referred to as the Atlantic Multi-decadal Variability, AMV⁴⁰). Mann-Kendall P values with Theil-Sen trends (solid black lines) are shown in (a–c). Data in (a–c) are from IBTrACS, Version 4.

important for predicting future impacts. A standardized synthesis of case studies across various response variables and dominant coastal marine ecosystems may help to elucidate general trends and lay the groundwork for predictive models.

North Atlantic TC (NATC) activity has accelerated in recent decades compared to other ocean basins¹. For example, in the North Atlantic, there has been a recent 42% increase per decade (1979–2017) in the probability of major TC exceedance, which is the probability of a storm reaching or exceeding Saffir–Simpson category 3²⁷. This increase dramatically surpasses the global average rate of 6% per decade over the same timeframe²⁷. Recent NATC trends have likely been driven by a combination of anthropogenic and natural climate forcing^{4,27,28}, and may reflect a “rebound” from a deep local minimum in the 1960–1980s²⁸. Nonetheless, a corresponding multi-decadal rise in NATC activity may provide a useful model system for understanding ecosystem damages as TCs intensify globally under climate warming, particularly given that all globally dominant types of coastal marine ecosystems are found in the North Atlantic²⁹ and many ecological studies have documented NATC impacts to marine foundation species and associated species and communities in recent decades (e.g., refs. 20,21,30–37). This is akin to how ocean warming hotspots have been identified as sentinels of ecosystem change under global warming^{38,39}.

Here, we first quantify recent trends (1970–2019) in landfalling NATCs for comparison against anticipated general changes in global TC activity at 2 °C of anthropogenic warming³. Second, we synthesize five decades of NATC landfall data and published records of ecological responses to NATC landfalls across five dominant coastal marine ecosystems: coral reefs, mangrove forests, salt marshes, seagrass meadows, and oyster reefs. More specifically, we analyze, with standardized effect sizes, the immediate (i.e., days to months) post-storm effects on marine species performance (e.g., growth, recruitment, and mortality) and community structure or processes (e.g., community diversity or carbon stocks). In addition, we assess and evaluate possible underpinning physical drivers of NATC impacts (winds, waves, surge, sediment changes, and salinity changes – as identified in the individual case studies) to better understand relationships between storm attributes and ecosystem damages. We find that the recent rising NATC trend provides a useful warning system for the general types of changes anticipated globally at 2 °C of anthropogenic warming, with evidence that increasing NATC activity correlates with greater ecological damages across coastal marine ecosystems, and especially in mangrove forests.

Results

NATC Landfall Activity

The annual frequency (count) of landfalls of lifetime maximum intensity (LMI) very intense NATCs increased 68% per decade from 1970 to 2019 (Mann-Kendall $P = 0.005$, Theil-Sen slope = 0.031 yr^{-1}) (Fig. 1a). Additionally, the proportion of LMI very intense NATC landfalls (i.e., the proportion of LMI category 4–5 to all LMI category 1–5 NATCs) increased 29% per decade from 1970 to 2019 (Mann-Kendall $P = 0.035$, Theil-Sen slope = 0.005 yr^{-1}) (Fig. 1b). NATC landfall wind speeds (for all LMI category 1–5

refs. 16,24,25), recent global analyses have revealed variation among ecosystems, with an intensity-damage relationship observed for mangrove forests but not necessarily for seagrass meadows^{25,26}. How intensity-damage interactions are modulated by ecosystem-specific physical drivers of impact (e.g., winds versus waves or surge) remains largely unexplored but will be

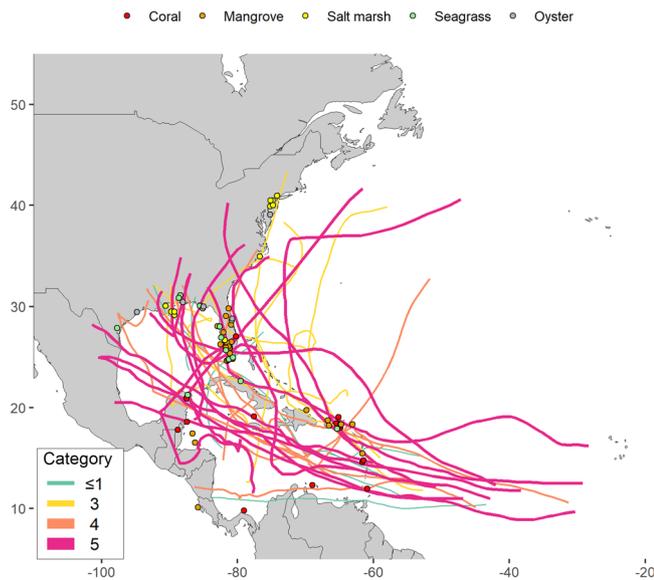


Fig. 2 | North Atlantic tropical cyclone (NATC) tracks (lines) and locations of impact in coastal marine ecosystems (circles) reported in the ecological literature (1970–2019). Tracks and impacts are color-coded based on NATC lifetime maximum intensity (Saffir-Simpson scale category ≤ 1 –5) and ecosystem type.

