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ECOSPHERE

SPECIAL FEATURE: HIGH-ENERGY STORMS

Resistance, resilience, and vulnerability of social-ecological systems to hurricanes in Puerto Rico

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Abstract. Subject to hurricane disturbance for millennia, natural ecosystems of Puerto Rico exhibit clear patterns of resistance (e.g., many tree species have little immediate storm-related mortality) and resilience (e.g., leaf litterfall and stream chemistry returned to pre-hurricane levels in as little as five years). Contemporaneous studies of near-shore areas also suggested no long-term impacts of hurricanes; however, anthropogenic effects (coral bleaching, sedimentation) dominate the long-term condition of marine systems in Puerto Rico, many of which have slowly evolved into novel ecosystems. A key characteristic of novel marine ecosystems is their long-term loss of benefits and resilience, coupled to declining biodiversity and loss of structural or functional redundancy, signaling increased vulnerability to subsequent hurricanes. Human systems are also strongly affected by cyclonic storms, as evidenced by the recent impacts of Hurricanes Irma and Maria in the Caribbean. The lack of short-term recovery from disturbance by coral reef ecosystems, coupled with an increasing recurrence of anthropogenic impacts, increasing hurricane frequency or severity, and sea-level rise, may have irreversible long-term socioeconomic consequences for coastal social–ecological systems and for community livelihoods. A comprehensive social–ecological understanding of hurricane effects in Puerto Rico is lacking in part because hurricane effects on human populations are not comprehensively followed. Although some studies suggest a path forward, finding effective methods to link measurements of storm intensity to the diverse components of tropical social–ecological systems remains a challenge.

Key words: anthropogenic effects; coastal ecosystems; cyclonic storms; forested ecosystems; Hurricane Irma; Hurricane Maria; marine ecosystems; novel ecosystems; ridge to reef; Special Feature: High-Energy Storms.

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Introduction

High-energy storms in tropical areas (hurricanes, typhoons, and cyclones, hereafter HES) challenge our understanding of disturbances in social–ecological systems (SES) because of their variable size, meteorological characteristics (course, size, wind strength, speed), and diverse effects (wind, rainfall, flooding in uplands, surf, strong currents, and storm surge in coastal and marine areas) on ecosystems (Anthes 1982, Scatena et al. 2012). It becomes especially challenging when one includes ecosystems dominated by human populations, structures, and economic systems (Adger et al. 2005, Wagner et al. 2014). Social ecology is a relatively new discipline with deep roots in both systems ecology and environmental sociology (e.g., Holling et al. 1973, Kinzig et al. 2006, Miller et al. 2010, Collins et al. 2011) that enables researchers to conceptualize how coupled human–natural systems respond to large-scale disturbances like HES (e.g., Colding et al. 2003, Adger et al. 2005). Social–ecological systems can be described by the characteristics that lend resistance or resilience (or both) to them in the face of intense disturbances like HES. Here, we use "resilience" in the narrow sense, as originally proposed by Hollings et al. (1973), to mean positive feedback processes that restore the system state through time. Thus, resistance and resilience describe the capability of a SES to remain at or return to normal (however defined) after a disturbance. We recognize that some authors combine resistance and resilience into a single term "resilience" (which we call broad-sense resilience; Walker et al. 2004), but we use the term sensu stricto because it distinguishes important SES characteristics, that is, permanence in response to disturbances (not dynamic) vs. positive feedback processes (dynamic in nature) that restore normal structure or function.

Vulnerability is a notion that is often treated as the inverse of broad-sense resilience but has more nuanced meanings (Miller et al. 2010). Having intellectual roots in the social sciences, vulnerability generally refers to particular components of SES. Although difficulties still exist in how the terms are combined in the conceptualization of SES (Miller et al. 2010), we find that vulnerabilities are points of weakness in an SES that, once exposed by disturbance, can cascade in effects to influence the status and dynamics of the SES as a whole (Kinzig et al. 2006, Miller et al. 2010). Kinzig et al. (2006) provide a number of examples of cross-scale interactions where small-scale component change results in altered SES state or dynamics as a whole. The challenge then is to identify the components of an SES that are vulnerable to disturbance by HES and determine how they have the potential to influence the state and function of the entire SES.

Puerto Rico represents a nexus for studies of the effects of HES on SES (López-Marrero and Wisner 2012, Brokaw et al. 2012*a*, Hernández-Delgado 2015) because of the availability of local research programs that monitor and illuminate their impacts (López-Marrero et al. 2019). This review of responses by SES to hurricanes (as HES are called in the Western Hemisphere) in Puerto Rico first delimits the hurricane disturbance history of the island. Special attention is given to the paleohistory of hurricane disturbance in the Caribbean to test the idea that, given millennia of hurricane disturbances, the natural components of SES should exhibit ecological adaptation to disturbance by HES. We then focus on the northeast corner of the island, an area that has been especially well studied because of the presence of the Luquillo Long-Term Ecological Research Program (Brokaw et al. 2012*a*) and other research programs (López-Marrero et al. 2019). Separating the area into three subsystems, the forested uplands of the Luquillo Experimental Forest ("ridge" in the parlance of this Special Feature), the mosaic of human-influenced lowlands ranging to the coast (lowlands), and the coastal and marine ecosystems (reef) beyond, we review the key elements of our knowledge of responses by SES to hurricane disturbance. We find that resistance, resilience, and vulnerability differ strongly among the three subsystems, increasing from ridge to lowlands to reef. These patterns are controlled by.

1. The history of anthropogenic disturbance, which is least on the ridges, intermediate (currently) in lowlands, and greatest in marine systems;
2. The accumulation and compounding of anthropogenic stressors from ridge to reef, especially sedimentation, overfishing and warming in the reef, leave marine systems especially vulnerable to storms; and
3. The variation in adaptation by particular components of SES, either ecological (i.e., evolved wind resistance in trees) or via human behaviors (e.g., wind-resistant construction, coping mechanisms), that can enhance resistance and resilience to HES. Lacking adaptation to the current combination of stressors can leave systems particularly vulnerable to HES.

Thus, in northeastern Puerto Rico, evolutionary history and human history interact to produce a distinct gradient in resistance, resilience, and vulnerability to HES from ridge to reef.

Context

Puerto Rico emerged as an island approximately 30 million years ago as a result of tectonic uplift related to the interactions of the Caribbean and North American plates, (Erickson et al. 1990). A secondary period of uplift beginning 4 million years ago (Brocard et al. 2015) gave the island its current relief. Former shorelines are apparent in some areas that, interestingly, appear to influence modern-day forest structure via undetermined mechanisms (though probably related to enhanced nutrient availability; Wolf et al. 2016). Today, the island has six life zones based on the Holdridge system (Ewel and Whitmore 1973), with a distinct northeast (wet and rainforests) to southwest (dry forest) gradient in rainfall influencing their spatial distribution.

Since the beginning of the 20th century, the major socio-ecological change in Puerto Rico has involved forest cover driven by changes in the economy. Much of Puerto Rico was deforested for agriculture by the 1940s owing to a combination of industrial (sugar, coffee, tobacco) and subsistence agriculture (Zimmerman et al. 2007). Only 5% of the forest cover remained at that time, much of which was in the Luquillo Mountains. Socioeconomic development led to a forest transition (Rudel et al. 2000) that resulted in the expansion of secondary forest. Now, 65% of the island has forest cover (Brandeis and Turner 2013). Much of the human population now lives in dense urban zones often near the coasts (Rudel et al. 2000, Muñoz-Erickson et al. 2014).

The domain of this study is the northeastern corner of Puerto Rico, which includes the Luquillo Mountains (see McDowell et al. 2012) and the surrounding lowlands, as well as associated coastal and marine zones (Fig. 1). In general, the region can be divided into three zones: uplands (ridges) from about ~300 m asl to the summits of the mountains (~1000 m asl), the (historically) human-dominated lowlands from the coast to ~300 m asl, and the coastal and marine zone (reef), which includes estuaries, islands, seagrass beds, and coral reefs to the island shelf.

The undisturbed terrestrial vegetation of northeastern Puerto Rico ranges from dry forest in the eastern fringes, to humid, wet, and rain forests with increasing elevation (Ewel and Whitmore 1973) toward the summits. Native vegetation in uplands comprises four major types based on dominant tree species and their physiognomy (Harris et al. 2012): short-statured elfin woodland at the summits above 900 m asl; mid-elevation palo colorado (*Cyrilla racemiflora*) forest between 600 and 900 m asl; tabonuco (*Dacryodes excelsa*) forest below 600 m; and palm forest (*Prestoea accuminata*) with a characteristic patchy distribution that interdigitates with the three other forest types at elevations above ~500 m.

The uplands are largely primary forest but include areas up to 600 m asl that were formally in agriculture but now host older (>50 yr post-abandonment) secondary forests (Zimmerman et al. 1995*a*, 2007). The lowlands include extensive areas of past human use for pastures or sugarcane fields (Thomlinson et al. 1996) but are now predominantly covered by secondary forests (20–50 yr post-abandonment) that are interspersed within expanding urban areas of various densities (Aide et al. 1996, Martinuzzi et al. 2007). Dense urban areas occur on the coastal plain, near town centers, the largest being Fajardo. Beaches and mangroves line the coast. Much of the original *Pterocarpus* forest was likely eliminated by logging to allow sugarcane production in the early part of the 20th century (Zimmerman et al. 2007). Rivers drain from the uplands through the lowlands, and empty into estuaries, seagrass beds, and reefs perched on the narrow Puerto Rico Platform (Fig. 1), forming the coastal and marine zone. This zone, which includes the offshore islands of Culebra and Vieques, ends to the north at the Puerto Rican Trench, one of the deepest locations in the Atlantic Ocean.

