Divergent mercury ~~sequestration~~ accumulation dynamics in tropical dry and moist broadleaf forests

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Abstract. Forests are major sinks for atmospheric mercury (Hg) due to the efficiency of stomatal uptake and litter deposition. Tropical forests, highly productive ecosystems, remain understudied despite their pronounced climatic and phenological variability. We investigated whether seasonal rainfall regimes and associated tree adaptations influence Hg dynamics in secondary tropical moist broadleaf (TMBF) and tropical dry broadleaf (TDBF) forests in Costa Rica by examining foliar Hg concentrations, litter Hg standing stocks, and soil Hg concentrations.~~We investigated whether seasonal rainfall regimes and associated tree adaptations regulate the Hg dynamics – its uptake by leaves, deposition through litter, and storage in soils – in secondary tropical moist broadleaf (TMBF) and tropical dry broadleaf (TDBF) forests from Costa Rica.~~ Seasonal differences in rainfall and associated environmental conditions strongly~~Seasonality strongly~~ ~~controlled~~ influenced foliar Hg ~~sequestration~~ concentration in the TDBF. ~~There, Dd~~Deciduous trees showed 4.7 times higher foliar Hg concentration in the wet season, when leaves were mature, compared to the dry season, when newly flushed leaves emerged after leaf shedding. Evergreen trees in TDBF demonstrated 2.3 times lower foliar Hg concentrations in the dry season than in the wet season (23 vs. 53 µg kg^{-1}), likely due to various associated physiological processes (e.g., leaf flushing). However, the primary mechanism remains unclear given the complex and unexplored Hg dynamics in TDBF. TMBF showed no clear seasonal variation in foliar Hg in either deciduous (dry: 48; wet: 54 µg kg^{-1}) or evergreen trees (dry: 57; wet: 53 µg kg^{-1}), likely due to longer leaf lifespan sustaining year-round transpiration and stomatal Hg uptake under high humidity. Atmospheric Hg concentrations in TDBF were two times higher than in TMBF (1.2 vs. 0.~~7~~6 ng m^{-3}) across both seasons, likely reflecting greater Hg capture per unit area in TMBF due to denser vegetation and enhanced wet deposition via rainfall. Foliar Hg was not correlated with stomatal density or specific leaf area in either forest type. Soil Hg concentrations, however, were correlated with litter-derived inputs, supporting litter as the dominant Hg transfer pathway. Higher seasonally averaged ~~Hg inputs via litter~~litter Hg standing stocks (34 µg m^{-2}) in TMBF than in the TDBF (19 µg m^{-2}) resulted in 3.4 times higher soil Hg concentrations (0–30 cm) in TMBF (115 µg kg^{-1}) than in TDBF (34 µg kg^{-1}). Soil Hg ~~stocks~~ concentrations were 2.6 times lower at a previously deforested TMBF

site, indicating persistent disturbance effects despite almost three decades of reforestation. Overall, foliar Hg concentrations in the TDBF varied markedly between seasons, while both TDBF and TMBF appeared ~~seasonality regulated Hg sequestration in TDBF, yet both TDBF and TMBF serve as~~ to be important ~~global~~ Hg^0 ~~sinks~~ reservoirs, with contrasting dynamics that are potentially sensitive to climate change.

1 Introduction

Mercury (Hg) is a highly toxic metal ranked among the top ten chemicals of public health concern, originating from both natural sources (volcanism and rock weathering) and anthropogenic sources (gold mining and biomass burning) (WHO, 2017; Gworek et al., 2020). In the atmosphere, 90%–99% of Hg exists as gaseous elemental mercury (GEM, Hg^0), with the remainder as gaseous oxidized mercury (Hg^{2+}) and particulate-bound mercury (Hg^p) (Gustin et al., 2013). Due to its high volatility, Hg^0 undergoes long-range atmospheric transport from emission sources until deposition (Selin, 2009)

Forests are major sinks for ~~atmospheric Hg (~~Hg^0~~)~~, with vegetation accounting for ~60–90% of the uptake, and depositing ~1180–1410 Mg Hg yr^{-1} to soil (Denzler et al., 2025; Zhou et al., 2021). Plant uptake involves (I) stomatal assimilation of Hg^0 followed by oxidation and internal transport (tree rings store atmospheric Hg) (Peng et al., 2024), although the site of foliar oxidation remains uncertain (Gustin et al., 2022), ~~-~~and (II) non-stomatal (cuticular) uptake, including diffusion of lipophilic Hg^0 through the cuticle and co-entry/oxidation of Hg^{2+} deposited on leaf surfaces (Laacouri et al., 2013; Rea et al., 2002; Stamenkovic and Gustin, 2009). Once incorporated into foliage, Hg is transferred to soils through litter, with more than 80% of global soil Hg originating from litter deposition (Jiskra et al., 2015; Wang et al., 2016). Additional mechanisms, including dry and wet Hg deposition, binding to organic matter, and soil erosion, also contribute to Hg accumulation in soils (Gerson et al., 2022; Monteiro et al., 2024; Silva-Filho et al., 2006).

Recent global estimates found that forests remove ~2200–3400 Mg Hg yr^{-1} (~40–65% of the Hg^0) and store ~500–1100 Gg in surface soils and vegetation (Wang et al., 2022). Litter Hg fluxes are ~~driven~~ controlled by multiple interacting factors, including vegetation structure (leaf area and canopy density), phenology and ~~(~~leaf age~~)~~, and environmental conditions such as ~~(~~climate , temperature, and ~~and humidity/~~moisture availability~~)~~ (Guentzel et al., 1998; Jiskra et al., 2018; Rea et al., 2002; Wang et al., 2019). These controls~~These fluxes~~ are especially pronounced in tropical forests, where high ~~biodiversity~~ productivity, large leaf area, continuous or prolonged growing seasons, and rapid biogeochemical cycling can promote substantial Hg^0 ~~atmospheric Hg~~ uptake by vegetation and subsequent Hg transfer to soils through litter fall. ~~turnover under warm, wet, and high-irradiance conditions enhance Hg uptake and recycling bound to organic matter degradation~~ (Poorter, 2004; Schneider et al., 2023; Wang et al., 2016~~a~~). Once deposited ~~in~~on the forest floor, Hg can be retained through interactions with soil organic matter, while rapid litter and organic-matter turnover in tropical forests can enhance post-depositional Hg transformations and redistribution, including Hg reduction and subsequent Hg^0 re-emission (Yuan et al., 2023~~a~~)~~decomposition and associated biogeochemist processes that influence it subsequent redistribution and mobility might be enhanced under faster turnover times~~

~~(CHECK refecences).~~ ~~-~~Tropical trees also exhibit elevated foliar Hg concentrations, linked to higher stomatal pore density and higher ~~photosynthesis capacity relative to~~photosynthetic capacity than temperate and boreal species (Larcher, 2003; Teixeira et al., 2018). Consequently, ~~regions~~ tropical regions such as the Amazon Basin and Central Africa exhibit the highest global Hg^0 removal via litter (65.0 ± 30.0 g km^{-2} yr^{-1}; Wang et al. 2016~~a~~). ~~Tropical forest, with those soils~~Soils in tropical forests represent a major Hg sink, with concentrations up to 10 times higher than in temperate forests ~~serving represent as the principal Hg sink with up to 10 times higher than in temperate forests~~ (Teixeira et al., 2017). Despite their global importance, tropical forests remain understudied compared to temperate and boreal forests (Yuan et al., 2023), even though they exhibit ~~contrasting~~ distinct ~~dynamics~~ patterns ~~in climate~~of climatic seasonality, vegetation productivity, and hydrology (Bonan, 2008; Cusack et al., 2024; Klock et al., 2022).

There are two main types of tropical forests: tropical rainforests and tropical seasonal forests (Holzman, 2008). Tropical rainforests, or more specifically referred to as tropical moist broadleaf forests (TMBF), are predominantly ~~mostly~~ evergreen, species-rich systems with~~evergreen vegetation and, species-rich systems with~~ annual precipitation typically > 2,000 mm - and as high as 10,000 mm- ~~-~~and ~~limited~~ relatively small seasonal differences in climatic conditions ~~low seasonality~~. They~~. They~~ generally experience ~~due to~~ short or weakly pronounced dry periods, which may ~~also~~ be interrupted by episodic rainfall events (Stork et al., 2008). By contrast, tropical seasonal forests, also ~~known~~ referred to as tropical dry broadleaf forests (TDBF), are characterized by pronounced wet and dry periods and predominantly deciduous vegetation structure, with substantial leaf shedding during the dry season. ~~distinct wet and dry periods characterized by leaf fall and long~~The dry season typically lasts 5 - 6 months, with monthly precipitation ~~with <~~below 100 mm~~)~~ (Bunyavejchewin et al., 2011), ~~with~~ while~~a~~ total annual rainfall ~~of~~ ranges from 700 to 2,000 mm (Ruangpanit, 1995).

To date, studies of Hg dynamics in tropical forests have focused on TMBF affected by artisanal small-scale gold mining pollution, leaving natural Hg cycling poorly characterized and limited to local study areas, often without considering the role of seasonal variation (Escobar-Camacho et al., 2024; Fostier et al., 2015; Gerson et al., 2022~~a, a~~; Lima et al., 2022; Lucchini et al., 2025; Rodriguez-Pascual et al., 2024; Silva do Nascimento et al., 2025; Silva-Filho et al., 2006; Teixeira et al., 2017, 2018). In some of those contaminated areas,~~,~~ ~~with high concentrations of~~elevated atmospheric Hg concentrations may further~~in polluted areas likely~~ overrid~~e~~~~ing~~ seasonal ~~effects~~patterns in Hg uptake and cycling, making it difficult to distinguish natural seasonal controls from pollution-driven effects. ~~-~~Moreover, the role of Hg sequestration in TDBF remains unexplored, despite their wide distribution across tropical and subtropical regions (~42%; Hasnat and Hossain, 2020) and ~~being~~ their status as one of the most threatened tropical ecosystems due to extensive deforestation and high vulnerability to climate change. In~~,~~ ~~particularl~~particular~~,y to~~ longer and more intense dry seasons ~~that could~~ may alter key phenological processes such as leaf flushing, leaf shedding, and~~,~~ flowering, among others~~-~~ (Chidumayo, 2025; Hasnat and Hossain, 2020; Siyum, 2020; Stivanello et al., 2024). These changes may have consequences for Hg uptake, litterfall Hg fluxes, and Hg sequestration in forest soils.

~~Season~~Studies in the Northern Hemisphere have shown that seasonal changes in Hg^0 concentrations are linked to seasonal changes in plant photosynthetic activity, as vegetation acts as a Hg^0 pump

~~Forest seasonality strongly influences atmospheric Hg^0 concentrations in the Northern Hemisphere due to variations in leaf uptake~~ (Jiskra et al., 2018), yet the ~~effect~~ influence of ~~these~~ seasonal patterns on ~~atmospheric~~ Hg^0 uptake and sequestration remains largely~~is~~ unexamined in tropical forests. This ~~might~~ may be especially relevant in TDBF, which experiences severe water deficits during the dry season, leading deciduous trees to shed leaves as a water-conservation strategy (Zhang et al., 2014). During this dry period, ~~remaining~~ leaves retained on trees typically exhibit ~~decrease~~ reduced stomatal conductance, ~~reduce~~ leaf transpiration, and net photosynthesis rates ~~,~~ as adaptive responses to water stress (Ávila-Lovera et al., 2019; Hasselquist et al., 2010; Mendes et al., 2020). These physiological responses may, in turn, influence ~~, which may directly impact on~~ Hg^0 uptake by vegetation and subsequent Hg sequestration in those forest ecosystems.

