A Research Framework to Integrate Cross-Ecosystem Responses to Tropical Cyclones

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Tropical cyclones play an increasingly important role in shaping ecosystems. Understanding and generalizing their responses is challenging because of meteorological variability among storms and its interaction with ecosystems. We present a research framework designed to compare tropical cyclone effects within and across ecosystems that: a) uses a disaggregating approach that measures the responses of individual ecosystem components, b) links the response of ecosystem components at fine temporal scales to meteorology and antecedent conditions, and c) examines responses of ecosystem using a resistance–resilience perspective by quantifying the magnitude of change and recovery time. We demonstrate the utility of the framework using three examples of ecosystem response: gross primary productivity, stream biogeochemical export, and organismal abundances. Finally, we present the case for a network of sentinel sites with consistent monitoring to measure and compare ecosystem responses to cyclones across the United States, which could help improve coastal ecosystem resilience.

Keywords: hurricane, typhoon, cyclone, research framework, ecosystem response.

Coastal regions are home to over 40% of the global population, 21 of the world's 33 megacities, and more than 77% of global economic output (Martínez et al. 2007, United Nations Department of Economic and Social Affairs 2014). The proportion of the world's population living in coastal areas is predicted to increase to 75% by 2025 (Crossett et al. 2013). This large coastal population will face many challenges associated with climate change in the next century, including stronger tropical cyclones (IPCC 2013). Since 1900, over $179 billion in damages and approximately 874,000 deaths across the globe have been attributed to tropical cyclones (Costanza 2008). However, these costs can potentially be mitigated by managing ecosystems and connected human infrastructure for increased resistance and resilience to storms (Grimm et al. 2017, Gaiser et al. 2020). As human populations continue to grow disproportionately in coastal areas (Crossett et al. 2013), the reliance on ecosystem services (i.e., coastal vegetation, freshwater drainages, and natural areas) that buffer the effects of tropical cyclones is increasing (Martínez et al. 2011). Therefore, there is an urgent need to better understand how variation among tropical storm events affects natural, urban, and coupled natural–urban ecosystems.

Tropical cyclones (hurricanes and typhoons) are extreme weather events that affect coastal systems through direct and indirect perturbations from high winds, heavy precipitation, storm surge, saltwater intrusion, and flooding (Paerl et al. 2001, Wetz and Yoskowitz 2013). Global climate models predict that the intensity of these extreme weather events will increase in the tropics and subtropics over the coming decades and affected areas will expand in size over the next century (Webster et al. 2005, Mann and Emanuel 2006, Elsner et al. 2008, Sobel et al. 2016, Emanuel 2017, Altman et al. 2018). Undoubtedly, such an increase in tropical cyclone intensity and geographic breadth will increase their influence on natural ecosystems and human systems

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*Figure 1. (a) A wall more than 3 meters tall of coarse wood debris deposited ashore a montane reservoir in southern Taiwan by high winds and extreme rainfall of Typhoon Morakot (August 2009). Typhoon Morakot was the deadliest typhoon to affect Taiwan in modern recorded history. Photograph: Chung-Te Chang. (b) Aerial photograph of a coastal Puerto Rican stream in the weeks following Hurricane Maria (September 2017). Brown hydrological flow shows the export of sediment, organic matter, and nutrients from a disturbed watershed. Photograph: William H. McDowell. (c) Aerial photo of the impact of Hurricane Michael (October 2018) at the Jones Ecological Research Center in Newton, GA. Many pines were tipped over and uprooted by high-speed winds. Photograph: Scott Taylor. (d) Exposed seagrass (***Thalassia testudinum***) rhizomes in the Florida Keys National Marine Sanctuary, Florida, following Hurricane Irma (September 2017). The storm surge, wave action, and strong currents created by Hurricane Irma disturbed the seafloor, creating erosion fronts and exposing seagrass rhizomes as sediments were sheared away. Photograph: Sara Wilson.*

(Lugo 2020). Tropical cyclones are not the only large-scale wind and water storms; gales occur in temperate zones, and derechos (i.e., blowdowns) occur in the Amazon and elsewhere. Studying the factors that modulate tropical cyclone effects on ecosystems is thus important for informing disturbance ecology more generally.

The influence of tropical cyclones on ecosystems is complicated, in part because of the substantial variation among storms in terms of size, wind-speed intensity, movement, and rainfall (Merrill 1984, Knapp et al. 2010, Ritchie et al. 2012, Wetz and Yoskowitz 2013). Topography, landscape exposure, and aspect interact with winds and precipitation to determine effects on local habitats and create spatial heterogeneity in storm damage (White and Pickett 1985, Morton and Barras 2011). Extreme rainfall and flooding cause material export across the terrestrial landscape and into coastal aquatic ecosystems (figure 1a; Villarini et al. 2011, Woodruff et al. 2013, Paerl et al. 2018). Winds damage natural and human-built environments, contribute pulses of organic matter and nutrients to waterways, and alter habitat structure (figure 1b, 1c; Armentano et al. 1995, Everham and Brokaw 1996, Adger et al. 2005, Laurance and Curran 2008). In upland forested watersheds that are damaged, increases in stream nutrient concentrations can be observed for years to decades, depending on lithology (McDowell et al. 2013), and watershed hydrology can be altered (McDowell 2011). Storm surge introduces large amounts of saltwater to coastal freshwater and terrestrial ecosystems physically disrupting benthic and coastal terrestrial habitats (figure 1d; Mallin et al. 1999, Smith et al. 2008), and can damage fisheries (Sainsbury et al. 2018). Storm surge can also cause rapid changes in coastal geomorphology because of erosion or deposition processes, affecting coastal hydrology, ecosystem productivity and biogeochemical cycling (Cahoon et al. 2003, Smoak et al. 2013, Feagin et al. 2015), which often leads to mortality or displacement of biota (Steneck et al. 2019, Radabaugh et al. 2019).

