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ARTICLE

Special Feature: Tropical Forest Responses to Repeated Large-Scale Experimental Hurricane Effects

Context dependence in a tropical forest: Repeated disturbance reduces soil nitrate response but increases phosphate

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Abstract

Hurricanes and other extreme events are increasing in many regions, yet their long-term impacts on ecosystem function are uncertain. In forested ecosystems, soil solution chemistry provides an important tool to assess the impacts of disturbance on nutrient cycling and dissolved organic carbon dynamics. Here, we address the dependence of soil solution chemistry on disturbance regime using a novel combination of both experimental and observational results collected over a period of 16 years in montane tropical sites in the Luquillo Experimental Forest of Puerto Rico. Soil solution was sampled following various combinations of canopy trimming and detrital manipulation (2004), repeated manipulation (2014), drought (2015), and Hurricane Maria (2017). Soil solution was sensitive to disturbance but resilient, with return to baseline after 12–18 months. Any disturbance regime that involved loss of canopy and detrital inputs to the forest floor resulted in increased nitrate concentrations, but the response declined with repeated disturbance. Lysimeters in plots that had received no experimental manipulation had 1.5 times higher response to Hurricane Maria than those previously manipulated. The response to disturbance thus showed clear context dependence, with disturbance history affecting disturbance response. Among the nutrients and major ions, only nitrate showed a response to experimental manipulations, drought, and Hurricane Maria. In contrast to nitrate, soil solution potassium was unaltered by initial experimental manipulation but increased dramatically following drought and Hurricane Maria. Phosphorus only increased following Hurricane Maria and only in plots that had twice received experimental trimming and deposition of cut branches on the forest floor. Stoichiometry of dissolved organic matter also changed in these plots, with decreased carbon to nitrogen ratios. The potassium response suggests that damage to roots from tropical cyclones and drought is an important driver of the biogeochemical response to tropical storms. Dampening of soil nitrogen losses and increases in phosphorus losses following successive disturbance events indicates that increased frequency of tropical storms

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and droughts will result in fundamental alteration of soil biogeochemical cycles, with uncertain effects on forest structure.

KEYWORDS
context dependence, dissolved organic carbon, dissolved organic nitrogen, disturbance, drought, hurricane, Luquillo Experimental Forest, Long Term Ecological Research site, nitrate, phosphate, potassium, soil solution chemistry, Special Feature: Tropical Forest Responses to Repeated Large-Scale Experimental Hurricane Effects, tropical forest

INTRODUCTION

The frequency and intensity of disturbance to forest ecosystems is likely to increase in many biomes and geographic regions due to ongoing climate change that results in increased frequency of extreme events (Hayhoe et al., 2007; Mann et al., 2017). In many forests throughout the tropics and subtropics, tropical cyclones such as hurricanes are important disturbance events with consequences for a wide range of biota and ecosystems (Hogan et al., 2020). Repeated hurricanes have effects on forest structure and ecosystem function that persist for decades, with canopy architecture and stem density appearing to respond globally to hurricane frequency (Ibanez et al., 2019; Tanner et al., 1991). Large transfers of leaves, branches, and boles from the canopy to the forest floor occur following hurricanes (e.g., Lodge et al., 1991), with subsequent impacts on groundwater chemistry and watershed export in streams, especially of nitrate (NO_3^-) and potassium (K^+) (McDowell et al., 1996, 2013; Schaefer et al., 2000). Droughts also occur widely and can have important impacts on tropical forest structure (Nepstad et al., 2007) and soil biogeochemistry (Cleveland et al., 2010; O'Connell et al., 2018).

Although the impacts of individual hurricanes on forests have been widely studied, information on their long-term effects on soils and soil biogeochemistry is relatively limited. Soil solution provides an integrated signal of nutrient availability and potential flux that mirrors the time course of forest disturbance, litter decomposition, microbial response, canopy closure, and root regrowth (e.g., McDowell & Liptzin, 2014). In contrast to the long-term changes in soil nutrients and C that may be driven by disturbance (Gutiérrez Del Arroyo & Silver, 2018), the impacts of hurricanes on microbial communities and extractable soil nutrients are typically evident within months (Eaton et al., 2020). One of the earliest studies of hurricane impacts on soil solution in a lowland coastal forest showed significant increases in inorganic carbon, Na^+, Cl^-, and ammonium following inundation by storm surge, with maximum mineral soil concentrations detected 2 months after Hurricane Hugo (Blood et al., 1991). Hurricane impacts on soil solution at upland sites appear to be similar to those of other disturbances in which an increase in NO_3^- is the most pronounced response in soil solution following deforestation (Fakhraei et al., 2020), ice storms (Houlton et al., 2003), soil freezing (Boutin & Robitaille, 1995; Fitzhugh et al., 2001), and even heated cable installation (McHale & Mitchell, 1996). The response of tropical forests to similar disturbances is not as well understood. Schrumpf et al. (2007) quantified effects of forest regrowth on soil solution chemistry in montane forests of Tanzania following cutting; McDowell and Liptzin (2014) showed that soil solution NO_3^- responded to experimental simulation of hurricane canopy damage in a wet tropical forest. At the whole-watershed scale, Jaramillo et al. (2018) showed changes in stream nitrate chemistry following a hurricane in Mexican tropical dry forest, but little information on soil solution response to disturbance events is available from the tropics.

Legacies of past land use are evident in many landscapes (e.g., Lajtha & Jones, 2018). These legacy effects typically involve a press disturbance such as land use conversion that alters species composition (Foster et al., 2003; Thompson et al., 2002). The legacy impacts of repeated pulse disturbances on watershed biogeochemistry are not as well documented and are perhaps best conceptualized using the framework of context dependence (Bracewell et al., 2021) to assess whether the sequence of past transitory (pulse) disturbance events at a site has an impact on the response to a given disturbance. Understanding the dependence of responses to droughts and hurricanes on site-specific context is likely to become a major research question in ecosystem ecology with increased frequency of such extreme events (Hayhoe et al., 2007).

In this paper, we address the response of soil solution in a wet tropical forest to repeated disturbance. Using a combination of long-term experimental manipulations that simulated several aspects of hurricane disturbance, as well as the occurrence of a major drought and hurricane, we address the following questions: (1) What are the magnitude and nature of biogeochemical responses to these distinct disturbances? (2) Is the response to disturbance context-dependent, varying by past disturbance history? and (3) Do repeated disturbances decouple the elemental interactions that govern nutrient availability in soil solution? Answering these questions about forest biogeochemistry will be critical to understanding the effects that an increased frequency of droughts and hurricanes is likely to have on stand dynamics and ecosystem function in the coming decades.