Methods

We supplemented the substantial reviews about hurricane-related dynamics in Puerto Rico (e.g., López-Marrero and Wisner 2012, Brokaw et al. 2012*a*, Hernández-Delgado 2015) with searches in Google Scholar based on keyword combinations such as (“hurricane +"Puerto Rico" + ecology or ecosystem) or (“hurricane” +"Puerto

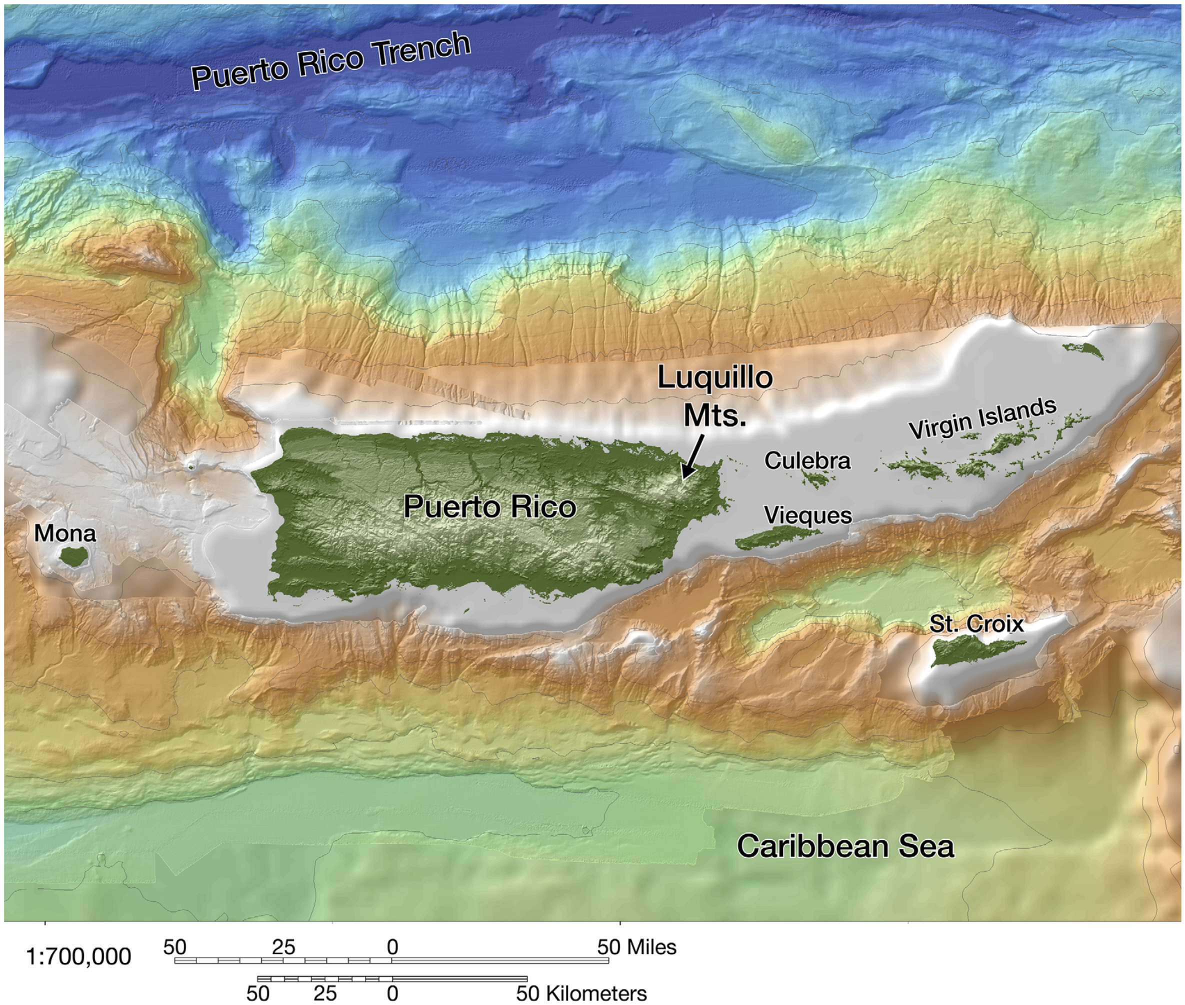

Fig. 1. Map of Puerto Rico showing the configuration of nearby coastal areas. The Luquillo Mountains are located in the northeast corner of the island. Extracted from Andrews et al. (2013).

Rico" + social or economic or socioeconomic) to make sure we had not over-looked critical resources. A recent publication by López-Marrero et al. (2019) used a similar approach to summarize the literature in this area and confirmed that much of what is known about hurricane disturbance to ecosystems on the island is from northeastern Puerto Rico. We used an outline for the article developed at a workshop on the topic. This suggested that we divide responses into immediate- and long-term responses, as well as among physiographic setting along the ridge to reef continuum. This led to an unbalanced presentation as more publications exist on immediate rather than long-term effects, and some physiographic zones are better treated (uplands and coastal/marine zones) than others (lowlands). Thus, the quantity and quality of coverage for particular responses or particular zones reflects a lack of information rather than a disinterest on our part.

Disturbance Regime

High-energy storms

High-energy storms are a dominant component of the disturbance regime in Puerto Rico (Scatena et al. 2012) with many storms affecting the island since detailed records began in the mid-1800s (Table 1; Scatena and Larsen 1991,

Table 1. Summary of hurricanes since 1851 that caused damage at F2 or higher on the Fujita scale in Puerto Rico.

Year	Name	Saffir-Simpson category	Storm surge (m)	Maximum sustained winds (m/s)	Maximum rainfall (cm/d)	Peak stream flow (cm/d)	Deaths	Economic losses ($1000 in 2017)
1876	San Felipe I	3	. . .	57	12	. . .	19	. . .
1893	San Roque III	3	. . .	43.7	8	. . .	4	. . .
1899	San Ciriaco	4	. . .	51.4	25	. . .	3396	$740,000
1916	San Hipolito II	3	. . .	51.4	75	. . .	1	$25,000
1928	San Felipe II	5	. . .	72	75	. . .	312	$1,330,000
1931	San Nicolas	1	. . .	41.2		. . .	2	$3200
1932	San Ciprián	4	. . .	48.9		. . .	22	$540,000
1956	Sta. Clara (Betsy)	3	. . .	43.7	22		0	$90,000
1989	Hugo	3	~1	61.7	25	5.2	12	$1,756,000
1998	Georges	3	3	45.6	75	1.8	8†	$3,000,000
2017	Irma	5	0.5	24.7	38	. . .	3	. . .
2017	Maria	4	2-3	69.5	96	. . .	~2975	$90,000,000

Notes: Saffir-Simpson category and maximum wind speed from Boose et al. (2004) through 1997; Guiney (1998), Cangialoso et al. (2018), and Paschet al. (2018) provided the others. Maximum rainfall is from Miner Solá (1995) through 1997 and Guiney (1998), Cangialoso et al. (2018), and Pasch et al. (2018). Storm surge is from Miner Solá (1995) and Guiney (1998), Cangialoso et al. (2018), and Pasch et al. (2018). Deaths and economic losses are from Miner Solá (1995) except that for Hurricane Georges, which were taken from Guiney (1998) and CDC (1998), respectively. Information on Hurricane Irma is from Cangialoso et al. (2018); that of Maria is from Pasch et al. (2018) and Santos-Lozada and Howard (2018). Ellipses denote no data.

† Acosta and Irizarry (2018) estimate ~1300 deaths from Hurricane Georges.

Miner Solá 1995, Boose et al. 2004). Following Boose et al. (2004), we define HES as cyclonic storms capable of causing F2 or higher damage on the Fujita scale (Table 1). Especially, intense hurricanes in 1876, 1899, and 1928 caused upward of thousands of deaths along with as much as $1 billion U.S. dollars (2017) of damage to agriculture and habitations. In 1965, Hurricane Betsy made landfall on Puerto Rico (Fig. 2) but caused little socioeconomic damage and no recorded deaths as it traversed the island (Miner Solá 1995). Other than Hurricane Betsy, Hurricane Hugo (1989) was the first cyclonic storm since 1932 (57 yr) to affect Puerto Rico (Table 1) with F2 damage or higher.

Hurricane Hugo generated a great deal of scientific attention, in part because of the establishment of the Luquillo Long-Term Ecological Research Program (LTER) in 1988, but also because of the presence of federal agencies (e.g., the USGS, NOAA) on the island that were eager to describe hurricane impacts as part of their missions (López-Marrero et al. 2019). Recent HES (i.e., Hurricanes Hugo and Georges) generated similar or higher levels of economic losses compared to previous storms, but recorded human deaths were generally much fewer (Table 1), with the death toll from Hurricane Maria being a despairing exception (Santos-Lozada and Howard 2018). Increased human population, and socioeconomic expansion of the island since World War II (Pielke et al. 2003), especially in coastal zones (Ramos-Scharrón et al. 2015), provides the likely explanation for the increase in economic losses to hurricanes. Improved house construction (reinforced concrete vs. wooden structures) and substantially improved warning systems combined to explain the apparent lowered loss of life. Only recently has the death toll from Hurricane Maria come into focus (e.g., Santos-Lozada and Howard 2018); the causes of the high mortality remain to be comprehensively understood but are likely linked to a collapsed healthcare system, especially in rural areas or for those with less socioeconomic capacity (Acosta and Irizarry 2018).

