



Divergent mercury sequestration dynamics in tropical dry and moist broadleaf forests

Juan Francisco Morales Arteaga¹, Grace Tatiana Páez-Barrera², Matthias Beyer¹, Christian Birkel^{3, 4}, Werner Huber⁵, María Auxiliadora Zúñiga Amador⁶, Harald Biester¹, Marta Pérez-Rodríguez¹

5 ¹Department of Environmental Geochemistry, Technische Universität Braunschweig, Brunswick, 38106, Germany

²Departamento de Ciencias de la Vida y la Agricultura, Universidad de las Fuerzas Armadas ESPE, Sangolquí, 171103, Ecuador

³Department of Ecohydrology and Biogeochemistry, Leibniz Institute of Freshwater Ecology and Inland Fisheries Berlin, Germany.

10 ⁴Department of Geography, University of Costa Rica, San José, 11501-2060, Costa Rica

⁵Department of Botany and Biodiversity Research, University of Vienna, Vienna, 1030, Austria

⁶Escuela de Ciencias Exactas y Naturales, Universidad Estatal a Distancia, Montes de Oca, 474-2050, Costa Rica

Correspondence to: Marta Pérez-Rodríguez (m.perez-rodriguez@tu-braunschweig.de), and Juan Francisco Morales Arteaga (juan-francisco.morales-arteaga@tu-braunschweig.de)

15 **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 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. Seasonality strongly controlled Hg sequestration in TDBF. Deciduous trees
20 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 $\mu\text{g kg}^{-1}$), 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 $\mu\text{g kg}^{-1}$) or
25 evergreen trees (dry: 57; wet: 53 $\mu\text{g kg}^{-1}$), 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. 0.6 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.
30 Higher seasonally averaged Hg inputs via litter (34 $\mu\text{g m}^{-2}$) in TMBF than in the TDBF (19 $\mu\text{g m}^{-2}$) resulted in 3.4 times higher soil Hg concentrations (0–30 cm) in TMBF (115 $\mu\text{g kg}^{-1}$) than in TDBF (34 $\mu\text{g kg}^{-1}$). Soil Hg stocks were 2.6 times lower at a previously deforested TMBF site, indicating persistent disturbance effects despite almost three decades of reforestation. Overall, seasonality regulated Hg sequestration in TDBF, yet both TDBF and TMBF serve as important global Hg sinks with contrasting dynamics that are potentially sensitive to climate change.

35



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 (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 by vegetation structure (leaf area and canopy density), phenology (leaf age), and environmental conditions (climate and humidity/moisture) (Guentzel et al., 1998; Jiskra et al., 2018; Rea et al., 2002; Wang et al., 2019). These fluxes are especially pronounced in tropical forests, where high biodiversity and rapid biogeochemical 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., 2016a). Tropical trees also exhibit elevated foliar Hg concentrations, linked to higher stomatal pore density and higher photosynthesis capacity relative to temperate and boreal species (Larcher, 2003; Teixeira et al., 2018). Consequently, regions such as the Amazon Basin and Central Africa exhibit the highest global Hg^0 removal via litter ($65.0 \pm 30.0 \text{ g km}^{-2} \text{ yr}^{-1}$; Wang et al. 2016a), with soils serving as the principal Hg sink 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 dynamics in climate 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 tropical moist broadleaf forests (TMBF), are mostly evergreen, species-rich systems with annual precipitation typically > 2,000 mm - and as high as 10,000 mm- and limited seasonality due to short dry periods, which may also be interrupted by rainfall (Stork et al., 2008). By contrast, tropical seasonal forests, also known as tropical dry



broadleaf forests (TDBF), are predominantly deciduous, with distinct wet and dry periods characterized by leaf fall and long dry seasons (5 - 6 months with < 100 mm) (Bunyavejchewin et al., 2011), with a total annual rainfall of 700 to 2,000 mm
70 (Ruangpanit, 1995).

To date, studies of Hg dynamics in tropical forests focus 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; Lima et al., 2022; Lucchini et al., n.d.; Rodriguez-Pascual et al., 2024; Silva do Nascimento et al., 2025; Silva-Filho et al., 2006; Teixeira et al., 2017, 2018), with
75 high concentrations of atmospheric Hg in polluted areas likely overriding seasonal 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 one of the most threatened tropical ecosystems due to extensive deforestation and high vulnerability to climate change, particularly to longer and more intense dry seasons that could alter key phenological processes such as leaf flushing, leaf shedding, flowering, among others (Chidumayo, 2025; Hasnat and Hossain, 2020; Siyum, 2020;
80 Stivanello et al., 2024).

Forest seasonality strongly influences atmospheric Hg⁰ concentrations in the Northern Hemisphere due to variations in leaf uptake (Jiskra et al., 2018), yet the effect of these seasonal patterns is unexamined in tropical forests. This might 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 decrease stomatal conductance,
85 reduce leaf transpiration, and net photosynthesis as adaptive responses (Ávila-Lovera et al., 2019; Hasselquist et al., 2010; Mendes et al., 2020), which may directly impact on Hg⁰ sequestration.

