Received: 4 November 2024 | Accepted: 24 May 2025

DOI: 10.1111/1365-2745.70108

BRITISH ECOLOGICAL SOCIETY Journal of Ecology

RESEARCH ARTICLE

Increasingly conservative N cycling in a wet tropical forest: Litter and stream N concentrations decline over 29 years despite surges from hurricanes

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Funding information
International Institute of Tropical Forestry; Universidad de Puerto Rico; Directorate for Biological Sciences, Grant/Award Number: DEB-1831952; University of New Hampshire Agricultural Experiment Station

Handling Editor: Peter Bellingham

Abstract

1. Long-term litterfall trends are unexplored in hurricane-prone regions but are needed to understand the consequences of altered hurricane regimes. In a wet tropical forest in northeastern Puerto Rico, we monitored litterfall mass (leaf fall, <2.5 cm diameter wood fall and miscellaneous), litterfall carbon (C) and nitrogen (N) and stream nitrate every 2 weeks for 29 years (1989–2017).
2. Litterfall from the nine observed hurricanes averaged 500 $g\,m^{-2}$ $hurricane^{-1}$ (CV = 90%), nearly half of the long-term mean of 951 $g\,m^{-2}$ $year^{-1}$. Hurricane-generated leaf fall and wood fall increased with increasing disturbance intensity (peak wind speed) and time since a previous hurricane. Wood fall from the two most intense hurricanes exceeded corresponding leaf fall and mean annual wood fall.
3. Litterfall increased over the 29 years due to increases in wood fall and miscellaneous materials but not leaf fall. Recovery of litterfall after individual hurricanes was distinctive and illustrated the varying effects of hurricane intensity and history on litterfall dynamics.
4. Leaf fall N concentrations [N] surged immediately after hurricanes yet decreased by around 33% over the 29 years. Similar changes were observed at the watershed scale, with increasing nitrate in streams following major hurricanes but then a long-term decline. Mean annual leaf fall [N] was negatively related to the previous year's fine wood fall but positively related to that wood fall's [N], suggesting a link between fine wood dynamics and plant N uptake. Stream nitrate-[N] showed a strong positive correlation with leaf fall [N] after hurricanes and across years, demonstrating tight coupling between terrestrial and aquatic N cycling throughout periods of cyclonic disturbances and recovery.
5. The decadal decreases in litterfall [N] and stream nitrate-[N] and the increase in wood fall suggest a trend towards more conservative cycling of N. Microbial immobilization of N in wood fall from hurricanes and during recovery likely contributed to the lower N availability.

6. *Synthesis*. More conservative cycling of N can be expected under the current hurricane disturbance regime. However, with increased hurricane frequencies and intensities, the lack of high wood fall typical of mature canopies may alter present N cycling trends.

KEYWORDS
Caribbean, forest succession, hurricane frequency, hurricane intensity, litterfall, Luquillo Experimental Forest, stream nitrate, tropical nitrogen cycle, tropical wet forest, woody litter

1 | INTRODUCTION

Forest litter, consisting of fallen leaves, branches and boles and reproductive parts, represents an important transfer of carbon (C) and nutrients from forest canopies to soils (Bray & Gorham, 1964; Sayer & Tanner, 2010), and may be key for maintaining aboveground forest productivity (Sayer et al., 2024). Wet tropical forests have some of the highest rates of litterfall (Bray & Gorham, 1964; Shen et al., 2019; Zhang et al., 2014) and are among the most productive forests globally (Brown & Lugo, 1982; Pan et al., 2011). Litterfall is an important source of nitrogen (N) for plant growth, as primary productivity in many ecosystems is limited by insufficient N supply (LeBauer & Treseder, 2008; Vitousek & Howarth, 1991). Litterfall N affects numerous ecological processes in tropical forests (Erickson et al., 2001; Osborne et al., 2020; Sayer et al., 2012). For example, soil emissions of nitrous oxide, a powerful greenhouse gas, correlate negatively with litterfall C/N ratios across multiple wet tropical ecosystems (Erickson et al., 2001). Experimental N additions, proxies for litterfall N, show strong coupling between N and P cycling (Marklein & Houlton, 2012) and increase tree reproductive output in a lowland Panamanian forest (Kaspari et al., 2008). Thus, even though productivity of some mature lowland wet tropical forest soils may be more phosphorus (P) than N limited (Cleveland et al., 2011; Du et al., 2020; Vitousek, 1984), understanding N cycling in tropical forests is fundamental to better understanding how tropical forests contribute to global elemental budgets in a changing earth system.

Litter production is not static across time. Tropical cyclones (termed hurricanes in the Atlantic and typhoons in the northwestern Pacific) create large surges of forest litterfall through defoliation, branch loss and tree mortality followed by variable recovery periods (Lin et al., 2017; Lugo et al., 2011; Scatena et al., 1996). The magnitude of litter inputs depends on cyclone intensity (wind speed) (Beard et al., 2005; Bomfim et al., 2022; Lin et al., 2003; Van Beusekom et al., 2018) and on the history of past cyclones (Brokaw et al., 2012; Lugo, 2008). Recovery to pre-cyclone conditions depends on resulting severity. In subtropical wet Taiwan, where typhoons are frequent (roughly averaging 1.5/year), canopy leaf area and litterfall return to pre-typhoon values within a year (Lin et al., 2017), although multiple cyclones in a year can slow recovery of litterfall. In contrast, after a severe hurricane in Puerto Rico (Hugo, Category 3, Saffir-Simpson scale), leaf litterfall took 5 years to reach over 90% of pre-hurricane values, while woody litterfall remained low compared to pre-hurricane values (Scatena et al., 1996). This suggests that recovery of woody inputs may be reduced if slowed by frequent or severe hurricanes. Tropical cyclone frequency and intensity are likely increasing with rising temperatures (Emanuel, 2020; Kossin et al., 2020; Murakami et al., 2020), yet litterfall responses to these expected changes, especially over the long term, are largely unknown.

Tropical cyclones often produce litterfall with higher nutrient concentrations than naturally senesced litter (Bomfim et al., 2022; González et al., 2014; Lodge et al., 1991; Lugo et al., 2011; Wang et al., 2013), with significant ecosystem-wide consequences. In a wet tropical forest in northeastern Puerto Rico, for example, high litter N concentrations [N] in litter generated from Hurricane Hugo (Lodge et al., 1991; Scatena et al., 1996) were associated with increases in both stream N concentrations (McDowell et al., 2013; Schaefer et al., 2000) and soil nitrous oxide emissions (Steudler et al., 1991). After other hurricanes in the region, high fluxes of nitrous oxide (Erickson & Ayala, 2004; Quebbeman et al., 2022) and stream or soil solution N (McDowell et al., 2013; McDowell & Potter, 2022) have been documented and are likely related to increased litter [N], yet quantitative data are lacking.

Litter [N] returned to pre-hurricane levels within a few years after Hurricane Hugo in Puerto Rico (Scatena et al., 1996), coincident with post-Hugo decreases in export of fluvial and atmospheric N (Schaefer et al., 2000; Silver et al., 1996; Steudler et al., 1991), also observed after other hurricanes (Erickson & Ayala, 2004; McDowell et al., 2013) and field experiments simulating various aspects of hurricane damage (McDowell & Liptzin, 2014). The large amount of wood fall generated by hurricanes may contribute to the decreasing N availability observed after hurricane-induced pulses of N. Experimental removal of woody litter after Hurricane Hugo resulted in increased soil inorganic N (Zimmerman et al., 1995), highlighting the key role woody debris plays in N immobilization after hurricanes. Despite this basic understanding, the trajectory of litter N concentrations [N] and wood fall have only been documented for a few years after hurricanes.

Woody litter may come into play again in the hurricane-recovery cycle. Eventually, as more biomass is allocated to structural tissues during stand development, wood fall begins to increase (Aryal et al., 2015). Small diameter woody debris also immobilizes N during decomposition (Herbert et al., 1999; Jones et al., 2019; Smith et al., 2011), potentially further limiting N availability. Yet long-term trends in litter N associated with woody biomass accumulation or wood fall during forest succession have not been documented in hurricane-prone forests.

Studies of N dynamics during forest succession in the tropics have typically focused on sites with known human disturbance. Among many young tropical secondary forests, where biomass containing N is removed in forest clearing and burning, N availability is initially low, yet chronosequence studies show relatively rapid recovery of the N cycle in these forests (Davidson et al., 2007; Sullivan et al., 2019; Winbourne et al., 2018). Biological N fixation likely plays a key role, especially during periods of rapid biomass accumulation (Batterman et al., 2013; Taylor et al., 2019). Whether litter N after hurricanes in forests lacking major human disturbance follows trajectories like those found after forest clearing for agriculture is largely unknown due to the lack of long-term studies in hurricane-prone regions.

We examined long-term (29 years, 1989–2017) trends in litter production, litter C and N dynamics and stream N in a wet tropical evergreen forest in Puerto Rico subject to multiple hurricanes and largely undisturbed by human activity (Scatena & Lugo, 1995). Hurricane litterfall in the region has been examined previously (e.g. Beard et al., 2005; Lodge et al., 1991; Ostertag et al., 2003; Scatena et al., 1996; Vogt et al., 1996), yet these studies often covered single, high-intensity and infrequent hurricanes, or a much shorter time series. By separating leaf fall from wood fall (and a combined miscellaneous category), we could assess relationships among these components and N availability over the long term. We also tracked stream [N] because of the similarity in pulses of stream and litter N observed in the immediate years after Hurricane Hugo. Beyond that, we are not aware of any studies in the tropics examining temporally linked litter N and stream N dynamics.

Ten hurricanes (litterfall from two combined) occurred during the 29 years, with differing intensities and lengths of time until the next hurricane, allowing us to explore effects of disturbance strength and frequency on litterfall and litterfall recovery. We expected that (1) hurricane-generated litterfall mass would be related to local hurricane intensity and time since a prior hurricane, (2a) fine woody litter inputs would increase with forest recovery and cause subsequent decreases in leaf litter and stream [N] due to N immobilization during wood decomposition or, (2b) based on studies of secondary successions after agricultural abandonment, litter [N] would increase over the three decades. We also expected that stream [N] would correspond with leaf fall [N] after multiple hurricanes, given their similar responses to Hurricane Hugo. We examined additional relationships between stream [N] and litterfall mass as negative correlations between stream [N] and leaf fall or litterfall mass have been noted elsewhere in the tropics (Ardón et al., 2023; McDowell & Asbury, 1994).

2 | MATERIALS AND METHODS

2.1 | Study site

Litter was collected from two adjacent Bisley Experimental Watersheds (18°20′ N, 65°50′ W), part of the Luquillo Experimental Forest (also known as El Yunque National Forest) in northeast Puerto Rico. The watersheds (hereafter 'Bisley') cover 13 ha, range between 265 and 456 m a.s.l. (Harris et al., 2012), and have received extensive study (McDowell et al., 2021). Rainfall, based on data collected from a meteorological tower located between the two watersheds (1993–2016), averaged 3588 mm/year, with a slight drier period from January to late March (Figure S1). Mean annual temperature was 24.4°C, with August and September averaging 3°C warmer than February (Figure S1). Soils are acidic (0–10 cm, pH 4.7–4.8), clayey Ultisols and Oxisols, and in upper topographic positions where the litterfall plots are located, generally well-drained (Scatena & Lugo, 1995; Silver et al., 1994).

