Disturbance and resilience in the Luquillo Experimental Forest

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ABSTRACT

The Luquillo Experimental Forest (LEF) has a long history of research on tropical forestry, ecology, and conservation, dating as far back as the early 19th Century. Scientific surveys conducted by early explorers of Puerto Rico, followed by United States institutions contributed early understanding of biogeography, species endemism, and tropical soil characteristics. Research in the second half of the 1900s established the LEF as an exemplar of forest management and restoration research in the tropics. Research conducted as part of a radiation experiment funded by the Atomic Energy Commission in the 1960s on forest metabolism established the field of ecosystem ecology in the tropics. Subsequent research has built on these early advances to develop new theories on ecosystem response to disturbance regimes and the role of the biota in ecosystem resilience. Recent and current research in the LEF has advanced understanding of resilience to hurricane disturbances, human land use, gamma irradiation, landslides, drought, and warming, showing that even following the most severe disturbances (e.g., landslides, agriculture) forests reestablish within 60 years. Work in the LEF has reversed the paradigm that tropical ecosystems are fragile, but instead exhibit remarkable resilience to many forms of disturbance present at multiple spatial and temporal scales. Current research is already advancing understanding of how climate change and attendant effects on the disturbance regime might affect the composition, structure, and function of tropical forest ecosystems.

1. Introduction

The Luquillo Experimental Forest (LEF; Fig. 1), one of the oldest forest reserves in the Western Hemisphere, is also distinguished by one of the longest continuous research histories in the tropics ((Sastre-Ines and Santiago-Valentín, 1996); Wadsworth, 1997; Harris et al., 2012; Brokaw et al., 2012). Throughout this time, scientific discoveries in the LEF have shaped fundamental understanding of tropical forest ecology and conservation, primarily in the areas of forest restoration and management, ecosystem energetics and food web structure, and more recently, disturbance and ecosystem dynamics. From conservation efforts undertaken in the early 19th Century, to the inception of the Luquillo Long-Term Ecological Research Program, scientists in the LEF have utilized a wide range of approaches for understanding forest ecosystems, including the assessment of long-term data, the study of naturally occurring disturbances, and manipulation experiments. Research on disturbance and succession spawned innovative field experiments to test resilience of ecosystems, defined as "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" (Walker et al., 2004). This research has greatly improved predictive understanding of ecosystem dynamics. This "institutional" history, coupled with the changing goals and theoretical frameworks of ecologists and conservationists through time, have led to revolutions of thought, which have continued to evolve as new tools have brought new perspectives on ecosystem conservation and ecology. This review follows the evolution of ideas that contributed to our current understanding of tropical forest ecology and conservation and explores how

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this understanding can be used to better predict the response of these invaluable ecosystems in a rapidly changing world.

2. Early conservation efforts

As early as the 1820s, the flanks of the Luquillo Mountains and surrounding areas were logged for timber and mined for gold (Domínguez Cristóbal, 2000). Under Spanish rule, concern for the conservation of forest, fish, and wildlife in what is now the LEF soon followed. In an effort to slow the ongoing degradation of the land, forest preserves were established in Puerto Rico in 1876, including 5012 ha of the Luquillo Mountains. At this time, a Forest Service was established with a guard assigned to the area, laws were created to protect timber for the Spanish Crown, and buffer areas were designated to protect streams from mining activities. These actions helped control excessive deforestation, making the LEF the largest area of forested land in Puerto Rico at the time the island was ceded to the U.S. in 1898.

Spanish Crown lands became U.S. federal lands after 1898 (Harris et al., 2012). Until 1918, however, the U.S. did little with the LEF except sort out ownership records, and survey and mark the boundaries. Placer gold mining, timber extraction, charcoal production and farming were allowed to continue, sometimes under permit. The foresters that visited

wrote about the forests in a utilitarian way (Brokaw et al., 2012). They saw the abundant palms as a nuisance. Unfamiliar with tropical forests, they could not suggest species to plant to control the erosion of the steep, degraded slopes in many of the lower elevations of the mountains. Critical advances in this area would come later (Section 4).

3. Scientific surveys

Beginning in 1906, Nathaniel and Elizabeth Britton began a long-term scientific survey of Puerto Rico (Sastre and Santiago, 1996). By 1933, they had conducted 16 expeditions to Puerto Rico, usually in interdisciplinary teams of botanists, zoologists, ecologists, and geologists (Brokaw et al., 2012). Their contributions to biological knowledge of the island were substantial. For example, 10,139 botanical collections were deposited in the New York Botanical Gardens during this period (Sastre and Santiago, 1996) and 38 new species representing over 10% of the island's endemic flora were described. The Brittons and their collaborators traveled through a deforested landscape, seeking patches of remnant forest. This experience naturally turned their attention to the issue of forest management, concerns which they shared with the governor of Puerto Rico. The Brittons also developed an interest in horticulture and non-native species that could be utilized to revegetate
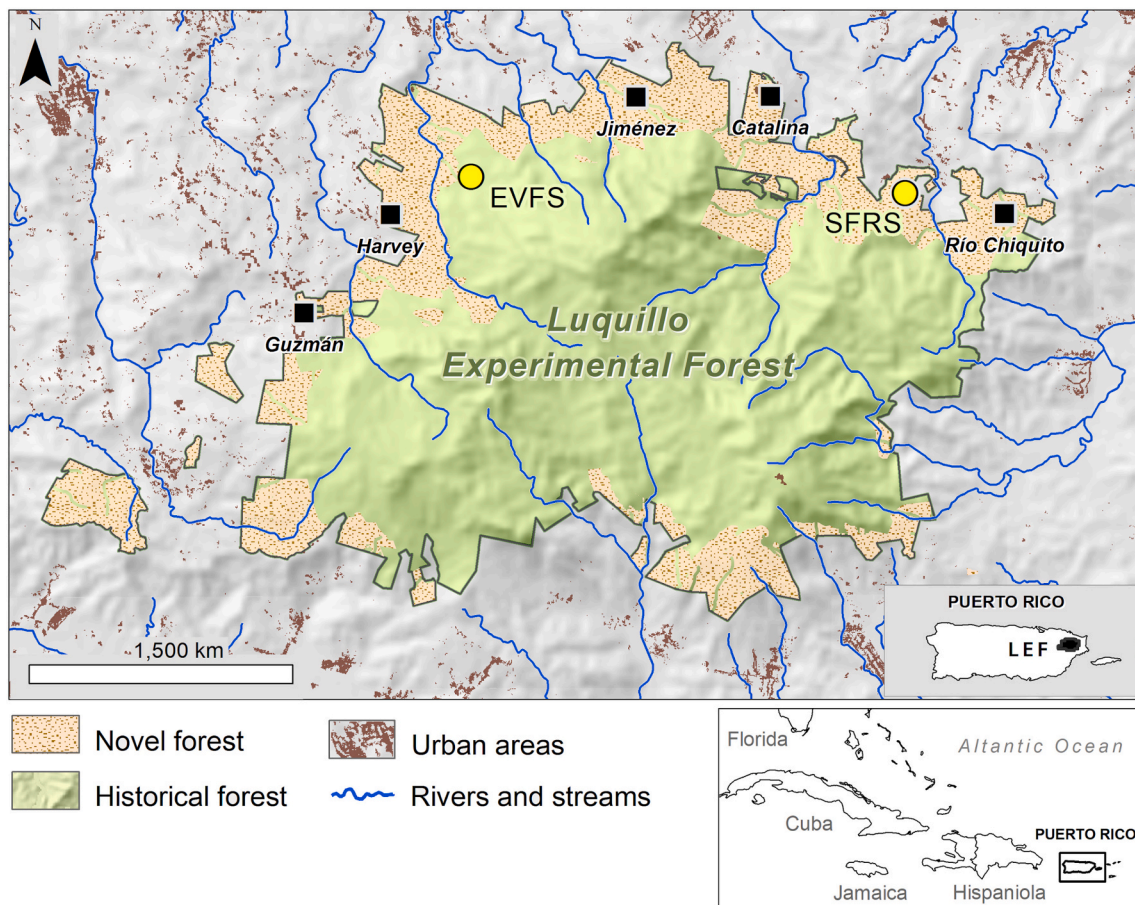

