



25TH ANNIVERSARY PAPER

A Severe Hurricane Increases Carbon Dioxide and Methane Fluxes and Triples Nitrous Oxide Emissions in a Tropical Forest

Andrew W. Quebbeman,¹ Duncan N. L. Menge,¹ Gabriel Arellano,^{2,3} Jazlynn Hall,¹ Tana E. Wood,⁴ Jess K. Zimmerman,⁵ and María Uriarte^{1*}

¹Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York, USA; ²Ecology and Evolutionary Biology, University of Michigan, New York, Michigan, USA; ³Oikobit LLC, Albuquerque, New Mexico, USA; ⁴USDA Forest Service International Institute of Tropical Forestry, Río Piedras, Puerto Rico, USA; ⁵Department of Environmental Sciences, University of Puerto Rico, Río Piedras, Puerto Rico, USA

ABSTRACT

Tropical cyclones (for example, hurricanes, typhoons) are expected to intensify under a warming climate, with uncertain effects on tropical forests. These ecosystems contribute disproportionately to greenhouse gas (GHG; carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O)) fluxes globally but there is high uncertainty in how these fluxes will respond to the projected increase in the frequency of severe tropical cyclones. To examine how these natural disturbance events may alter ecosystem processes in tropical forests, we studied the effects of Hurricane María (2017), a category 4 storm, on soil GHG fluxes from a forest in Puerto

Rico. We also asked how environmental conditions, namely severity of tree canopy damage and topographic position, influenced spatial heterogeneity in post-hurricane soil GHG emissions. Seven months after Hurricane María, we observed an 18% increase in soil CO₂ fluxes, a switch in CH₄ fluxes from net consumption toward net production, and a threefold increase in N₂O emissions relative to pre-hurricane fluxes. None of these fluxes were sensitive to topographic heterogeneity or the magnitude of tree canopy damage, in contrast to the marked soil GHG flux sensitivity to topography prior to the storm. Upscaling the increase in soil N₂O emissions to the ecosystem level shows that greater emissions of soil N₂O following hurricanes also led to high rates of nitrogen loss that, if sustained over a year, would be equivalent to 30% of estimated losses of inorganic nitrogen to runoff and groundwater. Additionally, the combined hurricane-induced increases in soil GHGs suggest a 25% increase in the contribution of soil GHG emissions from this forest to global warming, an effect that can persist for several months after the storm. Taken together, our results show that hurricane disturbance in coastal tropical forests can, at least temporarily, shift the radiative forcing of soils in these forests, exacerbating climate change.

Received 29 March 2022; accepted 18 September 2022

Supplementary Information: The online version contains supplementary material available at <https://doi.org/10.1007/s10021-022-00794-1>.

Author contributions AQ: Conceived of or designed study, performed research, analyzed data, contributed new methods or models, wrote the paper. DM: Conceived of or designed study, wrote the paper. GA: Collected tree damage data. JH: Collected tree damage data, analyzed data. TW: Wrote the paper. JZ: Collected pre-hurricane tree census data, wrote the paper. MU: Collected pre-hurricane tree census and damage data, conceived of or designed study, analyzed data, wrote the paper.

*Corresponding author; e-mail: mu2126@columbia.edu

Published online: 13 October 2022

Key words: Tropical forest; greenhouse gas emissions; hurricanes; puerto Rico; wind damage; topography.

INTRODUCTION

Tropical forests represent major gross sources of greenhouse gases (GHG) globally (Bouwman and others 1995; Curry 2007; Bond-Lamberty and Thomson 2010; Spahni and others 2011) but how these ecosystems will respond to increases in temperature and more variable precipitation with a changing climate remains highly uncertain (Huntingford and others 2013; Cavaleri and others 2015). Climate warming is expected to increase the frequency and severity of several natural disturbance events (McDowell and others 2020), including cyclonic storms (aka hurricanes, cyclones, and typhoons) (Balaguru and others 2018; Bhatia and others 2019), which represent the dominant natural disturbance in many coastal forests across the tropics (Lugo 2008). Increases in the severity of hurricanes further complicate our ability to predict forest responses to climate change (Knutson and others 2010; Richardson and others 2010; Shiels and others 2015; Bhatia and others 2019). More generally, predicting the effects of changing disturbance regimes on tropical ecosystems, and the consequences for GHG fluxes, is a key challenge for global change research.

Severe hurricanes have the potential to alter the short- and long-term dynamics of tropical forests ecosystems and consequently, their contribution to global GHG fluxes (McDowell 2001; Erickson and Ayala 2004; Chambers and others 2007; Vargas 2012; Chen and others 2015; Reed and others 2020a). Changes in the soil environment following a hurricane can increase both the magnitude and variation in GHG fluxes compared to pre-hurricane conditions. These changes include elevated light and temperature in the understory (Richardson and others 2010; Shiels and others 2015), reduced evapotranspiration and increased throughfall and soil moisture (Steudler and others 1991; Heartsill-Scalley and others 2007; Richardson and others 2010), as well as high nutrient deposition and decomposition rates (Lodge and others 1991; Ostertag and others 2003).

Debris from hurricane-induced tree damage and mortality represent massive transfers of biomass and nutrients that can significantly influence the soil environment. Typically, nutrient supply to forest soils increases following a hurricane (Lodge

and others 1991; Ostertag and others 2003; Silver and others 2014; Gutierrez Del Arroyo and Silver 2018), reflecting rapid decomposition of litter and woody debris generated by the storm (Chambers and others 2007; Chen and others 2015) as well as high rates of root mortality (Parrotta and Lodge 1991; Silver and Vogt 1993; Beard and others 2005; Yaffar and others 2021). The loss of aboveground biomass from trees can release up to 45% of nutrients previously sequestered in plant tissues (Scatena and others 1993). Higher soil inorganic N concentrations and rates of soil nitrification after hurricanes (Steudler and others 1991; Silver and Vogt 1993; McDowell 2001; Erickson and Ayala 2004; Reed and others 2020a) are responsible for an increased rate of soil N₂O production (Steudler and others 1991; Erickson and Ayala 2004). At the same time, tree mortality and canopy damage can lead to short-term declines in vegetation nutrient demand (Richardson and others 2010) and aboveground leaf litter production (Scatena and others 1996; Silver and others 2014). Increases in nutrient availability can also lead to higher rates of root production after the hurricane (Yaffar and others 2021), which could be amplified in trees with more damage (Raich and others 2014).

Canopy damage also increases light penetration to the understory for 18–24 months after a hurricane (Fernandez and Fetcher 1991; Bellingham and others 1996; Shiels and Gonzalez 2014), which together with reduced vegetation demand for water, can lead to increases in soil temperature, and shifts in soil moisture and oxygen (Steudler and others 1991; Richardson and others 2010; Shiels and Gonzalez 2014; Reed and others 2020b). Increases in nutrient availability coupled with changes in soil temperature, moisture and oxygen can in turn alter microbial community activity and corresponding rates of soil carbon (C) and nitrogen (N) cycling, which strongly depend on soil conditions (Cantrell and others 2014). Additionally, leaching can remove soluble portions of these nutrients from the ecosystem (McDowell 2001). Elevated nutrient leaching after a hurricane can persist as long as a decade (McDowell and others 2013; McDowell and Liptzin 2014). These changes to soil nutrients and environmental conditions in response to hurricanes have the potential to alter soil GHG fluxes, which are likely to vary significantly across small spatial scales, corresponding to topographic position and the magnitude of tree damage, among other factors (for example, Wood and Silver 2012).