Recent models estimating Hg in vegetation biomass, litter, soil, and the atmosphere have been developed and applied across various forest types, using machine learning and simulation approaches. Thus, Chen et al. (2024a) 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. Zhou and Obrist (2021b) reported annual vegetation Hg assimilation of 3062 ± 607 Mg yr⁻¹, with tropical forest mosses and lichens
90 showing the highest mean concentrations. Feinberg et al. (2022) estimated global Hg⁰ dry deposition to land at 2276 Mg yr⁻¹, with ~29% attributed to the Amazon. However, these studies highlighted substantial uncertainty, especially 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 seasonal photosynthesis, leaf fall (Tiwareti et al., 2025), species heterogeneity, and evergreen–deciduous transitions, all of which are highly variable in tropical forests. In
95 addition, TDBF remains unstudied and not considered in estimations, despite being strongly season-dependent and widely distributed. This lack of data likely constrains model performance and reduces predictive accuracy. Climate change adds further complexity by altering vegetation patterns, potentially increasing Hg mobilization to the atmosphere (Teixeira et al., 2017) and reducing sequestration due to tree mortality from longer dry periods.

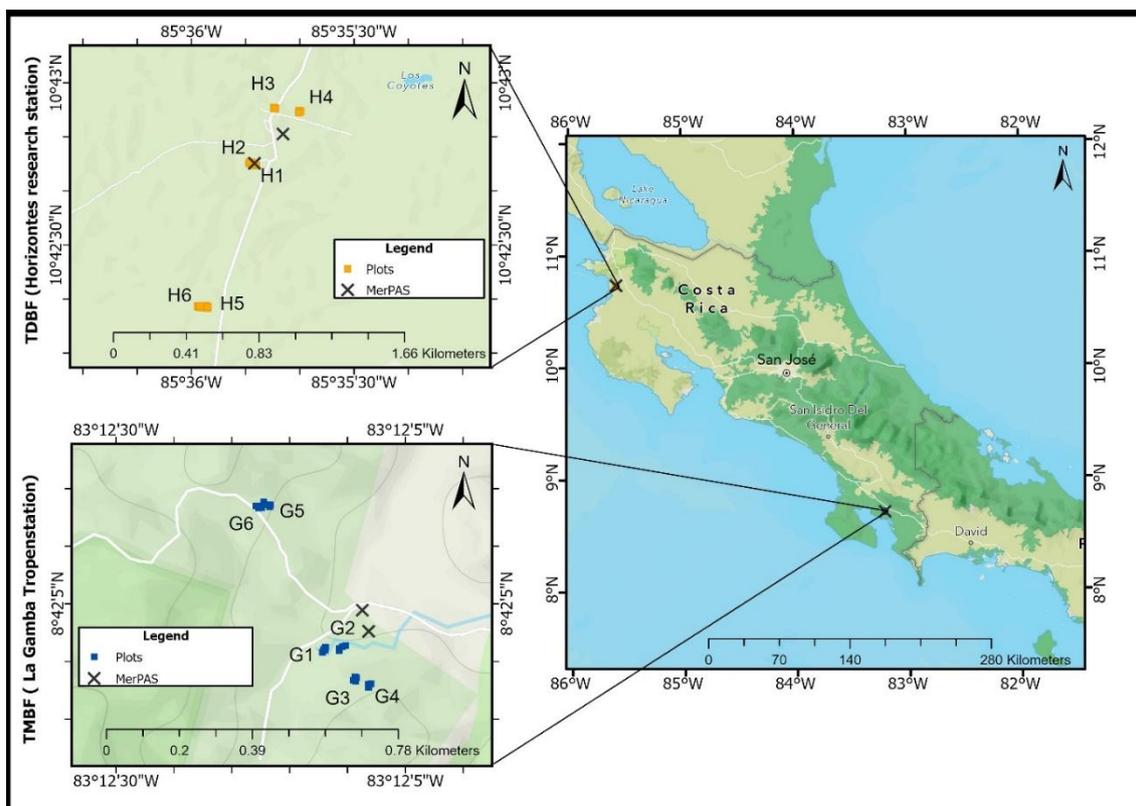


100 Our study aimed to evaluate how seasonality influences Hg dynamics in trees from TDBF and TMBF by quantifying Hg concentrations in key uptake, transfer, and storage compartments (foliage, litter, and soil), and by assessing the role of litter as a pathway for Hg transfer to soils in both forest types.

2 Materials and methods

2.1 Study area

105 The study was conducted in twelve plots (~100 m² each, adjusted to site orography) located in secondary forests in Costa Rica (Fig. 1), with six plots in tropical dry broadleaf forest (TDBF; H1–H6) and six plots in 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.; Mora-Chacón et al., 2022), northwestern Costa Rica.



