CHAPTER SIX

Soil biogeochemical responses of a tropical forest to warming and hurricane disturbance

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Abstract

Tropical forests represent <15% of Earth's terrestrial surface yet support >50% of the planet's species and play a disproportionately large role in determining climate due to the vast amounts of carbon they store and exchange with the atmosphere. Currently, disturbance patterns in tropical ecosystems are changing due to factors such as increased land use pressure and altered patterns in hurricanes. At the same time, these regions are expected to experience unprecedented warming before 2100. Despite the importance of these ecosystems for forecasting the global consequences of multiple stressors, our understanding of how projected changes in climate and

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disturbance will affect the biogeochemical cycling of tropical forests remains in its infancy. Until now, no studies to our knowledge have evaluated forest recovery following hurricane disturbance within the context of concurrent climatic change. Here, we present soil biogeochemical results from a tropical forest field warming experiment in Puerto Rico where, a year after experimental warming began, Hurricanes Irma and María greatly altered the forest, allowing a unique opportunity to explore the interacting effects of hurricane disturbance and warming. We tracked post-hurricane forest recovery for a year without warming to assess legacy effects of prior warming on the disturbance response, and then reinitiated warming treatments to further evaluate interactions between forest recovery and warmer temperatures. The data showed that warming affected multiple aspects of soil biogeochemical cycling even in the first year of treatment, with particularly large positive effects on soil microbial biomass pools (e.g., increases of 54%, 33%, and 38% relative to the control plots were observed for microbial biomass carbon, nitrogen, and phosphorus, respectively after 6 months of warming). We also observed significant effects of the hurricanes on soil biogeochemical cycling, as well as interactive controls of warming and disturbance. Taken together, our results showed dynamic soil responses that suggest the future of biogeochemical cycling in this tropical wet forest will be strongly shaped by the directional effects of warming and the episodic effects of hurricanes.

1. Introduction

Disturbances, such as hurricanes, play a key role in shaping forest landscape patterns and processes over years, decades, and centuries (Johnstone et al., 2016; Lugo, 2008; Lugo and Scatena, 1995). Most ecosystems are commonly recovering from past events, and thus interpretation of current forest dynamics should ideally be considered within the context of the historical disturbance regime (Bormann and Likens, 1979; Cooper, 1926; Turner, 2010; White, 1979). However, we are now entering a time when directional changes in climate, such as increasing temperatures, are likely to disrupt key ecosystem processes, which can increase vulnerability to other disturbances and endanger the persistence of the affected ecosystems (Folke et al., 2004). A strong interaction between disturbance and climate change severely limits our ability to predict how ecosystems respond to perturbation, as the outcomes of these interactions may not be apparent until a disturbance event has occurred (Johnstone et al., 2016). Despite the large potential for interactive effects between climate change and disturbance in tropical ecosystems, our understanding of the consequences of these combined effects for ecosystem function remains poor, in part because disturbance events, such as strong hurricanes, are relatively infrequent. Here, we took advantage of an ongoing field warming experiment in

Puerto Rico that was struck by two major hurricanes to ask the questions: (1) Does prior warming affect soil biogeochemical responses to hurricane disturbance? and (2) Does increased temperature affect the speed and magnitude of recovery of biogeochemical processes following disturbance?

Tropical forests are ideal ecosystems for addressing these questions, given the high rate of biogeochemical cycling and the speed of forest recovery. For example, within 15 years of forest regrowth following hurricanes, tropical forest canopy structure can be nearly indistinguishable from old growth forests (Heartsill-Scalley et al., 2010). Further, tropical forests play a disproportionately large role in Earth's biogeochemical cycling relative to the spatial extent of their land cover (Townsend et al., 2011). Lowland tropical forests make up only 15% of the planet's terrestrial surface, yet these productive ecosystems account for over 2/3 of our live terrestrial plant biomass (Pan et al., 2013), nearly one-third of all soil carbon (C) (Jobbagy and Jackson, 2000; Tarnocai et al., 2009), and exchange more carbon dioxide with the atmosphere than any other biome (Beer et al., 2010; Foley et al., 2003). Tropical forests also represent large uncertainties in our capacity to forecast future C cycling and thus climate (Cavaleri et al., 2015). For example, although data suggest tropical forest ecosystems determine the size of the land C sink (Ahlström et al., 2015), our understanding of how tropical forests will respond to global changes, such as increased temperature and altered precipitation, is lacking (Wood et al., 2012). Nevertheless, the implications for such uncertainty related to the biogeochemical consequences of tropical forest responses are particularly important. If the massive amount of C stored in tropical forest soils increases or decreases in response to change, even seemingly subtle alterations could have large implications for the amount of CO_2 in the atmosphere (see also "Protecting environmental and socio-economic values of selectively logged tropical forests in the Anthropocene" by Bousfield et al., this issue).

Most ecosystems are adapted to some form of disturbance regime. Hurricanes, for example, affect nearly every continent in the world and are among the most intense weather disturbances in forested ecosystems (McDowell, 2011). Strong hurricanes are known to cause significant disruption to forest structure and reductions in canopy height (Heartsill-Scalley et al., 2010; Fig. 1), which has cascading consequences for biogeochemical and hydrologic cycling in forests (Comita et al., 2009; Heartsill-Scalley et al., 2007; Herbert et al., 1999; Lodge et al., 1991; Lugo et al., 1983; McDowell, 2011; McDowell and Liptzin, 2014; Sánchez-Sánchez and Islebe, 1999; Silver and Vogt, 1993). For example, green leaves stripped from vegetation and deposited on the forest floor can deliver a substantial

