### Response and recovery of tropical forests after cyclone disturbance

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November 22, 2022

#### Abstract

Tropical cyclones dominate the disturbance regime experienced by forest ecosystems in many parts of the world. Interactions between cyclone disturbance regimes and nutrient availability strongly influence forest ecosystem dynamics. However, uncertainty exists over the importance of soil fertility properties (i.e., total soil phosphorus-P concentration) in mediating forest resistance and recovery from cyclone disturbance. We hypothesized that forests on soils with low total P (e.g., developed on limited-P parent material) have a higher resistance to but a slower recovery from cyclone disturbance than forests on high P soils. We investigated cyclone impacts on litterfall, an essential conduit for nutrient recycling in forest ecosystems. We compiled site-level forest litterfall data from 53 studies and datasets associated with 15 naturally-occurring one simulated tropical cyclone in 23 sites within five regions (Taiwan, Australia, Mexico, Hawaii, and the Caribbean) and four cyclone basins. We calculated the effect sizes of cyclone disturbance on the litterfall mass and nutrient (P and nitrogen-N) concentrations and fluxes during the first (< five) years post-disturbance across a total soil P gradient. We also assessed the effect of 20 covariates on the degree of cyclone impact on litterfall. Total litterfall mass flux increased by 4820% following cyclone disturbance. Such an initial increase in litterfall mass reflects the magnitude of cyclone-derived plant material input to the forest floor, which was highest in the Caribbean and lowest in Taiwan. Among 20 covariates, soil P and region were the best predictors of cyclone effects on total litterfall mass, explaining 80% of the variance. The effect sizes increased linearly with soil P and region, from significantly lower in Taiwan (low-P) to largest in the Caribbean (high-P). Total litterfall P and N fluxes increased significantly post-cyclone, whereas the increase in leaf P flux was twice as that in Nflux. Results highlight the importance of understanding the interactions between disturbance and nutrient gradients in forest ecosystems to understand forest responses to altered cyclone regimes expected under climate change.

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# **BACKGROUND & OBJECTIVE**

# Does soil fertility influence tropical forest stability in response to cyclone disturbance?



Damage caused by a hurricane in a Puerto Rican forest. Image credit: Dr. Maria Uriarte

- Quantifying ecosystem stability in response to disturbance is critical for predicting how disturbance regimes altered by climate change will affect ecosystem structure and function.

- Tropical cyclones, whose intensities are expected to increase with warming (Reed et al. 2020), dominate the disturbance regime experienced by forest ecosystems worldwide.

- Forest ecosystem dynamics are strongly influenced by interactions between cyclone disturbance regimes and nutrient availability.

- Uncertainty exists over the importance of soil fertility properties, like total soil phosphorus (P) concentration, in mediating forest resistance and recovery from cyclone disturbance.

To understand the role of soil P in mediating forest stability in response to cyclone, we investigated the response, resilience, and recovery of litterfall across a pantropical total soil P gradient.

### **HYPOTHESIS & APPROACH**

Forests on low-P soils are more resistant but less resilient to cyclone disturbance than forests on high-P soils.



Fig 1. Graphical hypothesis.

# The hypothesis was tested by a pantropical meta-analysis of published studies and data sets.



Fig 2. Schema of the research approach.

- 53 studies and data sets;
- 15 naturally-occurring and 1 simulated tropical cyclone;
- 23 sites within 5 regions Taiwan, Australia, Mexico, Hawaii, and the Caribbean;
- 4 cyclone basins.



Fig 3. Study sites located in five regions and four cyclone basins.

Table 1. Studies included in this meta-analysis.