The effects of tropical cyclones on ecosystems interact with other disturbances and stressors at variable spatiotemporal scales to generate complex and novel responses across landscapes (Dale et al. 2001, Lugo 2008, Peters et al. 2011, Johnstone et al. 2016). For example, damage due to tropical storms accelerated the long-term decline in Caribbean coral reef cover from 2% to 6% (Gardner et al. 2005). Similarly, the structural damage caused by high-speed winds is amplified by the fragmentation of tropical forests (Laurance and Curran 2008, Schwartz et al. 2017), and long-term cyclone return frequencies are hypothesized to explain some of the differences in forest structure and canopy height throughout the tropics (de Gouvenain and Silander Jr. 2003, Hogan et al. 2018, Ibañez et al. 2019, Simard et al. 2019). Cyclones can also result in shifts in ecosystem states (*sensu* Scheffer et al. 2001). Aquatic ecosystems may transition from net autotrophy to net heterotrophy (Klug et al. 2012, Van Dam et al. 2018), because of an influx of suspended sediment and organic matter that limits light availability and alters system biogeochemistry (Russell and Montagna 2007, Wetz and Yoskowitz 2013, Geyer et al. 2018). Suspended sediment and organic matter inputs can also create secondary, indirect effects such as hypoxia (Paerl et al. 1998), whereas added nutrient inputs can amplify storm damage to ecosystems and decrease their resistance and resilience (Feller et al. 2015).

The complexity of responses to tropical cyclones suggests that a major synthesis and measurement campaign is needed to reconcile responses across tropical cyclone-affected ecosystems and develop a framework for predicting future impacts. To expand on individual cyclone case studies and incorporate the variance in storm impacts across complex landscapes, a unified research framework is required. In the present article, we present a framework to facilitate the analysis and comparison of storm effects within and among ecosystems and coupled human–natural systems.

Research framework: Comparing cross-ecosystem effects of tropical cyclones

Studying tropical cyclone disturbances in a synoptic way that measures the multitude and variability of ecosystem responses is challenging. We use a disaggregating approach (Peters et al. 2011), in which ecosystem responses are broken down into individual components (e.g., leaf area index, species abundance, biomass, nutrient concentration) during these discrete disturbance events. We build on the general disturbance model of Peters and colleagues (2011), operationalizing it for cross-system comparisons of response to cyclone disturbance. Analyzing the responses of individual ecosystem components maximizes the potential to compare the variation in response, both within and among storms and across the landscape. In addition to characterizing individual components of the ecosystem response, we also propose a conceptual approach that disaggregates the meteorological attributes of tropical cyclones (i.e., storm surge, wind speed, rainfall, and storm duration and size), such that the response of ecosystem components to individual storm events can be placed in a resistance–resilience framework (figure 2).

This framework uses an ecosystem approach to link the response of a single variable that is measured repeatedly at fine temporal resolution (weeks to months) to storm strength, which is measured by meteorological attributes (e.g., wind speeds, rainfall, storm surge). This approach is recommended because not all tropical cyclones are the same; in fact, there is a large degree of variation among them. For example, Hurricane Harvey (August 2017) made landfall in Texas as a category 4 storm with winds of 130 miles per hour (mph; 209 kilometers per hour) but slowed tremendously and stalled because of high wind shear to create heavy rainfall and flooding in the Houston, Texas metro area (Emanuel 2017). In contrast, Hurricane Irma (September 2017), which made landfall in Florida also as a category 4 storm with 130-mph winds, was a faster moving, larger storm, which caused quite different effects. The storm surge from Hurricane Harvey was 1 meter (standard error = 0.33) for most of the Houston area, with rainfall over 150 centimeters (Blake and Zelinsky 2017), whereas storm surge from Irma was greater than 1 meter and as high as 3.5 meters for the majority of South Florida, but the precipitation totals were approximately 50 centimeters (Cangialosi et al. 2018). Within our framework, important distinctions among storm characteristics, and other contributing factors related to the environment can be considered and linked to differences in storm impacts. Linking storm characteristics and additional environmental factors that modulate ecosystem response across and within more cyclone disturbances should help develop new theoretical insights.

Our research framework (figure 2) makes use of several ecological concepts (box 1), which we define in mathematical terms useful for quantitative analyses. Qualitatively, there are large disparities in the definitions of the ecological concepts presented in box 1 among the scientific community. In the present article, we provide unambiguous quantitative definitions that can be used to assess change in any ecosystem component over time and in association with one or more tropical cyclones. We propose that each cyclone be