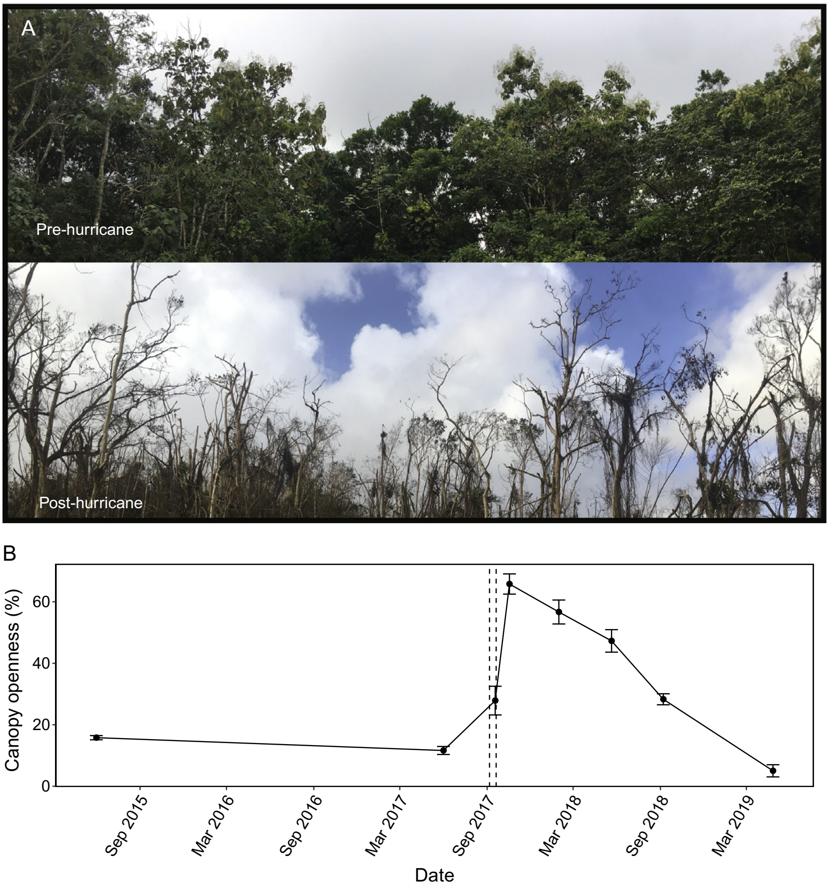

Fig.1 (A) Photographs showing canopy cover before and after the 2017 hurricanes at the warming experiment site in the Luquillo Experimental Forest, Puerto Rico. (B) Percent canopy openness before the hurricanes and following Hurricane Irma and Hurricane María. Dashed lines indicate dates the 2017 hurricanes in Puerto Rico. These data underscore both the large effects of hurricanes on the structure of tropical forests, as well as the rapid pace of recovery.

pulse of C and nutrients that are equivalent to more than a year's worth of litter inputs, resulting in 1.3 and 2.4 years' worth of phosphorus (P) and nitrogen (N), respectively deposited on the forest floor in less than 1 week (Lodge et al., 1991). The opening of the forest canopy also affects a range of processes via large changes in forests' microclimate. As much as 40% of rainfall can be intercepted by an intact forest canopy, and rainfall that does pass through the canopy (i.e., throughfall) is chemically altered due to leaf nutrient leaching and the washing off of dust and debris (Heartsill-Scalley et al., 2007). Immediately following hurricanes, canopy rainfall interception is negligible, and the chemistry of throughfall most closely reflects that of rainfall (Heartsill-Scalley et al., 2007). Canopy disturbance also significantly alters understory microclimate and light availability (Comita et al., 2009; Scatena et al., 1996), driving a much more variable microclimate without the buffering effect of the forest canopy, which is also likely to alter patterns of soil biogeochemical cycling (González et al., 2014; Lodge et al., 2014; Silver and Vogt, 1993). However, in places where such events are a long-term component of the disturbance regime, plant communities that experience frequent hurricanes have often developed adaptation strategies that provide both resistance and resilience to these forms of disturbance (Lugo et al., 1983; Sánchez-Sánchez and Islebe, 1999).

Research also suggests that tropical forests are facing a significant shift toward a novel temperature regime in the coming decades, with temperatures in the tropics and subtropics increasing by 3–5 °C within the next 20 years (Anderson, 2011; Diffenbaugh and Scherer, 2011). Given the narrow temperature range under which tropical forests typically operate, combined with evidence that these forests may be near high temperature thresholds, there is potential for tropical forest C cycling to respond dramatically to rising temperatures (Clark et al., 2003; Doughty and Goulden, 2008; Wood et al., 2012, 2019). Responses from warming experiments in other types of ecosystems show the likelihood of soil biogeochemical responses to increased temperatures (e.g., Bai et al., 2013; Rustad et al., 2001), but a lack of such experiments in tropical forests has hindered our capacity to explore similarities or differences in tropical environments (Cavaleri et al., 2015). Natural temperature gradients (e.g., elevational gradients) in the tropics offer important opportunities for observational studies of temperature effects on plant and ecosystem functioning (Malhi et al., 2010; Nottingham et al., 2019; Selmants et al., 2014; Townsend et al., 1995), yet the warmer temperature regimes predicted for the already-warm lowland tropics do not currently exist in tropical forests today (Wright, 2010). Thus, warming experiments are needed to achieve the projected temperatures and to assess how tropical forests change as temperatures rise (Cavaleri et al., 2015).

Given this potential for increased temperatures to “stress” tropical forested ecosystems, the combined effects of hurricane disturbance and warmer temperatures could fundamentally alter the functioning and the resilience of these ecosystems, resulting in direct and legacy effects of prior warming on soil biogeochemical cycling in the months following disturbance.

Furthermore, as the forest progresses through the expected stages of post-hurricane recovery, increased temperature could alter the trajectory and duration of forest recovery patterns, resulting in shifted ecosystem states (Johnstone et al., 2016) and changes to coupled biogeochemical cycles. An improved understanding of how hurricane disturbance and temperature interact to regulate tropical forest biogeochemical cycling is essential not only for considering the overall fate of these forests, but for improving predictions of future global C cycling and climate (Ahlström et al., 2015; Cavaleri et al., 2015; Reed et al., 2012; Van Gestel et al., 2018). Using the Tropical Responses to Altered Climate Experiment (TRACE) in situ manipulation and an opportunity to assess interactions of this experimental warming with forest responses to 2017's Hurricanes Irma and María, we hypothesized that prior warming would significantly alter soil C and nutrient cycling in the months following hurricane disturbance. We further predicted that warming in a post-hurricane environment would drive trajectories of recovery divergent from those in the unwarmed plots, resulting in fundamentally altered coupled C and nutrient cycles and a system with altered resilience to future disturbance (Johnstone et al., 2016).

2. Methods

2.1 Site description

The study site is a lowland subtropical wet forest (sensu Holdridge et al., 1971) located near the U.S. Forest Service Sabana Field Research Station, which is within the Luquillo Experimental Forest in northeastern Puerto Rico (18° 19′ 28.56"N, −65° 43' 50.16"W). The study area is ~100 m.a.s.l. and is a secondary forest that has regenerated from pasture since the early 1950s (Kimball et al., 2018). The site has a long history of hurricane disturbance, including Hurricanes Hugo (1989) and Georges (1998), which both occurred within the timeframe of this forest's regeneration. The mean annual temperature is 24 °C, and mean annual precipitation is ~3500 mm. Rainfall occurs throughout the year and, on average, no month receives less than 200 mm of precipitation (Heartsill-Scalley et al., 2007). Temperature exhibits relatively low seasonal variation, with mean monthly temperatures varying just 4 °C throughout the year (Kimball et al., 2018). Soils are classified as Ultisols and are deep and rich in clay (Scatena, 1989). The site has relatively steep slopes that range from 15 to 26 degrees with an average slope of 21 degrees (Kimball et al., 2018).