METHODS

Site description and sample collection

The study was conducted in the Luquillo Experimental Forest of northeastern Puerto Rico, in which extensive long-term research on forest ecology and watershed biogeochemistry has been conducted for decades (McDowell et al., 2021). The study site is located adjacent to the El Verde Field Station, with lysimeters installed in various locations in tabonuco forest type, which is dominant at mid-elevations in the Luquillo Mountains (McDowell et al., 2021). Three experimental blocks were established in 2003 as part of the canopy trimming experiment (CTE), with detailed site characteristics including overstory and understory composition described by Shiels et al. (2010). Two key effects of hurricanes were simulated: the loss of canopy branches and the deposition of leaves and branches on the forest floor. Replicated treatments (three plots per block and nine total per treatment) included canopy trimming of branches >10 cm (trim), application of trimmed debris to the forest floor (debris), trim plus debris, and no manipulation (control). Details of the experimental design and the manipulations are provided in Shiels et al. (2014). Nine porous cup tension lysimeters (5 cm diameter; Soil Moisture Corporation, Santa Barbara, CA, USA) were installed at a depth of 30 cm (McDowell & Liptzin, 2014) in each treatment plot, for a total of 36 lysimeters. Soil solution was collected monthly for 20 months before and 5 years after the experimental treatments of CTE 1. Samples from the 36 lysimeters were analyzed individually. Over the entire course of the study, lysimeters were collected weekly to monthly and evacuated for a week prior to retrieval of water samples. One of the treatments, trim plus debris, was repeated in 2014 in CTE 2. Only trim plus debris and control lysimeters were sampled before and after the experimental manipulations in CTE 2, for a total of 18 individual lysimeters sampled during that manipulation. Sampling of these 18 lysimeters continued during a major drought that occurred in 2015–2016 and resulted in very dry soil conditions from April to December 2015 (O'Connell et al., 2018). Following Hurricane Maria in late September 2017, we resumed sampling of all 36 lysimeters. To summarize, all 36 lysimeters were sampled in CTE 1, 18 lysimeters (control and trim plus debris) were sampled from 2006 to September 2017 (CTE 2 and drought), and all 36 were sampled following Hurricane Maria (2017–2018).

Analytical methods

Sample volume, pH, and conductivity were measured in a field laboratory at El Verde Field Station. Soil solution samples were filtered through precombusted (425°C) glass fiber filters (Whatman GF/F; nominal pore size 0.7 μm) and then frozen and shipped to the Water Quality Analysis Laboratory at the University of New Hampshire. For SiO_2 only, an aliquot of the sample was held refrigerated for several months prior to analysis. Ion chromatography (Dionex 1000 and 1100; Dionex, Sunnyvale, CA, USA) was used for anions (NO_3^-, NO_2^-, SO_4^{2-}, and Cl^-) and cations (Na^+, K^+, Ca^{2+}, and Mg^{2+}). Nitrite was typically never present and is not reported here. Additional nutrient analyses (NH_4^+; soluble reactive phosphorus, hereafter referred to as PO_4^{3-}; and total dissolved silica, hereafter referred to as SiO_2) were conducted using robotic colorimetry with a SmartChem 200 (Unity Scientific, Brookfield, CT, USA) or Seal AQ2 (Seal Analytical, Mequon, WI, USA). Dissolved organic matter was quantified as dissolved organic carbon (DOC) and dissolved organic nitrogen (DON). Both were analyzed using a Shimadzu Total Organic Carbon analyzer (TOC-VSH or TOC-LSH; Shimadzu Corporation, Kyoto, Japan), with DOC measured as nonpurgeable organic carbon and DON estimated as the difference between total dissolved nitrogen and inorganic nitrogen ($NH_4^+ + NO_3^-$). Half the detection limit was used when values were below the detection limit for each analyte. Detection limits and further analytical details can be found in McDowell et al. (2021). For most analytes, values obtained were well above detection limits. Ammonium, NO_3^-, DON, and PO_4^{3-} were below detection limits in 46%, 18%, 15%, and 70% of samples, respectively. Repeated analysis of a standard river water sample, repeated analysis of analytical blanks, duplicate analysis of individual samples every 12 samples throughout a sample run, analysis of commercially available standard reference materials, and participation in an annual laboratory quality assurance round robin of blind samples were all used to provide quality assurance throughout the project.

Statistical methods

A repeated-measures ANOVA was tested with time as the fixed effect. We used individual lysimeters within treatments over time as the replicates. To simplify the effects of time, we lumped the data from each experiment or disturbance based on the time course of lysimeter chemistry in response to previous manipulations in CTE 1 (McDowell & Liptzin, 2014): measurements 12–18 months prior to disturbance event (before) and up to 18 months after the beginning of the disturbance event (after). Significant effects were further investigated with a Tukey post hoc (Tukey's honestly significant difference in base R) on interaction terms between before and after fixed effects. We examined the differences between treatments prior to disturbance events to determine whether there were background differences between the plots. The ANOVAs were conducted on log-transformed data due to the frequently non-normal distribution of the data. Lysimeter installation increased K^+ concentrations in all experimental treatments from the outset of initial sampling and slowly declined in both control and experimental treatments through the initial CTE manipulations (McDowell & Liptzin, 2014). Establishment of the "before" values to pair with samples taken after Hurricane Maria (2017–2018) was thus somewhat problematic for potassium. For these plots only (CTE 1 debris and CTE 1 trim), we used the average K^+ concentration in the control lysimeters prior to the drought to assess the effects of Hurricane Maria on K^+ concentrations, rather than the pretreatment values obtained more than a decade earlier, prior to CTE 1.

Log response ratio (LRR) of peak concentrations was used to allow comparisons of the magnitude of response among solutes that were found to have significant changes after disturbance. The LRR was calculated by taking the natural log of the difference in mean solute concentration for the "before" time period and the peak value in the "after" time period, divided by mean solute concentration before the treatment. All statistical analyses were performed using R Statistical Software (version 3.6.2; R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Repeated hurricane simulation, drought, and passage of Hurricane Maria in 2017 resulted in little change in soil solution for most nutrients, organic matter, and major ions. Concentrations of most solutes were low to moderate and were unaltered by experimental manipulations or disturbances (Table 1). Among the solutes measured in each treatment before the first disturbance event, only Ca^{2+} exhibited treatment plot differences between trim and control, debris and control, and trim and trim plus debris. Concentrations of many of the major ions (Ca^{2+}, Mg^{2+}, SO_4^{2-}, and SiO_2) were unaffected by any treatment or disturbance; concentrations of Na^+ responded only in control plots following Hurricane Maria when compared to pre-Hurricane conditions (Table 1; $p < 0.05$). Concentrations of Cl^- also responded in control plots following Hurricane Maria and in trim plus debris plots after CTE 2. Among important inorganic nutrients in soil solution (NO_3^-, NH_4^+, and PO_4^{3-}), only NO_3^- consistently responded to almost every disturbance (Table 1), with concentrations in soil solution reaching values in individual lysimeters as high as 6 mg L^{-1} as N following CTE 1 (Figure 1). Ammonium concentrations were typically 10–30 μg L^{-1} as N prior to treatment or disturbance and were unresponsive to CTE manipulations, but were responsive to drought and Hurricane Maria (Table 1). Phosphate concentrations increased to average levels of >100 μg P L^{-1} following Hurricane Maria, but only in the most heavily manipulated plots (trim plus debris, manipulated in both CTE 1 and CTE 2); no other treatments or disturbances resulted in significant changes in phosphorus concentrations. Dissolved organic nitrogen ranged from 0.06 to 0.23 mg L^{-1}, with increases observed after drought and Hurricane Maria. Dissolved organic carbon concentrations ranged from 1.5 to 3 mg L^{-1} and increased during drought but were unaffected by experimental manipulations or Hurricane Maria.