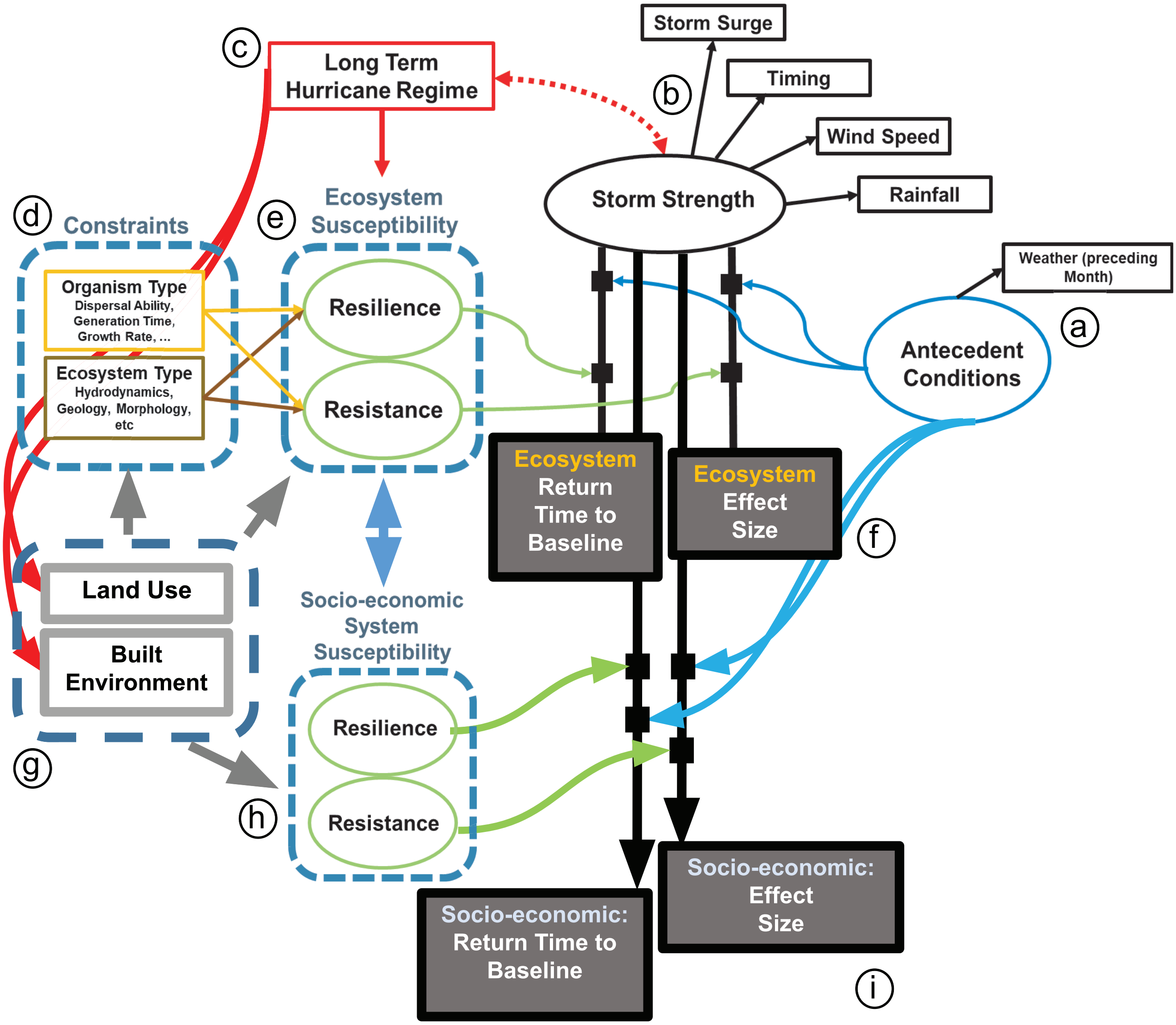

Figure 2. A research framework for evaluating the response of a single ecosystem component to cyclone disturbance. The framework applies to the use of a data time series for a single species abundance (e.g., bird or fish abundance), biogeochemical variable (e.g., stream nitrate), or another univariate ecosystem component (e.g., litterfall, biomass, percent vegetation cover, etc.). The boxes represent observed variables that are measurable, whereas the ovals represent latent variables, which are not directly measurable. The dashed, double-headed arrows represent covariances, whereas solid lines with arrows show direct causal links. The recent weather history of the site and an understanding of the historical (c) and present (i.e., antecedent) state of the ecosystem (a), and meteorological data from the tropical cyclone (b), are inputs into the framework. The green ovals represent ecological resistance and resilience (see box 1), which are directly influenced by the long-term hurricane disturbance regime (c) and ecosystem and organismal constraints (d) to control the magnitude of the response in an ecosystem component of interest (f). The human dimension (g and h) is also influenced by the long-term hurricane disturbance regime and interacts with the natural ecosystem to control the socioeconomic resistance and resilience of coupled human–natural systems, which can be quantified in the same manner as ecosystem variables using effect size and return to baseline intervals for socioeconomic variables of interest (i).

treated separately within the research framework, although any effects of previous disturbance may be considered, depending on their contextual significance. The research framework begins with knowledge of the recent climatological history of the study area that sets the environmental context for the antecedent conditions of the ecosystem (figure 2a). The historical tropical cyclone disturbance regime (figure 2c) and the meteorology and strength of the tropical cyclone of interest (i.e., the disturbance event) are inputs to the framework (figure 2b). Each tropical cyclone

Box 1. Defined terminology.

Antecedent conditions. The variable ecosystem condition that may change over the short term (i.e., months to years) prior to disturbance, encompassing the natural variability in ecosystem state over time. For example, soil moisture, water salinity, photosynthetic active radiation, etc. Given that we may not always have decades of data on ecosystem dynamics, we can attempt to represent that natural variability in ecosystem state by quantifying the antecedent conditions when we make cross-system comparisons.

Constraints. Immutable characteristics of the ecosystem and its constituent biota that do not vary over the short term (i.e., months to years) prior to disturbance. These encompass factors that limit the possible extent of ecosystem response—for example, the geomorphology of a basin, the mean generation time of organisms in the ecosystems, etc.

Baseline. The long-term (at least 1 year) average predisturbance value of a measurable ecosystem component (β). The baseline value should encompass any seasonal variation. The standard deviation of the baseline is also informative with respect to measurement variation.

Resistance. The capacity of an ecosystem to resist physical damage from tropical cyclone disturbance and remain unchanged (Connell and Souza 1983, Odum 1988, Volker and Wissel 1997). Within the research framework, resistance is quantified by the maximum magnitude of the deviation in a measurable ecosystem component from the baseline following, and because of, the disturbance event (α).

Resilience. The capacity of and rate at which an ecosystem returns to predisturbance conditions following a tropical cyclone (Holling 1973, Scheffer et al. 2001). Alternatively, the degree of disturbance an ecosystem can sustain without changing ecosystem organizational processes (i.e., undergoing a state change; Peterson et al. 1998, Folker et al. 2004). Within the research framework, resilience is quantified as the return interval of a measurable ecosystem component to the baseline following disturbance.

Effect size. The relative amount of change in the measurable ecosystem component following disturbance. The effect size can be expressed in terms of a log-response ratio calculated as the natural logarithm of the deviation of the baseline value divided by the baseline value or $\log\frac{\alpha}{\beta}$ (figure 3). Note that the effect size is negative when $\alpha < \beta$ (i.e., when the measurable ecosystem component decreases because of disturbance).

has a set of unique and quantifiable meteorological attributes (i.e., timing, duration, trajectory, wind speed and variability, amount of rainfall, height of storm surge; figure 2b). The storm interacts directly with the ecosystem, and its effects depend on the ecosystem and organismal constraints, which largely determine the extent to which energy, water, and matter can move into and out of the ecosystem.