Recent models have estimate~~d~~~~ing~~ Hg pools in vegetation biomass, litter, soil, and the atmosphere ~~have been developed and applied~~ across ~~various~~ a range of forest types~~,~~ using machine learning and process-based simulation approaches. Thus, Chen et al. (2024~~a~~) estimated a global mean foliar Hg concentration of 24 μg kg^{-1} and a total foliar Hg pool of 4561.3 Mg, with TMBF accounting for nearly half of the global pool. Zhou and Obrist (2021~~b~~) reported annual vegetation Hg assimilation of 3062 ± 607 Mg yr^{-1}, with tropical forest mosses and lichens showing the highest mean concentrations. Feinberg et al. (2022) estimated global Hg^0 dry deposition to land at 2276 Mg yr^{-1}, with ~29% ~~attributed~~ occurring in~~to~~ the Amazon. However, these studies also ~~highlighted~~ identified substantial uncertainty, ~~especially particularlly~~particularly in tropical forests, where field measurements remain scarce compared to forests from East Asia, Europe, and North America (Chen et al., 2024; Feinberg et al., 2022; Zhou and Obrist, 2021). The above-mentioned models omit the pronounced seasonal variations in plant photosynthetic activity reported among tropical tree species (Tiwari et al., 2025), as well as interspecific differences, ~~and~~ evergreen–deciduous phenological transitions, ~~all of which~~~~despite the strong seasonallyty~~ and other forms of vegetation heterogeneity~~heterogeneity characteristic~~characteristic of tropical forests. In addition, TDBF remains unstudied in this context and is not considered in estimations, despite being strongly season-dependent and widely distributed. This ~~lack of data likely~~limitation may constrain model performance and reduce~~s~~ the ~~predictive~~ accuracy of regional and global Hg flux estimates. Climate change may ~~adds~~ further ~~complexity~~ increase uncertainty by altering vegetation ~~patterns~~dynamics and water availability, potentially ~~increasing~~ affecting Hg^0 ~~evasion~~ exchange with ~~to~~ the atmosphere (Teixeira et al., 2017) and reducing Hg sequestration ~~due to~~through increased tree mortality ~~from longer~~ during prolonged or intensified dry periods (Yuan et al., 2024).

Our study aimed to evaluate how seasonal rainfall patterns influence Hg dynamics in TDBF and TMBF across the dry and wet seasons by quantifying Hg concentrations in key forest compartments involved in Hg uptake, transfer, and storage (i.e., foliage, litter, and soil) and by assessing litter as a pathway for Hg transfer from vegetation to soils.

~~Our study aimed to evaluate how seasonality influences Hg dynamics in trees from TDBF and TMBF by quantifying Hg concentrations in involved inkey uptake, transfer, and storage compartments (i.e., foliage, litter, and soil), and by assessing the role oflitter as a pathway for Hg transfer from vegetation to soils, in both forest types.~~

2 Materials and methods

2.1 Study area

The study was conducted in twelve plots (~100 m^2 each, adjusted to site orography) located in secondary forests in Costa Rica (Fig. 1), with six plots in the tropical dry broadleaf forest (TDBF; H1–H6) and six plots in the tropical moist broadleaf forest (TMBF; G1–G6). The TDBF plots were located at the Horizontes Experimental Research Station, in the Área de Conservación Guanacaste (60-184 ~~m.a.s.l~~m.a.s.l.; Mora-Chacón et al., 2022), northwestern Costa Rica.

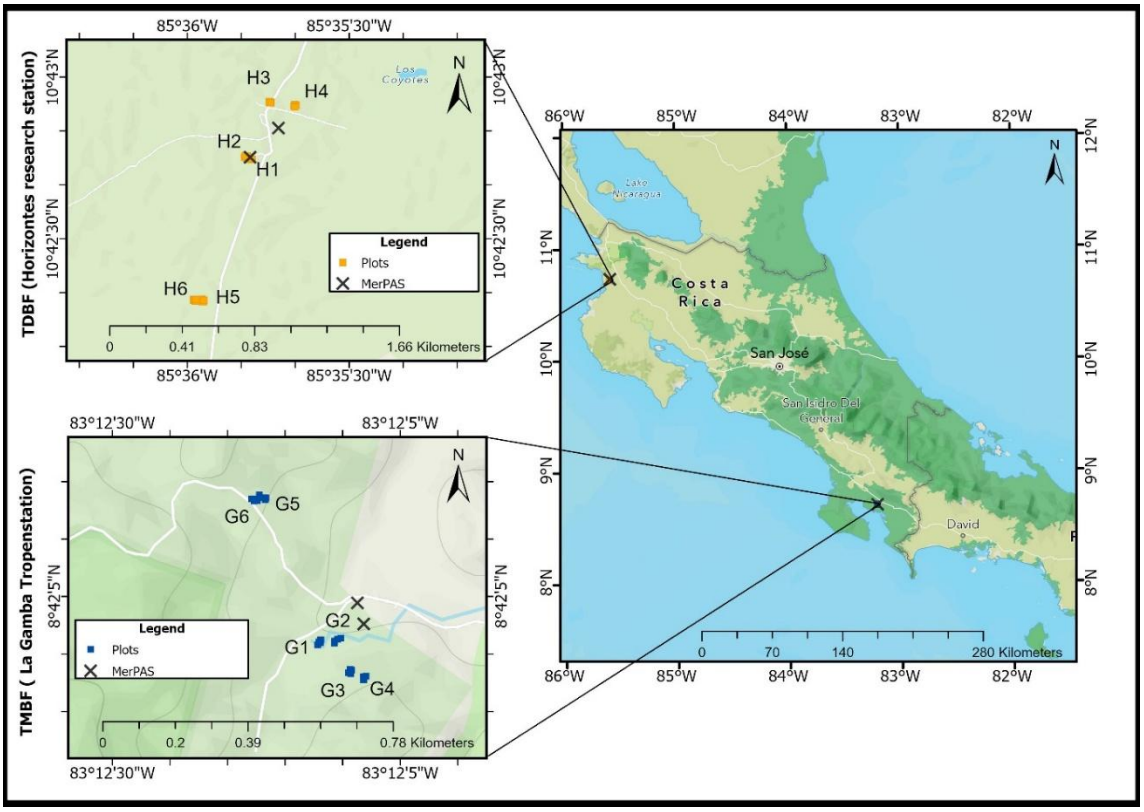


Figure 1: Location of the sampling sites in the tropical dry broadleaf forest (TDBF) and tropical moist broadleaf forest (TMBF) in Costa Rica and the sites where the atmospheric mercury samplers (MerPAS) were deployed.

The TMBF plots were near the La Gamba Tropenstation (60-345 m.a.s.l.; Höbinger et al., 2012) in the Golfo Dulce region, on the edge of Piedras Blancas National Park (Área de Conservación Osa). GPS coordinates are listed in Table S1 in the Supplementary Material (SM).

The TDBF site has a mean annual temperature of 25 °C, a six-month dry season from mid-November to mid-May, and an average annual rainfall of ~1575 mm (interannual range 880–3030 mm) (Gei and Powers, 2013; Höbinger et al., 2012). The area of study in TDBF has undergone natural regeneration for ~37 years (since approximately 1989), following the cessation of rice cultivation and cattle grazing, and is now dominated by deciduous trees with some evergreen species (Werden et al., 2018). The TMBF has a mean annual temperature of 28.2 °C and receives ~5,900 mm of rain annually, with a short, nominal dry period from December to April that is often interrupted by rainfall (Huber et al., 2008; Huber and Weissenhofer, 2019). Owing to its wet climate, biogeographic setting, and environmental heterogeneity, it supports humid evergreen lowland forest and is considered one of the most species-rich lowland rainforests in Central America (Yumpu.com, 2025). The TMBF study area was previously affected by partial land-use impacts from cattle grazing, plantations, and pasture use. It has undergone reforestation for ~33 years (since approximately 1993) and now consists of a mosaic of primary and secondary forest (Huber and Weissenhofer, 2019). The specific sites sampled in both TDBF and TMBF are secondary forests without any known close source of anthropogenic Hg emission (e.g., gold mining, cement production, etc.) (Fig. 1).

Three sampling campaigns (SC1, SC2, and SC3) were conducted, two at the end of the dry season and one at the end of the wet season, as shown in Table 1. This design enabled evaluation of seasonal effects in both TDBF and TMBF. Climate data for each season in both forest types, including daily precipitation, UV radiation, and earth skin temperature, were obtained from 15 November 2023 to 15 June 2026 from NASA's Prediction of Worldwide Energy Resources (POWER) project (NASA POWER | Data Access Viewer (DAV), 2026).

Table 1~~2~~: Design of the sampling campaigns in the tropical dry broadleaf forest (TDBF) and tropical moist broadleaf forest (TMBF).

Sampling Campaign	Month, Year	Season[a]	Leaf phenology in deciduous species[b]	Sampling objective
SC1	May 2024	Dry	TDBF, leaves are newly flushed after the first sporadic rainfall~~s~~	Set plots, tag plant species, sample soil, collect leaves and litter, deploy MerPAS[c].
SC2	November 2024	Wet	TDBF, mature leaves[d]	Resample leaves from tagged plants, sample litter, collect deployed MerPAS from SC1, and replace them with new ones.
SC3	May 2025	Dry	Similar to SC1	Sample leaves to assess within-individual variability~~,~~ ; collect deployed MerPAS in SC2

[a] Samples were taken at the end of the ~~specify~~ specified season
[b] In TMBF, deciduous trees behaved more like evergreens, renewing leaves periodically throughout the year. They were found with mature leaves during all sampling campaigns; i.e., only mature leaves were collected.
[c] Mercury passive samplers
[d] Fully expanded, non-senescent leaves were considered mature leaves

2.2 Leaves, litter, and soil sampling and processing

Sampling of living leaves: In each forest (TDBF and TMBF), composite leaf samples were collected primarily from trees, with fewer bushes, ferns, and lianas, in proportion to their local distribution across the twelve plots (TDBF: H1–H6; TMBF: G1–G6) during SC1, SC2, and SC3 (Table 1). In SC1, 60 samples were collected per forest (n = 120); in SC2, 90 samples were collected per forest (n = 180); and in SC3, a total of 91 samples were collected across both forests. This yielded an overall total of n = 391 samples to fulfill the sampling objectives detailed in Table 1. ~~Sampling of living leaves: In each forest (TDBF and TMBF), composite leaf samples were collected primarily from trees, with fewer bushes, ferns, and lianas, in proportion to their local distribution (n= 391) across the twelve plots (TDBF: H1–H6; TMBF: G1–G6) during SC1, SC2, and SC3 (Table 1).~~ As most of the sampled species in both forests were trees, we refer to them as tree species throughout the manuscript. The leaves were sampled using a telescopic pruner at heights between 1 and 5 m. In SC3, to assess within-individual repeatability of foliar Hg, we sampled ≥ 3 leaves from different branches or positions of the same tagged individual. After sampling, the leaves were washed thoroughly with tap water to remove soil, dust or moss, rinsed with deionized water, dried, and stored until analysis. Most plant individuals were classified to the species level, with a few identified to the genus level due to the high similarity between species. All samples were then classified by leaf habit (evergreen vs. deciduous), a trait strongly

influenced by ~~seasonality~~seasonal dynamics. Total Hg concentrations ~~was~~ were analyzed in all the samples ~~after~~ following sample preparation.

Litter sampling: Excluding green leaves and twigs, litter was sampled ~~in~~ from four replicates per plot ~~(n= 96)~~ at the end of the dry season (SC1) and the wet season (SC2), resulting in 96 samples in total (n=96). This sampling design ~~enable~~enables the ~~to~~ assessment of ~~differences in seasonality~~seasonal differences. All litter within a ~400 cm^2 sampling square was collected into sealed plastic bags, dried to constant weight (50 °C, ~14 days), and weighed ~~before grinding~~ to estimate litter accumulation (~~per~~ g m^{-2}) before grinding. Total Hg concentrations ~~was~~ were analyzed ~~after~~ following sampling preparation.

Soil sampling. Four soil ~~profile~~ cores ~~samples~~ were collected ~~per~~ from each of six plots ~~from~~ in each~~both~~ forest type s ~~(n = 24 cores)~~ during the SC1 sampling campaign, resulting in 48 cores in total. Each ~~-~~core was sectioned into~~Sampling was conducted at~~ four depth intervals (0–5, 5–10, 10–20 cm, and 20–30 cm~~, n = 192~~), yielding 96 ~~soils~~soil samples per forest ~~plot~~ and 192 samples in total (n=192). Soil samples were collected using a stainless-steel soil corer~~;~~ ~~-~~sampling ~~(~~coordinates are provided in Table S1~~)~~. All samples were dried, sieved (< 2mm), and ground prior to analysis. Total Hg concentrations w~~as~~ere analyzed ~~after~~ following sampling preparation.

Sample preparation: Litter, soil, and leaf samples were dried to constant weight at 50 °C, homogenized, and ground to a fine powder with a zirconia ball mill (MM40, Retsch, Germany).

2.3 Mercury analysis

Total Hg concentrations ~~was~~ were measured in dried, milled, homogeneous litter, soil, and leaf samples using a direct mercury analyzer (DMA-80; MWS, Germany). Analytical quality control included instrument triplicates for every tenth sample. For foliage and litter, NIST SRM 1515 (Apple Leaves) and IPE-181 (Mango Leaves; WEPAL-QUASIMEME) yielded mean recoveries of 96% and 102%, respectively. For soils, Chinese SRMs NCS DC7303 (soil) and NCS DC73048 (sediment) (NCS Testing Technology Co., Ltd., China) gave recoveries of 94% and 97%, respectively.