2.2 Experimental design

The Tropical Responses to Altered Climate Experiment (TRACE) is made up of six 4-m diameter hexagonal plots: three control and three heated. All plots were at least 10 m apart. For the heated plots, six infrared (IR) heaters (Model Raymax 1010, Watlow Electric Manufacturing Co., St. Louis, MO) were installed on crossbars at ~2.6 m height from the ground. Heating from this height warms the understory canopy and the soils. The same infrastructure (crossbars, posts, and concrete footings) used for the warming plots was also constructed around the unwarmed control plots to control for any effects of treatment installation and/or shading. Instead of IR heaters for these plots, aluminium panels were installed on crossbars as false heaters. Multiple soil microclimate sensors were installed (Campbell Scientific CS655; Logan, UT): Each plot has one soil temperature and moisture sensor at 40–50 cm depth, one sensor at 20–30 cm depth, and three surface sensors at 0–10 cm depth. The surface sensors are at the edge of the plot, midway to the center of the plot, and at the center of the plot. The deeper soil sensors are in the center of the plot. Warming treatments began on September 28, 2016. The IR heaters were designed and controlled so heated plots maintained temperatures 4.0 °C higher than the mean of control plot temperatures ±0.1 °C, as sensed by IR thermometers (Kimball et al., 2018). During the first year of heating prior to the hurricanes, heating was homogeneous, and there was little observable difference among temperatures of the 0–10 cm depth soil at the plots' centers, edges, and midway between. During this first year with the warming treatments, soil temperatures at 40–50 cm depth increased ~3 °C compared to the control plots. Details about the warming treatment's design, installation, and performance can be found in Kimball et al. (2018).

In 2017, the coastal U.S. and Puerto Rico were struck by a series of major hurricanes that will have long-lasting implications for these tropical forests. On September 5, 2017, after 11.5 months of experimental warming, the IR heaters were turned off in preparation for the hurricanes. On September 7, 2017 the eye of category 5 Hurricane Irma passed just 15 miles north of Puerto Rico. Less than 2 weeks later, Hurricane María made landfall on the island as a Category 4 storm with sustained winds up to 250 km/h, and 500 mm of precipitation fell in 24 h. Hurricanes Irma and María strongly affected forest structure across the island. This disturbance completely defoliated all vegetation, severed large branches, and drove a large number of treefalls, all of which substantially increased canopy openness (Uriarte et al., 2019; Fig. 1), with significant consequences for forest structure and function (e.g., Heartsill-Scalley et al., 2007; Lodge et al., 1991; Silver and Vogt, 1993). Although the majority of branches and leaves were lost from the canopy, most trees survived, and forest regeneration began quickly (Fig. 1).

While TRACE infrastructure was designed to withstand hurricane-force winds and precipitation, falling trees and branches during Hurricanes Irma and María damaged portions of the heating and plot infrastructure. Tree trunks and large branches were removed from the plots following the hurricanes, but leaf litter and small woody debris (≤3 cm diameter) were left in place. Warming treatments were fully re-initiated approximately 1 year later, on September 28, 2018. Following the reinstatement of warming, changes to forest structure significantly altered the way warming occurred in the soils (Fig. 2). Hurricane-induced increases in understory growth

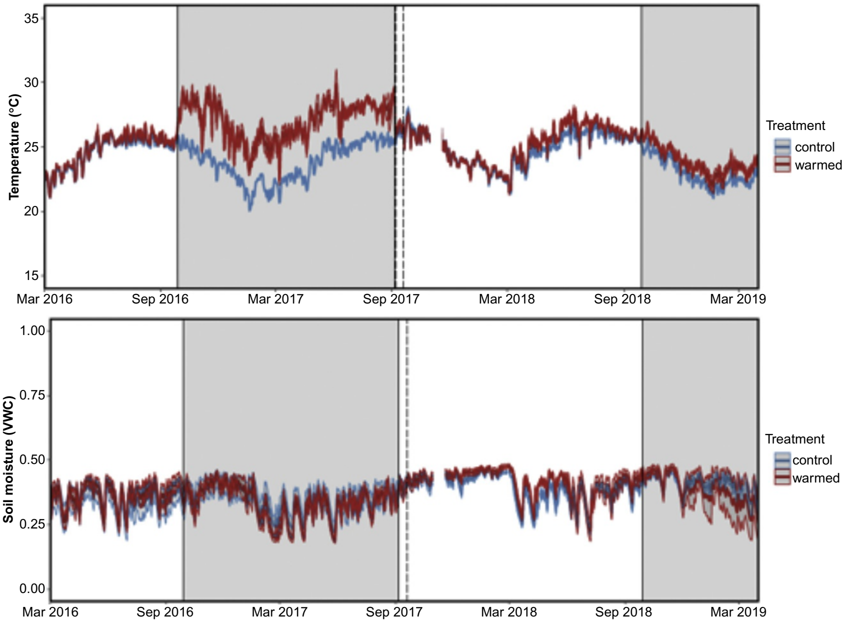

Fig. 2 (A) Soil temperature (°C) and (B) soil moisture (volumetric water content, unitless) values for the top 10 cm of soil in the control (blue) and warmed (red) plots ($n = 3$ for each treatment). The data are daily means with standard error for among plot variation shown with coloured shading. There is a gap in the soil microclimate data in November, 2017 due to problems with the data logger battery system. The gray shading blocks show the times when the warming treatments were active and the vertical dashed lines show when Hurricanes Irma and María struck the site. Results show that the warming increased soil temperatures at all measurement times, but the warming effects were larger prior to the hurricanes. The warming also caused significant but small reductions in volumetric water content.

intercepted more energy from the IR lamps, and as a result the soils warmed on average + 1 °C at 0–10 cm depth as opposed to the +3.2 °C observed at the same soil depth prior to the hurricanes.

The hurricanes that struck Puerto Rico were, of course, not a planned treatment and because the entire forest was affected, the disturbance left an experimental design without a disturbance control (i.e., all plots, warmed and unwarmed, were affected by the hurricanes). A lack of power throughout Puerto Rico following Hurricane María and damage to warming infrastructure also meant that warming treatments were not possible for several months following the hurricanes. With that in mind, the warming treatments were stopped for a full year so that we could fully assess the legacy effects of warming on a recovering tropical forest without the confounding effects of active warming. While the need to stop the warming did inhibit assessment of the consequences of active warming during the first year of regrowth, the in situ warming experiment combined with the potentially once-in-a-century Category 4 hurricane offered a unique opportunity to assess the effects of prior warming on forest responses to hurricane disturbance and to explore the interacting effects of warming and disturbance on the trajectory of forest recovery. Taken together, the data presented here show pre-treatment data, nearly a year of warming, a year of forest regrowth without warming following large hurricane disturbance, and then recovery from hurricane disturbance with warming treatments reinitiated.