Fig. 1. Map of the Luquillo Experimental Forest in northeastern Puerto Rico. The LEF (coterminous with El Yunque National Forest), at just over 11,000 ha, includes much of the Luquillo Mountains, which rise to peaks at ~1000 m asl (Brokaw et al., 2012; Harris et al., 2012). There is a steep rainfall gradient from ~2000 mm yr^{-1} at low elevations (~200 m asl) to almost 4500 mm yr^{-1} at the summits. Much of the upper elevations (above ~600 m asl) are classified as wetlands because of the high rainfall which saturates soils and reduces their oxygen concentration. Mean annual temperatures range from 27 °C at the lowest elevations to 20 °C at the highest. As a result, five subtropical Holdridge Life Zones are included: moist forest, wet forest, rain forest, lower montane wet forest, lower montane rain forest. Classification of the forest with regard to dominant vegetation yields four forest types: tabonuco (*Dacryodes excelsa*) forest, palo colorado (*Cyrilla racemiflora*) forest, palm brake (*Prestoea montana*), and elfin woodlands (located along the highest ridges). The main soil orders of the LEF are Ultisols and Inceptisols. Lower elevation areas, marked in stippling, were deforested and later allowed to regenerate as novel forests, with mixtures of native and introduced species, or planted into forest plantations (locations denoted with black squares). Historical forests were never in agriculture or cut-over. Key study locations in the LEF include El Verde Field Station (EVFS) and the Sabana Field Research Station (SFRS).

the island (Sastre and Santiago, 1996).

The first soil survey in Puerto Rico was led by Clarence W. Dorsey and published in 1902 (González et al., 2020). Descriptive accounts of the soils of the LEF date back to the 1920s (Gleason and Cook, 1927; cited in Howard, 1968) with a focus on upper elevation cloud forests. Early studies were purely descriptive and focused on the wet, mucky condition of the soil surface and lack of a deep litter layer on the forest floor. More detailed analyses began with Gaztambide de Urrutia (1950) and Lyford (1969), setting the stage for our current understanding of the chemical and physical characteristics of soils in the LEF, as well as proposing hypotheses regarding the dominant soil forming processes. Research in the LEF provided an important counterpoint to early biogeochemistry research in the South American tropics conducted in the Río Negro region of Venezuela, an area underlain by old sandstones yielding some of the most nutrient depleted soils known to support tropical forests (Jordan, 1982). Although researchers generally assumed that most New World tropical forests were similarly highly nutrient poor, they began to question how these soils could support such high net primary productivity. A key paper published by Jordan and Herrera (1981) questioned whether nutrients were really limiting in tropical forests, citing data from the LEF on high calcium content of soils. However, a unit conversion error discovered years later would show that the supposed high calcium availability was considerably overestimated (Silver et al., 1994).

4. A new era of forest management in the tropics

Two devastating hurricanes in 1928 and 1932, coupled with the Great Depression, changed economic fortunes for many of those living in and around the Luquillo Mountains, heralding abandonment of farmland there (Scatena, 1989) and eventually throughout Puerto Rico (Rudel et al., 2000). Under the Weeks Act, the U.S. Department of Agriculture (USDA) Forest Service began purchases that would eventually double the size of the LEF to 11,000 ha. Much of what is now the lower elevations of the LEF entered into the early stages of forest succession, leaving legacies of prior land use for future researchers to discover and describe (García-Montiel and Scatena, 1994; Zimmerman et al., 1995; Thompson et al., 2002).

In 1942, the arrival of Frank Wadsworth in Puerto Rico began a critical phase of forestry research that would lead to important discoveries for years to come. Wadsworth established forest plots throughout the island and across the LEF, ranging in elevation from 200 to 640 m (Harris et al., 2012; Wood et al., 2019a). Information gained on tree growth through 1947 in the plots provided guidance for the development of a forest management plan, which Wadsworth published as his dissertation (1949). With time, improvement thinning and harvest to reduce tree crowding were tested to see if it could improve the productivity of commercial species. At the same time, Marrero (1948) summarized the results of efforts to reforest degraded lands at the lowest elevations. Many of the species' trials failed. Two that did not were those of *Tabebuia heterophylla* (*roble blanco*) and *Calophyllum calaba* (*palo maria*). Today, every spring, swaths of the Luquillo Mountains are blanketed in the mauve flowers of *Tabebuia*, a result of these early restoration efforts. Plantations of valuable timber species were also established, including mahogany, mahoe, pine and other species. These studies were revolutionary (Wood et al., 2019a). They were the first attempts in the modern era of restoration and silviculture in tropical America and continue to inform restoration efforts in the tropics to this day. Further, the plots established by Wadsworth continue as an invaluable resource for long-term research (e.g., Heartsill Scalley, 2017), helping contribute to the establishment of the LEF in 1956 and the Luquillo LTER Program 32 years later.

5. A radiation experiment

H.T. Odum pioneered the "steady state" perspective, that the cycling of materials and flow of energy in natural ecosystems were largely balanced. This perspective was refined in the LEF, where it was used to guide the "radiation experiment", a study of the effects of gamma radiation on tropical forest structure and function. Indeed, the radiation experiment remains one of the most comprehensive studies of the ecology of a single site in the history of tropical research (Odum and Pigeon, 1970). The results of the radiation experiment helped advance new ecological paradigms that were in development in the mainland United States but had not been tested in the tropics. For example, the ecosystem concept initially proposed by Tansley (1935) became more widely accepted in ecology after 1969 (Golley, 1993), and H.T. Odum, being one of the pioneers in its application, did so with eloquence and authority in presenting the results of the radiation experiment in the LEF (Odum and Pigeon, 1970).

Based on extensive quantitative data and experiments that disturbed the forest with both ionizing radiation and mechanical cutting, Odum was able to explore, and even model, the dynamics of tropical forests following extreme disturbances and under different levels of human activity (Odum, 1995). His models were based on forest productivity, diversity, and nutrient and mass cycles, clearly pioneering a systems level approach to the subject of the interactions of humans and tropical forests. They also helped develop notions of self-organization through tropical succession, a process that is fundamental to restoration and understanding of tropical biota (Odum, 1988).

The radiation experiment also influenced global understanding of the interrelations of ecological systems across latitudes. This was accomplished with some of the early empirical evidence of the movement of radionuclides from atmospheric atomic explosions from the Pacific to the epiphytic organisms on roofs in Guaynabo, Puerto Rico and the LEF (Odum and Pigeon, 1970). The world's geochemical cycles affected everyone.