Mature tabonuco (*Dacryodes excelsa*) forests (classified as subtropical wet forest in the Holdridge life zone system), largely undisturbed by human activities since the 1940s (Scatena & Lugo, 1995), cover the watersheds. Beginning in the early 1800s, the watersheds were used for small-scale shade-coffee production involving selective harvesting of trees to encourage growth of those with desirable features, such as high litter [N] (García-Montiel & Scatena, 1994). When the USDA Forest Service purchased the land in 1934, the forest was dominated by mature and overmature tabonuco but had been severely damaged by the 1932 Hurricane Capriano (Category 4) (Scatena & Lugo, 1995). Minor selective harvesting of trees for off-site charcoal production continued for a short period thereafter.

By 1989, *D. excelsa*, *Guarea guidonia* and *Sloanea berteriana* dominated tree biomass. In 1994, 5 years after another major hurricane (Hurricane Hugo, Category 3), *D. excelsa*, *Cecropia schreberiana* and *G. guidonia* dominated tree biomass (Heartsill Scalley et al., 2010), with the early successional *C. schreberiana* then decreasing in abundance through 2014 (Heartsill Scalley, 2017). A palm (*Prestoea acuminata*, formerly *P. montana*) nearly tripled in biomass from pre-Hugo to 2004.

2.2 | Hurricane history

Hurricanes (on the Saffir-Simpson scale, sustained wind speeds >33 m s^{-1}) and tropical storms (18–33 m s^{-1}) are major and frequent disturbances in the Caribbean. Because Atlantic hurricanes typically move from east to west, northeastern Puerto Rico is affected more than elsewhere on the island (Boose et al., 2004). In the Luquillo Mountains, the historical return interval for hurricanes ≥Category 1 (Saffir-Simpson) was 17–21 years and was 50 years for hurricanes ranging from mid Category 2–mid Category 4 (46–62 m s^{-1}) (Boose et al., 2004; Scatena & Larsen, 1991).

We considered tropical storms and hurricanes whose centres passed within 130 km of Bisley; distance was expanded to 240 km for hurricanes ≥Category 4 (https://coast.noaa.gov/hurricanes), to account for an average hurricane radius of 235 km, including outer tropical storm force winds (Zhai & Jiang, 2014). For the 10 hurricanes over the 29-year study period, all but two occurred in September (Table 1). Nine tropical storms were identified (Table S1), including two hurricanes near the edge of the radius that we reclassified as tropical storms as their effects on wind speeds at our site were negligible. The two strongest hurricanes in our record, hurricanes Hugo (1989) and the closely occurring Irma and Maria (2017) occurred

TABLE 1 The hurricanes passing by Bisley during this study, their dates, maximum recorded wind speed at or when near Bisley and hurricane litterfall.

Named hurricane (Saffir-Simpson category assessed when closest to Bisley)	Month and year of occurrence	Daily maximum wind speed ($m\,s^{-1}$)	Hurricane-generated litterfall[a] ($g\,m^{-2}$ collection^{-1}), percent of total in parentheses			
			Leaf	Wood	Total	Litterfall N
Hugo (Cat 3)	Sept 1989	43.8[b]	386.1 (35%)	578.2 (53%)	1098	17.94
Luis (Cat 4)	Sept 1995	24.9	324.0 (73%)	80.2 (18%)	441	7.93
Marilyn (Cat 2)	Sept 1995	24.1	109.2 (82%)	17.4 (13%)	133	1.85
Bertha (Cat 1)	July 1996	30.9	212.1 (75%)	47.7 (17%)	282	4.05
Hortense (Cat 1)	Sept 1996	13.3	43.6 (81%)	5.2 (10%)	54	0.97
Georges (Cat 3)	Sept 1998	32.5	361.7 (76%)	95.6 (20%)	477	7.31
Earl (Cat 4)	Sept 2010	23.1	278.1 (68%)	95.9 (23%)	410	5.65
Irene (Cat 1)	Aug 2011	21.1	99.8 (45%)	91.3 (41%)	223	2.55
Irma and Maria (Cat 5–4)	Sept 2017	69.3[b]	558.3 (40%)	763.1 (55%)	1384	15.02
Hurricane means, % CV			264, 62 (53%)	197, 139 (39%)	500, 90	7.03, 84

[a]Collection periods are normally every 2 weeks, except when collected after 21, 7, and 76 days during which hurricanes Luis, Marilyn and Irma-Maria occurred, respectively. For Luis and Marilyn, this was 5 days post-hurricane, and 59 and 46 days post-hurricane for Irma and Maria, respectively. Despite variable collection times, these are the best estimates we have of hurricane inputs.

[b]Wind speed sensors were destroyed at Bisley and across much of Puerto Rico after these hurricanes; values reported are at landfall (from Mitigation Assessment Team, 2018).

during the first and final years of our study. The 1990s saw multiple hurricanes, while the decade from 1999 to 2009 lacked hurricane activity yet had a few tropical storms (Figure 1). Between 2010 and 2017, four hurricanes and a relatively strong tropical storm (Erika, August 2015) occurred.

2.3 | Wind speed

Reliable, consistent frequency wind speed data collection began in 1993 from the meteorological tower between the watersheds. Maximum wind speed per litterfall sampling period was based on the highest value for a 5-min interval. Because wind speed sensors were damaged during hurricanes Hugo and Maria, we used published maximum sustained winds at landfall (Mitigation Assessment Team, 2018) acknowledging that these are likely higher than what occurred in the forest. Note that maximum wind speed during hurricanes did not always match Saffir-Simpson categories (Table 1).

2.4 | Litterfall

From 1989 to 2017, forest litter was collected every 2 weeks, hereafter 'biweekly' (with few exceptions and except after hurricanes, see Table 1) from 60 baskets (0.25 m^2) located ~3 m apart on either side of a 425 m transect bisecting the watersheds on ridgetop or slope positions. Palm fronds and pieces of wood (generally <2.5 cm diameter, rarely including larger pieces) straddling a basket were cut at the basket boundary. Access to the site was non-existent after the 2017 hurricanes, resulting in a 76-day delay in collecting litterfall (Table 1).

At the International Institute of Tropical Forestry Chemistry Laboratory (Río Piedras, Puerto Rico) litter from each basket was hand separated into leaves, woody material, fruits and flowers combined and a miscellaneous class, prior to drying at 65 °C and weighing. Separated contents were composited into two subsamples for chemical analyses, based on a protocol developed in the 1980s. Thus, each 2-week period consists of potentially 240 mass weights (60 baskets × 4 litter types) and eight samples for elemental analyses (2 composited subsamples × 4 litter types).

Ground samples (18 mesh screen, Wiley Mill) were analysed for C and N by combustion using either a LECO TruSpec CN Analyzer (samples collected 1989 to March 1995, and after June 2007) or a LECO CNS-2000 Analyzer (April 1995 to June 2007). LECO tobacco leaves were used for calibration, with additional certified standards used to track potential inter-annual bias. For example, standard alfalfa leaf [N] varied randomly across years from expected values by ≤1.5%. Biweekly C and N concentrations (dry weight (65°C) basis) for each litter type are weighted by masses for the two subsamples.

2.5 | Stream chemistry

Stream water nitrate-[N], the dominant fraction of dissolved N in the Bisley watersheds, was measured biweekly from the two watersheds (referred to in previous publications as Bisley 1 or Q1 and Bisley 2 or Q2). Samples were filtered (pre-combusted glass fibre filter, Whatman GF/F), immediately frozen, and analysed using either spectrophotometry (1989) or ion chromatography (1990–2017). Details are provided in McDowell et al. (2021).

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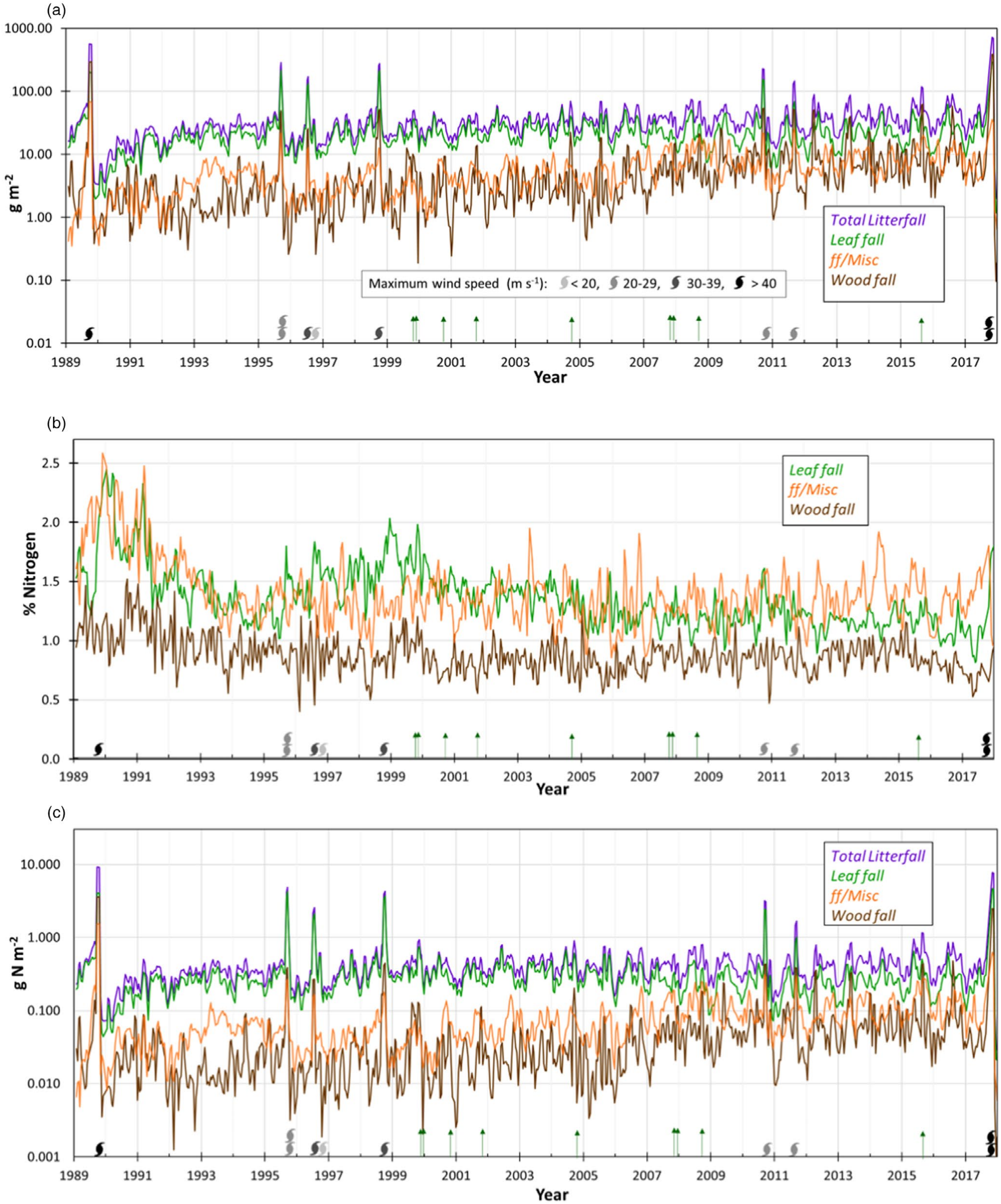

FIGURE 1 Moving average (roughly monthly) trend lines for litterfall mass (a), N concentrations (b) and litterfall N mass (c) over the 29 years. Hurricane symbols and green arrows indicate hurricanes and tropical storms, respectively. Graded scale of hurricane symbols plotted on (a) show wind speed at Bisley or at landfall (see Table 1). Nonparametric fitted lines on annual means used to calculate relative change (Helsel & Hirsch, 2002): for (a), total litterfall = −43132.8 + (22.0 × year); for (b), leaf fall [N] (%) = 39.8577 + (−0.01923 × year), wood fall [N] (%) = 12.853 + (−0.006 × year); and for (c), annual N litterfall mass = −261.628 + (0.1361 × year).