2.3 Soil sampling and analysis

At each sampling timepoint, soil samples were taken from 0 to 10 cm depth and were analysed for total C and total N, KCl-extractable inorganic N (NH_4^+ + NO_3^-), Bray-extractable PO_4^{3-}, K_2SO_4-extractable organic C and N, and microbial biomass C, N, and P concentrations. Unfortunately, unanticipated problems with the chloroform methods resulted in unusable soil microbial biomass data for the pre-warming timepoint of March 10, 2016. Chloroform methods were refined and were successful at all other timepoints. Soils were harvested from each plot and were returned to the on-site laboratory where roots and visible organic matter were manually removed from each sample. All soil processing and extractions were conducted on the same day soils were collected. For all extractions, extracts were filtered through Whatman #1 filter paper (GE Healthcare, Chicago, IL), frozen immediately, and stored frozen until analysis.

To assess total C and N concentrations, soils were dried at 60 °C, ground, and were analysed for total C and N using an elemental analyser (Elementar Vario Micro Cube, Elementar Inc., Langenelsbold, Germany). For extractable inorganic N concentrations, fresh soil was shaken with 2 N KCl for 1 h, allowed to sit overnight, and filtered (as described in Reed et al., 2008). Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were analysed using colorimetry with the indophenol blue method and a cadmium reduction-Greis Ilosvay method on an autoanalyser (Unity Scientific Smartchem 200 Discrete autoanalyser, Milford, MA; Reed et al., 2008). To assess Bray-extractable PO_4^{3-}, fresh soil was extracted with Bray solution (dilute $HCl+NH_4F$) and shaken for 1 min (Bray and Kurtz, 1945). Samples were filtered immediately and PO_4^{3-} concentrations were measured colorimetrically using an ascorbic acid molybdate analysis on the SmartChem autoanalyser (Sparks et al., 1996). For TOC and TDN analyses, fresh soil was extracted with 0.5 M K_2SO_4. Samples were shaken for 1 h, filtered, and analysed on a Shimadzu TOC/TDN (TOC-V_{CPN} with TNM-1 attachment, Shimadzu Corporation, Kyoto, Japan).

A chloroform addition method was used to assess microbial biomass C, N, and P. Briefly, the method is a modification of the chloroform fumigation method (Brookes et al., 1985; Vance, 1987), and ethanol-free chloroform is directly added to soil instead of fumigating with chloroform in a sealed chamber headspace. For microbial C, N, and P, fresh soil was placed into an Erlenmeyer flask, and 1 mL of chloroform was added before sealing the flask with a neoprene stopper. The flasks were left in the dark for 14–16 h before being unstoppered and aired for 1 h. Samples for microbial biomass C and N concentrations were extracted with K_2SO_4 and were analysed for TOC and TDN concentrations as described above. Samples for microbial biomass P were extracted with Bray and were analysed for PO_4^{3-} concentrations as described above. Initial K_2SO_4 extract values (for C and N) or initial Bray extract values (for P) were subtracted from the K_2SO_4 or Bray values from the samples with chloroform addition to estimate microbial biomass C, N, and P concentrations. The data provided here have not been converted using the proportionality constants sometimes used for C, N, and P (Brookes et al., 1985, Vance et al., 1987; e.g., $Kc=0.45$ for C). Canopy openness was measured from the center of each of the six experimental plots on the dates shown in Fig. 1 using a spherical densiometer (Forestry Suppliers, Inc.). Measurements were taken following the manufacturer's instructions.

All data were tested for normality and homoscedasticity before analysis. Variation in all soil biogeochemical pools were assessed over time, by treatment, and with associated interactions using a repeated measures general linear model (GLM). Plots were treated as a random variable to account for native differences among them. For single time points, significant differences between treatments were explored with multi-variate GLM. Significance was determined at $\alpha < 0.05$ and all analyses were performed using SPSS statistical software (IBM Inc., Armonk, NY).

3. Results

3.1 Warming treatment effects on soil moisture

The volumetric water content was an average of 1.45% lower in the warmed plots relative to the control plot for the first round of warming (10/4/2016–9/5/2017), and an average of 3.79% lower in the warmed plots relative to the control plots for the second round of warming (9/29/2018–8/27/2019; Fig. 2).

3.2 Total carbon and nitrogen

Total soil C and N concentrations in the top 10 cm of soil varied significantly with time ($P < 0.001$), showing significant increases in C and N concentrations in the year following the hurricanes and subsequent declines after that time (Fig. 3). Although there was some suggestion of warming-induced increases in total soil C and N during the first year of warming before the hurricanes struck, these trends were not significant and there were no interactive effects of warming on the patterns of soil C and N over the course of post-hurricane forest recovery. The C:N ratios of the soil did not change through time or with the warming treatment.

3.3 Extractable carbon, nitrogen, and phosphorus

Similarly to total soil C and N, there were not significant warming treatment effects for extractable organic C or total dissolved N concentrations at any timepoint. Extractable organic C and N concentrations did increase through time. In contrast, the concentrations of inorganic forms of extractable soil N and P did respond significantly to warming (for NH_4^+, NO_3^-, and PO_4^{3-} there was a significant effect of warming ($P < 0.05$) for at least one time point of every extractable pool; Figs. 4 and 5). Concentrations of these highly available extractants were also affected by the hurricane and showed interactive effects of hurricane disturbance and warming. For example, patterns in inorganic N showed strong responses to these global change