At the time, the U.S. was experimenting with radiation effects in temperate and boreal biomes, and results from the LEF provided comparative information about the resilience of tropical forests to ionizing radiation. Tropical trees in the LEF were more resilient than temperate pine trees. From then on, the resilience of tropical forests became a subject of attention at the LEF and subsequent research on disturbances such as hurricanes and landslides helped focus attention on the high, rather than low, resilience of these systems (Brokaw et al., 2012).

6. A tropical food web

Biodiversity in the LEF is the product of the tropical location of Puerto Rico as well as its size and isolation (MacArthur and Wilson, 1967). Research at the LEF has provided a detailed study of trophic structure of the subtropical wet forest community (Reagan and Waide, 1996). Many more plant species exist in the LEF than in areas of comparable size in the temperate zone, but animal species richness is similar. Characteristics of the resulting food web include the absence of large herbivores and predators, a low faunal richness compared to the tropical mainland, and an abundance of frogs and lizards (Reagan and Waide, 1996).

These distinctive characteristics of the animal community determine to a great extent the structure of the food web in the LEF. Reagan and Waide (1996) lumped 2601 species of consumers into 156 "kinds of organisms", representing species, stages in the life cycle within a species, or collections of functionally or taxonomically related species. With this, 214 species of plants were classified into 20 structural categories. Even when species were combined in this way, the resulting food web was much more diverse than most published food webs at the time. This situation, coupled with the abundance of ectothermic frogs and lizards, led to several conclusions that were at odds with conventional wisdom about food webs.

Food webs structure should reveal, theoretically, how stable the system is (Pimm, 1982). For example, transitive feeding loops (in which

species A eats B, B eats C, and C eats A) are common in the LEF even though theory suggests that such loops should destabilize natural systems. Some of these loops involve reciprocal predation among different life history stages of mutual predators. For example, *Eleutherodactylus coqui* (a common frog) eats juvenile centipedes, wolf spiders, tarantulas, and whip scorpions, all of which consume juvenile coquí as adults. Omnivory (species that feed at more than one trophic level; Pimm and Lawton, 1978), also linked to food web stability, is pervasive in the web. Some omnivores feed at several trophic levels, including many species of birds, frogs, lizards, and large invertebrates feed on more than one trophic level. A typical example is *Anolis evermanni*, a lizard, which consumes all but the smallest arthropods regardless of trophic level. Compartmentalization of food webs influences stability and Pimm and Lawton (1980) suggested based on empirical evidence that webs within the same habitat are not divided into compartments. The most abundant consumers in the LEF food web are anoline lizards, which are diurnal, and coquí frogs, which are nocturnal. Major anole predators (Puerto Rican lizard cuckoo, pearly-eyed thrasher, hawks) are also diurnal while most coquí predators (tarantulas, crab spiders, whip scorpions, Puerto Rican screech owl) are nocturnal. Thus, day-night activity differences lead to distinct subwebs (compartments) within the same habitat.

Some of the patterns that have emerged from work in the LEF may result from general characteristics of tropical ecosystems and hence should be observable in other tropical communities (Reagan and Waide, 1996). For example, tropical breeding patterns maintain various life stages of many species throughout the annual cycle, providing the opportunity for feeding loops to be more prominent. The day-night separation of feeding interactions may also be a general pattern in species-rich tropical communities, where specialization is high. The disturbance regime in the LEF may contribute to the structure of the food web by periodically re-organizing the abundance of species and the strength of links in the web. Thus, the high degree of omnivory may be an adaptation to a dynamic environment in which disturbance causes rapid shifts in the relative availability of different food types.

The food web of the LEF offers opportunities for interesting comparisons with temperate systems, which have similar faunal richness but many fewer plant species, as well as mainland tropical systems, where plant species density is similar to Puerto Rico, but faunal richness is much higher. The Luquillo food web is more tractable analytically than highly diverse mainland tropical forests, and thus represents a point of entry for testing how well food web theory derived from simple mathematical models holds up in diverse natural systems. As our work has shown, predictions from models or simple laboratory experiments often fail when confronted with highly resolved webs from diverse systems. This conclusion emphasizes the continued importance of studies of natural history and systematics in understanding the principles underlying tropical food webs. The forest ecosystems of the LEF also provide an excellent laboratory to examine the effects of repeated disturbance on food web structure and stability. As we have shown, cyclonic storms alter physical and chemical characteristics of ecosystems but have relatively fewer effects on biological characteristics (e.g., species richness). Our long-term studies of the effects of intense hurricanes Irma and Maria on the flora and fauna of the LEF will provide continued insights into the stability of tropical food webs.

7. The Luquillo Long-Term Ecological Research Program

Funding for the Long-Term Ecological Research (LTER) program by the U.S. National Science Foundation began in 1980 to address the many ecological questions that require more than three years of study, the typical length of funded proposals, to understand ecosystem dynamics (Hobbie et al., 2003; Willig and Walker, 2016). Luquillo was added as an LTER site in 1988 at least in part because of the growing recognition of the disturbance regime as the dominant factor affecting the structure and functioning of ecosystems. The first Luquillo LTER research proposal preceded the popular move from a "balance of nature" approach in

ecology and conservation (Kricher, 2009). Instead, an approach was pioneered in which the influence of self-organizing mechanisms of ecosystems that embodied a balance approach (e.g., succession) are disrupted by periodic disturbances (e.g. hurricanes, landslides, logging), on the one hand, and constrained by legacies and large-scale, slow-tempo environmental change (i.e., land use and global climate change) on the other (Waide and Lugo, 1992; Lugo and Waide, 1993; Lugo, 2020). Armed with this conceptual framework, where ecosystems respond to disturbances differing in timing, intensity, and extent, researchers began to study how hurricanes, landslides, tree falls, and humans influenced the ecology and functioning of the LEF. Multiple hurricanes brought into focus the notion that disturbance was a key regulator of ecosystems structure and function (Brokaw et al., 2012). One of the main conclusions from long-term studies was that ecosystems of the LEF were resilient to both non-anthropogenic and anthropogenic disturbances. Such resilience was a surprise and countered a prevailing view that tropical forest ecosystems are quite fragile (Goméz-Pompa et al., 1972; Farnworth and Golley, 1974).

7.1. Hurricanes

Large-scale windstorms affect forests throughout the world. The Luquillo LTER experienced its first intense hurricane one year after its founding, in 1989. Though hurricanes were anticipated in its planning, hurricane Hugo drastically realigned the goals of the program for years to come and, in turn, illuminated how periodic wind disturbances shape a tropical forested ecosystem (Walker et al., 1991, 1996; Brokaw et al., 2012). As devastating as the effects of Hurricane Hugo were (Walker et al., 1991; Fig. 2), the resilience to the storm's effects was equally surprising (Walker et al., 1996). Initial tree mortality (7–9%) was greater than background rates (Lugo and Scatena, 1996) but not as high as suggested by the large reduction in canopy structure witnessed after the storm. Delayed mortality was high, however, (Uriarte et al., 2019), and those tree species with the densest wood appeared protected from the worst trunk damage (Zimmerman et al., 1994).