2.4 Soil physical properties

The 2 mm-sieved, air-dried soil was used for the analysis of the physical properties. Soil texture was determined using the Pario sedimentation analysis system (Meter Group Inc., USA, 2021), which applies Stokes' Law to estimate the relative proportions of fine soil particles based on the integral suspension pressure method (Durner et al., 2017). Soil pH was measured in a 2 mm, air-dried soil ~~suspension~~ collected from the~~(~~ 0-5 cm depth~~)~~, using ~~in~~ water as the extractant at a ~~(~~soil~~-~~to~~-~~ water ratio of~~,~~ 1:5 (w/v) (ISO 10390, 2005).

2.5 Specific leaf area and stomatal density determination

Specific leaf area (SLA) was determined using the method proposed by Pérez-Harguindeguy et al. (2013). Briefly, mature leaves were collected during sampling SC2, rinsed, gently blotted dry with absorbent paper, and scanned. The scanned ~~files~~ images were processed using a Python script to estimate leaf surface area. The leaves were then dried to constant weight and weighed. SLA was calculated by dividing the surface area by the weight of the dried sample.

For stomatal density (SDN), mature leaves collected in the second campaign (SC2) were analyzed following Millstead et al. (2020). Nail polish epidermal impressions of the abaxial surface were prepared, and stomata were counted under a light microscope at 40X magnification. Counts were performed in triplicate from three different sections of the leaf abaxial surface (all stomata were found ~~-~~abaxial in this study).

For SLA and SDN, at least one individual per species was assessed. When additional individuals were available, extra measurements were taken, depending on the species' distribution across plots. For SDN, when more than three individuals were sampled, three random individuals were measured, and values were averaged.

2.6 Determination of atmospheric mercury concentrations

A total of 32 mercury passive samplers (MerPAS®, Tekran) were deployed in both the TDBF and TMBF. In each forest, two sites were selected (Table S1, SM). At each site, ~~16~~ four MerPAS® ~~(~1.5 m above the soil)~~ were deployed at approximately 1.5 m above the soil surface, including three active samples and one field blank. Samplers were initially deployed at the end of the dry season (May 2024) and ~~in such a way that three replicates of the MerPAS® and one field blank per location were present. After deployment, they were~~ left in the field ~~-~~for ~~about~~ ~~aproximately~~approximately 6 months~~,~~. They were then collected~~,~~ and replaced with new ~~units~~ samplers to assess ~~seasonality~~ seasonal variation in atmospheric Hg concentrations (Table 1). Total Hg concentrations ~~was~~ were analyzed using the DMA-80 instrument (described above), based on the method suggested by McLagan et al. (2016). To assess measurement quality control, SRM 2685c (NIST, USA) was used, with an average recovery of 101%.

2.~~7~~6 Statistical analysis

Statistical analysis included the Shapiro-Wilk test for normality and Levene's test for homogeneity of variances. Group differences were assessed using the Wilcoxon rank-sum test, two-sample Student's t-test, or the Welch two-sample t-test, depending on data distribution and variance structure. Correlation patterns were evaluated using Spearman's and Pearson's ~~rank~~ correlations. Statistical significance was defined as $p < 0.05$~~A significance level of significance (p value < 0.05) was applied~~. All analyses were conducted in ~~R Studio~~RStudio (version 2025.05.0).

Leaf Hg concentrations for the dry season were calculated as the mean of the two dry season campaigns (SC1 and SC3) ~~if~~ when ~~samples~~ data from both ~~campaings~~campaigns were available. When data were available from only one campaign, that ~~;~~ single ~~dry season~~ measurement~~s~~ w~~as~~ere used ~~when only one campaign provided data~~to represent the dry season (Fig. 3~~S1~~, Fig. S3~~2~~ in SM~~; Fig. 2~~). Soil and litter data are reported separately per sampling event.

In the manuscript, mean values are expressed as ± standard error, except for Hg concentrations in different species from TDBF and TMBF (~~Fig. 2;~~ Fig. S3~~2~~ in SM), and Hg concentrations in MerPAS® samplers (Fig. 2~~1~~), where means are expressed with standard deviation.

3 Results and discussion

3.1 Atmospheric Hg in tropical dry and moist broadleaf forests

Given that elemental atmospheric Hg (Hg^0) is the primary source of natural Hg to tropical forests, we measured its concentrations using MerPAS® to assess seasonal and forest-level differences between tropical dry broadleaf forest (TDBF) and tropical moist broadleaf forest (TMBF), and their potential ~~influence~~ relationship~~on~~ with foliar Hg. In the TDBF, Hg^0 did not differ significantly between seasons (dry: 1.3 ± 0.2 ng m^{-3}; wet: 1.1 ± 0.2 ng m^{-3}; n = 6; Fig. 2~~1~~).

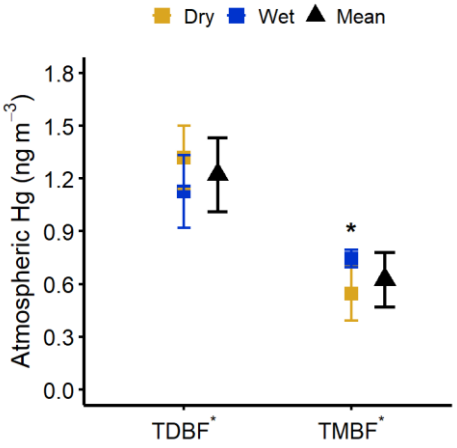


Figure ~~1~~2: Mean (± standard deviation) of atmospheric Hg concentration in tropical dry broadleaf forest (TDBF) and tropical moist broadleaf forest (TMBF) during the dry and wet seasons (TDBF dry n = 6, TDBF wet n = 6, TMBF dry n = 6, TMBF wet n = 4; two Hg passive sampler measurements from the TMBF wet season could not be obtained because of a catalyst-related instrument malfunction during Hg analysis; total n = 22). Forest means across both dry and wet seasons (TDBF n = 12, TMBF n = 10) are represented with a black triangle ± standard deviation. (*) on the x-axis indicates statistically significant differences between the forests, while within the graph indicates significant seasonal differences according to the two-sample *t*-test.

The TMBF showed slightly higher Hg^0 concentrations during the wet season (0.8 ± 0.1 ng m^{-3}, n = 4) than during the dry season (0.6 ± 0.2 ng m^{-3}, n = 6), ~~likely~~ potentially reflecting air mass dynamics associated with rainfall events (Koenig et al.,

2021). However, the main difference was observed between forests, as Hg^0 concentrations in TDBF (1.2 ± 0.2 ng m^{-3}, n = 6) were approximately twice those in TMBF (Fig. 2~~1~~). The lower atmospheric Hg^0 concentration in TMBF is consistent with higher wet deposition, but alternative explanations (e.g., differences in regional air mass history) cannot be ruled out.~~Higher Hg^0 concentrations in TDBF may be due to lower canopy density and humidity, whereas the denser and more humid conditions in TMBF likely enhance foliar Hg^0 uptake per unit area and wet Hg^0 deposition through rainfall, as Hg^0 is strongly dependent on meteorological conditions (Xu et al., 2022).~~

Compared to global background levels, Hg^0 concentrations in TDBF were close to the reported Southern Hemisphere background (1.1 ng m^{-3}) (Lindberg et al., 2007; Sprovieri et al., 2010), ~~while~~ whereas concentrations in TMBF were approximately 1.6 times lower. The lower Hg^0 concentration in TMBF compared to the background concentration in the Southern Hemisphere may be attributable to greater vegetation-mediated Hg^0 uptake resulting from higher canopy density, combined with other factors such as meteorological conditions, as explained above. To our knowledge, baseline values for Hg^0 concentrations in non-polluted areas have not previously been reported for TDBF. ~~,~~ ~~while for TMB~~For TMBF, Gerson et al. (2022) reported Hg^0 concentrations of approximately 1 ng m^{-3} at remote, non-mining background sites in Madre de Dios, Peru, which is still roughly 1.4 times higher than our seasonally averaged value of 0.7 ng m^{-3}. Thus, our study provides baseline values for Hg^0 concentrations under natural conditions in TDBF, and adds a comparison point for TMBF. ~~a Hg^0 concentration of approximately 1 ng m^{-3} has been reported in remote areas from TMBF located in la Madre de Dios, Peru affected by gold mining, which is still 1.4 times higher than our findings of 0.7 ng m^{-3} seasonally averaged (Gerson et al., 2022b). Thus, our study provides the baseline values for atmospheric Hg^0 concentrations under natural conditions.~~ However, ~~further studies with~~ additional MerPAS® deployments across multiple seasons and locations are needed to better understand ~~the~~ seasonal dynamics in Hg^0 concentrations ~~dynamics~~ in both forests.

3.2 Foliar Hg among different plant species from TDBF and TMBF

3.2.1 Seasonal patterns of Hg concentration in tropical forest plant species

Seasonal patterns in foliar Hg concentrations were observed in both deciduous and evergreen trees in the TDBF. Deciduous trees showed a more pronounced seasonal difference, with leaf Hg concentrations 4.7 times higher in the wet season (49 ± 27 μg kg^{-1}, n = 53) than in the dry season (10 ± 11 μg kg^{-1}, n = 50) (Fig. 3a). Evergreen trees showed the same pattern, although

less pronounced, with leaf Hg concentrations 2.3 times higher in the wet season (53 ± 27 μg kg^{-1}, n = 37) compared to the dry season (23 ± 18 μg kg^{-1}, n = 35). The higher wet-season leaf Hg concentrations were also observed when plants were analyzed at the species level (Fig. S1, SM).

~~Seasonal patterns in foliar Hg concentrations appeared in both deciduous and evergreen trees in the TDBF. Deciduous trees showed a more pronounced seasonal shift, with leaf Hg concentrations 4.7 times higher in the wet season (49 ± 27 μg kg^{-1}, n = 53) than in the dry season (10 ± 11 μg kg^{-1}, n = 50) (Fig. 2a).~~

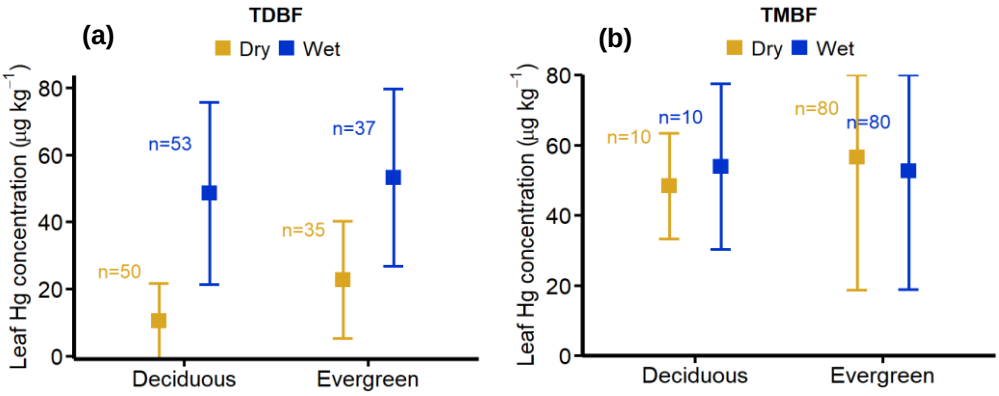


Figure 3: Mean (± standard deviation) concentrations of Hg in leaves of deciduous and evergreen species during the dry and wet seasons in the tropical dry broadleaf forest (TDBF, a) and tropical moist broadleaf forest (TMBF, b). Dry season values represent the average of two sampling campaigns (SC1 and SC3); wet season values represent a single sampling campaign (SC2). Sampling campaign details are explained above in Table 1.