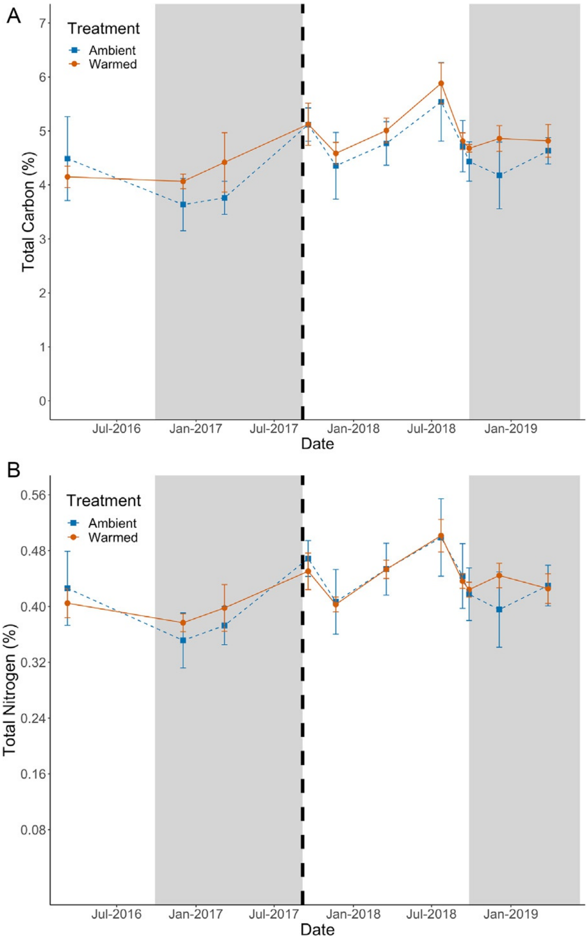

Fig. 3 Total soil (A) carbon and (B) nitrogen concentrations from 0–10 cm depth in the ambient (blue squares) and warmed (red circles) plots. Measurements were made through time and values are means ± 1 standard error. Gray shading shows the times when the warming treatments were active, and the dashed vertical line represents when Hurricane Irma occurred. Total carbon and nitrogen concentrations varied through time, most notably changing after the hurricanes, and there were no significant warming treatment effects.

pressures and different forms of N responded in different ways. Extractable ammonium concentrations increased significantly following the hurricane, with values that remained elevated above all pre-hurricane values for all post-hurricane sampling points (Fig. 4A; $P < 0.01$). In addition to hurricane effects, warming significantly decreased ammonium concentrations prior to the hurricanes, but although concentrations of ammonium were consistently lower in the warmed plots relative to control plots after the

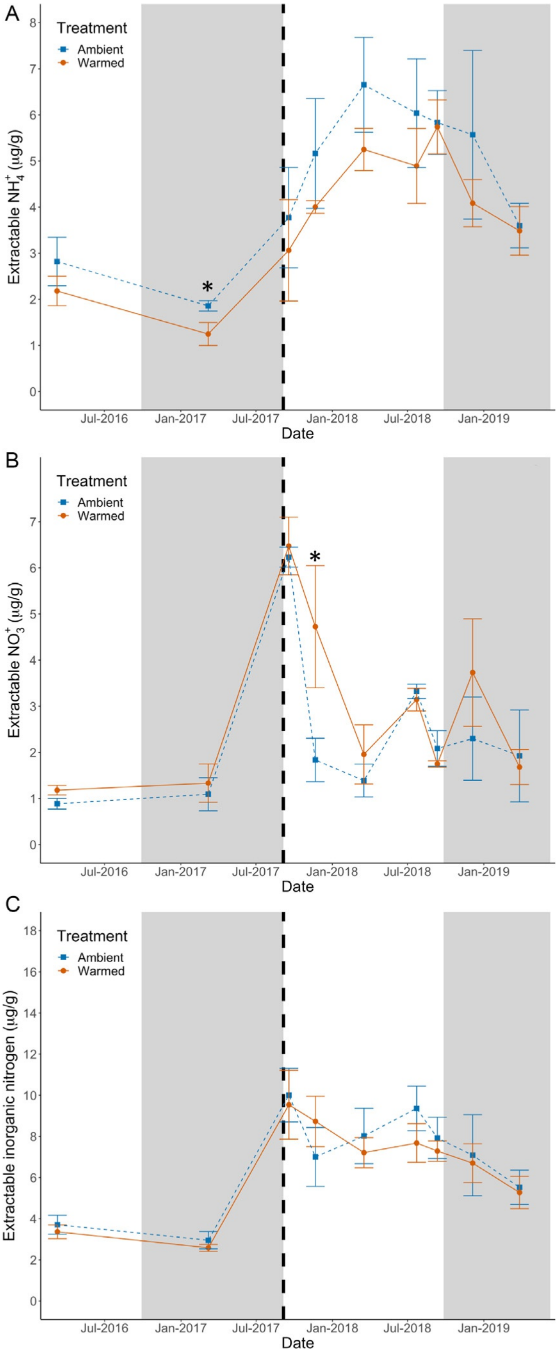

Fig. 4 Extractable (A) soil ammonium (NH_4^+), (B) nitrate (NO_3^-), and (C) inorganic nitrogen concentrations from 0–10 cm depths in the ambient (blue squares) and *(Continued)*

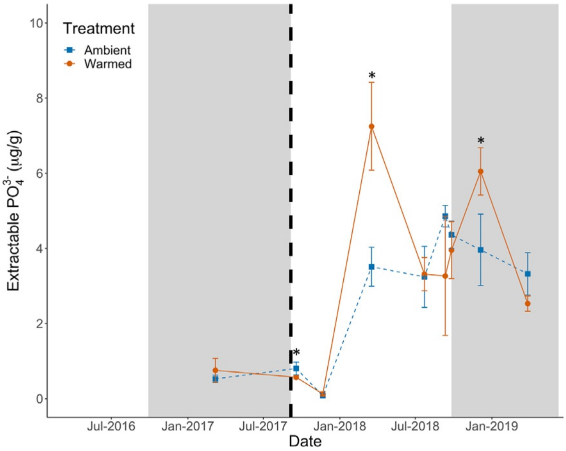

Fig. 5 Extractable soil phosphorus (PO_4^{3-}) concentrations from 0–10 cm depths in the ambient (blue squares) and warmed (red circles) plots. Measurements were made through time and values are means ± 1 standard error. Gray shading shows the times when the warming treatments were active, and the dashed vertical line represents the occurrence of Hurricane Irma. Data showed concentrations varied through time, especially following hurricane activity, with warming treatment effects at specific times (depicted with asterisks). Results show that both hurricane disturbance and warming significantly affected dynamic soil phosphorus concentrations.

hurricane, these differences were not significant. For nitrate, warming alone did not significantly affect concentrations prior to the hurricanes, but following hurricane disturbance, nitrate concentrations were significantly higher in the warmed plots during the year of recovery before warming was reinitiated ($P = 0.012$). The hurricane did not have as sustained an effect on nitrate concentrations as it did ammonium concentrations. When summing ammonium and nitrate to explore changes in inorganic N concentrations, we found that the hurricanes significantly increased the extractable inorganic N concentrations and that these concentrations remained elevated nearly 2 years after the hurricanes

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Fig. 4—Cont'd warmed (red circles) plots. Measurements were made through time and values are means ± 1 standard error. Gray shading shows the times when the warming treatments were active, and the dashed vertical line represents the occurrence of Hurricane Irma. Data show that extractable nitrogen concentrations varied through time, especially following hurricane activity, with warming treatment effects at specific times (significant differences among treatments depicted with asterisks). Results show that both hurricane disturbance and warming significantly affected dynamic soil nitrogen concentrations of this tropical wet forest.