NATCs) also increased 4% per decade from 1970 to 2019 (Mann-Kendall $P = 0.011$, Theil-Sen slope = 0.222 yr^{-1}) (Fig. 1c).

Knutson et al.³ provide predictions for the percent change in various global TC metrics at 2 °C of anthropogenic warming, based on available high-resolution models relative to the 1986–2005 global baseline, and with a range of confidence levels in these predictions (see Methods). Given the NATC baseline (1986–2005; black dashed lines in Fig. 1a–c), we find that NATC trends have surpassed the median percent changes (dashed orange lines) but remain below the maximum percent changes (dashed red lines) predicted by Knutson et al.³ for similar global TC metrics. Specifically, the trend in annual frequency of LMI very intense NATC landfalls has surpassed the median and is below the maximum increase that Knutson et al.³ predict may occur in the global annual frequency of very intense TCs at 2 °C of anthropogenic warming (Fig. 1a). Moreover, the trend in proportion of LMI very intense NATC landfalls has surpassed the median and is below the maximum increase that Knutson et al.³ predict may occur in the proportion of global very intense TCs at 2 °C of anthropogenic warming (Fig. 1b). Finally, a trend in NATC landfall wind speeds has reached the median and is below the maximum increase that Knutson et al.³ predict may occur in global maximum TC surface wind speeds at 2 °C of anthropogenic warming (Fig. 1c). These data indicate that NATCs provide a useful warning system for the general types of changes that may occur globally under anthropogenic climate change. However, basin-scale variability in TC projections at 2 °C of anthropogenic warming³ mean that global impacts may be heterogeneous. Specifically, the projections of Knutson et al.³ indicate a greater rise in very intense TCs in the Northeast Pacific and North Atlantic compared to the North and South Indian Ocean, and with potential decreases in these storms in the Northwest and Southwest Pacific.

A subset of the landfalls in Fig. 1a–c are also recorded in published ecological literature documenting their impacts on coastal marine ecosystems (Fig. 1d). These reported impacts occurred across five dominant coastal marine ecosystems and the geographic footprint of landfalling NATCs, but with poorer coverage in South America, Central America, and Mexico as compared to the United States and islands of the Caribbean Sea (Fig. 2). The ecological literature followed the expected pattern of more frequent impacts reported after a 1995 rise in NATC activity and corresponded to a shift from a negative to positive phase of the Atlantic Multi-decadal Oscillation (Fig. 1), now referred to as the Atlantic Multi-decadal Variability⁴⁰, a potential driver of NATC activity⁴. Peaks in reports of

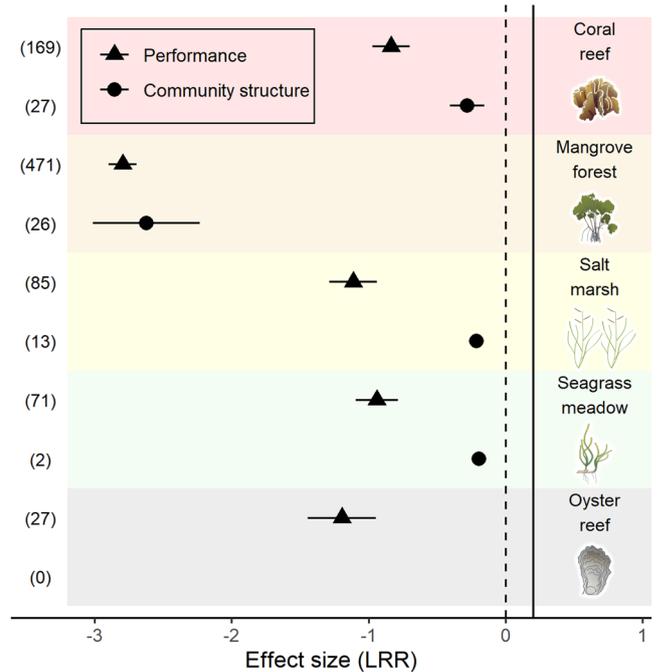


Fig. 3 | Effect sizes (log response ratios, LRR) across two ecological response measures (species performance and community structure or processes) and five coastal marine ecosystems after North Atlantic tropical cyclone landfalls. Values at left are sample sizes. Data are pooled for habitat forming and associated species. Community structure or processes is a nondirectional metric, shown here as negative for visual clarity. Error bars are SEs. Image credits: Integration and Application Network (ian.umces.edu/imagelibrary/).

ecological impacts in the early–mid 2000s and late 2010s coincided with peaks in the frequency of LMI very intense NATC landfalls during those periods (Fig. 1a, d). Indeed, the frequency of LMI very intense NATC landfalls was strongly correlated with the frequency of ecosystem impact reports (GLM: $F_{1,6} = 2.03$, $p < 0.001$, $R^2 = 0.533$), with the possible interpretation that five decades of rise in NATC activity correspondingly led to a rise in impacts (Fig. 1). These data were corrected for research effort by plotting only unique ecosystem landfall events (see Methods).

