

RESEARCH ARTICLE

Linking soil phosphorus with forest litterfall resistance and resilience to cyclone disturbance: A pantropical meta-analysis

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Abstract

While tropical cyclone regimes are shifting with climate change, the mechanisms underpinning the resistance (ability to withstand disturbance-induced change) and resilience (capacity to return to pre-disturbance reference) of tropical forest litterfall to cyclones remain largely unexplored pantropically. Single-site studies in Australia and Hawaii suggest that litterfall on low-phosphorus (P) soils is more resistant and less resilient to cyclones. We conducted a meta-analysis to investigate the pantropical importance of total soil P in mediating forest litterfall resistance and resilience to 22 tropical cyclones. We evaluated cyclone-induced and post-cyclone litterfall mass ($\text{g}/\text{m}^2/\text{day}$), and P and nitrogen (N) fluxes ($\text{mg}/\text{m}^2/\text{day}$) and concentrations (mg/g), all indicators of ecosystem function and essential for nutrient cycling. Across 73 case studies in Australia, Guadeloupe, Hawaii, Mexico, Puerto Rico, and Taiwan, total litterfall mass flux increased from $\sim 2.5 \pm 0.3$ to $22.5 \pm 3 \text{g}/\text{m}^2/\text{day}$ due to cyclones, with large variation among studies. Litterfall P and N fluxes post-cyclone represented $\sim 5\%$ and 10% of the average annual fluxes, respectively. Post-cyclone leaf litterfall N and P concentrations were $21.6 \pm 1.2\%$ and $58.6 \pm 2.3\%$ higher than pre-cyclone means. Mixed-effects models determined that soil P negatively moderated the pantropical litterfall resistance to cyclones, with a $100 \text{mg P}/\text{kg}$ increase in soil P corresponding to a 32% to 38% decrease in resistance. Based on 33% of the resistance case studies, total litterfall mass flux reached pre-disturbance levels within one-year post-disturbance. A GAMM indicated that soil P, gale wind duration and time post-cyclone jointly moderate the short-term resilience of total litterfall, with the nature of the relationship between resilience and soil P contingent on time and wind duration. Across pantropical forests observed to date, our results indicate that litterfall resistance and resilience in the face of intensifying cyclones will be partially determined by total soil P.

KEYWORDS

Biogeochemistry, ecosystem function, hurricane, litterfall, nitrogen, nutrient cycling, soil fertility, typhoon

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1 | INTRODUCTION

Tropical cyclones are pulse disturbances with large global environmental and socio-economic effects (Baade et al., 2007). In 2020, tropical cyclones affected over 36 million people and caused nearly \$56 billion in damages globally (CRED, 2022). By likely becoming more intense (Knutson et al., 2020) and occurring closer to coastal regions (Wang & Toumi, 2021), changing tropical cyclone regimes (Bakkensen & Mendelsohn, 2019; Reed et al., 2020; Wehner et al., 2018) may lead to long-lasting effects on tropical forests under climate change. While the influence of tropical cyclone frequency and intensity on the structure and function of tropical forests have been widely studied (e.g., Everham & Brokaw, 1996; Hogan et al., 2020; Ibañez et al., 2019; Lin et al., 2020; Lugo, 2008; Walker et al., 1996; Zimmerman, Aide, et al., 1995; Zimmerman, Pulliam, et al., 1995), much less attention has been given to the role of resource availability on the functional stability of tropical forests across the globe in the face of cyclone disturbance.

The stability of ecosystems—the set of system properties that determines the magnitude, duration, and reversibility of change resulting from a perturbation (Noy-Meir, 1974; Van Meerbeek et al., 2021)—may be influenced by the availability of limiting nutrient resources (e.g., Lepš et al., 1982; MacGillivray et al., 1995), with nutrient limitation tending to stabilize ecosystem dynamics (DeAngelis et al., 1989). Specific life history and resource allocation traits (e.g., relative growth rate, leaf and twig longevity, antiherbivore defense; Coley et al., 1985; Lavorel & Garnier, 2002) may be universal moderators of the resistance (i.e., the ability to withstand instantaneous disturbance-induced change) and resilience (i.e., the capacity to return to a pre-disturbance reference condition; Van Meerbeek et al., 2021) components of stability in plant communities exposed to disturbances (Lepš et al., 1982). For instance, in herbaceous plant communities of contrasting soil fertility, nutrient stress tolerance correlated positively with resistance and negatively with resilience to frost, drought, and fire disturbance (MacGillivray et al., 1995). Further, the availability of limiting nutrient resources is related strongly to the resistance and resilience of subtropical mangrove (Feller et al., 2015) and tropical forests to cyclone disturbances (Gleason et al., 2008, 2010; Herbert et al., 1999). However, the pantropical importance of nutrient availability to the resistance and resilience of tropical forest litterfall to cyclone disturbances remains unexplored.

Tropical forest productivity can be limited by phosphorus (P) or co-limited by P and multiple other elements (e.g., calcium, potassium, nitrogen) (Kaspari & Powers, 2016; Townsend & Asner, 2013; Vitousek, 1984; Wright, 2019). As a rock-derived element with low atmospheric input (Chadwick et al., 1999; Walker & Syers, 1976), the stock and availability of P may be a moderator of tropical forest resistance and resilience to matter-redistributing disturbances like tropical cyclones. Empirical evidence from a phosphorus fertilization experiment in P-poor forests in Hawaii suggests that cyclone-induced tree defoliation severity increased following

P addition (Herbert et al., 1999). The authors associated the increased leaf stripping with a P-induced increase in leaf area and aerodynamic drag (Jackson et al., 2021), consequently decreasing the wind resistance of leaves compared to co-located unfertilized plots. Evidence from Australia suggests that plant species growing on high-P basalt soils had higher branch breakage after a cyclone than those growing on low-P schist soils—including and excluding nutrient-poor specialists (Gleason et al., 2008). Also, leaf stripping in Australia was significantly lower in low-P soil specialists relative to species occurring on low-P and high-P soils, suggesting strong linkages between cyclone resistance and resilience and plant resource use strategies. The influence of P as a limiting resource on cyclone resistance and resilience may reflect a greater investment of carbon per unit nutrient acquired into structurally robust components (Chapin, 1980) by tropical trees on low-P soils compared to those on high-P soils. Such an allocation strategy allows structural resistance and component longevity, especially for leaves (Reich et al., 1991), while boosting the residence time of P and decreasing long-term costs of acquisition (Bloom et al., 1985). Therefore, further understanding the differential resistance and resilience of tropical forest canopies on soils of contrasting P concentration can lead to more robust predictions of post-cyclone trajectories.

The most immediate effect of tropical cyclones is a rapid redistribution of aboveground litter mass and nutrients (Zimmerman et al., 1996) that alters energy flow and nutrient cycling (Lodge et al., 1994; Ostertag et al., 2003). Hence, cyclone-caused changes in litterfall, an ecosystem function, and crucial nutrient cycling process, provide a valuable basis for quantifying the resistance and resilience components of stability in forest canopies affected by tropical cyclones across the tropics. Besides, litterfall represents a significant proportion of the aboveground net primary productivity (NPP)—e.g., 47% of NPP in tabonuco forests in Puerto Rico (Weaver & Murphy, 1990; Zimmerman, Aide, et al., 1995; Zimmerman, Pulliam, et al., 1995), and strongly relates to forest composition, stature and structure, and soil fertility (Coley et al., 1985; Dent et al., 2006). While an ecosystem's stability, as defined by quantitative metrics, is generally defined in terms of structure and function (Van Meerbeek et al., 2021), only ~2% of studies included in an ecosystem stability review (Donohue et al., 2016) examined the stability of an ecosystem function.

To elucidate the role of soil P in mediating forest litterfall stability in response to tropical cyclones, we conducted a pantropical meta-analysis of litterfall resistance and resilience across sites that varied widely in total soil P concentration to answer: (i) How do litterfall resistance and resilience to cyclone disturbance vary across the tropics? (ii) Does soil P mediate resistance and resilience to cyclones pantropically? (iii) How do soil P, cyclone intensity and regime, and key environmental variables interact to influence resistance and resilience to cyclones pantropically? We expected forests on low-P soils to be more resistant and less resilient to cyclone disturbance than forests on high-P soils (Figure 1), and that this P effect would be modulated by cyclone intensity.

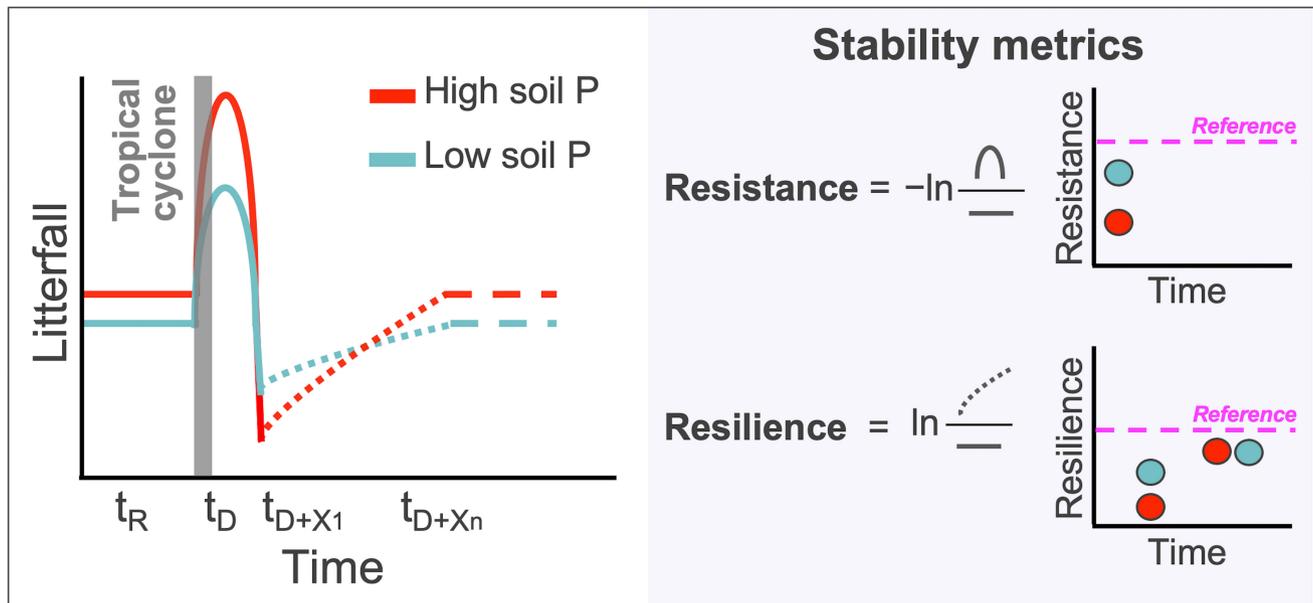


FIGURE 1 Conceptual framework depicting the predictions of reference conditions (pre-cyclone reference litterfall or litterfall_{t_R}), cyclone-induced pulses (litterfall_{t_D}), and post-cyclone trajectories of litterfall (litterfall_{t_D+X_n}) for forests growing on soils with different total phosphorus concentrations (high in red and low in light blue). The stability component of resistance refers to the ability to withstand immediate changes, and resilience refers to the capacity to return to reference values over time following a disturbance. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16223)]

2 | MATERIALS AND METHODS

2.1 | Literature search

We conducted a primary literature search following a systematic review protocol (Moher et al., 2009) to identify publicly available data sets and published articles. To be considered for inclusion within our meta-analysis, published articles and data sets needed to:

1. report forest litterfall (excluding mangrove forests because of the influence of salinity, tidal inundation, redox status, and their effects on litterfall (Day et al., 1996), nutrient availability, plant photosynthetic rates, and nutrient uptake; He et al., 2021; Reef et al., 2010) within the Tropics of Cancer and Capricorn (23.5°N–23.5°S) (note: we made one exception to include a published study from central Taiwan at 23.9°N because of its proximity to the Tropic of Cancer);
2. include twice a month or, in the case of dry forests (Murphy & Lugo, 1986) and dry season sampling, monthly litterfall collection reporting mass or nitrogen (N) and P concentration measurements before and after a cyclone (Tables S1 and S2; Appendix A includes additional details on the few exceptions to this criterion);
3. include the cyclone name to allow for the collection of disturbance variables (Appendix B); and
4. be published in English, Spanish, Portuguese, or French (Nuñez & Amano, 2021) between 1970 and 2019.