~~**Figure 2: Mean (± standard deviation) concentrations of Hg in leaves of deciduous and evergreen species during the dry and wet seasons in the tropical dry broadleaf forest (TDBF, a) and tropical moist broadleaf forest (TMBF, b)**~~

~~Seasonal patterns in foliar Hg concentrations were observed in both deciduous and evergreen trees in the TDBF. Deciduous trees showed a more pronounced seasonal difference, with leaf Hg concentrations 4.7 times higher in the wet season (49 ± 27 µg kg^{-1}, n = 53) than in the dry season (10 ± 11 µg kg^{-1}, n = 50) (Fig. 2a). Evergreen trees in TDBF showed the same pattern, although less pronounced, with leaf Hg concentrations 2.3 times lower higher Hg concentration in the wet season (53 ± 27 µg kg^{-1}, n = 37) compared to the dry season (23 ± 18 µg kg^{-1}, n = 35) compared to the wet season (53 ± 27 µg kg^{-1}, n = 37).. The higher wet season leaf Hg concentrations wasere also observed when plants were analyzed at the species level (Fig. S1, SM).~~

The lower leaf Hg concentration observed in deciduous trees during the dry season most likely reflects seasonal leaf turnover ~~phenology~~. In TDBF, deciduous trees shed their leaves during the dry season as a strategy to reduce water loss and~~limit~~ drought stress~~, avoid drought induced water loss,~~ and to protect their hydraulic function (Bullock et al., 1995; Eamus, 1999; Wolfe et al., 2016). ~~Thus~~Consequently, leaves sampled at the end of the dry season were likely newly flushed following ~~early rains~~the onset of rainfall, as in the field they seemed young, small, not well developed ~~(REFERENCE TO SUPPLEMENTARY), (Bullock et al., 1995; Eamus, 1999; Wolfe et al., 2016)~~ and therefore had less time to ~~accumulated~~ accumulate ~~less~~ Hg than older leaves. This interpretation is ~~,~~ consistent with previous studies showing that foliar Hg concentrations generally ~~increases~~ increase with leaf age (Laacouri et al., 2013; Pleijel et al., 2021) ~~(Bullock et al., 1995; Eamus, 1999; Wolfe et al., 2016)~~.

For evergreen trees, the influence of several mechanisms may have contributed to the lower foliar Hg concentrations in the dry season. First, leaves collected during the dry season may have been newly flushed shortly before sampling. Although classified as evergreen trees, some species lose their leaves during dry periods and rapidly develop new foliage ~~after~~ following ~~subsequent~~ incipient rainfall. Therefore, some authors call them semi- or brevi-deciduous depending on the degree and timing of leaf shedding ~~ir shading characteristics~~ (Eamus, 1999). This ~~hypothesis~~explanation is consistent with our field observations. While all selected trees had ~~enough~~sufficient foliage for ~~could be~~ sampling~~ed~~ during the first campaign, the same individuals showed substantial variation in canopy coverage and visually estimated leaf age during the second dry-season campaign. Thus, some trees could still be sampled despite reduced or predominantly young foliage, while others were completely leafless and could not be sampled. ~~individuals leafless.~~ For example, all sampled individuals of *Tabernaemontana glabra* had foliage during the first dry-season campaign, whereas during the second dry-season campaign, three individuals were completely leafless and eight individuals had predominantly ~~visually~~ young leaves (visually determined)~~,~~. Canopy coverage among those individuals ~~with the canopy coverage~~ rang~~inged~~ from 5 to 90% ~~among these individuals~~ (Table S2, SM). Consistent with our field observations and interpretation~~this~~, Borchert (1994) described evergreen trees in the same ~~area of our study~~region as facultative evergreens, ~~with~~ whose leaf phenology is primarily driven by water status. This suggests that ~~Hg sequestration~~foliar Hg accumulation~~, even~~ for evergreen trees from TDBF ~~, might~~may also be controlled by ~~seasonality~~ seasonal variation in ~~and plant~~ water availability, as happens for deciduous trees.~~.~~

Second, although research on foliar Hg re-emission is limitedA second potential mechanism is Hg^0 re-emissions from leaves;. Although research on foliar Hg re-emission remains limited, Yuan et al. (2019) found that stomatal uptake of Hg^0 followed by internal oxidation to Hg^{2+} cancan be reversed through photochemical reduction, apotentially allowing Hg^0 to be re-emitted from leaves. Canopy-scale studies suggest that up to ~45% of Hg taken up throughby foliage leaves may return to the atmosphere via this pathwayre-emission (Graydon et al., 2012). Therefore, higher UV radiation during the dry season in TDBF could potentially have enhanced Hg re-emission via light-driven reductive loss from leaves (Yuan et al., 2019), although the roles of lower humidity and higher leaf temperature observed during the dry season may also contribute to Hg re-emission; however, this process has not yet been investigated specifically in TDBF.including, and higher leaf temperaturesfoliar Hg re-emission Consistent with this possibilitypossible Hg re-emission mechanism, the evergreen *Hymenaea courbaril*, which retained visually mature leaves during the dry season (Table S2, SM), showed substantially lower foliar Hg concentrations in both dry season campaigns (14 and 24 μg kg^{-1}) than in the wet season (82 μg kg^{-1}), as shown in ; Fig. S1, SM).

Although we did not directly evaluate foliar Hg^0 of re-emission in this study, weather station data indicatesindicate that environmental conditions were potentially a more favourable for re-emission during the dry season. This pattern is concordant with the observed differences in weather conditions: UV radiation was slightly higher in the dry season (2.2 averaged across the two dry seasons) than during the wet season (2.2 averaged across the two dry seasons vs. (1.9 W m^{-2} x 40), and ,the median temperature was approximately 1 °C higher across both dry seasonsduring the dry season (29 °C, average of the two dry seasons) comparedthan during thethe wet season (28 °C). The dry season also had more days exceeding 28 °C, with 137 days during the first dry season and 102 days during the second dry season, compared with only 43 days during the wet season, as shown in experiencingFig. S2 in SM. In contrast, and cumulative precipitation was 11 times higher induring -the wet season (3083 mm) than induring the dry season (349 mm, averaged across the two dry season campaigns). Moreover, Gerchow et al. (2025) used UAV-based thermal imaging to analyse leaf-scale forest canopy temperatures in the same study area. They and found that daytime canopy temperatures in some areascan exceed 42 °C during the dry season. ,Together, higher radiation and temperature, sparser canopy cover, and lower precipitationTogether, the higher radiation and temperatures, more sparse canopy cover, combined with lower precipitation, suggest environmental conditions that could –potentially favour foliar Hg^0 re-emission during the dry season. conditions that all together might further facilitate Hg re-emission.

Finally, Hg translocation-, defined as the transport of Hg from leaves to woody tissues via phloem, may also contribute to lower foliar Hg concentration during the dry season. Estimates suggest that approximately 5-15% of foliar Hg can be translocated to woody tissues, (Gerchow et al., 2025)Second, although research on foliar Hg re-emission is limited, Yuan et al. (2019) indicate that stomatal uptake of Hg^0 followed by internal oxidation to Hg^{2+} can be reversed through photochemical reduction, allowing Hg^0 to be re-emitted from leaves. Canopy-scale studies suggest that up to ~45% of Hg taken up through leaves may return to the atmosphere via this pathway (Graydon et al., 2012). Therefore, dry season conditions in TDBF, characterized by high irradiance and low humidity, likely enhance this process; however, no studies have confirmed this

~~mechanism in TDBF. Lastly~~Another ~~mechanism that might have contributed to lower foliar Hg concentrations during the dry season, foliar Hg could be translocated~~is translocation, ~~as studies have shown that (~5–15% of Hg from leaves can be) via the phloem and transported~~transported via the phloem ~~to woody tissues,~~ contributing to dendrochemical records of atmospheric Hg (Monaci and Baroni, 2025; Peng et al., 2024).

Although all of these mechanisms – including variation in the timing of shedding, foliar Hg re-emission, and Hg translocation– m~~ight~~ay have contributed to the decline in foliar Hg concentrations in evergreen trees from the TDBF during the dry season, none was directly measured in this study. Moreover, to our knowledge, ~~and~~ their contribution to seasonal foliar dynamics in evergreen trees in ~~no prior work has confirmed these processes specifically in the~~ TDBF has not been evaluated. Therefore, the ~~drivers~~mechanisms ~~underlaying~~underlying ~~of~~ the lower foliar Hg concentration ~~observed~~ observed in evergreen trees during the dry season warrant further investigation. ~~It is worth noting that f~~Future studies should consider normalizing foliar Hg by time-integrated stomatal conductance or by leaf age to try to ~~separate seasonal uptake dynamics~~seasonal variations in Hg uptake from age-related accumulation~~.~~. They should ~~and should~~ account for ~~the high~~ substantial inter-individual ~~variability~~variation in canopy coverage ~~among individual trees~~, ~~wich~~which may ~~driven by heterogeneous~~reflect ~~hetergenous~~heterogeneous plant water availability conditions. ~~However, the complex water-dependent dynamics of evergreen trees in TDBF further complicate identifying the main mechanism driving lower foliar Hg during the dry season.~~ To our knowledge, our data provide the baseline ~~for~~ foliarge Hg concentrations ~~in~~ for TDBF, ~~as no studies have yet been conducted in this forest type for cross-comparison~~for which comparable measurements have not previously ~~reposted~~been reported.

No seasonal patterns in foliar Hg concentrations were observed in the TMBF. Deciduous trees showed similar Hg concentrations ~~in~~ during the dry (48 ± 15 μg kg^{-1}, n = 10) and wet seasons (54 ± 24 μg kg^{-1}, n = 10). Evergreen trees showed ~~the~~ a ~~same~~ similar pattern, with ~~similar~~ comparable ~~values~~ concentrations ~~in~~during the dry (57 ± 38 μg kg^{-1}, n = 80) and wet (53 ± 34 μg kg^{-1}, n = 80) seasons (Fig. 3~~2~~b). At the species level, ~~high variability in~~ foliar Hg concentrations varied substantially ~~was found~~, but no ~~clear~~ consistent seasonal differences were observed~~, as shown in~~ (Fig. S1, SM). The absence of seasonal variation in foliar Hg concentrations in evergreen trees is likely ~~due to~~related to leaf age, as the sampled leaves were mature during both the dry and wet seasons, and foliar Hg accumulation is known to be correlated with leaf lifespan (Pleijel et al., 2021). Evergreen trees can retain leaves for 1.6 to 4.7 years, depending on species and light conditions (Reich et al., 2004), allowing continuous Hg accumulation over time. ~~Moreover~~In addition, the absence of a pronounced dry season and the resulting relatively ~~persistent~~ high humidity~~,~~ ~~resulting from the absence of a pronounced dry season, likely~~may reduce seasonal constraints ~~maintained optimal~~ on stomatal conductance ~~,in both seasons, promoting continuous~~ photosynthesis, and transpiration, ~~which~~ potentially supporting relatively continuous atmospheric~~have been linked to high~~ Hg ~~foliar Hg uptake~~uptake by foliage throughout the year (Teixeira et al., 2018~~e~~). ~~In addition, d~~Dense canopy structure may further enhance foliar Hg ~~uptake~~ retention and limit Hg^0 re-emission by reducing light penetration and, consequently, the potential for Hg re-emission from foliage (Yuan et al., 2019).~~.~~

~~A similar absence of~~Regarding the lack of seasonal variation i~~o~~n foliar Hg ~~was~~ ~~also~~ observed in trees classified as deciduous ~~trees~~based on the typical phenology of those species, ~~For these species, w~~w~~W~~e assumed that the sampled leaves were mature during both the dry and wet seasons based on ~~of those species~~ our field observations, which is consistent with the high foliar Hg concentrations found in both seasons. This assumption is supported by the typical phenology of deciduous trees in TMBF, where leaf shedding is followed by fast regrowth under favorable moisture conditions, with phenology patterns regulated by drought and light availability (Kearsley et al., 2024). Leaves from deciduous trees therefore remain mature for longer periods, allowing continuous Hg accumulation and sustained high foliar Hg concentrations across seasons. However, leaf age was not quantitatively determined, representing a limitation of this study.

~~quantitatively determinedrepresentingthis, as the sampled leaves were mature during both seasons. In TMBF, leaf shedding is typically followed by fast regrowth under abundant favorable moisture conditionsand rainfall, with phenology patterns regulated by drought and light availability (Kearsley et al., 2024). Consequently, most leaves remain mature for extended periods, potentially allowing continuous foliar Hg accumulation. As discussed above, older leaves under may ideal net photosynthesis conditions exhibit higher Hg foliar concentrations under conditions favorable for atmospheric Hg^0 uptake.~~

~~lack of seasonal variation in mayreflect the relatively favorablethroughout the year as observable for weather data from the time span of sampling campaings(), suggesting that seasonal water limitation was, as expected, substantially weaker in the TMBF~~

~~Overall, water availability~~Overall, water availability, ~~—~~which differed markedly between seasons~~strongly regulated by seasonality, — emerged~~appeared to be ~~as the~~an ~~primary~~ important driver of foliar Hg ~~sequestration~~ accumulation ~~in both~~across both fores t types~~s~~. During the dry season, accumulated precipitation in TMBF was almost three times higher than in TDBF (937 mm vs. 349 mm; Fig. S2, SM), which likely sustained continuous plant water availability, supporting both stomatal activity and the extended leaf maturity explained above, potentially contributing to the consistently high foliar Hg concentrations observed in TMBF across seasons. Although foliar Hg concentrations declined during the dry season, both evergreen and deciduous trees showed rapid foliar Hg accumulation during the wet season, reaching concentrations in mature leaves comparable to those observed in TMBF.