2.6 | Calculations and statistics

2.6.1 | Biweekly (2-week) data

Litterfall was based on the means of all baskets. Biweekly element inputs per litter type (mass times concentration) were calculated as the sum of inputs. If insufficient samples were available for analyses, C and/or N concentrations were modelled from significant linear correlations between the two subsamples for each litter type. Because of a potential bias distinguishing fruits and flowers from miscellaneous litter over time, here, they are combined and indicated as *ff-misc*. Element concentrations for *ff-misc* are weighted by the masses of each component.

Stream nitrate-[N] was expressed as flow-weighted averages for each biweekly period. When either stream was not flowing during the biweekly sampling period, the values from the flowing stream were used. When both streams were dry or data were not available, the biweekly period was not included in the stream chemistry record.

2.6.2 | Monthly and annual data

Monthly litterfall was calculated from biweekly data. For collections straddling 2 months, mass was apportioned by the number of days falling within a month. Annual litterfall was calculated by summing across the 12 months (Table S2). Data were missing from two collections (in August 2008 and July 2016) and not infilled for monthly or annual totals.

For streams, mean annual nitrate-[N] was calculated as the average of flow-weighted concentrations for each sampling period, except for 1994–1996 lacking sufficient data. Annual nitrate-[N] fluxes were calculated as the annual nitrate-[N] times annual stream runoff for each calendar year.

2.6.3 | Statistics

We analysed broad temporal trends (1989–2017) on annual means of litterfall and stream chemistry using the nonparametric Mann-Kendall test, which assesses monotonic trends and has advantages over parametric tests as it is robust against non-normality and extreme values (i.e. those produced during hurricanes) (Helsel & Hirsch, 2002). Kendall's tau (τ) measures the degree of association between two samples, with the associated slope following Sen (1968). Nonparametric fitted lines were calculated following Helsel and Hirsch (2002) and used to estimate relative change over time.

We assessed finer-scale post-hurricane temporal trends (i.e. recovery) in leaf fall and fine wood fall (the largest contributors to litterfall) and leaf fall [N] (dominating N inputs) after three hurricanes with the longest times until the next hurricane: post-Hugo (1989, 6 years hurricane free), post-Georges (1998, 12 years hurricane free) and post-Irene (2011, 6 years hurricane free). Of these hurricanes, Hugo was the strongest (wind speed at landfall 43.8 m s^{-1}), followed by Georges (maximum wind speed at Bisley 32.5 m s^{-1}), then Irene (maximum wind speed at Bisley 21.5 m s^{-1}). To avoid including hurricane-generated litterfall in these analyses, we removed the first 100 days from the time series. First, we tested for serial autocorrelation with the Durbin–Watson statistic; if significant, autoregressive error term(s) were accounted for in regressions. If autocorrelation was not apparent, we used ordinary least squares regression. Responses were modelled as a function of days since a hurricane, and if significant, we added a squared term to account for levelling off. Model residuals were checked for normality; outliers showing high influence were removed from final models.

We accounted for seasonality of leaf fall (see Figure S2) in regressions using the following variable, which places peak fall between May and June in the absence of hurricanes:

$$\text{CosVar1} = \cos\left(2 \times \pi \times (\text{Julian date} - 151) / 365\right). \quad (1)$$

For woody litter containing multiple peaks (Figure S2) or for leaf fall [N] with a broad peak from October–March, we modelled seasonality with the general periodic function (Helsel & Hirsch, 2002):

$$\text{CosVar2} = \cos\left(2 \times \pi \times \text{Julian date} / 365\right). \quad (2)$$

To examine how hurricane-generated leaf fall and wood fall changed with maximum wind speed and time since a previous hurricane, we conducted regression analyses. Because of the temporal dynamics of fine wood decay (mineralizing N after a year, Jones et al., 2019), we assessed the effect of the previous year's fine wood fall or its [N] on leaf fall [N] following the same protocol. Mean annual stream nitrate-[N] was compared to annual litterfall, wood fall and litterfall N inputs, and leaf fall [N] and peak hurricane stream nitrate-[N] was compared to hurricane leaf fall [N] using correlation analysis.

Statistical analyses were performed in SAS (version 9.4, SAS Institute Inc., Cary, NC, USA), except for Sen's slope, calculated using an Excel add-on (Real Statistics). Residuals from multiple regressions were checked for normality. Variables were ln-transformed if necessary. This study meets all permit requirements as per USDA FS Forest Service Manual 4062.14.

3 | RESULTS

3.1 | Hurricane litterfall and annual summaries

Surges in litter production over the 29 years corresponded to hurricanes and tropical storms (Figure 1a). Eight of the nine hurricanes (with hurricanes Irma and Maria combined, hereafter 'Hurricane Maria') produced leaf fall close to or greatly exceeding 100 g m^{-2} collection^{-1} (Table 1; Figure 1a), an amount only exceeded by one tropical storm (2015, Erika, 178 g m^{-2}). Litterfall from the two strongest hurricanes, Hugo (1989, Cat 3) and Maria (2017, Cat 4), occurring during the first and last years of the study, exceeded the 29-year annual average of 951 g m^{-2} year^{-1} by 15% and 46%, respectively (Tables 1 and 2). Similarly, wood fall from hurricanes Hugo and Maria exceeded the 29-year annual average by over 200% and 300%, respectively (Tables 1 and 2). On

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TABLE 2 Average annual ($n=29$, + SE) litterfall and litterfall N and C ($g\,m^{-2}\,year^{-1}$) for total litter and litter classes.

Input type	Total	Leaves	Wood	*FF-Misc*
Litterfall mass	951.2 (63.9)	612.7 (32.1)	188.2 (33.5)	150.2 (11.8)
N mass	12.0 (0.82)	8.37 (0.55)	1.59 (0.29)	2.04 (0.16)
C mass	480.4 (32.1)	308.9 (16.4)	96.4 (16.8)	75.1 (5.9)

average, hurricanes produced 53%, 43%, 105% and 33% of the 29-year average annual litterfall, leaf fall, wood fall and *ff-misc*, respectively (Tables 1 and 2).

Leaf fall averaged 53% of hurricane-generated litterfall, with wood fall averaging 39% (Table 1); this contrasts with the 29-year average, with leaf fall comprising 64% and wood fall 20% of total litterfall inputs (Table 2). Wood fall surpassed 50% of hurricane-generated litterfall with the strong hurricanes Hugo (1989) and Maria (2017), contributing to high variation (Table 1). Litterfall from Hurricane Hortense (1996, Cat 1, and with the lowest maximum wind speed of the hurricanes) was substantially less than the other hurricanes and had the lowest proportion and amount of wood fall (Table 1). Two months before hurricane Hortense, Hurricane Bertha (1996, Cat 1, with maximum wind speeds more than twice those of Hortense) resulted in litterfall nearly five times that of Hortense and with a greater proportion of wood fall. Two other back-to-back hurricanes (1995, Luis and Marilyn) had similar peak winds, yet litterfall was 70% less for the second hurricane. Litterfall from Hurricane Irene (2011, Cat 1), occurring a year after Hurricane Earl (2010, Cat 4, though with maximum wind speeds like Irene's), continued a trend of increasing wood fall for hurricanes (Table 1). In 2015, the strong tropical storm Erika (maximum wind speed of $16.9\,m\,s^{-1}$) resulted in litterfall of $178\,g\,m^{-2}$, 65% of which was wood fall, the highest proportion of any hurricane or tropical storm.

Taken together, maximum hurricane wind speed explained 73% ($p=0.003$) and 77% ($p=0.002$) of the variation in hurricane-generated leaf fall and wood fall, respectively (Figure 2a). Similarly, time since a previous hurricane explained 59% ($p=0.016$) and 72% ($p=0.004$) of the variation in leaf fall and wood fall, respectively (Figure 2b). Litterfall from the less intense tropical storms (mean maximum wind speed $=12.5\,m\,s^{-1}$, $n=8$) was nearly an order of magnitude less than from hurricanes, averaging 66, 32 and $25\,g\,m^{-2}$ for total litterfall, leaf fall and wood fall, respectively (Table S1). Nonetheless, tropical storm wind speed explained 53% ($p=0.039$) and 60% ($p=0.024$) of the variation in leaf and wood fall, respectively.

Annual litterfall was also highly variable because of hurricanes, with a high of $2001\,g\,m^{-2}$ in 2017, the year of the strongest hurricane, Hurricane Maria, to a low of $284\,g\,m^{-2}$ in 1990, the year following the second strongest hurricane, Hurricane Hugo (Table S2, also showing high within-year variation for hurricane years. Litterfall for 2017 may be underestimated given the 76-day delay in collecting litterfall). However, the greatest input of N ($26.2\,g\,N\,m^{-2}$) occurred the year of Hurricane Hugo, 1989, rather than in 2017. Like total litterfall, the lowest N input occurred in 1990 ($4.9\,g\,N\,m^{-2}$) (Table S2).

Hurricane-generated litterfall N averaged $7.03\,g\,m^{-2}$, over half the annual average (Tables 1 and 2). Average annual litterfall N was only exceeded with hurricanes Hugo (1989) and Maria (2017) by 50% and 25%, respectively (Tables 1 and 2). Leaf fall contributed 70% of the 29-year average litterfall N inputs, followed by *ff-misc* and wood at 17% and 13%, respectively (Table 2).