Potassium concentrations ranged widely, averaging from 0.15 to 1 mg L^{-1} depending on disturbance regime (Table 1) and reaching concentrations of several milligrams per liter in individual lysimeters (Figure 1). Interpretation of K^+ over time was made more difficult by the strong disturbance effect that persisted for several years after lysimeter installation (McDowell & Liptzin, 2014); as reported in that paper, we saw no response in K^+ concentrations to any of the original CTE treatments. The drought and hurricane had large effects on K^+ concentrations (Table 1, Figure 1). In the experimental manipulation of CTE 2, the trim plus debris treatment also showed a significant increase in K^+ concentrations to 0.16 mg L^{-1}, but a much larger response was observed in these same lysimeters following drought (0.73 mg L^{-1}) and Hurricane Maria (0.37 mg L^{-1}; Table 1). Sodium and Cl^- covaried and ranged from 5 to 8 mg L^{-1} (Na^+) and 10 to 14 mg L^{-1} (Cl^-). Concentrations of other major anions and cations showed little response to disturbances, with SO_4^{2-} ranging from 0.2 to 0.4 mg L^{-1} as S, Mg^{2+} from 0.9 to 1.5 mg L^{-1}, and Ca^{2+} from 1 to 2 mg L^{-1}. SiO_2 concentrations ranged from 1 to 5 mg L^{-1}.

Clear context dependence was observed for the response of most nutrients, but no major ions, to experimental treatments and disturbances. Phosphate, for example, only responded in the most heavily manipulated plots (trim plus debris treatments in CTE1 and CTE 2) following Hurricane Maria. Soil solution collected

TABLE 1 Response of soil solution chemistry to experimental treatments in the two canopy trimming experiments (CTE1 and CTE2), sustained drought, and Hurricane Maria by solute and treatment/disturbance

Solute	C, DT		C, HM		T, HM		D, HM		TD1		TD2		TD1 + 2, DT		TD1 + 2, HM	
	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After	Before	After
NH_4-N	23.0 (53.1)	**106.7** **(99.8)**	23.0 (53.1)	22.6 (30.7)	44.9 (20.1)	26.4 (34.5)	25.2 (27.0)	43.0 (28.0)	23.1 (5.8)	12.3 (1.6)	7.3 (11.9)	17.1 (23.9)	13.3 (12.1)	**81.6** **(203.1)**	13.3 (12.1)	**173.0** **(860.7)**
NO_3-N	0.03 (0.05)	**0.12** **(0.19)**	0.03 (0.05)	**0.60** **(0.72)**	0.07 (0.11)	0.13 (0.26)	0.05 (0.11)	**0.41** **(0.60)**	0.05 (0.11)	**1.00** **(1.54)**	0.02 (0.04)	**0.35** **(0.56)**	0.02 (0.04)	**0.23** **(0.33)**	0.02 (0.04)	**0.25** **(0.45)**
DON	0.08 (0.06)	**0.13** **(0.09)**	0.08 (0.06)	0.10 (0.11)	0.13 (0.29)	0.12 (0.13)	0.09 (0.05)	0.09 (0.10)	0.11 (0.08)	0.13 (0.12)	0.08 (0.06)	0.07 (0.06)	0.06 (0.05)	**0.14** **(0.15)**	0.06 (0.05)	**0.23** **(1.48)**
PO_4-P	4.0 (5.6)	32.7 (75.5)	4.0 (5.6)	5.7 (13.3)	7.1 (20.2)	4.2 (3.6)	3.5 (3.1)	8.4 (37.6)	3.5 (2.5)	3.2 (2.2)	6.4 (27.1)	22.8 (112.7)	25.7 (120.9)	17.5 (38.2)	25.7 (120.9)	**167.4** **(781.9)**
N:P	86 (54)	**24** **(28)**	86 (54)	**274** **(109)**	165 (121)	153 (109)	92 (80)	138 (91)	111 (81)	**782** **(752)**	142 (106)	**41** **(45)**	142 (106)	**55** **(61)**	142 (106)	**8** **(11)**
DOC	2.19 (1.86)	**3.14** **(2.48)**	2.19 (1.86)	2.34 (2.54)	2.67 (2.32)	2.44 (1.98)	2.11 (1.24)	1.46 (1.07)	2.61 (2.65)	2.02 (2.31)	2.06 (1.66)	1.63 (1.76)	1.30 (0.76)	**2.85** **(3.31)**	1.30 (0.76)	2.21 (6.82)
DOC:DON	30 (36)	27 (32)	30 (36)	32 (27)	21 (9)	22 (18)	27 (29)	25 (12)	29 (39)	23 (22)	6 (32)	**33** **(34)**	25 (18)	28 (26)	25 (18)	**13** **(5)**
Na	4.91 (2.06)	6.17 (2.79)	4.91 (2.06)	**7.71** **(2.88)**	6.52 (4.75)	8.09 (3.05)	6.16 (4.11)	6.26 (2.05)	5.81 (2.65)	5.96 (2.81)	4.74 (1.11)	5.88 (2.09)	5.31 (1.76)	4.68 (2.10)	5.31 (1.76)	6.19 (2.42)
K	0.09 (0.09)	**0.91** **(1.76)**	0.09 (0.09)	**0.35** **(0.53)**	0.09 (0.09)	**0.46** **(0.38)**	0.09 (0.09)	**0.39** **(1.33)**	0.43 (0.23)	0.30 (0.16)	0.07 (0.08)	**0.15** **(0.10)**	0.13 (0.08)	**0.73** **(1.27)**	0.13 (0.08)	**0.37** **(0.87)**
Ca	0.81 (0.32)	2.22 (1.88)	0.81 (0.32)	0.97 (0.55)	1.27 (1.16)	1.67 (1.62)	0.52 (0.41)	0.67 (0.77)	0.67 (0.63)	0.68 (0.86)	0.74 (0.77)	0.80 (0.67)	0.73 (0.49)	1.34 (1.27)	0.73 (0.49)	1.27 (1.92)
Mg	1.00 (0.39)	1.52 (1.06)	1.00 (0.39)	1.29 (0.61)	1.14 (1.07)	1.53 (0.82)	0.92 (0.75)	1.09 (0.52)	0.85 (0.52)	1.10 (0.63)	0.71 (0.26)	0.99 (0.41)	0.91 (0.29)	0.91 (0.40)	0.91 (0.29)	0.90 (0.56)
SO_4-S	0.37 (0.20)	0.46 (0.28)	0.37 (0.20)	0.44 (0.27)	0.74 (0.57)	0.60 (0.52)	0.60 (0.45)	0.47 (0.22)	0.76 (0.69)	0.56 (0.28)	0.35 (0.12)	0.46 (0.21)	0.44 (0.19)	0.53 (0.23)	0.44 (0.19)	0.56 (0.37)
Cl	10.08 (3.07)	10.19 (4.69)	10.08 (3.07)	**12.84** **(5.30)**	12.49 (7.70)	14.15 (6.09)	11.39 (8.33)	9.78 (3.51)	11.87 (6.96)	7.90 (4.29)	7.75 (1.86)	**10.39** **(2.32)**	10.12 (2.19)	10.27 (2.54)	10.12 (2.19)	9.70 (5.45)
SiO_2	3.10 (2.89)	2.63 (5.46)	3.10 (2.89)	2.51 (4.91)	5.51 (2.64)	4.32 (7.42)	4.31 (3.76)	1.15 (1.60)	3.31 (2.66)	2.12 (3.42)	3.01 (2.45)	2.98 (3.34)	2.57 (2.62)	4.74 (7.72)	2.57 (2.62)	2.22 (2.62)

Note: Mean and SD (in parentheses) are shown by treatment and event pairs. Bold typeface indicates statistically significant differences (ANOVA, $p < 0.05$) between before and after experimental manipulations or disturbance events. Before and after are defined by samples collected 12–18 months prior to the treatment or disturbance event and up to 18 months following the event. Treatment pairs: control plus drought (C, DT); control plus Hurricane Maria (C, HM); trim plus Hurricane Maria (T, HM); debris plus Hurricane (D, HM); trim and debris manipulation 1 (TD1), trim and debris manipulation 2 (TD2), trim and debris plus drought (TD1 + 2, DT), and trim and debris plus Hurricane Maria (TD1 + 2, HM). Treatments to the CTE plots as described in Shiels et al. (2014). Soil solution data from the first CTE were initially presented in McDowell and Liptzin (2014). Concentrations in milligrams per liter, except NH_4^+-N and PO_4^{3-}-P in micrograms per liter.