110

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.



115 The TMBF plots were near the La Gamba Tropenstation (60-345 m.a.s.l.; Hübinger 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).

120 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; Hübinger 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 (Die Tropenstation La Gamba, 2025).
125 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 source of anthropogenic Hg (e.g., gold mining, cement production, etc.) (Fig. 1).

130 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.

135

140

145



Table 1: 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 rainfalls	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 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

155 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
 160 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. Total Hg was analyzed in all the samples after sample
 preparation.

165 Litter sampling. Excluding green leaves and twigs, litter was sampled in four replicates per plot (n= 96) at the end of the dry
 season (SC1) and the wet season (SC2) to assess differences in seasonality. All litter within a ~ 400 cm² square was collected
 into sealed plastic bags, dried to constant weight (50 °C, ~ 14 days), and weighed before grinding to estimate litter accumulation
 (per m²). Total Hg was analyzed after sampling preparation.

170



Soil sampling. Four soil profile samples were collected per plot from both forest types (n= 24 cores) during the SC1 sampling campaign. Sampling was conducted at four depth intervals (0–5, 5–10, 10–20, and 20–30 cm, n = 192) using a stainless-steel soil corer (coordinates are provided in Table S1). All samples were dried, sieved (< 2mm), and ground prior to analysis. Total Hg was analyzed after sampling preparation.

175

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 was 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.

180

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 (0-5 cm depth) in water (soil to water ratio, 1:5 w/v) (ISO 10390, 2005).

185

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 were processed using a Python script to estimate 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.

190

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 abaxial in this study).

195



200 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 averaged.

2.6 Determination of atmospheric mercury concentrations

205 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 MerPAS[®] (~1.5 m above the soil) were deployed at the end of the dry season (May 2024) in such a way that three replicates of the MerPAS[®] and one field blank per location were present. After deployment, they were left for about 6 months, collected, and replaced with new units to assess seasonality (Table 1). Total Hg was 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%.

210 2.6 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. A significance level of significance (p -value < 0.05) was applied. All analyses were conducted in R-Studio
215 (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 samples from both were available; single dry season measurements were used when only one campaign provided data (Fig. S1, Fig. S2 in SM; Fig. 3). Soil and litter data are reported per sampling event.

220

In the manuscript, mean values are expressed \pm standard error, except for Hg concentrations in different species from TDBF and TMBF (Fig. 2; Fig. S2 in SM), and Hg concentrations in MerPAS[®] samplers (Fig. 2), where means are expressed with standard deviation.

225

230



3 Results and discussion

3.1 Atmospheric Hg in tropical dry and moist broadleaf forests

Given that 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 influence on foliar Hg. In the TDBF, Hg^0 did not differ significantly between seasons (dry: $1.3 \pm 0.2 \text{ ng m}^{-3}$; wet: $1.1 \pm 0.2 \text{ ng m}^{-3}$; $n = 6$; Fig. 2).

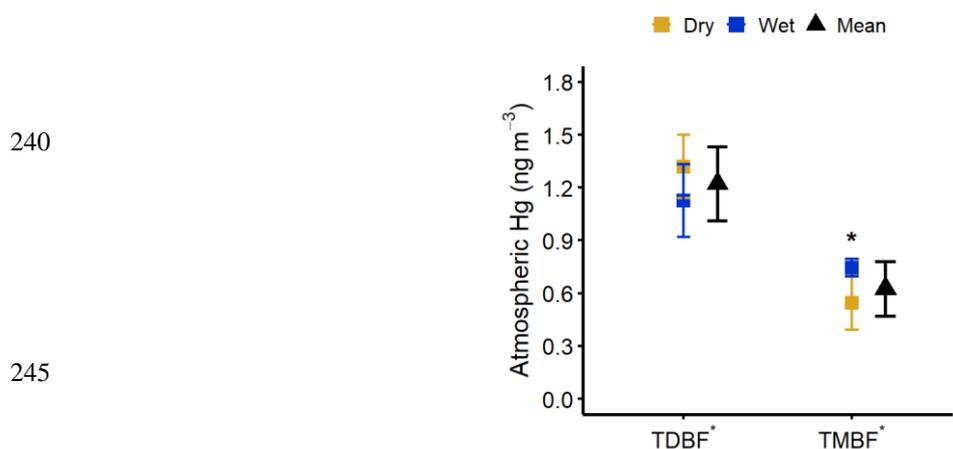


Figure 2: Mean (\pm standard deviation) of atmospheric Hg concentration ($n = 6$) in tropical dry broadleaf forest (TDBF) and tropical moist broadleaf forest (TMBF) during the dry and wet seasons. In the TMBF wet season data, two Hg passive samplers were lost during analysis due to issues with the catalyst in the instrument used for Hg measurement. Seasonal means are represented with a black triangle \pm 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 ($0.8 \pm 0.1 \text{ ng m}^{-3}$, $n = 6$) than during the dry season ($0.6 \pm 0.2 \text{ ng m}^{-3}$, $n = 6$), likely 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 ($1.2 \pm 0.2 \text{ ng m}^{-3}$, $n = 6$) were approximately twice those in TMBF (Fig. 2). 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).