NATC ecosystem damages

A meta-analysis of quantitative data in the published impact reports, focusing on the severity of immediate post-storm impacts and including all taxa pooled within ecosystems, indicated overall strong negative effects (negative log response ratios) on species performances and community structure or processes, with the strongest negative impacts occurring in mangrove forests (Fig. 3, Supplementary Information Table S1). Of all the unique ecosystem–storm events, 30%, 29%, 15%, 14%, and 11% were from coral reefs, mangrove forests, seagrass meadows, salt marshes, and oyster reefs, respectively. 85% of the reported impacts were to foundation species, while 15% were to associated species. 92% of the reported impacts were to the performance of species, while 8% were to community structure and processes. Linear mixed effects models showed a significant negative relationship between effect size and landfall wind speed for mangrove forests, but not for the other ecosystems (Fig. 4, Supplementary Information Table S2). Inclusion of the linear distance of the storm to the landfall impact site did not improve model fit (additional deviance explained = 0.2%; $\Delta AIC = 12.6$, $\chi^2 = 7.1$, $p = 0.714$).

The storms in these analyses made landfall on average 431 (± 285 SD) km from the location of the recorded ecosystem impact. This demonstrates a geographically wide footprint of TC impacts, consistent with a typical TC outer radius of $> 800 \text{ km}^{41}$. Almost all (95%) of the NATCs causing these impacts were classified as LMI category ≥ 1 , with 74% being classified as

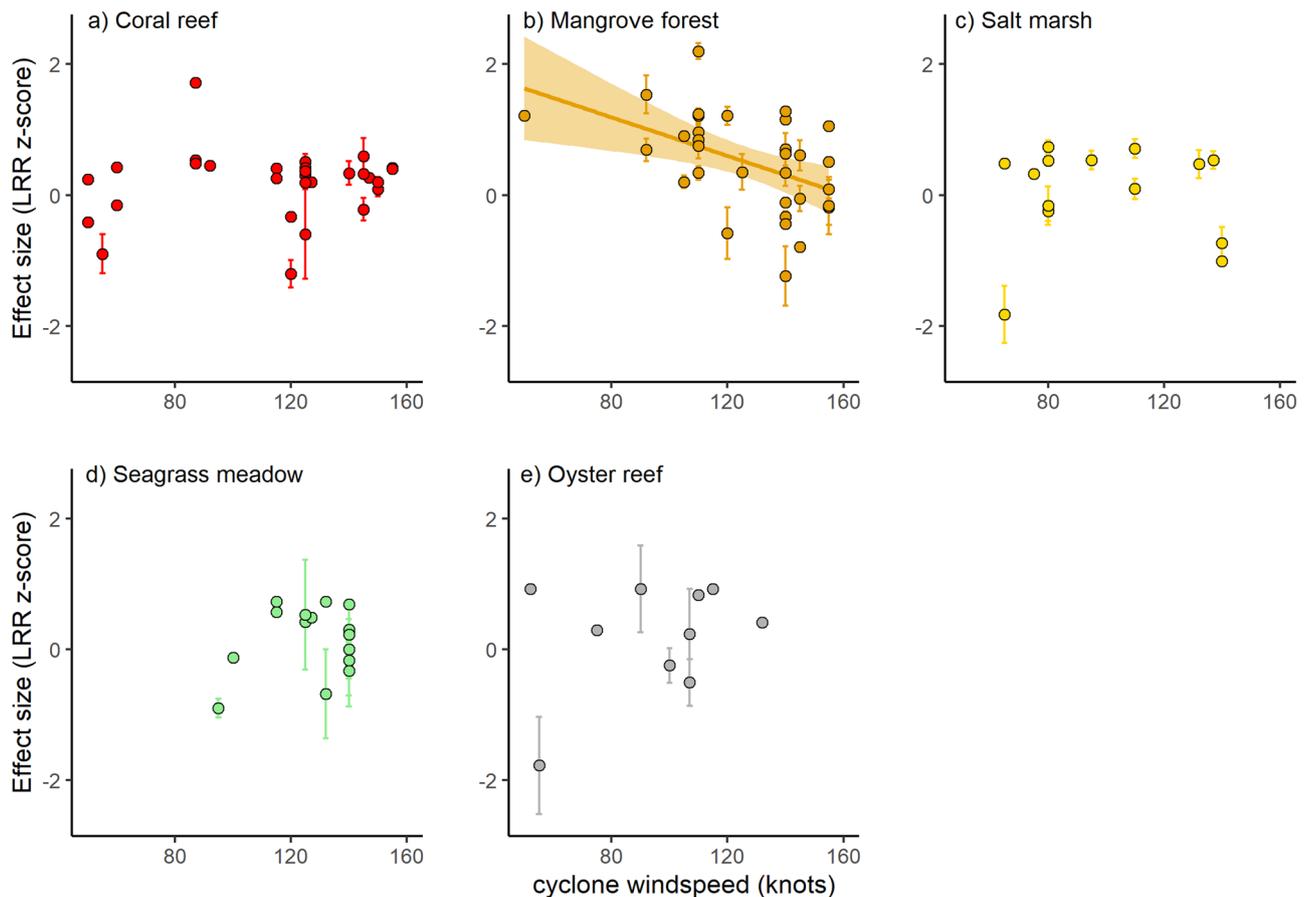


Fig. 4 | Relationships between effect size (log response ratio, LRR, z-score) and landfall wind speed (knots) across five coastal marine ecosystems. Line in (b) is a linear relationship from a linear mixed effects model (Supplementary Information Table S2). Data in (a–e) are z-scores of LRR pooled across measures of performance

and community structure or processes and include both habitat forming and associated species. Three statistical outliers were removed for visual clarity. Error bars are SEs.