Our systematic search identified a total of 27 published articles and data sets (details available in Appendix A) that described

73 case studies—53 related to litterfall mass and 20 related to N and P. Each case study represented a combination of site, treatment, and cyclone disturbance for litterfall mass or nutrients (Tables S1 and S2). The case studies spanned 26 sites representing nine Holdridge life zones across Australia, Guadeloupe, Hawaii, Mexico, Puerto Rico, and Taiwan (Figure 2), and 22 tropical cyclones and one canopy trimming experiment (CTE; El Verde, Puerto Rico; Shiels et al., 2014) occurring between 1977 (cyclone Keith, Australia) and 2017 (cyclones Irma and Maria, Puerto Rico). The compiled data covered four cyclone basins with site-level cyclone frequency between 0.14 and 0.94 per year between 1955 and 2000.

2.2 | Data extraction

Our compiled database was used to quantify litterfall resistance and resilience, and the effects of moderator variables for each case study (Bomfim et al., 2021; details in supporting information Appendix B). We extracted sample sizes (i.e., number of baskets deployed in the forest) and all available pre- and post-disturbance data points to calculate pre-cyclone means and standard deviations of litterfall mass flux ($\text{g m}^{-2} \text{ day}^{-1}$), litterfall N and P flux ($\text{mg m}^{-2} \text{ day}^{-1}$), and N and P concentration (mg g^{-1}) from text, figures, tables, and appendices of the published articles, or directly from the data sets or article authors. We included the total litterfall and the leaf, fine wood (diameter ≤ 2 cm), reproductive (i.e., fruits, flowers, and seeds), and miscellaneous (non-identifiable plant material) fractions whenever available. To extract data from figures, we used the web-based plot digitizing tool *WebPlotDigitizer* version 4.4 (Rohatgi, 2021).

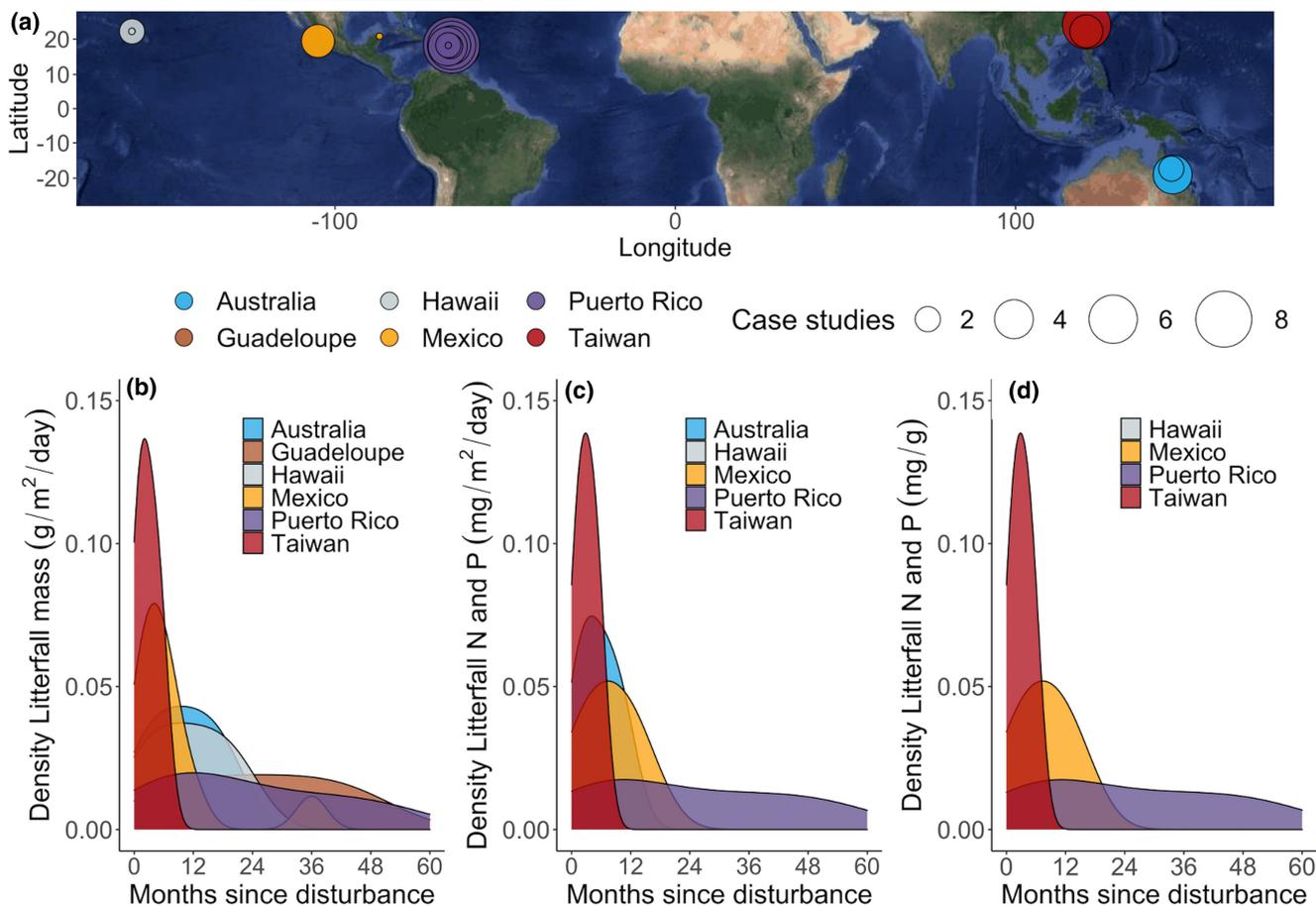


FIGURE 2 (a) Geographical location of the case studies included in this meta-analysis (size of the circle represents the number of case studies per site). Distribution of compiled observations of (b) litterfall mass flux, (c) N and P flux, and (d) N and P concentration by study region and time since cyclone disturbance (in months). Because, in Hawaii, the N and P flux and concentration data are limited to a few observations, the density plots (c) and (d) do not show Hawaii's data distribution. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16223)]

When the published articles did not report pre-disturbance standard deviations, we estimated it as 25% of the mean (Dynarski & Houlton, 2018).

We assembled other case study-level variables and tested 17 of them (Table 1; Appendix B) as effect modifiers (Gurevitch et al., 2018). The retrieved moderators consisted of total soil phosphorus concentration (soil P), soil order and parent material, and lithology (Porder & Ramachandran, 2013). Cyclone variables included peak wind speed and gale wind duration from the HURRECON model (<https://github.com/hurrecon-model/HurreconR>; Boose et al., 1994, 2001, 2004), which used cyclone track data from HURDAT2 and IBTrACS (Knapp et al., 2010). This model does not consider local topography or convective-scale effects such as spiral trainbands but generated site wind speed that is related strongly to wind speed data from the World Meteorological Organization (WMO) and the distance to cyclone track ($R^2 = .84$; Figure S4). Storm frequency represents the number of storms listed in IBTrACS over the 1955–2020 period for the 1° latitude × 1° longitude grid cell (where the site is located) divided by the number of years between 1955 and 2020. While not a precise measure, storm

frequencies are autocorrelated in space across scales (Lugo et al., 2000). This approach assures a reasonable determination of whether the site is located in an area of frequent versus low hurricane disturbance during the last 65 years. Time since the previous storm is the number of years between the cyclone and the last storm detected in the 1°-grid within which the site is located. Cyclone rainfall is the precipitation amount associated with the cyclone extracted from the original article or NOAA's cyclone report.

To account for large-scale differences in biogeography and consider possible correlations between biogeography and cyclone resistance (Griffith et al., 2008, 2013) and resilience (e.g., Cole et al., 2014), we assembled site elevation, longitude, latitude, and geographic region information. Other moderators included forest type as described in the original article and according to the Holdridge life zone classification (Holdridge, 1947); nutrient or biomass treatment (ambient conditions, full or element-specific fertilization, or debris removal); and climate (mean annual temperature and precipitation). We also compiled information on time since the cyclone occurred for each case study and associated data points. Time since the cyclone ranged from 0.5 to 60

TABLE 1 Summary of the site- and cyclone-level explanatory variables used as moderators of the resistance and resilience of litterfall mass flux ($\text{g}/\text{m}^2/\text{day}$) to cyclone disturbance across the tropics

Variable	Unit	Range
Total soil phosphorus (0–20 cm)	mg P kg^{-1} dry soil	20–2400
Soil order (USDA taxonomy)	Categorical with 7 levels	Alfisol, Andisol, Inceptisol, Entisol, Mollisol, Ultisol, and Oxisol
Soil parent material	Categorical with 14 levels	Acid volcanic, Basalt, Granite, HA Volcaniclastic, Hengchun Limestone, Limestone, Metamorphic schist, Noncarbonate sedimentary, Residuum Coluvium Volcanic, Quartzitic sandstone, Rhyolitic rhyodacitic volcanic, Volcanic ash, Volcanic siltstone, and Volcaniclastic
Geological group	Categorical with 6 levels	Acid volcanic, Basalt, Basic Intermediate Volcanic, Shale, Sandstone, and Carbonate
Phosphorus class of geological group	Categorical with 3 levels	Low, Intermediate, and High
WMO wind speed ^a	m s^{-1}	11.3–77.2
Distance from site to cyclone track ^a	km	3–177
Peak wind speed ^b	m s^{-1}	18–63
Gale wind duration ^b	minutes	80–6040
Time since the previous storm	Years	0.03–12.1
Storm frequency	Storms year^{-1}	0.14–0.94
Cyclone rainfall	mm	10–860
Site longitude	Decimal degrees	–159.72–146.17
Elevation	m	60–1134
Holdridge life zone	Categorical with 9 levels	Subtropical dry, Subtropical lower montane rain, Subtropical lower montane wet, Subtropical lower montane moist, Subtropical moist, Subtropical premontane dry, Subtropical wet, Tropical dry, and Tropical moist
MAT/MAP ^c	$^{\circ}\text{C}/\text{mm} \times 100$	0.4–3.2
Treatment	Categorical with 6 levels	Ambient, debris removal, full fertilization, N fertilization, P fertilization, and N + P fertilization
Time since cyclone	Months	1–36

^aSite-level WMO wind speed was compiled from IBTrACS (Knapp et al., 2010), and the distance from the site to the point in the cyclone track where the WMO wind speed was obtained.

^bSite-level peak wind speed and gale wind duration were obtained from the HURRECON model (Boose et al., 1994, 2004).

^cMean annual temperature to precipitation ratio multiplied by 100.

months, with most data concentrated within 21 months post-disturbance (Figure 2b–d).