Several studies reported a significant influence of micro-topographic position on soil GHG fluxes in tropical forests as a result of variation in soil nutrients, pH, and water content, on soil GHG fluxes in tropical forests (for example, Wood and Silver 2012 (nutrients, CO₂, CH₄, N₂O); see Courtois and others 2018). In wet forests, soils in valleys are typically wetter and have lower soil oxygen than ridges, which creates soil redox conditions that favor higher production of CH₄, consumption of N₂O, and reduction of CO₂ effluxes (McSwiney and others 2001; Wood and Silver 2012; O’Connell and others 2018; Quebbeman and others 2021). However, although the proximal effects of topography on soil GHG fluxes may be long-lasting, many of the changes to the soil temperature, moisture, and nutrient availability following a hurricane are transient, lasting between a few months to 1–2 years while the forest recovers (Stuedler and others 1991; McDowell 2001; Erickson and Ayala 2004; Shiels and others 2014; Shiels and Gonzalez 2015).

Patchiness in tree species coupled with high interspecific variation in tree litter (Condit and others 2000; Hattenschwiler and others 2008) and throughfall chemistry (Wood and Silver 2012) also creates spatial heterogeneity in soil nutrients (C, N, and P) (Keller and others 2013; Waring and others 2015; Osborne and others 2017; Quebbeman and others 2021). Hurricanes also cause differential damage across tree species, with damage severity related to species traits like successional status and wood density (Zimmerman and others 1994; Canham and others 2010; Uriarte and others 2019). Areas with high tree damage after the hurricane will have reduced nutrient demand and evapotranspiration, leading to increases in substrate availability and soil moisture during the initial phase of post-hurricane recovery (Stuedler and others 1991; Silver and others 1996; Richardson and others 2010). Increases in litterfall, decomposition, and soil nutrient availability in damaged areas are also likely to lead to higher CO₂ fluxes (Ostertag and others 2003; Cleveland and Townsend 2006; Vargas 2012). However, decreases in autotrophic (that is, roots, mycorrhizae, and other rhizospheric microorganisms) respiration due to the immediate increase in root mortality following a hurricane (Parrotta and Lodge 1991; Silver and Vogt 1993; Beard and others 2005) or changes in rates of soil gas diffusion (Wood and others 2013; Schimel 2018) may dampen hurricane-induced increases in soil CO₂ fluxes. In contrast, areas with low hurricane damage may have soil properties more similar to pre-hurricane conditions. Thus, the

response of soil properties and GHG fluxes to hurricanes is likely to be spatially variable and related to differences in hurricane-induced damage, topography, and species characteristics, resulting in high spatial heterogeneity in the magnitude of change in soil GHG fluxes.

In September 20, 2017, Hurricane María hit Puerto Rico as a category 4 storm (Pasch 2018), causing wide-scale defoliation, and tree damage and mortality (Uriarte and others 2019; Hall and others 2020). In this study, we examined the storm’s effects on soil GHG fluxes from a subtropical forest in Puerto Rico. We compared pre- and post-hurricane soil GHG fluxes at the ecosystem scale, evaluating how topography and spatial heterogeneity in tree damage severity influenced changes in soil GHG fluxes during the initial phase of forest recovery. Specifically, we ask:

- (1) To what degree do pre-hurricane soil GHG fluxes change seven months after the hurricane? In response to increases in soil temperature and moisture and the balance of nutrient supply and demand, we hypothesized an increase in soil CO₂, CH₄, and N₂O fluxes (either increased emission or a shift from consumption to emission) following Hurricane María.
- (2) Do fine-scale soil GHG fluxes vary spatially with the severity of tree damage and topographic position? We hypothesized that fluxes of soil CO₂, CH₄, and N₂O will be higher in areas with more severely damaged trees during the initial recovery phase due to associated increased nutrient inputs and decreased nutrient demand. Finally, we hypothesized that canopy damage will lead to larger changes in soil CH₄ and N₂O fluxes in topographically flatter than steep areas post-hurricane, because of larger increases in soil moisture in valleys.

METHODS

Site Description

Soil GHG fluxes were measured in the Luquillo Forest Dynamics Plot (LFDP) in the Luquillo Experimental Forest in northeastern Puerto Rico (SW corner 18° 20’ N, 65° 49’ W). The forest is classified as a subtropical wet forest in the Holdridge life zone system and has an average annual rainfall of 3,500 mm per year (Ewel and Whitmore 1973). The LFDP is a 16-hectare forest plot established in 1990. All stems in this plot with a diameter greater than 1 cm at 1.30 m height (dbh) have been mapped, identified to species, and measured

based on the protocol fully described in (Thompson and others 2002). Approximately every five years since 1990, stems are re-measured and their status is assessed, and new stems are added. The last census of the LFDP prior to Hurricane María was completed in 2016, representing pre-hurricane conditions in this study.

Beginning in January 2018, all trees at least 10 cm dbh in the LFDP were surveyed to assess damage and immediate mortality from H. María (Uriarte and others 2019). The survey recorded several qualitative and quantitative observations of tree damage resulting from the hurricane, such as uprooting or stem break, and type of damage to stems, tree crowns and branches. Using this information, we classified each stem at least 10 cm in dbh into three damage classes: (1) no or light damage ($\leq 25\%$ of crown volume removed by the storm), (2) medium damage (25–75% of crown volume lost through a combination of branch damage and crown break), or (3) heavy or complete ($> 75\%$ of the crown lost, stem snapped, root break or tip-up) (see Canham and others (2010) and Arellano and others (2021) for details).

We calculated concavity and slope for all trees included in the analyses using a high-resolution digital elevation model derived from a LiDAR fly-over of the forest in 2011 (Wolf and others 2016). We computed continuous measures of concavity and slope by fitting a six-term polynomial over a spatially moving window with a radius of r (m) to the digital elevation model following methods described in (Hurst and others 2012).

Pre-hurricane Gas Soil Flux Collection

Net fluxes of CO_2 , CH_4 , and N_2O were measured from the soil at the base of 24 individuals of each of five focal species (120 trees total) in the LFDP. These species (*Casearia arborea*, *Dacryodes excelsa*, *Inga laurina*, *Manilkara bidentata*, and *Prestoea acuminata* var. *montana*) represent a range of life history strategies and are the five most abundant species in the plot, accounting for 68% of stems with a dbh at least 10 cm in the 2016 census of the LFDP. Individual trees at least 10 cm dbh were randomly chosen using the 2016 LFDP census data after stratifying for topographic position (ridge, valley) within each species. For individuals selected in locations where GHG flux measurements were not possible, (that is, rocky outcrops), a nearby individual of the same species was selected. Each tree was sampled for pre-hurricane measurements once in May 2017 and again in July 2017. To capture a single, pre-hurricane measurement for

each of the CO_2 , CH_4 , and N_2O fluxes, we averaged the two pre-hurricane samples into a single estimate for each individual tree.

To measure soil GHG fluxes, a 40 cm diameter, 6.4 cm height (8.04 L) chamber was placed on the soil surface at 50 cm from the base of each individual tree. A seal was created between the chamber edges and the soil surface by fitting robust plastic sheeting tightly around the base of the chamber and weighting the sheeting with heavy chains (Min and others 2021; Quebbeman and others 2021). This method does not require inserting collars into the soil, so it minimizes soil disturbance, but the tradeoff is that the seal from the weighted sheeting is not as tight as a collar base. At intervals of 0, 5, 15, and 25 min after sealing the chamber, gas samples were withdrawn from the chambers through a septum in the top of the chamber and transferred to pre-evacuated Restek vials fitted with robust Geo-Microbial Technologies septa, which our internal tests have shown are gas tight for at least a year. As an additional check on sample leaks, we over pressurized the sample vials (15 mL sample in 10 mL vials). Prior to extracting each sample, we used the sampling syringe to mix the air in the chamber by plunging the full volume of the syringe three times. After sampling, septa were sealed with silicon sealant to maintain positive pressurization. All gas samples were air transported back to Columbia University in New York for analysis. Soil moisture (HydroSense II: 12 cm depth) was measured at the end of each gas sampling. To examine potential differences in soil moisture that may have resulted from differences in rainfall prior to sampling, we used cumulative rainfall data for the 2-days preceding each sampling event collected at the nearby El Verde Field Station. This time window is most closely associated with soil moisture at the site (Uriarte and others 2018).