LMI very intense NATCs (Fig. 2). An apparent bias towards reporting on LMI very intense NATCs may reflect a tendency for authors to report positive results as compared to negative or null results. Nonetheless, the findings here indicate the potential for strong ecosystem impacts in response to LMI very intense NATCs, and that impacts across mangrove forests scale with NATC landfall wind speeds.

Qualitative assessment of the impact reports indicated that the primary physical drivers of impact reported by study authors varied across ecosystems, with winds reported as the primary driver only in mangrove forests (in support of our regression analyses), while other oceanographic changes caused by TCs were the most reported direct drivers in coral reefs (waves), salt marshes (surge), seagrass meadows (deposition and erosion of sediments), and oyster reefs (salinity changes) (Fig. 5). Furthermore, many studies also reported secondary drivers, e.g., 97 of the 414 impacts in mangroves that were attributed to winds also reported surge flooding as a secondary impact-driver.

Discussion

The repercussions of climate change for coastal marine ecosystems are receiving increased attention, as the role of these ecosystems in sustaining and enhancing human lives and livelihoods has come into sharp focus⁴². Awareness, research, and management of climate-driven stressors and extreme events have grown substantially, particularly evident in the burgeoning research on the consequences of ocean warming and marine heatwaves for marine ecosystems^{29,43}. In contrast, far less climate-change research has investigated the changes and impacts of intense storms on coastal ecosystems. For example, a recent global synthesis of cumulative

anthropogenic impacts on 21,159 marine animal species identifies 13 climate and non-climate stressors but omits TCs⁴⁴. Indeed, unlike the ecological impacts reported for climate change drivers such as incremental warming⁴⁵, marine heat waves⁴⁶, or ocean acidification⁴⁷, there are no analogous quantitative analyses of impacts for altered storm activity. This study uncovers the impacts of rising NATCs across diverse coastal marine ecosystems. Specifically, we found compelling evidence that coastal marine ecosystems, particularly mangrove forests, have been heavily damaged by NATCs, with impacts increasing alongside rising NATC activity. Furthermore, we suggest that trends in NATC impacts from 1970–2019, driven by anthropogenic and natural climate forcing^{4,27,28}, can serve as a warning system for potential future global impacts at 2 °C of anthropogenic warming – a threshold likely to be reached within this century^{48,49}.

Our analyses of standardized effect sizes suggest that the magnitude of impacts can, at least partially, be predicted from attributes of the NATC itself (in particular wind speed at landfall) and the attributes of the impacted ecosystems, such as the identity and traits of the dominant habitat-forming taxon (e.g., being flexible like seagrass or rigid like corals) and whether these organisms are submergent (e.g., corals) or emergent (e.g., mangroves), of marine (e.g., oysters) or terrestrial (e.g., salt marsh) origin, or inhabiting hard (e.g., corals) or sedimentary (e.g., seagrass) substrates. For example, mangrove forest damages were strongly correlated to landfall wind speeds, where the powerful TC winds interact directly with the emergent large and woody vegetation (with high drag), and clear areas of forest by uprooting the loosely buried roots and breaking the rigid mangrove tree trunks^{12,32,50,51}. These findings corroborate earlier studies on mangrove forests, demonstrating a correlation