Coming only 9 yr after Hurricane Hugo, another Category 3 storm, Hurricane Georges (Table 1, Fig. 2) provided a fruitful comparison to Hurricane Hugo for understanding the impacts of HES on the social–ecological systems (e.g., Canham et al. 2010). The impact of Hurricane Georges on a number of Caribbean islands and on the U.S. mainland is the topic of another article in this special feature (van Bloem and Martin 2020).

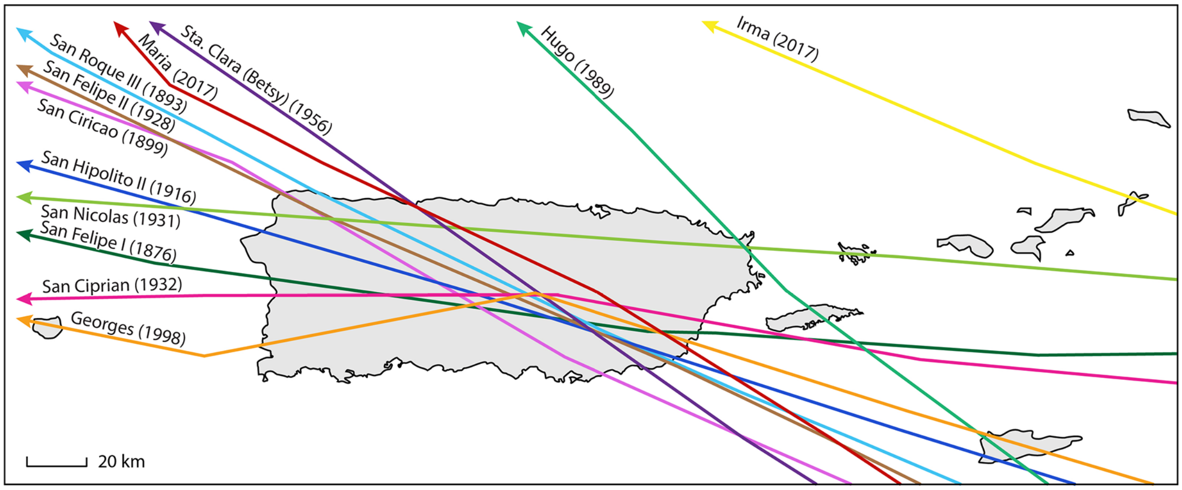

Fig. 2. Tracks of hurricanes since 1851 that caused damage at F2 or higher on the Fujita scale in Puerto Rico (Table 1).

The 2017 hurricane season was devastating in the Caribbean and the mainland of the southern United States (Cangialoso et al. 2018, Pasch et al. 2018). Hurricane Irma passed 50 km to the northeast of Puerto Rico, causing some significant damage in northeastern Puerto Rico (Fig. 2). Before the effects of Hurricane Irma could be documented, it was followed by Hurricane Maria. It was the most intense storm in 90 yr to strike the island (since San Felipe II, Table 1), and its toll on the SES remains to be evaluated fully.

The return interval for hurricanes (Category 1 on the Saffir-Simpson Scale or higher) passing over the Luquillo Mountains is 50–60 yr during the time period of 1851–1990 (Scatena and Larsen 1991); accounting for recent storms (to 2017) reduces this interval to ~42 yr (N. Brokaw, *personal communication*). The storms are most common from July to October, during which they contribute greatly to peak annual discharge rates of streams draining the Luquillo Mountains (see Figure 4.3b, Scatena et al. 2012).

Scatena et al. (2012), reviewing the meteorological characteristics of named storms in Puerto Rico, concluded "there is no simple direct relationship between the magnitude and the destructive powers" of hurricanes because of variability in hurricane path, local aspect and topographic exposure, amount of moisture entrained in the storms, wind velocity, forward velocity of the eye, time period that a storm directly affects the land mass, and the positions of the storm and site relative to oceans. Boose et al. (2004) developed a unique approach to the issue of storm intensity and severity. They converted storm damage to the Fujita Scale (ranging from 0 to 5), utilizing historical storm damage reports from local periodicals to record damage type and extent in human habitations beginning in 1851 (Fig. 3). Thus, they used the damage expressed by the SES to back-calculate storm meteorological characteristics. Meteorological reconstructions of each hurricane affecting the island from 1851 to 1997 were done utilizing the HURRECON model (Boose et al. 1994), which summarized the path, forward speed, and wind intensity (but not moisture content, rainfall amounts, or storm surge) of each storm affecting the island. Integrating historical damage records into the model, they were able to calculate the return intervals of damaging winds of different levels on the Fujita Scale for the 146-yr period. The geographical pattern (Fig. 3) showed that cumulative damage frequency and intensity were highest in the northeastern part of the island. This transpires because storms approach from the east, but often turn to the north because of steering air currents in the region, creating a locus of high storm frequency just east of Puerto Rico and the Virgin Islands (see Fig. 16.7 in Lugo et al. 2000*a*). Storms sometimes clip the northeast corner of the island (e.g.,

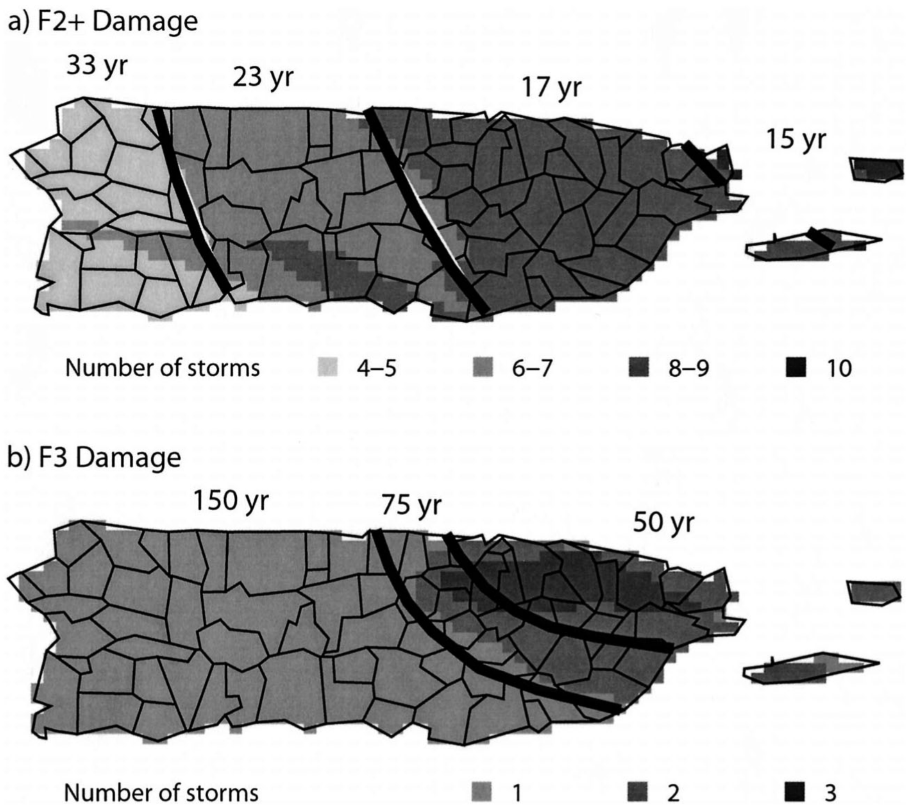

Fig. 3. Recurrence interval of hurricanes (1851–1997) with differing severity (Fujita scale) as described by Boose et al. (2004).

Hurricane Hugo). Those storms that do not make the turn north, often cross the island from the southeast to the northwest (Scatena and Larsen 1991, Boose et al. 2004) and are generally the most severe storms, that is, S. Ciprian, S. Felipe II, S. Ciriaco, Hurricanes Georges, and Maria (but not Hurricane Betsy; Table 1, Fig. 2). Interestingly, Hurricane Irma passed well to the northeast of Puerto Rico (Fig. 2) yet due to its high intensity was able to generate F2 damage levels in Puerto Rico.

The importance of high sea surface temperatures (SSTs) on the hurricane formation (Knutson et al. 2010) leads to the question of whether hurricanes have always been as frequent as they are now. Researchers have assumed that the contribution of hurricanes to the disturbance regime has not changed over time, thereby representing a strong selection pressure on the evolution of the biota (Francis and Alemañy 2003, Brokaw et al. 2004, Griffith et al. 2008). During glacial periods when SSTs were lower, storm generation might have been reduced compared to during the more recent, warm interglacial period. Modeling of cyclonic storms during the last glacial maximum (LGM), approximately 18,000 yr ago, suggests that HES were prevalent in the northwest Pacific Ocean even during the coldest periods of the Pleistocene (Yoo et al. 2016). A study of the Atlantic that used earlier versions of global circulation models suggested that storm intensity might have been somewhat lower during the LGM compared to recent times (Hobgood and Cerveny 1988). Taken together, these results suggest that hurricanes and tropical storms have been a prevalent part of the disturbance regime of Puerto Rico and the Caribbean throughout much of the Pleistocene and probably before, with a reasonable likelihood of affecting the evolution of native biota or of filtering the species that are able to persist after immigrating to the islands.