The leaf fall/wood fall ratio also changed across years: lowest in 1989 and 2017, years of the strong hurricanes with their high wood fall and highest in 1992–1993 reflecting low wood fall and the rebound in leaf fall several years after Hugo (from Table S2). Shifts after other hurricanes were less dramatic but followed similar patterns, with relatively low leaf fall/wood fall ratios during hurricane years and increasing afterwards (Table S2 and see next section). Throughout the relatively quiet hurricane years in the 2000s, the leaf fall proportion fell to around 50% while the wood fall proportion increased to around 25% (from Table S2). Due to the low variation in [C] among the three litter classes (29-year means range: 50.2%–51.9%), their relative C inputs were equal to their proportional mass contributions.

3.2 | Broad temporal trends

Based on our nonparametric analyses, total litterfall nearly doubled (a 98% increase) over the 29 years (*analysis on untransformed annual means*, $\tau=0.591$, $p<0.0001$, $n=29$), due to increases in wood fall ($\tau=0.596$, $p<0.0001$) and the *ff-misc* class ($\tau=0.532$, $p<0.0001$) (Figure 1a). Leaf fall, the largest component of litterfall, showed no increase over the 29 years ($p=0.06$), despite increases in the early years (Figure 1a, Table S2, and next sections).

Mean annual N concentrations decreased over the 29 years for litter classes except *ff-misc* ($p=0.13$). Leaf fall [N] (29-year *mean* [N] = 1.37%) ($\tau=-0.596$, $p<0.0001$, $n=29$, Figure 1b) decreased by 33%, while fine wood fall [N] (29-year *mean* [N] = 0.86%) decreased by 18% ($\tau=-0.537$, $p<0.0001$). Leaf fall C/N mass ratios (*mean* = 37.6, data not shown) increased ($\beta=0.572$, $\tau=0.606$, $p<0.0001$), reflecting changes in N rather than C concentrations. Mean annual litterfall N inputs increased by 42% over the 29 years ($\tau=0.299$, $p=0.023$, Figure 1c, Table S2), from increases in woody and *ff-misc* litter N inputs ($\tau=0.520$, $p<0.0001$ and $\tau=0.510$, $p=0.0001$, respectively) as driven by their mass inputs. Annual leaf fall N inputs showed no change ($p=0.837$).

3.3 | Detailed post-hurricane trajectories

Litterfall after individual hurricanes (Figure 3, listed in order of occurrence) showed the immediate surge and subsequent decrease of total litterfall (Figure 3a), leaf fall (Figure 3b) and wood fall (Figure 3c). While leaf fall [N] in the 3 months immediately following hurricanes demonstrated the expected short-term increase, several hurricanes showed additional (though lesser) peaks around 1.5 years (Figure 3d).

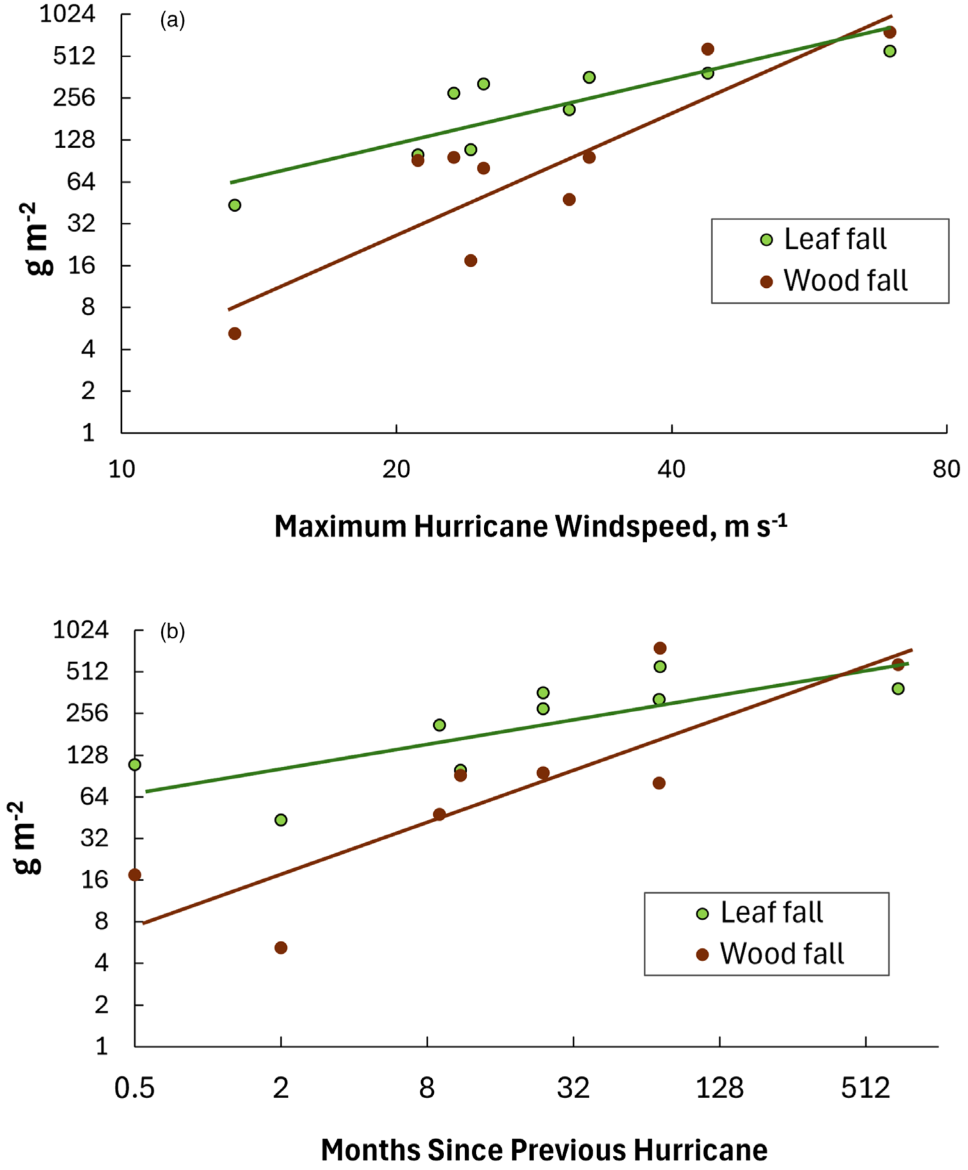

FIGURE 2 Hurricane-generated leaf fall and wood fall as a function of (a) maximum hurricane wind speed and (b) time since a previous hurricane. For (a), Log_2Leaf fall = 1.487Log_2X + 0.52, R^2 = 0.728, p = 0.003; Log_2Wood fall = 2.896Log_2X − 7.663, R^2 = 0.771, p = 0.002. For (b), Log_2Leaf fall = 0.2958Log_2X + 6.460, R^2 = 0.587, p = 0.016; Log_2Wood fall = 0.6218Log_2X + 3.716, R^2 = 0.723, p = 0.004. For Hurricane Hugo we used 1932 for the previous hurricane (from Scatena & Larsen, 1991). Litterfall from hurricanes Irma and Maria are combined. Wind speeds for hurricanes Hugo and Irma were recorded at landfall, likely higher than at Bisley (see text).

Further analyses after the three hurricanes with the longest time trajectories lacking additional hurricanes (post-Hugo (1989), post-Georges (1998) and post-Irene (2011)) allowed us to track the individual recovery patterns of litterfall, ignoring the immediate inputs from the hurricanes (first 100 days). Litterfall trajectories varied by hurricane, showed seasonal variation (Table 3), and exhibited first order serial correlations (see methods, data not shown). Leaf fall post-Hugo (Cat 3) responded strongly with time since the hurricane (Table 3) indicating rapid recovery, with the significant (negative) polynomial term suggesting eventual slowing. Leaf fall post-Georges (Cat 3) responded similarly, though at less magnitude than for post-Hugo. Post-Irene (Cat 1), leaf fall did not change with time; mean leaf fall was equal across the post-Georges and post-Irene trajectories (Table 4). Fine wood fall increased post-Hugo and post-Georges (Table 3), but not post-Irene, suggesting wood fall may have stabilized after initial hurricane inputs with Irene. Fine wood fall increased over 300% during recovery from the intense and earlier Hurricane Hugo (1989) to the least intense and most recent recovery post-Irene (Table 4; Figure 3c). Average leaf fall/wood fall ratios for the post-Hugo, post-Georges and post-Irene trajectories were 7.3, 4.9 and 2.4, respectively. Leaf fall [N] post-Irene was the lowest among hurricanes (Figure 3d; Table 4) and, as with leaf fall and wood fall, showed no consistent temporal trend after the first 100 days (Table 3). Overall, the lower intensity of Hurricane Irene (Cat 1, Table 1) enabled fast litterfall rebound (Figure 3a), continued high fine wood fall (Figure 3c) and maintained low leaf fall [N] (Figure 3d).

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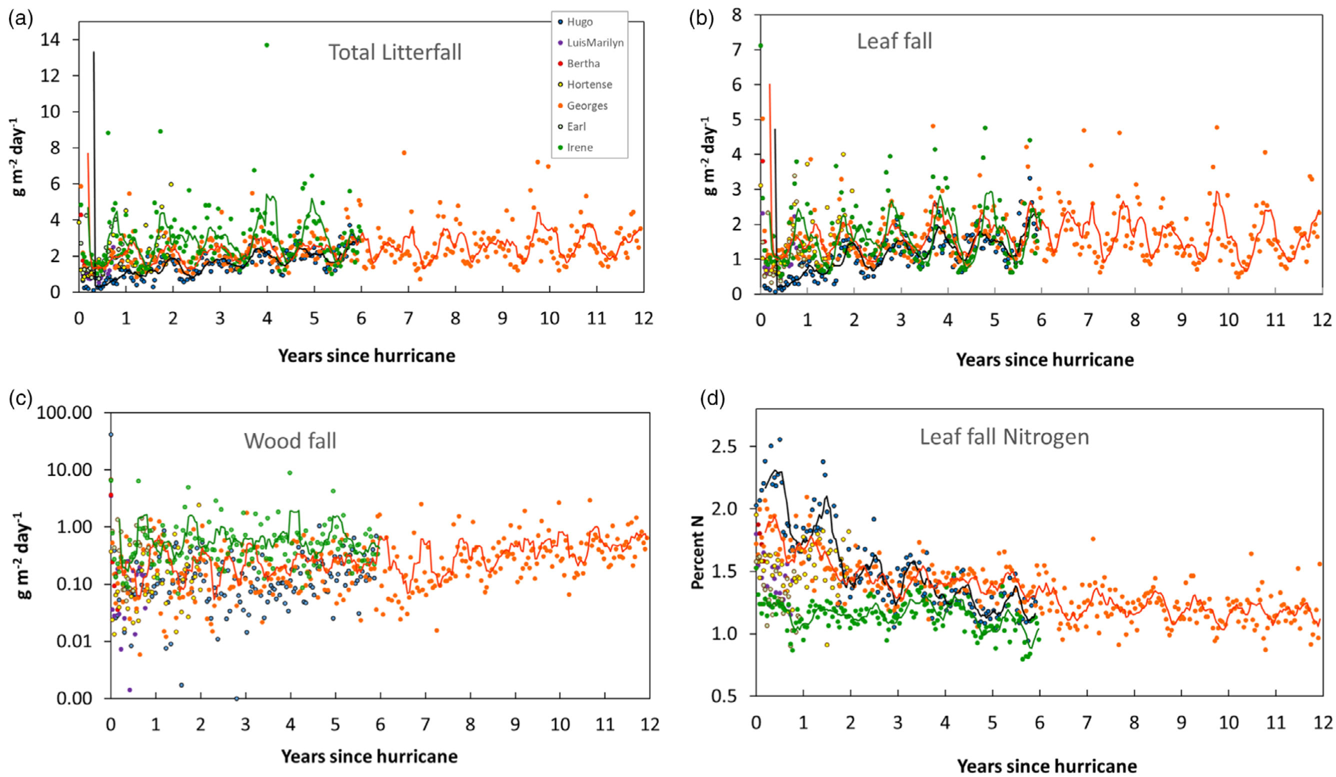