In a few months, the understory became alive with herbs and shrubs and newly recruited tree saplings. Some forest processes such as soil nutrient cycling and stream chemistry returned to near pre-hurricane levels quickly, exhibiting a high degree of resilience (Silver et al., 1996; Zimmerman et al., 1996; Brokaw et al., 2012; McDowell et al., 2013). Some species, like coquís and shrimp, became more abundant, responding positively to increased habitat and resources. Others, like snails, declined strongly in abundance in the hot, dry conditions immediately following the storm (Willig and Camilo, 1991), only to increase to near or above pre-storm numbers as the understory became quickly shaded and their favored plant species became abundant (Bloch and Willig, 2006). Forest structure, stream-water exports of coarse particulate matter, and abundances of some plants and animals recovered slowly or never fully recovered their pre-Hugo values (Heartsill-Scalley et al., 2010, 2012; Willig et al., 2011). However, resilience overall was high.

Another intense hurricane followed nine years later, Hurricane Georges, facilitating a refinement of knowledge concerning hurricane effects and recovery trajectories. Comparisons of the two storms showed differences in effects on terrestrial and on aquatic ecosystems (Brokaw et al., 2012; Schowalter et al., 2017). Hurricane Georges (1998) resulted in much less structural and compositional change, largely because the branch structure of the forest had not fully recovered from hurricane Hugo, reducing the effects of the second storm on the forest canopy and the amount of generated woody debris. Topography emerged as an important predictor of structural effects and mortality, with trees on ridges and in valleys being more susceptible (Brokaw et al., 2012). These results demonstrate contingency (Scheiner and Willig, 2011), that response to disturbance is dependent upon pre-existing conditions. Just as every storm is different, the forest condition is different at the time of every storm, being in a unique state since the passing of the previous
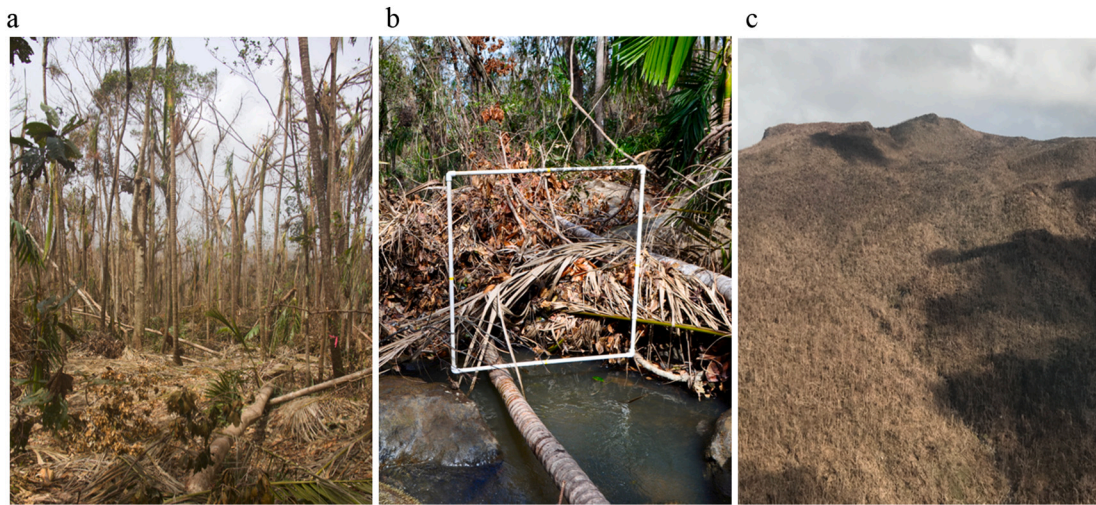
Fig. 2. a–c. Hurricane disturbance in the LEF. Illustrated are examples following the passage of Hurricane María. a) A forest scene one-week post-hurricane, showing the open canopy and hurricane debris typical of most areas (J. Zimmerman photo). b) A debris dam in a stream with a 1×1 m quadrat for scale (Pablo Gutiérrez, photo). c) View of the summit of the mountains from a helicopter, two weeks post hurricane (S. Wallace photo).

storm and other intervening events (Walker and Willig, 1999; Brokaw et al., 2012; Fig. 3).

Data from hurricanes Hugo and Georges suggested that canopy opening, and detrital inputs were the dominant drivers of ecosystem responses to intense storms (Walker et al., 1991, 1996; Brokaw et al., 2012; Shiels and González, 2014). The results prompted development of a long-term, factorial experiment (the Canopy Trimming Experiment – CTE) to explore the separate and combined effects of canopy opening and detrital deposition. In general, canopy openness was a more important predictor of abiotic (Van Beusekom et al., 2020) and ecological response (Shiels et al., 2015), favoring pioneer trees, reducing the abundance and diversity of key animal groups, reducing decomposition rates via inhibition of lignin-degrading fungi, and increasing nitrate export in soil water. Debris deposition was an important source of C and nutrients deep into the soil profile (Gutiérrez del Arroyo and Silver, 2018) and contributed to a slight increase in tree basal area growth (Shiels et al., 2010), but no increase in litterfall production (Silver et al., 2014). A large flush of labile C and nutrients leached into soil from the deposited litter within the first three weeks following the experimental

trim. Soil microbial biomass increased quickly, and microbial communities in litter and soil shifted from lignin-degrading basidiomycete fungi towards microfungi that degrade cellulose and hemicellulose (Shiels et al., 2015). Lysimeters, which provide an integrated measure of the response of forest floor processes over time by collecting soil water from 30 cm depth (McDowell and Liptzin, 2014), exhibited peaks in stream nitrate following debris deposition, closely mimicking the response of stream chemistry to hurricanes Hugo and Georges (McDowell et al., 2013). These results demonstrate the strong connection between forest soil and stream chemistry in this rainforest system, as well as the effectiveness of the CTE as an analog for hurricane disturbance (Fig. 4).

Recently, the LEF was struck by two hurricanes, Irma and María, in close succession. Hurricane Irma (September 7, 2017) passed to the north and had mild to moderate effects on the site. Hurricane María (September 20, 2017), with strong, category 4 winds (69 ms^{-1} at landfall), passed near the LEF and caused widespread defoliation and significant alteration of forest and stream structure. Hurricane María was the strongest hurricane to make landfall in Puerto Rico since hurricane San Felipe in 1928 (Zimmerman et al., 2020; Lugo, 2020). Hurricane María killed twice as many trees as Hurricane Hugo, and for all but two species, broke 2- to 12-fold more stems than Hurricanes Hugo or Georges. Hurricane María had higher wind velocities and dissipated more energy over the forest (Van Beusekom et al., 2018) than did Hurricane Hugo. The result was, for example, that aspects of stem breakage were decoupled from tree species wood density (Uriarte et al., 2019) as found in previous lower intensity storms. Thus, patterns of species vulnerabilities became less predictable even though overall patterns of effects are predictable (Lugo, 2008, 2020; Hall et al., 2020; Van Beusekom et al., 2020). Regardless, the recent storms have allowed the Luquillo LTER program to delve deeper into the characteristics of tropical forests that lend resilience to repeated hurricane disturbance.