260



265 Compared to global background levels, Hg^0 concentrations in TDBF were close to the reported Southern Hemisphere
 background (1.1 ng m^{-3}), while concentrations in TMBF were approximately 1.7 times lower (Lindberg et al., 2007; Sprovieri
 et al., 2010). The combined effects of dense vegetation cover in TMBF and local meteorological conditions, as explained
 above, likely explain these differences. To our knowledge, baseline Hg^0 concentrations have not previously been reported for
 these forests. Thus, our study provides the baseline values under natural conditions. However, further studies with additional
 270 MerPAS[®] deployments are needed to better understand the seasonal Hg^0 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 appeared in both deciduous and evergreen trees in the TDBF. Deciduous trees
 275 showed a more pronounced seasonal shift, with leaf Hg concentrations 4.7 times higher in the wet season ($49 \pm 27 \mu\text{g kg}^{-1}$, $n = 53$)
 than in the dry season ($10 \pm 11 \mu\text{g kg}^{-1}$, $n = 50$) (Fig. 3a).

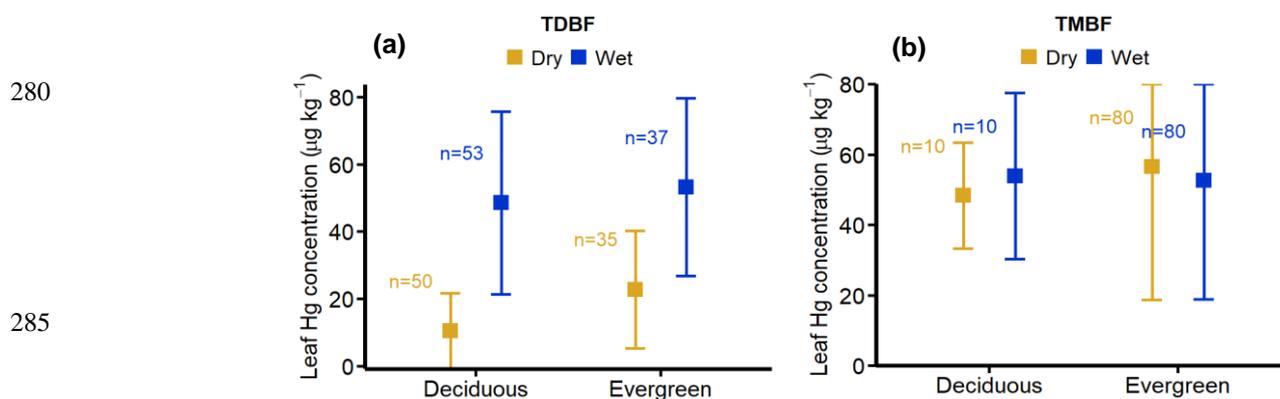


Figure 3: Mean (\pm standard deviation) concentrations of Hg in leaves of deciduous and evergreen species during the dry and wet seasons in the tropical dry broadleaf forest (TDBF, a) and tropical moist broadleaf forest (TMBF, b)

290

295



Evergreen trees in TDBF showed the same pattern, although less pronounced, with 2.3 times lower Hg concentration in the dry season ($23 \pm 18 \mu\text{g kg}^{-1}$, $n = 35$) compared to the wet season ($53 \pm 27 \mu\text{g kg}^{-1}$, $n = 37$). The higher wet-season leaf Hg concentration was 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 leaf phenology. In TDBF, deciduous trees shed their leaves during the dry season to limit drought stress, avoid drought-induced water loss, and protect their hydraulic function (Bullock et al., 1995; Eamus, 1999; Wolfe et al., 2016). Thus, leaves sampled at the end of the dry season were newly flushed following early rains and had therefore accumulated less Hg, consistent with previous studies showing that Hg increases with leaf age (Bullock et al., 1995; Eamus, 1999; Wolfe et al., 2016). For evergreen trees, the influence of several mechanisms may contribute to 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 lose their leaves during dry periods and rapidly develop new foliage after subsequent rainfall. Therefore, some authors call them semi- or brevi-deciduous depending on their shading characteristics (Eamus, 1999). Consistent with this, Borchert (1994) described evergreen trees in the same area of our study as facultative evergreens, with leaf phenology primarily driven by water status. This suggests that Hg sequestration, even for evergreen trees from TDBF, might be controlled by seasonality and water availability. 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 absorbed Hg 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, foliar Hg could be translocated (~5–15%) via the phloem and transported to woody tissues, contributing to dendrochemical records of atmospheric Hg (Monaci and Baroni, 2025; Peng et al., 2024). 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, we provide the baseline for foliage Hg concentrations in TDBF, as no studies have been conducted in this forest type for cross-comparison.