FIGURE 3 Litterfall dynamics after individual hurricanes for (a) total litterfall, (b) leaf fall, (c) wood fall and (d) leaf fall N concentrations. Trajectories for individual hurricanes continue until the next hurricane. The 2017 hurricanes are not included because of lack of reliable daily rates for the first collection post-hurricane (see text). Lines for hurricanes with the longest trajectories (Hugo, Georges, and Irene) are 3-month moving averages; omitted in (c) for Hugo as seasonality was not significant (see Table 3). For (a), the first collection of litterfall is off scale for Hugo (78.5 $g\,m^{-2}\,day^{-1}$), Luis and Marilyn (20.5 $g\,m^{-2}\,day^{-1}$), Bertha (21.7 $g\,m^{-2}\,day^{-1}$), Georges (34.1 $g\,m^{-2}\,day^{-1}$), Earl (29.3 $g\,m^{-2}\,day^{-1}$) and Irene (15.9 $g\,m^{-2}\,day^{-1}$). For 3b, the first collection of leaf fall is off scale for Hugo (27.6 $g\,m^{-2}\,day^{-1}$), Luis and Marilyn (15.5 $g\,m^{-2}\,day^{-1}$), Bertha (16.2 $g\,m^{-2}\,day^{-1}$), Georges (25.8 $g\,m^{-2}\,day^{-1}$) and Earl (19.9 $g\,m^{-2}\,day^{-1}$). Note the different collection times post-hurricane for hurricanes Luis, Marilyn and Maria (Table 1).

3.4 | Stream nitrate

Stream nitrate-N concentration ([N]) varied little with flow and was highly correlated with stream N fluxes ($r=0.701$, $p=0.0003$, $n=28$), hence we focus on nitrate-[N] hereafter. Stream nitrate-[N] increased following hurricanes (Figure 4), peaking on average 88 days later. Like leaf fall [N], mean annual stream nitrate-[N] decreased over time ($\tau=-0.471$, $p=0.0007$, $n=26$). Mean annual stream nitrate-[N] was strongly correlated with mean annual leaf [N] ($r=0.706$, $p<0.0001$, $n=26$; Figure 5), but not with total litterfall, N mass inputs, or any of the wood fall characteristics ($p>0.05$). Peak stream nitrate-[N] after hurricanes was highly correlated with hurricane leaf fall [N] ($r=0.865$, $n=6$; Figure 5 inset).

4 | DISCUSSION

4.1 | Hurricane litterfall dynamics

Annual litterfall varied sevenfold over the 29 years in this wet tropical forest (Table S2), providing an extraordinary opportunity to address the fundamental drivers of temporal variability in litterfall. Clearly, hurricanes and their aftermath are key influences, with high litterfall during hurricanes (and hurricane years) and low litterfall immediately following (Figure 1a; Table S2), as in cyclone-impacted areas elsewhere in the tropics (Lin et al., 2003, 2017; Martínez-Yrízar et al., 2018). Collectively, these studies point to the dynamic nature of litterfall in cyclone-prone regions.

Here we show that variability in hurricane-generated leaf and wood fall is driven by a combination of maximum local wind speed during hurricanes and time since a previous hurricane, confirming our initial hypothesis. We also found a significant, though much reduced, effect of maximum wind speed on leaf fall and wood fall during the less intense tropical storms. Maximum site wind speed integrates effects of hurricane path and topography (Boose et al., 2004; Van Beusekom et al., 2018) and is a well-established influence on hurricane litterfall (Beard et al., 2005; Bomfim et al., 2022; Ibanez et al., 2024; Lin et al., 2003, 2017). For example, the two strongest hurricanes, Hugo and Maria, occurring during the first (1989) and final years (2017) of our study, had the highest amounts of leaf fall and wood fall, the largest proportions of wood fall and the lowest leaf fall/wood fall ratio of the hurricanes. Moreover, of the nine hurricanes occurring over the 29 years, only these two hurricanes yielded wood fall that exceeded the 29-year average. For both

TABLE 3 Regression coefficients (*p*-values) for three post-hurricane trajectories.

Litter component	Hurricane	Seasonality	Days since	Days since SQ	R^2 transformed	R^2 adj.
Leaf fall $g\,m^{-2}\,day^{-1}$ (ln)	Hugo	0.219 (0.032)	0.0022 (<0.0001)	-6.8×10^{-7} (<0.0001)	0.46	na
	Georges	0.290 (<0.0001)	0.0003 (0.015)	-5.6×10^{-8} (0.015)	0.14	na
	Irene	0.396 (<0.0001)	NS	NS	0.17	na
Wood fall $g\,m^{-2}\,day^{-1}$ (ln)	Hugo	NS	0.0004 (0.0054)	NS	0.06	na
	Georges	0.250 (0.002)	0.0003 (<0.0001)	NS	0.22	na
	Irene	−0.299 (0.0011)	NS	NS	na	0.07
Leaf fall N % (ln)	Hugo	0.085 (<0.0001)	−0.0006 (<0.0001)	1.4×10^{-7} (0.0001)	0.64	na
	Georges	0.053 (<0.0001)	−0.0002 (<0.0001)	1.9×10^{-8} (0.0040)	0.40	na
	Irene	0.070 (<0.0001)	NS	NS	0.20	na

Note: The R^2 transformed measures model fit after accounting for autocorrelation; estimates determined by maximum likelihood. If autocorrelation was not indicated, the adjusted R^2 is shown. NS = not significant at $\alpha = 0.05$. Sample sizes reported on Table 4.

TABLE 4 Means (+ SE), after the first 100 days, of litterfall ($g\,m^{-2}\,day^{-1}$) and [N] (%) during recovery after three hurricanes with the longest periods without additional hurricanes, listed in order of occurrence.

Hurricane	No. collections	Total litterfall	Leaf fall	Wood fall	Leaf fall [N]	Wood fall [N]
Hugo	145	1.60 (0.059)	1.19 (0.048)	0.163 (0.013)	1.48 (0.027)	1.00 (0.021)
Georges	303	2.43 (0.059)	1.66 (0.043)	0.342 (0.023)	1.33 (0.012)	0.84 (0.010)
Irene	147	2.95 (0.136)	1.66 (0.075)	0.692 (0.087)	1.14 (0.010)	0.84 (0.012)

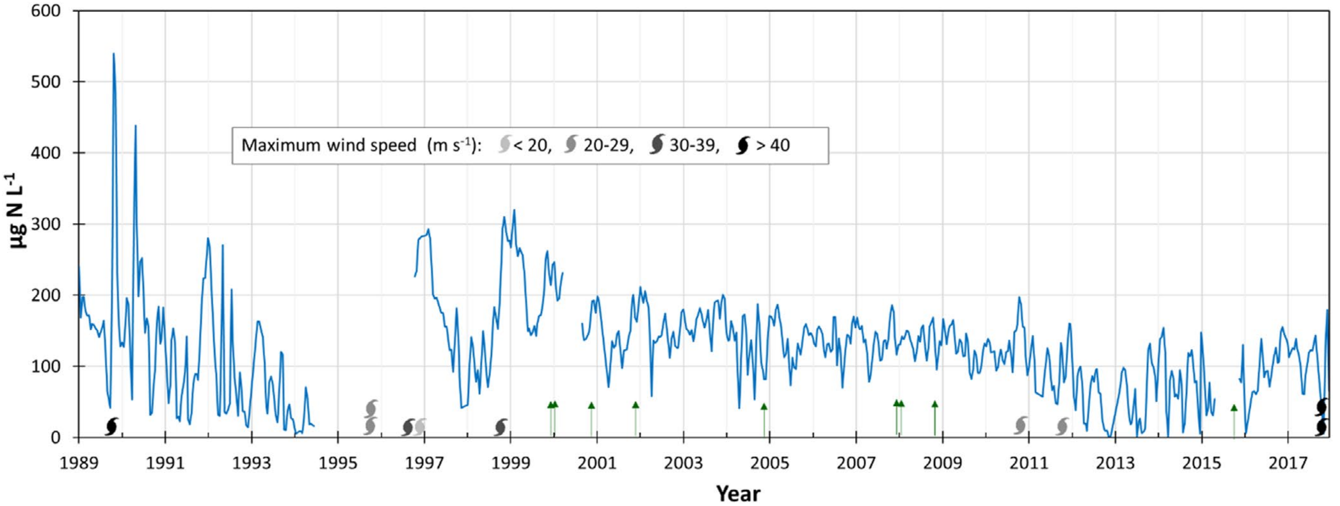

FIGURE 4 Moving average (roughly monthly) trend line of flow-weighted average concentrations of stream water nitrate-N from two sub-catchments in Bisley. A break in the trend line indicates ≥10 missing consecutive observations. Hurricane symbols and green arrows show hurricanes and tropical storms, respectively.

hurricanes, nearly two decades or more had passed since a prior hurricane with wind speeds $>30\,m\,s^{-1}$ had occurred. In an area close to our study, Liu et al. (2018) also documented high wood fall from the 2017 hurricanes compared to estimates made 1 year prior, consistent with exceptional tree damage and branch litterfall from intense hurricanes (Ibanez et al., 2024; Lin et al., 2017).

While largely intuitive, to our knowledge this is the first study to show the combined effects of wind speed and time since a previous hurricane on litterfall at a single site. Bomfim et al. (2022) found that as modelled wind speed increased, litterfall resistance (cyclone litterfall/pre-cyclone litterfall) decreased. In our case, time since the previous hurricane may be a proxy for pre-hurricane litterfall, which may be difficult to assess where litterfall varies seasonally (Figure S2) and is a moot point when hurricanes occur at very short intervals. For example, hurricanes Luis and Marilyn (both September 1995) had similar peak winds at Bisley, but litterfall (and total and proportional wood fall) was much lower with Marilyn than with the earlier Luis, as much of the litter was brought down with Luis.