On evolutionary timescales, the long-term disturbance regime has already shaped the ecosystem attributes and the organisms present in an ecosystem (Lugo 2008, Hogan et al. 2018, Ibañez et al. 2019). This set of ecosystem attributes, which is relatively stable over time, acts as a constraint on the limits of ecosystem response to disturbance (box 1, figure 2d). The long-term historical hurricane disturbance regime and the immediately antecedent conditions of the ecosystem interact to determine the susceptibility of the ecosystem at the time of the disturbance (figure 2e), which is linked to the average susceptibility of the ecosystem via the long-term disturbance regime. Therefore, the immediate antecedent conditions, which are more variable over time than constraints, function within the lifespan of an ecosystem component of interest (e.g., vegetation percent cover, population size, etc.; box 1). In addition, the ecosystem susceptibility (figure 2e), in terms of resistance and resilience to tropical cyclone disturbance, is constrained by various ecosystem attributes (figure 2d; e.g., hydrology and drainage network, geomorphology and grain size of sediments, biogeochemistry, canopy structure, etc.). Similarly, organismal traits such as dispersal ability, generation time, and functional differences among species will constrain the temporal trajectory of the responses of the ecosystem components following disturbance. Organismal traits interact with the attributes of the ecosystem as the ecosystem reorganizes and recovers from the disturbance event along a successional trajectory.

Empirically defining baseline ecosystem conditions (see box 1) is a crucial first step in quantifying disturbance effect. The direction and magnitude of the recovery can be understood from the perspective of ecological resistance and resilience (Peterson et al. 1998, Folker et al. 2004). Disturbance effect can be quantified for a single ecosystem component in terms of the magnitude of change from baseline or the effect size, because of disturbance. This represents a measure of resistance. Similarly, the recovery of an ecosystem can be measured with return time to baseline conditions of an ecosystem component after a disturbance, a measure of resilience (figure 2f, figure 3). The research framework tests the hypothesis that the return time to baseline and the effect size are conditional on the antecedent conditions of the ecosystem, such as the state of ecosystem development (*sensu* Odum 1969), the extent of resource limitation, or the presence of other ecosystem stressors such as drought or fire. Return time and effect size can also interact; for example, if disturbance induces a very large deviation from the historical baseline, it may cause an ecosystem state change, wherein the component may take a very long time to return to baseline, if at all. In

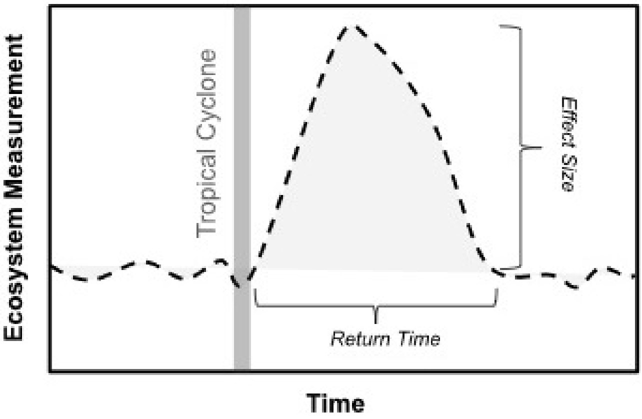

Figure 3. Illustration of the response of a time series of a single ecosystem attribute to tropical cyclone disturbance (figure 2f). Following a tropical cyclone, the magnitude of the deviation of the attribute from its long-term baseline is the effect size or a measure of the ecosystem's resistance to disturbance. The amount of time it takes for the measured ecosystem attribute to return to its baseline level represents the ecosystem's resilience to disturbance (see box 1).

addition, the framework can identify ecosystem tipping points (Scheffer et al. 2001), as is reflected in the recovery time. In theory, if an ecosystem undergoes a state shift with respect to a single ecosystem component, the time needed to return to baseline approaches infinity. The value in treating the return time to baseline and effect size as separate ecological response variables that measure resilience and resistance, respectively (see box 1), lies in the ability to decouple their response to disturbance and examine them in context of the research that is being conducted (i.e., by relating them to the other parts of the research framework).

In many coastal systems, the human-built environment is highly integrated into the ecological environment. The research framework can be extended to encompass how the human-built environment interacts with natural ecosystems. Like ecological systems, the long-term hurricane regime (figure 2c), the land-use type and the state of the infrastructure it contains (figure 2g) will significantly influence the socioeconomic susceptibility of coupled human–natural systems to cyclone disturbance (figure 2h). The susceptibility of the system interacts with storm strength to affect socioeconomic system resistance (i.e., effect size) and resilience (i.e., return to baseline; figure 2i).

Framework examples: Marsh productivity, stream nitrate, and fish abundance

The framework presented in the present article is not only an organizational approach to help guide the research on the causes and effects of tropical cyclone disturbances but may also be used to analyze ecosystem data in the context of disturbance ecology. We illustrate the utility of the framework by applying it to three commonly measured ecosystem response variables: gross primary productivity (GPP), watershed biogeochemical export, and organismal abundances.

The GPP of an ecosystem is a summary metric that we might expect to vary as a function of the disturbance size and intensity (Najjar et al. 2018). A reasonable first proposition is that the magnitude of the effect size is dependent on the seasonal timing of the disturbance. For example, Hurricanes Katrina, Gustav, and Isaac all hit a Louisiana salt marsh site (figure 4a left panel) near the peak of the tropical cyclone season, with respective strike dates of 29 August 2005, 1 September 2008, and 28–29 August 2012. The GPP dropped precipitously immediately after each storm, decreasing by about 3 grams of carbon per square meter per day, and remained below the seasonal average until winter plant senescence. In contrast, Superstorm Sandy hit a New Jersey salt marsh (figure 4a middle panel) after senescence had already begun on 29 October 2012, and the GPP did not noticeably decrease from the baseline because the growing season had ended.