from the same lysimeters showed no PO_4^{3-} response to either of the CTE experiments or to the drought, with average concentrations that ranged from 4 to 30 μg P L^{-1} (Table 1). Following Hurricane Maria, however, we observed concentrations averaging 170 μg L^{-1} (Table 1) in the most heavily manipulated plots. The LRR of phosphate concentrations across treatments and disturbances was striking (Figure 2a). In plots with no or minor experimental manipulation prior to Hurricane Maria, PO_4^{3-} concentrations were unaffected by hurricane disturbance, but the LRR was 4 in plots that had twice been trimmed and debris deposited during experimental manipulations. Nitrate concentrations also showed clear context dependence following Hurricane Maria. Plots with the least prior manipulation showed the largest increase in NO_3^- response (control), while the plots with repeated manipulations (trim plus debris manipulations in CTE 1 and CTE 2) showed a smaller NO_3^- response (Figure 2b). The response to Hurricane Maria also was greater in comparison with the original CTE 1 manipulation in the trim plots but did not change in the debris plots. In the most heavily manipulated plots, NO_3^- concentrations showed progressive decreases in the magnitude of response to each subsequent disturbance event (Figure 3). Dissolved organic nitrogen responded similarly to PO_4^{3-} across the series of manipulations and disturbances, showing clear context dependence in the response to Hurricane Maria. In plots that had previously been trimmed, or had debris

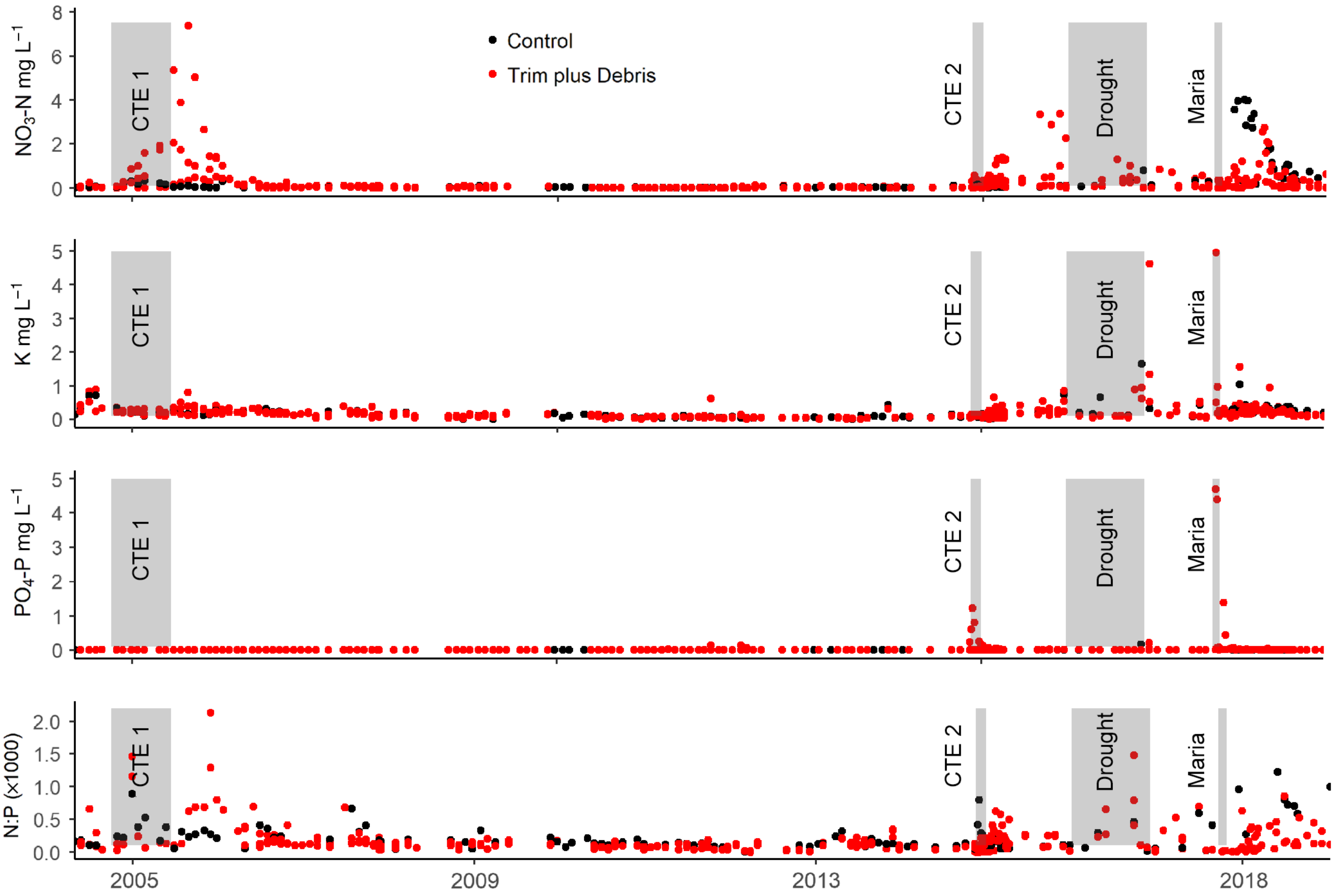

FIGURE 1 Response of nitrate (NO_3-N), soluble reactive phosphorus (PO_4-P), and potassium (K) concentrations, and molar N:P ratio, in representative individual lysimeters sampled weekly to monthly over 15 years from control, and trim plus debris treatments in the canopy trimming experiment. Vertical gray areas denote the occurrence of an experimental treatment or disturbance event.

deposited, the response to Maria was minimal and not statistically significant. The plots that had twice been manipulated by trimming and deposition of debris on the forest floor, however, showed a fourfold increase in DON concentrations, increasing from 0.06 to 0.23 mg L^{-1}.

The series of manipulations and disturbances resulted in a large alteration in nutrient stoichiometry. In the control plots, which were subject to drought and Hurricane Maria only, N:P (molar ratio of the sum of NH_4, NO_3, and DON divided by PO_4^{3-}) was 86 prior to Maria and 274 following Maria, with a statistically significant change (Table 1). In the plots that received the greatest level of disturbance during the two CTEs, N:P ratios declined from 142 to 8 following Maria (Table 1) and declined following CTE 2 and drought after increasing following CTE 1. Decreases in the N:P ratio also occurred when considering inorganic N and PO_4^{3-}. Although not as large as the changes in total dissolved N:P ratios, they were also statistically significant in the trim plus debris plots following Hurricane Maria. The stoichiometry of dissolved organic matter also changed with disturbance regime. At the most intensely disturbed plots, DOC:DON (molar) declined from 25 to 13 but was largely unchanged following other disturbances (Table 1).