The rise and fall in litter N concentrations [N] (Figures 1b and 3d), litterfall N flux (Figure 1c) and stream nitrate-[N] (Figure 4) that we have documented after multiple hurricanes is consistent with our current understanding of factors driving their dynamics. The lack

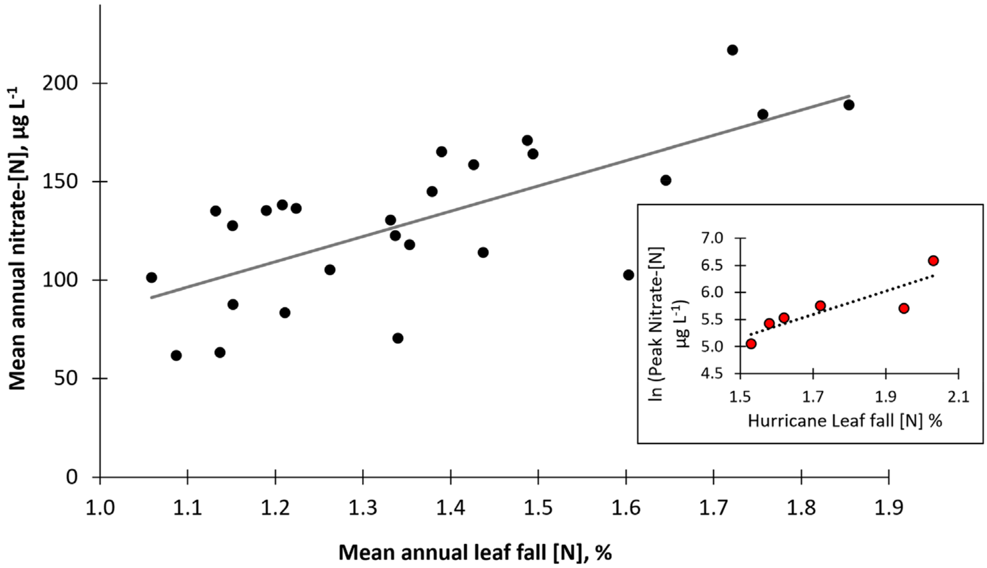

FIGURE 5 Mean annual stream nitrate-[N] versus mean annual leaf fall [N] ($r=0.706$, $p<0.0001$, $n=26$). Excluding hurricane years retained the significant correlation ($r=0.675$, $p=0.0008$, $n=21$). Inset: Hurricane-generated peak stream nitrate-[N] versus hurricane leaf fall [N] ($r=0.865$, $p=0.026$).

of leaf senescence and nutrient resorption in hurricane leaf litter enables greater concentrations than in senesced litterfall (Bomfim et al., 2022; Lodge et al., 1991; Wang et al., 2013; but see Lin et al., 2003; Martínez-Yrízar et al., 2018). Hurricane-produced leaf fall decomposes and mineralizes faster than senesced leaf fall (Fonte & Schowalter, 2004; González et al., 2014); taking less than a year at sites close to Bisley (Ostertag et al., 2003; Vogt et al., 1996). The rapid release of N from this green litter, combined with a decrease in N demand by a hurricane-diminished canopy (Scatena et al., 1996; Schaefer et al., 2000), leads to greater soil inorganic N pools often dominated by mobile nitrate (Erickson & Ayala, 2004; Gavito et al., 2018; McDowell & Potter, 2022; Reed et al., 2020; Silver et al., 1996; Steudler et al., 1991), resulting in nitrate leaching (this study; McDowell et al., 2013; McDowell & Liptzin, 2014; Schaefer et al., 2000) and increased emissions of nitrous oxide (Erickson & Ayala, 2004; Quebbeman et al., 2022; Steudler et al., 1991). High litter [N] several months post-hurricanes (Figures 1b and 3d) may be due to green leaves detached by hurricanes not immediately reaching the forest floor (Lodge et al., 1991). In Taiwan where litter [N] often changes little with typhoon disturbances, increased stream water N lasts only days (Lin et al., 2011) not months, which these authors attribute to low overstory mortality, fast regrowth of understory vegetation and exceptionally low decomposition rates for the subtropics.

The peaks in leaf fall [N] 1.5 years after hurricanes Hugo, Hortense and Georges (Figure 3d) may correspond to early successional, light-demanding species gaining dominance locally (Brokaw et al., 2012; Shiels et al., 2010), with higher foliar [N] than low-light adapted species (Heartsill Scalley et al., 2010; Uriarte et al., 2015). The peaks in leaf fall [N] after Hurricane Hortense were somewhat surprising in that maximum wind speeds and litterfall were the lowest with this hurricane (Table 1). Likely the sustained high leaf fall [N] from Hurricane Hortense is a legacy from the three back-to-back hurricanes occurring over the previous year, maintaining conditions suitable for high N availability (open canopy, high foliage production).

The eventual decrease in litter [N] a few years after the initial surges (Figures 1b and 3), previously documented at the site after Hurricane Hugo (Scatena et al., 1996), is consistent with the decreases in atmospheric and fluvial export of N noted after other hurricanes (Erickson & Ayala, 2004; Schaefer et al., 2000; this study). As the large mass of hurricane-generated fine wood fall (<2.5 cm diameter) begins to decompose, it likely contributes to lower N availability via N immobilization (Herbert et al., 1999; Jones et al., 2019; Smith et al., 2011). Moreover, the large-diameter (>2.5 cm) hurricane-generated wood fall that we did not measure was likely substantial with high wind speeds. These slowly decomposing branches and boles can also withdraw N from the soil pool due to microbial immobilization (Zimmerman et al., 1995). Early stand development and recovery from hurricanes favours foliage over wood production (Brandeis & Woodall, 2008; Weaver & Gillespie, 1992), seen in the high leaf fall/wood fall ratios we note in the early years following hurricanes. Production of leaves requires relatively large amounts of N compared with wood, likely contributing to the subsequent decreases in soil nitrate and leaching a few years following disturbance (McDowell & Liptzin, 2014; Silver et al., 1996).

4.2 | Hurricane recovery and long-term trends

At Bisley, litterfall increased over the 29 years due to increases in wood fall and *ff-misc* but not leaf fall. The observed increase in wood fall (and lowering of the leaf fall/wood fall ratio) is likely due to the reduced hurricane intensities and frequencies later in our study (except for the final year) allowing development of a more mature canopy. Others have shown increases in litterfall with secondary succession (Aryal et al., 2015; Lohbeck et al., 2015) yet examining multi-decadal shifts in litterfall components is uncommon. Consistent with our findings, twig fall increased with forest succession in a semi-evergreen forest in SE Mexico (Aryal et al., 2015) and the relative importance of leaf fall decreased from secondary forest to old growth in Brazilian Atlantic forests (Martinelli et al., 2017). These general findings contrast with a 17-year litterfall record in typhoon-affected Taiwan, which showed that increases in total litterfall were mainly due to increases in leaf litter and a miscellaneous category, but not to changes in woody litterfall (Lin et al., 2017). These authors attribute the observed increases partly to increases in typhoon frequency, which did not occur in the latter part of our study.

Our study reveals the effects of important nuances in disturbance history and hurricane intensity on litterfall dynamics during hurricane recovery. The three post-hurricane trajectories we track (post-Hugo (1989), post-Georges (1998), post-Irene (2011)) were initiated with varying intensity, with Hurricane Hugo > Hurricane Georges > Hurricane Irene (Table 1). Although leaf fall was unchanged when analysing over the 29 years of record, these finer event-scale analyses revealed leaf fall increased relatively rapidly post-Hugo, levelled out post-Georges and remained unchanged post-Irene, suggesting stabilization of canopy production during recovery after Georges and occurring earlier than stabilization of wood production.

Natural stand thinning (c.f. Lugo, 2008) likely contributed to the increase in wood fall that we observed during recovery post-Hugo and post-Georges and the continued high wood fall post-Irene. Delayed hurricane-induced mortality could also contribute to wood fall several years after hurricanes (Brokaw et al., 2012). At our site, basal area and tree biomass recovered after 15 years post-Hugo (4 years post-Georges), yet stem density exceeded pre-hurricane levels by almost 80% (Heartsill Scalley et al., 2010). Increases in stem densities after hurricanes reflect infilling into areas receiving more light exposure (Ibanez et al., 2019; Shiels et al., 2010), and as more biomass is allocated to structural tissues during continued stand development (Aryal et al., 2015; Lohbeck et al., 2015), wood fall increases with density-dependent mortality (Lugo, 2008) and branch turnover. The less intense Hurricane Irene affected a well-developed woody canopy and enabled continued fine wood fall during recovery. The 2015 tropical storm Erika (occurring during the post-Irene trajectory) with the highest proportion of wood fall to total litterfall of any tropical storm or hurricane also points to a highly developed wood-rich canopy. At a neighbouring forest, Brokaw et al. (2012) reported its canopy returned to its former smoothness 18 years after Hurricane Hugo, consistent with canopy and wood production stabilization at that site.

Forests of northeastern Puerto Rico are considered resilient, returning relatively rapidly to pre-disturbance conditions (c.f. Bomfim et al., 2022) after hurricanes (Brokaw et al., 2012; Ostertag et al., 2003; Zimmerman et al., 2021). Our data show that wood fall is slow to recover to pre-hurricane rates, taking at least 22 years after Hurricane Hugo (1989). The mean leaf fall/wood fall ratio of 2.4 for the post-Irene (2011) period is remarkably close to an estimate made for the pre-Hugo years of 2.34 (calculated from Lodge et al., 1991), considered a stable forest with peak wood production. The similar values (and sustained high wood fall after Hurricane Irene) provide further evidence that wood fall had presumably stabilized during the final years of our study. Results from these analyses confirm the previously proposed slow recovery of wood fall based on limited temporal data (Scatena et al., 1996) and simulation modelling (Zimmerman et al., 1995).

Litter [N], especially leaf litter [N], marks another exception to presumed resiliency and suggests resiliency is highly dependent on temporal scale. Contrary to our hypothesis (2b), we found a substantial, multidecadal decrease in litterfall [N] for Bisley—around a 33% decrease for leaf fall [N]. Previous studies have based recovery on the return to pre-disturbance conditions on limited pre- and/or post-disturbance data, perhaps only months or several years (e.g. Scatena et al., 1996). Only with our long-term data were we able to observe the slow decline in litter fall [N] over several decades. To our knowledge, this is the first documented case of a long-term decrease in litterfall [N] for a tropical forest.