Post-hurricane Soil Gas Flux Collection

Between April 18 and May 2, 2018, we used the same methods to sample post-hurricane GHG fluxes from the base of 22 to 33 individuals (Supp. Table 1) of each of the five focal tree species sampled before the hurricane. These five focal tree species accounted for 72.5% of trees at least 10 cm dbh at the time of the damage census and suffered a range of damage severities (Figure 1).

Individuals sampled in 2017 were resampled if they survived the hurricane (Supp. Table 1). When selected pre-hurricane trees were either sacrificed or could not be accessed because of fallen debris, we selected a nearby tree (< 30 m distance) of the

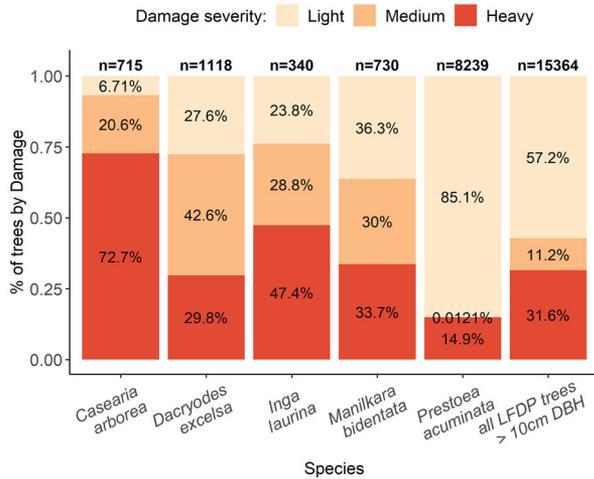


Figure 1. Proportion of trees ≥ 10 cm dbh in the LFDP in each canopy damage category following Hurricane María. The five focal species represent 72.5% of trees ≥ 10 cm dbh in the LFDP. See Supplementary Table 1 for damage categories in sampled individuals.

same species with similar canopy damage status and topographic position, such that we had approximately 10 individuals representing each of the three canopy damage classes (light, medium, or heavy damage) for each of the five focal tree species. For the palm *P. acuminata*, we were only able to sample individuals with light canopy damage because this species cannot survive if the single terminal bud is damaged (Zimmerman and others 1994; Uriarte and others 2019). We also calculated proportion of trees damaged within various distance of the focal tree using various metrics (See Supplementary Methods and Supp. Figure 1 for details).

GHG Laboratory Analysis

For both pre- and post-hurricane gas samples, the concentrations of soil CO_2 , CH_4 , and N_2O were analyzed using gas chromatography (a series of two, 2 m Haysep-D columns; SRI 8610C, SRI Instruments, Torrance, CA, USA) with a Nickel-63 electron capture detector for N_2O and a flame ionization detector equipped with a methanizer for soil CO_2 and CH_4 . Soil GHG fluxes were calculated from the quadratic change of the gas concentrations over time after considering the chamber volume and air temperature at the time of collection. Chamber flux measurements that had quadratic fits with $R^2 < 0.60$ were discarded, as in Quebbeman and others (2021). Negative fluxes represent net uptake into the soil, whereas positive values represent net soil emissions. All soil GHG flux mea-

surements with negative CO_2 flux estimates were discarded, as they suggest an issue with the sampling chamber placement and seal. The final total number of usable samples is provided in Supp. Table 2.

Statistical Analysis

To compare pre- and post-hurricane soil GHG flux measurements, we fitted a Bayesian linear model to both pre- and post-hurricane measurements combined for each gas (hereafter referred as M1). Because previous work found significant relationships between topography and pre-hurricane soil GHG flux measurements (Quebbeman and others 2021), we also included concavity and slope as model covariates in this model. Positive values of concavity correspond to valleys and negative values represent ridges. The optimal spatial window for these topographic metrics were estimated for each soil GHG flux by maximizing the likelihood of the data using a model that included only concavity and slope as covariates (see details in Quebbeman and others (2021)). Measurements across damage severities were treated as one category for post-hurricane measurements in M1, that is, we did not include damage severity as a covariate in this model.

To compare the effect of canopy damage severity and topographic position on post-hurricane soil GHG flux measurements, we fitted an additional model with damage classes (light, medium, and heavy) and topographic position (concavity and slope) as covariates (hereafter referred as M2). Posterior distributions of parameters were estimated using Markov chain Monte Carlo (MCMC) methods using the *rjags* R package (Plummer 2003). Normal likelihood distributions were used for soil CO_2 , CH_4 , and N_2O fluxes and three chains were computed for each parameter with uninformative priors. The first 5,000 iterations were discarded, and each chain ran for 10,000 iterations. Convergence was assessed by visually inspecting trace plots of chains. Significant differences were determined by determining overlap in the 95% credible intervals for parameter estimates.

We then assessed the effects of the hurricane on scaled-up estimates of ecosystem soil GHG emissions, using parameter estimates from M1 and M2 to estimate overall ecosystem-scale soil GHG emissions for the 16-ha LFDP. To test for differences between pre- and post-hurricane ecosystem-scale GHG emissions, we used parameter estimates from M1 to derive pre-hurricane soil flux for each tree at least 10 cm dbh in the LFDP. For post-hur-

ricane conditions, we examined the effect of damage severity on estimates of ecosystem-scale GHG emissions using the canopy damage severity recorded for trees during the 2018 hurricane damage assessment and parameter estimates from M2. We then scaled each individual tree's soil gas flux estimate by a fraction of area of the LFDP using Dirichlet tessellation (spatstat: Baddeley and others (2016)). The tessellation was calculated by dividing the area of the LFDP into convex, non-overlapping and perfectly complementary polygons for each individual tree at least 10 cm dbh regardless of species identity (see detail in (Quebbeman and others 2021)). The size of each polygon was influenced by the distance to nearest neighbors and scaled by tree size, such that, on average, a large tree represents a larger fraction of LFDP area than a small tree. Ecosystem-scale soil GHG emission estimates were then calculated by summing soil GHG fluxes across the estimates for all individual trees. To incorporate uncertainty in coefficient estimates into our ecosystem-scale GHG estimates, we calculated ecosystem-scale soil GHG emissions as a derived parameter within each model; this allowed us to estimate credible intervals for each ecosystem-scale soil GHG estimate. Differences between model estimates were significant if the 95% credible intervals are non-overlapping.

To compare the combined effect of ecosystem-scale soil CO_2 , CH_4 , and N_2O emissions, we used global warming potentials at the standard 20 and 100 year equivalencies to calculate a CO_2 -equivalent ecosystem emission for each model. Soil CH_4 fluxes were scaled by 72 (20 year) and 25 (100 year), N_2O fluxes by 289 (20 year) and 298 (100 year), and carbon dioxide fluxes by 1. Total CO_2 -equivalent estimates for each model were calculated as the sum of scaled soil CO_2 , CH_4 , and N_2O estimates.