Patterns of hurricane disturbance dating to 5000 yr before present were revealed by studies of sediment deposits in a coastal bay on Vieques (Donnelly and Woodruff 2007). The frequency of landfall by intense hurricanes in the record has varied on centennial to millennial scales over this interval, with periods (~1000 yr) of highly frequent and intense hurricanes alternating with relatively calm periods. This variability was probably modulated by atmospheric dynamics associated with variations in the El Niño–Southern Oscillation and the West African monsoon (Donnelly and Woodruff 2007). Thus, storm frequency has varied considerably over time in Puerto Rico, but intense storms have been a dominant part of the disturbance regime for millennia. This disturbance regime would be expected to select for trees adapted to frequent wind disturbance (Francis and Alemañy 2003, Griffith et al. 2008), including resistance to withstand and survive high winds or resilience to quickly re-colonize and dominate the canopy (Zimmerman et al. 1994, Uriarte et al. 2012). Similarly, other components of the biota should evolve traits to enable broad-sense resilience to the direct and indirect effects of HES (e.g., Donihue et al. 2018).

Other components of the disturbance regime

Additional atmospheric sources of disturbance in Puerto Rico include non-cyclonic tropical storms and extratropical frontal systems (Scatena et al. 2012) that may produce local storms of high intensity, yielding localized, intense flooding events, and lesser storms that last several days over the entire region, and therefore trigger widespread landslides in mountainous areas (Walker et al. 1996).

Droughts are a more recently appreciated part of the disturbance regime to forests of eastern Puerto Rico (Beard et al. 2005). The impact of droughts on forest and stream ecosystems has been summarized by Scatena et al. (2012), with more context and information on consequences to human populations provided by Larsen (2000). Landslides, which occur following heavy rains and are frequently associated with roads (Walker et al. 1996), typically affect about 1% of the Luquillo Mountains per century. Wildland fires are not extensive in the area, being generally restricted to small patches (<0.5 ha) of disturbed vegetation along roadsides or in abandoned fields (Scatena et al. 2012).

Human disturbance of the study site includes conversion of forest to agriculture or agroforestry, water diversions from streams, hunting and fishing, recreation, road building, and urbanization (Scatena et al. 2012). Much of the coastal plain and lower flanks of the mountains was dominated by sugarcane production until the mid-20th Century (Grau et al. 2003, Zimmerman et al. 2007) but was eventually converted to pastures before being abandoned beginning in the 1960s (Thomlinson et al. 1996). Coffee cultivation dominated in the uplands throughout Puerto Rico (less so in the LEF), but now only continues in the western Cordillera Central (Zimmerman et al. 2007).

Future disturbance regimes

Future disturbance regimes are likely to be dominated by more frequent, intense hurricanes and by a more variable precipitation regime, including more frequent and intense flooding events and droughts. Knutson et al. (2010) reviewed the evidence for how a warming world will affect hurricane frequency and intensity, concluding that overall storm frequency will be lower in a warmer world because higher average wind shear caused by warming will dissipate storms before they can intensify. However, once formed, higher sea surface temperatures will cause storms to develop at higher intensities, with an overall shift of storm intensities to the highest categories (4 and 5 on the Saffir-Simpson scale). Nonetheless, hurricane destructiveness has increased across the western tropical Atlantic since the 1970s (Emanuel 2005). Some have linked such trends to sea surface warming associated with climate change (Webster et al. 2005, Mann and Emanuel 2006). In contrast, others have warned about the complex uncertainties associated with factors other than sea surface warming, such as the shifting position of the mid-Atlantic ridge and low-altitude easterly winds (Trenberth 2005).

Working from climate downscaling results from Hayhoe (2013), Henereh et al. (2016) showed that the climate should become warmer in Puerto Rico, particularly in the lowlands. They predict that humid forest, which dominates lower elevations, will become dry and thorn scrub forests by the end of the century. Declines in precipitation (20–50%) are likely, with reductions in rainfall in very wet forests at high elevations being the greatest. Declining precipitation with be accompanied by steady increases in total number of dry days (less than a mm of rainfall). Hayhoe (2013) noted the increase in the number of dry days in the climate simulations for the last decades of the century, but emphasized that an increase in high rainfall events will likely to lead to an increase in the number of flooding episodes. Thus, the future will likely be dominated by a climate with hotter and drier conditions, on average, combined with more frequent extreme events (droughts, floods, and heat waves). Moreover, sclerochronological evidence from Mona Island (Fig. 1) using Sr-U proxies from Laminar star coral, *Orbicella faveolata*, suggests that a significant sea surface warming trend characterized the 20th century and early 21st century (Alpert et al. 2017). This further corroborates the overall warming trends of this region of the Caribbean.

Physical Manifestation of Hurricane Disturbance

Data on wind speed, rainfall, and peak stream flow associated with cyclonic storms in Puerto Rico since the late 1950s demonstrate that storms differ greatly in critical characteristics (Scatena et al. 2012). Particular storms also differ in aspects of severity due to storm path and intensity, as well as due to the topography of the land at which they cross the island. For example, Hurricane Hugo approached the island as a Category 3 storm, but decreased in intensity as it passed over the northeast corner of the island (Scatena and Larsen 1991), departing the region as a Category 1 storm. Damaging winds most strongly affected the eastern and northern slopes of the Luquillo Mountains; the effect of the storm west of San Juan was small. In contrast, Hurricane Georges entered the island near Humacao as a Category 2 storm, and continued along the center of the island before departing as a Category 3 storm. Island-wide damage was concomitantly much more widespread. Storm surge due to Hurricane Hugo ranged from 0.6 to 1.0 m along the coast to the east of San Juan (Rodriguez et al. 1994; Table 1), with waves adding an additional 1.5–3.0 m. Importantly, coastal geomorphology can significantly magnify storm surge effects. For example, storm surge during Hurricane Hugo reached 3.0 m in Ensenada Honda, Culebra, a bay whose opening faced into the strongest winds. The storm surge due to Hurricane Georges was 3.0 m, with an additional 6.0 m due to waves (Guiney 1998). Storm surge and waves flatten beach profiles and move sand inland along exposed coastal areas (Bush 1991, Rodriguez et al. 1994). Flooding from streams and due to ponding is a localized effect of hurricanes in Puerto Rico, but was a major impact of Hurricane Hugo in San Juan (Rodriguez et al. 1994). Similarly, residents at the mouth of the Fajardo River remembered Hurricane Hugo as one of two major flooding events to most strongly affect their communities (López-Marrero 2010, López-Marrero and Yarnal 2010).

In coastal and marine ecosystems, storms can cause extensive coral colony fragmentation and dislodgment (Lirman and Fong 1997), incidental coral mortality due to sediment bedload associated with horizontal transport (Hubbard 1986), and even mechanical destruction of coral reef frameworks (Rogers 1992). Hurricanes may stimulate major macroalgal blooms (Roff et al. 2015), and in the long term alter benthic community structure (Hughes 1994), with limited resilience (Stoddart 1969, Mallela and Crabbe 2009). Indeed, the recent impact of two consecutive Category 5 storms, Hurricanes Irma and María, across the northeastern Caribbean in 2017 caused extensive and unprecedented impacts on coral reefs of northeastern Puerto Rican, particularly near Culebra. This included the nearly total extirpation of shallow water populations of Staghorn coral (*Acropora cervicornis*), the extensive destruction of biotopes of Finger coral (*Porites porites*), and unprecedented mechanical destruction of reef spur systems. These resulted in the formation of extensive rubble fields (E. A. Hernández-Delgado, *unpublished data*).

Storms can also alter the distribution of sediments, sometimes burying associated seagrass habitats (Rodriguez et al. 1994, Cabaço et al. 2008, van Tussenbroek et al. 2014) and fostering the formation of extensive bottom gaps that were quickly colonized by the rapidly spreading invasive seagrass, *Halophila stipulacea* (E. A. Hernández-Delgado et al., *unpublished manuscript*). This opportunist species has largely displaced native seagrasses across the eastern Caribbean region since 2002, and hurricanes may play a critical role in their dispersal. Moreover, intense hurricanes have the potential to produce significant wave scouring of the bottom and thereby destroy the seagrass matrix (E. A. Hernández-Delgado et al., *unpublished manuscript*).

Immediate Effects to Uplands

Producers

The immediate impacts of hurricanes to tabonuco forest in Puerto Rico have been studied extensively (e.g., Walker et al. 1991, Zimmerman et al. 1994, Scatena et al. 1996, Beard et al. 2005) and reviewed elsewhere (Crowl et al. 2012, Brokaw et al. 2012*a*). Only key elements are described hereafter. Wind damage by Hurricane Hugo to trees was quite severe (Walker et al. 1991), particularly in topographically exposed areas (Basnet et al. 1992, Boose et al. 1994). Hurricane Hugo reduced canopy height by as much as 14 m (Brokaw et al. 2012*b*) and caused a marked decline in fine root biomass in tabonuco forest (Parrotta and Lodge 1991, Silver and Vogt 1993). Despite severe damage to forest canopies, relatively few trees (9–20% of stems) died in the storm (Basnet et al. 1992, Zimmerman et al. 1994). This indicates one aspect of tree resistance to hurricane damage. Moreover, pioneer species, such as *Cecropia schreberiana*, suffered greater mortality (~40%) than did mature forest species, such as *Dacryodes excelsa*, for which mortality was ~1% (Zimmerman et al. 1994). Recent data for Hurricane Maria suggest similar patterns as found following Hurricane Hugo, but with increased levels of stem damage caused by higher wind speeds and greater rainfall (Uriarte et al. 2019). Life-history characteristics (i.e., wood density) did not strongly determine the mortality of particular tree species in response to disturbance from Hurricane Maria compared to Hurricane Hugo, suggesting that intense hurricanes have stronger but less predictable effects on tree communities.