2.3 | Resistance and resilience calculations

We recorded individual case studies in our database because individual published articles and data sets often reported more than one site, treatment, or cyclone (Tables S1 and S2). We calculated the cyclone effect sizes (Hedges et al., 1999) for each case study (i.e., a unique combination of site, cyclone and treatment in the case of studies with more than one treatment) using the following stability metrics: resistance (r_r) = $\ln(\text{mean litterfall}_{t_D}/\text{mean litterfall}_{t_R})$ and resilience (r_s) = $\ln(\text{mean litterfall}_{t_{D+x}}/\text{mean litterfall}_{t_R})$, where t_D is the litter-basket collection time immediately following the cyclone, t_R is the mean of all available pre-disturbance or reference period measurements, and t_{D+x} is a post-disturbance time point (Figure 1). The resistance reflects the cyclone-induced change in litterfall mass

flux (originally in $\text{g m}^2 \text{day}^{-1}$), N and P flux (originally in $\text{mg m}^2 \text{day}^{-1}$) and N and P concentration (originally in mg g^{-1}) at a single point in time, while the resilience varies with time post-cyclone. Due to limitations in data reporting, our resilience metric was calculated following Lloret et al. (2011), is not a return rate post-perturbation, and has been characterized as a “recovery” metric by others (e.g., Ibáñez et al., 2019), as explained in Van Meerbeek et al. (2021).

To calculate the resistance, we included case studies (48 out of 73 from 27 publications) reporting post-cyclone litterfall data within two weeks post-cyclone (Tables S1 and S2). Because litterfall mass flux varies seasonally (e.g., Dent et al., 2006), we considered two resistance calculations with alternate pre-disturbance reference periods: (a) a mean of all available pre-disturbance litterfall observations ($N = 48$ total litterfall mass flux case studies); and (b) a month-specific pre-disturbance mean ($N = 22$ case studies as 26 did not report sub-annual means) (Figure S1). We used this approach to assess the effect of seasonality on the pantropical resilience of total litterfall mass flux (Figure S2).

We calculated the resilience only for case studies reporting litterfall mass flux, N and P flux, and N and P concentration more than two weeks following the cyclone (Tables S1 and S2). We considered resilience as the capacity of litterfall to return to pre-disturbance levels (Pimm, 1984), excluding the initial post-cyclone observations used in the resistance calculations (Lloret et al., 2011). Because most of the pantropical data were concentrated within the first 21 months post-disturbance (Figure 2b–d), we analyzed data for this time frame. We grouped the observations based on time since cyclone, with one-month groups of post-disturbance litterfall mass flux data and two-month groups for N and P.

We used the *pcurve* function (package *dmatar*) to detect “p-hacking” and article publication bias—driven by publication-bias for statistically significant results (Nakagawa & Santos, 2012; Simonsohn et al., 2014). We conducted bias detection for all individual resistance and resilience effect sizes and sampling variances (Tables S3–S7). We found evidence for true effect sizes in the resistance and resilience data.

2.4 | Statistical analysis

We analyzed data and created plots in R (version 3.6.2; R Core Team, 2019), using packages *ggplot2* (Wickham, 2016) for all plots and *ggmap* (Kahle & Wickham, 2013) for Figure 2.

This meta-analysis (Gurevitch et al., 2018) consisted of three parts. First, we calculated the individual resistance and resilience effect sizes and the corresponding sampling variances (*escalc* function in package *metafor*) to standardize data across case studies (Hedges et al., 1999; Lajeunesse, 2011; Pappalardo et al., 2020; Viechtbauer, 2010, 2015). During this step, we calculated the resistance effect size (hereafter resistance) of total litterfall and leaf, fine wood, reproductive, and miscellaneous mass flux reported within two weeks post-cyclone (originally in $\text{gm}^{-2} \text{day}^{-1}$). We calculated the P and N flux (originally in $\text{mgm}^{-2} \text{day}^{-1}$) and concentration (originally in mgg^{-1}) resistance of total litterfall and litterfall fractions. We calculated the mass flux, P and N flux and concentration resilience effect size (hereafter resilience) of total litterfall and fractions at multiple time points following the cyclone.

2.4.1 | Random-effects meta-analysis

Second, we applied multilevel random-effects meta-analysis models (*rma.mv* function) to estimate the pantropical effect of cyclones on litterfall (Fernández-Castilla et al., 2020), using the Knapp–Hartung adjustment (Higgins & Thompson, 2004; Knapp & Hartung, 2003) to decrease risk of type 1-errors (Assink & Wibbelink, 2016) and the restricted maximum likelihood (REML) estimator (Konstantopoulos, 2011). To minimize a dependency of effect sizes induced by a multilevel data structure (Assink & Wibbelink, 2016), the models considered sampling variability of

the observations as the first level, and site and cyclone as crossed random effects as the second level ($\sim 1|\text{Site}$, $\sim 1|\text{Cyclone}$) (Harrison et al., 2018). We calculated the pantropical resistance of litterfall mass flux, N and P flux (total and fractions), and N and P concentration in leaf and wood litterfall, as explained above. We included a random effect for site in the final meta-analysis model for wood N and P concentration as informed by a likelihood-ratio test for the significance of the between-site variance (Assink & Wibbelink, 2016).

We calculated the pantropical resilience of mass, N, and P flux of total litterfall and litterfall fractions, and leaf and wood litterfall N and P concentration considering non-independent effect sizes (Cheung, 2019; Nakagawa & Santos, 2012). We divided the data to analyze effect sizes under ambient (i.e., non-manipulated) conditions, including and excluding the CTE data to verify its influence on the results. We used the *rma.mv* function in an intercept-only model, with an autoregressive variance structure in the random argument to consider temporal autocorrelation, and included site and cyclone as crossed random effects ($\sim 1|\text{Site}$, $\sim 1|\text{Cyclone}$) to calculate the pantropical resilience over the first 21 months post-cyclone. Model estimates are presented in the text as percentages for clarity.

2.4.2 | Meta-analytic random forests for exploratory moderator selection

Third, we used the random forest algorithm for meta-analysis (<https://github.com/cjvanlissa/metaforest>; MetaForest R package; Van Lissa, 2017, 2020) to explore the moderating effect of soil P and 16 covariates on the between-case study heterogeneity (Grueber et al., 2011; Schielzeth, 2010) in the resistance (ambient conditions only) and resilience (ambient conditions with and without CTE), for total and leaf litterfall mass flux. This non-parametric random forest analysis ranks moderators based on their influence on the effect size through bootstrap sampling. It is, by design, inclusive to understand the relative importance of all moderators for which we had data. This approach allowed us to identify the moderators contributing to the final model's predictive power across (non-)linear and interaction effects. We standardized all continuous moderators by subtracting the mean and dividing by two standard deviations so that the estimated coefficients were unitless and directly comparable to untransformed categorical moderators (Gelman, 2008). We included all observations between 1 and 21 months for total and leaf litterfall mass flux resilience. We used Hugo disturbance wind data for the CTE because this experiment considered the patchiness of altered forest canopies created by Hugo in El Verde (Brokaw & Grear, 1991; Shiels et al., 2014). To understand the influence of the resistance on the resilience, we included the former as a moderator in resilience random forests run for case studies that also reported the immediate cyclone impact. The full syntax of all meta-forest analyses is available at <https://github.com/bdbomfim/Pantropical-MetaAnalysis-Cyclones>.

2.4.3 | Mixed-effects meta-analysis

Finally, to test the effect of soil P on cyclone resistance, we fit linear mixed-effects meta-analysis models including soil P as a moderator of total and leaf litterfall mass flux resistance (Nakagawa & Santos, 2012). To test whether cyclone regime and intensity and environmental factors interact with soil P in moderating cyclone resistance across case studies, we further added the most important continuous and categorical moderators, as revealed by the random forest analysis. We only included moderators that were uncorrelated (Pearson's $r < .4$; Dormann et al., 2013). We checked the omnibus test of moderators to assess the null hypothesis that all coefficients except the intercept were simultaneously zero (Viechtbauer, 2010) and Cochran's Q (Q_E) to assess the significance of residual heterogeneity (e.g., Harrison, 2011). We considered effects significant at the 95% confidence level. We estimated the coefficient of determination (R^2) as $(\text{sum of random-effects model } \sigma^2 - (\text{sum of model P } \sigma^2)) / \text{sum of random-effects model } \sigma^2$, where random-effects model is that fit to calculate the pantropical resistance of litterfall mass flux including only random effects, model P is the mixed-effects model including soil P as the single moderator (Table 2, model 1a), and σ^2 is the variance (Harrer et al., 2021).

In all meta-analysis models, we ran sensitivity analyses to test the influence of case studies where total soil P could only be obtained through a fixed estimate from the available soil P concentration (Appendix B, Table B3). We tested the influence of the Milolii, Makaha 1, Halemanu, and Kumuwela case studies where the pre-cyclone litterfall mean was not included in the published article but obtained from a prior study conducted in these sites (Appendix A), and the influence of Puerto Rico case studies on the pantropical litterfall resistance and the moderator effect of soil P on resistance (Table S8).

To test the effect of soil P, cyclone regime and intensity, and environmental factors on the resilience of total and leaf litterfall mass flux, we fit mixed-effects generalized additive mixed models (GAMMs) (Bates et al., 2015; Wood, 2004) including the weights generated in random-effects meta-analysis models. The weights (w_i) were calculated as $w_i = 1 / (\sigma_1^2 + \sigma_2^2 + v_i)$, where σ^2 is the heterogeneity from the random effects and v_i is the sampling variance (Konstantopoulos, 2011). We fit several GAMMs with different combinations of fixed effects using maximum likelihood estimation, which allows comparison of models using Akaike information criterion corrected for finite sample size (AICc) (e.g., Walker et al., 2019). Once the fixed-effects terms were selected according to the minimum adequate model (lowest AICc using the *AICcmodavg* package; Mazerolle, 2020), GAMMs with the same fixed effects but different random effects (site and cyclone as sole or crossed random effects) were fit using REML parameter estimates. The GAMMs were fit to total and leaf litterfall mass flux under ambient conditions, including and excluding the CTE data to detect differences. Random effects were site and cyclone disturbance, and fixed effects were soil P, time since cyclone and

wind duration for total litterfall, and time since cyclone and wind speed for leaf litterfall.

To test the influence of the resistance on the resilience of total litterfall when litterfall returned to the reference value (in two-month groups due to limitation in the number of observations), we ran mixed-effects meta-analysis models including resistance as a random and soil P as a fixed effect.

3 | RESULTS

3.1 | Pantropical resistance of forest litterfall mass to cyclone disturbance

The meta-analysis model including crossed random effects for site and cyclone revealed a significant overall positive effect of cyclones on total litterfall mass flux, with significant heterogeneity across case studies ($Q = 22,881.6$, p -value $< .001$). The model estimated a mean pantropical increase in litterfall by $901 \pm 57\%$ (standard error; t -value = 5.1, p -value $< .001$; Figure 3a) due to cyclones, from -2.5 ± 0.3 to $22.5 \pm 3 \text{ g/m}^2/\text{day}$. This estimate of the cyclone-induced litter flux was calculated relative to a pre-disturbance mean including all available pre-cyclone data points (from three months to multiple years) rather than the typical litterfall mass flux during the month of the cyclone event (which was less available). We found no difference in the pantropical increase in litterfall by excluding the four sites in Hawaii where pre-cyclone means were retrieved from an earlier study in the same sites (Scowcroft, 1986), or when a random subset of Puerto Rico case studies is removed (Table S8). When we considered the typical litterfall mass flux when the cyclone occurred, where measurements were available, we found no difference between resistances calculated with annual versus sub-annual pre-disturbance means (Figure S1).