No seasonal patterns in foliar Hg concentrations were observed in the TMBF. Deciduous trees showed similar concentrations in the dry ($48 \pm 15 \mu\text{g kg}^{-1}$, $n = 10$) and wet seasons ($54 \pm 24 \mu\text{g kg}^{-1}$, $n = 10$). Evergreen trees showed the same pattern, with similar values in the dry ($57 \pm 38 \mu\text{g kg}^{-1}$, $n = 80$) and wet ($53 \pm 34 \mu\text{g kg}^{-1}$, $n = 80$) seasons (Fig. 3b). At the species level, high variability in foliar Hg concentration was found, but no clear 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 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 environment (Reich et al., 2004), allowing continuous Hg accumulation over time. Moreover, persistent high humidity, resulting from the absence of a pronounced dry season, likely maintained optimal stomatal conductance in both seasons, promoting continuous photosynthesis and transpiration, which have been linked to high foliar Hg uptake (Teixeira et al., 2018c). In addition, dense



canopy structure may enhance foliar Hg uptake and limit Hg⁰ re-emission by reducing light penetration (Yuan et al., 2019). A similar absence of seasonal variation on foliar Hg was also observed in deciduous trees, as the sampled leaves were mature during both seasons. In TMBF, leaf shedding is typically followed by fast regrowth under abundant moisture and rainfall, with phenology regulated by drought and light availability (Kearsley et al., 2024). Consequently, most leaves remain mature for extended periods, allowing continuous foliar Hg accumulation. As discussed above, older leaves under ideal net photosynthesis conditions exhibit higher Hg foliar concentrations.

Overall, water availability—strongly regulated by seasonality—emerged as the primary driver of foliar Hg sequestration in both forests. In TDBF, although foliar Hg 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 in TMBF. Additionally, foliar Hg concentrations in TMBF remained consistently higher in both dry and wet seasons, although higher Hg⁰ was found 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, *Tabebuia ochracea* (deciduous) exhibited the highest mature leaf Hg concentration ($99 \pm 45 \mu\text{g kg}^{-1}$, $n = 4$) (wet-season), while among evergreens, the *Tabernaemontana glabra* reached the highest concentration ($72 \pm 12 \mu\text{g kg}^{-1}$; $n = 11$) (Fig. S2, SM). In the TMBF, *Psychotria elata* (evergreen) showed the highest Hg concentrations (dry season: 92 ± 15 , $n = 5$; wet season: $86 \pm 12 \mu\text{g kg}^{-1}$, $n = 5$), whereas *Amphirrhox longifolia* accumulated most Hg among deciduous species (dry: 57 ± 9 , $n = 5$; wet: $68 \pm 24 \mu\text{g kg}^{-1}$, $n = 5$) (Fig. S2, SM).

Among leaves, Hg concentrations varied markedly in both evergreen and deciduous trees. This pattern was especially pronounced for TDBF species such as *Amphilophium paniculatum* (Percentual deviation from the mean for individual samples (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 similar variability 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). This variability is most likely a result of differences in leaf age, light exposure, humidity, stomatal conductance, net photosynthesis, presence of pests, among 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, as described in the materials and methods, 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.