7.2. Landslides

Landslides are important sources of disturbance in montane regions (Walker and Shiels, 2013). Landslide research in the LEF established a close relationship between geomorphological conditions and vegetation turnover as a result of different disturbance events that cause landslides (Guariguata, 1990; Scatena and Lugo, 1995). The vegetation of the LEF undergoes a rapid succession after landslides, overcoming the dramatic changes in substrate conditions during succession (summarized by Harris et al., 2012; p 24 to 30). This rapid recovery of vegetation back to forest within 60 years (Guariguata, 1990) is consistent with vegetation
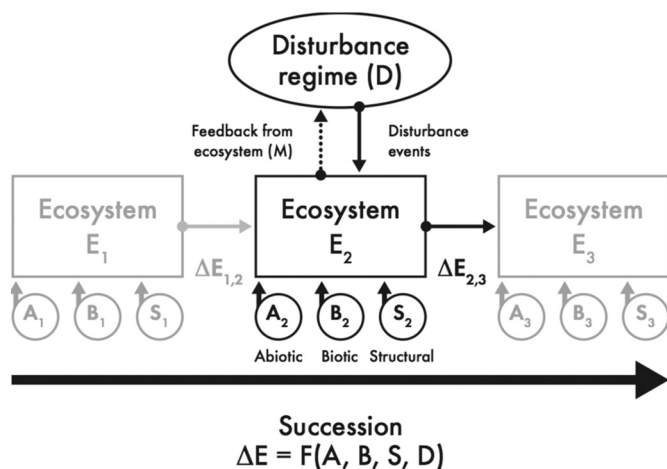

Fig. 3. A model linking disturbance and succession at LUQ. Abiotic, biotic, and structural environments interact with one another and the disturbance regime to determine the state of the ecosystem. Meanwhile, the state of the ecosystem can influence the disturbance regime and future ecosystem states, implying contingency. From Willig and Walker (1999).
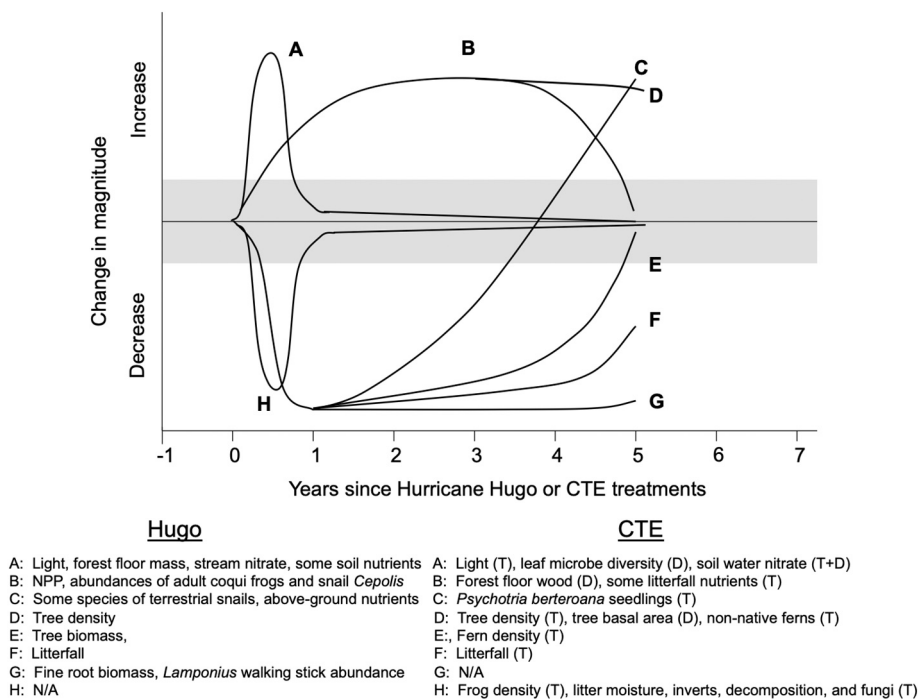
Fig. 4. Responses of key biotic, abiotic, biogeochemical, and ecosystem processes in the LEF following Hurricane Hugo (September 1989; Zimmerman et al., 1996) or following the experimental hurricane manipulations performed during the Canopy Trimming Experiment (CTE; manipulations completed early 2005 and followed 1–7 years; Shiels et al., 2014). The shaded portion of the graph represents values that are indistinguishable from pre-hurricane (or pre-treatment) values. The response curves in the CTE reflect trimming trees and branches to open the canopy (T), or the addition of canopy debris to the forest floor (D) or a combination of both treatments (T + D). Figure adopted from Shiels et al. (2014).

Hugo

A: Light, forest floor mass, stream nitrate, some soil nutrients
B: NPP, abundances of adult coqui frogs and snail *Cepolis*
C: Some species of terrestrial snails, above-ground nutrients
D: Tree density
E: Tree biomass,
F: Litterfall
G: Fine root biomass, *Lamponius* walking stick abundance
H: N/A

CTE

A: Light (T), leaf microbe diversity (D), soil water nitrate (T+D)
B: Forest floor wood (D), some litterfall nutrients (T)
C: *Psychotria berteroana* seedlings (T)
D: Tree density (T), tree basal area (D), non-native ferns (T)
E:, Fern density (T)
F: Litterfall (T)
G: N/A
H: Frog density (T), litter moisture, inverts, decomposition, and fungi (T)

recovery after the abandonment of paved roads (Heyne, 2000), and underscores the inherent resilience of wet tropical forest vegetation to alteration of the substrates that anchor plants.

Landslide research at LEF not only has provided critical information for the management of landslide effects, but also supplemented other research in demonstrating the mechanisms by which vegetation reorganizes following extreme disturbance events. At large spatial scales in montane environments, landslides can be a major type of landcover, of the same order of magnitude as is deforestation (Restrepo and Alvarez, 2006). Landslides have the potential to sequester large amounts of carbon, up to 19% of the residual land sink in 2012 (Ramos Scharron et al., 2012). Landslides also add heterogeneity to the environment favoring a diversity of soil environments for plant colonization and succession (Walker and Shiels, 2013). Exposed saprolite can lead to enhanced weathering and the release of nutrients providing an important source of nutrients to highly weathered soils. Thus, this research has been instrumental in the development of the field of landslide ecology in the tropics (Walker and Shiels, 2013).

7.3. Human-initiated disturbance

The tide of humanity rose and receded in the LEF, leaving behind evidence of past human activities as represented by ox cart trails, mines, roads, charcoal pits, coffee plantations, pastures, and dams. LTER researchers began to study the implications of past land use in earnest in the 1980s (e.g., Zimmerman et al., 2007; Marín-Spiotta et al., 2009) as a way of understanding the resilience of tropical forests to deforestation and agricultural activities. They were among the first investigations of old-field succession in a tropical context. Benefiting from aerial photographs taken beginning in 1936 (Foster et al., 1999; Thompson et al., 2002) and interviews with elderly residents (e.g., García-Montiel and Scatena, 1994), researchers were able to identify key past land use activities (e.g., Thomlinson et al., 1996) and describe the key processes of tropical forest ecosystems recovering from different land uses (Grau et al., 2003). Chronosequence studies (Zimmerman et al., 2007; Marín-Spiotta et al., 2009) indicated that forests had the potential to recover soil C stocks, structure, biomass, and diversity (but not the same species composition and proportions) to near pre-disturbance levels surprisingly

quickly, in 50–80 years from the estimated time of abandonment. Again, these studies suggested that the tropical forests, at least those represented by the LEF, were not as fragile as originally perceived.