Another reasonable proposition is that antecedent conditions or location of the ecosystem affect the time it takes an ecosystem to return to baseline. In each of the storms mentioned above, GPP had recovered to the baseline by the time that plants emerged from senescence in the following spring. In each case, GPP was within the standard deviation from the baseline (assessed using 16-day cumulative productivity from 2000–2018). However, in the unique case of Hurricane Ike on the Chenier Plain of Texas (figure 4a right panel), the GPP fell below the baseline for the entirety of the following year. During Ike (13 September 2008), hundreds of square kilometers of wetlands in this area were inundated by a surge of approximately 6.5 meters in height, with saltwater penetrating over 20 kilometers inland (Williams et al. 2009). The flooding waters drained relatively slowly because of impoundments, levees, and low topographic relief. Abnormally high salinities severely depressed plant growth. Comparing Ike versus Katrina, Gustav, and Isaac, we can see initial evidence that the GPP recovery time was likely related to the degree of salt stress to the plants. Relatively fresher antecedent conditions both preselected the species and preconditioned their plastic responses to saltwater inundation, and both mechanisms likely affected the longer recovery time of GPP (table 1).

Another common approach to quantifying ecosystem response to disturbance is to measure watershed biogeochemical export in streams. Seminal works that have furthered nutrient balance theory about ecosystems have used these methods (e.g., Bormann et al. 1974). We illustrate the variation and differential responses among and within ecosystems to cyclone disturbance using data on stream nitrate concentrations from two tropical, montane headwater streams: the Quebrada Sonadora in Luquillo, Puerto Rico, and watershed 1 in Fushan, Taiwan (figure 4b). Puerto Rico experiences a category 3 or greater (Saffir–Simpson index) hurricane on average every 50 to 150 years (Booze et al. 2004, Knapp et al. 2010), whereas Fushan, Taiwan,