Storm damage to forest canopies varied with elevation (Brokaw and Grear 1991). Least damaged was short-statured elfin forest at the mountain summits. In turn, palo colorado forest at intermediate elevations was less damaged than was taller tabonuco forest at the lowest elevations. Thus, patterns of storm resistance were elevation-specific and related to differences among forests in stature and species composition.

Nutrient flux

Intense HES like Hurricane Hugo deposit a great deal of litter and associated nutrients to the forest floor. Fine litterfall during Hurricane Hugo exceeded usual yearly total mass by 20%. Because leaves deposited on the forest floor by Hurricane Hugo were green, they contained higher levels of N and P compared to the usual litter that is dominated by senescent leaves. The result was that hurricane litter from a single day contained high nutrient levels (e.g., 3.3 times the annual average for phosphorus; Lodge et al. 1991, Scatena et al. 1996).

Stream characteristics

Flooding associated with hurricanes is not substantially different than that occurring through the year from other causes. However, hurricane-induced damage to the forest canopy results in deposition of large woody debris (tree branches and trunks) into stream channels that produce large debris dams that strongly affect stream architecture (pool and riffle characteristics) and influence long-term responses of the biota (Covich et al. 1991).

Heterotrophs

Species vagility, combined with tolerance of high light levels and dry conditions that prevail immediately after a hurricane, strongly influenced responses of consumers to Hurricane Hugo (Zimmerman et al. 1996). The response to Hurricane Hugo, however, was compounded by a severe drought that persisted for the three months after the hurricane (Scatena and Larsen 1991). Although some birds and bats decamped following the storm, insectivorous species were influenced less than were species that consume flowers and fruits (Waide 1991, Gannon and Willig 1994). In contrast, the abundances of four species of terrestrial gastropod (*Caracolus caracolla, Polydontes acutangual, Nenia tridens, and Gaeotis nigrolineata*) and two species of walking stick (*Lamponius portoricensis and Agamemnon iphemedeias*) declined sharply in tabonuco forest immediately after hurricane impact (Willig and Camilo

1991). Moreover, the resistance of populations of *L. portoricensis* to Hurricane Hugo (97% reduction in abundance) was much less than resistance to Hurricane Georges (21% reduction in abundance), likely a consequence of marked differences in the physical effects of the two storms (Willig et al. 2010). Yet, not all responses by less vagile species were negative. The abundances of frogs (*Eleutherodactyus coqui*) and decapod shrimp increased initially in response to hurricane disturbance (Woolbright 1991, 1996, Covich et al. 1991). This probably occurred because debris provided refuge (frogs) or resources (shrimp) that compensated for other negative effects of the hurricane. The responses of anoline lizards to hurricane disturbance were diverse and related to species-specific habitat associations in forest canopies (Reagan 1991). Those species that occur in the shady understory of closed canopy forest declined sharply in abundance. Those found in tree crowns increased greatly, probably because the lack of over story in the damaged forest resulted in the downward movement individuals to occupy ground-level habitats. The immediate effects of Hurricane Hugo on common bats in tabonuco forest were species-specific (Gannon and Willig 1994). After a year, the abundance of *Artibeus jamaicensis* declined to less than 10% of pre-hurricane numbers and the abundance of *Stenoderma rufum* declined to less than 50% of pre-hurricane numbers. In contrast to these two frugivores, the abundance of *Monophyllus redmani*, a nectarivore, declined initially but within a year had essentially returned to pre-hurricane numbers. Moreover, the home ranges and foraging ranges of *S. rufum* increased significantly after the hurricane and did so in the same manner for males and females. This was likely a behavioral response that reflected the need to traverse larger areas to obtain food or secure roosting sites in the canopy of trees.

Foraging range of the Puerto Rican boa (*Epicrates inornatus*) increased after Hurricane Georges (Wunderle et al. 2004) for two reasons. First, individuals traveled longer distance to seek favorable cover conditions in the heterogeneous and rapidly changing understory of the forest. Second, longer foraging bouts were required to find and secure suitable prey as a consequence of the altered abundance and spatial distribution of prey species in the post-disturbance forest.

Immediate Effects to Lowlands

Producers

The short-term dynamics (4–5 yr) of secondary forest stands 15–81 yr post-abandonment were investigated in the Luquillo and Carite Mountains of eastern Puerto Rico in response to disturbance by Hurricane Georges (Pascarella et al. 2004). Stem densities decreased in all sites, with sites of intermediate-age exhibiting the greatest decrease in density and the largest change in the size distribution of trees. The density of the largest stems increased due to growth of survivors, whereas that of small size classes significantly decreased, apparently due to physical damage from falling debris. Overall, basal area decreased in 11 of 15 sites while exhibiting only a slight gain in the other sites. In all but one site, species richness decreased, largely because of decreases in stem density (number of individuals). The proportional loss in species was greater for shrubs than for tree species. Thus, the immediate impacts of Hurricane Georges on secondary forests in lowland areas were greatest in intermediate-aged stands (Pascarella et al. 2004).

Sociological characteristics

Total estimated property damage by Hurricane Hugo exceeded $1 billion U.S. dollars (Miner Solá 1995; Table 1). Twelve human deaths were associated with the storm, and many of these deaths were caused by electrocutions during the effort to restore electrical power (CDC 1998). Although electrical power to many areas was restored in about ten days, residents in more rural areas waited as much as two months for power services to return (J. Bithorn, *personal communication*). Although many people in Puerto Rico occupy concrete structures that are resistant to storm damage, over 80 percent of the wooden structures on the off-shore islands of Culebra and Vieques were destroyed by the storm, temporarily leaving more than 30,000 people homeless (Schwab et al. 1996).

Hurricane Georges was the first intense hurricane to traverse the length of the island since Hurricane San Ciprian in 1932 (Miner Solá 1995). Winds damaged 72,605 houses and destroyed an additional 28,005 more, leaving tens of thousands of people homeless after the storm's passage. Nearly half of the island's electric lines were lost, leaving 96% of the population without electricity. In contrast, only 8.4% of the population lost telephone service. Lack of electricity left water pumps without power, resulting in the loss of water and sewer service to 75% of the island. Moreover, the storm caused significant damage to the agricultural industry, including the loss of 95% of the year's banana and plantain crop, 75% of its coffee crop, and 65% of its poultry production. In total, Hurricane Georges caused $3 billion U.S. dollars in damage (Table 1) and resulted in few apparent casualties (although Acosta and Irizarry [2018] suggest this number was much higher). Sattler et al. (2002) and van Bloem and Martin (2020) provide additional details. In contrast to Hurricane Hugo, which damaged or destroyed many thousands of homes on Culebra, Hurricane Georges only destroyed 74 houses and damaged 89 others.

The immediate effects of Hurricanes Irma and Maria were especially severe. Although still being evaluated, the death toll was in excess of 1,000 persons (e.g., Santos-Lozada and Howard 2018; Table 1), much more than the 64 reported by local authorities. The damage resulted in the loss of electricity and cell phone service to the entire island (Pasch et al. 2018). Many buildings and bridges were destroyed by high winds, flooding, and coastal surge; surges particularly affected the eastern coast. Total damage was estimated at $90 billion U.S. dollars (Table 1), albeit with a wide confidence interval (Pasch et al. 2018).

Immediate Effects to Coastal and Marine Ecosystems

Intense hurricanes can have devastating effects on coral reefs and associated ecosystems. Hurricane Hugo strongly affected coastal and marine areas of northeastern Puerto Rico (Rodriguez et al. 1994), resulting in flattened beach profiles and inland wave incursions ranging widely from 30 to 250 m. Impacts were influenced by shoreline composition (sandy vs. rocky stretches) and morphology, with the rocky portions of shoreline offering greater protection from wind-driven waves (Bush 1991). Hurricane impacts depend on multiple factors, including the geographic orientation of the reef in relation to the pathway of the storm (Bries et al. 2004), as well as factors such as geographic location (i.e., windward, leeward), reef zone, wave energy, bottom topography, and benthic composition of the reef (Bonem 1988). Reef crest depth might also have a critical influence on the effect of hurricanes to backreef communities (Graus and Macintyre 1989). Shallow reefs play a critical role in reducing up to 97% of wave energy. However, models based on increasing sea level, in combination with reef flattening, suggest that the wave energy environments across reef flats and backreef communities will be enhanced by future HES (Storlazzi et al. 2011). Thus, shallow degraded reef systems and their adjacent coastlines can be more exposed to effects of HES across the shallow reef flats, and backreef or lagoonal habitats (i.e., seagrasses) because reefs have been lowered by previous storms.