				Soil parent	Total soil P	Storm frequency	Cyclone name and
Region	Study	Holdridge life zone	Site	material	(mg/kg)	(year <sup>-1</sup> )	year
Australia	Gleason et al. 2008	Tropical rain	Wooroonooran 1	Basalt	1520	0.28	
			Wooroonooran 2	Metamorphic schist	240	0.28	Larry 2006
	Herbohn & Congdon 1993	Tropical rain	Mt Spec	Granite	130	0.28	Charlie 1988
	Benson & Pearson 1993	Subtropical lower montane wet	Birthday Creek	Granite	210	0.28	Charlie 1988
Caribbean	Zimmerman et al. 1995	Subtropical wet	El Verde	Volcaniclastic	340	0.21	Hugo 1989
	Walker et al. 1996 Lodge et al. 1991						
	Ramirez 2017	Subtropical wet	El VerdeTrim <sup>a</sup> & TrimDeb <sup>b</sup>	Volcaniclastic	340	0.21	CTE 2005
	Ostertag et al. 2003	Subtropical moist	Cubuy	Volcaniclastic	255	0.21	Georges 1998
		Subtropical wet	Bisley	Volcaniclastic	320	0.21	Georges 1998
	Lodge et al. 1991	Subtropical wet	Bisley	Volcaniclastic	320	0.21	Hugo 1989
	Scatena et al. 1996	Subtropical wet	(watersheds 1 & 2)	Volcaniclastic	320	0.21	Hugo 1989
	Covich 2015	Subtropical wet	Bisley (La Prieta)	Volcaniclastic	320	0.21	Hugo 1989
	Liu et al. 2018	Subtropical wet	Bisley	Volcaniclastic	320	0.21	Irma & Maria 2017
	Ostertag et al. 2003	Subtropical lower	East Peak Palm forest	HA Volcaniclastic	140	0.21	Georges 1998
		Subtropical lower	East Peak	HA	317.3	0.21	Georges 1998
		Subtranical lower	Colorado	Volcaniclastic			
		subtropical lower	East Peak Cloud	voicanic	260	0.21	Georges 1998
	Walker et al. 1996	Subtropical lower	East Peak Cloud	Volcanic			Hugo 1989
		montane rain	forest	siltstone	260	0.21	
	Lugo et al. 2011	Subtropical moist	Utuado	Noncarbonate sedimentary	330	0.21	Georges 1998
	Van Bloem et al. 2005	Subtropical dry	Guanica	Limestone	500	0.21	Georges 1998
	Liu et al. 2018	Subtropical dry	Guanica	Limestone	500	0.21	Irma & Maria 2017
		Subtropical wet	Rio Abajo	Limestone	820	0.21	Irma & Maria 2017
		Subtropical moist	Guayama	Residuum Coluviuum Volcanic	340	0.21	Irma & Maria 2017
	Beard et al. 2005	Subtropical wet	Bisley/El Verde <sup>¢</sup>	Volcaniclastic	320	0.21	Bertha 1996
	Imbert & Portecop 2008	Tropical dry	Grande-Terre	Coral limestone	670	0.33	Hugo 1989
Hawaii	Herbert et al. 1999	Subtropical lower montane wet	Kokee	Basalt	220	0.12	Iniki 1992
	Harrington et al. 1997	Subtropical premontane dry	Makaha 1	Basalt	110	0.12	
		Subtropical lower montane wet	Milolii	Basalt	110	0.12	
			Kumuwela	Basalt	20	0.12	
			Halemanu	Volcanic ash	52	0.12	
Mexico	Whigham et al. 1991	Tropical dry	San Felipe	Limestone	2900	0.44	Gilbert 1988
	Martínez-Yrízar et al. 2018	Tropical dry	Chamela- Cuixmala	Rhyolitic Rhyodacitic Volcanic	291	0.33	Jova 2011
		Tropical dry	Chamela- Cuixmala	Rhyolitic Rhyodacitic Volcanic	291	0.37	Patricia 2015
Taiwan	Wang et al. 2013	Subtropical wet	Lienhuachi	Quartzitic sandstone	460.9	0.97	Kalmaegi 2008
	Liao et al. 2006	Tropical moist	Kengting III	Hengchun	87.9	0.97	Mindulle 2004
			Kengting IV	Limestone	70.5	0.97	



**Fig. 4 a** Litterfall mass flux, **b** nutrient flux and **c** concentration by region and time since disturbance, and **d-f** by Holdridge life zone and region.

### **Response variables**

Using litterfall mass flux data during the first (< five) years post-disturbance, we calculated:

### Response

 $Rp = In (Litterfall t_i/t_0)$ 

### R<sub>p</sub> near zero indicates high resistance

Resilience

### R<sub>s</sub> near zero indicates high resilience

Recovery

 $R_c = ln (Litterfall t_x/t_i)$ 

### **Moderator variables**

Using Random Forest for meta-analysis and multivariate random-effects models, we assessed the influence of soil phosphorus and 20 variables related to cyclone disturbance, soil, geology, geography, and vegetation (Fig. 2) on the stability indices.

# **RESULTS: RESPONSE**





Fig. 5 The pantropical overall response to cyclone disturbance, and response by region.

- The pulse of litter was highest in the Caribbean and lowest in Taiwan.