DISCUSSION

Magnitude and nature of disturbance response

Our data provide some of the first evidence that repeated disturbances to tropical forests can alter the concentrations of nitrogen, phosphorus, organic matter, and potassium in soil solution despite the strong biotic and abiotic controls that result in relatively low levels for these solutes in tropical forests (Lin et al., 2018; McDowell, 1998). Of the major nutrients for which we documented a response to disturbance, increased nitrate concentrations are one of the most commonly observed responses to all types of disturbance globally. Many studies have documented whole-watershed response (increased concentrations of NO_3^- in stream

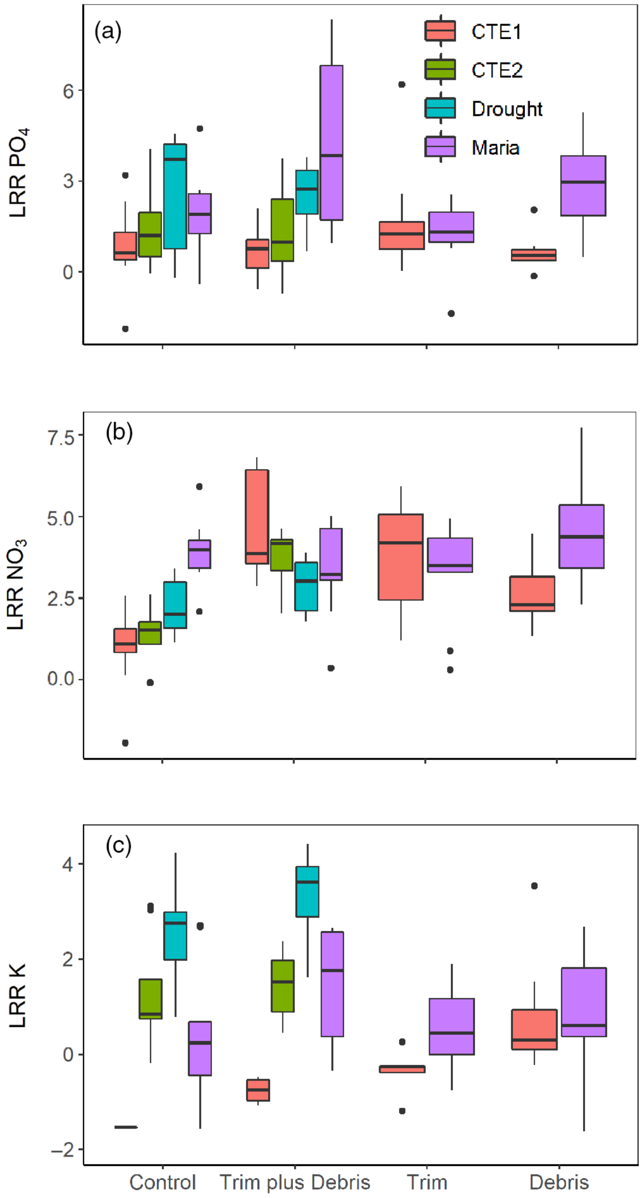

FIGURE 2 Box and whisker plots of solute response to experimental manipulation, drought, and Hurricane Maria expressed as the log response ratio (LRR) calculated for individual lysimeters ($n = 9$ lysimeters per original canopy trimming experiment [CTE] treatment; total $n = 106$ except $n = 105$ for PO_4). Line inside box is median, lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles; interquartile range [IQR]), whiskers are 1.5 × IQR from the hinge, and points are individual outliers. Canopy trimming experiment treatments included control, trim plus debris, trim only, and debris only (as described in McDowell & Liptzin, 2014). For each lysimeter, the response ratio was the maximum observed concentration divided by the average pretreatment or predisturbance concentration, expressed as natural log of the response ratio. Data for response in CTE 1 were originally published in McDowell and Liptzin (2014) but were not described using the LRR

water) to disturbances such as ice storms (Houlton et al., 2003), insect infestation (Swank et al., 1981), wildfire (Rodríguez-Cardona et al. 2020), and hurricanes (McDowell et al., 2013) in forested landscapes, as well as to commercial harvesting of trees (Fakhraei et al., 2020). The literature is not as extensive for disturbance response in soil solution chemistry. Nitrate flux in soil solution increased by 50% following insect infestation in a German Scots pine forest (Grüning et al., 2017; Table 2). Extensive canopy damage by an ice storm resulted in 15%–350% increase in NO_3^- concentrations of soil solution collected in B-horizon soils at Hubbard Brook in New Hampshire, USA (Fakhraei et al., 2020; Houlton et al., 2003). Experimental manipulation at the plot scale shows that soil freezing results in a doubling of NO_3^- concentrations in sugar maple stands but no response in yellow birch stands (Fitzhugh et al., 2001). The magnitude and timing of the NO_3^- response in soil solution is remarkably similar in many disturbances, with peak concentrations in stream water or soil solution approaching several milligrams of NO_3^--N per liter and return to baseline in about a year or 18 months post-disturbance (Dodds et al., 2012). Despite wide-ranging differences in forest type and climatic regime, this 12- to 18-month response of NO_3^- concentrations in soil solution to watershed disturbance seems typical (Table 2).

Flushes of DOC in soil solution following disturbance appear to be associated with damage or death of fine roots rather than inputs of debris to the forest floor, based on the observation that increases in DOC only occurred following drought and not during experimental manipulations of debris inputs (Table 1). Dissolved organic carbon concentrations in mineral soils are typically controlled by sorption reactions that keep DOC at equilibrium values driven by interactions with clay minerals and reactive sesquioxides (Kalbitz et al., 2005), and mineral soils at our study site are very efficient at removing DOC from solution in comparison with many other sites (McDowell, 1998; Neff & Asner, 2001). Despite the large inputs of organic matter to the forest floor from experimental manipulations and hurricanes, the subsequent leaching (Schreeg et al., 2013) and decomposition of this organic matter on the forest floor (González et al., 2014) resulted in no change in DOC concentrations at 30-cm depth. This suggests that soluble organic matter produced by decomposing litter is either stored or metabolized during passage through the mineral soil, a conclusion that is supported by the increase in deeper soil C stocks following canopy manipulations (Gutiérrez Del Arroyo & Silver, 2018). The flush of decaying fine roots at depth following drought thus seems to be the most likely cause of the observed increase in DOC, rather than the input of leaf litter that also occurs during drought.

Increases in the nitrogen-rich fraction of organic matter (DON) occurred in several plots where DOC was

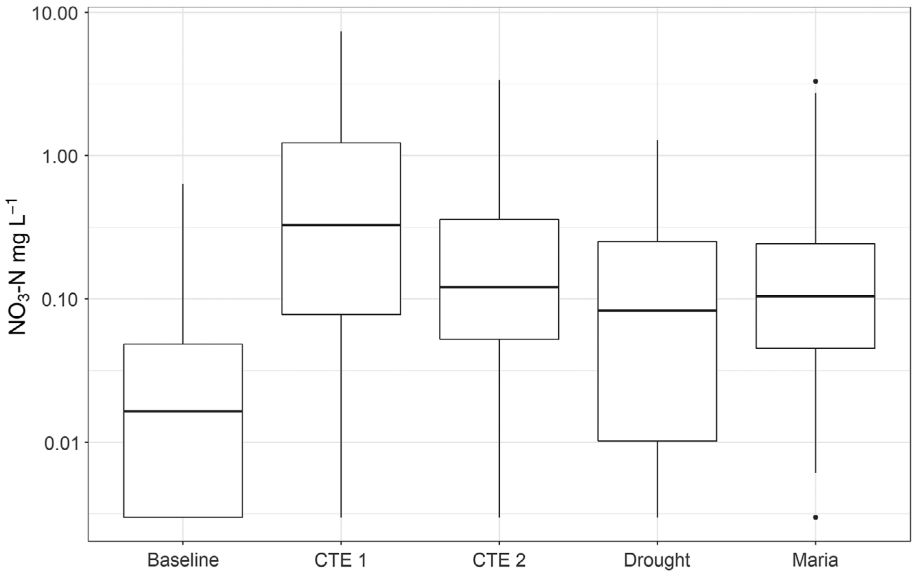

FIGURE 3 Box and whisker plots of NO_3 concentrations for each disturbance event and over long-term baseline in trim plus debris lysimeters only ($n = 9$). The baseline includes 6 months before CTE 1 and 7 years between CTE 1 and CTE 2 when response had returned to background levels. The disturbance events include up to 16 months of sampling after the event.