Wind-driven currents from Hurricane Hugo damaged exposed coral reefs and dispersed marine sediments. For example, the extent of a large and prominent sand deposit, the *Escollo de Arenas* near the western tip of Vieques, increased by 60% as a consequence of a hurricane-driven sand. Turbulent seas dispersed sediment deposits and buried nearby seagrass beds (Rodriguez et al. 1994). Nonetheless, little sediment was lost to the Puerto Rico Trench. Natural geologic barriers, such as the petrified beaches that parallel the coast, prevent loss of sediment to the trench. Consequently, lateral movement of sediment dominated during the storm (Schwab et al. 1996).

Strong wave action during hurricanes can stochastically re-shape benthic assemblages in coral reefs, mostly due to significant coral and sponge dislodgment as well as habitat fragmentation (Álvarez-Filip and Gil 2006). Damage can be dependent on the topography of reef benthos: Flattened locations are more vulnerable with depth as a significant controlling effect (Harmelin-Vivien and Laboute 1986). Although the most significant damage generally occurs within a depth of 5 m (Hernández-Avila et al. 1977), depending on storm intensity, distance, and pathway, damage from intense hurricanes has been documented down to 10–12 m and as much as 50 m in the Caribbean (Woodley et al. 1981). Critically, coral reef formations that are characterized by short wave-breaking zones over the steep reef faces can facilitate the formation of highly destructive, tsunami-like, infra-gravitational waves (Roeber and Bricker 2015). Consequently, under some local circumstances extreme wave action can play a significant destructive role. Windward coral reefs to the east of Culebra, dominated by Elkhorn coral, *Acropora palmata*, were heavily damaged by Hurricane Hugo, whereas leeward reefs suffered almost no damage (Rodriguez et al. 1994). Reefs flattened by storms show little ability to recover (Gardner et al. 2003, 2005) and can have profound long-term impacts on reef fish assemblages (Alvarez-Filip et al. 2009, 2015). Such reef flattening has been associated with the widespread decline of *A. palmata*, historically the most important coral reef builder supporting associated shallow Caribbean reef assemblages (Lugo et al. 2000*b*). The combination of rapidly declining coral cover, rapid colonization by algae, and fishing impacts may further affect recovery to pre-hurricane conditions (Rogers et al. 1997). These anthropogenic effects will likely make reefs even more susceptible to future HES.

An indirect form of hurricane damage results from extreme rainfall events and massive runoff. Extreme rainfall can produce catastrophic flooding and localized coral mortality across shallow coral reefs adjacent to the shoreline (Goenaga and Canals 1979). Staghorn coral, *A. cervicornis*, is particularly vulnerable to freshwater exposure (Hernández-Delgado et al. 2014*a*). Moreover, recruitment patterns following hurricanes and other major types of disturbances (i.e., recurrent mass bleaching and coral mortality events) have resulted in long-term shifts that favor ephemeral species in contrast to dominance by typical large-sized, persistent species (Loubersac et al. 1988, Hernández et al. 2014*b*). Recurrent runoff events in Puerto Rico have had long-term, persistent effects on fringing coral reef assemblages (Hernández-Delgado et al. 2017, Otaño-Cruz et al. 2017, 2019), producing novel ecosystems. These runoff events increase the vulnerability of shallow coastal reef assemblages to future storm events. This suggests the increasing need for coral farming and reef rehabilitation as emerging tools for restoration after hurricane damage to catalyze reef accretion and restore coastal resilience (Hernández-Delgado et al. 2018*a*, *b*).

Long-Term Responses in the Uplands

The intermediate- to long-term responses of the uplands to the impacts of Hurricane Hugo were summarized briefly by Zimmerman et al. (1996) and more thoroughly by Brokaw et al. (2012*b*). Key classes of response to disturbance were characterized as recovery trajectories based on observational (Zimmerman et al. 1996) and experimental studies (Shiels et al. 2015) in tabonuco forest.

Producers

Most trees regenerated new crowns within 20 weeks of Hurricane Hugo (Walker 1991) and rates of fine litterfall approached pre-storm levels within five years after the storm (Scatena et al. 1996, Brokaw et al. 2012*b*). Root biomass, however, had not recovered pre-Hugo levels ten years later (Yaffar and Norby 2020). As the forest recovered, recruitment of pioneers led to net increases in the nitrogen and phosphorus contained in forest biomass compared to that measured before the storm (Scatena et al. 1996). Uriarte et al. (2019) recently demonstrated substantial delayed mortality (to 1995) in Hugo-damaged trees in many species, challenging the perception that upland forests are resistant to the effects of hurricanes in the long-term. Tracking the effects of Hurricane Maria on long-term mortality patterns will be important in resolving this issue.

Nutrient flux

Green leaf litter deposited during storms, despite high nutrient levels compared to senescent litter, had little long-term effects on the nutrient content of forest soils (Ostertag et al. 2003). Decomposing course woody debris (CWD) can immobilize soil N, thereby reducing its availability to plants and temporarily reducing primary productivity (Zimmerman et al. 1995*b*). As pioneers began to numerically dominate forest stands after Hurricane Hugo, nutrient fluxes in litterfall increased dramatically, exceeding pre-storm levels (Scatena et al. 1996).

Stream characteristics

The flux of NO^{-3} and K^{+} increased in streams in response to Hurricane Hugo (Schaefer et al. 2000), a pattern repeated after Hurricane Georges (McDowell et al. 2013), albeit to a lesser degree. Fluxes of NO^{-3} may be attributed to decomposition of hurricane-formed debris and dead roots in watersheds following the storm, and not primarily due to in-stream sources, although these could have contributed (McDowell and Liptzin 2014).

Heterotrophs

One of the biophysical surprises associated with Hurricane Hugo was the transient positive impacts (i.e., increases in abundance) on some animal populations, such as frogs and shrimps (Woolbright 1991, 1996, Covich et al. 1991). Such surprises can be understood in terms of hurricane-caused increases in resource availability or habitat quality (Zimmerman et al. 1996). In tabonuco forest, abundances of some terrestrial gastropod species exhibited dramatic increases five years after Hurricane Hugo (e.g., *C. caracolla*, 3-fold increase; N. *tridens*, 7-fold increase; *P. acutangula*, 2-fold increase; *G. nigrolineata*, 6-fold increase), reversing initial declines as they exploited favorable microhabitats and augmented resources associated with plant secondary succession (Secrest et al. 1996). Nonetheless, long-term population trends of 17 species of terrestrial gastropod indicate that each species responded to disturbances from Hurricanes Hugo and Georges in a consistent fashion (Bloch and Willig 2006): Two species linearly increased in density, two species linearly decreased in density, and 13 species exhibited no significant linear trend in density following disturbance. Population responses probably hinge on trade-offs between sensitivity to microclimatic changes, understory structure, and resource availability. Community-level responses (species richness, evenness, and nestedness) of gastropods to hurricane-induced reconfiguration of the landscape within tabonuco forests suggest the importance of cross-scale interactions (Willig et al. 2007). Nonetheless, the structure of the gastropod metacommunity in tabonuco forest was remarkably consistent over time, suggesting a canonical structure characterized by compartments associated in part with previous land use (M. R. Willig et al., *unpublished manuscript*).

In tabonuco forest, temporal trajectories of abundance of the walking stick *L. portoricesis* during secondary succession (i.e., patterns of resilience) differed statistically between Hurricanes Hugo and Georges, as well as among historical land-use categories (i.e., agricultural practices and associated canopy opening) on the Luquillo Forest Dynamics Plot (Willig et al. 2010). Moreover, the effects of hurricanes and land-use histories were independent of each other. These complex results likely arise because of differences in the intensities of the two hurricanes with respect to microclimatic effects of the hurricanes (i.e., temperature and moisture) in the forest understory, as well as because of time-lags in the response of walking sticks to changes in the abundance and distribution of preferred food plants (*Piper*) in post-hurricane environments.

Long-term changes in populations and communities of arboreal arthropods in tabonuco forest are complex (Schowalter et al. 2017) and depend on the legacy of previous disturbances. As a main effect or via an interaction with time, gaps created by Hurricane Hugo affected taxon abundance in 15 of 58 (26%) analyses, guild abundance in 13 of 42 (31%) analyses, and taxonomic biodiversity in 6 of 30 (20%) analyses. As a main effect or via an interaction with gap legacy, time after Georges affected taxon abundance in 13 of 58 (22%) analyses, guild abundance in 10 of 42 (24%) analyses, and taxonomic biodiversity in 11 of 30 (37%) analyses.

Recently, Lister and Garcia (2018, 2019) contended that many animal populations (i.e., walking sticks, canopy arthropods, frogs, and birds) in the Luquillo Forest were declining as a consequence of global warming, and that this was leading to the collapse of food webs. In contrast, Willig et al. (2019*a*, *b*), using the same or augmented data, found little evidence to support for either claim. Instead, long-term trajectories of populations were species-specific and reflected dynamics associated with disturbance and secondary succession linked to HES. Nonetheless, disentangling the effects of global warming from those derived from local cooling during the process of post-hurricane canopy closing, as well as from successional changes in the structure, microclimate, and composition of the forest at spatial scales relevant to target animal species, needs to be undertaken over many cycles of hurricane disturbance to confidently ascribe causation to press or pulse disturbances that occur in concert.