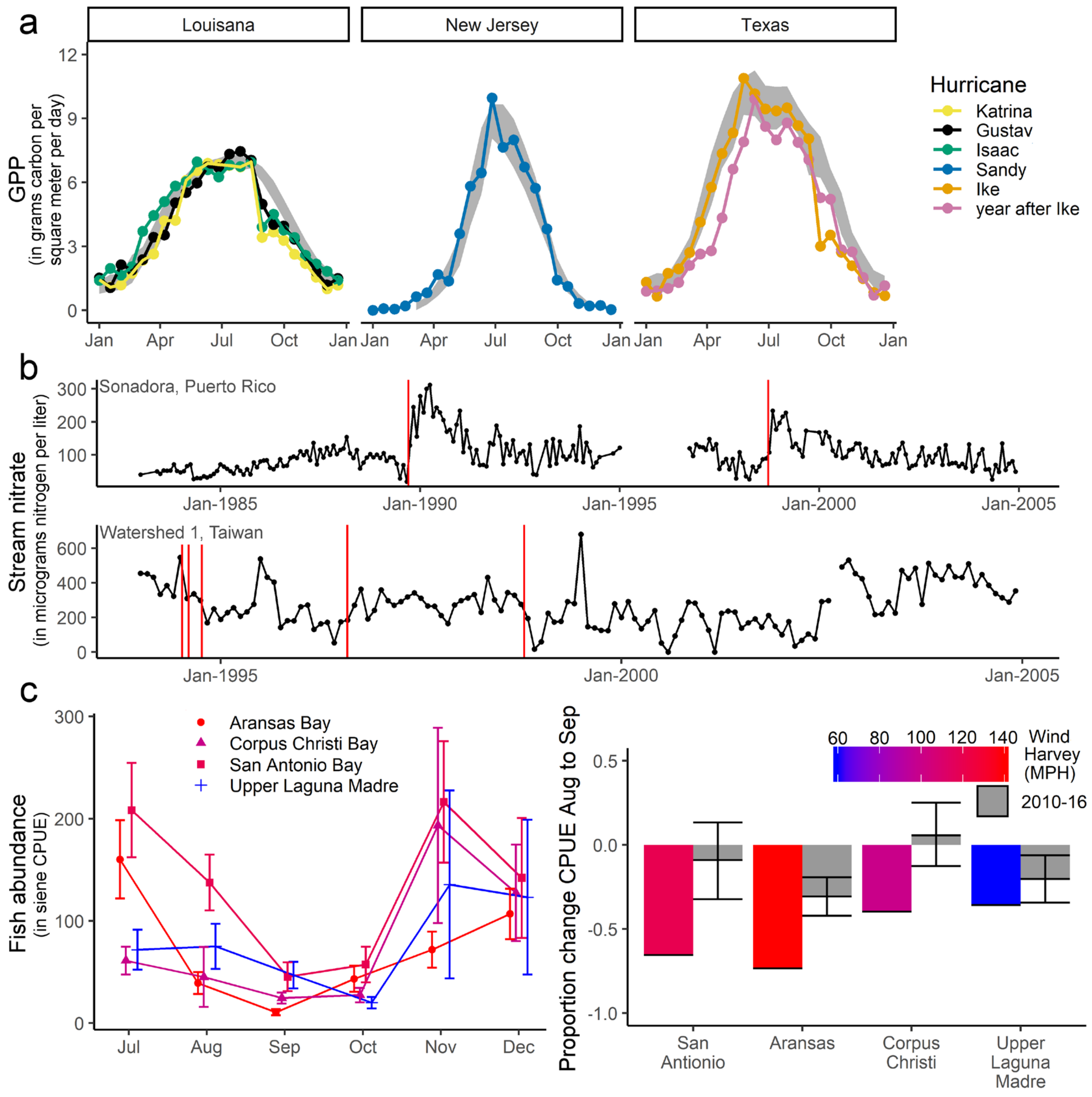

Figure 4. (a) Gross primary productivity (GPP) in relation to hurricane timing for three American coastal marshes in Louisiana (left panel), New Jersey (middle panel) and Texas (right panel). Shaded gray ribbons show average 16-day marsh productivity, with 95% confidence intervals, from 2000 to 2018 (i.e., baselines). Colored lines show the 16-day productivity for the selected years during and following hurricane disturbance. GPP dropped in the Louisiana salt marsh when Hurricanes Katrina, Gustav, and Isaac hit at the end of August, whereas it did not in a New Jersey salt marsh when Sandy hit at the end of October when plant senescence had already begun; GPP dropped in a Texas marsh when Ike hit mid-September, and continued to be lower for well over a year afterward. (b) Monthly stream nitrate-nitrogen concentrations from Quebrada Sonadora in the Luquillo Experimental Forest, Puerto Rico (1983–2005, top), and watershed 1 in the Fushan Experimental Forest, Taiwan (1994–2005, bottom). Vertical red lines represent category 3 or greater cyclonic storm occurrences: Hurricane Hugo (September 1989) and Hurricane Georges (September 1998) for Quebrada Sonadora and Typhoon Tim (July 1994), Typhoon Doug (August 1994), Typhoon Seith (October 1994), Typhoon Herb (July 1996), and Typhoon Zeb (October 1998) for watershed 1. Likely because of differences in cyclone recurrence, increases in stream nitrate in Quebrada Sonadora in response to cyclones were an order of magnitude higher and took about four times longer to return to baseline than those of watershed 1, (c) Changes in fish abundance in response to Hurricane Harvey for four coastal estuaries along the Texas Gulf Coast. The left panel shows the average in seine catch per unit exertion (CPUE) from 2010 to 2016 (i.e., baseline); the error bars represent the standard error. The right panel shows the proportional change in seine CPUE before and after Hurricane Harvey in 2017 in comparison to that of the baseline; the error bars represent the standard error. Colors denote average wind speed in each bay during Hurricane Harvey. Estuaries that experienced wind speeds over 100 miles per hour (i.e., San Antonio and Aransas Bays) had greater decreases in fish abundances than those that experienced weaker (i.e., Corpus Christi Bay and the Upper Laguna Madre).

Table 1. Measures of ecosystem response to cyclones for three commonly measured response variables: Primary productivity, stream biogeochemistry, and organismal abundance.

Response variable	Site	Hurricane or typhoon	Date	Baseline mean	Baseline standard error	Post-disturbance value	Time to return to baseline (in days)	Percent change	Log-response ratio
GPP (in grams of carbon per square meter per day)	Louisiana Salt Marsh	Hurricane Katrina	August 2005	6.4	0.4	3.4	80	–44	–0.82
		Hurricane Gustav	September 2008	6.4	0.4	5.0	48	–17	–1.75
		Hurricane Isaac	August 2012	6.4	0.4	3.9	48	–35	–1.04
	New Jersey Salt Marsh	Hurricane Sandy	October 2012	0.6	0.2	0.3	<16	–50	–0.69
	Texas Salt Marsh	Hurricane Ike	September 2008	7.2	1.0	3.8	381	–47	–0.75
Nitrate-nitrogen (in micrograms per liter)	Quebrada Sonadora, Puerto Rico	Hurricane Hugo	September 1989	84	22	312	722	270	1.30
		Hurricane Georges	September 1998	62	26	234	1081	275	1.32
	Watershed 1, Fushan, Taiwan	Typhoon Tim	July 1994	316	79	420	21	33	0.28
		Typhoon Doug	August 1994	303	86	239	14	–21	–0.23
		Typhoon Seth	October 1994	359	115	544	28	52	0.42
		Typhoon Herb	July 1996	194	113	291	21	50	0.41
		Typhoon Zeb	October 1998	262	106	70	21	–73	–1.32
Fish abundance (Seine CPUE)	Aransas Bay	Hurricane Harvey	August 2017	39	11	10	45[a]	–74	–1.35
	Corpus Christi Bay			45	29	27	45[a]	–40	–0.52
	San Antonio Bay			138	27	46	75[a]	–66	–1.08
	Upper Laguna Madre			78	22	48	75[a]	–36	–0.45

Note: Ecosystem data, including mean baseline values, disturbance effect (percentage change and log-response ratio), and time to return to baseline are shown graphically in figure 4. The gross primary productivity data come from three coastal American marshes in response to five hurricanes. The stream nitrate data are from seven cyclones from two tropical montane watersheds that differ substantially in the frequency of disturbance events. Finally, the fish abundance data are from seine drags from four Texas waterways affected by Hurricane Harvey. Abbreviations: CPUE, catch per unit exertion; GPP, gross primary productivity. [a]Monthly temporal resolution of the fish abundance data limits the sensitivity of estimates for the return to baseline interval.

experiences, on average, three typhoons per year, with 60% of those being category 3 or greater (Lin et al. 2011, Knapp et al. 2010). From 1983 to 2005, two hurricanes (Hugo and Georges) affected the Puerto Rican watershed that was instrumented for nutrient sampling, whereas, from 1994 to 2005, five typhoons affected the instrumented watershed in Taiwan. The research framework is used to compare the response of watershed nitrate export to Hurricane Georges in the Quebrada Sonadora to several typhoons that have affected watershed 1 (table 1; Lin et al. 2011).

The baseline (1-year average) for the Quebrada Sonadora in Puerto Rico before Hurricane Georges was 62 micrograms (μg) per liter (L) nitrate-nitrogen (standard deviation [SD] = 26), which increased to 234 μg per L (SD = 45; figure 4b) and took approximately 1081 days to return to baseline. For watershed 1 in Fushan, responses of nitrate-nitrogen to typhoons produced concentrations as wide ranging as baseline values (47–407 μg per L) with concentrations increasing following some typhoons, decreasing after others, and remaining unchanged for many typhoons (i.e., all typhoons between 1994 and 1995). In the context of the framework, we quantify the disturbance effect size (i.e., how large a deviation from the baseline occurred because of the cyclone) and the log-response ratio. Deviations of ecosystem components following disturbance can be quite large, explaining the use of logarithms. For watershed 1, log-response ratios ranged from –1.32 to 0.53 (averaging 0.02) and were negative in one-third of cases. In comparison, the log-response ratio of stream nitrate for Quebrada Sonadora after Hurricane Hugo was 1.30 and after Hurricane Georges was 1.32 (table 1).