RESULTS

Pre- and Post-hurricane Soil GHG Fluxes

Post-hurricane soil CO_2 fluxes were higher ($P < 0.05$; 95% credible intervals) than pre-hurricane measurements (medians of 3.36 vs. 2.83 $\text{g CO}_2\text{-C m}^{-2} \text{day}^{-1}$, respectively; Figure 2a; Supp. Table 3). Similarly, net soil CH_4 fluxes increased marginally ($P < 0.10$; 90% credible intervals) shifting from net soil CH_4 consumption to net production in the LFDP following Hurricane María (medians of 0.69 post- vs. $-0.41 \text{ mg CH}_4\text{-C m}^{-2} \text{day}^{-1}$ pre-hurricane; Figure 2b; Supp. Table 3). Net soil N_2O fluxes in the LFDP differed substan-

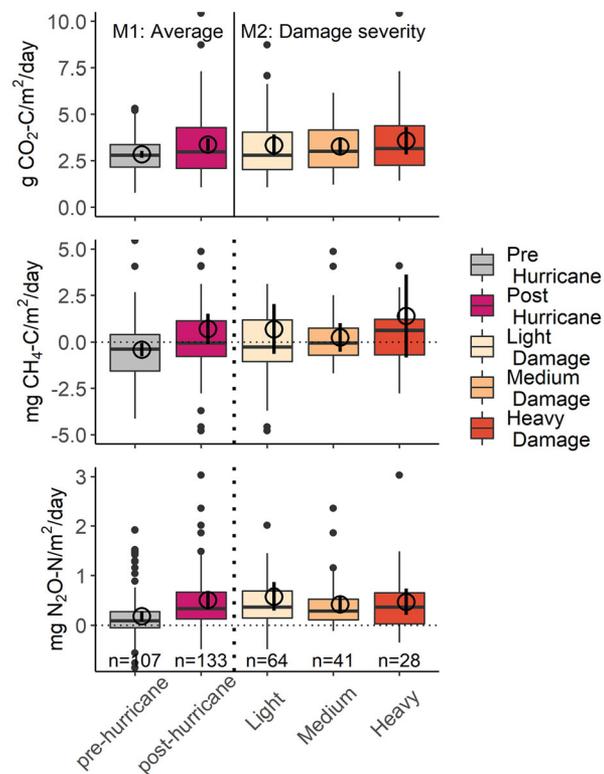


Figure 2. Boxplots of soil GHG flux measurements pre- and post-hurricane. CO_2 (a), CH_4 (b), and N_2O (c) for pre- and post-hurricane measurements, (M1) and measurements by damage severity (M2). All models include topographic position. Open circles with lines represent the model coefficient estimates and 95% credible intervals.

tially between pre- and post-hurricane ($P < 0.05$; 95% credible intervals), increasing from 0.18 to 0.51 $\text{mg N}_2\text{O-N m}^{-2} \text{day}^{-1}$ (Figure 2c; Supp. Table 3). This represents a nearly threefold increase in net soil N_2O production.

Differences in rainfall and soil moisture might account for these changes in soil GHG fluxes. Rainfall was lower during the post-hurricane sampling period than in the pre-hurricane campaign (Mean_{pre} = 30.33 mm, Mean_{post} = 9.75 mm, $F = 82.16$, d.f. = 1, 992, $P < 00,001$) but soil moisture was slightly higher after the hurricane (Mean_{pre} = 42.24 mm, Mean_{post} = 45.59 mm, $F = 17.01$, d.f. = 1, 788, $P < 00,001$). Although rainfall was lower after the hurricane, under the same antecedent rainfall conditions, average soil moisture was slightly higher after the hurricane (Figure 3, Supp. Table 4).

Prior to the hurricane, we observed significant relationships between concavity and soil fluxes of CH_4 ($0.53 \text{ mg CH}_4\text{-C m}^{-2} \text{day}^{-1}$ per standard deviation in concavity) and N_2O ($-0.18 \text{ mg N}_2\text{O-N}$

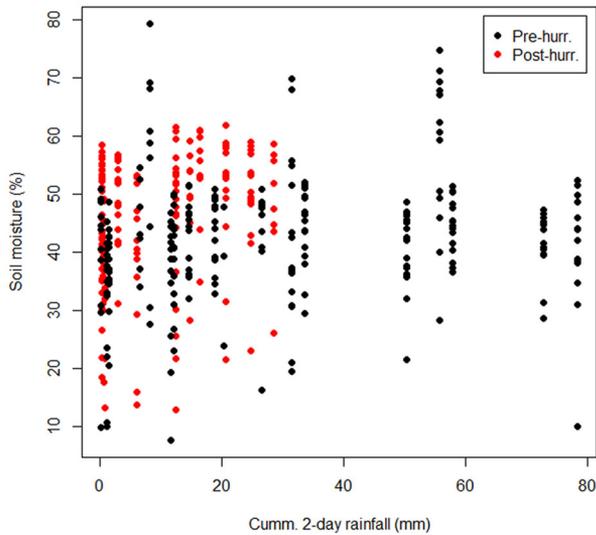


Figure 3. The relationship between 2-day cumulative antecedent rainfall and soil moisture differed between the pre-hurricane and post-hurricane campaigns. Under the same antecedent rainfall conditions, soil moisture was higher after the hurricane (See Supplementary Table 4 for ANCOVA results).

$\text{N m}^{-2} \text{ day}^{-1}$ per standard deviation in concavity) (Quebbeman and others 2021) and lower soil CO_2 fluxes in steeper slopes ($-0.2 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$ per standard deviation in slope). The relationship between topography and soil CH_4 and N_2O fluxes was not evident after the storm. However, soil CO_2 fluxes were lower in valleys than ridges after the storm ($-0.44 \text{ g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$ per standard deviation change in concavity).

Soil GHG Fluxes Across Damage Severities

There was no statistical difference in any soil GHG fluxes across damage severity. Median soil CO_2 fluxes for light, medium, and heavy damaged categories were 3.33, 3.26, and 3.57 $\text{g CO}_2\text{-C m}^{-2} \text{ day}^{-1}$, respectively (Figure 2a; Supp. Table 3). Median net soil CH_4 fluxes for light, medium, and heavy damage categories were 0.69, 0.22, and 1.3 $\text{mg CH}_4\text{-C m}^{-2} \text{ day}^{-1}$, respectively (Figure 2b; Supp. Table 3). Median soil N_2O fluxes for light, medium, and heavy damage severities were 0.55, 0.39, and 0.43 $\text{mg N}_2\text{O-N m}^{-2} \text{ day}^{-1}$, respectively (Figure 2c; Supp. Table 3). We also failed to uncover any significant interactions between topography (neither concavity nor slope) and damage severity.

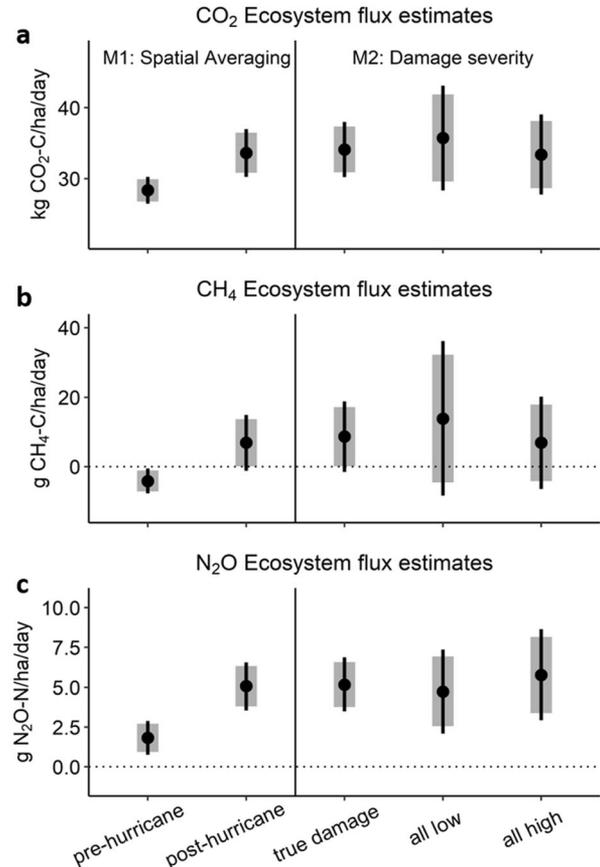


Figure 4. Scaled-up soil GHG emission estimates. Each panel shows estimates using M1 in the left half (the pre-hurricane average and the post-hurricane average) and M2 in the right half (true damage severity in the LFDP and estimates assuming that all trees had low or high damage severity). Points depict the median model estimates, black lines represent 95% credible intervals for that median, and gray lines 90% credible intervals.