~~In TDBF, although foliar Hg concentrations declined during the dry season, both evergreen and deciduous trees showed rapid rapidfoliar foliar Hg accumulation accumulation during the wet season, reaching concentrations in mature leaves comparable to those observed in TMBF. Additionally, fFoliar Hg concentrations in TMBF remained consistently higher high in both dry~~

and wet seasons,between seasons and although higher Hg^0 was found inwere generally higher than those in TDBF in both seasons.

3.2.2 Leaf Hg concentration in TDBF and TMBF at the tree species level and intra-individual variation.

In the TDBF, considering the most sampled species, the deciduous species *Tabebuia ochracea* (deciduous) exhibited the highest mature leaf Hg concentration (99 ± 45 μg kg^{-1}, n = 4) (wet seasonwet season), while among evergreens, the *Tabernaemontana glabra* reached the highest concentration (72 ± 12 μg kg^{-1}; n = 11) (Fig. S32, SM). In the TMBF, *Psychotria elata* (evergreen) showed the highest Hg concentrations (dry season: 92 ± 15, n = 5-; wet season: 86 ± 12 μg kg^{-1}, n = 5), whereas *Amphirrhox longifolia* accumulated mossshowed the highestt Hg concentartionsconcentrations among deciduous species (dry: 57 ± 9, n = 5; wet: 68 ± 24 μg kg^{-1}, n = 5) (Fig. S32, SM).

At the forest level, foliar Hg concentrations varied substantially among individual trees in both TDBF (range: 4–161 μg kg^{-1}, n = 90) and TMBF (range: 2 – 167 μg kg^{-1}, n = 90), reflecting considerable interspecific variability that should be considered when estimating global foliar Hg budgets.show To investigateexplore potential mechanisms underlying the high variability in foliar Hg concentrations among speciesunderlayingconcentrations, we evaluated the relationship between foliar Hg concentrations and two static morphological traits, specific leaf area (SLA) and stomatal density (SD). However, nNeither trait showed a strongly or statistically significant relationship with foliar Hg concentrations (Fig. S4 a-d, SM), suggesting that thesesthese morphological traittraits alone do not adequately explain the observed interspecific variability. These findings highlightshighlight the need thatfor future studies to incorporate direct physiological measurements (e.g., WHICH ONESstomatal conductance, net photosynthesis, transpiration rate) and the weak correlations found underscore the need for direct physiological measurements in future studies. To address this limitation, future work should strategically measure morphological and physiological traits on the same leaves used for Hg analysis to identify which mechanisms are most closely related to foliar Hg accumulation, while minimizing bias from high intra-individual variability, as described below. to avoid a vias due to the

Among leaves,Marked variability in foliar Hg concentrations was observed among leaves collected from different parts of the canopy within thethe same individual tree, Hg concentrations varied markedly in both evergreen and deciduous treesspecies. This was expressed as the percentage deviation of each subsample from the tree-level mean foliar Hg concentration (MPD), where positive and negative values indicate Hg concentrations above and below that mean, respectively. ,This pattern variability was especially pronounced for in TDBF species such as *Amphilophium paniculatum* (Percentual deviation from the mean for individual samples (MPD)MPD range from: -29% to 19%, n = 3), *Hymenaea courbaril* (MPD range: -73% to 57%,

n = 3), and *Bromelia pinguin* (MPD range: -59% to 63%, n = 3)~~,~~. ~~with s~~Similar variability was observed in TMBF species including *Theobroma cacao* (MPD range: -71% to 42%, n = 3), *Cyathea arborea* (MPD range: -70% to 72%, n = 3), *and Cardulovica palmata* (MPD range: -66% to 71%, n = 3) (Fig. 4~~3~~). This within-tree variability ~~is most likely a result of~~may reflect differences among ~~in leaf~~leaves in age, light exposure, humidity, stomatal conductance, net photosynthesis, ~~presence of pests~~pest presence, ~~among other factors~~ and other factors (Pleijel et al., 2021; Teixeira et al., 2017, 2018). These results highlight the importance of collecting a large number of leaf samples (multiple leaves per individual) to ensure representative foliar Hg measurements. ~~-~~It is also worth noting that our sampling strategy covered a maximum height of 5 m, whereas trees in TDBF and TMBF can reach heights of up to 20 and 50 m, respectively (Brienen et al., 2010). Therefore, variability in foliar Hg concentrations may be even greater along the canopy height gradient, which was not captured by our sampling design.

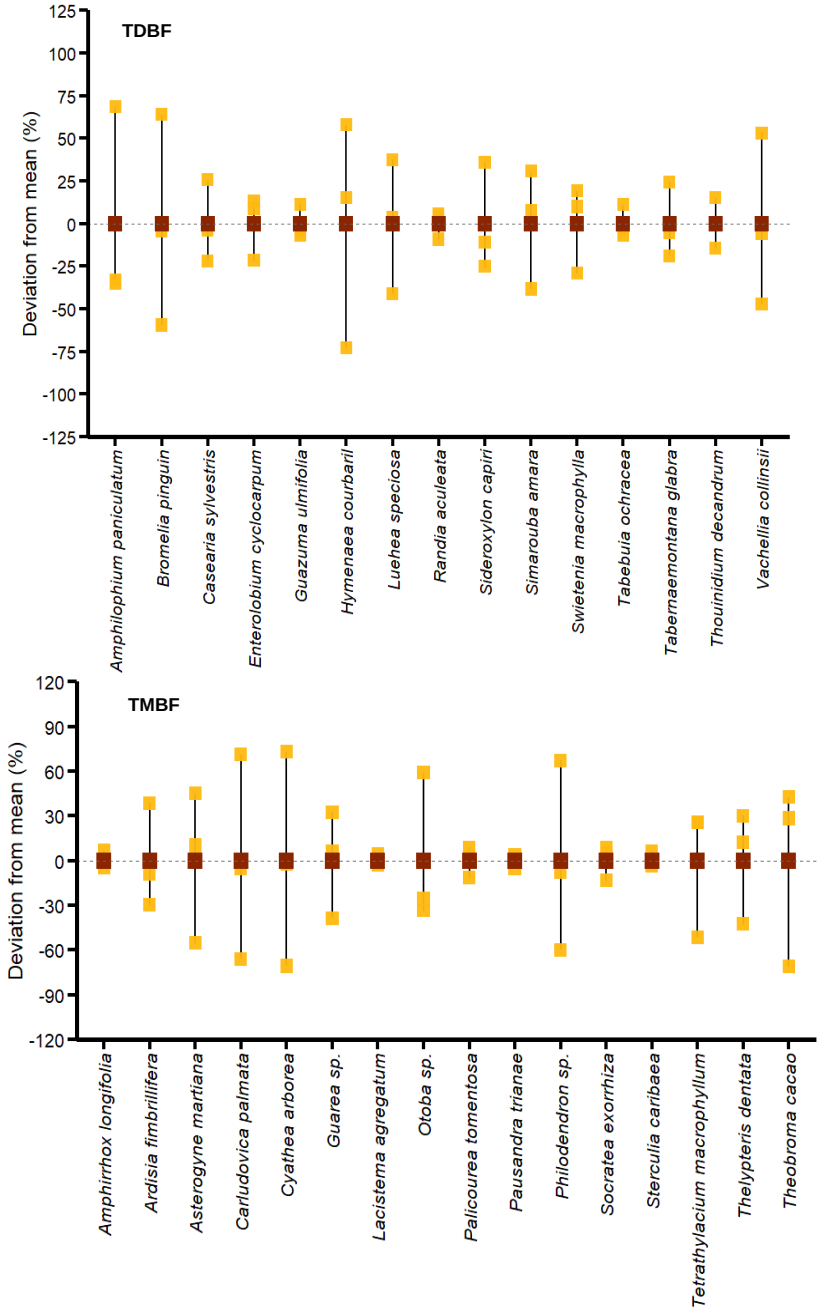


Figure 43: Within-individual variability in leaf subsamples collected from different parts~~leaf Hg concentration based subsamples collected from different parts~~ of the same plant across multiple species in the tropical dry broadleaf forest (TDBF) and the tropical

moist broadleaf forest (TMBF) during the dry season (SC3). Yellow squares represent Hg concentrations in individual subsamples, brown squares indicate the mean of the three measurements, and black lines connect subsamples belonging to the same plant.

3.2.3 Foliar functional traits and their relationship with Hg accumulation in tropical forests

Most studies agree that Hg^0 is primarily taken up through stomata (Denzler et al., 2025; Monaci and Baroni, 2025; Rutter et al., 2011; Wang et al., 2016; Wohlgemuth et al., 2022), although some authors suggest that non-stomatal pathways may also contribute significantly to foliar Hg^0 accumulation (Stamenkovic and Gustin, 2009). Leaf area and stomatal density have further been proposed as factors influencing Hg^0 uptake (Pleijel et al., 2021). In our study, specific leaf area index (SLA) and stomatal density index (SDN) were weakly correlated with foliar Hg concentration in TDBF and TMBF (Fig. S3 a-d,). The high intra-individual variability in foliar Hg concentrations (as explained above), driven by leaf age and heterogeneous environmental conditions such as light exposure, moisture, and slope, likely weakens these relationships. Leaf position (sun exposure and canopy height) within the canopy is known to affect foliar Hg uptake (Anderson, 1955; Laacouri et al., 2013), further weakening any direct correlation with morphological traits. This aligns with Teixeira et al. (2018d), who emphasized physiological processes such as net photosynthesis rather than SLA as key drivers of foliar Hg concentrations. Their work also emphasized the role of stomatal function through measurements of stomatal conductance. However, they did not assess the relation between SDN and foliar Hg concentrations. To our knowledge, information on the influence of SDN in tropical forests remains scarce, and no study has yet analyzed SDN on the same leaf samples used for Hg analyses. Such an approach would offer greater accuracy.

3.2.43 TDBF and TMBF contributions to the global foliar Hg pool

Across all species, mature leaves in the TDBF averaged 50 µg kg^{-1} Hg (n = 90)(range: 4–161 µg kg^{-1}, n = 90), while those in the TMBF averaged 53 µg kg^{-1} (n = 90)(range: 2–167 µg kg^{-1}, n = 90). These values are 2.1-fold (TDBF) and 2.2-fold (TMBF) times higher than the estimated global foliar Hg mean concentration (24 µg kg^{-1}; Chen et al., 2024b) and exceed typical concentrations reported for temperate and boreal forests (e.g.,including 16.3 µg kg^{-1} in U.S. temperate forests, (Yang et al., 2018); 20 – 40 µg µg kg^{-1} in Canadian temperate deciduous forests, (Siwik et al., 2009) and; 11 – 26 µg kg^{-1} in European forests, (Wohlgemuth et al., 2020). Although atmospheric higher Hg^0 concentrations have been reportedare generally higher in the Northern Hemisphere, where most temperate and boreal forests are located (1.5 – 1.7 ng m^{-3}; Sprovieri et al. 2010b), where most temperate and boreal forests are located, they were lower in our study forest (TBDFTDBF values and TMBF values). Despite these lower atmospheric Hg concentrations, foliar Hg concentrationconcentrations in both tropical forest types were higher thant those typically repostedreported for temperate and boreal forestforests. This contrast highlights that

atmospheric Hg^0 concentrations alone do not determine foliar Hg ~~conctrations~~concentrations. Importantly, atmospheric Hg^0 concentrations measured ~~withing~~within the forest ~~reflects~~reflect not only regional and local atmospheric Hg emission and transport but also the removal of Hg^0 by vegetation and other atmospheric sinks. Taken together, these findings underscore~~All together underscores , compared to our results of Hg^0 in TMBF and TDBF, foliar Hg concentrations in both tropical forests were significantly higher. This underscores~~ the importance of tropical forests as ~~a major~~~~important~~relevant ~~global Hg sink~~contributors to the global foliar Hg pool, ~~with favorable~~as their dense vegetation and relatively sustained stomatal conductance~~, dense vegetation, abundant species, high net~~ and ~~photosynthesis~~photosynthetic activity may promote ~~, and year-round light availability likely creating conditions for enhanced~~ foliar Hg uptake and subsequent ~~retation~~retention in foliage.