The individual mass flux resistances varied from a minor change in Taiwan with Haima to an instantaneous flux that was ~ 2 times the annual input in Bisley, Puerto Rico with Irma (Figure 3a). Of the 18 case studies whose litterfall mass flux resistance fell below the pantropical mean, 15 were in Puerto Rico. Among Puerto Rico case studies, 79% were lower than the pantropical resistance. By contrast, all cyclone resistances in Taiwan were above the pantropical resistance. Australia's resistances showed considerable variation in magnitude, from a small increase in Birthday creek to over 15,000% increase ($\sim 41\%$ the annual input in $\text{g/m}^2/\text{year}$) in Wooroonooran on soil derived from schist and 16,000% (45% the annual input in $\text{g/m}^2/\text{year}$) on basalt-derived soil. Finally, in Chamela-Cuixmala (Mexico) and all sites in Hawaii, the change in litterfall following cyclones Jova, Patricia, and Iniki were within the pantropical confidence interval.

We found a large variation in pantropical cyclone resistances across biomass components (Figure 3b). Overall, the mass flux of wood increased by $4067 \pm 76\%$, from ~ 0.92 to $37.4 \text{ g/m}^2/\text{day}$, followed by $830.9 \pm 77\%$ in leaf (-1.85 to $15.4 \text{ g/m}^2/\text{day}$), $1029 \pm 202\%$

TABLE 2 Results of the mixed-effects meta-analysis models for the pantropical resistance of total litterfall and leaf litterfall mass flux to cyclones, including crossed random effects for site and cyclone disturbance. Models 1a and 1b include total soil P concentration as the single moderator, and models 2a and 2b include total soil P concentration and wind speed as moderators

Total litterfall mass flux				Leaf litterfall mass flux			
Model 1a (N = 48 case studies) $R^2 = .33$							
Random effect	Estimate	Sqrt	Levels	Random effect	Estimate	Sqrt	Levels
Site	0.70	0.84	24	Site	1.38	1.17	18
Cyclone	3.69	1.92	19	Cyclone	2.26	1.50	14
Test of moderators Q_M : p -value < .0001							
	Estimate	SE	t	p-value	CI	SE	t
Intercept	-2.28	0.50	-4.57	<.0001	-3.28 to -1.27	0.46	-4.26
Soil P	-1.67	0.07	-22.7	<.0001	-1.78 to -1.49	0.74	-1.18
Model 2a (N = 45 case studies ^a) $R^2 = .39$							
Random effect	Estimate	Sqrt	Levels	Random effect	Estimate	Sqrt	Levels
Site	1.22	1.10	23	Site	1.46	1.81	18
Cyclone	1.05	1.03	17	Cyclone	2.67	1.63	14
Test of moderators Q_M : p -value < .001							
	Estimate	SE	t	p-value	CI	SE	t
Intercept	-3.07	0.39	-7.91	<.001	-3.85 to -2.28	0.60	-3.60
Soil P	-1.97	0.23	-8.47	<.001	-2.44 to -1.50	0.95	-0.27
Wind speed	-1.71	0.55	-3.13	.003	-2.81 to -0.6	0.88	-1.03
Soil P:Wind speed	-2.40	1.75	-1.37	.18	-5.94 to -1.14	2.11	-0.93
Model 1b (N = 30 case studies) $R^2 = .05$							
Random effect	Estimate	Sqrt	Levels	Random effect	Estimate	Sqrt	Levels
Site	0.70	0.84	24	Site	1.38	1.17	18
Cyclone	3.69	1.92	19	Cyclone	2.26	1.50	14
Test of moderators Q_M : p -value = .25							
	Estimate	SE	t	p-value	CI	SE	t
Intercept	-2.28	0.50	-4.57	<.0001	-3.28 to -1.27	0.46	-4.26
Soil P	-1.67	0.07	-22.7	<.0001	-1.78 to -1.49	0.74	-1.18
Model 2b (N = 30 case studies ^a) $R^2 = .01$							
Random effect	Estimate	Sqrt	Levels	Random effect	Estimate	Sqrt	Levels
Site	1.22	1.10	23	Site	1.46	1.81	18
Cyclone	1.05	1.03	17	Cyclone	2.67	1.63	14
Test of moderators Q_M : p -value = .47							
	Estimate	SE	t	p-value	CI	SE	t
Intercept	-2.28	0.50	-4.57	<.0001	-3.28 to -1.27	0.46	-4.26
Soil P	-1.67	0.07	-22.7	<.0001	-1.78 to -1.49	0.74	-1.18

Note: The site-level moderator variables soil P and wind speed were standardized as explained in the Statistical Analysis section. Bold values denote significance at the 95% confidence level.

^aModels 2a and 2b included all case studies where site-level HURRECON-derived wind data was available. CI is the confidence interval.

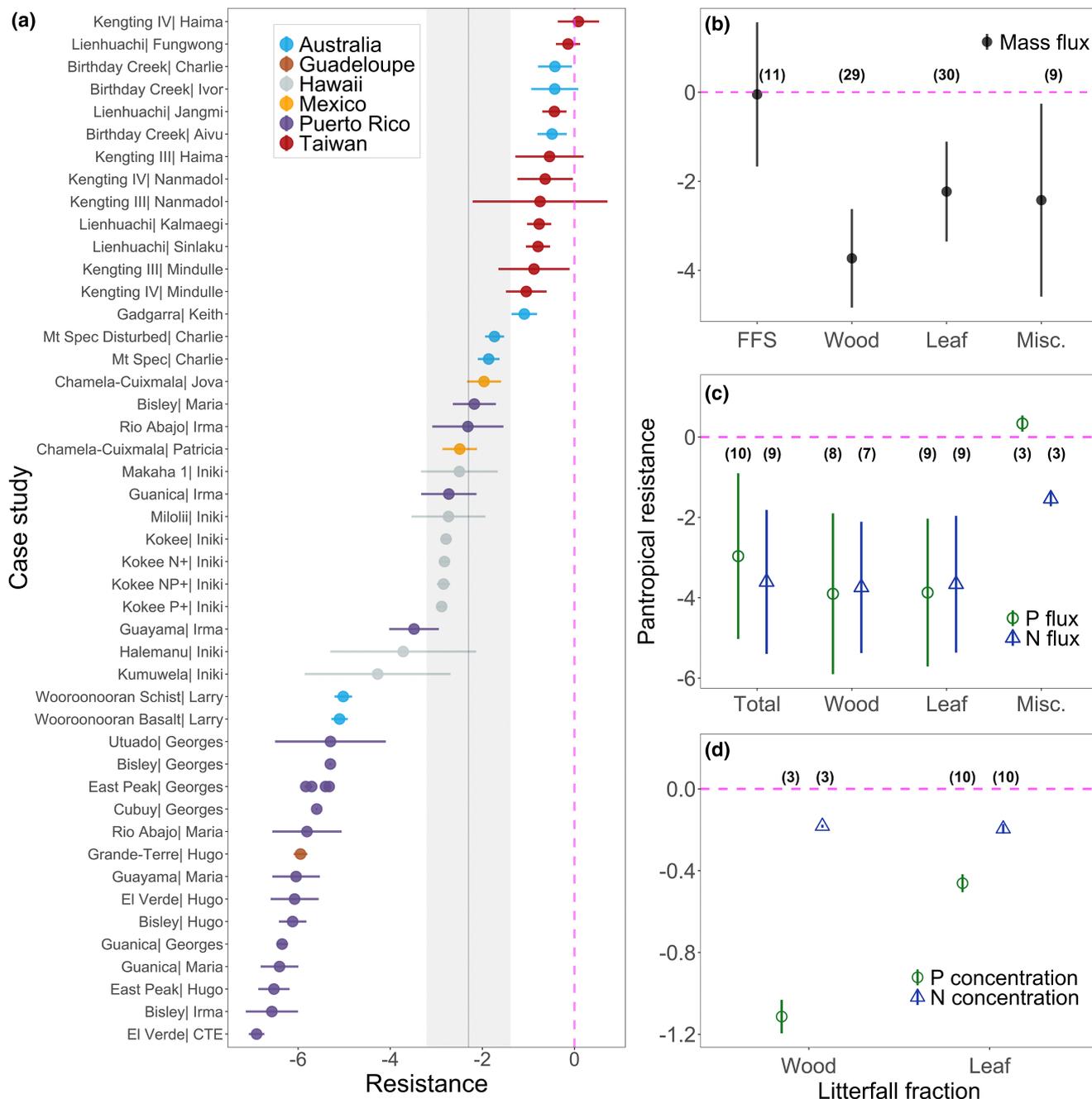


FIGURE 3 (a) Total litterfall mass flux resistance [x-axis; in $\ln(\text{litterfall}_{\text{TD}}/\text{litterfall}_{\text{TR}})$], originally in $\text{g}/\text{m}^2/\text{day}$, to cyclone disturbance with 95% confidence interval for each case study (y-axis; site|cyclone; $N = 48$ case studies). The gray vertical line is the pantropical resistance (weighted overall effect size), and the shaded area is the 95% confidence interval. The four points in East Peak|Georges represent distinct forest patches in that site; Kokee N+, NP+, and P+ denote fertilized plots with the respective element additions. El Verde|CTE is the trimming + debris addition treatment (not included in the pantropical mean calculation). Pantropical resistances with 95% confidence interval [y-axes; in $\ln(\text{litterfall}_{\text{TD}}/\text{litterfall}_{\text{TR}})$] of (b) reproductive (FFS denotes fruits, flowers, and seeds), fine wood, leaf, and miscellaneous litterfall mass flux, (c) P and N flux (originally in $\text{mg}/\text{m}^2/\text{day}$) in total litterfall and fine wood, leaf, and miscellaneous litterfall fractions, (d) and wood and leaf litterfall P and N concentrations (originally in mg/g). All magenta dashed lines indicate the pre-disturbance reference, and numbers in parentheses in (b)–(d) are the number of case studies included in each pantropical resistance. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

in miscellaneous (unidentified plant material), and little change in reproductive material litterfall following cyclones. These values did not differ from the month-specific resistances (i.e., utilizing month-specific pre-disturbance mean, as explained in Section 2.3), except for the miscellaneous fraction (Figure S1).

3.2 | Pantropical resistance of litterfall nutrients

The pantropical resistances of P and N flux were large and significant for total litterfall and fine wood and leaf fractions (Figure 3c). Total litterfall P flux increased by $1838 \pm 186\%$, representing an

instantaneous cyclone-caused input ~5% of the average annual flux of ~3.4 kg P/ha/year. P flux via leaf litterfall increased by $4700 \pm 156\%$, and wood litterfall by $4846 \pm 177\%$, representing an input of approximately 13% of the average annual flux of ~1.75 and ~0.5 kg P/ha/year, respectively. Total litterfall N flux increased by $3588 \pm 149\%$, representing ~10% of the average annual flux of ~84 kg N/ha/year. N flux via leaf litterfall increased by $3800 \pm 138\%$, representing nearly 10% of the average annual flux of 58.9 kg N/ha/year, which was a little smaller than the increase by $4123 \pm 130\%$ via fine wood litterfall, or ~11% of the annual flux of 11.2 kg N/ha/year.

These large changes in N and P fluxes reflected the increase in litterfall mass and N and P concentration (Figure 3d), as the cyclone-induced increase in total P flux was 1.3 and in total N flux 1.1 times higher than that in total mass flux, considering the same case studies ($N = 9$). Overall, cyclone-induced leaf and wood litterfall P concentrations were, respectively, $58.6 \pm 2.3\%$ and $204.5 \pm 4.3\%$ higher than the mean reference values. N concentration was $21.6 \pm 1.2\%$ and $20 \pm 0.4\%$ higher in leaf and wood litterfall after cyclone disturbance relative to the pre-disturbance means.

3.3 | Moderators of litterfall mass resistance to cyclone disturbance

We used random forest models to explore the importance of soil P and 16 other moderators of the total and leaf litterfall mass flux resistance to cyclones. Out of the final 14 moderator variables (distributions shown in Figure S3), HURRECON-derived site wind speed showed the highest importance in explaining the resistance of total litterfall (Figure 4a) and second-highest for leaf litterfall mass flux (Figure 4b). Soil P had higher importance for leaf than total litterfall and had weak and no correlation with wind speed in each data subset, respectively (Figure 4c,d). For the case studies of total litterfall resistance, wind speed correlated significantly with storm frequency ($r = -0.53$) and longitude ($r = -0.71$).