Pre- and Post-hurricane Ecosystem-Scale Soil GHG Emissions

We observed higher upscaled soil ecosystem GHG emissions post-hurricane. We estimated median post-hurricane upscaled soil CO_2 emissions to be 33.67 compared to 28.36 $\text{kg CO}_2\text{-C ha}^{-1} \text{ day}^{-1}$ for pre-hurricane conditions ($P < 0.05$; Figure 4a). Similarly, upscaled soil CH_4 fluxes shifted from a net CH_4 consumption of 4.1 $\text{g CH}_4\text{-C ha}^{-1} \text{ day}^{-1}$ pre-hurricane toward a net CH_4 production of 6.9 $\text{g CH}_4\text{-C ha}^{-1} \text{ day}^{-1}$ post-hurricane (Figure 4b). Estimates of soil N_2O emission, upscaled to the ecosystem, showed an increase in median N_2O production from 1.8 to 5.07 $\text{g N}_2\text{O-N ha}^{-1} \text{ day}^{-1}$ ($P < 0.05$) following Hurricane María (Figure 4c).

Pre- and post-hurricane differences in estimates of scaled-up soil ecosystem GHG emissions trans-

late to significant differences in the global warming potential at both 20- and 100-year equivalencies. Pre-hurricane 20- and 100-year equivalencies were 28.58 and 28.70 kg CO₂-C ha⁻¹ day⁻¹, respectively (Figure 5) compared to the respective post-hurricane estimates of 35.62 and 35.34 kg CO₂-C ha⁻¹ day⁻¹. There were no significant differences in global warming potentials across damage severities, at least over the time period we considered.

DISCUSSION

Comparing pre- and post-hurricane soil GHG fluxes, we found an increase in emissions even seven months after the storm. The most dramatic change we found was an increase in ecosystem-scale soil N₂O production that was nearly 3 times higher than pre-hurricane production. Generally, soil N₂O production rises following hurricane-driven increases in leaf litter and woody debris, which increase nitrogen availability (ammonium pools and rates of net N-mineralization and net nitrification). The stark rise in N₂O production in our study is consistent with the higher soil inorganic N availability (Silver and others 1996; Erickson and Ayala 2004; Wood and Silver 2012) and elevated N leaching (McDowell and others 2013; McDowell and Liptzin 2014) observed in this forest following previous hurricanes. These conditions can last as long as 18 months (Shiels and others 2014). This forest is characterized by high N availability that is readily leached from soils, unlike available soil P, which is generally considered the limiting nutrient and is known to bind closely to the iron-rich soils

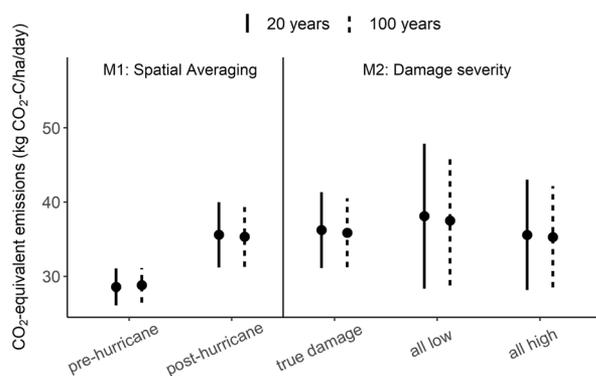


Figure 5. CO₂-equivalent ecosystem GHG emissions. Values represent the 20-year (solid lines) and 100-year (dashed lines) CO₂-equivalent estimates (combined CO₂, CH₄, and N₂O fluxes) for each model. Left half (M1): the pre-hurricane average and the post hurricane average. Right half (M2): true damage severity in the LFD, and estimates assuming all trees had low or high damage severity. Error bars show 95% credible intervals.

(Vitousek and Sanford 1986; Chacon and Dezeo 2004).

Increases in soil CO₂ and CH₄ post-hurricane fluxes were more modest in comparison with changes in N₂O fluxes. The increase in these fluxes is consistent with previous studies in Puerto Rico identifying increases in decomposition and microbial activity following hurricanes (Ostertag and others 2003; Cantrell and others 2014). However, high rates of fine root mortality immediately following hurricanes (Parrotta and Lodge 1991; Silver and Vogt 1993; Yaffar and others 2021) could lead to a temporary decrease in autotrophic soil respiration and thereby dampen the increase in CO₂ fluxes. However, in a nearby forest Yaffar and others (2021), found a 2.8-fold increase in root biomass in the 9 months following Hurricane María, which could account for the observed increase in soil CO₂ fluxes. The shift from net CH₄ consumption toward net production, coupled with the higher soil moisture observed after the storm, suggests a more anoxic post-hurricane soil environment compared pre-hurricane conditions (Shiels and others 2014; Reed and others 2020b), given that methanogens thrive under anoxic conditions. Higher anoxia post-hurricane may result from reduced vegetation uptake and evapotranspiration and higher throughfall (Shiels and Gonzalez 2014).

Contrary to our expectations, the increase in GHG fluxes post-hurricane María did not differ by damage severity of the focal trees. It is possible that individual tree assessments of damage do not reflect canopy changes in the neighborhood of the focal trees, which together with variation species' vulnerabilities to hurricane damage (Uriarte and others 2019), may have shifted the nearby soil environment. However, in addition to the focal tree method, we also used metrics of neighborhood damage calculated as the average of nearby tree damage categories, which also showed no effect of damage on GHG fluxes. Homogenization of debris and leaf litter deposition following a hurricane (Lodge and others 1991) is another possible reason for the pattern. A canopy trimming experiment in this forest (Shiels and others 2014) found that litter deposition had more significant effects on soil C, N, and P pools than canopy opening (that is, simulated damage) (Gutierrez Del Arroyo and Silver 2018), which primarily affected the nutrient demand of canopy trees by shifting plant community composition (Shiels and others 2010) and litterfall nutrient concentrations (Silver and others 2014). Our finding that GHG fluxes did not vary by canopy damage seven months after the hurricane, in

addition to this trimming experiment, suggest that the magnitude of canopy damage is a poor predictor of soil processes and soil GHG fluxes in this forest following a hurricane.

The effects of canopy damage and differences in nutrient inputs associated with species' litter chemistry may also be dampened by other environmental factors. Topography (both slope and concavity) has previously been shown to affect GHG fluxes in this forest (McSwiney and others 2001; Quebbeman and others 2021). The relationship between topography and GHG fluxes was weaker post-hurricane. The overall negative relationship between CO₂ and concavity, the only significant relationship, indicates that soil CO₂ fluxes were lower in valleys compared to ridges. This may be due to lower rates of gas diffusion or decreases in microbial activity in wetter valley soils (Silver and others 1999).