Our study provides, to our knowledge, the first baseline data ~~for~~ on foliar Hg concentrations in TDBF and highlights the importance of accounting for ~~seasonality~~ seasonal differences when sampling and modeling foliar Hg, particularly in highly seasonal systems such as TDBF. Although our results are consistent with the modelled mean foliar Hg concentration for TMBF (~53 ± 24 µg kg^{-1}, n = 263~~;) proposed by~~ Zhou et al. (2021~~b~~)), ~~they~~ our data ~~show~~ also reveal high variability, including marked intra-individual differences in foliar Hg concentrations in both forests. Given the limited availability of field-based Hg data ~~data available~~, the~~i~~se findings ~~highlights~~ highlight the need for more in-field measurements that account for ~~the seasonality of~~seasonal differences in tropical forests to improve model accuracy.

3.3 Mercury inputs from litter in tropical forests

3.3.1 Seasonal patterns in litter accumulation in TDBF and TMBF

~~At TDBF, litter mass accumulation in soil was significantly higher during the dry season compared to the wet season at all plots except H3 (Fig. 4a).~~

~~At~~ In the TDBF, litter mass accumulation in soil was significantly higher during the dry season compared to the wet season ~~at~~in all plots except H3 (Fig. 5~~4~~a).

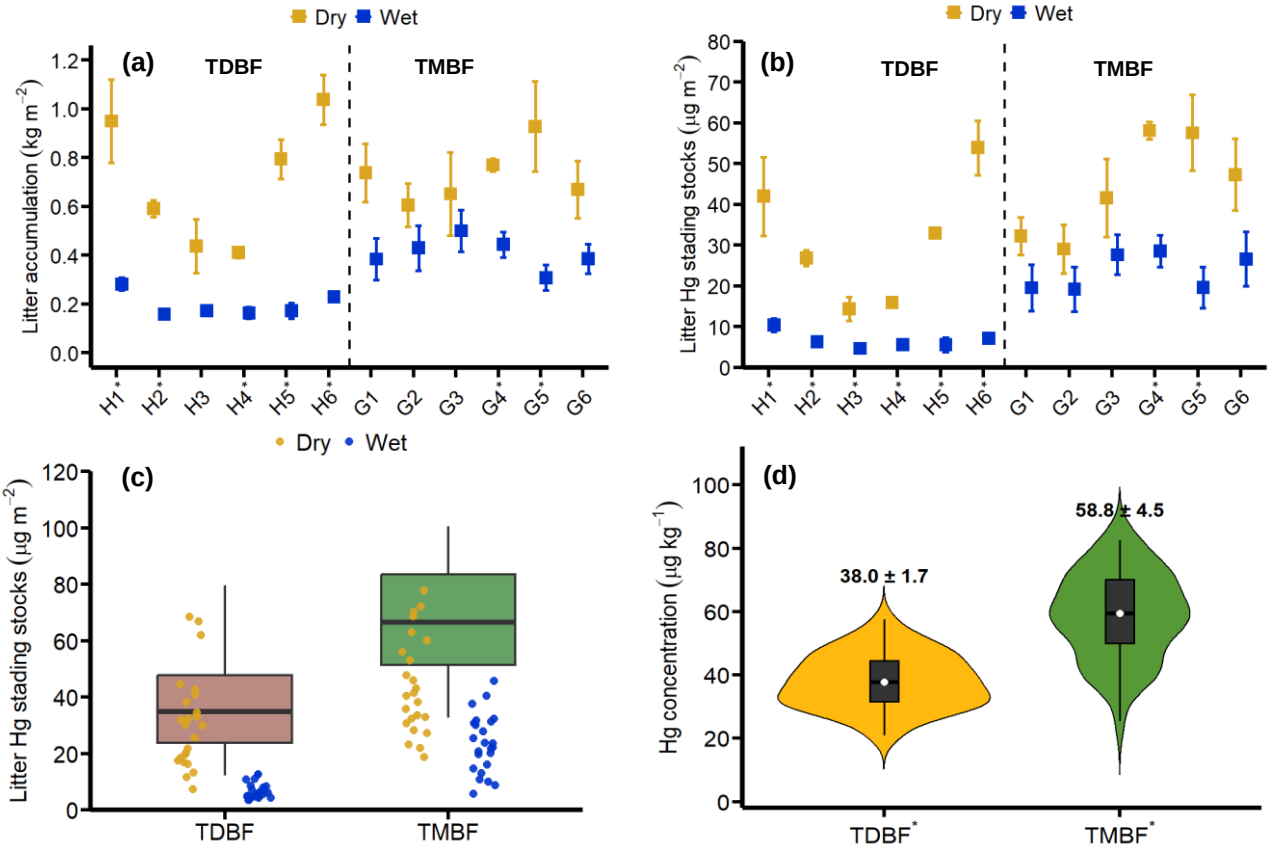


Figure 5: Mean (± standard error) of litter accumulation and litter Hg standing stocks (n = 4 individual samples) across different plots in the tropical dry broadleaf forest (TDBF), plots H1–H6; and the tropical moist broadleaf forest (TMBF), plots G1 – G6, during the dry (yellow) and wet (blue) seasons (a, b). (c) Mean (± standard error) of litter Hg standing stocks during the dry and wet seasons per forest. Individual data points are shown as dots, coloured by season. (d) Violin plot of the Hg concentration mean (± standard error) in litter per forest (n = 6 plots), values represent plot-level averages for the dry and wet seasons. (*) at the x-axis indicates statistically significant differences according to the Wilcoxon signed-rank test, or Student's t-test ($p < 0.05$), depending on data distribution.

~~**Figure 4: Mean (± standard error) of litter Hg accumulation (n = 4) across different plots in the tropical dry broadleaf forest (TDBF), plots H1–H6; and the tropical moist broadleaf forest (TMBF), plots G1–G6 during the dry (yellow) and wet (blue) seasons (a, b). (c) Mean (± standard error) of litter Hg accumulation during the dry and wet seasons per forest. Individual data points are shown as dots, coloured by season. (d) Violin plot of the Hg concentration mean (± standard error) in litter (n=6), values represent plot-level**~~

~~averages for the dry and wet seasons. (*) at the x-axis indicates statistically significant differences according to Wilcoxon signed-rank test, or Student's t-test ($p < 0.05$), depending on data distribution.~~

~~On average~~Averaged across plots (~~plots~~ H1-H6), dry-season litter mass was 3.6 times higher (0.7 ± 0.1 kg m^{-2}, n = 24) than wet-season litter mass (0.2 ± 0.0 kg m^{-2}, n = 24). At TMBF, no significant seasonal differences in litter mass accumulation were found at most plots, except for G4 and G5 (Fig. 5~~4~~a). However, when averaged across all plots (G1-G6), litter accumulation at forest level was 1.8 times higher during the dry season (0.7 ± 0.1 kg m^{-2}, n = 24) than during the wet season (0.4 ± 0.0 kg m^{-2}, n = 24). Plot-level differences in litter accumulation likely reflect the high heterogeneity in species distribution in both forests, as litter inputs are influenced by the phenology of dominant species, in situ water availability, and species drought tolerance (Tonin et al., 2021). The ~~increased~~ higher litter accumulation observed during the~~overall~~ dry ~~-~~season ~~litter observed~~ in both forests is consistent with previous reports of intensified leaf shedding in Mexican TDBF ~~driven~~ associated ~~by~~ with deciduous leaf abscission (Morffi-Mestre et al., 2020) and in secondary rainforest (TMBF) in Brazil as a tree response to moisture stress (Oliveira de Morais et al., 2021).

It is important to note that we quantified forest-floor litter present at the time of sampling (end of each season), rather than trap-based litter. Our measurements, therefore, represent net litter accumulation, which is shaped not only by leaf shedding but also by decomposition dynamics influenced by temperature, tree species composition, precipitation, soil moisture, and other environmental factors (Bothwell et al., 2014; Wood et al., 2012). ~~-~~The lower litter mass observed during the wet season is consistent with reduced leaf shedding and higher decomposition rates, whereas during the dry season, limited soil moisture likely constrains microbial activity, slowing decomposition and allowing greater litter accumulation. However, our study design does not allow the relative contributions of increased leaf shedding and reduced decomposition to the seasonal litter pool to be distinguished, as both processes are likely to contribute. Differences among plots presumably reflect local variation in microclimate, successional stage, topography, tree species diversity, and forest structural patterns (Giweta, 2020).

When comparing the ~~both~~ two forest types across seasons, the TMBF showed 1.3 times higher mean litter accumulation (0.57 ± 0.0 kg m^{-2}, n = 6 plots~~48~~, Fig. S5~~4~~a, SM) than the TDBF (0.45 ± 0.1 kg m^{-2}, n = 6 plots). Although litter mass in the TDBF was low during the wet season, the higher accumulation ~~in~~ during the dry season resulted in overall~~total~~ seasonal ~~masses litter~~litter masses comparable to those observed ~~of~~in the TMBF. These patterns broadly align with previous reports showing higher litter in TMBF (~8–14 Mg ha^{-1} yr^{-1}; Chave et al., 2010a) compared to TDBF (4–8 Mg ha^{-1} yr^{-1}; Montañez-S. et al., 2023; Morffi-Mestre et al., 2020~~b~~; Souza et al., 2019~~b~~), though ranges overlap between forest types.

3.3.2 Hg concentration in litter and its relationship to foliar Hg

Litter Hg concentrations averaged across all plots in the TDBF were 43 μg kg^{-1} (n = 24) ~~in~~during the dry season~~,~~ and 33 μg kg^{-1} (n = 24) ~~in~~during the wet season. At the plot level, seasonal differences were not statistically significant (Welch's two-sample t-test, n = 4 per season per plot), except for H6 (p = 0.003) ~~as shown in~~(Fig. S5 b, SM). In the TMBF, plot-averaged litter Hg concentrations were 61 μg kg^{-1} ~~(Hg), (~~n = 24~~),~~ during the dry season and 57 μg kg^{-1}~~(,~~n = 24~~,~~) during the wet season. Similarly, ~~showing the same pattern of~~ no significant seasonal ~~effect~~differences were observed at ~~at the plot level in~~ most plots, except for G4 (p = 0.028). The relatively small sample size within individual plots (n = 4 per season) may have limited our ability to detect modest seasonal effects.~~Hg concentrations in litter from the TDBF showed an average value of 43 μg kg^{-1} (n = 24), in the dry season, compared to 33 μg kg^{-1} (n = 24), in the wet season. Differences were not statistically significant at the plot level, except for H6 (Fig. S4 b, SM). The same pattern of a lack of significant seasonality effect in most plots (except G4) was found for TMBF, with totals of 61 μg kg^{-1} (Hg), n = 24, during the dry season and 57 μg kg^{-1}, n = 24, during the wet season.~~ Slightly higher dry-season litter Hg concentrations in some plots are plausible because wet-season rain has been shown to leach/dilute dry-deposited Hg, diverting it to throughflow and streams (Silva-Filho et al., 2006; Teixeira et al., 2017). Overall, ~~litter~~ Hg concentration in litter in TMBF was comparable to ~~those~~ that reported by Fostier et al. (2015~~b~~) and Wright et al. (2016~~b~~), in rainforests from Brazil and French Guiana (~60 μg kg^{-1}). To our knowledge, there are no data on Hg concentration in litter from TDBF.

In the TDBF, the average foliar Hg concentration of mature living leaves during the wet season (50 μg kg^{-1}, n = 90)~~,~~ was 34% higher than in litter, ~~likely~~ potentially reflecting~~due to~~ Hg losses from litter ~~though~~through leaching, decomposition~~, re-emission~~, and other post-shedding ~~processes~~processes ~~factors~~. ~~Conversely~~In contrast, ~~in~~ during the dry season, Hg concentration in litter was 64% higher than in living leaves (15 μg kg^{-1}, n = 85). This pattern may indicate~~, suggesting~~ that dry-season litter consisted~~s~~ primarily of older, Hg-enriched leaves, which are shed after prolonged Hg^0 accumulation, ~~while~~~~whereas~~whereas many~~most~~ living leaves ~~remain~~had relatively low ~~in~~ Hg concentration ~~due to the different mechanisms described above~~because of the seasonal processes described above, including the presence of ~~(e.g.~~ newly flushed foliage ~~from~~in deciduous trees and~~,~~ potential re-emission~~)~~. This seasonal reversal pattern, in which litter Hg concentrations exceed those of living ~~leaf~~leaves ~~Hg concentrations in~~during the dry season but ~~falls below foliage Hg concentrations in~~were lower during the wet season, ~~indicates~~suggests that litter Hg dynamics ~~are~~may be driven by ~~driven~~ both ~~by~~ the timing of leaf senescence relative to Hg accumulation and ~~by~~ post-shedding losses through leaching and decomposition.~~, suggesting that most litter consisted primarily of mature leaves shed early in the season.~~ In the TMBF, litter Hg concentrations were 8 % and 7 % higher than those in living leaves during the dry (56 μg kg^{-1}, n = 90) and wet seasons (53 μg kg^{-1}, n = 90), respectively. This pattern may reflect a greater contribution of older, Hg-enriched leaves to the litter layer, which had accumulated Hg over longer periods before senescence. Post-shedding Hg losses through different mechanisms (e.g., leaching and re-emission) in TMBF may not have offset the

higher Hg concentrations of older leaves. However, this difference was much smaller than the pronounced dry-season difference observed in the TDBF, as described above.