(e.g., inorganic N concentrations were >50% higher at all timepoints post hurricane relative to all pre-hurricane measures).

Extractable soil P concentrations varied greatly with time ($P<0.001$), with large increases in P observed following the hurricanes (extractable PO_4^{3-} concentrations were over four times higher post-hurricane relative to values observed prior to the hurricanes). Overall, the amount of extractable P remained elevated relative to any of the pre-hurricane measurements almost 2 years after the hurricanes occurred (Fig. 5). In contrast, warming treatments significantly reduced extractable P prior to Hurricane Maria ($P<0.05$). Warming also interacted with the effects of hurricane disturbance such that extractable P was more than doubled in the plots that had been previously warmed 6 months after the hurricanes occurred than in the controls which had received no warming (Fig. 5). The extractable P concentrations were also significantly higher in the warmed plots during the second round of warming in December 2018 for one measurement timepoint.

3.4 Microbial biomass carbon, nitrogen, and phosphorus

Surprisingly, the hurricanes did not significantly affect microbial biomass C or N in the year following the events (Fig. 6). In contrast to microbial biomass C and N, microbial biomass P did significantly increase during the year following the hurricanes and remained higher than pre-treatment concentrations for all post-hurricane timepoints ($P<0.001$). Warming affected microbial biomass C, N, and P concentrations only during times when the warming treatments were active (Fig. 6). Although we did not have pre-treatment data for microbial biomass due to methodological issues, none of the other pre-treatment values, including those for the highly dynamic extractable N pools, showed significant differences prior to the warming treatment, supporting the idea that microbial biomass concentrations likely did not have spurious differences between treatment plots prior to the initiation of warming. Further, for all microbial biomass element pools, the differences between the warming and the control plots disappeared when the warming was not active (i.e. the timepoints during the year post-hurricane when warming was ceased; Fig. 6), lending further support for the suggestion that the warming treatment, when active, caused strong differences in microbial biomass C, N, and P. In all cases, when warming had a significant effect on microbial biomass concentrations of any element, the effect was a warming-induced increase in concentrations (Fig. 6).

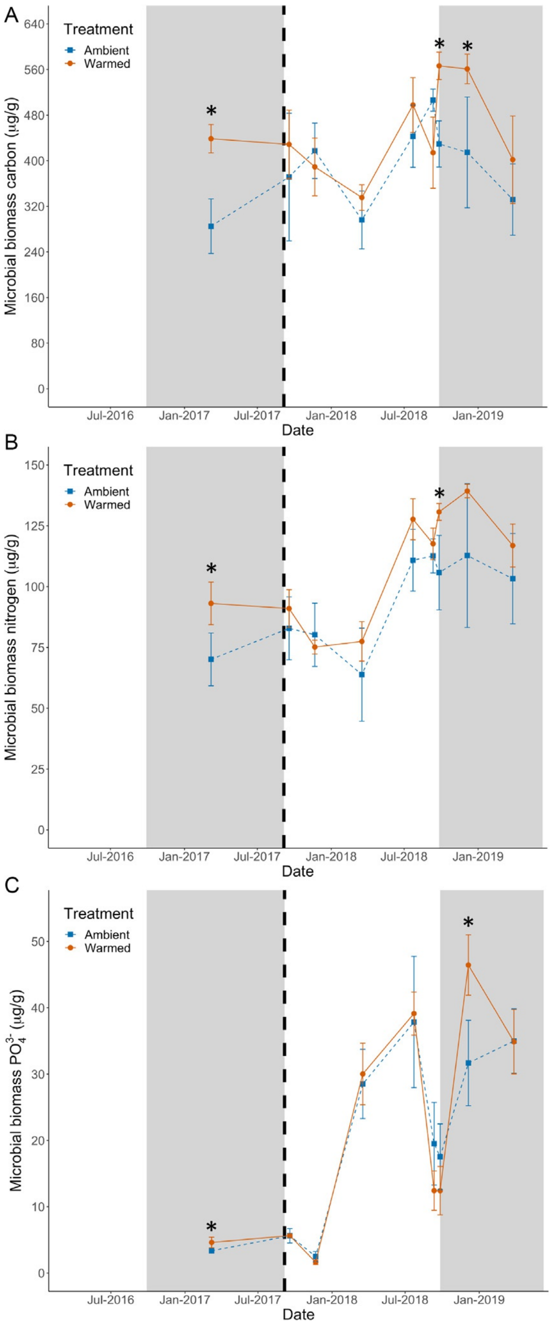

Fig. 6 Soil microbial (A) carbon, (B) nitrogen, and (C) phosphorus concentrations from 0–10 cm depths in the ambient (blue squares) and warmed (red circles) plots. Measurements were made through time and values are means ± 1 standard error. Gray shading shows the times when the warming treatments were active, and the dashed vertical line represents the occurrence of Hurricane Irma. Data showed that concentrations varied through time, especially with warming, and significant warming treatment effects are depicted with asterisks.

4. Discussion

This study assessed the soil biogeochemical responses of a tropical wet forest to an in situ warming treatment and subsequent interactions with disturbance following a once-in-a-century hurricane (i.e., Hurricane María). Like the majority of tropical forest sites (Chazdon, 2003; Houghton and Nassikas, 2018), the study area is a secondary forest (regenerating from pasture for ~70 years). While no tropical forest can be a proxy to predict the responses of all tropical forests, the data described here are relevant to the large number of tropical forests that have legacies of land use history and disturbance (see chapter "Novelty in the tropical forests of the 21st century" by Lugo et al., this issue), which can help us begin to constrain tropical responses to concurrent global changes. We observed a high responsiveness of this forest's soil biogeochemical cycles to both warming and hurricane disturbance, as well as their interactive effects. The data from the warming experiment demonstrated a rapid response of tropical soil's faster-cycling C and nutrient pools to increased temperature. Multi-timepoint biogeochemical data following Hurricanes Irma and María showed the dynamism with which tropical forest soils responded to and the new trajectories of change following large-scale hurricane disturbance. The interactions between the effects of warming and hurricanes lend insight into the consequences of hurricanes in a warmer world and provide a novel look into a potential future for some tropical forest soils.

4.1 Warming effects

To our knowledge, the soil biogeochemical data from the year of in situ experimental warming prior to the hurricanes represent the first such published values for any tropical wet forest and lend unique insight into tropical forest belowground responses to increasing temperatures. While no warming experiment can perfectly mimic the manner, extent, or variation that will occur with actual warming (Amthor et al., 2010; Aronson and McNulty, 2009), in situ warming experiments can provide a mechanistic understanding of how systems interact with, are driven by, and respond to temperature change (Aronson and McNulty, 2009; Cavaleri et al., 2015; Hanson et al., 2017; Kimball et al., 2008).