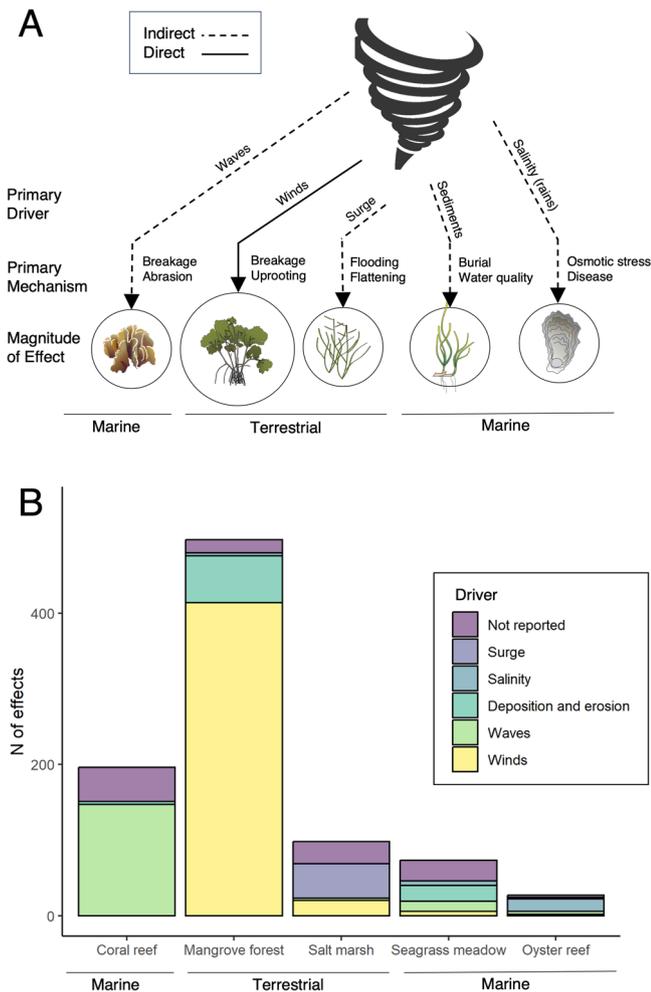


Fig. 5 | Physical drivers of impact. **A** Conceptual diagram showing the primary drivers of impact by tropical cyclones, corresponding impact mechanisms, and magnitude of effects across five coastal marine ecosystems composed of habitat formers that are marine or terrestrial in origin. **B** Frequency (n of effects) of the physical drivers of impact (drivers) reported by individual study authors. ‘Not reported’ indicates no reported physical driver and may include habitat changes. Data are pooled for measures of species performance and community structure or processes and habitat forming and associated species. Image credits: Integration and Application Network (ian.umces.edu/imagelibrary/).

between TC winds and damages^{26,52}, and underscore the vulnerability of mangrove forests to future increases in intense TCs.

Among the other dominant coastal marine ecosystems, impacts did not scale with winds in our analyses. On coral reefs, damages appear to occur primarily by waves (Fig. 5), where breaking waves physically break, abrade, and dislodge large rigid stony corals and their associated species^{20,53,54} – in some instances toppling the largest coral heads, 100 s of years old⁵⁵. Yet, we found that the magnitude of these (wave) impacts were not predicted by the landfall wind speed. Instead, wave generation during TCs often depends on more complex interactions between local and distant storm attributes modified by local bathymetry (e.g., wave-dampening structures)⁵⁶. For example, coastal waves can originate from both local air-sea interactions and distantly generated swell waves⁵⁶. Accordingly, coral reefs can be damaged at distances up to 800 km from the path of a TC²⁴. A recent study has shown that the wave hazard posed by TCs (in terms of the footprint of TC waves) has increased from 1979 to 2022, a rise that may accelerate with future climate change⁵⁷. Thus, we anticipate an increasing risk of future TCs for coral reefs, adding to the plight of coral reefs, already thought to be the most climate-vulnerable marine ecosystem²⁹.

In salt marshes, seagrass meadows, and oyster reefs, direct physical damage from strong winds (or waves), were again of low importance, as these habitat-formers are relatively short (low drag) and flexible (low drag coefficient) (salt marsh and seagrass) or very short (low drag) and rigid (oysters). Instead, more indirect effects associated with storm surge, altered sediments (erosion or sediment burial), and rapid changes to water quality (in particular salinity, but also potentially eutrophic pulses, turbidity, spread of diseases, and hypoxia) were identified as the most important physical drivers of impact, respectively (Fig. 5). In this context, storm surges inundate the marsh habitat, flattening and potentially uprooting marsh grasses^{15,30}, erosion or sediment burial uproot or smother the seagrass habitat^{33,58}, and low salinity associated with strong rainfall causes osmotic stress and susceptibility to diseases and increases oyster mortality^{21,59,60}. There is an expectation that TC rains will increase with warming sea surface temperatures⁶¹, and the joint hazard posed by extreme rainfall and surge also may increase⁶². Increased rains may in turn increase sediment discharge⁶³. These projections suggest a climate-driven rise in TC damages across salt marshes, seagrass meadows, and oyster reefs, yet the magnitudes of these changes remain unknown.

Often coastal marine ecosystems exhibit resilience to TCs, recovering with time following a storm^{16,64}, or display resistance, where damages are superficial, such as the temporary flattening of salt marsh grasses¹⁵. Previous studies across multiple ecosystems provide compelling evidence for an inverse relationship between ecosystem capacity for recovery and resistance to TC damages, indicating a resilience-resistance trade-off that represents two alternate evolutionary strategies: to “rebuild” versus to “resist”^{23,65}. Here, we find that mangrove forests experience the greatest immediate impacts of TCs. Given the potential for additional delayed mangrove mortality from surge flooding, this may represent an underestimate of the magnitude of TC damages to mangrove forests¹⁶. Accordingly, mangrove forests are broadly considered TC “resilient” (rather than resistant) and tend to rebuild with time following damages^{16,64}. Specifically, while larger stature trees are felled and broken by TC winds, smaller trees often survive due to the wind-buffering effects of submergence in storm surge, and these individuals can repopulate the mangrove forest¹⁶. Yet, during very intense (category 4 and 5) TCs, even smaller stature trees are impacted as the buffering effect of surge is overcome by high winds¹⁶. Given that mangrove forest damages scaled directly with landfall wind speeds here, we infer that despite anticipated variation in impacts across global mangrove forests⁶⁶, future global increases in the most intense TCs may compromise mangrove forest resilience. Other stressors, such as altered hydrodynamic conditions, may further compound these impacts^{16,67}. Already, 45% of global mangrove forest loss due to natural causes since the 1960s has been attributed to TCs⁶⁸. We posit that other marine ecosystems, which appear to have higher resistance to TC damages (less negative LRRs), would be at risk under future TC activity if immediate post-storm damages rise, given their lower capacity for recovery. Notably, evidence for ecosystem regime shifts in response to TCs in some marine ecosystems (e.g., coral to macroalgal dominance⁶⁹; mangroves to mudflats⁷⁰), indicates the potential to move beyond the capacity of ecosystems to respond to stressors, with long-term changes in ecosystem structure following these extreme events that are difficult to reverse⁷¹.