The mixed-effects meta-analysis model indicated that soil P had a significant negative effect on cyclone resistance of total litterfall ($R^2 = .33$; Table 2, model 1a). By reversing the moderator standardization, we found that for a total soil P increase of 100 mg P/kg, resistance drops by 32%. This soil P effect remained significant when the five sites with total soil P estimated from the available P pool were removed (Table S9). The effect of soil P on leaf litterfall resistance to cyclones was not significant (Table 2, model 1b; Table S9).

The mixed-effects meta-analysis model with wind speed and soil P indicated that both negatively affected litterfall mass resistances pantropically, and predicts that a 100 mg P/kg increase corresponds to a 38.2% decrease in resistance ($R^2 = .39$; Table 2, model 2a; Figure 5a). This effect was also observed when the five sites with estimated total soil P were removed from the analysis, although a significant interaction between soil P and wind speed emerged (Table S9, model 2a). The same model fit for leaf litterfall indicated a non-significant effect of wind speed on cyclone resistances (Table 2, model 2b; Figure 5b). However, when the same five sites were

removed, a significant negative interactive effect of soil P and wind speed on leaf litterfall resistance emerged (Table S9, model 1b).

3.4 | Pantropical cyclone resilience of litterfall mass

Only 33% (16 out of 48) of the case studies included in the resistance analysis contained pre- and post-cyclone litterfall mass flux observations that allowed us to calculate resilience trajectories. Litterfall mass flux resilience varied over time, with similar temporal trends among fractions (Figure 6a-d; Table S10). The random-effects meta-analysis models revealed that litterfall mass flux (total and each fraction) reached pre-disturbance levels within the first year after the disturbance. Total litterfall mass flux resilience reached a minimum of $65 \pm 28\%$ below the reference five months post-disturbance. Leaf litterfall mass reached a minimum of $70 \pm 54\%$ below the reference one-month post-cyclone and showed a consistent increase until 21 months post-cyclone. Wood litterfall reached a minimum of $70.5 \pm 128\%$ lower than the reference three months post-cyclone and varied widely across the tropics and through time. The reproductive litterfall resilience was reported in very few case studies. Still, it showed a similar pattern over the same period, returning from 76.4 ± 58 below the reference one-month post-cyclone to the reference level within 12 months.

3.5 | Pantropical cyclone resilience of litterfall nutrients

The pantropical total litterfall P and N fluxes were $76.9 \pm 4.0\%$ and $66.8 \pm 2.4\%$ below the reference level during the first two months after the cyclone, respectively (Figure 7a,b; Table S11). The resilience trajectories for both nutrient fluxes were similar. While N and P flux mainly remained below the reference during the first months after the cyclone, P concentration in leaf litterfall mainly remained above the reference during that period (Figure 7c,d; Table S11).

The random-effects models fit for leaf litterfall N and P concentration indicated that both were significantly positively affected by cyclones during the first-year post-disturbance. P concentration in the leaf fraction peaked at $69.4 \pm 2.8\%$ above the reference between three and four months after the disturbance. Leaf litterfall N concentration peaked at $19.2 \pm 2.1\%$ above the reference between five six-months post-cyclone.

3.6 | Moderators of the pantropical resilience of litterfall mass flux to cyclones

The random forest models indicated that gale wind duration and time since cyclone were the moderators with the highest permutation importance for total litterfall. Time since cyclone and wind speed were the strongest moderators of leaf litterfall mass resilience

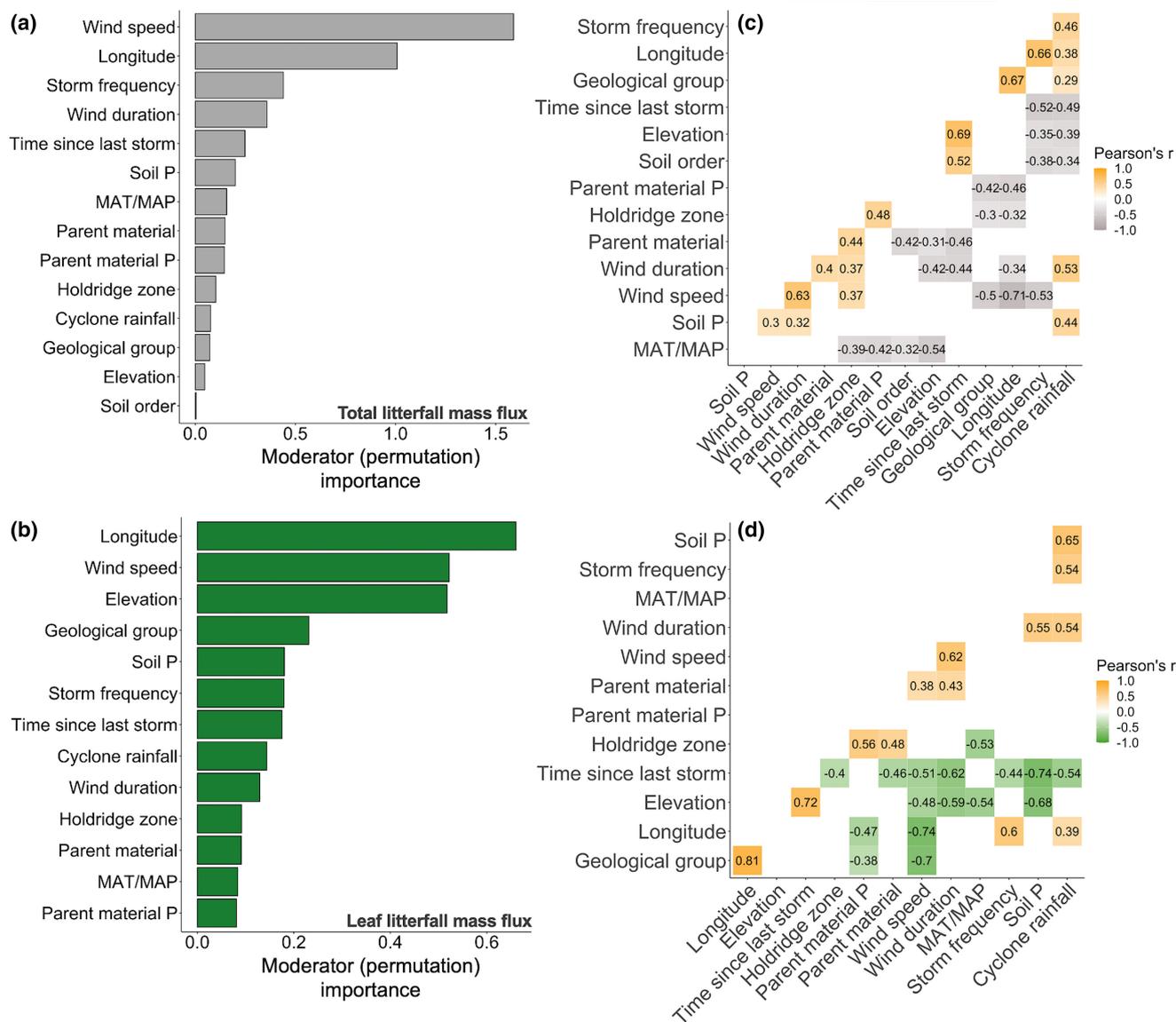


FIGURE 4 Moderator importance from the random forest models predicting cyclone resistance [$\ln(\text{litterfall}_{\text{LD}}/\text{litterfall}_{\text{TR}})$] of (a) total litterfall ($N = 45$ case studies, estimate of predictive performance or $R^2_{\text{Oob}} = .45$, predictive performance or $R^2_{\text{cv}} = .5$) and (b) leaf litterfall mass flux ($N = 30$ case studies, $R^2_{\text{Oob}} = .20$, $R^2_{\text{cv}} = .74$). Moderator (permutation) importance measures how strongly each moderator explains differences in effect size, capturing (non-)linear relationships and higher-order interactions. Pearson's correlation coefficients among the moderator variables included in the final random forest model for (c) total litterfall and (d) leaf litterfall mass flux, where blank squares indicate lack of correlation at the 95% confidence level. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16223)]

(Figure 8a,b). Soil P was more important for total litterfall relative to leaf litterfall mass resilience; distinguishing soil P from cyclone intensity effects on leaf litterfall resilience was challenged by the collinearity of variables ($r > .7$; Figure S5b). Moderator importance rankings and correlations among moderators did not change when the canopy trimming experiment (CTE) data were excluded (Figures S5 and S6). The resistance was an important moderator of the total litterfall resilience (Figure S7a), but not as much for leaf litterfall (Figure S7b), considering the case studies where the resistance could be calculated (86% of total litterfall and 84% of leaf litterfall case studies).

Based on the results of the random forest models, we fit GAMMs to test the influence of total soil P and top-ranked moderator

variables on total and leaf litterfall mass flux resilience (1–21 months post-disturbance). The GAMM fit for total litterfall indicated a significant joint effect of total soil P and time since the cyclone on the short-term resilience ($R^2 = .25$; Table 3, model 1a). At 12 months, an increase in soil P from the median (291 mg P/kg) to the 75th percentile (330 mg P/kg) yields a decrease in resilience by 23%, from -0.43 to -0.53 ; this trend was consistent within the first-year post-cyclone (Figure S8a). Forty percent of the variability in total litterfall resilience was explained by an interaction between the joint effect of soil P and time since cyclone with gale wind duration (Table 3, model 2a; Figure 9). At low (25th percentile) gale wind duration, resilience increased with soil P for the first ~ 9 months, but at higher gale wind duration (75th percentile) resilience declined with increasing soil P in

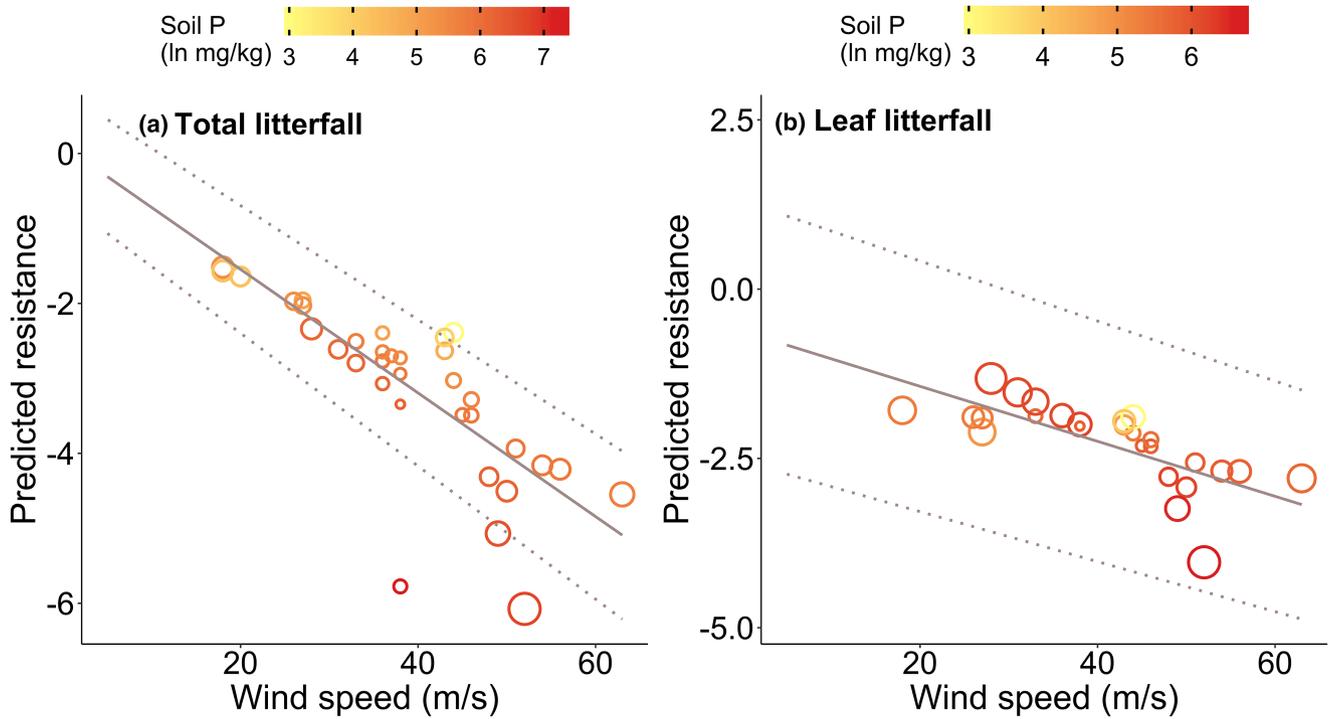


FIGURE 5 Predictions of (a) total ($N = 45$ case studies) and (b) leaf litterfall mass flux ($N = 30$ case studies) resistances [y-axes; in $\ln(\text{litterfall}_{\text{D}}/\text{litterfall}_{\text{R}})$] to cyclones across the tropics based on site-level wind speed and total soil P (ln mg P kg^{-1} soil). Point sizes are proportional to the standard error of the predictions. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16223)]