Comparing the two streams, we can see a large difference in the response of stream nitrate concentrations to tropical cyclones between watershed 1 and Quebrada Sonadora. Responses of watershed 1 were variable. Despite that variability, the main difference in ecosystem response between the two streams is the return to baseline interval, which occurs after a week to a month for watershed 1 but takes years to return for Quebrada Sonadora (table 1). In addition, watershed 1 illustrates within-ecosystem variation in response to tropical cyclone disturbance, wherein there is a large degree of variability over time, with typhoons sometimes leading to a change in stream nitrate concentrations and other times not. The research framework presented in the present article provides a means to investigate the reasons behind such within- and among-ecosystem variation in response to tropical cyclones.

Third, long-term monthly fish abundance data from four Texas estuaries illustrate a typical seasonal dynamic, where abundances decline steadily until September and October and then increase as fall recruits arrive in November and December (figure 4c left panel). Hurricane Harvey affected all four estuaries in mid-August 2017, reducing abundances in catch surveys for 1–2 months. The decreases in the catch per unit exertion (CPUE) from August to September 2017 were greater in all estuaries than was common from their past 6-year historic baselines (figure 4c right panel). Fish abundances following Hurricane Harvey in Aransas, San Antonio, Corpus Christi Bays, and the Upper Laguna Madre decreased by 74%, 66%, 40%, and 36%, respectively, whereas historical mean (M) changes in CPUE from August to September (2010 to 2016) for Aransas, San Antonio, Corpus Christi Bays, and the Upper Laguna Madre measured M = –31%, standard error (SE) = 11; M = –10%, SE = 23; M = 6%, SE = 19; and M = –21%, SE = 13, respectively.

Generally, animals are more resilient than other ecosystem components (e.g., GPP or biogeochemical fluxes). The short response time to return to the baseline in fish abundances compared to those of GPP and stream nitrate illustrate this point. The increased resistance of animals relative to other ecosystem components may be explained by a combination of adaptation to environmental fluctuations, and in the case of mobile animals, the ability to move away from storms and colonize new areas after the storm. Estuaries and rivers are inherently dynamic environments when compared to terrestrial ecosystems, and therefore, their associated animals are often adapted to tolerate large fluctuations in environmental conditions, such as shifts in salinity or flood regime. However, when comparing responses across estuaries, those with higher wind speeds during Hurricane Harvey (i.e., Aransas and San Antonio Bays with wind speeds higher 100 miles per hour) showed greater decreases in fish abundances relative to historical baselines than those with less wind (i.e., Corpus Christi Bay and the upper Laguna Madre with wind speeds below 100 miles per hour; figure 4c right panel).

The quantitative application of the framework allows for a wide variety of different response variables to be treated similarly to the examples that have been provided. Many ecological data sets are multivariate, meaning they measure the response of many species or ecosystem properties simultaneously. Although, this is a strength of ecological data sets and there are many tools for their analysis, often, the relatively simple univariate responses are overlooked. The key feature of this framework is the reduction of complex ecological variables into numerical terms. This reduction allows comparisons across study locations and storms. In addition, the quantification of univariate responses, and the disaggregated approach in general, is much more amenable to translation into numerical models of ecosystems than responses identified using multivariate analytical approaches. It also allows for comparisons across species, trophic levels, or even disciplinary metrics for very different phenomena (see table 1). Creative application of the framework could even allow it to accommodate a single multivariate or composite measure of ecosystem response (i.e., those arising from an eigenanalysis or other data reductive procedure).

For example, the framework can accommodate and compare the response curves for fish abundance, invertebrate diversity, sediment export, carbon dioxide exchange, or salinity, among many other variable types. It can elucidate the time domains required for recovery at the various hierarchical levels of ecosystem organization—for example, the recovery time of a forest to return to prestorm leaf light interception levels versus prestorm forest canopy cover levels. The research framework can address spatial heterogeneity in ecosystem response to cyclone disturbance, if the data permits (e.g., sites along a transect), in that each site may be examined using the framework separately and their responses compared. Moreover, the framework may be adapted to other systems and potentially other disturbances, although careful editing of the framework in consideration of different disturbance drivers and the ecosystem attributes governing responses would be needed. We have avoided any explicit references to the mechanisms of ecosystem recovery from disturbance, because they can be categorical and can differ substantially among ecosystems. To allow for maximum quantitative cross-system comparison, our model allows for multiple mechanisms to be quantified as system attributes, whether they be antecedent conditions or constraints (see box 1) and evaluates them using real data.

Call to action: Research and funding agency coordination

Ideally, a unified framework allows scientists from disparate disciplines to synthesize their findings within a broader context. This can then lead to meta-analyses, discoveries, and the creation of new paradigms that will aid in advancing the scientific community's knowledge regarding disturbance events that are occurring across various spatial and temporal scales (e.g., Collins et al. 2011, Grimm et al. 2017, Gaiser et al. 2020). To date, however, most studies of the ecological effects of tropical cyclones have come from opportunistic poststorm sampling of predesigned studies rather than well planned, prestorm sampling designs and protocols (but see Shiels et al. 2015). In some cases, single-investigator, prestorm study designs exist and can identify the differences among repeated cyclones affecting a single site, but meta-analyses that examine the effects of multiple cyclonic storms across a wide range of locations are still needed to fully understand their global importance (Ibañez et al. 2019, Pruitt et al. 2019).