While maximum sustained wind speed is considered the standard metric of TC intensity², we found that landfall maximum sustained winds only predict the level of damage for one of five coastal marine ecosystems studied. This metric could be representative of the maximum winds anywhere within the storm at a given time and may be located far from particular study sites, highlighting a limitation of this metric for assessing future risk to ecosystems. Regardless, it appears that maximum sustained winds are a strong predictor of ecosystem damages only in cases where the physical driver of impact is related directly (i.e., mangrove trees downed by winds) to winds. Maximum sustained winds at landfall did not predict damages in cases where the physical impact-driver is typically linked to other storm attributes, such as distantly generated waves (coral reefs) and storm surges (salt marshes), sediment erosion/burial (seagrass meadows), and intense rainfall or elevated riverine flow (oyster reefs). Given the range of

mechanisms by which TCs affect ecosystems, and the complex role of TC attributes in determining these biological changes (Fig. 5), high-resolution quantification of the magnitude of drivers at study sites (e.g., winds, waves, surge, sediments, and salinity), their resultant mechanisms of biological effects (e.g., abrasion, burial, disease), and the response at the ecosystem level (e.g., population collapse or regime shifts) is required. Other measures of storm intensity, such as the power dissipation index (PDI) and accumulated cyclone energy (ACE)⁷² may warrant consideration. Pairing detailed biological sampling with existing physical models of coastal storm changes would act to leverage and improve current capacities to better predict TC damages and develop ecosystem management and climate change adaptation plans.

A number of data gaps were identified that should be filled to improve the spatial and temporal resolution of future predictions of TC ecosystem damages. Firstly, our literature search revealed that TC impact research on kelp forests is sparse with only two studies in the North Atlantic^{17,73}. This precluded the analysis of TC impacts to kelps, which form one of the most globally extensive coastal marine habitats^{29,74}. Both studies reported significant impacts to kelp forests across multiple TCs by defoliating kelps¹⁷ and modifying grazing dynamics⁷³. An increased emphasis in TC research on temperate marine ecosystems could become relevant as TCs continue to undergo poleward expansion with global warming⁷⁵. Secondly, reports of community level responses to TCs were relatively rare (only 8% of reported impacts), yet these data will be critical for understanding broader ecosystem changes such as regime shifts. Ongoing temporal data collection on TC ecosystem damages, both globally and in the well-studied North Atlantic, across many storm events and biological response variables, will improve the potential for high-quality temporal regression analysis in future studies. Finally, future data collection should include measurement and reporting of data variability so that weighted meta-analysis will become possible, improving the robustness of statistical analyses, as only 23% of data values extracted here had an associated variance value. With these improved data, future studies can begin to develop multiple predictive relationships across marine ecosystems for real-time impact assessment and management.

Given the potentially devastating consequences of marine habitat loss for ecosystems and people¹ and the critical need to develop strategies to enhance ecosystem resilience for human lives and livelihoods⁴², the NATCs studied here provides a critical warning system for future TC impacts. Our overlying findings – that across ecosystems TCs yield overall negative immediate effects (particularly in mangrove forests), that wind speeds drive damages in only one type of coastal ecosystem, and finally, that future increases in TC activity may yield significant negative effects, globally – provide a glimpse into a future where extreme events are a more fundamental driver of ocean change. Better knowledge of the specific drivers and mechanisms of TC ecosystem damages (e.g., Fig. 5) will improve our ability to manage and enhance ecosystem resilience to TCs. This should include directly targeting local stressors shown to amplify TC damages (e.g., sedimentation, hydrological dynamics, and disease). Given the high magnitude of impacts to mangrove forests and direct response of this ecosystem to TC intensities (which are anticipated to rise at a global scale³), management of mangrove forests for resilience is a high priority. Yet, our analyses imply that a potential rise in TC frequency at a global scale³ may alone increase damages across coastal marine ecosystems, even in the absence of direct intensity-damage relationships. Hence, management for resilience across coastal marine ecosystems is likely needed to weather the storm of rising TC impacts.

Materials and Methods

North Atlantic tropical cyclone trends

To assess how the recent rise in North Atlantic tropical cyclone (NATC) landfall activity generally relates to the predicted rates of change in similar global metrics at 2 °C of anthropogenic warming³, we first analyzed best-track data for the North Atlantic basin from IBTrACS (Version 4.0)^{76,77}. These data include wind intensity (knots), TC category (Saffir-Simpson scale categories < 1–5), and geographic position at 6-hour intervals (0, 6, 12,

and 18 UTC) throughout each storm's lifetime, with higher frequency tracking at landfall (3 h intervals). The 3–6 h interval data are commonly referred to as “fixes”. NATC category is determined based on the lifetime maximum intensity (LMI) of the storm, where storms with ≥ 64 knot winds are considered category 1 or higher storms, and NATCs with an LMI of ≥ 113 knots are considered category 4–5 storms and termed “very intense” (after ref. 3). LMI is defined as the maximum category reached in the lifetime of the storm. For example, where a storm reached category 4 in any of the fixes in its lifetime, it is categorized as a category 4 NATC.