We observed upscaled soil N₂O emissions nearly 3 times higher than pre-hurricane N₂O losses, which is undoubtedly an underestimate of total gaseous N loss to the system. Other N losses through nitrification and denitrification include N₂, NO, and NO₂, all of which may equal or exceed N₂O losses (Pilegaard 2013), not to mention ammonia volatilization. Additionally, if we scale our estimates of soil N₂O loss up to annual fluxes by assuming constant fluxes throughout the year (which has many caveats), the value (1.84 kg N₂O-N ha⁻¹ year⁻¹) is nearly 30% that of estimates of nitrogen losses through runoff and groundwater following Hurricane Hugo in 1989 (5.29 kg NO₃-N ha⁻¹ year⁻¹ and 0.54 kg NH₄-N ha⁻¹ year⁻¹, respectively; (Schaefer and others 2000)) and 50% that of a previous estimate of total gaseous N losses in this forest (1–4 kg N ha⁻¹ year⁻¹ including N₂, N₂O, NO₂, and NO; (Chestnut and others 1999)). Gaseous soil N₂O losses following Hurricane María, if constant for a year, account for 0.27% of the estimated aboveground nitrogen pool for this forest (~ 670 kg N ha⁻¹; Scatena and others (1996)). This represents a major nitrogen loss from this forest, nearly equal to rates of atmospheric N deposition (2–4 kg N ha⁻¹ y⁻¹; (Chestnut and others 1999)), though lower than biological N fixation (10 kg N ha⁻¹ y⁻¹; (Cusack and others 2009)). Previous studies at the site have shown that nitrate concentrations in soil solution can remain elevated for almost a decade after the passage of a storm (McDowell and others 2013). Thus, more frequent or intense hurricanes could shift forests into a new state characterized by high nitrogen loss and lower soil N concentrations, which may slow

forest biomass recovery (Walker and others 1996; Beard and others 2005).

Improving our understanding of nitrogen and carbon losses may help us predict shifts in the carbon balance of forests under climate change. Our work suggests that hurricanes increase soil GHG emissions, at least temporarily. However, predicting the long-term effects of more frequent severe hurricanes on GHG fluxes is far more complicated since it will depend on the degree of forest recovery and productivity, and therefore on long-term forest carbon uptake after storms. Tree species differ in their susceptibility to disturbance by a wind of a given intensity, the nature of the damage they sustain from a given wind storm intensity, their recovery from wind disturbance at both the individual plant level through repair of damage, and at the population level through reproduction, seedling establishment, and juvenile response to enhanced light availability (Canham and others 2010; Uriarte and others 2009; Walker 1991; Zimmerman and others 1994; Uriarte and others 2019). Because hurricanes tend to damage larger trees, storm damage may increase short-term productivity by favoring rapid understory tree growth (Uriarte and Papaik 2016). However, losses of carbon in downed biomass and differences among species that benefit from wind damage in carbon uptake relative to those present before a storm may counteract these short-term gains over a longer time period (Fisk and others 2013; Uriarte and Papaik 2016). Understanding the relative importance of these seemingly countervailing impacts on long-term changes in forest composition and carbon uptake can be furthered by the use of models (Fisk and others 2013).

Although most models estimating tropical forest response to climate change ignore hurricanes (Huntingford and others 2013; Zhou and others 2013; Cavaleri and others 2015), models of temperate forests that include hurricanes predict a shift from net carbon sinks to net carbon sources with increasing hurricane severity and frequency (Fisk and others 2013). However, these studies in temperate forest primarily focus on carbon storage in aboveground biomass and do not consider the effect of nitrogen losses on biomass recovery. Including N₂O emissions in the calculation could change the predictions considerably. According to our results, N₂O losses accounted for 4.2% of the post-hurricane GHG-induced radiative forcing (compared to 1.8% pre-hurricane) and the combined increase in upscaled CO₂, CH₄, and N₂O soil emissions we observed translates to an increase in forest soil GHG emissions of about 25% in global

warming potential equivalency compared to pre-hurricane emissions. These results suggest that more frequent severe hurricanes may exacerbate climate change by switching tropical forests from long-term net carbon sinks to contributors of global warming potential equivalent GHG emissions, at least temporarily.

Although the limitation of forest recovery by nitrogen after hurricanes is poorly understood, there is evidence that forests on soils with increased nitrogen pools from previous land-use recover faster than nearby forests (Beard and others 2005) and that increases in coarse woody debris can immobilize soil nitrogen and limit biomass recovery (Zimmerman and others 1995). Following Hurricane Hugo, live aboveground biomass and nitrogen in our study site decreased by nearly 50% (Scatena and others 1996) and both took approximately 5 years to recover to pre-hurricane levels (Scatena and others 1996). Frequent hurricanes could therefore lead to a depleted nitrogen pool due to increased losses to groundwater leaching and gaseous emissions and could affect the recovery of forests and the role tropical forests will play in climate change mitigation in the future.

As large-scale disturbances, hurricanes have the power to drastically alter the trajectory and state of tropical forests (Uriarte and others 2009; McDowell and others 2020). These ecosystems have the potential to shift from net carbon sinks to net sources if the frequency or intensity of storms increase to the point that forests fail to recover between hurricane events. Constraints on biomass recovery have primarily focused on successional trajectories and species growth rates and few have considered nutrients as a limiting factor in forest regeneration post-hurricanes. However, removal of debris after Hurricane Hugo at the study site caused a significant decline in tree diameter increment relative to controls (Walker and others 1996) and a canopy and debris manipulation study also found that debris increased forest productivity (Shiels and others 2014). We observed a dramatic shift in soil GHG emissions following Hurricane María, driven largely by increases in soil N₂O emissions that, in addition to nitrogen leaching through groundwater, represent a net loss of nitrogen from the forest that has the potential to limit biomass recovery in the future. Based on these findings, we recommend that soil GHG production in forests following hurricanes, and the subsequent loss of nitrogen from the system, both be considered when modeling forest responses to climate change. Without such considerations, projections of forest growth may

overestimate the ability of tropical forests to sequester carbon and mitigate climate change.

ACKNOWLEDGEMENTS

We thank the field crews who collected tree census data. Research was supported by NSF awards DEB-1831952 and 1546686 to the Luquillo LTER. Tree damage data was collected with funding from NSF RAPID award DEB-1801315 to MU and JKZ and the Next Generation Ecosystem Experiments-Tropics, funded by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research (<https://ngee-tropics.lbl.gov/>). The findings and conclusions in this publication are those of the author(s) and should not be construed to represent any official USDA or U.S. Government determination or policy.

REFERENCES

- Arellano G, Zuleta D, Davies SJ. 2021. Tree death and damage: a standardized protocol for frequent surveys in tropical forests. *J Veg Sci* 32:38.
- Baddeley A, Rubak E, Turner R. 2016. Spatial point patterns: methodology and applications with R.
- Balaguru K, Foltz GR, Leung LR. 2018. Increasing magnitude of hurricane rapid intensification in the central and eastern tropical atlantic. *Geophys Res Lett* 45:4238–4247.
- Beard KH, Vogt D, Vogt D, Scatena FN, Covich A, Sigurdardottir R, Siccama TG, Crowl AT. 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecol Monogr* 75:345–361.
- Bellingham PJ, Tanner EVJ, Rich PM, Goodland TCR. 1996. Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. *J Trop Ecol* 12:699–722.
- Bhatia KT, Vecchi GA, Knutson TR, Murakami H, Kossin J, Dixon KW, Whitlock CE. 2019. Recent increases in tropical cyclone intensification rates. *Nat Commun* 10:635.
- Bond-Lamberty B, Thomson A. 2010. A global database of soil respiration data. *Biogeosciences* 7:1915–1926.
- Bouwman AF, Vanderhoek KW, Olivier JGJ. 1995. Uncertainties in the global source distribution of nitrous-oxide. *J Geophys Res-Atmos* 100:2785–2800.
- Canham CD, Thompson J, Zimmerman JK, Uriarte M. 2010. Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42:87–94.
- Cantrell SA, Molina M, Lodge DJ, Rivera-Figueroa FJ, Ortiz-Hernandez ML, Marchetti AA, Cyterski MJ, Perez-Jimenez JR. 2014. Effects of a simulated hurricane disturbance on forest floor microbial communities. *For Ecol Manag* 332:22–31.
- Cavaleri MA, Reed SC, Smith WK, Wood TE. 2015. Urgent need for warming experiments in tropical forests. *Glob Change Biol* 21:2111–2121.
- Chacon N, Dezzio N. 2004. Phosphorus fractions and sorption processes in soil samples taken in a forest-savanna sequence of the Gran Sabana in southern Venezuela. *Biol Fertil Soils* 40:14–19.