Forest stands of different land use, while of similar structure, however, were often found to host different tree and shrub species (e.g., Zimmerman et al., 1995; Grau et al., 2003). The mark of last crop is also found in species composition in temperate forests (e.g., Foster et al., 1998). For example, in the LEF, as foresters found before (Zimmerman et al., 1995), *Tabebuia heterophylla* recruited readily into abandoned pastures, in part because of high propagule availability (Zimmerman et al., 2000). *Guarea guidonia* is abundant in abandoned shade coffee (Grau et al., 2003) in part because of its physiological adaptations to the high light and high nutrient conditions (Fernández, 1997). This species is the second most abundant species in Puerto Rico (Marcano-Vega, 2017), largely because of the extensive history of coffee farming.

What is the conservation value of secondary forests whose composition is altered compared to presumed pre-disturbance assemblages, particularly when stands are dominated by nonnative species (i.e., novel forests; Lugo and Helmer, 2004; Lugo, 2004)? Forested landscapes, regardless of species composition, retard erosion and reduce extreme flooding while providing habitat structure for generalist wildlife. Nonnatives, such as *Spathodea campanulata*, the most abundant tree in Puerto Rico (Marcano-Vega, 2017), encourage the establishment of native species beneath their stands (Zimmerman et al., 2007), as they do in Singapore (Lum and Ngo, This issue). Although counterexamples have been suggested (e.g., Brown et al., 2006), the general conclusion was that forests with "novel" assemblages of species (i.e., assemblages without historical precedent) provide important ecosystem benefits.

Humans were found to negatively affect streams in the LEF via the construction of intakes and low head dams to divert water for human consumption (March et al., 2003). These diversions disrupt the connectivity of the streams and have negative effects on many migratory organisms (e.g., fish, shrimps, snails). Shrimps breed in headwaters, letting eggs and larvae drift downstream to estuaries, where, having completed a key stage of development, begin migrating back to the headwaters. Intakes divert part or all the larvae to public water systems, depending on flows, and dams impede upstream migration (March et al., 2003). Shrimps are key for ecosystem function in headwater streams, as

they process and consume much of the leaf litter that enters the streams, while feeding on periphyton from stream surfaces. Reaches upstream from large dam's lack shrimps and have abundant accumulations of fine sediments and benthic algae (i.e., slime), a clear change in ecosystem condition (Greathouse et al., 2006).

Armed with this knowledge, LEF researchers led the opposition to the construction of a dam on the Mameyes River, representing the largest undammed wild and scenic river in Puerto Rico (March et al., 2003). This opposition eventually resulted in the construction of a unique intake placed in the gravel of the river bottom. No structures impeded migration of the biota and water intakes did not affect migrating shrimp. Flows were monitored to maintain at least minimum flows recorded for the stream. The experience led water and regulatory authorities in Puerto Rico to adopt new methods for water diversions throughout the island, resulting in greater conservation of stream resources (March et al., 2003).

7.4. Drought in the rainforest

When the LTER project began in 1988, few expected that drought would be a major consideration for a forest receiving in excess of three meters of rainfall per year. Intense droughts occurred in 1994 and 2015, and other less intense droughts have taken place in between (Brokaw et al., 2012; Mote et al., 2017). Global climate models currently predict substantial changes in precipitation patterns in the tropics, with a strong potential for an increase in the frequency and intensity of drought (Bhardwaj et al., 2018; Ramseyer et al., 2019). Thus, one of the current goals of the LTER program is to understand implications of drought if it becomes a more frequent component of the disturbance regime. Within the LEF, researchers have explored the effects of drought on a wide range of ecosystem processes spanning terrestrial and aquatic interfaces, as well as a diversity of spatial scales, ranging from microbial to the ecosystem. Field experiments and long-term observations have been deployed, as well as mathematical models, to provide an integrated understanding of how tropical forests are likely to respond to future changes in precipitation regimes.

A replicated small-scale throughfall exclusion study was used to evaluate the effects of drought on soil biogeochemistry in 2008 (Wood and Silver, 2012; Wood et al., 2013). Results from this experiment showed that soil moisture exerts a strong influence on soil P availability and on greenhouse gas emissions from tropical forest soils, and that responses vary substantially with topographic position (Wood and Silver, 2012; Wood et al., 2013). In addition, tropical forest soil microbes that had experienced recent drought were able to adapt to future, longer-term drought, and critical microbial functions, such as the types of soil carbon utilized, was fundamentally altered (Bouskill et al., 2013; Bouskill et al., 2016a, 2016b).

In 2015, the LEF experienced an intense drought, with only 50% of long-term average rainfall for that year. Water availability declined substantially, with visible effects on the forest soils and vegetation, and ultimately leading to widespread water rationing for human populations on the island. The seasonal pattern of rainfall was similar to preliminary climate model predictions for end-of-century warming trends (Ramseyer et al., 2019). As such, this extreme event provided a unique opportunity to test hypotheses that were developed as a result of the small-scale throughfall exclusion experiment and from long-term data collected on plant demography and soil processes. Scientists capitalized on an ongoing, intensive study using a continuous sensor array along a hillslope to assess the effects of drought on biogeochemical processes. This work revealed that drought significantly increased soil oxygen availability and lowered soil phosphorus (P) availability, and that biogeochemical responses varied along a *catena*, similar to previous findings using rainout shelters. Soil CO_2 emissions increased during the 2015 drought event (O'Connell et al., 2018), in contrast to results from the experimental drought, when CO_2 emissions declined. Overall, these results suggest that tropical soils respond rapidly to changes in soil

moisture content, and that topographic position is an important driver of spatial variation; however, work is still needed to understand why the direction of this response was not consistent across observational and experimental conditions. Furthermore, longer-term research is needed to determine if these responses will diminish with repeated drought due to microbial acclimation or adaptation (Wood and Silver, 2012; Bouskill et al., 2013).

Utilizing long-term forest productivity and climate data, Feng et al. (2018) found that a scenario of steadily increasing drought and temperature, as predicted for the Caribbean, could cause forest net ecosystem productivity to decrease to zero by 2036 in mid-elevation forest, assuming that plants are unable to acclimate to drier conditions and that community composition does not change. Given these caveats, the model predicted that the LEF could switch from being a C sink to becoming a C source in response to drought. However, strong effects of the 2015 drought on species-specific patterns of seedling (but not tree or understory herbaceous community) mortality were recorded (Uriarte et al., 2018; Kennard et al., 2020) that may portend alteration of community composition in the future. Moreover, African dust inputs that may have caused the drought (Mote et al., 2017) reduced irradiance levels to the forest floor, and when combined with reduced precipitation, could influence species-specific seedling mortality and further alter species composition (Uriarte et al., 2018). For example, positive density-dependence controls were observed on seedling mortality under drought conditions, such that seedling survivorship was higher when in close proximity to an individual of the same species (Bachelot et al., 2020). Thus, over the longer term both a change in tree species composition as well as a reduction in species diversity in response to drought could occur, which could in turn mediate the projected modeling scenario of Feng et al. (2018). Overall, the life history of the trees in Puerto Rico might suggest there are species with pre-existing tolerance to a wide range of moisture conditions and that the potential for many of these species to acclimate to climate drying has yet to be explored.

