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Manuscript title

Canopy litterfall and soil respiration under rainfall and fog reduction in tropical montane cloud forests.

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Abstract

Tropical montane cloud forests (TMCFs) are globally important ecosystems that act as large carbon sinks. However, climate-driven declines in rainfall and cloud immersion threaten these forests, and their responses to declines in these distinct water sources remain poorly understood. Two separate large-scale experiments to reduce throughfall (TE) and fog (FE) in a Peruvian TMCF were conducted, to compare the temporal patterns and drivers of canopy litterfall and soil respiration, with nearby control (CON) plots. Litterfall and soil respiration declined during the relatively dry season on the CON plots. Seasonal patterns of soil respiration were related to soil moisture, while litterfall was related to air temperature.

Litterfall and soil respiration on the TE plot were suppressed overall and aseasonal, although litterfall pattern was offset FE-induced increases in litterfall from fine wood structures and epiphytes. On the FE plot, the only sign of altered seasonality was elevated litterfall from reproductive structures in the late dry season relative to the CON plot. There was little consistent interannual trend in either litterfall or respiration over time under the FE treatment. By contrast, the TE treatment was associated with a consistent decline in total litterfall, mainly caused by leaf litterfall while soil respiration initially declined for the first four years of the treatment followed by a rise likely associated with a concomitant increase in soil moisture. TE and FE appear to alter the amount and seasonality of reproductive activity in the canopy which could have major consequences for stand structure in a drier future climate.

Key words: Tropical montane cloud forests; precipitation manipulation experiment; drought; carbon cycling; litterfall; climate change; soil carbon dioxide efflux.

Highlights

1. Canopy litterfall and soil respiration were suppressed by throughfall exclusion

2. Throughfall and fog exclusion decreased canopy reproductive components seasonality
3. Throughfall and fog exclusion increased litterfall fine woods and epiphytes

1. Introduction

Tropical montane cloud forests (TMCFs) comprise only a small portion of global tropical forests, but they provide a range of key ecological services regionally and globally (Aldrich et al. 1997; Spracklen & Righelato, 2014; Bruijnzeel et al., 2011; Gotsch et al. 2016). The plant communities which support these services depend on high rainfall and persistent cloud immersion, a defining feature of TMCFs that has driven specialized plant adaptations (Bruijnzeel et al., 2011; Fahey et al. 2016; Eller et al. 2020). However, both the extent and frequency of cloud immersion are projected to decline sharply over the coming decades as rising temperatures lift cloud-base elevations, while regional deforestation reduces atmospheric moisture and weaken orographic cloud formation (Guzmán et al., 2024). Given their limited exposure to soil water deficits, TMCFs may be particularly vulnerable to these shifts, yet their climatic sensitivity remains poorly constrained relative to other ecosystems.

As droughts intensify across tropical regions (Cheng et al. 2026), the need to predict ecosystem responses has become increasingly urgent. A key advance has been the development of large-scale rainfall manipulation experiments (Knapp et al., 2024). Multiple applications of such experiments in tropical lowlands have yielded critical insights into drought effects on forest carbon cycling, substantially improving the representation of drought processes in ecosystem models (McDowell et al., 2013; Powell et al., 2013). Compared to the lowland tropics, relatively few such drought experiments, or other manipulations of climatic factors of interest, have been installed in TMCFs (Krashevska et al. 2012; Delsinne et al. 2013; Moser et al. 2014; Bartholomew et al. 2026). Furthermore, the relatively greater importance of fog water inputs and the distinctive structure, physiology and species composition of TMCFs, (Bruijnzeel

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et al., 2011; Fahey et al. 2016; Eller et al. 2020), make it difficult to directly predict TCMF responses from experiments performed in lowland forests.

Two major components of the ecosystem carbon (C) balance, which may respond strongly to water availability, are canopy productivity, usually estimated via litterfall, and carbon flux from the soil surface. However, results from available experiments have generated mixed results in terms of the direction, magnitude and seasonality of responses. For example, in a lowland eastern Amazon forest, initial declines in soil moisture associated with experimental rainfall reduction caused a slight suppression in leaf litter but a major drop in reproductive litterfall (e.g.: seeds, fruits, flowers) (Rowland et al., 2018). In a rainfall reduction experiment in the central Amazon lowlands, lower soil moisture caused minimal shifts in litterfall but a strong decline in canopy density, indicating an overall shift in canopy turnover (Brando et al., 2008). Similarly, some experiments demonstrate a strong drought-induced decline in soil carbon efflux as might be expected from suppressed microbial activity (Wood & Silver 2012; van Straaten et al., 2011; da Costa et al., 2013; Bartholomew et al., 2026), while others have shown little change (Brando et al., 2008) or even increased respiration (Cleveland et al., 2010, Zhang et al., 2015; Cusack et al., 2023). By comparison with lowland forest, relatively little information exists about the magnitude and climatic sensitivity of litterfall and soil respiration in TMCF (Rapp & Silman 2014; Girardin et al., 2014; Bartholomew et al., 2026).

To understand the effects of fog and throughfall reduction on canopy and soil carbon fluxes, we analysed monthly variation in these components over 7 years after installation of two adjacent large-scale experiments to reduce throughfall (TE) and fog (FE) in a Peruvian old-growth TMCF. Our study addressed the following research questions: (1) How do different components of precipitation – fog and throughfall – affect litterfall productivity and total soil respiration in TCMF? (2) What controls seasonal and interannual variations in litterfall productivity and total soil respiration in TCMF?

2. Materials and Methods

2.1. Study site

The experimental infrastructure is part of the Wayqecha Amazon Cloud Curtain Ecosystem Experiment (WACCEE) to manipulate fog, together with an adjacent canopy throughfall reduction experiment (Brum et al., 2023; Metcalfe et al., 2025). The sites are located in a TCMF in the southeastern Peruvian Andes within the private conservation area of the Wayqecha Biological Station which is administered by the Amazon Conservation Association (ACA). The region experiences frequent cloud immersion (Clark et al., 2014; Halladay et al., 2012), precipitation over 1800 mm per year, with six consecutive months of the year where less than 100 mm falls from May to October, and a mean annual temperature of around12 ^{o}C (Girardin et al., 2015). The forest is dominated by tree species of *Weinmannia crassifolia, Weinmannia bangii, Weinmannia reticulata, Clusia alata, Clusia trochiformis, Myrsine coriacea, Clethra cuneata, Prunus integrifolia, and Persea mutissi* (Farfan Rios et al., 2015). Ferns, liverworts, and mosses are the most dominant epiphytes (Horwath et al., 2015; Rapp et al., 2014).

2.2. Sampling design

In February 2017, two 30 × 30 m plots were installed in the TCMF at the site (-13.18959, -71.58709), and basic monitoring of litterfall, soil respiration, and meteorology began (see below). In August 2017, one of the plots was covered with transparent plastic panels suspended on a wooden frame at around 2.5 m above ground, excluding ~ 95% of throughfall input to the ground (TE-EXP). The adjacent plot was left unmodified to serve as an experimental control (TE-CON) (Brum et al., 203). Around 500 m away from the throughfall experiment, two other plots were installed in TCMF (-13.19335, -71.58823) in September 2017 (Metcalfe et al., 2025). At one of these plots a 30 m high, 40 m long mesh curtain was suspended along the downslope side, to reduce ingress of fog moving upslope in a ~ 420 m^2 patch of forest behind the curtain (FE-EXP). The adjacent plot was left unmodified to serve as an experimental control (FE-CON).

2.3. Litterfall sampling

Canopy litterfall < 2 cm in diameter was collected once a month at 9 locations in all plots using 50 x 50 cm litter trap baskets, following the GEM protocol (Marthews et al., 2013). In the TE-EXP plot nine litter traps were secured with wires ~1 m above the plastic panels. Litterfall was sorted into leaves, reproductive parts (flowers, fruits, and seeds), fine wood (< 2 cm diameter), and epiphytic plant material then oven-dried at 70 °C to a constant mass, and weighed to calculate the litterfall for each component, and per litter trap. Three litterfall traps from the TE-CON plot exhibited anomalously high litterfall which we attribute to the proximity of a single large, fast-growing N-fixing tree (*Alnus acuminata*) which did not occur in any of the other plots. We removed data from these traps for the present analysis, but included them in the Supplementary material. To convert litterfall dry biomass to carbon mass we assumed a C fraction of 0.492 (Fyllas et al. 2009).

2.4. Soil respiration sampling

Soil CO_2 efflux respiration was measured once a month at the middle of each subplot in all plots, where PVC permanent collars were installed to record CO_2 fluxes with an infra-red gas analyzer (EGM-5 and SRC-1 chamber, PP systems, Hitchen, UK), following the GEM protocol (Marthews et al., 2014). After CO_2 measurements, air and soil surface temperature (T260 probe, Testo Ltd., Hampshire, UK) and soil moisture (Hydrosense probe, Campbell Scientific

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Ltd., Loughborough, UK) were recorded at the same location to 10 cm soil depth. Respiration was estimated from accumulation of CO_2 over time (120 min) within the chamber sealed to the soil surface. The linear slope obtained from the relationship between CO_2 concentration and time of measurement, and it was used to calculate total CO_2 flux (Metcalfe et al., 2018; Riutta et al., 2021).