TABLE 2 Soil solution (B-horizon or mineral soil) response to disturbances

Location	Vegetation	Type	Response duration	N concentration or flux		PO_4^{3-}-P		K^+		Reference
				Before	After	Before	After	Before	After	
Germany	Scots pine	Insect		**5.4**	**8.6**	NA	NA	NA	NA	Grüning et al. (2017)
Germany	Oak	Insect		**1**	**3**	NA	NA	NA	NA	Arnold et al. (2016)
New Hampshire	Mixed hardwood	Harvest	1–2 years	0.090	2.98	NA	NA	0.42	1.72	Fakhraei et al. (2020)
New Hampshire	Mixed hardwood	Ice storm	18 months	0.28	0.32	NA	NA	0.61	0.27	Fakhraei et al. (2020)
New Hampshire	Mixed hardwood	Ice storm	18 months	0.51	0.95	NA	NA	0.32	0.66	Fakhraei et al. (2020)
New Hampshire	Sugar maple	Soil freezing	1 year	0.28	0.60	2.91	4.03	NA	NA	Fitzhugh et al. (2001)
New Hampshire	Yellow birch	Soil freezing	1 year	0.60	0.50	74.3	16.1	NA	NA	Fitzhugh et al. (2001)
Brazil	Tropical evergreen	Harvest	1–2 year	0.24	11.3	18.6	1.54	0.043	2.28	Williams et al. (1997)
Puerto Rico	Tropical evergreen	Drought	6 months	0.03	0.12	4	32.7	0.09	0.91	This study (C, DT)
Puerto Rico	Tropical evergreen	Hurricane	1 year	0.03	0.6	4	5.7	0.09	0.35	This study (C, HM)
Puerto Rico	Tropical evergreen	Hurricane simulation plus hurricane	1 year	0.02	0.25	25.7	167	0.13	0.37	This study (T + D1, T + D2, HM)

Note: Nitrogen response is shown for NO_3^- where available; otherwise, TDN is reported here. All values are concentrations (milligrams per liter of N, P, or K) except those in bold typeface, which are monthly fluxes (in kilograms per hectare). NA means data not available.

unchanged, suggesting a fundamental decoupling of the C-rich and N-rich fractions of organic matter in disturbed environments, as has been observed in rivers draining an urban tropical watershed (McDowell et al., 2019). A few earlier studies have shown DOC response in soil solution or stream water following disturbance, with mixed results depending on the nature and intensity of the event or manipulation. Following deforestation, a decrease in stream DOC export was observed by both Meyer and Tate (1983) and Drake et al. (2019). Others have shown no apparent response in stream chemistry after deforestation (Hobbie & Likens, 1973) or in groundwater chemistry after a hurricane (McDowell et al., 1996). This is likely due to very efficient removal of DOC from soil solution by adsorption on mineral soil at most sites (McDowell, 1998; McDowell & Wood, 1984) but may also be related to biogeochemical linkages between NO_3^- and DOC. At Coweeta Hydrologic Observatory, for example, experimental manipulation of streams by long-term nutrient addition (N and P) resulted in declines in DOC concentration (Rosemond et al., 2015). In regional surveys, declining N has been associated with increasing DOC in small lakes and streams, although the statistical association of DOC with NO_3^- is typically weaker than between SO_4^{2-} and DOC (Gavin et al., 2018) or ionic strength and DOC (Hruška et al., 2009; Lawrence & Roy, 2021). Thus, accumulation of NO_3^- in soil solution postdisturbance may also contribute to minimal response in DOC concentrations, while DON concentrations can be highly responsive to NO_3^- additions (e.g., Wymore et al., 2015). Nitrogen availability may also drive changes in the stoichiometry of dissolved organic matter (DOC:DON) found in soil solution posthurricane, as observed previously in soil solution following N fertilization (McDowell et al., 1998). A recent synthesis of DOC:DON in streams from multiple biomes also shows that elevated levels of N are associated with lower C:N of dissolved organic matter (Wymore et al., 2021), suggesting that the nitrogen content of dissolved organic matter in both soils and streams is surprisingly plastic in response to disturbance.

Differences in the timing, magnitude, and duration of soil solution increases in K^+ and NO_3^- suggest that their concentrations are controlled by different mechanisms, even though their dynamics are linked at the plant physiological level (Raddatz et al., 2020) and both ions show increased concentrations in stream water in response to whole-watershed disturbances in temperate watersheds and our topical montane study site (Fakhraei et al., 2020; McDowell et al., 2013). During the first CTE, for example, we saw no response in K^+ concentrations in any treatment (McDowell and Liptzin, 2014; Figure 4). There was a minor response to the second CTE manipulation (Table 1, Figure 4) but much smaller than the increases seen in the subsequent drought, and those that followed Hurricane Maria. The drought and hurricane response increased K^+ concentrations by fourfold, in some cases to almost 1 mg L^{-1}, compared to no effect in CTE 1 and doubling in CTE 2. The timing of the K^+ and NO_3^- responses also showed clear differences. During the drought, NO_3^- responded during the middle of the drought, but K^+ responded only as the drought broke (Figure 4). By contrast, following Hurricane Maria, soil solution K^+ responded almost immediately, with NO_3^- responding months later. As noted earlier by McDowell and Liptzin (2014), the response of nitrogen to the CTE manipulations suggests that both reduced plant uptake and increased organic matter mineralization contribute to the observed sharp increase in NO_3^- concentrations. The fact that hurricane simulation increased NO_3^- concentrations in CTE 1 and CTE 2 in a manner similar to the effects of an actual hurricane (Hurricane Maria) provides strong evidence that the drivers of increased NO_3^- are indeed both canopy disturbance and mineralization of organic debris.

The pulse of K^+ following the drought and Hurricane Maria is more difficult to attribute to a specific source. The minimal response of K^+ to experimental simulation of hurricane damage to the forest canopy and subsequent leaching and mineralization of organic debris suggests that root damage, the only driver that is absent in the CTE experiments but occurs following drought and actual hurricanes, is the primary source of the flush of K^+ that we observed in soil solution of the Luquillo Mountains. Although K^+ is known to leach readily from tropical vegetation (Schreeg et al., 2013) and is present in high concentrations in throughfall collected in the Luquillo Mountains (McDowell et al., 2020), the modest response of K^+ to experimental manipulations that included leaf leaching (CTE 1 and CTE 2) suggests that leaf leaching is not the primary source of K^+ postdisturbance. Other potential drivers of increased K^+ posthurricanes include root mortality (Parrotta & Lodge, 1991) that both reduces K^+ uptake and also provides a release of K^+ as root tissue leaches and decomposes. During droughts, another plausible source is release of K^+ by the microbial lysis that is driven by pulsed wetting and drying cycles (Lodge et al., 1994). Because K^+ concentrations are controlled by both biotic and abiotic factors at the watershed scale in our study site (McDowell & Asbury, 1994), a geochemical interaction associated with hurricanes and droughts may also be important in regulating soil solution K^+ concentrations following disturbances.