**Does soil P explain differential responses?** 



Fig. 6 Moderator variables ranked by their importance in explaining forest response to cyclone disturbance.

# Total soil P is a significant predictor of forest response to tropical cyclone disturbance.



**Fig. 7** Predictions of forest response (Rp: ln litterfall  $t_i/t_0$ ) to cyclone disturbance by linear regression including total soil phosphorus (mg/kg) and study region as predictors.

Rp = 1.496 +

- 0.00173 soil P Australia
- 3.957 soil P (Caribbean)
- 1.321 soil P Hawaii
- 0.228 soil P Mexico
- 0.582 soil P Taiwan

# **RESULTS: RESILIENCE & RECOVERY**





**Fig. 8** Overall forest resilience to cyclone by time since disturbance. Asterisks denote a significant difference from the baseline at the 95% confidence level.

# Resilience in the first year post-disturbance is negatively related to soil phosphorus.



**Fig. 9 (a)** Predictor importance ranking using resilience calculated for the first 14 months post-cyclone response. (**b**) Resilience by total soil P, storm frequency (number of storms per year), and tropical region. (**c**) Resilience predictions using storm frequency and elevation as predictors.

### Forest recovery after cyclone disturbance can be predicted by total soil P.



Fig. 10 Recovery index (ln litterfall  $t_x/t_i$ ) predictions by linear regression, including total soil phosphorus as a significant predictor.

# FUTURE DIRECTIONS

- How do P and N fluxes from the canopy to the floor change after cyclone disturbances?



**Fig. 11** The overall response of **a** litterfall mass, P and N fluxes (by fractions), and **b** wood and leaf fall N and P concentrations to cyclone disturbance.

- How does plant functional composition influence the response and resilience to cyclone disturbance?

- Can we extrapolate the response, resilience, and recovery predictions across the tropics?

# **HIGHLIGHTS & ACKNOWLEDGMENTS**

- Across the tropics, forests on high-P soils were less resistant and resilient to tropical cyclones, at least in the first year post-disturbance.

- Forest recovery after tropical cyclone disturbance was negatively related to soil P concentration.

### Acknowledgments

- U.S. Department of Energy Office of Science, Office of Biological and Environmental Research

- NGEE-Tropics project
- Luquillo LEF-LTER and Critical Zone Observatory
- USDA International Institute of Tropical Forestry (IITF)
- Ariel Lugo, USFS Puerto Rico
- Alonso Ramírez, North Carolina State University
- Whendee Silver, UC Berkeley
- Daniel Imbert, Université des Antilles
- Choy Huang and Hsueh-Ching, National Taiwan University

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### ABSTRACT

Tropical cyclones dominate the disturbance regime experienced by forest ecosystems in many parts of the world. Interactions between cyclone disturbance regimes and nutrient availability strongly influence forest ecosystem dynamics. However, uncertainty exists over the importance of soil fertility properties (i.e., total soil phosphorus-P concentration) in mediating forest resistance and recovery from cyclone disturbance. We hypothesized that forests on soils with low total P (e.g., developed on limited-P parent material) have a higher resistance to but a slower recovery from cyclone disturbance than forests on high P soils. We investigated cyclone impacts on litterfall, an essential conduit for nutrient recycling in forest ecosystems. We compiled site-level forest litterfall data from 56 studies and datasets associated with 15 naturally-occurring and one simulated tropical cyclone in 23 sites within five regions (Taiwan, Australia, Mexico, Hawaii, and the Caribbean) and four cyclone basins. We calculated the effect sizes of cyclone disturbance on the litterfall mass and nutrient (P and nitrogen-N) concentrations and fluxes during the first (< five) years post-disturbance across a total soil P gradient. We also assessed the effect of 20 covariates on the degree of cyclone impact on litterfall. Total litterfall mass flux increased by 4820% following cyclone disturbance. Such an initial increase in litterfall mass reflects the magnitude of cyclone-derived plant material input to the forest floor, which was highest in the Caribbean and lowest in Taiwan. Among 20 covariates, soil P and region were the best predictors of cyclone effects on total litterfall mass, explaining 80% of the variance. The effect sizes increased linearly with soil P and region, from significantly lower in Taiwan (low-P) to largest in the Caribbean (high-P). Total litterfall P and N fluxes increased significantly post-cyclone, whereas the increase in leaf P flux was twice as that in N flux. Results highlight the importance of understanding the interactions between disturbance and nutrient gradients in forest ecosystems to understand forest responses to altered cyclone regimes expected under climate change.



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