2.5. Canopy and soil-level meteorology

We continuously recorded air temperature and humidity, precipitation, and solar radiation since 2012 from a weather station installed in a clearing outside of the forest ~1 km from the experimental plots. Soil-level meteorology - air temperature 15 cm above the ground, soil temperature at 2 and 5 cm soil depth and soil moisture - was recorded at five points in each experiment plot (TMS-4 sensors, TOMST s.r.o, Czech Republic). Raw moisture data were converted to volumetric soil moisture using a conversion equation applied by Halbritter et al. (2024) from a location near the current study.

2.6. Statistical analyses

The daily variation of climatic variables from the canopy and soil were summarised into monthly and yearly averages, to understand the effect on canopy productivity and soil respiration in the experimental treatments and control plots. Error propagation for all litterfall components and soil respiration was carried out using conventional quadrature rules (Hughes & Hase, 2010). Generalised additive models were fit to understand the relationships between mean respiration and productivity values and temporal variation in climate variables, to quantify seasonal and annual patterns.

Multiple linear regression analyses were conducted in order to understand the relationship between monthly variability of litterfall components and canopy meteorology. The monthly variation of productivity of total litterfall and components was analysed with cross-correlation analysis with meteorological variables, and then generalised linear models were performed on total litterfall, leaves, reproductive parts, and fine wood, and epiphyte litterfall as response variables with one month lagged relative humidity, temperature, solar radiation, and precipitation as independent variables, alongside the dependent variables to remove autocorrelation. Models were fitted using the *mgcv* package for R (Wood, 2011).

Linear mixed-fixed effects modelling was used to examine the effects of soil temperature and soil moisture on soil respiration. Soil-level meteorological variables (soil temperature and moisture) in the treatment (FE-EXP, TE-EXP), and control plots (FE-CON, FE-EXP) were treated as fixed effects, and the treatment and control plots and their sub plots were treated as random effects. The linear mixed-effect models were fitted using the *glmmTMB* package in the R statistical software (Brooks et al., 2017). The modelling approaches began with all predictors and then predictors were removed with lowest statistical significance to improve the model fit. Akaike information criterion (AIC) was used to compare the models and the model with a lower AIC was selected as the best predictor of response variable for litterfall components and total soil respiration. All analyses were carried out using R version 4.5.0 (R core Team 2025).

3. Results

3.1. Climatic variables

The study site shows strong climatic seasonality, with lowest air relative humidity, precipitation, and air temperature over May - August (Figure 1a, b, c). Solar radiation showed a distinct seasonal pattern, peaking over August - November (Figure 1d).

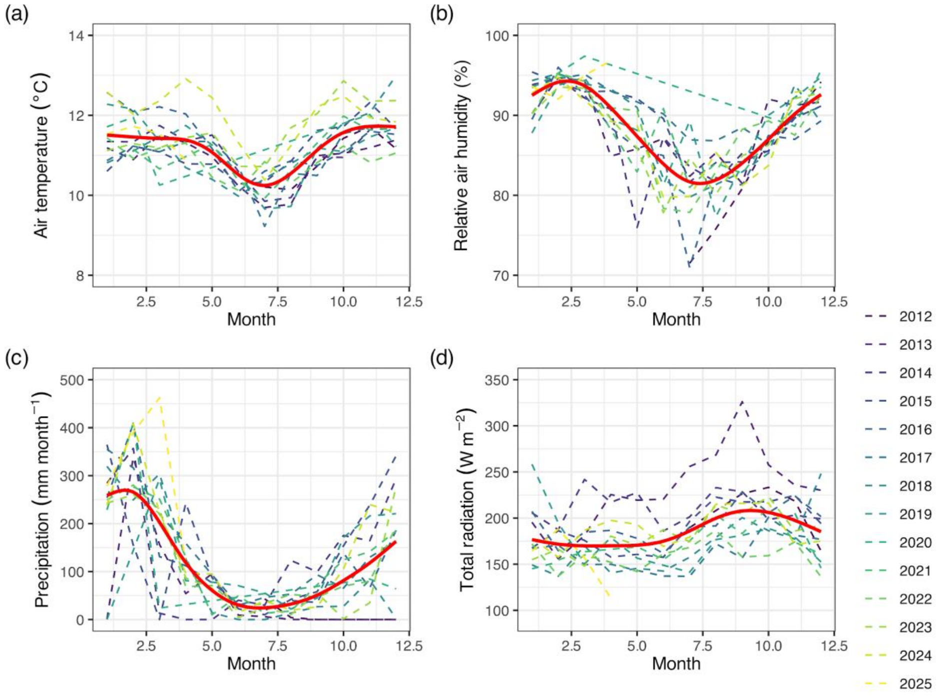

Figure 1. *(a) Monthly average variation of air temperature (˚C), (b) relative air humidity (%), (c) precipitation (mm), and (d) total radiation (W* m^{-2}*). The dashed lines represent the interannual monthly variations of climate variables, and the red solid lines show the marginal predictions fitted with the generalised additive model for each climatic variable.*

The FE treatment caused a strong reduction in air humidity and a smaller reduction in above-canopy air temperature (Metcalfe et al., 2025). Soil-level meteorology changed with both the FE and TE treatments (Figures S1 & S2). FE-EXP decreased soil temperature, deep and shallow soil temperatures and soil adjacent air temperatures but only during the dry season (Figures S1a-c & S2a-c). By contrast, the TE-EXP caused no shift in deep soil temperature, and a relatively minor dry season reduction in shallow soil temperatures (Figures S1a, b & S2a, b). Soil adjacent air temperatures were consistently elevated on the TE-EXP throughout the

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year (Figure S1c). Further, the FE-EXP increased soil moisture, however TE-EXP suppressed soil moisture to a relatively constant level through the year (Figure S1d).

3.2. Overall plot differences in litterfall and soil respiration

Total annual litterfall was similar among the FE-CON (3.72 ± 0.72 Mg C ha^{-1} yr^{-1}) and FE-EXP (3.77 ± 0.73 Mg C ha^{-1} yr^{-1}) plots (Figure 2a). However, on the TE-EXP total litterfall was notably suppressed (2.94 ± 0.67 Mg C ha^{-1} yr^{-1}) relative to the TE-CON (3.86 ± 0.58 Mg C ha^{-1} yr^{-1}) (Figure 2a), and declined consistently over seven years after initiation of the TE treatment (Figure 3, 4). Leaf litter decreased 27% on TE-EXP (Figure 2b), reproductive parts decreased on FE-EXP and TE-EXP by 39% and 31% respectively (Figure 2c). By contrast, fine wood litterfall increased on the FE and TE (Figure 2d) by 10% and 4% respectively, and epiphytic litterfall increased by 29% on the FE-EXP and 130% on the TE-EXP (Figure 2e) relative to their respective control plots.

Overall, across the 7 years of the TE treatment, soil respiration decreased by 54%, from 8.74 ± 0.20 Mg C ha^{-1} yr^{-1} (TE-CON) to 4.05 ± 0.14 Mg C ha^{-1} yr^{-1} (TE-EXP). Total annual soil respiration was significantly lower on the TE-EXP than the TE-CON, FE-CON, and FE-EXP plots (Figure 2f).