Drought effects on streams in the LEF are severe but transitory. During the last drought event in 2015, a long-term study stream in the LEF became a series of unconnected pools after base flow decreased and overland flow disappeared in several areas (Gutiérrez-Fonseca et al., 2020). Water-stressed riparian vegetation lost more leaves than normal, increasing leaf litter inputs and allowing more sunlight to reach the stream channel. Large inputs of leaf litter and reduced flow resulted in altered water physicochemical characteristics, including large diurnal fluctuations in dissolved oxygen. Low oxygen reduced invertebrate diversity and caused mobile taxa (e.g., shrimps) to actively move among pools in search of better conditions. During the 1994 drought, some shrimp species (*Atya lanipes*) increased in abundance in some pools relative to pre-drought conditions (22 vs 75 individuals/m^2 of pool area, Covich et al., 2003). As organic matter accumulates in pools and rates of decomposition decrease, it can be expected that drought increases the production of greenhouse gases. As drought conditions become prolonged or if their frequency increases, as predicted by climate change models, these transitory changes may become more common or continuous in nature.

Although no introduced species inhabit stream ecosystems within the LEF, coastal streams are inhabited by a large number of non-native fishes. At least in one lowland urban stream, t drought facilitated the establishment of an introduced cichlid fish (Ramírez et al., 2018). Increased drought events in the LEF could reduce the resistance of stream ecosystems to invasion and establishment of non-native species.

7.5. Rising temperatures

Temperatures are expected to increase significantly in tropical regions within the next two decades, shifting much of the warm lowland tropics into a wholly novel temperature regime (Wood et al., 2019b). Although the absolute change in temperature might be small relative to high latitude ecosystems, even small increases in temperature are likely

to strongly affect tropical forest processes due to the critical role that temperature plays in the fitness of organisms and the narrow temperature ranges under which they have evolved (Wood et al., 2019b). Temperature directly affects basic metabolic functions (e.g., respiration and photosynthesis) that mitigate the energetic costs and benefits of alternative life history characteristics (Hall et al., 1992; Brokaw et al., 2012; Wood et al., 2019b) that ultimately determine the ability of species to persist in changing or new combinations of environmental characteristics. For example, there is evidence to suggest that tropical canopy trees may be nearing a high temperature threshold, beyond which their ability to take up large amounts of carbon might decline (Wood et al., 2019b).

For physiological reasons, ectotherms may be especially sensitive to elevated temperatures (Seebacher et al., 2015), which may be exacerbated in the tropics because the smaller amplitudes of seasonal variation in temperature might not select for intraspecific variation in thermal tolerance (e.g., narrow thermal niches) or the capacity of individuals to acclimate or exhibit phenotypic plasticity in response to warming temperature (Janzen, 1967; Deutsch et al., 2008). If such changes occur at an accelerating rate, it may lead to an "Insect Armageddon," (i.e., permanent decline in insect populations that have popularized in the press). Such concerns are particularly relevant to tropical islands and their endemic species, because local extinctions are less likely to be "rescued" (sensu Brown and Kodric-Brown, 1977) from large source populations that occur elsewhere. Recently, Lister and Garcia (2018) suggested that climate-driven changes in arthropod abundance, especially those related to mean annual daily maximum temperatures, have led to sustained declines in abundances of animals, including birds, lizards, frogs, and arthropods, over a two-decade period in the LEF, and that such population declines may precipitate food web collapse. This claim generated widespread media coverage and was widely cited in scholarly articles and reviews (e.g., Sánchez-Bayo and Wyckhuys, 2019). However, empirical evidence does not substantiate either claim (Schowalter et al., 2019, 2020; Willig et al., 2019), but rather reflects dynamics associated with disturbance and secondary succession initiated by hurricanes (Schowalter et al., 2020). Thus, even though warming of ~0.02 °C per year has been demonstrated in the LEF (Van Beusekom et al., 2015), any substantial long-term effects on arthropod abundance have yet to be demonstrated.

In addition to the effects of warming on diversity and population dynamics, the response of tropical organisms to warming is additionally important given the large role that tropical forests play in the global carbon cycle, where even small changes in the exchange of carbon with the atmosphere could have dramatic consequences for atmospheric carbon dioxide concentrations, globally, and ultimately feedback on future climate (Wood et al., 2019b). Despite this potential for significant climate feedbacks, little is known about how these changes will affect critical biological processes related to carbon cycling, or the ability of tropical organisms to adapt or acclimate to these changes (Wood et al., 2019b). Observational data suggest that trees within the LEF are already operating above their optimum temperature for photosynthesis, and that when moisture is available, temperature significantly increases soil respiration rates (Mau et al., 2018; Wood et al., 2013; Wood et al., 2019b). In an effort to better understand the potential for warmer temperatures to affect this balance, the first field warming experiment in the tropics was established in 2015, where three 4 m diameter areas in the LEF were warmed with an array of infrared heaters by 4 °C above ambient temperature measured in three control plots from 2016 to 2017 (Kimball et al., 2018). After one year of warming, photosynthesis of two common understory shrubs exhibited limited ability to acclimate to warmer temperatures while foliar respiration showed no ability to acclimate (Carter et al., 2020). Taken together, these findings suggest that warmer temperatures will negatively affect the carbon balance of tropical plants (Carter et al., 2020). Over this same timeframe, the understory herbaceous community was highly resistant to effects of increased temperature on community composition (Kennard et al.,

2020). Increased temperature does, however, appear to affect density-dependent controls on the woody seedling community (Bachelot et al., 2020).

Following the first year of warming, two major storms, hurricanes Irma and Maria, struck the island of Puerto Rico in September 2017, including the site of the warming experiment. This disturbance, overlaid on an existing climate change experiment, provided an unprecedented opportunity to evaluate forest recovery following major hurricane disturbance in the context of climate change. This led to the development of two new post-hurricane "treatments". First, a new post-hurricane baseline was established and assessed to determine whether there were legacy effects of prior warming on ecosystem processes following the disturbance. Thus, no warming treatment was applied for the first year of forest succession following the hurricanes. After this year of forest recovery, the warming treatment was re-initiated, to evaluate how hurricane disturbance and warmer temperatures interact to affect the trajectory of forest recovery (Reed et al., 2020). This diverse array of warming and disturbance "treatments" allowed for the direct effects of warming to be differentiated from that of disturbance and identify interactions between disturbance and increased temperature. Thus, while there were no effects of warming on composition of the understory herbaceous community there were substantial changes in composition following hurricane disturbance, with no differences between areas that had experienced prior warming and the controls (Kennard et al., 2020). However, legacy effects of prior warming were noted on available soil P. Prior to the hurricanes, there was a small decline in available P in the warmed relative to the control plots, yet after the hurricanes, available soil P increased across all plots, but did not differ between the two treatments. However, when warming was reinitiated, available soil P pools increased significantly in the warmed relative to the control plots, suggesting a strong interaction between temperature and disturbance on the cycling of this key nutrient (Reed et al., 2020). Microbial biomass tells a different story. Prior to the hurricanes, microbial biomass was 50% higher in the warmed relative to controls (Reed et al., 2020), yet this difference disappeared post-hurricane when the warming treatment was not active. Once the warming treatment was re-initiated, microbial biomass in the warmed plots once again increased relative to the controls, suggesting a significant, direct, positive effect of warming on microbial biomass carbon only when soil is actively warmed (Reed et al., 2020). As part of this ongoing research, the effects of increased temperature and hurricane disturbance on key components of the carbon cycle are being explored, including plant ecophysiology and soil carbon fluxes.