Long-Term Responses of Lowlands

Secondary forest stands in north-central and eastern Puerto Rico, originally measured prior to

Hurricane Georges in 1996, were revisited 9 yr post-hurricane to study how hurricane disturbance alters post-abandonment succession (Flynn et al. 2010). As found previously (Pascarella et al. 2004), the dynamics were dependent on stand age but this study also accounted for exposure to hurricane effects using models of storm meteorology and topographic exposure to hurricane winds (Boose et al. 1994, 2004). In the oldest stands, the density and basal area of large trees declined with increasing exposure to hurricane winds, altering the stand structure to that characteristic of younger stands. In contrast, in younger stands, the basal area (but not density) of large trees generally increased with increasing hurricane wind exposure. Hurricanes can alter the successional trajectory of secondary forests recovering from previous human disturbances, although the overall patterns were complicated by site precipitation and soil type, in addition to site age and hurricane exposure (Flynn et al. 2010).

Little information documents the long-term recovery of the social component of social–ecological systems to Hurricanes Hugo or Georges in northeastern Puerto Rico. Relief efforts following each storm led to construction booms, as residents were able to replace destroyed wooden homes with new concrete structures using federal government relief funds (J. Bithorn, *personal communication*). But no detailed information exists on which homes were most vulnerable to storm damage or the degree to which residents utilized access to relief funds to mitigate the long-term negative effects of the storm. The great interest generated by the devastation of Hurricane Maria in Puerto Rico will likely lead to a deeper understanding of these patterns, and the role of resource subsidies from the federal government in enhancing resilience (a kind of socioeconomic source-sink dynamic or rescue effect).

Long-Term Responses in the Coastal and Marine Zone

For Puerto Rico, long-term responses of coastal and marine areas are poorly documented. Post-Hugo changes to beach profiles included a return to pre-storm conditions in many areas, although beach recovery was slow to occur where human infrastructure was damaged extensively (USGS 2016). In addition, reefs on the east side of Culebra, despite heavy damage from Hurricane Hugo, exhibited signs of healthy regrowth. Indeed, based on geological evidence, HES may be necessary for healthy growth of coral reefs in the same way that fire is necessary for healthy plant growth in other ecological systems (e.g., grasslands of the Great Plains, montane forests of California). Human-driven reef decline often results in the evolution of a novel coral reef ecosystem (sensu Hobbs et al. 2009). As such, highly altered reef communities exhibit little resilience and instead have a significantly increased vulnerability to storm events and a rapid turnover of species (Hoegh-Guldberg et al. 2007, Veron et al. 2009, Hernández-Delgado 2015).

Bleaching events and mass coral mortality across the northeastern Caribbean (Rogers and Miller 2006, Miller et al. 2006, 2009, Hernández-Pacheco et al. 2011), as well as impacts of sediment loads from rivers draining into the ocean, degrade reef systems (Rogers 1990, Larsen and Webb 2009). For example, over decadal time spans, warming ocean temperature and its effects on water quality via sediment dynamics have had a larger impact on the near-shore marine systems than have the intensity or frequency of hurricanes, including direct and indirect mechanisms of action (Hernandez-Delgado 2015). Long-term dynamics of coral reefs are also significantly influenced by land-based sources of pollution (Sladek Nowlis et al. 1997, Bonkosky et al. 2009, Hernández-Delgado et al. 2010, 2017, Otaño-Cruz et al. 2017, 2019) and by long-term alterations in land-use patterns (Ramos-Scharrón et al. 2012, 2015). In this broader context, the long-term response of marine systems to hurricanes must be interpreted carefully by fully considering the confounding effects of persistent anthropogenic influences such as warming seas, bleaching events, pollution, and sedimentation. Importantly, altered connectivity along the ridge-to-reef gradient plays a fundamental role in affecting trajectories of recovery. For instance, any meaningful hydromodification, alteration in land use at the watershed scale, or modification of water quality of streams and rivers due to land-based source pollution can result in altered terrestrial-marine connectivity. This can potentially result from altered flows of water, nutrients, and energy to estuarine and coastal habitats, increasing coastal vulnerability to potential turbid, sediment-laden, and nutrient-loaded pulse runoff events, which could lead to chronic degradation of adjacent coral reef ecosystems (Ennis et al. 2016, Hernández-Delgado et al. 2017, Otaño-Cruz et al. 2017, 2019).

Discussion

Utilizing a unique approach to measuring HES impacts that draws information from both natural and human components of SES (Boose et al. 2004), we find that the eastern portion of Puerto Rico has historically faced the greatest amount of hurricane disturbance in recent human history, and that this pattern has probably existed for millennia. Separating the area into three subsystems (i.e., ridge, lowlands, and reef), we find evidence of important variation in the resistance, resilience, and vulnerability that describe the response of the SES to HES (Table 2), and evidence of adaptation in human systems as well as in natural ones. We find a distinct pattern of broad-sense resilience that declines from the relatively resilient forested ridges to the marine systems, where multiple anthropogenic stressors convey high vulnerability to HES. The intermediate lowlands, where secondary forests and human habitations are found, appear intermediate in broad-sense resilience to HES because of relatively more vulnerable tree species in the aggrading forests and a limited degree of human adaptation to severe HES.

One general conclusion of our review is that the history and intensity of anthropogenic disturbance strongly influence patterns of broad-sense resilience and vulnerability to HES, from the uplands through the lowlands to marine systems. Upland forests exhibit the lowest anthropogenic disturbance, occurring at or above the elevation where the tide of humanity had risen and then receded in the Luquillo Mountains as human fortunes waxed and waned (Scatena 1989, Rudel et al. 2000, Thompson et al. 2002, Grau et al. 2003). In upland areas, hurricane effects on primary forests, including resident animal populations and communities, are well characterized and show evidence of resistance and narrow sense resilience that have likely evolved in the context of millennia of hurricane disturbances (Zimmerman et al. 1994, Brokaw et al. 2004, 2012*a*).

Broad-sense resilience to HES in lowland secondary forests is less than that in primary forests on ridges. Secondary tree species are fast-growing and, therefore, less wind firm (Zimmerman et al. 1994, Uriarte et al. 2012), and this contributes to less broad-sense resilience of forests to HES. Forest structure is an important additional factor in secondary forests. Younger, less tall forests are subject to less wind damage from hurricanes than are taller, older forests (Pascarella et al. 2004, Flynn et al. 2010). The combination of the two factors, wind resistance and structure, yields an overall intermediate level of resilience to HES compared to the situation in the uplands or in marine systems.

The lowlands also provide evidence of human adaptation to HES via improved house construction and increased responsiveness of social and political systems, which historically increased broad-sense resilience to hurricanes, as witnessed by reduced human deaths attributed to the storms. This is despite the fact that more human structures have been placed in harm's way, leading to increased economic losses during storms (Pielke et al. 2003). Recent experiences suggest that there is a limit to resilience to HES. Hurricanes Irma and Maria in the Caribbean clearly have shown how the most intense HES challenge human subsystems greatly. Moreover, the high death toll in Puerto Rico during Hurricane Maria suggests that authorities may be poorly preparing or accounting for the effects of HES on human populations. The experience brought doubt to the finding that there were only 12 storm-related deaths during Hurricane Georges, a less intense storm than Hurricane Maria that, nonetheless, traversed the entire island leading to long-term (over two months) power outages in rural and impoverished areas. Indeed, applying similar methods to that of Santos-Lozada and Howard (2018) to mortality data following Hurricane Georges, Acosta and Irizarry (2018) suggest that there may have been 1300 storm-related deaths during and following the hurricane. This inability to account for delayed effects on the way we quantify death tolls underscores like nothing else how poorly we are able to document the effects of HES on the human subcomponent of SES.

Table 2. Summary of the effects of HES on the ridge to reef social–ecological systems of northeastern Puerto Rico.

System	Immediate	Long-term
Ridge	Large increase in forest canopy openness and alteration of 3-dimensional structure; large inputs of debris and nutrients to forest floor	Rapid recovery of canopy restores key ecosystem functions (e.g., leaf litterfall rate) in as little as five years, accompanied by massive recruitment of pioneer species of trees and shrubs
	Low immediate mortality in many tree species except in most intense storms; high tree mortality in pioneer trees species at all times; reduction in fine root biomass	Decomposing coarse woody debris immobilizes some inorganic soil N. Large transitory losses of NO_3^- from streams attributed to decomposition of hurricane-generated fine debris
	Damage to forest canopies decreases with elevation (and forest type)	Increases in abundances of coqui and shrimp. Increases in other invertebrate populations common but species-specific variations reflect sensitivities to key ecological conditions such as microclimate or resource availability
	Stream flooding not unusual but large inputs of debris cause dam formation	
	Heterotroph responses varied but dependent on species-specific vagility and tolerance to hot or dry conditions	
Lowlands	Low resistance to HES in secondary forest stands of intermediate age and structure	Long-term dynamics of secondary forests determined by stand age interacting with hurricane wind exposure and other site factors
	Effects on human habitations depend on construction (wood vs. concrete); loss of electric and water service widespread and often long lasting (weeks to months)	Long-term responses of human populations poorly documented; anecdotal evidence of construction booms following hurricanes and improved housing (possibly linked to "subsidies" from the federal government that might not be available in developing countries)
	Human death attributed to storms often low; large numbers of deaths associated with collapse of health system recently documented	
Reef	Flattened beach profiles, inland wave incursions, large movements of marine sand deposits; no apparent loss of sediments to Puerto Rico Trench	Natural restoration of beach profiles
	Damage to exposed coral reefs; damage increased by anthropogenic stressors (pollution, coral bleaching) and freshwater exposure	Little apparent resilience of anthropogenically stressed coral reefs resulting in permanent loss without restoration efforts

López-Marrero and Wisner (2012) recently reviewed patterns of vulnerability to natural disturbance in the Caribbean, finding access to natural, physical, economic, human, social, and political resources all strongly determine how effectively humans are able to contend with and manage disasters like HES. In eastern Puerto Rico, López-Marrero (2010) and López-Marrero and Yarnel (2010) creatively documented the components of vulnerability of two coastal, low-income communities that are frequently flooded by hurricanes and other rainstorms. Residents rely strongly on neighbors following severe disturbances and employ various coping mechanisms to respond in the short term and to recover in the long term. Government agencies respond more slowly, if at all, to the needs of these poor communities. The recent effects of Hurricane Maria in Puerto Rico provided stark evidence of this dichotomy. The apparent failures of local and federal governments to respond to a natural disaster of this magnitude will hopefully be more fully documented than responses to earlier storms and will lead to improved policies and preparedness to minimize social injustice associated with potentially devastating consequences of HES.