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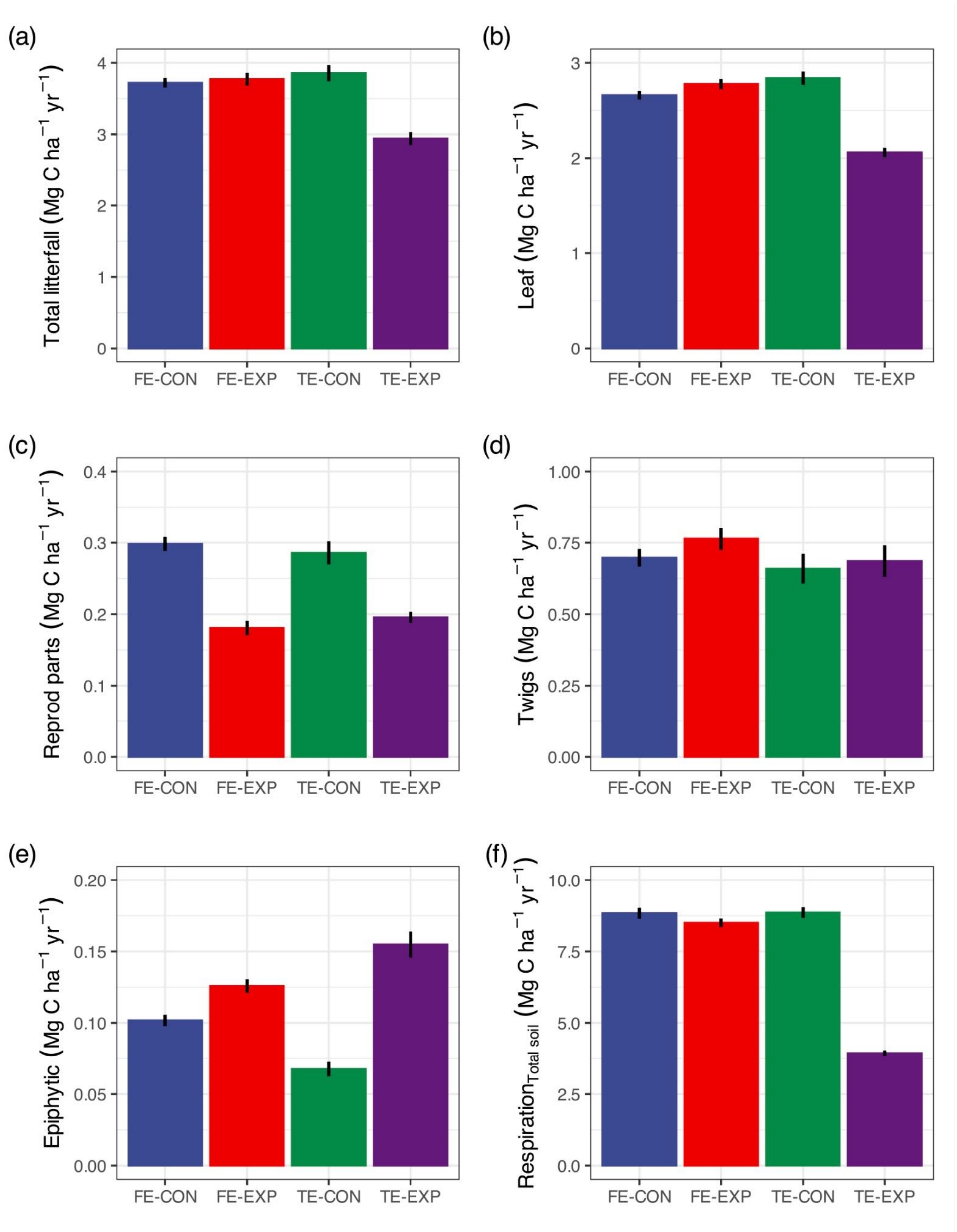

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231 **Figure 2.** *Annual productivity (Mg C ha^{-1} yr^{-1}) of (a) total litterfall, (b) leaf, (c) reproductive parts, (d) fine wood, (e) epiphytes and (f) total soil respiration on FE (blue and red bars) and TE (green and purple bars) plots. The black bars on each coloured bar plot shows the propagated standard error of the mean (n = 7).*

3.3. Temporal trends and climatic drivers of fine litterfall productivity

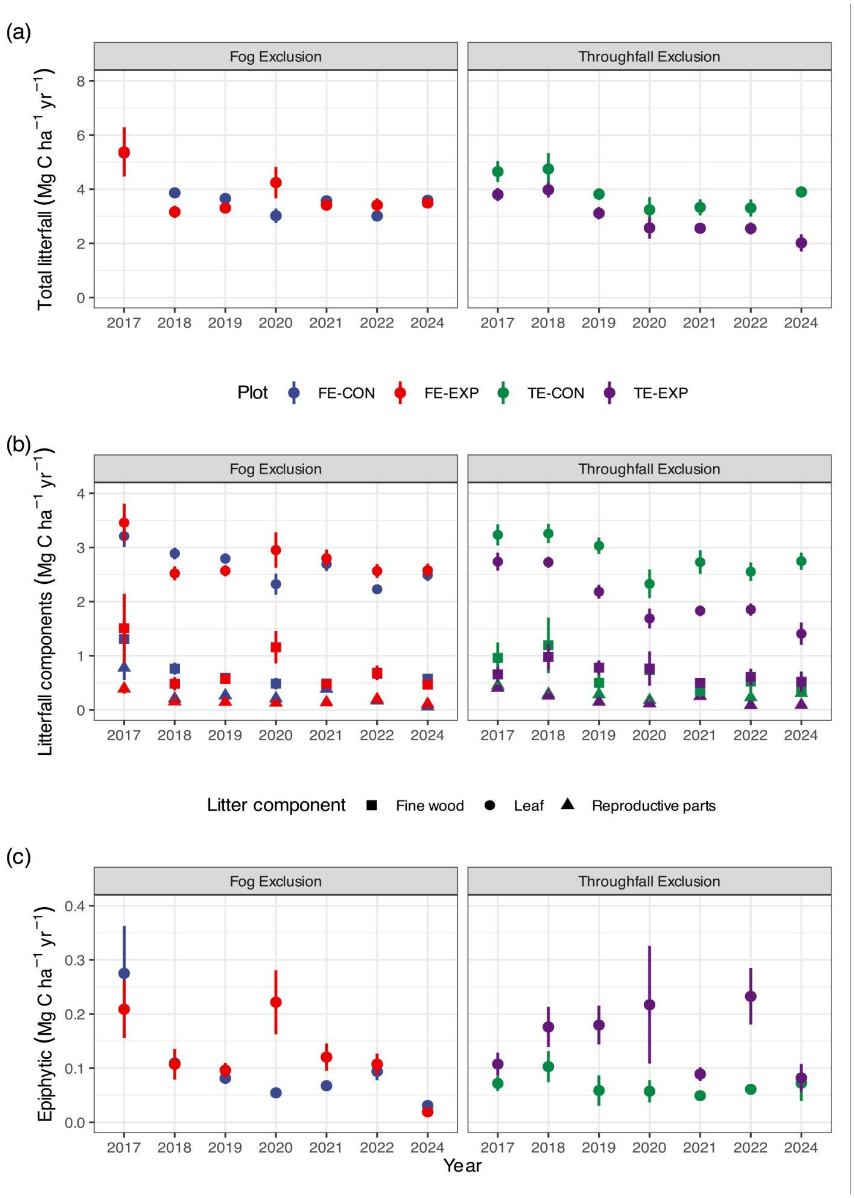
We did not observe any significant interannual differences between FE-EXP and FE-CON total litterfall productivity, and no significant trends of change over time from 2017 to 2024 (Figure 3a, left panel). However, total litterfall productivity was significantly lower on the TE-EXP plot relative to the TE-CON (Figure 3a, right panel). Total annual litterfall production declined significantly over time ($r = -0.86$, $p < 0.01$) by an average rate of 24% per year (Figure 3a, right panel). Annual leaf litterfall did not show any significant differences between FE-CON and FE-EXP plots. By contrast, leaf litter in the TE-EXP plot decreased significantly over time ($r = -0.83$, $p < 0.01$), since the imposition of the treatment in 2017 (Figure 3b, right panel). Canopy productivity of reproductive parts was suppressed on both precipitation treatments relative to their respective controls (Figures 3b & 4b). Fine wood litter did not exhibit any significant difference between the FE-CON and FE-EXP plots, while TE-EXP fine wood litterfall showed a small but consistent rise after the third year of the TE treatment compared to the TE-CON plot (Figure 3b, right panel). Epiphyte litter also showed no significant difference between the FE-CON and FE-EXP plots but was strongly and consistently elevated on the TE-EXP relative to the TE-CON plot (Figures 3c & 4d, right panels).

Mean monthly temperature was the main driver of total monthly litterfall with a positive and significant relationship ($p < 0.01$) for both FE-CON and FE-EXP, while relative air humidity was negatively and significantly related to month variation in total litterfall only in the FE-CON plot ($p < 0.05$). By contrast, monthly total litterfall in the TE-CON and TE-EXP was not clearly related to either temperature or relative air humidity (Table 1). Further analyses of litterfall components revealed different climatic sensitivities among components and plots. Monthly variation in leaf litterfall was positively and significantly related to temperature ($p < 0.05$) at the FE-CON and FE-EXP but not in the TE plots (Table 1). Monthly reproductive litter was positively and significantly related to solar radiation at the FE-CON ($p < 0.01$) and temperature at the FE-EXP ($p < 0.01$). While precipitation was negatively and significantly related at the TE-CON ($p < 0.05$), and solar radiation and relative humidity were positively related at the TE-EXP ($p < 0.05$). Precipitation was positively and significantly related to fine wood litterfall at the FE-EXP ($p < 0.001$) while no significant climatic drivers were found on the other plots for fine wood litterfall. Precipitation showed a significant positive relationship with monthly epiphyte litterfall at the FE-EXP ($p < 0.001$) but no clear effect on the FE-CON. Solar radiation was positively and significantly related to epiphyte litterfall in the TE-CON but not for the TE-EXP plot.