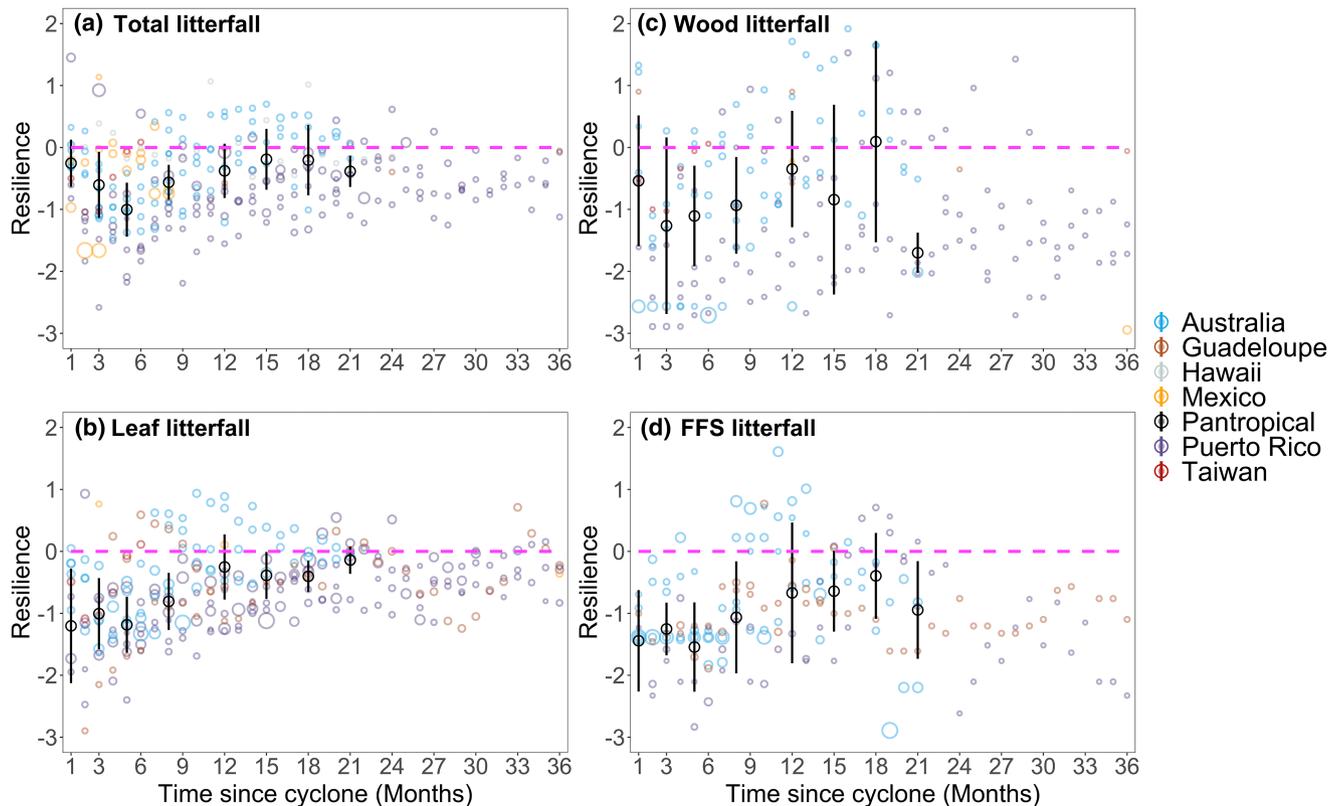


FIGURE 6 Resilience [y-axes; in $\ln(\text{litterfall}_{\text{D}+\text{x}}/\text{litterfall}_{\text{R}})$] of (a) total, (b) leaf, (c) wood, and (d) fruits, flowers and seeds litterfall mass flux to cyclone disturbance over the first 36 months post-cyclone (x-axes; in months). Points represent observed effect sizes colored by region (shown in the legend). Black points and lines are the pantropical resilience with 95% confidence intervals calculated for specific time points. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16223)]

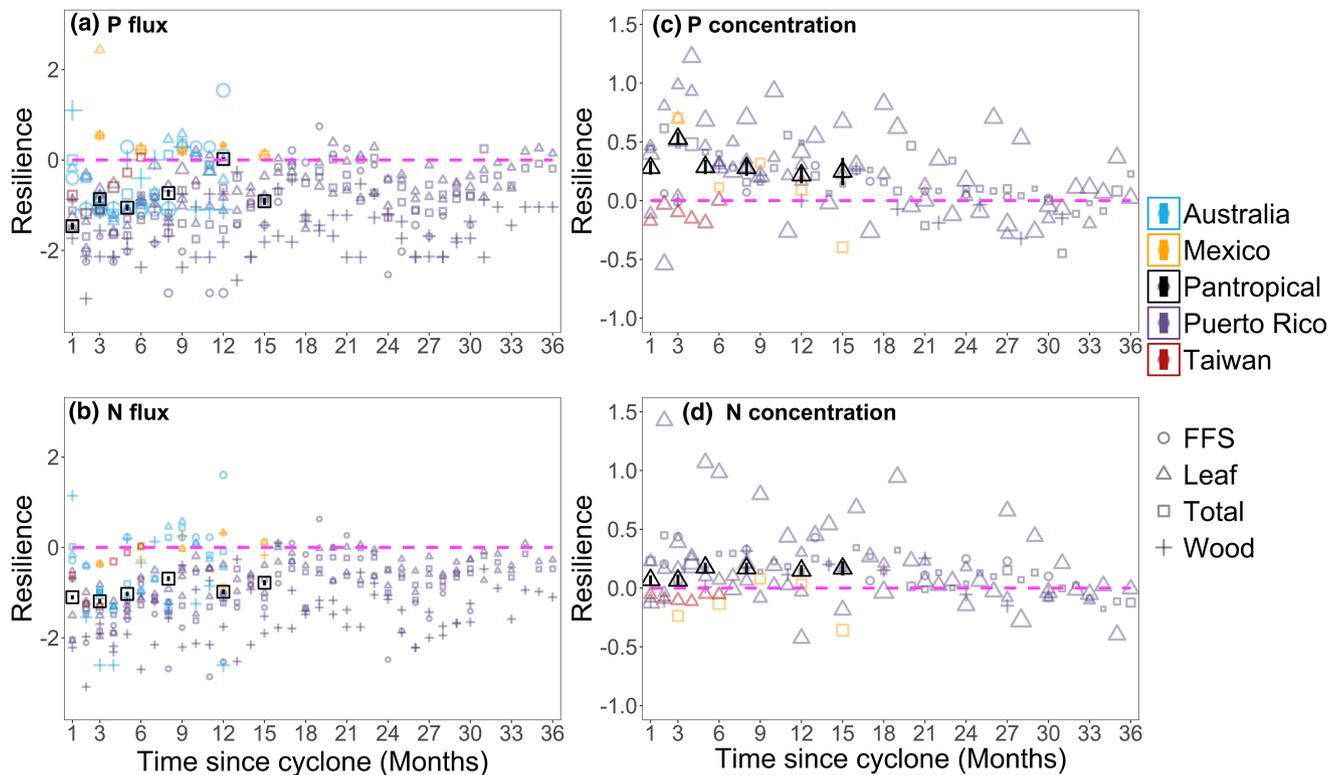


FIGURE 7 Cyclone resilience [y-axes; in $\ln(\text{litterfall}_{\text{TD}+\text{x}}/\text{litterfall}_{\text{TR}})$] of litterfall (a) P and (b) N fluxes (originally in $\text{mg}/\text{m}^2/\text{day}$), and (c) P and (d) N concentrations (originally in mg/g) with time since cyclone disturbance (in months). Points represent the observed resilience colored by region. Black shapes and lines are the pantropical resilience with 95% confidence intervals calculated for specific time points. Pantropical resilience in (a)–(b) represents total litterfall P and N flux, respectively, and in (c)–(d) leaf litterfall P and N concentration, respectively. In all panels, shapes represent total litterfall and each litterfall fraction, where FFS denotes the reproductive (fruits, flowers, and seeds) fraction. [Colour figure can be viewed at wileyonlinelibrary.com]

this initial period post-storm (Figure S8b,c). By 12 months, the effect of soil P was diminished, and at 15 months was reversed. A GAMM fit for leaf litterfall including only a joint effect of soil P and time since cyclone explained 34% in the variability (Table 3, model 1b). Due to the high correlation between total soil P and wind speed for this subset of the resilience data (Figure S5c), we fit a model with only wind speed and time since cyclone, which explained 46% of the variability in leaf litterfall resilience (Table 3, model 2b). Including only observations at 1-year post-cyclone, mixed-effects meta-analysis models including random effects for resistance revealed that soil P was not a significant moderator of total litterfall (p -value = .1) or leaf litterfall (p -value = .06) mass flux resilience (Table S9).

4 | DISCUSSION

4.1 | Large variation in litterfall resistance to cyclones relates to wind speed and soil phosphorus

Total litterfall mass flux resistance to tropical cyclones varied widely among case studies, corroborating earlier reviews (Lugo, 2008; Mitchell, 2013; Xi & Peet, 2011) and indicating highly variable cyclone resistances across tropical forests. While multiple biotic and abiotic factors influence the cyclone resistance of litterfall, among

17 moderators spanning soil types, lithologies, biogeographies, and cyclone regimes, site wind speed and total soil P concentration were among the strongest moderators of the pantropical variation in cyclone resistance. Site wind speed, which correlated strongly and negatively with the location of the forest site and cyclone frequency (Figure 4c), did not entirely explain the observed resistances. The Chamela-Cuixmala Reserve (Mexico), for example, received the strongest wind with Patricia (63 m/s) but did not show the lowest resistance (Figure 3a). Litterfall resistances in Puerto Rico, where wind speed and soil P fell between the mean and the high end of the data range, were >80% below the pantropical mean.