~~litter contained 9% and 7% less Hg than in living leaves during the dry (61 μg kg^{-1}, n = 90) and wet seasons (57 μg kg^{-1}, n = 90), likely reflecting Hg losses through leaching and decomposition as mentioned above.~~

3.3.3 Seasonal patterns of litter Hg ~~accumulation through litter~~standing stocks in TDBF and TMBF

Strong seasonal patterns in litter Hg ~~accumulation~~ standing stocks were observed in TDBF across all plots, except for H3 (Fig. ~~4b~~5b). ~~On a~~Averaged across plots (~~plots~~ H1-H6), ~~litter Hg inputs~~ standing stocks were 4.7 times higher ~~in~~ during the dry season (31 ± 6 μg Hg m^{-2}, n = 24) than ~~in~~ during the wet season (7 ± 1 μg Hg m^{-2}, n = 24), primarily due to greater litter mass accumulation during the dry season (Fig. ~~5~~4a). In TMBF, ~~similar~~ consistent with the pattern observed in~~to~~ litter accumulation, no significant seasonal differences in litter Hg ~~inputs~~ standing stocks were observed across plots, except for G4 and G5 (Fig. ~~5~~4b). However, at the forest level (plots G1- G6), higher overall litter accumulation during the dry season resulted in greater ~~Hg~~ ~~accumulation~~standing stocks, ~~being~~ which were 1.9 times higher~~,~~ during the dry season (44 ± 5 μg Hg m^{-2}, n = 24) ~~compared~~ than~~to~~ during the wet season (24 ± 2 μg Hg m^{-2}, n = 24).

Seasonal patterns of litter Hg standing stocks ~~accumulation~~ were ~~potentically~~potentially driven by both leaf phenology and decomposition dynamics in both ~~forests~~ forest types, but ~~most strongly in~~these effects were more pronounced in the TDBF. In TDBF, leaf shedding occurs mainly during the dry season, when litter consists mainly of mature leaves with higher Hg concentrations, ~~often~~ including leaves retained from the preceding growing season in ~~originating from the previous season in~~ deciduous trees. In addition, Hg concentrations in litter reflect not only the elemental content of leaves at abscission but also changes occurring during decomposition. This ~~, which~~ is particularly relevant because we measured net litter accumulation, which ~~reflect~~reflects litter inputs and post-abscission losses. Thus, seasonal differences in Hg (both concentration and ~~accumulation~~standing stocks) ~~as well as between forest types~~ are shaped by both the timing of leaf fall and the degree of post-abscission degradation.

Overall, our data indicate that litter Hg standing stocks in TDBF ~~soils is~~are strongly influenced by seasonal variations, with peak inputs occurring during the dry season. ~~Overall, our data indicate that Hg inputs from litter to soil in the TDBF are strongly influenced by seasonality, with peak inputs during the dry season.~~ In contrast, ~~litter derived Hg inputs~~ in the ~~TMBF~~TMBF, litter Hg standing stocks ~~occur~~~~occur~~appear to be maintained ~~s~~ more continuously throughout the year, ~~with~~ although some sites ~~peaking~~ exhibited higher standing stocks under dry-season conditions, potentially reflecting ~~depending on many factors such as~~differences in species composition and distribution, species-specific ~~plant species'~~ drought tolerance,

~~species distribution, among~~and ~~others~~other~~, as~~ factors described above (section 3.3.1). ~~Additionally, g~~Greater litter-derived Hg ~~accumulation~~ standing stocks during the dry season may also be ~~linked~~ associated ~~to~~ with reduced decomposition rates, as dry conditions ~~are known~~can ~~to~~ slow litter breakdown (Rowland et al., 2014; Teixeira et al., 2017; Yavitt et al., 2004). Thus, ~~seasonality~~ seasonal differences may influence Hg ~~trnasfer~~transfer from vegetation to soil not only through ~~its~~their effects on litter deposition but also ~~also~~ indirectly ~~influence Hg transfer~~ through ~~its~~ their effects on decomposition and potential reemission, although these mechanisms need further investigation. ~~It is worth noting that~~Importantly, our litter Hg standing stocks represent a snapshot of Hg retained in the litter layer at specific sampling times rather than annual Hg inputs. Consequently, the dry-season standing stocks should not be interpreted as equivalent to annual Hg transfer from litter to soil. Some of the Hg present in dry-season litter may remain in undecomposed material and may subsequently be lost through re-emission, leaching, or other processes before being incorporated into mineral soil. Therefore, the actual annual transfer of Hg from litter to mineral soil may be lower than suggested by the maximum dry-season standing stocks observed in this study.~~;~~ ~~the actual annual transfer of Hg from litter to mineral soil may be lower than our dry-season values suggest, because some dry-season litter Hg remains undecomposed and may be lost through re-emission or leaching before incorporation.~~

3.3.4 Litter Hg ~~fluxes~~ standing stocks ~~and concentrations~~ in TDBF and TMBF compared with global estimates

Seasonally averaged ~~litter-derived Hg inputs~~litter Hg standing stocks were 1.8 times higher in TMBF (34 ± 3 μg Hg m^{-2}, n = 6 plots) than in the TDBF (19 ± 3 μg Hg m^{-2}, n = 6 plots~~;), as shown in~~ Fig. 5~~4~~c). Although our estimates are seasonal sums rather than annualized values, they are comparable to findings from rainforests (34.6 ± 1.2 μg m^{-2} yr^{-1}; Teixeira et al., 2017d) and fall within modelled ranges in the Amazon (49 ± 14 μg Hg m^{-2} yr^{-1}; Fostier et al., 2015). Hg concentration in litter was 1.5 times higher in TMBF than in TDBF, with density peaks near ~60 μg Hg kg^{-1} and ~33 μg Hg kg^{-1}, respectively (Fig. 5~~4~~d). TMBF peaks are similar to the Amazon rainforest estimates by Fostier et al. (2015d) (~60.5 μg Hg kg^{-1}). For TDBF, ~~there is~~ a~~the~~ lack of datasets on litter Hg concentration ~~in litter, which impedes~~limits cross-study comparison, ~~and~~while direct comparisons with global means are further complicated by differences in Hg^0 concentration, climate, ~~and~~ vegetation characteristics, and species composition. Nevertheless, the mean litter ~~our~~ Hg concentration ~~in~~observed in the ~~litter from T~~TDBF in this study ~~falls~~was ~~below~~lower than the global forest litter estimate of 54 μg Hg kg^{-1}(~~,~~n = 168; ~~,~~Wang et al., 2016). This difference~~,~~ highlight~~s~~ing the need for additional measurements in ~~more~~ TDBF ~~specific data~~ to ~~improve~~establish more robust ~~the~~ baseline ~~littler~~litter Hg concentrations for this forest type.

~~While datasets on TDBF litter Hg are lacking, which impedes cross-study comparison, our results indicate that TDBF litter Hg concentration is lower than the mean global litter estimate from various forests of 54 μg Hg kg^{-1}, n = 168 (Wang et al., 2016), but similar to the mean estimate for deciduous needleleaf forests reported by Xu et al. (2022) of 36 μg Hg kg^{-1}.~~

Overall, our study shows that although TDBF can accumulate foliar Hg at levels comparable to TMBF in mature leaves, post-senescence processes (e.g., re-emission, leaching and ~~and~~ decomposition) may alter Hg concentrations and reduce the amount of Hg in litter before it ~~reaches~~ is incorporated into~~the~~ soil. ~~,~~These findings ~~-~~highlight~~ing~~ the importance of incorporating seasonal dynamics into Hg modelling estimates. Given the wide global distribution of TDBF and its high foliar Hg sequestration capacity, these ecosystems should be explicitly included in global Hg budgets.

3.4 Mercury dynamics in soils from TDBF and TMBF

3.4.1 Role of litter in Hg accumulation in tropical soils

Consistent with previous studies identifying litter as the primary Hg source to forest soils (Feng et al., 2019; Jiménez et al., 2025; Lu et al., 2016; Ma et al., 2022; Zhou et al., 2018), our results showed a positive correlation between litter Hg ~~inputs~~ standing stocks and soil Hg concentrations (0-30 cm depth-averaged) in both tropical forests (Fig. 6~~5~~a). However, it is worth noting that our correlation does not demonstrate causality; Hg transfer from litter to soil may be independently influenced by common environmental factors (e.g., organic matter accumulation). Moreover, post-senescence Hg losses from litter before incorporation into mineral soil remain unquantified.

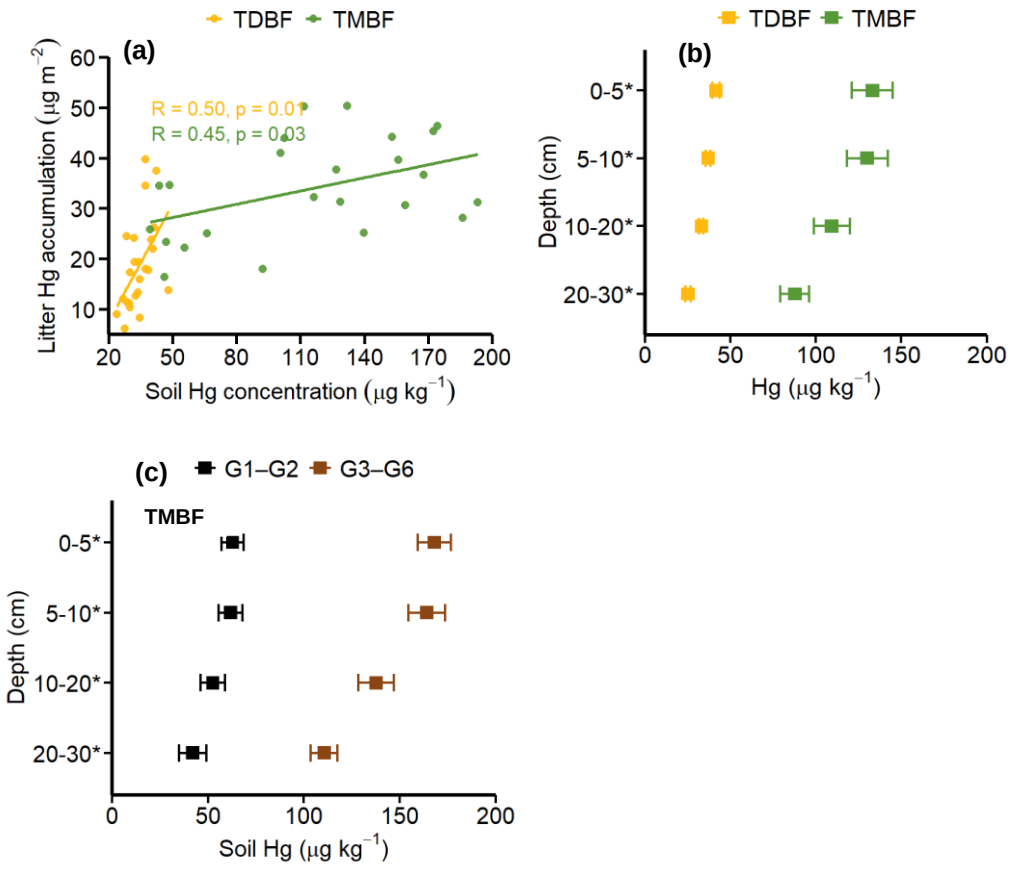


Figure 6~~5~~: (a) Pearson's ~~rank~~ correlations (based on data distribution), with the R coefficients and *p*-values, between Hg accumulation in litter across all six plots (mean of litter from dry and wet seasons) and soil Hg concentration (averaged at 0 – 30 cm depth) in tropical dry broadleaf forest (TDBF) and tropical moist broadleaf forest (TMBF). Trend lines were added to visualise overall patterns in the data. (b) Mean (± standard error) concentrations of Hg at different depths in the TDBF and TMBF. (c) Mean (± standard error) concentrations of Hg at different depths in the anthropogenically disturbed (G1-G2) and less disturbed (G3-G6) plots in TMBF. (*) on the y-axis indicates statistically significant differences between forests at each depth (Wilcoxon rank sum test $p < 0.05$).