- Chambers JQ, Fisher JJ, Zeng H, Chapman EL, Baker DB, Hurtt GC. 2007. Hurricane Katrina's carbon footprint on U.S. Gulf Coast forests. *Science* 318:1107.
- Chen Y, Randerson JT, Morton DC. 2015. Tropical North Atlantic ocean-atmosphere interactions synchronize forest carbon losses from hurricanes and Amazon fires. *Geophys Res Lett* 42:6462–6470.
- Chestnut TJ, Zarin DJ, McDowell WH, Keller M. 1999. A nitrogen budget for late-successional hillslope tabonuco forest, Puerto Rico. *Biogeochemistry* 46:85–108.
- Cleveland CC, Townsend AR. 2006. Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proc Natl Acad Sci U S A* 103:10316–10321.
- Condit R, Ashton PS, Baker P, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbell SP, Foster RB, Itoh A, LaFrankie JV, Lee HS, Losos E, Manokaran N, Sukumar R, Yamakura T. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288:1414–1418.
- Courtois EA, Stahl C, Van den Berge J, Brechet L, Van Langenhove L, Richter A, Urbina I, Soong JL, Penuelas J, Janssens IA. 2018. Spatial variation of soil CO₂, CH₄ and N₂O fluxes across topographical positions in tropical forests of the Guiana shield. *Ecosystems* 21:1445–1458.
- Curry CL. 2007. Modeling the soil consumption of atmospheric methane at the global scale. *Glob Biogeochem Cycles* 21:88.
- Cusack DF, Silver W, McDowell WH. 2009. Biological nitrogen fixation in two tropical forests: ecosystem-level patterns and effects of nitrogen fertilization. *Ecosystems* 12:1299–1315.
- Erickson HE, Ayala G. 2004. Hurricane-induced nitrous oxide fluxes from a wet tropical forest. *Glob Change Biol* 10:1155–1162.
- Ewel JJ, Whitmore JL. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. International Institute of Tropical Forestry.
- Fernandez E, Fetcher N. 1991. Changes in light availability following Hurricane Hugo in a subtropical montane forest in Puerto Rico. *Biotropica* 23:393–399.
- Fisk JP, Hurtt GC, Chambers JQ, Zeng H, Dolan KA, Negron-Juarez RI. 2013. The impacts of tropical cyclones on the net carbon balance of eastern US forests (1851–2000). *Environ Res Lett* 8:333.
- Gutierrez Del Arroyo O, Silver WL. 2018. Disentangling the long-term effects of disturbance on soil biogeochemistry in a wet tropical forest ecosystem. *Glob Chang Biol* 24:1673–1684.
- Hall J, Muscarella R, Quebbeman A, Arellano AG, Thompson J, Zimmerman JK, Uriarte M. 2020. Hurricane-induced rainfall is a stronger predictor of tropical forest damage in Puerto Rico than maximum wind speeds. *Sci Rep* 2:569.
- Hattenschwiler S, Aeschlimann B, Couteaux MM, Roy J, Bonal D. 2008. High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. *New Phytologist* 179:165–175.
- Heartsill-Scalley T, Scatena FN, Estrada C, McDowell WH, Lugo AE. 2007. Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico. *J Hydrol* 333:472–485.
- Huntingford C, Zelazowski P, Galbraith D, Mercado LM, Sitch S, Fisher R, Lomas M, Walker AP, Jones CD, Booth BBB, Malhi Y, Hemming D, Kay G, Good P, Lewis SL, Phillips OL, Atkin OK, Lloyd J, Gloor E, Zaragoza-Castells J, Meir P, Betts R, Harris PP, Nobre C, Marengo J, Cox PM. 2013. Simulated resilience of tropical rainforests to CO₂-induced climate change. *Nat Geosci* 6:268–273.
- Hurst MD, Mudd SM, Walcott R, Attal M, Yoo K. 2012. Using hilltop curvature to derive the spatial distribution of erosion rates. *J Geophys Res-Earth Surf* 117:5506.
- Keller AB, Reed SC, Townsend AR, Cleveland CC. 2013. Effects of canopy tree species on belowground biogeochemistry in a lowland wet tropical forest. *Soil Biol Biochem* 58:61–69.
- Knutson TR, McBride JL, Chan J, Emanuel K, Holland G, Landsea C, Held I, Kossin JP, Srivastava AK, Sugi M. 2010. Tropical cyclones and climate change. *Nat Geosci* 3:157–163.
- Lodge DJ, Scatena FN, Asbury CE, Sanchez MJ. 1991. Fine litterfall and related nutrient inputs resulting from hurricane Hugo in subtropical wet and lower montane rain-forests of Puerto Rico. *Biotropica* 23:336–342.
- Lugo AE. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Aust Ecol* 33:368–398.
- McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L, Clark JS, Dietze M, Grossiord C, Hanbury-Brown A, Hurtt GC, Jackson RB, Johnson DJ, Kueppers L, Lichstein JW, Ogle K, Poulter B, Pugh TAM, Seidl R, Turner MG, Uriarte M, Walker AP, Xu C. 2020. Pervasive shifts in forest dynamics in a changing world. *Science* 368:618.
- McDowell WH. 2001. Hurricanes, people, and riparian zones: controls on nutrient losses from forested Caribbean watersheds. *For Ecol Manag* 154:443–451.
- McDowell WH, Brereton RL, Scatena FN, Shanley JB, Brokaw NV, Lugo AE. 2013. Interactions between lithology and biology drive the long-term response of stream chemistry to major hurricanes in a tropical landscape. *Biogeochemistry* 116:175–186.
- McDowell WH, Liptzin D. 2014. Linking soils and streams: Response of soil solution chemistry to simulated hurricane disturbance mirrors stream chemistry following a severe hurricane. *For Ecol Manag* 332:56–63.
- McSwiney CP, McDowell WH, Keller M. 2001. Distribution of nitrous oxide and regulators of its production across a tropical rainforest catena in the Luquillo Experimental Forest, Puerto Rico. *Biogeochemistry* 56:265–286.
- Min E, Wilcots ME, Naeem S, Gough L, McLaren JR, Rowe RJ, Rastetter EB, Boelman NT, Griffin KL. 2021. Herbivore absence can shift dry heath tundra from carbon source to sink during peak growing season. *Environ Res Lett* 16:91117.
- O'Connell CS, Ruan L, Silver WL. 2018. Drought drives rapid shifts in tropical rainforest soil biogeochemistry and greenhouse gas emissions. *Nat Commun* 9:228.
- Osborne BB, Nasto MK, Asner GP, Balzotti CS, Cleveland CC, Sullivan BW, Taylor PG, Townsend AR, Porder S. 2017. Climate, topography, and canopy chemistry exert hierarchical control over soil N cycling in a neotropical lowland forest. *Ecosystems* 20:1089–1103.
- Ostertag R, Scatena FN, Silver WL. 2003. Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. *Ecosystems* 6:261–273.
- Parrotta JA, Lodge DJ. 1991. Fine root dynamics in a subtropical wet forest following hurricane disturbance in Puerto Rico. *Biotropica* 23:343–347.
- Pasch RJ, Andrew BP, Robbie B. 2018. Hurricane Maria (AL152017).