NATC landfall trends were examined from 1970–2019. We defined landfalls as fixes with a storm center less than 60 nautical miles from a coastline, including all continents and any islands larger than 1400 km², as per IBTrACS documentation. A storm with a center within 60 nautical miles of a coastline is considered very likely to impact the coast^{76,77}. We plotted three types of time-series: the annual frequency (count) of very intense NATCs that made landfall, the annual fractional proportion of very intense NATCs that made landfall (numerator: annual count of LMI category 4–5 NATCs that made landfall; denominator: annual count of LMI category 1–5 NATCs that made landfall), and the wind speed at landfall of all category 1–5 NATCs. Frequency and proportion time-series are plotted as triads (3-y bins; after ref. 27), except for the final datapoint which includes the years 2018 and 2019. The decision of whether to pair the two data points at the end or beginning of the time series did not considerably alter the trends. The remaining triads include: 1970–1972, 1973–1975, 1976–1978, 1979–1981, and so forth (using different bins did not change the results, unpubl. analyses).

We tested for monotonic increases in the time-series with nonparametric Mann-Kendall tests with the R package *kendall*⁷⁸. Slopes of the time-series were calculated with Theil-Sen regression with the R package *mblm*⁷⁹. Theil-Sen regression, also known as “robust regression”, provides a non-parametric alternative to ordinary least-squares regression, and is insensitive to outliers and heteroscedasticity⁷⁹.

We calculated a historical climatology for each of the three time-series as the median value over the baseline period of 1986–2005 (after ref. 3). From this baseline, we directly applied a median and maximum percent change taken from the high-resolution global models for similar global storm metrics at 2 °C of anthropogenic warming in Knutson et al.¹³. (the global frequency of very intense TCs, 30% and 105% increase, respectively [low confidence]; the global proportion of very intense TCs, 13% and 120% increase, respectively [high confidence]; and the global maximum surface wind speeds, 5% and 10% increase, respectively [high confidence]).

Literature search and data extraction

To identify studies that reported short term ecological impacts following NATCs, we conducted a systematic literature search of article titles in Web of Science. We focused the search on coastal marine ecosystems that dominate tropical, subtropical, and temperate coastlines globally²⁹: coral reefs, mangrove forests, salt marshes, seagrass meadows, kelp forests, and oyster reefs. Search strings included hurricane* or cyclone* or “tropical storm*”, in combination with coral*, or mangrove*, or marsh*, or alga*, or macroalga*, or kelp*, or macrophyte*, or seagrass*, or eelgrass*, or “submerged aquatic vegetation”, or seaweed*, or oyster*. Titles of articles were searched in Web of Science, as many early articles do not have digitized abstracts, and therefore searching abstracts as well as titles would bias the results toward later publication years. The search was conducted on or around 29 July 2021, covering years up to 2020. The ecological literature was analyzed through 2020 rather than through 2019, as occurred for the physical analysis described above under *North Atlantic Tropical Cyclone Trends*, to account for a lag between NATC landfall and publication.

A total of 248 articles were retrieved in the literature search (Supplementary Information Fig. S2). Only 1 and 6 records were returned for kelp forests and oyster reefs, respectively, so a more detailed but qualitative ‘expert search’ was conducted to ensure that no studies were missed, which returned 1 additional report for each ecosystem. Each article was read in detail, and studies were excluded that were not reporting ecological

responses to NATCs (e.g., studies from the Pacific Ocean, modeling studies of simulated storms, and geophysical studies). We identified a total of 109 relevant articles reporting an ecological response to a NATC; 80 articles reported quantitative responses: 22 for coral reefs, 26 for mangrove forests, 13 for seagrass meadows, 13 for salt marshes, 7 for oyster reefs (1 from the additional expert search) and 2 for kelp forests (1 from the additional expert search) (Supplementary Information Fig. S2). Given the limited studies on kelp forest responses to NATCs (2 total; both authored by the present investigators), we did not analyze these effects.