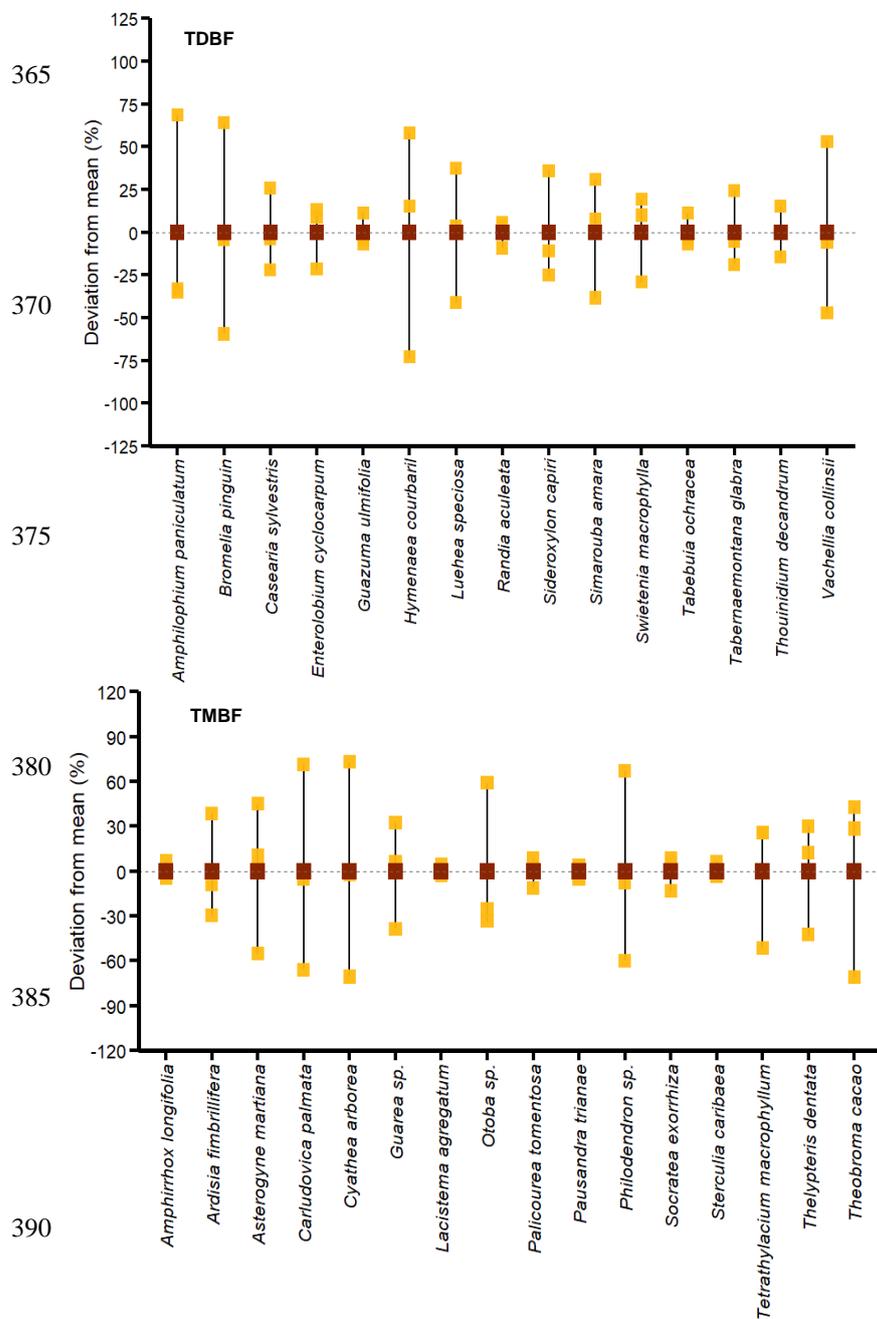


Figure 4: Within-individual variability in leaf Hg concentration-based subsamples collected from different parts of the same plant across multiple species in the tropical dry broadleaf forest (TDBF) and the tropical moist broadleaf forest (TMBF) during the dry season (SC3). Yellow squares represent Hg 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 Hg⁰ accumulation in tropical forests

Most studies agree that Hg⁰ 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 Hg⁰ accumulation (Stamenkovic and Gustin, 2009). Leaf area and stomatal density have further been proposed as factors influencing Hg⁰ 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.

3.2.4 TDBF and TMBF contributions to the global foliar Hg pool

Across all species, mature leaves in the TDBF averaged 50 $\mu\text{g kg}^{-1}$ Hg (range: 4–161 $\mu\text{g kg}^{-1}$, $n = 90$), while the TMBF averaged 53 $\mu\text{g kg}^{-1}$ (range: 2 – 167 $\mu\text{g kg}^{-1}$, $n = 90$). These values are 2.1 (TDBF) and 2.2 (TMBF) times higher than the estimated global foliar Hg mean concentration (24 $\mu\text{g kg}^{-1}$; Chen et al., 2024b) and exceed typical concentrations reported for temperate and boreal forests (e.g., 16.3 $\mu\text{g kg}^{-1}$ in U.S. temperate forests, Yang et al., 2018; 20 – 40 $\mu\text{g kg}^{-1}$ in Canadian temperate deciduous forests, Siwik et al., 2009; 11 – 26 $\mu\text{g kg}^{-1}$ in European forests, Wohlgemuth et al., 2020). Although higher Hg⁰ concentrations have been reported in the Northern Hemisphere, where most temperate and boreal forests are located (1.5 – 1.7 ng m^{-3} ; Sprovieri et al. 2010b), compared to our results of Hg⁰ in TMBF and TDBF, foliar Hg concentrations in both tropical forests were significantly higher. This underscores the importance of tropical forests as a major global Hg sink, with favorable stomatal conductance, dense vegetation, abundant species, high net photosynthesis, and year-round light availability likely creating conditions for enhanced foliar Hg uptake.