- Pilegaard K. 2013. Processes regulating nitric oxide emissions from soils. *Philos Trans R Soc B-Biol Sci* 368:5000.
- Plummer M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), March 20–22, Vienna, Austria.
- Quebbeman AW, Menge DNL, Zimmerman J, Uriarte M. 2021. Topography and tree species improve estimates of spatial variation in soil greenhouse gas fluxes in a subtropical forest. *Ecosystems* 3:72.
- Raich JW, Clark DA, Schwendenmann L, Wood TE. 2014. Aboveground tree growth varies with belowground carbon allocation in a tropical rainforest environment. *PLoS One* 9:6300.
- Reed SC, Reibold R, Cavaleri MA, Alonso-Rodriguez AM, Berberich ME, Wood TE. 2020a. Soil biogeochemical responses of a tropical forest to warming and hurricane disturbance. In: Dumbrell AJ, Turner EC, Fayle TM, Eds. *Tropical Ecosystems in the 21st Century*, pp. 225–52.
- Reed SC, Reibold R, Cavaleri MA, Alonso-Rodriguez AM, Berberich ME, Wood TE. 2020b. Soil biogeochemical responses of a tropical forest to warming and hurricane disturbance. In: Dumbrell AJ, Turner EC, Fayle EM, Eds. *Tropical Ecosystems in the 21st Century*, pp. 225+.
- Richardson BA, Richardson MJ, Gonzalez G, Shiels AB, Srivastava DS. 2010. A canopy trimming experiment in Puerto Rico: the response of litter invertebrate communities to canopy loss and debris deposition in a tropical forest subject to hurricanes. *Ecosystems* 13:286–301.
- Scatena FN, Moya S, Estrada C, Chinae JD. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley experimental watersheds, Luquillo experimental forest, Puerto Rico. *Biotropica* 28:424–440.
- Scatena FN, Silver WL, Siccama TG, Johnson AH, Sanchez-de Leon Y. 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico before and after Hurricane Hugo, 1989. *Biotropica* 25:15–27.
- Schaefer DA, McDowell WH, Scatena FN, Asbury CE. 2000. Effects of hurricane disturbance on stream water concentrations and fluxes in eight tropical forest watersheds of the Luquillo Experimental Forest, Puerto Rico. *J Trop Ecol* 16:189–207.
- Schimel JP. 2018. Life in dry soils: effects of drought on soil microbial communities and processes. In: Futuyama DJ, Ed. *Annual Review of Ecology, Evolution, and Systematics*, Vol 49, pp. 409–32.
- Shiels AB, Gonzalez G. 2014. Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. *For Ecol Manag* 332:1–10.
- Shiels AB, Gonzalez G. 2015. Tropical forest response to large-scale experiments. *Bioscience* 65:839–840.
- Shiels AB, Gonzalez G, Lodge DJ, Willig MR, Zimmerman JK. 2015. Cascading effects of canopy opening and debris deposition from a large-scale hurricane experiment in a tropical rain forest. *Bioscience* 65:871–881.
- Shiels AB, Gonzalez G, Willig MR. 2014. Responses to canopy loss and debris deposition in a tropical forest ecosystem: synthesis from an experimental manipulation simulating effects of hurricane disturbance. *For Ecol Manag* 332:124–133.
- Shiels AB, Zimmerman JK, Garcia-Montiel DC, Jonckheere I, Holm J, Horton D, Brokaw N. 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *J Ecol* 98:659–673.
- Silver WL, Hall SJ, Gonzalez G. 2014. Differential effects of canopy trimming and litter deposition on litterfall and nutrient dynamics in a wet subtropical forest. *For Ecol Manag* 332:47–55.
- Silver WL, Lugo AE, Keller M. 1999. Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. *Biogeochemistry* 44:301–328.
- Silver WL, Scatena FN, Johnson AH, Siccama TG, Watt F. 1996. At what temporal scales does disturbance affect belowground nutrient pools? *Biotropica* 28:441–457.
- Silver WL, Vogt KA. 1993. Fine-root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *J Ecol* 81:729–738.
- Spahni R, Wania R, Neef L, van Weele M, Pison I, Bousquet P, Frankenberg C, Foster PN, Joos F, Prentice IC, van Velthoven P. 2011. Constraining global methane emissions and uptake by ecosystems. *Biogeosciences* 8:1643–1665.
- Stuedler PA, Melillo JM, Bowden RD, Castro MS, Lugo AE. 1991. The effects of natural and human disturbances on soil-nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. *Biotropica* 23:356–363.
- Thompson J, Brokaw N, Zimmerman JK, Waide RB, Everham EM, Lodge DJ, Taylor CM, Garcia-Montiel D, Fluet M. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecol Appl* 12:1344–1363.
- Uriarte M, Canham CD, Thompson J, Zimmerman JK, Murphy SF, Sabat AM, Fetcher N, Haines BL. 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. *Ecol Monogr* 79:423–443.
- Uriarte M, Muscarella R, Zimmerman JK. 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Glob Chang Biol* 24:e692–e704.
- Uriarte M, Papaik M. 2016. Hurricane impacts on dynamics, structure and carbon sequestration potential of forest ecosystems in Southern New England, USA. *Tellus Dyn Meteorol Oceanogr* 59:519–528.
- Uriarte M, Thompson J, Zimmerman JK. 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. *Nat Commun* 10:1362.
- Vargas R. 2012. How a hurricane disturbance influences extreme CO₂ fluxes and variance in a tropical forest. *Environ Res Lett* 7:55.
- Vitousek PM, Sanford RL. 1986. Nutrient cycling in moist tropical forest. *Annu Rev Ecol Syst* 17:137–167.
- Walker LA, Silver WL, Willig MR, Zimmerman JK. 1996. Long-term responses of Caribbean ecosystems to disturbance. *Biotropica* 28:414–614.
- Waring BG, Alvarez-Cansino L, Barry KE, Becklund KK, Dale S, Gei MG, Keller AB, Lopez OR, Markestijn L, Mangan S, Riggs CE, Rodriguez-Ronderos ME, Segnitz RM, Schnitzer SA, Powers JS. 2015. Pervasive and strong effects of plants on soil chemistry: a meta-analysis of individual plant “Zinke” effects. *Proc R Soc B-Biol Sci* 282:91–98.
- Wolf J, Brocard G, Willenbring J, Porder S, Uriarte M. 2016. Abrupt change in forest height along a tropical elevation gradient detected using Airborne Lidar. *Remote Sens* 8:1004.

- Wood TE, Detto M, Silver WL. 2013. Sensitivity of soil respiration to variability in soil moisture and temperature in a humid tropical forest. *PLoS One* 8:93.
- Wood TE, Silver WL. 2012. Strong spatial variability in trace gas dynamics following experimental drought in a humid tropical forest. *Glob Biogeochem Cycles* 26:1222.
- Yaffar D, Wood TE, Reed SC, Branoff BL, Cavaleri MA, Norby RJ. 2021. Experimental warming and its legacy effects on root dynamics following two hurricane disturbances in a wet tropical forest. *Glob Change Biol* 27:6423–6435.
- Zimmerman JK, Everham EM III, Waide RB, Lodge DJ, Taylor CM, Brokaw NVL. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *J Ecol* 82:911–922.
- Zimmerman JK, Pulliam WM, Lodge DJ, Quinonesorfila V, Fetcher N, Guzmangrajales S, Parrotta JA, Asbury CE, Walker LR, Waide RB. 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forests from hurricane damage. *Oikos* 72:314–322.

Springer Nature or its licensor holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.