Table 1. *The explanatory variables of total litterfall, leaves, reproductive parts, fine wood, and epiphytes were used as response variables along fog exclusion control (FE-CON) and experiment (FE-EXP) plots, throughfall exclusion control (TE-CON), and throughfall exclusion experiment (TE-CON) plots. A summary of the generalized linear models was performed between the response variables (litterfall components and epiphyte productivity) and a one-month lag of the explanatory variables. Standard error (SE) and significance of the model coefficients p values of 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘NS’ 1 on signif column.*

Plot code	**Response variables**	**Explanatory variables**	**Estimate**	**SE**	**T-value**	**p-value**	**signif**	**AIC**
FE-CON	**Litterfall**	Intercept	-1.6186	0.5733	-2.82	0.0065	**	-132.15
		Temperature	0.1432	0.0440	3.25	0.0019	**	
		Relative humidity	-0.0139	0.0063	-2.20	0.0318	*	
FE-EXP		Intercept	-3.1159	0.6014	-5.18	0.0000	***	-121.40
		Temperature	0.1635	0.0533	3.07	0.0032	**	
TE-CON		Intercept	-2.1393	0.9110	-2.35	0.0218	*	-75.90
		Temperature	0.0870	0.0811	1.07	0.2872	NS	
TE-EXP		Intercept	-2.3727	0.9688	-2.45	0.0173	*	-93.69
		Temperature	0.0884	0.0870	1.02	0.3140	NS	
FE-CON	**Leaves**	Intercept	-1.4319	0.5874	-2.44	0.0179	*	-165.12
		Temperature	0.0909	0.0451	2.02	0.0486	*	
		Relative humidity	-0.0128	0.0065	-1.97	0.0534	.	
FE-EXP		Intercept	-2.6498	0.4821	-5.50	0.0000	***	-168.44
		Temperature	0.0994	0.0427	2.33	0.0234	*	
TE-CON		Intercept	-1.8702	0.7011	-2.67	0.0095	**	-136.41
		Temperature	0.0373	0.0624	0.60	0.5518	NS	
TE-EXP		Intercept	-1.6929	0.0783	-21.62	<2e-16	***	-152.37
		Precipitation	-0.0004	0.0005	-0.88	0.3810	NS	
FE-CON	**Reproductive**	Intercept	-6.3776	0.8323	-7.66	0.0000	***	-345.96

	parts	Solar radiation	0.0140	0.0048	2.91	0.0051	**	
FE-EXP		Intercept	-8.5830	1.4351	-5.98	0.0000	***	-439.70
		Temperature	0.3694	0.1272	2.90	0.0052	**	
TE-CON		Intercept	-3.4140	0.1742	-19.60	<2e-16	***	-382.52
		Precipitation	-0.0025	0.0011	-2.22	0.0300	*	
TE-EXP		Intercept	-11.6259	2.6552	-4.38	0.0000	***	-382.62
		Solar radiation	0.0131	0.0057	2.28	0.0260	*	
		Relative humidity	0.0601	0.0240	2.50	0.0152	*	
FE-CON	**Fine wood**	Intercept	-3.1352	0.1259	-24.90	<2e-16	***	-267.30
		Precipitation	0.0010	0.0008	1.30	0.1990	NS	
FE-EXP		Intercept)	-4.9160	0.9266	-5.31	0.0000	***	-266.13
		Solar radiation	0.0072	0.0051	1.41	0.1648	NS	
		Precipitation	0.0045	0.0011	4.15	0.0001	***	
TE-CON		Intercept	-5.3473	1.6293	-3.28	0.0016	**	-286.91
		Solar radiation	0.0114	0.0091	1.26	0.2129	NS	
		Precipitation	0.0028	0.0020	1.36	0.1801	NS	
TE-EXP		Intercept	-9.9008	3.5453	-2.79	0.0070	**	-225.78
		Solar radiation	0.0123	0.0077	1.60	0.1150	NS	
		Relative humidity	0.0558	0.0321	1.74	0.0874	.	
FE-CON	**Epiphytes**	Intercept	-5.1877	0.1590	-32.62	<2e-16	***	-501.96
		Precipitation	0.0009	0.0010	0.96	0.3410	NS	
FE-EXP		Intercept	-5.4883	0.1917	-28.62	<2e-16	***	-469.35
		Precipitation	0.0046	0.0012	3.92	0.0002	***	
TE-CON		Intercept	-13.2923	2.8915	-4.60	0.0000	***	-595.24
		Solar radiation	0.0230	0.0061	3.78	0.0003	***	
		Relative humidity	0.0462	0.0263	1.76	0.0836	.	
TE-EXP		Intercept	-6.8909	1.2559	-5.49	0.0000	***	-412.73
		Solar radiation	0.0128	0.0072	1.78	0.0802	.	
		Precipitation	0.0030	0.0015	1.97	0.0535	.	



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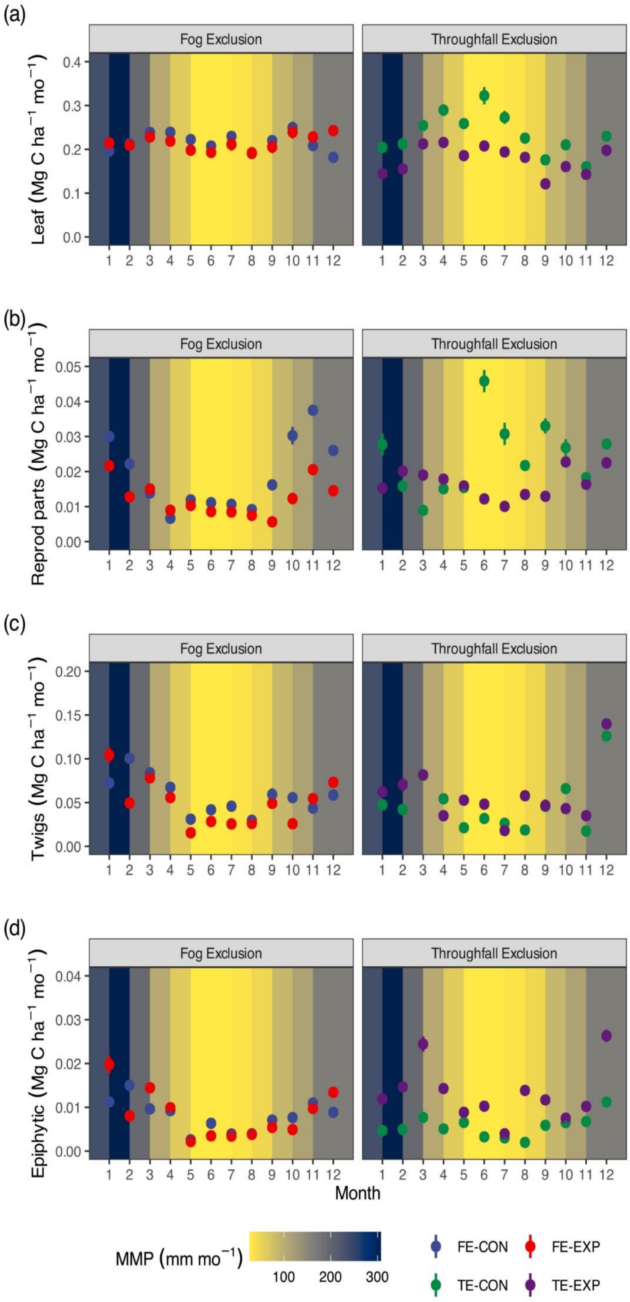
280 **Figure 3.** *(a) Yearly variation of total litterfall productivity (Mg C ha-^{1} yr^{-1}), (b) litterfall components (leaf, reproductive parts, and fine wood) and (c) epiphytic component for fog exclusion (Left panels: FE-CON, FE-EXP) and throughfall experiment plots (Right panels: TE-CON, TE-EXP). The coloured dots, squares, triangles and vertical bars show the mean and standard errors.*



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286 ***Figure 4.*** *Seasonal variation in (a) leaf, (b) reproductive parts, (c) fine wood, and (d) epiphytic*

287 *litterfall productivity (Mg C ha^{-1}mo^{-1}) along fog exclusion (left panels) and throughfall (right*

panel) experiment plots. The coloured dots are the mean values of monthly productivity, collected for fog exclusion control (FE-CON, blue) and experiment (FE-EXP, red) plots, and for canopy throughfall control (TE-CON, green) and throughfall experiment (TE-EXP, purple) plots recorded between 2017 and 2024. The coloured background bars show the monthly average precipitation input (mm mo^{-1}) recorded from 2012–2024.