In this tropical wet forest, warming treatments did not affect total soil C and N concentrations in a single year (Fig. 3). The hurricanes restructured the forest before we could assess longer-term total C and N pool responses to warming in the absence of recent disturbance, nevertheless, we did observe significant effects of warming on soil extractable and microbial C and nutrient pools in the first year of warming (Figs. 4–6), with different responses from different pools and elements. In contrast to our predictions, extractable organic C and total dissolved N did not vary significantly with warming, however, warming decreased extractable P by 30% (Fig. 5). Effects on extractable P are of particular interest as P is the element often believed most limiting to the activity of lowland tropical forest plants and microbes (Cleveland and Townsend, 2006, Elser et al., 2007, Cleveland et al., 2011, Camenzind et al., 2018; but see Wright, 2019). Determining the underlying mechanisms controlling a dynamic response of P to warming would be of great value, and many components of P cycling could be at play. For example, clay-rich Ultisols, which are common in lowland tropical forests (Reed and Wood, 2016), have a high affinity for P (Olander and Vitousek, 2004) and these interactions can be strongly mediated by soil moisture and soil redox conditions (Chacon et al., 2006; Lin et al., 2018; Wood et al., 2016). Thus, in addition to competition between roots and microbes, there is also competition with the soil mineral surface for available P pools. In addition to warming the soils, our treatments also resulted in a small reduction of soil moisture in the surface soils (Fig. 2), which could affect P adsorption to mineral soils. A wealth of data suggest that understanding how P availability responds to altered climate and disturbance is critical for our understanding and prediction of how tropical forests store and cycle C (Camenzind et al., 2018; Cleveland and Townsend, 2006; Fleischer et al., 2019; Reed et al., 2015; Turner et al., 2018; Wright, 2019; Yang et al., 2016), and the data presented here suggest that warming has strong potential to affect the P pools believed most biologically accessible (Fig. 5).

Microbial biomass C, N, and P all significantly increased with the warming during both sets of warming events (i.e., pre- and post-hurricane; Fig. 6). As in most ecosystems, tropical forest microbes are biogeochemical engines that drive myriad ecosystem processes and that can determine globally-relevant functions, such as soil C storage and CO_2 exchange with the atmosphere (Cleveland et al., 2003; Cleveland and Townsend, 2006; Sayer et al., 2007; Wood et al., 2012). An increase in the size of the microbial biomass pool has numerous implications for the cycling of nutrients and for the fate of the large amounts of C that enter tropical forest soils (e.g., Cleveland et al., 2010). For example, a larger microbial biomass pool could immobilize limiting nutrients, alter competition between plants and heterotrophs, and shift the proportion of C that is released to the atmosphere versus stored in soil. It is also noteworthy that microbial biomass C, N, and

P concentrations were affected by the warming treatments only during times when the warming was active, as there were no legacy effects of the warming treatment in the year following Hurricanes Irma and María when there was no active warming. Further, for microbial biomass C and N, it was warming alone that showed significant effects on soil concentrations in the year following the hurricanes (i.e., there was no effect of hurricanes on microbial biomass C or N in the unwarmed plots the year after hurricane disturbance). These results suggest that microbial communities are responding quickly to the temperature treatments: when temperatures rose with the treatments, so did microbial biomass, and when the treatments were stopped, microbial biomass pools quickly declined and the differences among treatments disappeared. As would be expected with real-world warming, the warming treatments resulted in altered soil moisture and, although these changes were small (Fig. 2), further research at the site is underway to disentangle the direct effects of temperature from any indirect effects of warming-induced changes to soil hydrology.

4.2 Hurricane effects

Most soil biogeochemical measurements showed significant change with hurricane disturbance and, for all measured values except microbial biomass C and N concentrations, the effects of the hurricanes were larger than the effects of warming (although we cannot yet know how the relative effects of warming and disturbance will compare with the effects of longer-term warming). While assessments of soil biogeochemistry through time in tropical forests recovering from hurricanes are rare, our results are in line with the observational data, experimental results, and model predictions that exist for lowland tropical forests (González et al., 2014; Lodge et al., 1991; Lugo, 2008; McDowell and Liptzin, 2014; Sanford et al., 1991; Silver et al., 2014). Specifically, we observed an increase in C and N concentrations in the year following the hurricanes, followed by a decline back to original values (Fig. 3). These changes may seem minor (e.g. soil total C concentrations ranged between ~, 4% to ~6%), but they are highly relevant differences from a C cycle and climate feedback perspective. This responsiveness of total soil C and N concentrations has implications for understanding the potential for rapid terrestrial biosphere effects on the global C cycle and for model representation of these productive ecosystems. An improved understanding of the mechanisms behind these changes remains important. For example, the build-up of soil total C and N in the year following the hurricanes likely comes from the large inputs of leaves, particularly green leaves, that accompany defoliation and represent important inputs into tropical forest soils (Lodge et al., 1991). Partitioning these inputs into C's fate as stabilized organic matter versus leached losses into waterways versus gaseous CO_2 and CH_4 emissions is critical for modelling potential feedbacks to climate change (Cavaleri et al., 2015; McDowell, 2011; Sanford et al., 1991).

The concentrations of extractable soil N pools were significantly affected by hurricane disturbance and changed as the forest recovered (Fig. 4). Extractable ammonium (NH_4^+) concentrations rose consistently following the hurricane. Increased concentrations of this biologically available pool of N could in part be an effect of the large reductions in root biomass often observed following hurricanes (Parrotta and Lodge, 1991; Silver and Vogt, 1993). Fewer roots to immobilize NH_4^+ could result in higher concentrations in the soil, as could increased mineralization of the elevated litter inputs observed with hurricane disturbance (Lodge et al., 1991). See also chapter "Revisiting nutrient cycling by litterfall—Insights from 15 years of litter manipulation in old-growth lowland tropical forest" Sayer et al. (this issue), for further discussion of the impacts of increased litterfall on nutrients. However, elevated soil NH_4^+ is not a response observed consistently with hurricane disturbance, as NH_4^+ concentrations have also been shown to decline (Erickson and Ayala, 2004). These discrepancies among results could be related to forest land use history, soil type, sampling frequency, and/or differences in the nature of the hurricane disturbance. More data are needed to improve our understanding of the patterns and mechanisms behind soil biogeochemical responses to hurricanes. In contrast to NH_4^+, extractable nitrate (NO_3^-) concentrations rose immediately after the hurricanes, but then declined. The relatively rapid decline in NO_3^- could be due in part to increased denitrification and/or leaching losses, which are loss pathways typically expected for NO_3^-. Hurricanes have been shown to stimulate N_2O losses (Erickson and Ayala, 2004), which could come from increased nitrification and/or denitrification rates. Elevated soil solution NO_3^- has been observed with other hurricanes and with simulated hurricane disturbance (Shiels et al., 2015), however, these patterns are not universal across hurricane events and sites (Erickson and Ayala, 2004). Nevertheless, long-term assessment of stream water chemistry following hurricanes supports the idea of sustained inputs in NO_3^- moving from soils into waterways for years following large hurricane events (McDowell, 2011; Schaefer et al., 2000).