From each study, we extracted data on (1) the type of ecosystem(s) impacted, (2) the year of the impact(s), (3) the causative storm name(s), (4) the geographical region(s) and approximate latitude and longitude of the study site/region, (5) depth (where appropriate), (6) whether there were co-occurring stressors (e.g., nutrient loading), (7) the linear spatial extent of observations (10 s m, 100 s m, or kms), (8) the taxa affected (all taxa including foundation species and associated flora and fauna were included), (9) the date of observation before and after the impact, (10) the type of metric measured (e.g., growth, abundance, density), (11) the mean, measure of error, and sample size for control (pre-storm) and impact (immediate post-storm) values (as available), and (12) the primary physical driver of impact interpreted by the study authors. Drivers were classified into winds, waves, sediment deposition or erosion, salinity changes, surge or other. The 'other' category included habitat loss and studies with no physical driver reported. We considered impacts of the same NATC to different marine ecosystem types (e.g., coral reefs and seagrass meadows) as independent events. We also considered the impacts of the same NATC to the same ecosystem type but in broadly different geographical locations or reported by different authors as independent events. We retrieved a total of 97 TC landfalls, here considered independent events. Within these independent landfalls there were 891 post-storm impact data points. Co-occurring stressors (e.g., nutrient enrichment, urbanization, or bleaching) were reported for a total of 21%, 8%, 18%, 23%, and 0% of coral reef, mangrove forest, salt marsh, seagrass meadow, and oyster reef impact observations, respectively. Given the potential for delayed mortality, particularly in mangrove forest ecosystems¹⁶, the magnitude of impacts may be underestimated in some cases.

To examine general temporal patterns in NATC landfall activity from the literature reports, we plotted the total number of unique NATC landfalls reported in each year from 1970–2019 for each ecosystem, to align with the best-track data time series. Given that NATC activity is mediated in part by the Atlantic Multidecadal Oscillation (AMO)⁴, more recently referred to as the Atlantic Multi-decadal Variability (AMV)⁴⁰, we also determined whether anomalies were positive or negative for each year based on the yearly average retrieved from the National Oceanic and Atmospheric Administration's (NOAA) Physical Sciences Laboratory⁸⁰. To establish a dataset of matching ecological impact and physical data, we cross-referenced the storm names, years, and locations of impact (latitude and longitude) from each study with IBTrACS and extracted for each ecological impact the LMI of the storm (e.g., category 1–5), landfall storm category and wind speed (knots), and landfall location (latitude and longitude).

Effect sizes and statistical analysis

Log response ratios (LRR) were calculated from reported mean control (\bar{x}_c , i.e., immediate pre-storm) and mean impact (\bar{x}_i , i.e., immediate post-storm) values extracted from the ecological studies as: $LRR = \ln(\bar{x}_i/\bar{x}_c)$. Immediate pre- and post-storm values were defined as the last recorded observation before and the first recorded observation after the storm. It was assumed that the authors of each study selected relevant immediate pre- and post-storm timeframes to document impacts for a particular ecosystem, taxon, and ecological response type. All pre-storm and post-storm observations were within 90 and 20 months of landfall (respectively), with a median of 4 and 3 months from landfall (respectively) (95% of all pre-storm observations occurred within 34 months of landfall). We used an unweighted effect size because measures of variance were not available for 77% of the control and mean values extracted.

Effect sizes were calculated for two categories of ecological responses: "species performance" and "community structure or processes". Species performance includes organism and population level metrics such as condition, cover, count, productivity, growth, mortality, recruitment, greenness, weight, density, size, volume, abundance, frequency, and area. Community structure or processes includes community and ecosystem level metrics such as species richness, indices of diversity, number of food web nodes, and carbon stock. Where ecological responses had clear directionality (performance measures only), we ensured that the direction of change reflected the direction of impact (e.g., an increase in mortality was assigned a negative effect size, while an increase in abundance was assigned a positive effect size). For community structure or processes, we assessed the magnitude but not the direction of impact.

For the mortality response variable, pre-storm rates of mortality often were not reported. Therefore, where authors reported mortality as related directly to a storm (e.g., newly downed trees in a mangrove forest or recently toppled corals on a coral reef), we assumed a mean pre-storm value for mortality of zero. Where either the pre- or post-storm value were zero, and therefore a natural log could not be calculated, we added a small constant (0.001) to the zero values (varying this constant between 0.01 or 0.0001 did not affect our general results). Where both the pre- and post-storm values were zero, the effect size was assigned as zero.

To test for a statistical relationship between ecosystem type and LRR, we used a linear mixed effects model that tested the effect of 'ecosystem type' (coral reef, mangrove forest, seagrass meadow, salt marsh, and oyster reef) on the LRR effect size using z-scores of the performance and community measures pooled, and where unique combinations of 'storm' for each ecosystem type was the random effect (*nlme* package in R). To examine the relationship between effect size and the intensity of a storm, we plotted LRR (z-scores) against landfall maximum sustained wind speed (knots) for each independent landfall in each ecosystem. Where sequential storms impacted an ecosystem (13.6% of observations), the greater of the landfall wind speeds was used in the model. Inclusion of the linear distance of the storm to the landfall impact site did not improve model fit (additional deviance explained = 0.2%; $\Delta AIC = 12.6$, $\chi^2 = 7.1$, $p = 0.714$). Residuals were examined graphically for normality, linearity, and fit.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data are publicly accessible at <https://doi.org/10.6084/m9.figshare.27316113.v1> (ref. 81).

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Author contributions

Designed research: C.J.F., K.F.D., M.S.T., T.W., T.M., Performed research: C.J.F., K.F.D.; Analyzed data: C.J.F., K.F.D.; Wrote paper: C.J.F., K.F.D., M.S.T., T.W., T.M.

Competing interests

The authors declare no competing interests.

Additional information

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