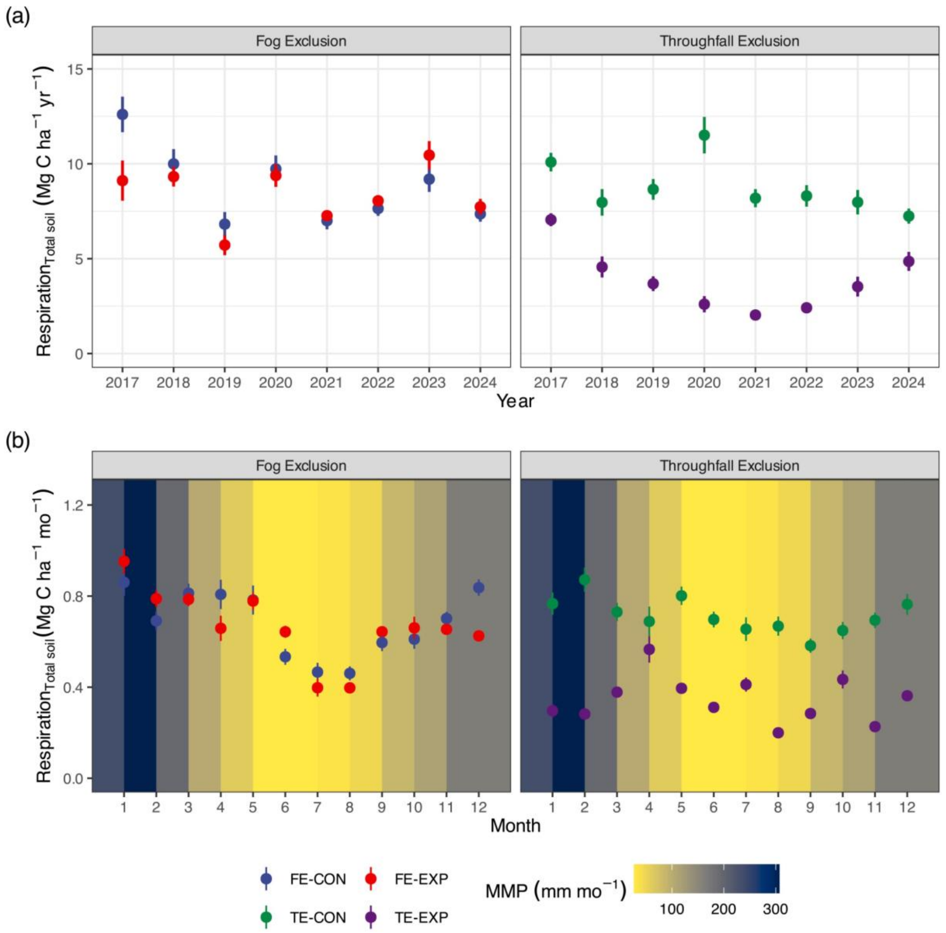

Figure 5. *(a) Yearly variation of total soil respiration fluxes (Mg C ha^{-1} yr^{-1}). (b) Seasonal variation in total soil respiration for FE, TE, and control plots. The coloured dots and bars on*

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the top and bottom panels show the mean values and standard error of the mean values recorded for fog exclusion control (FE-CON) and experiment (FE-EXP) plots, and for canopy throughfall control (TE-CON) and throughfall experiment (TE-EXP) plots. The coloured background bars on the bottom panel represent the monthly mean precipitation (mm mo^{-1}) recorded between 2012 and 2024.

The seasonal month variation of litterfall components productivity increased in the wet season and decreased in dry season (Figure 5). Leaf litterfall productivity FE plots did not reveal any significance differences, white a significant difference was observed between the TE-CON and TE-EXP plots ($p < 0.001$). Further the seasonal variation of leaf litterfall productivity at the TE-EXP was significantly lower ($p < 0.05$) than the FE-CON and FE-EXP plots (Figure 5a). Reproductive litterfall was higher in the wet season than the dry season for the FE plots and the TE-EXP, whereas on the TE-CON it peaked during the dry season. Fine wood litterfall productivity peaked in the wet season for FE and TE plots (Figure 5c). Highest epiphytic litterfall was recorded in the wet season for FE plots. Overall, epiphyte litterfall at TE-EXP was significantly ($p < 0.01$) higher than the TE-CON (Figure 5d).

3.4. Temporal trends and climatic drivers of total soil respiration

Annual soil respiration did not consistently differ between FE-CON and FE-EXP plots across all years of measurement (Figure 6a, left panel). In contrast, between the TE-CON and TE-EXP plots, the total soil respiration was significantly lower in TE-EXP (Figure 6a, right panel). In addition, soil respiration on the TE-EXP plot showed an U-shaped relationship over time from 2017 to 2024, decreasing strongly until 2021 then rising thereafter (Figure 6a, right panel). Overall, soil respiration observed at TE-EXP was lower than control and experimental plots.

This rise later in the experiment coincided with increasing soil moisture on the treatment as significant gaps developed in the plastic roofing which were only completely repaired in 2024.

Monthly soil moisture was the main factor that controlled total soil respiration, with strongly significant positive relationships ($p < 0.001$) for each plot. Interestingly, a significant interaction between soil temperature and total soil respiration was also observed for the FE-EXP and TE-CON plots, however for other plots were not observed (Table 2).

Strong seasonal variation of total soil respiration was observed for both FE plots, with low average values recorded during the dry season (Figure 6a, left panel). In contrast, a relatively weaker seasonality was observed for the TE-CON plot, while total respiration on the TE-EXP was highly variable with no apparent seasonality (Figure 6b, right panel).

Table 2. *Explanatory variables of total soil respiration in the fog exclusion experiment (FE-EXP) and control (FE-CON) plots. throughfall exclusion control (TE-CON) and throughfall exclusion experiment (TE-CON) plots. The independent variables of total soil respiration included the soil moisture and temperature. Mixed-effect models were carried out using the maximum likelihood, providing soil moisture and soil temperature variables as fixed effects and subplots (collars) as random effects. The best fixed-effect model was determined by the lowest AIC value and by comparing the full model to other models. Significant of the model coefficients p values of 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 'NS' 1*

Plot code	Explanatory variables	Parameter	SE	z value	p-value	signif	AIC
FE-CON	**Fixed effects**						
	Intercept	-1.137286	0.224843	-5.058	4.23e-07	***	141.6
	Soil moisture	0.015628	0.001935	8.077	6.64e-16	***	
	Soil temperature	0.028851	0.015123	1.908	5.64e-02	.	
	Random effects						
	Sub plot	0.1076	0.328				
FE-EXP	**Fixed effects**						
	Intercept	-0.30306	0.1899	-1.596	0.1105	NS	116.6
	Soil moisture	0.01174	0.001855	6.328	2.49e-10	***	
	Soil temperature	-0.031159	0.014252	-2.186	2.88e-02	*	
	Random effects						
	Sub plot	0.02185	0.1478				
TE-CON	**Fixed effects**						
	Intercept	-1.243238	0.166066	-7.486	7.08e-14	***	193.6
	Soil moisture	0.008748	0.001481	5.907	3.49e-09	***	

	Soil temperature	0.048185	0.012164	3.961	7.46e-05	***	
	Random effects						
	Sub plot	0.009199	0.09591				
TE-EXP	**Fixed effects**						
	Intercept	-1.52558	0.079641	-19.16	<2e-16	***	-342.4
	Soil moisture	0.037818	0.002895	13.06	<2e-16	***	
	Random effects						
	Sub plot	0.04416	0.2101				
All plots	**Fixed effects**						
	Intercept	-1.047751	0.151787	-6.903	5.1e-12	***	580.2
	Soil moisture	0.014581	0.001032	14.127	<2e-16	***	
	Soil temperature	0.014434	0.008458	1.707	0.0879	.	
	Random effects						
	Plot	0.04166	0.2041				

4. Discussion

4.1. Effects of fog and throughfall exclusion on litterfall and soil respiration

This study was designed to understand the distinct effects of water inputs via fog and throughfall on canopy litterfall and total soil respiration in TMCF. Our results provide some of the first insights into ecological responses to moisture availability in TMCF, highlighting similarities and differences with previous studies, mainly from lowland tropical forests. The FE treatment caused no clear shift in overall litterfall, whereas total litterfall productivity declined immediately after imposition of the TE treatment, and was lower than the control plot for most of the survey period (Figure 3). This trend was mainly driven by shifts in leaf litterfall, which accounted for ~70% of total litterfall. In contrast, in a Southeast Asian montane forest, 25 months of 80% throughfall reduction did not appear to affect leaf litter and other litterfall components (Moser et al., 2014). Throughfall reduction experiments in lowland tropical tropical forests also show distinct responses to our study, with drought-associated reductions in litterfall but usually only after several years (e.g., Brando et al., 2008; Meir et al., 2018; Nepstad et al., 2002; Rowland et al., 2018). The apparently more rapid and/or severe drought suppression of litterfall production in our study could reflect the more intense drought treatment imposed (~95% throughfall reduction, versus ~80% on other studies) and/or genuinely elevated sensitivity of the TMCF canopy to drought compared to most lowland forests. Further work in

TMCF and other tropical biomes is needed to understand and explain the diversity of observed drought responses to date.