Context dependence of disturbance response

Previous work shows context can be important in driving the biotic response to disturbance events (Bracewell et al., 2021), but our study is one of the first to illustrate the extent to which past disturbance alters the trajectory of nutrient dynamics following repeated disturbances. The response of soil solution chemistry to past manipulations in our study plots suggests that site history can play an important role in the response of N, P, and DOM to repeated disturbance. We have documented several examples that indicate the importance of context in characterizing the response to disturbance. The nearly

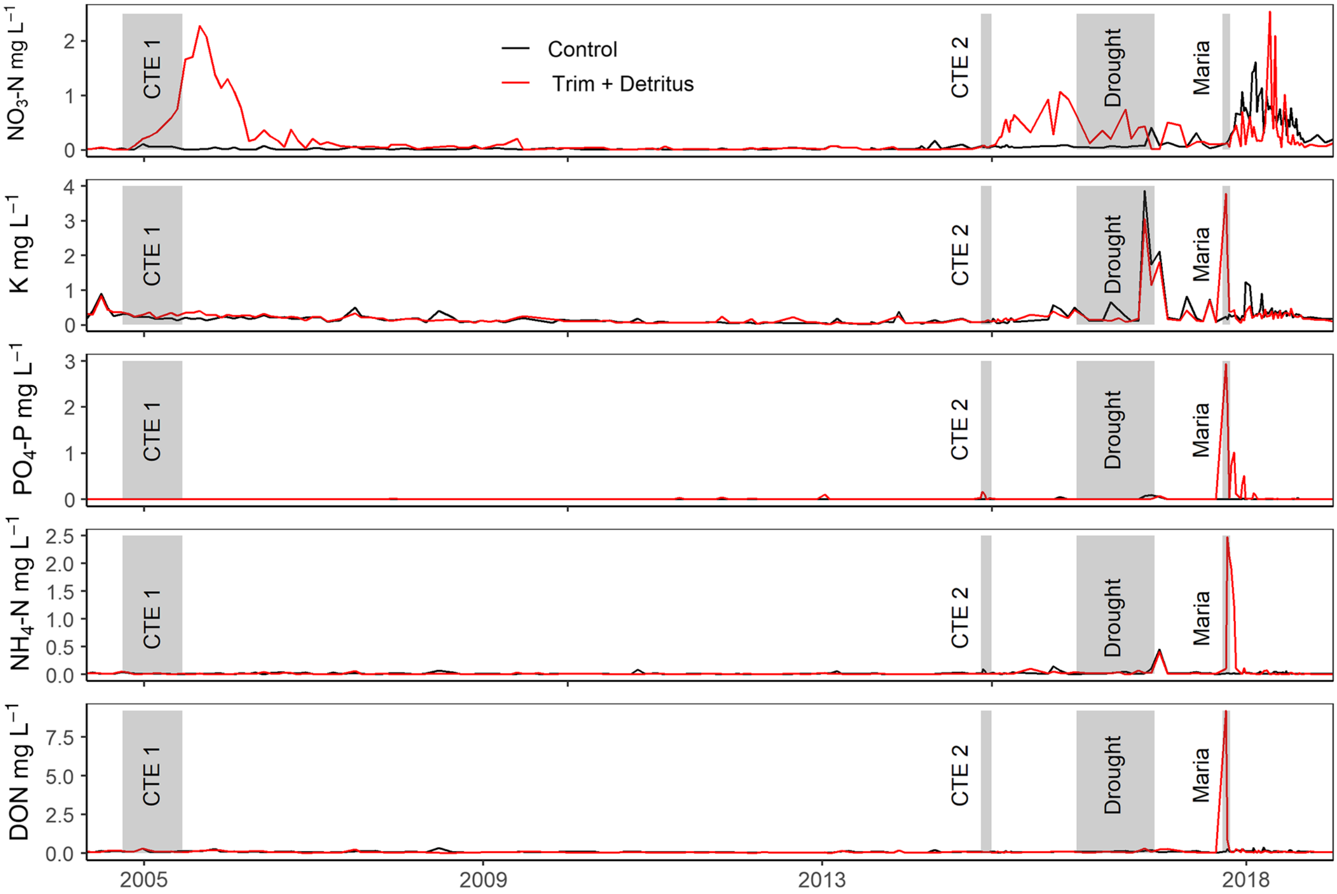

FIGURE 4 Response of nitrate (NO_3-N), potassium (K), soluble reactive phosphorus (PO_4-P), ammonium (NH_4-N), and dissolved organic nitrogen (DON) concentrations in soil solution of all lysimeters in the trim plus debris treatment plots and control plots. Individual lysimeters (nine each from trim plus debris and control plots) were sampled and analyzed weekly to monthly over 15 years and shown here as the average value obtained by date and treatment. Vertical gray areas denote the occurrence of an experimental treatment (canopy trimming; CTE 1 and 2) or a disturbance event

ubiquitous response of NO_3^- to forest disturbance (Fakhraei et al., 2020; Table 2) is altered by context at our site. Repeated disturbances to individual study plots over 15 years resulted in a declining response of soil solution NO_3^- to repeated disturbances (Figures 2 and 3), with concentrations averaging 1.00 mg L^{-1} as N after the first disturbance but only 0.25 mg L^{-1} in the same lysimeters after Hurricane Maria. Similar unmanipulated plots showed a robust response to Hurricane Maria, with concentrations of NO_3^- post-Maria averaging 0.60 mg L^{-1}. This declining strength of response to disturbance at the plot scale could be the result of nitrogen mining from the high soil N stocks at the site (Chestnut et al., 1999), decreased rates of N fixation following disturbance in plots with repeated disturbance, or increased rates of N uptake by the relatively young and rapidly growing biomass found in our experimental plots following canopy manipulation (Chevalier et al., 2022). Understanding the fundamental mechanism of this context-dependent response to disturbance is essential to predicting the long-term trajectory of these tropical montane forests to increased frequency or intensity of droughts and hurricanes, and requires additional study.

Changes in the relative abundance of essential nutrients such as N and P and how they are cycled can have profound influences on plant growth and are indicative of overall nutrient status in forests (Jiang et al., 2021; Wright et al., 2011). Although the literature assessing effects of experimental fertilization on growth of tropical forests is extensive (Wright, 2019), very limited information is available on the effects of repeated disturbances such as droughts and hurricanes on nutrient availability in soil solution. The declining NO_3^- response to repeated disturbances that we have observed (Figures 2 and 3) may be the result of increased N immobilization by microbial communities on coarse woody debris on the forest floor that was deposited following the CTE manipulations (Zimmerman et al., 1995). Lodge et al. (1994) argued that nutrient pulses associated with fluctuations in litter inputs or cycles of wetting and drying may be essential to maintaining productivity in many tropical forests, as the flush of nutrient availability facilitates new growth. Our results following repeated experimental treatments, drought, and hurricane clearly support the predictions of Lodge et al. (1994) that pulses of nutrients occur following disturbances. The frequency and magnitude of these flushes may have been sufficient, however, to draw down nutrient stocks in shallow soils and transfer them to deeper soil or export them in stream water. This may be especially true in the case of NO_3^-, which does not have abiotic controls on its transport such as the sorption on clays and reactive sesquioxides that control availability of inorganic P, NH_4^+, and organic nutrients (e.g., Kalbitz et al., 2005; Lin et al., 2018).