Inorganic N concentrations ($NH_4^+ + NO_3^-$) are commonly considered a highly available N pool for plants and microbes, and the patterns in the concentrations of extractable inorganic N observed here suggest that the availability of these pools varies through time following a hurricane event (Fig. 4C). There are relatively few data of which we are aware that assess these dynamic pools through time with hurricane disturbance, in part because the events themselves are infrequent, and those presented here show not only the magnitude of hurricane effects on soil N cycling, but also how the patterns of NH_4^+ and NO_3^- can vary. This is particularly interesting because results from other ecosystem types suggest that the form of N (i.e., NH_4^+ vs. NO_3^-) can be as or more important in determining the ecological consequences of N cycling changes as the total amount of N (Austin et al., 2006).

The hurricane also significantly affected soil P cycling: extractable P declined by over 50% immediately following the hurricanes, but then increased dramatically—increasing 4 times in the control plots and over 10 times in the warmed plots—and remained significantly higher than all pre-hurricane values (Fig. 5). Increases in these available forms of P have important implications for forest recovery. For example, research using experimental hurricane effects found that adding debris to forests with intact canopies could increase forest basal area by 10% for at least 7 years after applying the treatments (Zimmerman et al., 2014). In the context of forest canopies that close after hurricanes on timelines of less than 2 years (e.g., Fig. 1), this suggests that hurricane-induced increases in litter resources are likely to fuel forest recovery. Movement of P from the large amounts of debris that is deposited from the canopy to the forest floor during hurricanes has strong potential to increase the availability of limiting nutrients (Lodge et al., 1991, 2014; Wright, 2019). For example, in a litter manipulation experiment in Panama, results showed the litter layer was important in supplying P to biota: the addition of litter not only quickly stimulated nutrient cycling, but also had longer-term effects on soil microbes and C dynamics (Sayer et al., 2012; Sayer and Tanner, 2010). Lodge et al. (2014) showed that P from hurricane-induced litterfall was both immobilized in the forest floor and moved to the soil below, likely through litter leaching. Their calculations suggested that most of the P lost from the green leaves deposited after a hurricane likely enters the soil or is taken up directly by plant roots (Lodge et al., 2014). The soil extractable and microbial P data shown here support the idea that this P is moving into and is maintained in surface soils in multiple P forms. In light of the many studies suggesting P plays a critical role in regulating C and N cycling in terrestrial ecosystems, particularly in highly weathered tropical forest soils such as those described here (Camenzind et al., 2018; McGlynn et al., 2007; Reed et al., 2007; Reed and Wood, 2016), it will be important to determine how these observed effects change in concert with changes to plant and microbial communities through time. For example, the increases in extractable P occurred concurrently with large increases in microbial biomass P (Fig. 6C), which is in contrast to the more tightly-cycled P suggested by the data for the pre-hurricane timepoints (Figs. 5 and 6). Such increases could be due not only to changes in microbial stoichiometric ratios (Cleveland and Liptzin, 2007), but also to luxury consumption or microbial community composition shifts. Overall, hurricane effects on the aspects of the P cycle measured here were of a higher magnitude and were more sustained than for patterns observed in C or N.

4.3 Interactive effects of warming and hurricanes

We saw significant interactions between warming and hurricane disturbance, including legacy effects of warming even during times when the warming treatment was not active. For example, extractable NO_3^- and PO_4^{3-} concentrations were significantly higher in the warmed plots months after the warming treatments had ceased following Hurricane María (Figs. 4B and 5). Such changes to the N and P economies of the soils suggest the potential for longer-term effects for a range of forest organisms (Cleveland and Townsend, 2006; Elser et al., 2007; McGlynn et al., 2007). Of note, microbial biomass C, N, and P concentrations, which showed such strong warming effects during times when warming treatments were active, did not show significant legacy effects of warming (i.e., biomass concentrations were not different between control and warmed soils post-hurricane during the year when warming was not occurring). However, when we look at times when warming and recovery from hurricane co-occurred (i.e. the second warming event), we see significant effects of warming on the trajectory of recovery and interactions between warming and disturbance. For example, microbial biomass C, N, and P concentrations, as well as those of soil NO_3^- and PO_4^{3-}, are higher in the warmed plots relative to the control plots and higher than the concentrations observed before the hurricanes. These data suggest some potential increases in soil fertility for a warmer recovering forest. Over the longer-term, coupling the soil changes with plant growth and community composition will help determine if these changes to soil biogeochemistry help support ecosystem resilience or, instead, shift the system into a new state (Johnstone et al., 2016). It is important to mention that the concurrent effects of warming and hurricane disturbance in many cases would not have been predictable from summing the individual effects of a single change.

For example, the effects of warming on extractable soil PO_4^{3-} in a recovering forest were many times larger and opposite in direction than the effects of warming on that P pool prior to the Hurricane María. As in other systems, disturbance and climate change interactions may alter not only the magnitude of the effect of a single driver, but also the sign.

Taken together, the results from this study point to a highly dynamic soil biogeochemical response to warming and hurricane disturbance, with significant interactions between the two change factors. In the context of understanding how multiple global change stressors will affect terrestrial ecosystems (Johnstone et al., 2016; Turner, 2010), the data from this study point to the likelihood that disturbance and climate change will have profound effects on tropical rain forest soils and their function. In particular, these results suggest tropical secondary forests recovering from hurricane disturbance in a warmer environment will have a larger soil microbial biomass pool and greater access to available nutrients such as the N in NO_3^- and the P in PO_4^{3-} (Figs. 4–6), at least in the short-term. Opposite to our predictions, increases in these pools could result in increased productivity of tropical forests, with more fertility fueling faster response. However, increases in the size of these pools, and their large variation among sampling times, also suggest faster cycling and larger nutrient losses from the system (e.g., via leaching and denitrification). In this way, the faster turnover and decomposition that warming may stimulate when large inputs of litter fall from the canopy could result in an overall reduction in ecosystem fertility and thus lowered resilience over the long-term. Future studies that further elucidate the mechanisms and consequences of interactive changes for tropical wet forests in a warmer world will be of the utmost importance for forecasting the fate of these diverse, productive, and globally important ecosystems.

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