Notably, both fog and throughfall reduction suppressed productivity of reproductive structures (seeds, fruits, flowers) in our study site. This contrasts with typical seasonal reproductive phenology of tropical forests, where flowering tends to peak during periods with greater solar radiation and lower water availability (Pau et al. 2017). However, our results are consistent with multiple drought experiments both in lowland tropical forests (Brando et al., 2006; Nepstad et al., 2002; Rowland et al., 2018; Vogado et al., 2020) and also in temperate forests (Ogaya & Peñuelas, 2007). This suggests that the short-term cues guiding seasonal reproduction are overridden by longer-term constraints on productivity imposed by drought. If this suppression is representative of TMCF more widely, then predicted future shifts in moisture availability across these biomes could drive major shifts in community composition and structure. Throughfall reduction also increased epiphytic and, to a lesser extent, fine wood litter productivity after the third year. This may reflect increasing tree mortality and associated canopy structure changes, since drought often leads to a decline in photosynthesis rates and leaf area index, inducing an increase of branch turnover (Nepstad et al., 2002).

Throughfall reduction strongly suppressed soil respiration in our study while fog reduction had no clear effect. This result is consistent with some previous studies of soil respiration in long-term throughfall experiments in lowland and montane tropical forests (e.g. Cusack et al., 2023; Sotta et al., 2007; van Straaten et al., 2011). This reduction in soil respiration on the TE-EXP is closely correlated with soil moisture, which may affect both autotrophic and heterotrophic soil components (van Straaten et al., 2011). For example, the overall reduction could be related to likely to root biomass decreases on top soil layers, due to physiological stress provoked by long-term throughfall exclusion (Fan et al., 2021) and/or shifts in the soil microbial community due to lower soil moisture and slightly elevated

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temperature (Nottingham et al., 2025). These results indicate that the very substantial soil C stocks in TMCF (Spracklen & Righelato 2014) may be threatened by future drought, with important consequences for the ecosystem C sink potential. More drought experiments in TMCF, and further experimentation with different soil components are required to reinforce and add mechanistic detail to our findings.

4.2. Temporal trends in litterfall productivity and soil respiration fluxes

Air temperature was the main climatic factor controlling monthly variation of total and leaf litterfall for FE plots. Other long-term studies of litterfall productivity in tropical forest ecosystems confirm that air temperature is the most important climatic factor driving canopy productivity. For example, in lowland and montane forests of Malaysian Borneo, the daily mean air temperature is the most important factor correlated to total litterfall and leaf litter productivity (Kitayama et a., 2021; Nakaqawa et al., 2019). In addition, the positive relationship between canopy productivity and air temperature also increases the nutrient availability in tropical montane wet forests of Hawaii (Litton et al., 2020; Lyu et al., 2021). Notably, some litterfall components were more closely associated with solar radiation in our study. Specifically, reproductive structures, fine wood, and epiphytic litter components increased with increasing solar radiation for both FE control and treatment plots. Most tree species in the study plots started flowering during the dry season and then started fruiting at the beginning of rainy season, which is typical in tropical montane forests (Günter et al., 2008). The underlying mechanisms responsible for peaks in reproduction during high light are still unresolved, but may be related to strategies to enhance pollination success, or reflect knock-on effects of temporal coordination of other phenological stages (i.e. leaf flushing) (Rowland et al., 2018; Van Schaik et al., 1993; Wright and Van Schaik, 1994). This study reinforces a previous long-term study of net primary productivity in old-growth forest ecosystems from upper montane to the lowland Amazon which also revealed that the seasonal rhythm of canopy productivity is synchronised with solar irradiance, and that leaf litter productivity peaks in the late dry season (Girardin et al., 2014).

Precipitation was the main driver of fine wood and epiphytic litter seasonal productivity on the FE-EXP, and to a lesser extent on the FE-CON (Figure 5c, d). Rapp et al. (2012) reported a strong association between high rainfall and strong wind speed during the wet season at high elevation (~ 3400 m asl) close to our study area; this relationship may increase branch turnover and fine wood litter productivity during the rainy season (Figure 5c). However, the higher fine wood litter productivity observed for the TE plot at the beginning of the rainy season may also reflect drought-associated canopy disturbance and tree mortality. The high turnover of canopy branches would likely have a strong negative impact on epiphytes, thereby increasing epiphytic litterfall.

The total soil respiration on the long-term fog and throughfall exclusion experiment plots is driven by the soil moisture variation in TMCF. The increase of soil moisture during the rainy season enhanced soil CO_2 emissions while the lower soil moisture during the dry season suppressed total soil respiration (Figure 6b). In addition, this study also revealed that soil temperature exerts positive and negative relationships with the soil respiration on the control and FE plots respectively while soil moisture is not a limiting factor in these plots (Wood & Silver, 2013). Further work quantifying environmental controls over different components of soil CO_2 efflux, such as litter, soil organic matter, roots and associated mycorrhizae and mineral soil, remains a high priority for TMCF.

5. Conclusions

This study compares similarities and differences in ecological responses to shifts in two critical water sources in TMCF - fog and throughfall. We focus on litterfall and soil respiration responses as two major and dynamic components of the ecosystem carbon cycle. Throughfall reduction generally caused stronger effects than fog reduction, with a significant decrease in leaf litterfall and soil respiration over time after imposition of the throughfall reduction treatment. Further, climatic controls and phenological shifts differed between the two different experiments. Temperature was the main driver of total litterfall productivity, however soil moisture was the main control over total soil respiration. In addition, litterfall from reproductive parts, fine wood, and epiphytes are driven by solar radiation and precipitation. The seasonal cycle of litterfall components and soil respiration are driven by monthly precipitation, although decreased soil water content on the fog and throughfall reduction plots changed the seasonal pattern. The main ecosystem response observed in both the fog and throughfall reduction was a clear and consistent increase in litterfall from reproductive structures. While a minor component of litterfall mass, these shifts in flower, fruit and seed production could lead to major changes in species composition, forest demography and structure over time under predicted changes in moisture availability in TMCF. Further research on other ecosystem carbon fluxes and climatic drivers is urgently needed to predict the fate of TMCFs under climate change.

Code and data availability

All data and code supporting this study are publicly available via Figshare (https://figshare.com/s/e509498c310a402f977e)

Supplement

The supplement related to this article is available online.

Author contributions

D.M. and W.H.H conceived the study; W.H.H., M.E.C., D.C.A., B.E.O., D.G.C., B.P.V., R.S.C., Y.S.Q., L.A.M., J.C.P., A.H., D.B. and D.M. performed the study; W.H.H. and D.M. analysed the data and wrote the paper with input from all authors.

Competing interests

The authors declare no conflicts of interest.

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References

Aldrich, M., Billington, C., Edwards, M., Laidlaw, R. (1997). Locations of tropical montane cloud forest sites as recorded in a worldwide inventory in "*A Global Directory of Tropical Montane Cloud Forests*". Cambridge (UK): UNEP-WCMC.

Bartholomew, D. C., Bittencourt, P. R. L., Galiano Cabrera, D., Sacatuma Cruz, R., Chambi Paucar, J. R., Corrales Alvarez, D., Cosio, E., Espinoza Otazu, B., Mamani, D. M., Meir, P., Muñoz Hermoza, G. A., Oliveira, R. S., Puma Vilca, B. L., Rosalai, A., Salas Yupayccana, C., Salinas, N., Sanchez Tintaya, J., Yuca Palomino, J. A., & Metcalfe, D. B. (2026). Tropical montane cloud forests have high resilience to five years of severe soil drought. *Global Change Biology*, *32*(1), e70670. https://doi.org/10.1111/gcb.70670

Berry, Z. C., & Goldsmith, G. R. (2020). Diffuse light and wetting differentially affect tropical tree leaf photosynthesis. *New Phytologist*, *225*(1), 143–153. https://doi.org/10.1111/nph.16121

Brando, P. M., Nepstad, D. C., Davidson, E. A., Trumbore, S. E., Ray, D., & Camargo, P. (2008). Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: Results of a throughfall reduction experiment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1498), 1839–1848. https://doi.org/10.1098/rstb.2007.0031

Brooks, M., E., Kristensen, K., Benthem, K., J. ,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., & Bolker, B., M. (2017). Glmmtmb balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378. https://doi.org/10.32614/RJ-2017-066

Bruijnzeel, L. A., Mulligan, M., & Scatena, F. N. (2011). Hydrometeorology of tropical montane cloud forests: Emerging patterns. *Hydrological Processes*, *25*(3), 465–498. https://doi.org/10.1002/hyp.7974