As hypothesized, soil P had a moderating effect on total litterfall resistance, suggesting a lower resistance in pantropical sites with higher total soil P concentration. This moderating effect aligns with site-level studies in Australia (Gleason et al., 2008) and Hawaii (Herbert et al., 1999), which were included in the meta-regression analysis (Table 2) but represented a small fraction of the 48 case studies (Table S1). In addition, both studies were limited in describing the differing effects of cyclones in three tropical forests on contrasting soils. Our study provides empirical evidence for the role of soil P in mediating litterfall resistance in 26 tropical forests affected by 22 tropical cyclones with varying intensity. Herbert et al. (1999) had proposed that contrasting cyclone effects in Hawaii and Puerto Rico were due to nutrient availability differences, but this is the first

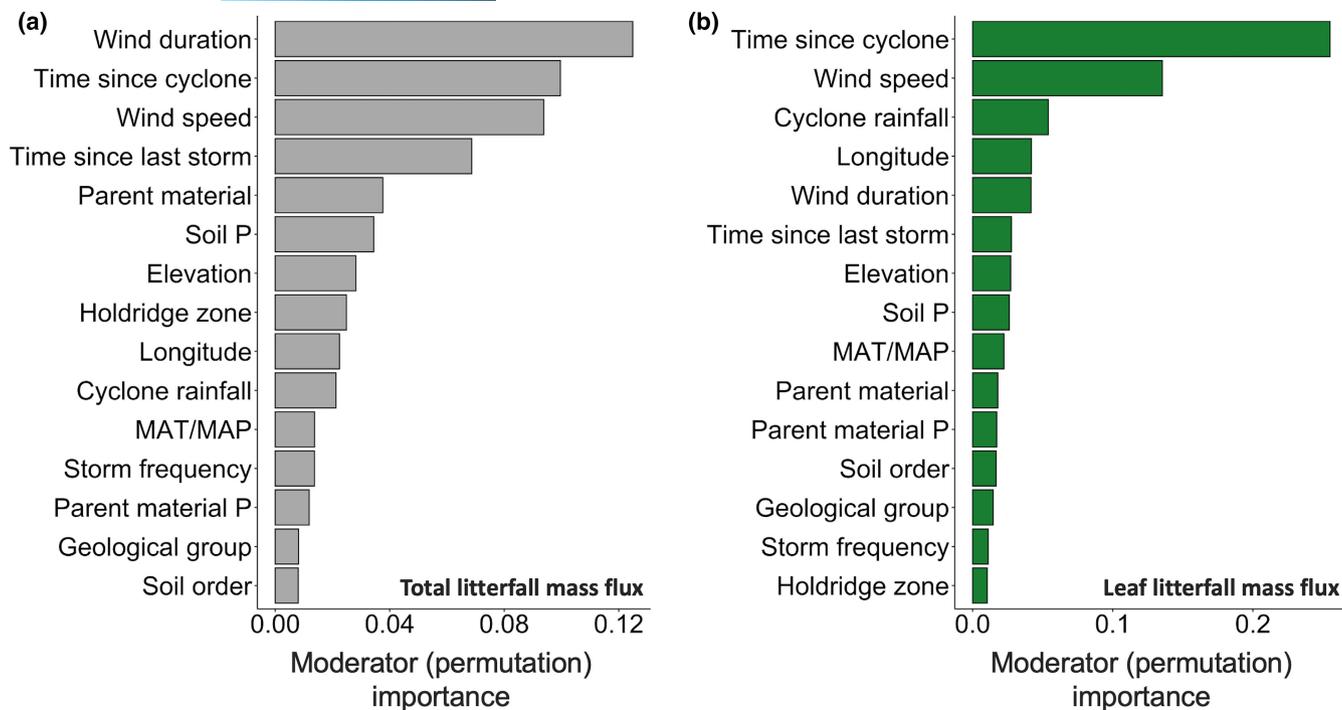


FIGURE 8 Moderator importance from the random forest models predicting the short-term (1–21 months) cyclone resilience [$\ln(\text{litterfall}_{\text{TD+X}}/\text{litterfall}_{\text{LR}})$] of (a) total litterfall ($N = 213$, $R^2_{\text{oob}} = .38$, $R^2_{\text{cv}} = .39$) and (b) leaf litterfall mass flux ($N = 193$, $R^2_{\text{oob}} = .48$, $R^2_{\text{cv}} = .54$). Moderator (permutation) importance is the measure of how strongly each moderator explains differences in effect size, capturing (non-)linear relationships and higher order interactions. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16223)]

study to quantitatively link soil resource availability and litterfall stability in response to cyclones across the world's terrestrial tropical forests. Although most studies of the role of resource availability in ecosystem stability have occurred in aquatic systems (DeAngelis et al., 1989), increasing nutrient availability has also decreased the functional and canopy resistance to hurricanes in subtropical mangrove forests (Feller et al., 2015). Here we provide empirical evidence that in tropical forests across the globe, resource availability plays a role in shaping litterfall response to cyclones.

Mechanisms related to forest structure and tree ecophysiology could explain the relationship between litterfall resistance to cyclones and soil P. As tall forest canopies are more vulnerable to wind than short ones (Mitchell, 2013), it is possible that tropical forests on low-P soils may be shorter (e.g., Aiba & Kitayama, 1999; Quesada et al., 2012) and have lower wind exposure than high-P forests (Coomes et al., 2007; Gorgens et al., 2021), which would be worth testing in future studies. Further, ecosystems that receive chronically low inputs of limiting nutrients like phosphorus generally have mechanisms and structures that increase nutrient recycling relative to the amount of nutrient input (DeAngelis et al., 1989). This can be reflected in phosphorus use differences (e.g., high leaf P retranslocation; Han et al., 2013), likely indicating a selection pressure toward efficient nutrient economics in low-P sites (DeAngelis et al., 1989) and adaptations for wind resistance (Zhang et al., 2018). Plant traits that vary with soil P may include growth rate, tissue lifespan, wood density (Asner & Goldstein, 1997), and antiherbivore defense (Chapin, 1980; Coley et al., 1985; Grime, 1979). High leaf nutrient

content may be associated with reduced proportions of structural tissues (e.g., lignin, cellulose, and hemicellulose) in plants (Gleason et al., 2008). The same leaf traits (e.g., total C, lignin, tannins negatively correlated with leaf decay) that make tropical trees meticulous with nutrients when they are scarce (e.g., Urbina et al., 2021) might also result in wind-resistant leaves and wood (Curran et al., 2008; Feller et al., 2015; Gleason et al., 2008).

Differences in species composition or relative dominance could also affect litterfall resistance and resilience. The high importance of longitude to litterfall resistance (Figure 4a,b) may serve as a biogeographic proxy reflecting these differences, given that this meta-analysis did not directly include species composition data. Prior work has found correlations between wind resistance and biogeography (Griffith et al., 2008, 2013) and has described differential cyclone effects among tree species (Basnet et al., 1992; Foster & Boose, 1992; Ostertag et al., 2005). Tree species with increased investment in P-conserving processes like high leaf longevity (Heberling & Fridley, 2012; Tian et al., 2016) might dominate the forest biomass in low-P soils as an adaptive response to phosphorus deprivation. Conversely, species with weaker wood (Webb, 1989), low leaf reconfiguration ability (Vogel, 1989), and shallow root systems (Gresham et al., 1991; Putz & Sharitz, 1991), which generally show low cyclone resistance (Everham & Brokaw, 1996; Xi, 2015), might dominate the forest biomass on high-P soils. In Australia, the properties of low soil-P specialists dominated forest functioning in low-P forests (Gleason et al., 2008). Therefore, the moderator effect of soil P on litterfall cyclone resistance could be partially related to tree species

TABLE 3 Results of the generalized additive mixed-effects models (GAMMs) fit for the pantropical resilience (r_s) of total and leaf litterfall mass flux to cyclone disturbance, including crossed random effects for site and cyclone disturbance, and country and cyclone disturbance, respectively

Total litterfall mass flux					Leaf litterfall mass flux				
Model 1a (N = 218 observations) $r_s \sim s(\text{soil P, Time since cyclone, } k = 20); R^2 = .25$					Model 1b (N = 198 observations) $r_s \sim s(\text{soil P, Time since cyclone, } k = 20); R^2 = .34$				
Random effects	Variance	SD	Levels		Random effects	Variance	SD	Levels	
Site	0.009	0.01	13		Country ^a	1.16×10^{-4}	0.01	6	
Cyclone	0.17	0.41	11		Cyclone	0.22	0.47	7	
Residual	0.99	1			Residual	0.65	0.81		
	Estimate	SE	t-value	p-value		Estimate	SE	t-value	p-value
Intercept	-0.43	0.14	-3.14	<.001	Intercept	-0.50	0.19	-2.68	.008
Approximate significance of smooth terms:					Approximate significance of smooth terms:				
	Edf	Ref df	F	p-value		Edf	Ref df	F	p-value
s(soil P, Time since cyclone)	14.1	14.1	5.66	<.001	s(soil P, Time since cyclone)	15.3	15.3	11.56	<.001
Model 2a (N = 218 observations) $r_s \sim s(\text{soil P, Time since cyclone, by = wind duration, } k = 20); R^2 = .4$					Model 2b (N = 198 observations) $r_s \sim s(\text{Time since cyclone, wind speed, } k = 20); R^2 = .46$				
Random effects	Variance	SD	Levels		Random effects	Estimate	Sqrt	Levels	
Site	0.009	0.1	13		Country ^a	0.11	0.34	6	
Cyclone	0.1	0.31	11		Cyclone	0.06	0.24	7	
Residual	1.06	1.03			Residual	0.66	0.81		
	Estimate	SE	t-value	p-value		Estimate	SE	t-value	p-value
Intercept	-0.50	0.12	-4.23	<.001	Intercept	-0.52	0.21	-2.54	.01
Approximate significance of smooth terms:					Approximate significance of smooth terms:				
	Edf	Ref df	F	p-value		Edf	Ref df	F	p-value
s(soil P, Time since cyclone, by wind duration)	12.9	12.9	5.16	<.001	s(Time since cyclone, wind speed)	15.44	15.44	11.35	<.001

Note: The GAMMs were fit using the weights (w_i) calculated as $w_i = 1/(\sigma_1^2 + \sigma_2^2 + v_i)$, where σ^2 is the heterogeneity from the random effects and v_i is the sampling variance obtained from the *escalc* function. Edf denotes effective degrees of freedom—the amount of the basis complexity used in the smooth, where high edf values (≥ 8) indicate a non-linear curve. Ref df denotes effective residual degrees of freedom. Bold values denote significance at the 95% confidence level.

^aThe categorical variable 'Country' included the levels: Australia, Guadeloupe, Hawaii, Mexico, Puerto Rico, and Taiwan.

compositions (Lepš et al., 1982; MacGillivray et al., 1995) that reflect distinct adaptive specializations related to the plant's acquisitive and retentive mechanisms of phosphorus utilization (Chapin, 1980; Coley et al., 1985; Endara & Coley, 2011; Fridley et al., 2011).

4.2 | Tropical forest litterfall mass flux is resilient to cyclones

Following the instantaneous cyclone-induced litterfall mass flux, this forest function resumed its average pre-disturbance reference within one-year post-cyclone, indicating resilience in the studied cyclone-prone forests (i.e., 33% of the case studies included in the resistance analysis). This matters because litterfall resilience reflects the recuperation of photosynthetic area and plant nutrient uptake to support stem growth (Harrington et al., 1997) and avoids net nutrient losses due to cyclones. The observed pantropical resilience

makes sense as energy acquisition in post-cyclone early-successional forests is maximized by a rapid leaf turnover (Coley et al., 1985). This pantropical litterfall resilience finding corroborates previous studies in tropical forests reporting leaf area index (Herbert et al., 1999; Whigham et al., 1991) and litterfall resilience (Scatena et al., 1996) following cyclones.