This litter-mediated influence was also reflected in the vertical ~~decline~~ distribution of soil Hg concentrations. In TMBF (pH 5.1 ± 0.1 at 0–5 cm; silty clay), soil Hg concentrations decreased with depth from~~,~~ 133 to 88 μg kg^{-1} across the 0–30 cm profile (Fig. 6~~5~~b). A similar depth-dependent decline was observed in TDBF (pH 6.6 ± 0.1; silty clay), with concentrations approximately 3.4 times lower than those in the TMBF across ~~at~~ all depths ~~(soil Hg declining range at~~ranging from ~~different depths:~~ 42 to ~~–~~25 μg kg^{-1}~~)~~. In both ~~forests~~ forest types, the vertical distribution of soil Hg concentrations closely followed ~~the same pattern as~~that of C (R > 0.7 for both forests; data not shown), consistent with the well-known Hg-C associations in soil (Ma et al., 2022; Semu et al., 1987).

Despite TDBF and TMBF exhibiting, on average, similar foliar Hg ~~concentration~~ concentrations in mature leaves (50 vs. 53 μg kg^{-1}, ~~respectivelly~~respectively), soils in TMBF contained substantially more Hg. This difference might be related to more continuous litter production in TMBF, which sustains a steady litter-mediated Hg input to the soil throughout the year, as relatively stable litter Hg standing stocks were found across both dry and wet seasons, as explained in the litter section. In contrast, TDBF showed a peak of litter Hg standing stocks during the dry season, followed by a decrease during the wet season, driven by the leaf-shedding phenology of deciduous trees. ~~This difference is likely~~may be related ~~driven to more~~by sustained ~~litter-mediated Hg inputs in TMBF, where litter Hg concentrations remained stable between seasons (~61 dry vs. ~59 wet μg kg^{-1}) when comparing the ratio of Hg inputs (μg m^{-2}) to litter accumulation (kg m^{-2}). In contrast, TDBF had exhibited lower litter Hg concentrations (44 and 35 μg kg^{-1} in dry and wet seasons, respectively) and marked pronounced seasonal variability in litter mass driven by deciduous leaf shedding, as explained above. T~~Thus, the combination of lower litter Hg standing stocks and the lower tree density and canopy cover observed in the field may have contributed to the lower soil Hg concentrations in the TDBF compared with the TMBF.~~ed effects of lower litter Hg inputs, more strongly seasonal litter inputs, lower species density, and potentially greater temporal variability in Hg transfer may strong seasonal dependence likely explain the~~contribute ~~to the lower soil Hg concentrations observed in TDBF compared to TMBF.~~ Differences in ~~Different forests'~~ Hg-soil dynamics between the two forest types ~~are also shown~~are also evident in ~~in~~ Fig. 6~~5~~a, where contrasting slopes in the soil–litter Hg relationship ~~between forests types~~ indicate ~~distinct~~ differences in long-term Hg accumulation and retention in soils. In TMBF, ~~consistent~~ consistently high foliar Hg concentrations and frequent rainfall likely promote steady Hg inputs but also increase leaching potential. In TDBF, episodic yet ~~intense~~ high dry-season ~~litter Hg inputs~~litter Hg standing stocks, combined with reduced leaching under drier conditions, may favour more efficient Hg retention over time.

3.4.2 Anthropogenic disturbances affecting ~~Hg sequestration dynamics~~soil Hg concentrations in tropical forests

The depth-averaged Hg concentration (0–30 cm) in soils from plots G1 and G2 (55 μg kg^{-1}) was 2.6 times lower than in plots G3 – G6 (Fig. ~~6~~5c). This pattern was consistent across the entire soil profile (0 – 5, 5 – 10, 10 – 20, and 20 – 30 cm), with Hg concentrations remaining approximately 2.6 times lower in G1 – G2 (63, 62, 53, 42 μg kg^{-1}) than in G3 – G6 (168, 164, 138, 111 μg kg^{-1}) at every depth. The lower soil Hg concentrations ~~are~~may be ~~most~~ attributable to human disturbance. ~~This difference is most likely due to human disturbance.~~ Although plots G1 and G2, similar to plots G3 – G6, were also deforested, they were subsequently grazed and reforested ~~mainly~~ predominantly with *Theobroma cacao* for ~33 years (since approximately 1993), ~~resulting~~ resulting in lower species diversity~~in lower species diversity~~ compared to G3 – G6~~;~~. litter Hg standing stocks in G1 – G2 were also, ~~Thus, plots G1 – G2 received~~ on average, 1.5 times lower ~~litter-derived Hg inputs~~ (25 ± 3 μg Hg m^{-2}, n = 16) than G3 – G6 (38 ± 11 μg Hg m^{-2}, n = 32)~~. , likely due to cacao monoculture with a foliar Hg concentration of ~ 61 μg kg^{-1}, which is similar to Hg content in soil.~~As we did not measure Hg loss pathways (e.g., volatilisation, leaching, erosion, re-emission), their relative contributions cannot be determined from our data, and, given the unbalanced number of plots in the disturbed sites (n = 2) compared with the less disturbed ones (n = 4), these findings should be interpreted as a case study rather than a definitive demonstration of deforestation effects. ~~-~~Nonetheless, the magnitude of Hg loss is comparable to Mainville et al. (2006), who reported up to 60 % lower topsoil Hg following forest to pasture conversion in Ecuadorian rainforests, linked to erosion, leaching, and reduced organic matter inputs (Almeida et al., 2005); similarly, reforested soils in deciduous forests have remained Hg-depleted even after 60 – 80 years of regrowth (Gamby et al., 2015).

~~(Bouchet et al., 2026)~~

Therefore, our findings ~~underscore~~suggest ~~the importance of~~ that forest maturity and disturbance history may be important considerations when evaluating ~~for effective~~ Hg sequestration in tropical forests. ~~. We~~Our data also ~~highlight~~suggest that ~~soils~~soil Hg concentrations in TMBF may ~~-~~remain altered for several decades following disturbance. ~~the long time required for soil Hg concentrations to recover in previously disturbed areas. (Gamby et al., 2015)Consistent with this, forest conversion to pasture can reduce topsoil Hg by up to 60% (Mainville et al., 2006) due to increased soil exposure to erosion, enhanced Hg leaching, and reduced organic matter inputs (Almeida et al., 2005). Our findings underscore the importance of forest maturity to preserve Hg stocks and maintaining species diversity for effective Hg sequestration in tropical forests, as some TMBF species exhibited foliar Hg concentrations of up to 167 μg kg^{-1}, which could increase litter-derived Hg inputs. We also highlight the long time required for soil Hg stocks to recover in previously disturbed areas. For the~~The TDBF site had also undergone ~~reforestation~~ spatially heterogeneous reforestation~~in an un-even way, the area was also reforested~~; however, soil Hg concentrations were consistent across plots. Because we did not sample comparable disturbed and undisturbed sites, we are unable to determine ~~wether~~whether forest maturity or disturbance contributed to the observed patterns. ~~, and the lack of data in both disturbed and undisturbed areas impeded any cross-comparison.~~

Overall, topsoil Hg concentrations at the forest level were 1.8 times higher in TMBF and 1.8 times lower in TDBF than the estimated global average (74 μg kg^{-1}) by Liu et al. (2023). Our results for TMBF fall within the range reported for less disturbed near primary forest areas (128 – 225 μg kg^{-1}) (Almeida et al., 2005; Mainville et al., 2006). However, our results highlight the substantial variability that can be found among sampling sites~~, as discussed above~~. As no baseline data exist for disturbed or undisturbed TDBF soils, further research is needed, particularly considering that TDBF represents one of the most extensive yet endangered tropical forest ecosystems (Hasnat et al., 2000). Future modelling approaches should therefore also include this ecosystem. Overall, soils in TDBF and TMBF have been shown to efficiently store Hg derived primarily from litter, but they are highly vulnerable to human disturbances and may require long periods and a diverse native species assemblage for proper recovery of soil Hg ~~stocks~~concentrations.

4 Conclusions and implications

Our study demonstrate~~d~~ that ~~Hg sequestration~~foliar Hg concentrations in TDBF ~~is~~ vary strongly between the dry and wet season~~strongly driven influenced by seasonality~~, likely as a result of seasonal differences in plant water availability and associated changes in leaf phenology.~~which influences affects plant water availability and, consequently, leaf phenology.~~ In both ~~forests~~ forest types, mature leaves had higher foliar Hg concentrations than newly flushed leaves~~mature leaves accumulated higher foliar Hg concentrations than newly flushed leaves~~. As a result, evergreen and deciduous trees in TDBF exhibited lower foliar Hg during the dry season due to leaf phenological patterns (leaf shedding and flushing). During the wet season, evergreen and deciduous trees in TDBF showed a rapid ~~foliar Hg uptake~~increase in foliar Hg concentrations, reaching concentrations similar to those of mature leaves of both deciduous and evergreen species in TMBF. In contrast, TMBF maintained consistently high foliar Hg across seasons, likely due to the longer leaf lifespan ~~under persistently moist conditions~~and less pronounced seasonal constraints on plant water availability. ~~Litter derived Hg transfer to soils was~~Litter Hg standing stocks were also ~~driven~~ influenced by ~~seasonality~~seasonal differences, particularly in TDBF, ~~with were~~where they peak~~ed~~s ~~litter derived Hg inputs occurring~~ during the dry season. A similar dry-season peak in litter Hg standing stocks ~~was~~ was observed at a few TMBF sites, potentially reflecting ~~spatial~~spatially heterogeneous species distribution and phenology, with some ~~of them~~species / ~~individuals~~species/individuals increasing litter production under drier conditions. ~~In this regard~~Thus, both forests, especially TDBF, appear highly vulnerable to year-to-year climate fluctuations, as their Hg accumulation capacity is strongly climate-dependent. Prolonged drought periods could delay leaf flushing, reducing the time available for foliar Hg uptake and accumulation.

Our findings also highlight the need to refine global Hg estimates by accounting for high species-level diversity, ~~strong~~ pronounced seasonal dynamics, and substantial within-individual local variability in tropical forests. For foliar Hg assessment,

collecting multiple leaves per individual ~~When sampling in tropical forests, composite leaf sampling~~ is essential, as foliar Hg concentrations varied considerably ~~even within individual trees~~among leaves from the same tree, potentially reflecting differences in ~~due to~~ canopy position~~,~~ ~~and~~ light exposure, leaf age, and other leaf-level factors.

Foliar Hg concentrations in both forest types exceeded global estimates and ~~values~~ concentrations reported for temperate, boreal~~,~~, and deciduous temperate forests, highlighting the~~ir~~ importance of tropical ~~forest~~forests as ~~Hg sequestration hotspots~~potential hotspots for Hg accumulation. Although soil Hg concentrations in TDBF were lower than in TMBF, the ~~sequestration~~ accumulation potential ~~in~~ of undisturbed TDBF (primary forest) ~~areas~~ remains unexplored. Further in situ measurements, combined with improved modelling approaches, are therefore essential to better quantify and refine global Hg budgets. Conserving both forest types is crucial, as deforestation ~~significantly reduces~~might reduce soil Hg ~~stocks~~concentrations, and recovery likely requires long-term ecosystem stability and native species diversity.

Data availability

~~Data will be made available on request.~~The data will be made available upon request, as they will be further used to estimate Hg accumulation and storage budgets in tropical dry forests and rainforests using the Normalized Difference Vegetation Index (NDVI) (manuscript in preparation).

Supplement link

The link to the supplement will be included by Copernicus, if applicable.

Author contributions

JFMA: Conceptualization, Investigation, Methodology, Data curation, Writing – original draft, Writing-Review; GTPB: Investigation; MB: Investigation; CB: Investigation; WH: Investigation; MAZA: Investigation; HB: Investigation, Writing-Review; MPR: Writing – original draft, Writing-Review, Project administration, Supervision, Methodology, Conceptualization, Funding acquisition.

Competing interests

The contact authors have declared that none of the authors have any competing interests.

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