Brum, M., Vadeboncoeur, M., Asbjornsen, H., Puma Vilca, B. L., Galiano, D., Horwath, A. B., & Metcalfe, D. B. (2023). Ecophysiological controls on water use of tropical cloud forest trees in response to experimental drought. *Tree Physiology*, *43*(9), 1514–1532. https://doi.org/10.1093/treephys/tpad070

Cheng, S., Liu, X., Cao, M., Fu, J., Qian, H., Pan, X., Yang, L., Feng, Y. (2026). Observed increase in tropical vegetation droughts over the past three decades. *Geophysical Research Letters*, 53, e2025GL121172, https://doi.org/10.1029/2025GL121172

Cleveland, C. C., Wieder, W. R., Reed, S. C., & Townsend, A. R. (2010). Experimental drought in a tropical rain forest increases soil carbon dioxide losses to the atmosphere. *Ecology*, *91*(8), 2313–2323. https://doi.org/10.1890/09-1582.1

Cusack, D. F., Dietterich, L. H., & Sulman, B. N. (2023). Soil respiration responses to throughfall exclusion are decoupled from changes in soil moisture for four tropical forests, suggesting processes for ecosystem models. *Global Biogeochemical Cycles*, *37*(4), e2022GB007473. https://doi.org/10.1029/2022GB007473

Delsinne, T., Arias-Penna, T, Leponce, M. (2013). Effect of rainfall exclusion on ant assemblages in montane rainforests of Ecuador. *Basic and Applied Ecology*, 14(4), 357-365, https:10.1016/j.baae.2013.04.002

Eller, C.B., Meireles, L.D., Sitch, S., Burgess, S. O., Oliveira, R. S. (2020). How Climate Shapes the Functioning of Tropical Montane Cloud Forests. *Current Forestry Reports*, 6, 97-114, https://doi.org/10.1007/s40725-020-00115-6

Fahey, T. J., Sherman, R. E., & Tanner, E. V. J. (2016). Tropical montane cloud forest: Environmental drivers of vegetation structure and ecosystem function. *Journal of Tropical Ecology*, *32*(5), 355–367. https://doi.org/10.1017/S0266467415000176

Fan, Y., Lu, S., He, M., Yang, L., Hu, W., Yang, Z., Liu, X., Hui, D., Guo, J., & Yang, Y. (2021). Long-term throughfall exclusion decreases soil organic phosphorus associated with reduced plant roots and soil microbial biomass in a subtropical forest. *Geoderma*, *404*, 115309. https://doi.org/10.1016/j.geoderma.2021.115309

Farfan-Rios, W., Garcia-Cabrera, K., Salinas, N., Raurau-Quisiyupanqui, M. N., & Silman, M. R. (2015). Lista anotada de árboles y afines en los bosques montanos del sureste peruano: La importancia de seguir recolectando. *Revista Peruana de Biología*, *22*(2), 145–174. https://doi.org/10.15381/rpb.v22i2.11351

Fyllas, N. M., Patiño, S., Baker, T. R., Bielefeld Nardoto, G., Martinelli, L. A., Quesada, C. A., Paiva, R., Schwarz, M., Horna, V., Mercado, L. M., Santos, A., Arroyo, L., Jiménez, E. M., Luizão, F. J., Neill, D. A., Silva, N., Prieto, A., Rudas, A., Silviera, M., … Lloyd, J. (2009). Basin-wide variations in foliar properties of Amazonian forest: Phylogeny, soils and climate. *Biogeosciences*, *6*(11), 2677–2708. https://doi.org/10.5194/bg-6-2677-2009

Girardin, C. A. J., Espejob, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca, L., Marthews, T. R., Aragao, L. E. O. C., Farfán-Rios, W., García-Cabrera, K., Halladay, K., Fisher, J. B., Galiano-Cabrera, D. F., Huaraca-Quispe, L. P., Alzamora-Taype, I., Eguiluz-Mora, L., -Revilla, N. S., Silman, M. R., Meir, P., & Malhi, Y. (2014). Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 107–123. https://doi.org/10.1080/17550874.2013.820222

Girardin, C. A. J., Malhi, Y., Feeley, K. J., Rapp, J. M., Silman, M. R., Meir, P., Huaraca Huasco, W., Salinas, N., Mamani, M., Silva-Espejo, J. E., García Cabrera, K., Farfan Rios, W., Metcalfe, D. B., Doughty, C. E., & Aragão, L. E. O. C. (2014). Seasonality of above-ground net primary productivity along an Andean altitudinal transect in Peru. *Journal of Tropical Ecology*, *30*(6), 503–519. https://doi.org/10.1017/S0266467414000443

Gotsch, S. G., Asbjornsen, H., & Goldsmith, G. R. (2016). Plant carbon and water fluxes in tropical montane cloud forests. *Journal of Tropical Ecology*, *32*(5), 404–420. https://doi.org/10.1017/S0266467416000341

Günter, S., Stimm, B., Cabrera, M., Diaz, M. L., Lojan, M., Ordoñez, E., Richter, M., & Weber, M. (2008). Tree phenology in montane forests of southern Ecuador can be explained by precipitation, radiation and photoperiodic control. *Journal of Tropical Ecology*, *24*(3), 247–258. https://doi.org/10.1017/S0266467408005063

Guzmán Q., J. A., Hamann, H. F., & Sánchez-Azofeifa, G. A. (2024). Multi-decadal trends of low-clouds at the Tropical Montane Cloud Forests. *Ecological Indicators*, *158*, 111599. https://doi.org/10.1016/j.ecolind.2024.111599

Halbritter, A. H., Vandvik, V., Cotner, S. H., Farfan-Rios, W., Maitner, B. S., Michaletz, S. T., Oliveras Menor, I., Telford, R. J., Ccahuana, A., Cruz, R., Sallo-Bravo, J., Santos-Andrade, P. E., Vilca-Bustamante, L. L., Castorena, M., Chacón-Labella, J., Christiansen, C. T., Duran, S. M., Egelkraut, D. D., Gya, R., … Enquist, B. J. (2024). Plant trait and vegetation data along a 1314 m elevation gradient with fire history in Puna grasslands, Perú. *Scientific Data*, *11*(1), 225. https://doi.org/10.1038/s41597-024-02980-3

Halladay, K., Malhi, Y., & New, M. (2012). Cloud frequency climatology at the Andes/Amazon transition: 1. Seasonal and diurnal cycles. *Journal of Geophysical Research: Atmospheres*, *117*(D23), 2012JD017770. https://doi.org/10.1029/2012JD017770

Holder, C. D. (2004). Rainfall interception and fog precipitation in a tropical montane cloud forest of Guatemala. *Forest Ecology and Management*, *190*(2–3), 373–384. https://doi.org/10.1016/j.foreco.2003.11.004

Horwath, A. B., Royles, J., Tito, R., Gudiño, J. A., Salazar Allen, N., Farfan-Rios, W., Rapp, J. M., Silman, M. R., Malhi, Y., Swamy, V., Latorre Farfan, J. P., & Griffiths, H. (2019). Bryophyte stable isotope composition, diversity and biomass define tropical montane cloud forest extent. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1895), 20182284. https://doi.org/10.1098/rspb.2018.2284

Hu, J., & Riveros-Iregui, D. A. (2016). Life in the clouds: Are tropical montane cloud forests responding to changes in climate? *Oecologia*, *180*(4), 1061–1073. https://doi.org/10.1007/s00442-015-3533-x

Hughes, N. M., Sanchez, A., Berry, Z. C., & Smith, W. K. (2024). Clouds and plant ecophysiology: Missing links for understanding climate change impacts. *Frontiers in Forests and Global Change*, *7*, 1330561. https://doi.org/10.3389/ffgc.2024.1330561

Kitayama, K., Ushio, M., & Aiba, S. (2021). Temperature is a dominant driver of distinct annual seasonality of leaf litter production of equatorial tropical rain forests. *Journal of Ecology*, *109*(2), 727–736. https://doi.org/10.1111/1365-2745.13500

Knapp, A. K., Condon, K. V., Folks, C. C., Sturchio, M. A., Griffin-Nolan, R. J., Kannenberg, S. A., Gill, A. S., Hajek, O. L., Siggers, J. A., & Smith, M. D. (2024). Field experiments have enhanced our understanding of drought impacts on terrestrial ecosystems—But where do we go from here? *Functional Ecology*, *38*(1), 76–97. https://doi.org/10.1111/1365-2435.14460

Krashevska, V., Sandmann, D., Maraun, M., Scheu, S. (2012). Consequences of exclusion of precipitation on microorganisms and microbial consumers in montane tropical rainforests. *Oecologia*, 170, 1067-1076, https://doi.org/10.1007/s00442-012-2360-6

Litton, C. M., Giardina, C. P., Freeman, K. R., Selmants, P. C., & Sparks, J. P. (2020). Impact of mean annual temperature on nutrient availability in a tropical montane wet forest. *Frontiers in Plant Science*, *11*, 784. https://doi.org/10.3389/fpls.2020.00784

Lyu, M., Giardina, C. P., & Litton, C. M. (2021). Interannual variation in rainfall modulates temperature sensitivity of carbon allocation and flux in a tropical montane wet forest. *Global Change Biology*, *27*(16), 3824–3836. https://doi.org/10.1111/gcb.15664

Marthews, T., Riutta, T., Oliveras Menor, I., Urrutia, R., Moore, S., Metcalfe, D., Malhi, Y., Phillips, O., Huaraca Huasco, W., Ruiz Jaén, M. del C., Girardin, C., Butt, N., & Cain, R. (n.d.). *Measuring tropical forest carbon allocation and cycling: A RAINFOR-GEM field manual for intensive census plots (V3. 0)*. Manual, Global Ecosystems Monitoring network, 10-39.