Litterfall resilience to cyclones varied across tropical forests and with time post-cyclone, wind disturbance factors, and soil P. The predicted resilience (Table 3, model 1a) decreased as soil P increased at 12 months post-cyclone (Figure S8a). When gale wind duration was included in the model as a predictor with soil P and time since disturbance, differential predicted resilience slopes by soil P were observed (Figure 9 and Figure S8b,c). These results only partially support our expectation of litterfall resilience increasing with soil P across cyclone-disturbed forests, suggesting a benefit of higher P only in the first 9 months following lower storm durations. The expectation of a positive influence of soil P on resilience arose from a

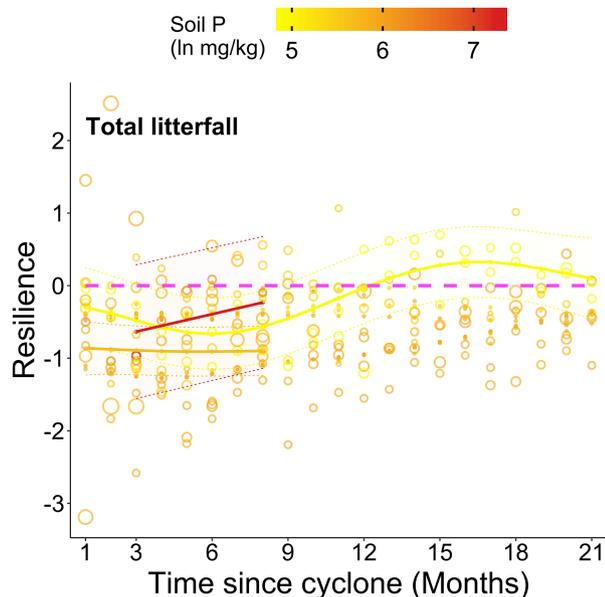


FIGURE 9 Predictions (lines; Table 3, model 2a) and observations (points) of temporal trends in total litterfall mass flux resilience [$\ln(\text{litterfall}_{\text{TD}+\text{x}}/\text{litterfall}_{\text{IR}})]$ by time since cyclone disturbance (months) and total soil P concentration ($\ln \text{ mg P kg}^{-1}$ soil; color gradient). Point sizes are proportional to the sampling variance. Lines with 95% confidence intervals are the predictions of three case studies with soil P values representing the minimum, median, and maximum total soil P within the total litterfall resilience data. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

previous study showing that phosphorus fertilization related positively to the resilience of Hawaiian forests affected by cyclone Niki (Herbert et al., 1999). In P-amended plots, the aboveground NPP (i.e., litterfall and wood biomass) reached pre-disturbance values earlier than co-located unfertilized plots. In addition, the removal of cyclone-induced debris and inorganic fertilization in tropical forest plots increased aboveground NPP by up to 40% 3 years after Hugo in Puerto Rico (Zimmerman, Aide, et al., 1995; Zimmerman, Pulliam, et al., 1995), indicating the positive influence of resource availability on forest functional resilience to cyclones. This influence, however, has been shown to differ between Puerto Rico forests that also differ in total soil P concentration (Walker et al., 1996). In mangrove forests, increasing nutrient availability decreased their ability to recover post-cyclone (Feller et al., 2015). Therefore, depending on the intensity of the cyclone event, and the forest structural or functional component assessed, resilience may be positively or negatively influenced by increased nutrient availability.

Besides litterfall resilience, tropical forests may present several mechanisms that promote functional resilience to cyclones, including increased stem sprouting (Bellingham et al., 1994; Tanner et al., 1991) and growth of the surviving trees in the post-cyclone environment of increased light, soil moisture, and nutrients (Xi, 2015). A rapid turnover rate of nutrients, mass and populations, biotic control of fluxes, and a high species turnover followed by self-organization of new communities are also characteristics of ecosystems that lead to resilience (Lugo & Scatena, 1995). Under typhoon regimes, tropical

forests tend to include low stature trees with resprouting ability as strategies that provide these forests with high resilience (and resistance) to wind (Chao et al., 2021). Furthermore, the rapid production of less durable leaves following cyclone-induced defoliation may involve a trade-off between fast recovery of photosynthetic area and resistance to defoliation (Herbert et al., 1999). Leaf mass area, those authors found, was 13% lower than the pre-disturbance value two years after cyclone Niki passed through their plots dominated by *Metrosideros polymorpha* plants. This could be a mechanism to capture nutrients and recover carbon assimilation quickly, later recycling the nutrients through resorption to make more sclerophyllous leaves.

4.3 | Cyclone disturbance as a lasting nutrient pulse in tropical forests

The N and P fluxes in the cyclone-caused litterfall were large pan-tropically, with short- to long-term consequences for nutrient cycling processes in cyclone-affected forests. The observed litterfall N and P flux resistances reflected both the magnitude of the instantaneous litterfall mass input and the elevated N and P concentration in plant parts that cyclone wind and rain knock down before senescence (Herbert et al., 1999; Lodge et al., 1991; Zimmerman et al., 1996). This fine litter material includes partially green or incompletely senesced plant parts containing higher nutrient concentration and lower carbon-to-nutrient ratios than normally senesced materials (Gavito et al., 2018; Harrington et al., 1997; Herbert & Fownes, 1995; Hidaka & Kitayama, 2011; Reich et al., 1991; Whigham et al., 1991). The greater increase in leaf litterfall P than N concentration corroborates the relative resorption hypothesis—plants resorb proportionally more of the relatively more limiting nutrient (Han et al., 2013; Massmann et al., 2021)—and the understanding that tropical forest P cycling is more conservative than N cycling (Sardans et al., 2021; Vitousek, 1984; Vitousek & Sanford, 1986). The cyclone-induced litter with high N and P may decompose and release nutrients faster than senesced leaves, providing positive feedback to high N and P availability (Chadwick et al., 1999). This directly influences nutrient availability to surviving, resprouting, and pioneer plants and soil organisms in cyclone-affected forests (Liao et al., 2006; Xi et al., 2012). Regardless of elemental differences, cyclone-driven maintenance of rapid cycling of both P and N and their temporarily increased availability in soil (Gavito et al., 2018) may have the effect of maintaining forest productivity.

As time progressed after a cyclone, N and P concentrations in leaf litterfall post-cyclone remained higher than the pre-disturbance values over the first year. This corroborates previous studies (e.g., Scatena et al., 1996) and could be explained by the increased recruitment and relative abundance of fast-growing pioneer species at the early stage of post-cyclone secondary succession. Acquisitive plant functional types, like *Cecropia schreberiana* in Puerto Rico (Brokaw, 1998), are associated with conditions enabling high resource capture and growth rates (Coley et al., 1985). Those conditions match

post-cyclone environments, wherein the disturbance increases the supply of limiting nutrients from the plant biomass. Nutrient concentrations in leaf litterfall likely recover from cyclones and resume the reference levels, as suggested by studies assessing litter quality and nutrient availability for six years post-cyclone (Gavito et al., 2018). Although our study did not include sufficient data, the Puerto Rico data support the recovery of leaf litterfall nutrient concentrations. In the long term, cyclones can be nutrient-conserving disturbances that redistribute mass and nutrients within the system. Therefore, certain pioneer species like *Cecropia* spp. play a crucial biogeochemical role by increasing the rate of nutrient cycling with low nutrient use efficiency that supports post-cyclone increase of vegetation biomass (e.g., Lovelock et al., 2011).

4.4 | Study limitations and future research directions

A relevant driver not assessed in this meta-analysis is the influence of previous or compound disturbances (Heartsill-Scalley & López-Marrero, 2021) like drought (e.g., Beard et al., 2005) and fire (Myers & van Lear, 1998). Ecological legacies related to prior land uses could also play a role in our study sites (Chazdon, 2003; Zimmerman, Aide, et al., 1995; Zimmerman, Pulliam, et al., 1995). Such legacies may be significant in sites where cyclones repeatedly occur over multiple decades, as effects on boles and branching architecture can limit litterfall resilience. Additional factors explaining variation in the functional resistance and resilience to cyclones across tropical forests may include stand properties like stem density (Ibañez et al., 2019) due to tree acclimation to wind and buffering effects of high winds (Herbohn & Congdon, 1993; Mitchell, 2013). Our moderator time since the last storm likely positively correlates with stem density but would be an imperfect proxy.

Assessing cyclone effects on trees to separate the structural and functional components of resistance and resilience (i.e., effects on stems versus litterfall) can be a way to characterize the response of tropical forests to future cyclone regimes (Herbert et al., 1999; Uriarte et al., 2019). Projected changes in tropical cyclone regimes in a changing climate may influence the structure and dynamics of disturbed forests (Ibañez et al., 2019). Nutrient conservation strategies in cyclone-prone tropical forests may increase under future cyclone regimes (e.g., more frequent cyclone disturbances). However, Gavito et al. (2018) hypothesized that repeated cyclones would gradually increase soil nutrient availability and nutrient acquisition strategies. Future research can test whether forests will become more or less functionally resistant and resilient to intensifying cyclone regimes or other disturbances like monsoons (Chao et al., 2021) under climate change. For instance, high wind events post-Iniki in Hawaii led to increased litterfall mass fluxes, reflecting a low resistance of new leaves to repeated disturbances which may substantially decrease leaf area with less force (Herbert et al., 1999). Therefore, an increased frequency and intensity of cyclone events could lead to an arrested succession of tropical forests.

Total soil P concentration is a proxy for but does not entirely explain soil fertility across forest ecosystems. Other soil variables like bulk density, saturation, texture, clay mineralogy (Sanchez et al., 2003), organic matter, carbon, nitrogen and phosphorus stock, cation exchange capacity, and depth could also influence soil fertility and tree anchorage. For instance, wet, sandy, and fertile soils may combine to decrease not only the structural but functional resistance to windthrow (Basnet et al., 1992; Xi & Peet, 2008). Besides, there is a high probability of tree uprooting on formerly disturbed soils, resulting from less compacted soil and, hence, impaired support for trees (Mayer, 1989; Šamonil et al., 2010).

Taken together, our findings support the influence of soil resource availability on the resistance and (partially) the resilience of terrestrial tropical forest litterfall to cyclone disturbance at a pan-tropical scale. Besides the negative effect of site wind speed on the resistance, higher total soil P concentration is related to higher litterfall mass flux—relative to pre-disturbance value—following numerous tropical cyclones of varying intensities. Because of limited data availability, the relationship between soil P and resilience is less robust even though our results suggest a dynamic interaction between the cyclone intensity, soil P and recovery through time, indicating the need for longer-term studies. We also observed that the resistance related to the resilience of total litterfall, but not as much for leaf litterfall mass flux. Our results suggest that soil P will partially determine the pantropical forest litterfall resistance and resilience in the face of intensifying cyclone disturbance.

This study is the first to document the pantropical role of phosphorus as a factor mediating tropical forest responses to cyclones. Litterfall mass and nutrient pulses caused by cyclones both respond and contribute to resource heterogeneity that can affect species regeneration, growth, and competitive interactions. Additional research can test how plant functional groups and species across pantropical forest ecosystems differ in their resistance and resilience to cyclones to represent cyclone disturbance responses in predictive modeling.

AUTHOR CONTRIBUTIONS

B.B., A.P.W., W.H.M., J.K.Z., and L.M.K. conceptualized the study. B.B. extracted, processed, and compiled the data. Y.F. extracted the hurdat2 wind data and generated the HURRECON wind data. B.B. conducted and A.P.W. and L.M.K. contributed to the data analysis. B.B., A.P.W., W.H.M., J.K.Z., Y.F., L.M.K. interpreted data. B.B. wrote and all authors read, edited, and approved the paper.

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CONFLICT OF INTERESTS

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data used to produce figures and conduct statistical analyses are available on <https://doi.org/10.15486/ngt/1821683>, and the code is available for download on <https://github.com/bdbomfim/Pantropical-MetaAnalysis-Cyclones>.

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