These responses may be partly explained by the expected loss of N-rich early successional species (Heartsill Scalley et al., 2010; Uriarte et al., 2015), and a potential decline of symbiotic N fixation with canopy closure (McCulloch & Porder, 2021; Taylor & Menge, 2018). At Bisley, the dominant N-fixing legume (*Inga laurina*) represented 3.9% of tree biomass immediately post-Hugo (1989), decreasing to 1.5%, 15 years later (Heartsill Scalley et al., 2010). In a survey across Puerto Rico, Erickson et al. (2014) found stand-scale fallen leaf [N] decreased with stand age and with the declining basal area of putative N-fixing legumes. Although symbiotic N fixation may be responsible for the initially high N status in many tropical forests (Batterman et al., 2013; Erickson et al., 2001; Winbourne et al., 2018), legume basal area does not always correlate with symbiotic N fixation (Taylor et al., 2019). Ardón et al. (2023) found that growth of streamside N-fixing legumes in Costa Rica correlated positively with stream nitrate concentrations, indicating that at their site legumes played a role in stream N flux. In a lowland forest in Costa Rica, canopies with high N (and high leaf fall [N]) were unrelated to legume abundance or asymbiotic N fixation, suggesting unique species assemblages may also account for differences in N cycling (Osborne et al., 2020). Given the low abundances of legumes at Bisley, the decadal decreases in leaf fall [N] that we observed may be driven more by transitions to less N-rich, shade-tolerant species.

A second possible explanation for the decrease in leaf fall [N] is the high amount of hurricane-generated wood fall we noted after Hurricane Hugo and the over 300% increase in fine wood fall we documented during the recovery after Hurricane Hugo up to Hurricane Maria (1989–2017, Table 4). Both the initial wood fall from Hurricane Hugo (1989) and the increase during recovery reflect a concomitant increase in the amount of N potentially immobilized by wood fall, limiting the N available for plant uptake and other ecosystem processes (Luo et al., 2004; Zimmerman et al., 1995). Omitting the 8 years with hurricane-generated wood fall, we found a negative relation between leaf fall [N] and previous year wood fall ($r = -0.66$, $p = 0.003$, Figure 6). Some of the high leaf fall [N]/low wood fall values reflect years following hurricanes, yet the trend of high wood fall coupled with lower leaf [N] occurs across the range of wood fall values.

Adding previous years wood fall [N], we found the following (adjusted $R^2 = 0.53$, $p = 0.0014$):

$$\text{Leaf fall } [N] = 1.89 - 0.113\,(\ln \text{ previous year wood fall}) + 0.462\,(\ln \text{ previous year wood fall } [N]). \quad (3)$$

This suggests positive feedback between fine wood fall quality and [N] in leaves; woody litter with lower N would mineralize more slowly than higher quality woody litter (Jones et al., 2019; Tian et al., 1992; Weedon et al., 2009), contributing to the lower leaf litter [N] (and reduced N availability) that we see over the long term. In addition, large-diameter wood fall, not measured in this study, decomposes more slowly than smaller pieces (van Geffen et al., 2010; Vogt et al., 1996), contributing to N immobilization and delayed release (Lodge et al., 2016; Nagy et al., 2017; Zimmerman et al., 1995). The shift from low to high density wood noted during wet forest succession (Poorter et al., 2019; van Gelder et al., 2006) also increases the resistance of wood to decay and N release (Chambers et al., 2000). Despite these plausible mechanisms related to stand development, the role of large wood in N cycling processes after hurricanes and during succession in the tropics remains largely unexplored (Giardina, 2019), although aspects have been addressed locally (Lodge et al., 2016; Torres & González, 2005; Zalamea et al., 2007, 2016). Given the opposite trends between wood fall and leaf fall [N] with recovery (Table 4), we propose that wood fall, both during hurricanes and in the absence of hurricanes, represents a keystone process regulating N availability in this hurricane-prone forest.

Another possibility for the decreasing leaf fall [N] is the increase in stand N requirements with age; more N is needed as biomass increases. Support for this comes from the observation that maximum leaf area index (indicated by stable leaf fall) occurred during the recovery from Hurricane Georges (1998, Table 4). However, the high wood fall in the later recovery trajectory (Table 4; Figure 3c), likely reflecting higher woody biomass, might not account for the decrease in leaf fall [N] (Table 4; Figure 3d), as wood requires much less N than foliage. Unfortunately, a stand-level N budget to assess the relative contribution of N requirements was not made prior to the 2017 hurricanes.

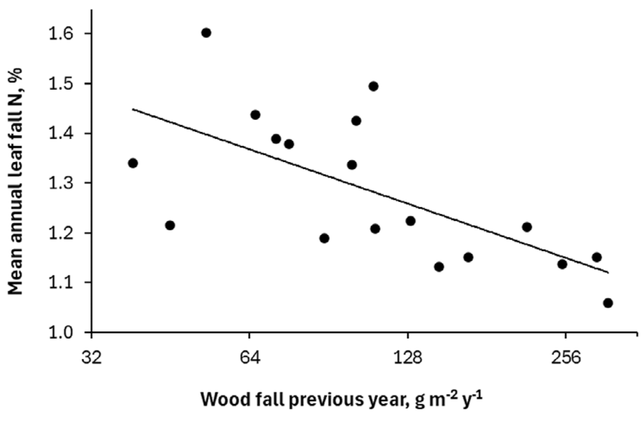

FIGURE 6 Correlation between mean annual leaf fall [N] (%) and previous year's wood fall ($g\,m^{-2}$), omitting data from years with hurricanes (1989, 1995, 1996, 1998, 2010, 2011, 2017). Pearson's $r = -0.66$, $p = 0.003$, $n = 18$.

Consistent with our hypothesis that leaf fall [N] would covary with stream nitrate-[N] after hurricanes, the tight coupling we found both immediately after hurricanes and across multiple years (Figure 5) indicates strong terrestrial–aquatic linkages at Bisley. This may be the first study to document this coupling for a tropical system. We did not anticipate the decadal decrease in stream nitrate-[N]. In northern US hardwood forests, stream nitrate N declines as pools of coarse woody debris increase (Fisk et al., 2002). This linkage has been implicated as a possible factor in the long-term decline of stream nitrate in a temperate zone watershed (Lajtha, 2020). Although we did not find a direct relationship between annual fine wood fall and stream N, the relationship with wood fall may be more related to coarse woody debris.

4.3 | Hurricane frequency-intensity litterfall (HurrFIL) model

We present a conceptual model of litterfall dynamics post-hurricane with broad-brush trends based on our findings (see Table S2) and earlier research, acknowledging the wide range in severity after hurricanes (Figure 7). The model contrasts low and high frequency hurricane return intervals (Figure 8), assuming hurricane intensity is negatively related to frequency (Bomfim et al., 2022). The high intensity, infrequent hurricane trajectory is modelled after hurricanes Hugo (1989) and Maria (2017), where total litterfall and wood fall are exceptionally high and leaf fall/wood fall ratios are low as is expected in a mature canopy. During recovery from these severe hurricanes, leaf fall/wood fall ratios increase rapidly as leaf production recovers and wood fall remains low. Following the initial surge of high N leaf fall, leaf fall [N] may begin to decrease as hurricane-produced coarse woody debris begins to immobilize N. On balance, leaf fall [N] remains relatively high as nutrient-rich early successional species become established, N fixation occurs or decomposition of hurricane-generated fine wood fall mineralizes N (Phase 1). Vegetation transitions from early phases with a relatively high abundance of fast-growing, light-requiring species to a closed forest with associated shifts in species and N cycling (Phase 2). The eventual decrease in leaf fall [N] occurs as non-hurricane wood fall increases from natural stand thinning and branch turnover, shade-tolerant species dominate, and N fixation, if occurring, diminishes. These processes continue to a mature forest with high total litterfall characterized by low leaf fall/wood fall ratios and low leaf fall[N], such as occurred up to Hurricane Maria (2017). Stream nitrate-[N] tracks leaf fall [N] throughout.

The greatest uncertainty in our model lies with the frequent hurricane trajectory (Phase 2 to Phase 1) which depends on hurricane

FIGURE 7 Photos showing the heterogenous responses to hurricanes, from nearly complete tree mortality to patchy or low mortality with large standing live or dead trees remaining.

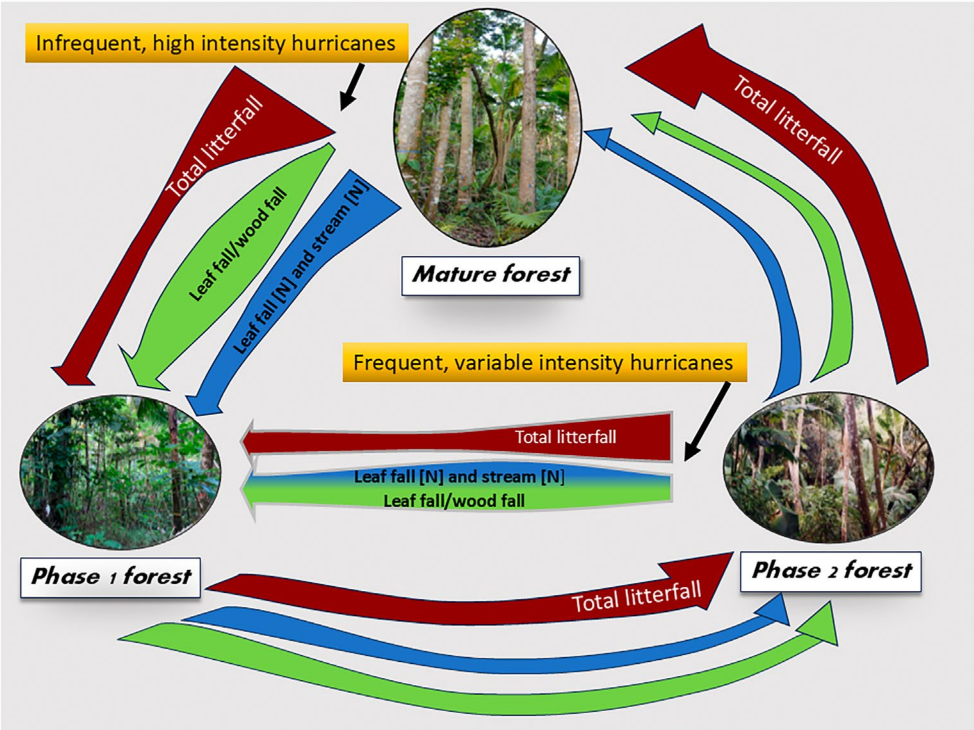

FIGURE 8 Conceptual model (HurrFIL) showing effects of varying hurricane frequency and intensity on forest structure and nitrogen cycling dynamics. Phase 1, reached in about 4–5 years after a high severity, infrequent hurricane (based on recovery after Hurricane Hugo), Phase 2 reached as early as 22–25 years (based on stable wood fall after Hurricane Irene), and the Mature Forest stage, based on continued increase in total litterfall, reached anywhere from 25+ years. The greatest uncertainty lies with the frequent hurricane pathway, where properties depend on tree species responses, return timing and intensity.

intensity, exact frequency and their interactions with forest development. The two sets of back-to-back relatively low intensity hurricanes in 1995 and 1996 show a greater reduction in total litterfall and wood fall relative to leaf fall with the second hurricane each year (Table 1); a similar reduction in litterfall was noted in Taiwan when typhoons occurred in close succession (Lin et al., 2017). The sustained high leaf fall/wood fall ratios we document for several years after hurricanes (Table S2) are coupled with high leaf fall [N] and stream [N] and, in our model, could be maintained with frequencies ≤1 year, yet would likely not be maintained with high stem infilling. In a global analysis of hurricanes occurring at least once per decade (Ibanez et al., 2019), stem densities increased, which would eventually lower the leaf fall/wood fall ratio. With increasing intensity and frequency combined, forest development may remain in early phases of foliage production and crown development (sensu Scatena et al., 1996), likely dominated by pioneer, wind-resistant species (Uriarte et al., 2019, 2023) and lacking the wood accrual characteristic of mature forests (essentially an 'arrested succession'). Our model does not consider infrequent low intensity hurricanes or tropical storms.