When disparate studies and their underlying data are integrated through a common framework, comparative inference can result in a deeper understanding. Funding agencies can leverage the findings of each study, as opposed to funding one-off studies that may be perceived as urgent and opportunistic during 1 fiscal year but limited in contribution to science by the next. Despite the value of rapid response programs (e.g., National Science Foundation RAPID grants) that quantify ecosystem responses to specific disturbance events, the overarching “experimental design” of these *post hoc* efforts may be ill suited for documenting the range of responses across a landscape and its associated ecosystems. Such studies often focus on a single or a few ecosystem components and struggle to produce generalizable conclusions across scales, between storms, and among ecosystems. Making such comparisons is imperative to advancing the scientific community’s knowledge of how ecosystems respond and informing management strategies that will improve ecosystem resistance to cyclone damage, and subsequent recovery (i.e., resilience). As a result, gaps exist in our ability to forecast the consequences of tropical cyclones on ecosystems and their services.

There is a need for a network of sentinel sites with the shared goal of understanding ecosystem response to tropical cyclones across the coasts of the United States, and potentially throughout the cyclone-affected areas of the world. High priority candidate sites that could be used to develop a network for the study of tropical cyclones have been suggested (Hopkinson et al. 2008); however, to date, this network has not emerged. An initial goal could be to develop a coordinated structure to sample during storms so that a synoptic picture emerges. As researchers, we believe a series of sites that share characteristics and measurements, not unlike the National Ecological Observatory Network (NEON) would be ideal. We envision that the most cost-effective approach is one of integration with other long-term programs. For instance, integrating the NEON system with other entities, such as the National Science Foundation’s Long Term Ecological Research Network, the National Oceanic and Atmospheric Organization’s National Estuarine Research Reserve System, and the US Geological Survey’s coastal programs to specifically target the study of tropical cyclones is one potential avenue forward toward a national network of sites. Given the societal impact of these disturbances and the importance of coastal ecosystems to national interests, current national research infrastructures (e.g., NEON sites) could be used to initiate this effort. The Gulf of Mexico Research Initiative program provides a potential example of leveraging multiple studies toward a common goal of understanding how the *Deepwater Horizon* hydrocarbon spill affected a variety of ecosystems (Martínez et al. 2012, GOMRI 2019, Kastler et al. 2019 and references therein) costing $500 million. Although this program emerged from a single event, there is no reason that funding cannot be similarly organized for a multiecosystem, multievent framework with a single emergent goal. With a common framework and quantitative approach, long-term studies can be planned across multiple sites for maximum scientific impact.

In addition, a network of field sites can provide ground truthing for satellite-based monitoring, and by upscaling, provide some representation of changes across the entire landscapes and regions. The combination of field-based measurements with remote sensing, GIS, and statistical modeling techniques can provide broader spatially explicit information on changes in ecosystem structure and function (Wang and Xu 2008, Zeng et al. 2009). Although remote sensing cannot capture all ecological field measurements, many attributes can be measured for both terrestrial (e.g., tree mortality, forest green cover, vegetation composition; Dolan et al. 2011, Han et al. 2018, Zhang et al. 2019) and aquatic ecosystems (e.g., sediment resuspension or discharge, phytoplankton blooms; Walker 2001, Shi and Wang 2007, Chen et al. 2009). Using the spatial disturbance legacies captured from satellite and airborne observations can inform locations where field-based measurements are needed to capture ecosystem state shifts. Increasing the range of variation in ecosystem monitoring on the ground will help couple ground-based field observations with remote airborne technological approaches, which hold immense promise in increasing the spatial scale and accuracy of quantifiable ecosystem responses to cyclones.

Implications for natural resource policy and management

Natural resource managers must often balance a variety of competing interests when making decisions about managing responses to tropical cyclones. These interests include ensuring the conservation and sustainable use of many ecosystem services across large areas, but management actions necessarily create tradeoffs among these services. For example, an action that seeks to increase the prestorm resistance of a forest to cyclonic wind damage at a National Wildlife Refuge will likely reduce the litterfall and poststorm export of organic materials to an adjacent riverine and estuarine watershed. In the adjacent aquatic systems, woody debris may be critical to create bathymetric diversity and therefore support fisheries, and the finer organic materials may provide a pulse in microbial productivity. Alternatively, organic materials could reduce water quality that a separate agency must manage. With a common framework, research managers can define the extent, relevance, and timing of these competing ecosystem services. We contend that meta-analysis across seemingly disparate variables will help managers weigh the relative value of different ecosystem services and improve management accordingly.

Policymakers must also evaluate ecosystem services, although socioeconomic needs are often more highly valued (Collins et al. 2011, Martínez et al. 2011). In general, laws, economic infrastructure, and policies are designed to promote stability, whereas disturbance events are dynamic and therefore, troublesome. Coastal policymakers generally embrace strategies that promote ecosystem resistance because a smaller magnitude of response to cyclonic disturbance coincides with landscape stability, less erosion, and a reduced transfer of materials across property lines (Feagin et al. 2015). Historically, policymakers have not fully embraced strategies that promote ecosystem resilience, because their implementation requires the vision to see the value of natural and social dynamism across longer time frames and multiple ecosystem services, as well as to make short-term economic sacrifices. A common framework can allow across-site comparisons and can aid in the creation of ecosystem and social vulnerability indices based on synchronized metrics (Gaiser et al. 2020). The development of a vulnerability ranking approach can then be implemented for coastal areas with increasing population and cyclonic impacts (Adger et al. 2005).

Conclusions

The research framework presented in the present article allows for the comparative study of the effect of tropical cyclones across ecosystems. Many scientists have previously investigated select responses to specific events using a variety of approaches, making it difficult to find commonalities between different response variables and events. The proposed framework reconciles the differences across ecosystems and variation in storm meteorology. Our ultimate hope is that the framework will lead to a standardized approach that benefits the scientific and ecosystem management communities, and ultimately helps identify ways to decrease societal susceptibility to cyclonic storm damage through advancement in the ecosystem science of tropical cyclone disturbances. Tropical cyclones will increasingly shape the world's natural and built systems. So a more general understanding of how these systems affect ecosystem resistance and resilience will help the global citizenry decide how to intervene to best preserve ecosystem services and benefits.

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Data availability

The data and the code used to produce figure 4 are available on GitHub at https://github.com/hoganhaben/A_framework_for_studying_cyclones.

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