425



430 Our study provides the first baseline data for foliar Hg concentrations in TDBF and highlights the importance of accounting
for seasonality when sampling and modeling foliar Hg, particularly in highly seasonal systems such as TDBF. Although our
results are consistent with the modelled foliar Hg concentration for TMBF ($\sim 53 \pm 24 \mu\text{g kg}^{-1}$, $n = 263$) proposed by Zhou et
al. (2021b), they show high variability, including marked intra-individual differences in both forests. Given the limited field-
based Hg data available, this highlights the need for more in-field measurements that account for the seasonality of tropical
435 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

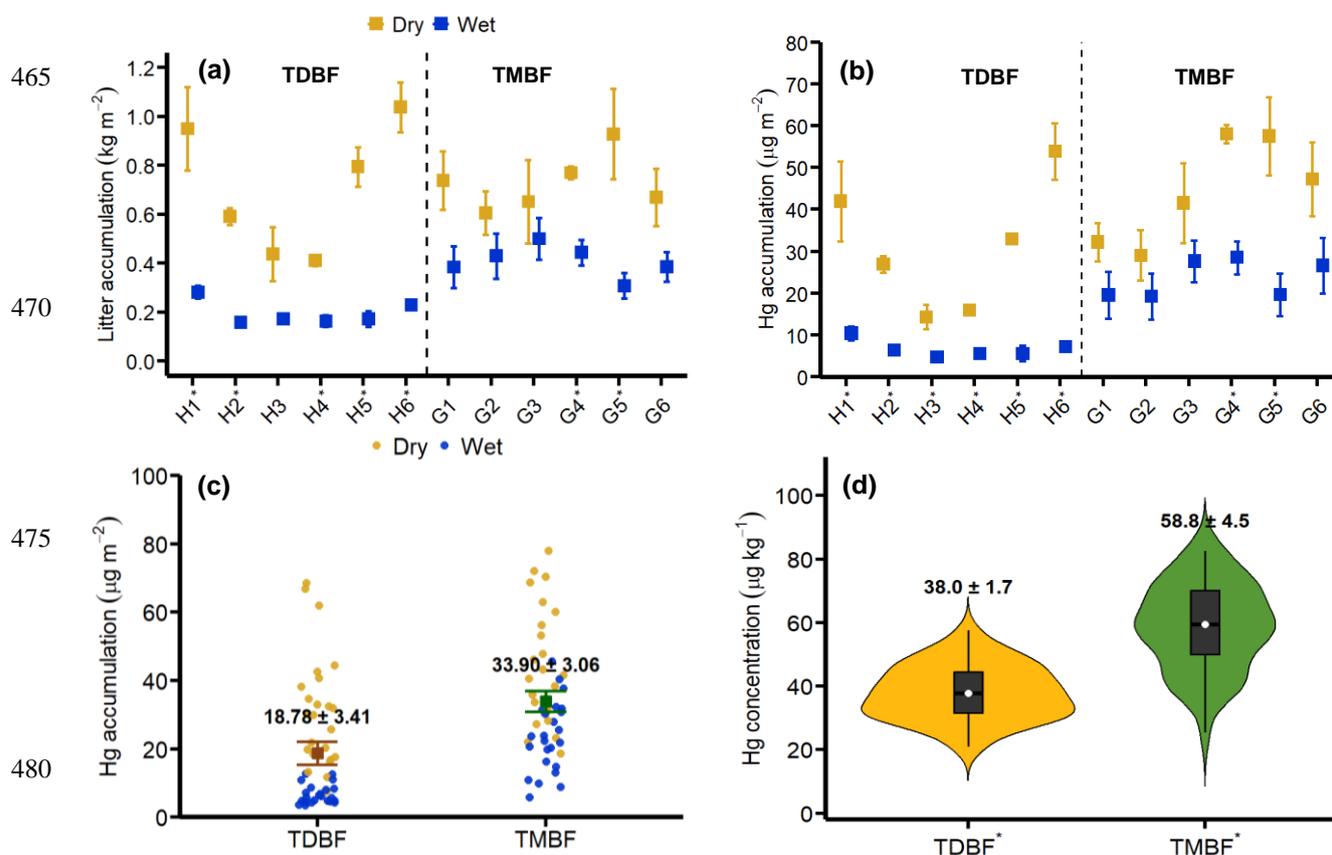
At TDBF, litter mass accumulation in soil was significantly higher during the dry season compared to the wet season at all
440 plots except H3 (Fig. 5a).

445

450

455

460



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



On average (plots H1-H6), dry-season litter was 3.6 times higher ($0.7 \pm 0.1 \text{ kg m}^{-2}$, $n = 24$) than wet-season litter ($0.2 \pm 0.0 \text{ kg m}^{-2}$, $n = 24$). At TMBF, no significant seasonal differences in litter mass accumulation were found at most plots, except for G4 and G5 (Fig. 5a). However, when averaged across all plots (G1-G6), litter accumulation at forest level was 1.8 times higher during the dry season ($0.7 \pm 0.1 \text{ kg m}^{-2}$, $n = 24$) than during the wet season ($0.4 \pm 0.0 \text{ kg m}^{-2}$, $n = 24$). 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 overall dry-season litter observed in both forests is consistent with previous reports of intensified leaf shedding in Mexican TDBF driven by deciduous leaf abscission (Morffi-Mestre et al., 2020) and in secondary rainforest in Brazil as a tree response to moisture stress (Oliveira de Moraes 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. Differences among plots presumably reflect local variation in microclimate, successional stage, topography, tree species diversity, and forest structural patterns (Giweta, 2020).