Partial support for the HurrFIL model comes from McDowell and Potter (2022), who found that the context of disturbance mediated the N response in soil solution. In that study, multiple experimental disturbances adding woody debris and leaf litter to forested plots in the Luquillo Mountains (Canopy Trimming Experiment) resulted in nitrate increases such as those observed in streams following previous hurricanes. When Hurricane Maria (2017) affected both the experimental plots and the untreated controls, the previously manipulated plots had significantly lower nitrate concentrations than those that had not received additional wood inputs prior to the hurricane. This implies that the hurricane response in the treated plots was dampened by previous canopy trimming manipulations and is consistent with our long-term decline in [N] following repeated hurricane disturbance. Our study shows a similar dampened response in leaf fall [N], litterfall N inputs and stream N export after the stronger Hurricane Maria compared to Hurricane Hugo (1989) (Figures 1b,c and 4). The HurrFIL model acknowledges these initial decreases in N concentrations but also anticipates the possibility of increased stream nitrate and leaf fall [N] with repeated frequent disturbances that might decrease wood fall when hurricane return intervals are shorter than recovery of wood production in a maturing canopy. Only with continued monitoring of species compositions, wood fall, and their N economies will these uncertainties be resolved.

4.4 | Implications of long-term N trends

In temperate forests, progressive tightening of the N cycle may be a general phenomenon with aging (Compton et al., 2007; Johnson, 2006), seen as a decrease in leaf fall [N] (Compton et al., 2007; Garten et al., 2011). Our data, showing long-term decreases in [N] for leaf fall and woody litter and in stream export (despite the immediate after-effects of hurricanes), hint that with succession, N may also be cycled relatively conservatively within this tropical forest.

Conservative cycling of N, while not unknown in mature wet lowland tropical forests (Koehler et al., 2009; Soper et al., 2018; Sotta et al., 2008), is considered rare. Theory and numerous experimental studies indicate that productivity in many mature tropical forests, especially those on highly weathered soils, is more P than N limited (Cleveland et al., 2011; Du et al., 2020; Vitousek, 1984), implying that excess N, after supplying biotic needs, is lost from the ecosystem. Although N limitation was not indicated in experimental fertilization of plots adjacent to our study watersheds (Cusack et al., 2011), recent experiments show the potential for both N and P limitation in lowland tropical forests (Wright, 2019; Wright et al., 2018). Using foliar $\delta^{15}N$ as an index of N availability across chronosequences, Tu et al. (2022) found that several tropical sites functioned more like temperate forests with decreasing N availability over time. The large hurricane-induced shifts in litter and stream N concentrations we document suggest an N cycle that oscillates between states of excess and limited N availability (see also Lin et al., 2020) that may not be captured with experimental fertilization studies.

Our study began in 1989, the year of the second strongest hurricane (Hugo) in our record. It is possible that these [N] declines indicate a return to pre-Hugo conditions, yet the stream data show otherwise, suggesting different drivers from pre-Hugo. Comparisons of stream nitrate-[N] from pre-Hugo (1987 and 1988) to the last year in our study (2017, which includes the Hurricane Maria surge) show a 36% drop, from 183 $\mu g\,N\,L^{-1}$ before our study to 118 $\mu g\,N\,L^{-1}$ in 2017.

4.5 | Bisley litterfall in context

Over the 29 years, litterfall at Bisley averaged 9.5 $Mg\,ha^{-1}\,year^{-1}$ (with hurricanes) or 8.2 $Mg\,ha^{-1}\,year^{-1}$ (ignoring months with hurricanes), comparable to an estimate for Bisley made prior to Hurricane Hugo (1989) of 8.7 $Mg\,ha^{-1}\,year^{-1}$ (Scatena et al., 1996) and slightly exceeding non-hurricane litterfall (7.5 $Mg\,ha^{-1}\,year^{-1}$) for a neighbouring tabonuco forest (Zalamea & González, 2008). Our value is remarkably close to annual litterfall estimates of 8.6 and 8.0 $Mg\,ha^{-1}$ for two old-growth forests in South America (Chave et al., 2010; Martinelli et al., 2017). Worldwide, litterfall in tropical evergreen forests averages 7.0 $Mg\,ha^{-1}\,year^{-1}$ (Zhang et al., 2014). These data suggest a broad geographic convergence of litterfall rates for tropical wet evergreen forests in the western hemisphere.

A main difference between the more common human-initiated secondary successions in the tropics and hurricane-generated successions lacking major human disturbance, such as at Bisley, lies in the quantity of wood remaining on site. In a meta-analysis of forest chronosequences commencing after agricultural and pasture use, where wood is mostly removed, Sullivan et al. (2019)

showed that several metrics of N availability, including the litter mass/litter N ratio, suggest a recovery of the N cycle with succession. In contrast, we show an overall rise in the litter mass/litter N ratio (Table S2), driven by decreasing [N]. Although the initial conditions vary greatly between these successional pathways, leading to different N dynamics, we propose that the long-term decline in [N] at Bisley, as indicated in the HurrFIL model, comes from the transition from early- to late successional species, characterized by lower growth rates, less N-rich foliage and litter (Heartsill Scalley et al., 2010; Uriarte et al., 2015), greater wood production and wood fall, and higher wood density (Poorter et al., 2019), properties likely also developing in secondary successions post-agriculture. Perhaps the reason declining N availability has not been observed in agricultural successions is that the focus has been on early-stage N recovery, not the nuances of N availability occurring in older forests.

Declining N availability may be a trend globally across terrestrial ecosystems, reflecting increases in atmospheric carbon dioxide, elevated temperatures and precipitation, longer growing seasons or disturbances removing N (Craine et al., 2018; Lie et al., 2021; Mason et al., 2022; Vitousek et al., 2024). Declining N availability, if significant at Bisley, could impact C storage, a global ecosystem service of tropical forests (Brown & Lugo, 1982; Xu et al., 2021) and numerous other N-dependent processes (Mason et al., 2022). Time since a major disturbance, and, as we emphasize, whether woody biomass is added or removed with disturbance, should be considered in regional or global assessments of N availability.

4.6 | Future perspectives

For forests like Bisley in the Luquillo Mountains under altered hurricane disturbance regimes, future species assemblages are likely to change. Uriarte et al. (2019, 2023) anticipate these forests will be shorter-statured (as in typhoon-frequent Taiwan (Lin et al., 2011)) and dominated by the pioneer *C. shreberiana* and the wind-resistant palm *P. acuminata*. Similarly, modelling by Zhang et al. (2022) projected greater palm abundance and reduced aboveground biomass by the end of the century with increasing hurricane intensities. Because *P. acuminata* lacks woody tissue, on a whole plant basis, this species has the highest N concentration among the dominant trees at Bisley (Scatena et al., 1993), implying sustained high N availability should this palm continue to increase with more frequent and intense hurricanes. How likely and fast these changes happen will depend on the dynamics of the new disturbance regimes.

The 29 years (1989–2017) of litterfall and stream data for the Bisley Experimental Watersheds allowed us to capture the dynamics of both short and long-term litterfall and litter and stream chemistry after hurricanes of varying intensities and frequencies. The two independent data sets of litter and stream chemistry corroborate a remarkable, nearly three-decade decline in leaf fall and wood fall litter N concentrations and stream N outputs. Including hurricane responses is essential for understanding the variability of long-term litterfall, especially considering that hurricane frequency and intensity are on the rise (Emanuel, 2020; Kossin et al., 2020; Murakami et al., 2020). Without these data, the exceptional decadal decreases in two major ecosystem properties, leaf fall and stream N concentrations, would not have been evident. However, given the expected shifts in species composition and N cycling dynamics with increased hurricane frequency and intensity, downward trajectories in N cycling may be short-lived. Continued long-term monitoring is critical as hurricane disturbances transform with a warming climate.

AUTHOR CONTRIBUTIONS

H. Erickson and G. González conceived of the initial ideas. G. González oversaw the litter collection and chemical analyses. H. Erickson performed data quality checks, litterfall calculations and statistical analyses, and led the writing and interpretation. W. McDowell and J. Potter assisted with stream chemistry sampling, oversaw the related analyses and interpreted the stream chemistry data. All authors contributed to the drafts and gave final approval for submission.

ACKNOWLEDGEMENTS

F. N. Scatena initially established the litterfall baskets and stream sampling at Bisley. R. Bemer, A. Colón, C. C. Domínguez, C. Estrada, S. Moya, C. Torrens, M. Salgado, H. Robles, M. M. Rivera and I. Vicens assisted with sample collecting and personnel of the International Institute of Tropical Forestry Chemistry Laboratory conducted chemical analyses of litterfall (L. Iglesias, M. Ittayem, E. López, M. J. Sánchez and E. Valcárcel). We thank J. Merriam of the University of New Hampshire Water Quality Analysis Laboratory for his supervision of many of the analyses of stream chemistry. We thank J. Compton, M. Huso, M. Keller, A. Lugo and E. Medina for feedback on the manuscript. This research was funded by the USDA Forest Service, International Institute of Tropical Forestry. Additional support was provided by the Luquillo Long-Term Ecological Research programme (National Science Foundation grant DEB-1831952), the University of Puerto Rico, the USDA National Institute of Food and Agriculture McIntire-Stennis Project 7003079, and the University of New Hampshire Agriculture Experiment Station. This is Scientific Contribution Number 3008. This is publication #1886 from the Institute of Environment at Florida International University. Any use of trade, product or firms' names is only for descriptive purposes and does not imply endorsement by the US Government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70108.

DATA AVAILABILITY STATEMENT

Litterfall mass and C and N chemistry are at https://doi.org/10.2737/RDS-2025-0024 (González & Erickson, 2025). Stream chemistry data are at https://doi.org/10.6073/pasta/570231c2807a6396ced6a89ef7547bd4 (McDowell & International Institute of Tropical Forestry, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Tropical storm wind speed and litterfall mass.

Table S2. Annual summaries for total litterfall, the three litterfall components and litterfall N inputs.

Figure S1. Monthly precipitation and temperature.

Figure S2. Monthly litterfall mass.

How to cite this article: Erickson, H. E., González, G., McDowell, W. H., & Potter, J. D. (2025). Increasingly conservative N cycling in a wet tropical forest: Litter and stream N concentrations decline over 29 years despite surges from hurricanes. *Journal of Ecology*, *00*, 1–21. https://doi.org/10.1111/1365-2745.70108