Tropical forests have historically been considered relatively resistant to warmer temperatures, with few studies that explicitly consider temperature as a predominant driver of change (Wood et al., 2019b). Research from the LEF supports that at least some aspects of the ecosystem are relatively resistant to variation in temperature and that large-scale disturbance, such as hurricanes, are the more dominant control (i.e., Willig et al., 2019; Kennard et al., 2020). While other ecosystem processes do appear to be sensitive to temperature, with complex interactions with disturbance (Wood et al., 2019b; Reed et al., 2020). Resolving how temperature is likely to affect tropical ecosystems will entail scientists utilizing the breadth of long-term data available for the LEF and combining it with experimental evaluation of mechanistic responses to better refine models.

7.6. Elevation gradient

The LEF includes a steep climate gradient from dry tropical forest just outside the boundaries of the forest to cloud forests at the summits. Average temperature declines with elevation from approximately 26.5 °C in the lowlands to approximately 20 °C at the summit (González et al., 2013). Average annual rainfall ranges from 2450 mm/year at lower elevations to about 5000 mm/year at higher-elevation sites. Rates of terrestrial net primary productivity in the LEF, like most tropical

forests, are among the highest on Earth, and decline with increasing elevation. Basal area, above-ground biomass, canopy heights, and mean plant species richness peak at mid elevations (Gould et al., 2006). The gradient in precipitation and temperature in the Luquillo Mountains can provide a surrogate for changing climate and facilitates understanding of how such change may influence the biota (González et al., 2013). The hypothesis has been that distributions of terrestrial heterotrophs (microbes, litter invertebrates, and gastropods; González et al., 2013) in the Luquillo Mountains are more closely related to changes in characteristics of autotrophs (e.g., changes in forest composition and physiognomy) than they are to gradual variation in abiotic characteristics (e.g., temperature, rainfall, light, and wind). Microbes and litter invertebrates more closely followed the hypothesis (González et al., 2013) whereas gastropods responded equivalently to both influences (Presley et al., 2010, Willig et al., 2011b). Much of the elevational variation in abundance biodiversity was related to variation in total number of individuals, consistent with the More Individuals Hypothesis (Srivastava and Lawton, 1998) or Theory of Random Placement (Coleman et al., 1982).

Campos-Cerqueira et al. (2017) showed the elevational distribution of eight of 21 avian species changed significantly over a span of 17 years (1998–2015). They hypothesize that this rapid response is driven by increasing temperature in Puerto Rico, rather than anthropogenic disturbances, given that the study site has been protected for >100 years. The elevation distributions of six bird species expanded, whereas the ranges of two species contracted. Elevation limits shifted upward with changes in upper limits more common. This distributional change of avian species in the best-protected forests in Puerto Rico may have significant ecological consequences for the dynamics in the LEF such as cascading effects and disruption of trophic interactions, because birds are the main top predators and seed dispersers on the island (Reagan and Waide, 1996).

Alterations to climate drivers can influence the composition and physiognomy of montane forests as they are strongly tied to regimes of rainfall and cloud cover (Dalling et al., 2016), which can feed back on soil aeration and biogeochemistry (Silver et al., 2013). Upper elevation forests are effectively upland wetlands, with low redox conditions that result in high methane emissions, and limit plant and microbial nutrient utilization (Yang et al., 2020). Climate change is predicted to have dramatic effects on montane forests by lifting cloud-base heights (Dalling et al., 2016). Van Beusekom et al. (2017) showed cloud levels in the dry season are consistently as low, or lower, than in the wet seasons at lower elevations in the Luquillo Mountains under the current climate regime, indicating that LEF ecosystems may be more vulnerable to wet season drought periods than was assumed previously. In contrast, a 42-year record showed no changes in cloud base height related to anthropogenic influences thus far (Miller et al., 2018). Continued long-term monitoring of the elevational gradient in the LEF will determine which climate drivers are most likely to affect change in the distribution of the biota and cause shifts in soil C storage and greenhouse gas emissions.

8. The future of the LEF

Results from the long research history in the LEF suggests the tropical ecosystems are highly resilient to many disturbances, both anthropogenic and non-anthropogenic in nature (Brokaw et al., 2012). How does the resiliency of this tropical ecosystem might change as the Caribbean confronts anthropogenic climate change, or a potential increase in frequency of natural disturbances? In the LEF, we anticipate three principal changes wrought by a warming world. One is the warming itself, which may challenge species' physiological tolerances and alter species demography. The other two potential changes accrue to shifts in the disturbance regime caused by increased warming: 1) an increase in the frequency of intense hurricanes driven by the warmed waters of the North Atlantic and; 2) an increase in the frequency or length of dry

periods caused by warming, coupled with a change in the seasonality of rainfall. Together the last suggests a world in which precipitation extremes become more common as extended dry periods are combined with more numerous heavy rainfall events. As none of these potential changes are mutually exclusive, the challenge is to understand how the combination of factors might affect ecosystems of the LEF in the future. In particular, we are interested in identifying tipping points of irreversible change (Johnstone et al., 2016), driven by conditions that exceed historical ranges (Duncan et al., 2010)?

It is difficult to speculate what would be the tipping points in the tropical forest ecosystems represented by the LEF. From a global perspective, the alternative stable state for a forested ecosystem is a grassland or savanna where fire is a key part of the disturbance regime, as discussed by Johnstone et al. (2016). We find an alteration of the disturbance regime to include fire difficult to fathom even under the most extreme drying scenarios. Brush fires do occur on the fringes of forests of the LEF during drought (Brokaw et al., 2012) but fire never penetrates the forest itself.

More fundamentally, we ask whether the range of conditions contemplated under the global change scenario for the Caribbean exceeds the historical range relevant to evolutionary time spans. Zimmerman et al. (2020) reviewed that evidence that the LEF forests have been subject to hurricane disturbance since at least the Last Glacial Maximum (during which cold ocean waters might be expected to shut down storm generation). Moreover, Donnelly et al. (2015) found that periods of frequent intense tropical cyclone landfalls (between 250 and 1150 C.E) exceeded historical levels at five sites across the Caribbean over the last 2000 years. Similarly, periods of drying in the last 10,000 years (e.g., Higuera-Gundy et al., 1999) may have created extinction filters favoring drought tolerant species (Borhidi, 1991).

Contemporary comparisons of tree dynamics in sites with different storm regimes, including sites in the western Pacific (Hogan et al., 2018; Lin et al., 2020) suggest one possible scenario. Frequent cyclone disturbance in Taiwan results in forests with reduced stature, but with demographic and trait dynamics not different from tall-statured forest in Panama that suffers little exposure to cyclonic storms, confirming Odum's (1970) hypothesis regarding storm frequency and forest stature. Two sites included in the Hogan et al. (2018) study with intermediate storm disturbance regimes and stature, including the LEF, had the highest demographic rates of all. This is because the prevailing storm interval and the timing of forest maturation via succession were matched closely; mature forests have more developed canopies for storm winds to affect. This aside, the comparison to Taiwan suggests a scenario where there is no distinct tipping point, but rather selection for increases in the abundances of species most resistant to the changing climate or disturbance regime, without a distinct change in ecosystem function (Uriarte et al., 2009). Although the composition of forest may change, the change may occur more gradually. We will be watching to see. In any case, the deep history of changing climate and disturbance regimes in the LEF likely explains the robust resilience to disturbance in the LEF that we have witnessed in the last century of research.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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