McDowell, N. G., Ryan, M. G., Zeppel, M. J. B., & Tissue, D. T. (2013). Feature: Improving our knowledge of drought-induced forest mortality through experiments, observations, and modeling. *New Phytologist*, *200*(2), 289–293. https://doi.org/10.1111/nph.12502

Meir, P., Mencuccini, M., Binks, O., Da Costa, A. L., Ferreira, L., & Rowland, L. (2018). Short-term effects of drought on tropical forest do not fully predict impacts of repeated or long-term drought: Gas exchange versus growth. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1760), 20170311. https://doi.org/10.1098/rstb.2017.0311

Metcalfe, D. B., Galiano Cabrera, D. F., Alvarez Mayorga, L. M., Cruz, R. S., Alvarez, D. C., Otazu, B. R. E., Huaraca Huasco, W., Chambi, J. R., Ezquerra, M. E., Puma Vilca, B. L., Mulligan, M., Vadeboncoeur, M. A., Asbjornsen, H., Bittencourt, P. R. L., Horwath, A. B., & Bartholomew, D. C. (2025). The Wayqecha Amazon Cloud Curtain Ecosystem Experiment: A new experimental method to manipulate fog water inputs in terrestrial systems. *Methods in Ecology and Evolution*, *16*(2), 400–413. https://doi.org/10.1111/2041-210X.14483

https://doi.org/10.5194/egusphere-2026-2882
Preprint. Discussion started: 11 June 2026

Metcalfe, D. B., Rocha, W., Balch, J. K., Brando, P. M., Doughty, C. E., & Malhi, Y. (2018). Impacts of fire on sources of soil CO_2 efflux in a dry Amazon rain forest. *Global Change Biology*, *24*(8), 3629–3641. https://doi.org/10.1111/gcb.14305

Moser, G., Schuldt, B., Hertel, D., Horna, V., Coners, H., Barus, H., & Leuschner, C. (2014). Replicated throughfall exclusion experiment in an Indonesian perhumid rainforest: Wood production, litter fall and fine root growth under simulated drought. *Global Change Biology*, *20*(5), 1481–1497. https://doi.org/10.1111/gcb.12424

Nakagawa, M., Ushio, M., Kume, T., & Nakashizuka, T. (2019). Seasonal and long-term patterns in litterfall in a Bornean tropical rainforest. *Ecological Research*, *34*(1), 31–39. https://doi.org/10.1111/1440-1703.1003

Nepstad, D. C., Moutinho, P., Dias-Filho, M. B., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., Ray, D., Guerreiros, J. B., Lefebvre, P., Sternberg, L., Moreira, M., Barros, L., Ishida, F. Y., Tohlver, I., Belk, E., Kalif, K., & Schwalbe, K. (2002). The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *Journal of Geophysical Research: Atmospheres*, *107*(D20). https://doi.org/10.1029/2001JD000360

Nottingham, A. T., Karhu, K., Salinas, N., Schnecker, J., Sietiö, O.-M., Martin-Vivanco, A. K., Wanek, W., & Meir, P. (2026). Microbial death in the Andes: Necromass declines despite growth and carbon-use-efficiency increases with decadal soil warming. *Soil Biology and Biochemistry*, *213*, 110002. https://doi.org/10.1016/j.soilbio.2025.110002

Ogaya, R., & Penuelas, J. (2007). Species-specific drought effects on flower and fruit production in a Mediterranean holm oak forest. *Forestry*, *80*(3), 351–357. https://doi.org/10.1093/forestry/cpm009

Pau, S., Okamoto, D. K., Calderón, O., & Wright, S. J. (2018). Long-term increases in tropical flowering activity across growth forms in response to rising CO_2 and climate change. *Global Change Biology*, *24*(5), 2105–2116. https://doi.org/10.1111/gcb.14004

Pau, S., Wolkovich, E. M., Cook, B. I., Nytch, C. J., Regetz, J., Zimmerman, J. K., & Joseph Wright, S. (2013). Clouds and temperature drive dynamic changes in tropical flower production. *Nature Climate Change*, *3*(9), 838–842. https://doi.org/10.1038/nclimate1934

Powell, T. L., Galbraith, D. R., Christoffersen, B. O., Harper, A., Imbuzeiro, H. M. A., Rowland, L., Almeida, S., Brando, P. M., Da Costa, A. C. L., Costa, M. H., Levine, N. M., Malhi, Y., Saleska, S. R., Sotta, E., Williams, M., Meir, P., & Moorcroft, P. R. (2013). Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytologist*, *200*(2), 350–365. https://doi.org/10.1111/nph.12390

Rapp, J. M., & Silman, M. R. (2014). Epiphyte response to drought and experimental warming in an Andean cloud forest. *F1000Research*, *3*, 7. https://doi.org/10.12688/f1000research.3-7.v2

Rapp, J., & Silman, M. (2012). Diurnal, seasonal, and altitudinal trends in microclimate across a tropical montane cloud forest. *Climate Research*, *55*(1), 17–32. https://doi.org/10.3354/cr01127

Riutta, T., Kho, L. K., Teh, Y. A., Ewers, R., Majalap, N., & Malhi, Y. (2021). Major and persistent shifts in below-ground carbon dynamics and soil respiration following logging in tropical forests. *Global Change Biology*, *27*(10), 2225–2240. https://doi.org/10.1111/gcb.15522

Rowland, L., Da Costa, A. C. L., Oliveira, A. A. R., Almeida, S. S., Ferreira, L. V., Malhi, Y., Metcalfe, D. B., Mencuccini, M., Grace, J., & Meir, P. (2018). Shock and stabilisation following long-term drought in tropical forest from 15 years of litterfall dynamics. *Journal of Ecology*, *106*(4), 1673–1682. https://doi.org/10.1111/1365-2745.12931

Sotta, E. D., Veldkamp, E., Schwendenmann, L., Guimarães, B. R., Paixão, R. K., Ruivo, M. D. L. P., Lola Da Costa, A. C., & Meir, P. (2007). Effects of an induced drought on soil carbon dioxide (CO_2) efflux and soil CO_2 production in an Eastern Amazonian rainforest, Brazil. *Global Change Biology*, *13*(10), 2218–2229. https://doi.org/10.1111/j.1365-2486.2007.01416.x

Spracklen, D. V., & Righelato, R. (2014). Tropical montane forests are a larger than expected global carbon store. *Biogeosciences*, *11*(10), 2741–2754. https://doi.org/10.5194/bg-11-2741-2014

Van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, *24*(1), 353–377. https://doi.org/10.1146/annurev.es.24.110193.002033

Van Straaten, O., Veldkamp, E., & Corre, M. D. (2011). Simulated drought reduces soil CO_2 efflux and production in a tropical forest in Sulawesi, Indonesia. *Ecosphere*, *2*(10), art119. https://doi.org/10.1890/ES11-00079.1

Vogado, N. O., Liddell, M. J., Laurance, S. G. W., Campbell, M. J., Cheesman, A. W., Engert, J. E., Palma, A. C., Ishida, F. Y., & Cernusak, L. A. (2020). The effects of an experimental drought on the ecophysiology and fruiting phenology of a tropical rainforest palm. *Journal of Plant Ecology*, *13*(6), 744–753. https://doi.org/10.1093/jpe/rtaa069

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical*

Society Series B: Statistical Methodology, *73*(1), 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wood, T. E., & Silver, W. L. (2012). Strong spatial variability in trace gasdynamics following experimental drought in a humid tropical forest. *Global Biogeochemical Cycles*, *26*(3), 2010GB004014. https://doi.org/10.1029/2010GB004014

Wright, S. J., & Van Schaik, C. P. (1994). Light and the phenology of tropical trees. *The American Naturalist*, *143*(1), 192–199. https://doi.org/10.1086/285600

Zhang, X., Zhang, Y., Sha, L., Wu, C., Tan, Z., Song, Q., Liu, Y., & Dong, L. (2015). Effects of continuous drought stress on soil respiration in a tropical rainforest in southwest China. *Plant and Soil*, *394*(1–2), 343–353. https://doi.org/10.1007/s11104-015-2523-4