Although the response of K^+ to droughts and hurricanes that we have observed mirrors that observed repeatedly in temperate forests subject to cutting and ice storms (Fakhraei et al., 2020), little information is available on the context dependence of potassium response to disturbance or the primary controls on K^+ concentrations in soil solution. Our data provide some evidence of context dependence in the response of soil solution K^+ concentrations to repeated disturbances, with no response to the initial CTE 1 manipulation, a minor response to CTE 2, but large increases following both drought and Hurricane Maria. The nature of the response to repeated disturbance differs from the experience at Hubbard Brook, where an ice storm resulted in similar responses in soil solution of recently harvested and reference watersheds (Fakhraei et al., 2020). The underlying reasons for differences between K^+ response to disturbance in our sites and those at Hubbard Brook are uncertain but may be associated with the high weathering rates in our tropical sites (McDowell & Asbury, 1994).

The large pulse of PO_4^{3-} that we observed in soil solution following Hurricane Maria is remarkable for both its magnitude and its context dependence. No other studies of forest response to disturbance have documented a similar magnitude of PO_4^{3-} response in mineral soil solution. Experimental soil freezing by snow manipulation in New Hampshire resulted in a 30% increase in B-horizon soil solution PO_4^{3-} under sugar maples, but a decline under yellow birch (Fitzhugh et al., 2001). The only plots in our study site to respond to the hurricane were those that had already been experimentally trimmed twice, prior to the hurricane, in which PO_4^{3-} concentrations increased sixfold following Hurricane Maria. We suspect that repeated disturbances at the site may have diminished plant uptake of P due to repeated trimming, drought, and hurricane. Alternately, the response of PO_4^{3-} to Hurricane Maria could have been driven by the successional state of vegetation on the experimental plots (Table 1, Figure 2). This highly context-dependent response of PO_4^{3-} to hurricane disturbance may be the result of the presence of relatively young vegetation with high nutrient content on our previously manipulated experimental plots (Chevalier et al., 2022), which upon hurricane passage resulted in deposition of large amounts of relatively P-rich leaves and saplings on the forest floor due to wind damage. Decomposition rates of fresh green material are very fast on these plots and P loss from leaves is rapid during the first 0.2 year of decay (González et al., 2014).

We propose a conceptual model (Figure 5) that incorporates most of the context-dependent responses to repeated disturbance that we have observed. The model highlights how the availability of N and P changes with increased disturbance frequency, but could also be applied to a metric that includes both frequency and intensity of individual disturbance events. A primary feature of the model is the extent to which the disturbance response of various nutrients diverges with increased disturbance frequency, resulting in decoupling of elemental cycles and changing stoichiometries under a high-frequency disturbance regime (Figure 5). The very low N:P ratios seen in soil solution following our most intense disturbance regime result in potentially important changes in nutrient availability that could affect the survival and recruitment of plant species that are typically limited by the relatively low levels of available P in tropical soils (Wright, 2019). Our model provides a different perspective from those proposed in earlier conceptual models such as Zimmerman et al. (1996) or Hogan et al. (2020), which focus on how various components of the system (e.g., stream nitrate, aboveground biomass) respond to a single hurricane (resistance) and recover to baseline conditions (resilience). By contrast, we emphasize how a functional component of

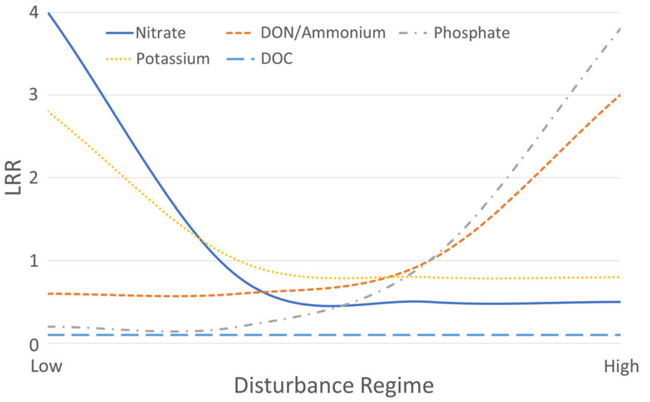

FIGURE 5 Conceptual model describing alteration of nutrient and organic matter availability (depicted as log response ratio, LRR) following repeated disturbance (low to high frequency of disturbance) in a tropical montane forest. Dissolved organic nitrogen (DON) and ammonium are included as a single line due to the similarity of their responses to disturbance. DOC, dissolved organic carbon

the entire ecosystem (soil biogeochemical cycles) is fundamentally altered by a high-intensity disturbance regime, with novel responses that may no longer return to "baseline" conditions in subsequent disturbances.

Implications for future disturbance scenarios

Understanding and anticipating the biogeochemical response to altered disturbance regimes requires mechanistic understanding of drivers and responses (e.g., Hogan et al., 2020). We have documented large increases in soil solution nutrient concentrations that represent a clear disturbance response. Yet, the underlying biotic or abiotic mechanisms behind these responses remain somewhat ambiguous, making it hard to predict future scenarios in a world of increased droughts and hurricanes. In the case of nitrogen, for example, increased concentration of NO_3^- in soil solution following disturbance represents a net ecosystem response resulting from competing processes such as increased N mineralization with subsequent nitrification, or decreased plant NO_3^- uptake. In fact, the results of the first CTE suggest that both increased sources (nitrification of mineralized N) and decreased plant uptake were required to generate the large signal in NO_3^- that was observed (McDowell & Liptzin, 2014).

Quantifying gross fluxes of nutrients and organic matter to understand the response to increasing frequency of disturbance is thus a central challenge for ecosystem science. For the N cycle, tools such as isotopic tracers and simple field incubations ("buried bag" approach) have been used to infer or directly measure various gross and net fluxes (e.g., Chestnut et al., 1999). For organic matter, potassium, and phosphorus dynamics, the tool kit is currently much more limited. Development of novel approaches to understanding controls on net versus gross elemental fluxes in soils and watersheds should be a high priority for ecosystem science, as fundamental alteration of nutrient cycling rates can feed back to affect forest structure and persistence. Several responses to repeated disturbance, which we have observed in the Luquillo Mountains, highlight the need for such new approaches. For the N cycle at our site, does the progressive decline in the magnitude of response to disturbance suggest that the soil stocks of available nitrogen are becoming depleted? Or that N fixation slows following repeated disturbance? Chestnut et al. (1999) argued that the loss of N in stream water following Hurricane Hugo was small relative to the total soil N pool. With a higher frequency of disturbance in the future, will this conclusion still hold, or will soils become measurably depleted in available nitrogen with implications for forest regrowth? Does the large increase in potassium in soil solution following drought and hurricanes signal an alteration of biotic sources and sinks, or is it driven more by previously unrecognized geochemical responses to disturbance? As with the N cycle, will loss of K^+ result in potential K^+ limitation to tree growth? Does the change in stoichiometry of dissolved organic matter signal a response to increased concentrations of inorganic N in soil solution such as observed by Wymore et al. (2021) for streams across the globe, or does it represent a change in the materials that are decomposing following a disturbance event? Each of these questions has important implications for developing scenarios of future forest trajectories following repeated frequent disturbance. The forests of the Luquillo Mountains have so far proven resilient in the face of disturbance (Shiels et al., 2015), but they may no longer prove resilient in the face of increased frequency or intensity of disturbance.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (McDowell, 2022) are available from the Environmental Data Initiative: https://doi.org/10.6073/pasta/aa67b1253fea7b0202c1af84e00c8757.

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