Extensive long-term studies of coral reefs have demonstrated significant anthropogenic declines in ecological health across large spatial scales (Gardner et al. 2003, 2005, Paddack et al. 2009, Jackson et al. 2014). Damage from HES can have strong impacts on reef framework (Harmelin-Vivien and Laboute 1986, Woodley 1993), often resulting in the loss of a significant proportion of live coral cover (Mah and Stearn 1986) and benthic spatial heterogeneity (Woodley et al. 1981), especially across shallow reef assemblages, leading to declines in fish populations (Kaufman 1983).

Impacts of HES on coral reefs and associated ecosystems will depend on the temporal and spatial scales under consideration, species-specific life-history traits, morphology of dominant species, depth of the reef zone, and the ecological and environmental history of each location (Rogers 1993). Resistance and resilience have been fundamental for the recovery of rainforests and coral reefs from HES (Lugo et al. 2000*b*). But chronically declining conditions of coral reef ecosystems due to a combination of cumulative and synergistic anthropogenic and climate change-related impacts are transforming reefs into novel ecosystems (sensu Hobbs et al. 2009), with limited natural ability to recover from disturbances. Therefore, in the context of ridge-to-reef perspective, novel coral reef systems react much more slowly than do terrestrial ecosystems, with greater lags in recovery because they integrate a combination of landscape impacts that have driven the ecosystem into a significantly compromised state. This condition points out the paramount importance of the implementation of rapid assisted interventions as a strategy to foster a faster recovery. Most of these approaches are based on the implementation of multiple methods such as in situ coral farming, land-based nurseries, larval rearing methods, and coral colony micro-fragmenting techniques to accelerate coral reef restoration and integrating community-based participation (Hernández-Delgado et al. 2018*a*, *b*). However, there is still a pressing need to expand the magnitude and spatial scales of restoration interventions to improve the recovery ability of coral reefs and foster the restoration of coastal resilience.

One interesting component of SES research is demonstrating how vulnerabilities at small scales cascade into transformed SES states at large scales (Kinzig et al. 2006). One example is land abandonment in the Luquillo Mountains, which preceded a generalized rural abandonment island-wide beginning in the late 1940s (Rudel et al. 2000), which spread to the lowlands on northeastern Puerto Rico (Thomlinson et al. 1996). This transformation was initiated by intense hurricanes in 1928 and 1932 that led to the choice by individual land tenants to abandon their farms and move elsewhere (Scatena 1989). Thus, disturbance acting at regional scales impacts human decisions at a local scale that eventually cascade (Kinzig et al. 2006) into the region-wide dynamics of forest cover, called the "forest transition" (Rudel et al. 2000). Interestingly, secondary forest communities arising from the interaction of the logging that took place in the 1920s (Thompson et al. 2002) have allowed the introduction of dense stands of secondary species. With time and further hurricane disturbance, a simulation model (Uriarte et al. 2009) predicted the colonization of increased numbers of these secondary species in nearby mature, unlogged forest communities, at abundances without historical precedence. The predicted result is a species composition that is very different from that before the human disturbance (Hogan et al. 2016). Thus, the forest transition yields novel forests with similar structures (Zimmerman et al. 1995*a*) but dominated by secondary species that are less resistant to future hurricane disturbances (Zimmerman et al. 1994).

Clearly, reef-building corals are susceptible to a combination of sedimentation and overfishing within the SES as well as to increasing ocean temperatures arising for global change drivers (Rogers 1990, Hughes 1994, Miller et al. 2006, 2009, Anthony et al. 2008, 2011, Hernández-Pacheco et al. 2011, Hughes et al. 2017, Muller et al. 2018). This makes coral communities vulnerable to destruction by HES, leading to the flattening of the reef structure, cascading to altered species compositions of corals and dependent biota, as well as to compromised ecosystem function (Alvarez-Filip et al. 2009, 2013, 2015). This may provide insights into what may happen to upland forests in the future. Upland forests maintain broad-sense resilience because of a lack of anthropogenic disturbance. Nonetheless, long-term effects of human-induced climate warming and drying may alter this scenario. The potential impacts of increased temperatures and drying on these forest ecosystems (Henereh et al. 2016) may, in a process parallel to that observed in marine habitats, drive systems to tipping points as dominant species decline in response to environmental change (e.g., Meir et al 2015). For example, in a simulation study, Feng et al. (2018) showed that net forest productivity in the

Luquillo Mountains might fall to zero within twenty years if current projections of increased temperatures and climate drying are accurate. The consequences of this to forest structure and composition are currently unclear, but the increasing negative effects of anthropogenic disturbance on forested uplands may portend declines in ecosystem structure and function similar to that currently witnessed in marine systems. In any case, large changes in tree forest species composition and structure in the Luquillo Forest would likely cascade, culminating in altered communities of consumer species as well.

How do we confront the difficulty of finding a common currency to describe HES effects on SES? Walker (2011) suggested a disturbance-severity gradient approach to the problem that takes advantage of the fact that the ecological processes are generally analogous during responses to both natural and anthropogenic disturbances. He suggests that indices of severity, including biomass loss or changes in substrate (fertility, texture, or stability) can be robust and serve to contrast natural and anthropogenic disturbances. The results of Boose et al. (2004) are interesting in light of this suggestion. They used the Fujita scale, which is normally used to describe tornado impacts, to provide an integrated understanding of wind and other storm-related impacts to the island. The Fujita scale is directly interpretable in terms of storm damage to trees and human infrastructure (i.e., is a measure of severity). Although their results focus on the effects of wind and not stream flooding or storm surge (at least not explicitly), their approach suggests a path forward toward an integrated measure of the impacts of HES on ridge-to-reef social–ecological systems.

Numerical modeling of waves has become a fundamental tool to address the destructive potential of hurricane-induced wave action on coral reefs (Poutinen et al. 2016), as well as on coastal SES. Rapidly declining ecological health of reef flat and shallow reef assemblages is an increasing concern for conservation (Sheppard et al. 2005, Péquignet et al. 2011, Storlazzi et al. 2011, Costa et al. 2016). The combined effects of altered wave environment, sea-level rise, and climate change still need to be integrated to fully understand vulnerabilities of coastal SES to future hurricane events (Quataert et al. 2015). Shallow fringing coral reefs can reduce 97% of the wave energy, and reef flats alone can dissipate 86% of that energy (Ferrario et al. 2014). Consequently, the conservation and ecological restoration of shallow coral reef assemblages has become a critical tool to replenish depleted coral populations of critical species such as Elkhorn coral across the Caribbean (Hernández-Delgado et al. 2018*a*, *b*). Restoring coral accretion along shallow reef crest and flat zones will increase wave buffering by shallow reef zones in the long-term, thereby increasing the resilience and resistance of backreef assemblages, and that of adjacent seagrass and shoreline communities. This will reduce vulnerabilities of coastal SES to future HES events.

Conclusions

The development of a comprehensive understanding of the effects of HES on SES is only in its beginning stages, and the example of eastern Puerto Rico is no exception. Detailed understanding of the responses of many but not all natural components is available because of research devoted to these topics. We find potentially broad parallels in the broad-sense resilience of forest and marine systems that suggests that forests in upland areas may be vulnerable to future climate change and HES in the way that are characteristic of marine systems. Research on the social impacts, however, has lagged and largely focused on the immediate impacts of the storm and short-term relief efforts. For example, the lack of documentation on long-term sociological effects, such as the degree to which a government-financed construction boom allowed many residents to replace wooden homes with hurricane-resistant concrete ones, leads us to rely on anecdotal information to paint a complete picture. Understanding the long-term societal benefits and legacies of government relief efforts to past storms and how this reflects on apparent recent failures has been addressed poorly. Finally, like research in all of ecology, it is critical to develop enhanced predictive understanding of the effects of HES on coupled human and natural systems. It is especially critical to identify common processes that play a major role in determining resistance and resilience as well as to understand site-, state-, and component-specific contingencies that modify these dynamics. In this context, comprehensive long-term studies at a number of locations are critical for advancing site-specific understanding, as well as for informing an evolving conceptual framework that is generalizable, especially during times of rapid global change.

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