When comparing both forest types across seasons, the TMBF showed 1.3 times higher litter accumulation ($0.57 \pm 0.0 \text{ kg m}^{-2}$, $n = 48$, Fig. S4 a, SM) than the TDBF ($0.45 \pm 0.1 \text{ kg m}^{-2}$, $n = 6$). Although litter mass in the TDBF was low during the wet season, the higher accumulation in the dry season resulted in total seasonal masses comparable to those of the TMBF. These patterns broadly align with previous reports showing higher litter in TMBF ($\sim 8\text{--}14 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; Chave et al., 2010a) compared to TDBF ($4\text{--}8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$; Montañez-S. et al., 2023; Morffi-Mestre et al., 2020b; Souza et al., 2019b), though ranges overlap between forest types.

525



3.3.2 Hg concentration in litter and its relationship to foliar Hg

530 Hg concentrations in litter from the TDBF showed an average value of $43 \mu\text{g kg}^{-1}$ ($n = 24$), in the dry season, compared to 33
 $\mu\text{g kg}^{-1}$ ($n = 24$), 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 $61 \mu\text{g kg}^{-1}$ (Hg), $n = 24$, during the dry season and $57 \mu\text{g kg}^{-1}$, $n = 24$, during the wet season. Slightly higher dry-season
535 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
TMBF was comparable to those reported by Fostier et al. (2015b) and Wright et al. (2016b), in rainforests from Brazil and
French Guiana ($\sim 60 \mu\text{g kg}^{-1}$). 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 ($50 \mu\text{g kg}^{-1}$, $n = 90$), was 34%
540 higher than in litter, likely due to Hg loss from leaching, decomposition, re-emission, and other factors. Conversely, in the dry
season, Hg concentration in litter was 64% higher than in living leaves ($15 \mu\text{g kg}^{-1}$, $n = 85$), suggesting that most litter consisted
primarily of mature leaves shed early in the season. In the TMBF, litter contained 9% and 7% less Hg than in living leaves
during the dry ($61 \mu\text{g kg}^{-1}$, $n = 90$) and wet seasons ($57 \mu\text{g kg}^{-1}$, $n = 90$), likely reflecting Hg losses through leaching and
decomposition as mentioned above.

545

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

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

Seasonal patterns of Hg accumulation were driven by both leaf phenology and decomposition dynamics in both forests, but
555 most strongly 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 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, which is particularly relevant because we measured net litter accumulation. Consequently, seasonal differences
in Hg (both concentration and accumulation) as well as between forest types are shaped by both the timing of leaf fall and the
560 degree of post-abscission degradation.



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 occur more continuously throughout the year, with some sites peaking under dry conditions, depending on many factors such as plant species' drought tolerance, species distribution, among others, as described above (section 3.3.1). Additionally, greater litter-derived Hg accumulation during the dry season may be linked to reduced decomposition rates, as dry conditions are known to slow litter breakdown (Rowland et al., 2014; Teixeira et al., 2017; Yavitt et al., 2004). Thus, seasonality may also indirectly influence Hg transfer through its effect on decomposition and potential reemission, although these mechanisms need further investigation.

570 3.3.4 Litter Hg fluxes and concentrations in TDBF and TMBF compared with global estimates

Seasonally averaged litter-derived Hg inputs were 1.8 times higher in TMBF ($34 \pm 3 \mu\text{g Hg m}^{-2}$, $n = 6$) than in the TDBF ($19 \pm 3 \mu\text{g Hg m}^{-2}$, $n = 6$), as shown in Fig. 5c. Although our estimates are seasonal sums rather than annualized values, they are comparable to findings from rainforests ($34.6 \pm 1.2 \mu\text{g m}^{-2} \text{yr}^{-1}$; Teixeira et al., 2017d) and fall within modelled ranges in the Amazon ($49 \pm 14 \mu\text{g Hg m}^{-2} \text{yr}^{-1}$; Fostier et al., 2015). Hg concentration in litter was 1.5 times higher in TMBF than in TDBF, with density peaks near $\sim 60 \mu\text{g Hg kg}^{-1}$ and $\sim 33 \mu\text{g Hg kg}^{-1}$, respectively (Fig. 5d). TMBF peaks are similar to the Amazon rainforest estimates by Fostier et al. (2015d) ($\sim 60.5 \mu\text{g Hg kg}^{-1}$). 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 $54 \mu\text{g Hg kg}^{-1}$, $n = 168$ (Wang et al., 2016), but similar to the mean estimate for deciduous needleleaf forests reported by Xu et al. (2022) of $36 \mu\text{g Hg kg}^{-1}$.

580

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 and decomposition) may reduce Hg in litter before it reaches the soil, highlighting 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.

585

3.4 Mercury dynamics in soils from TDBF and TMBF

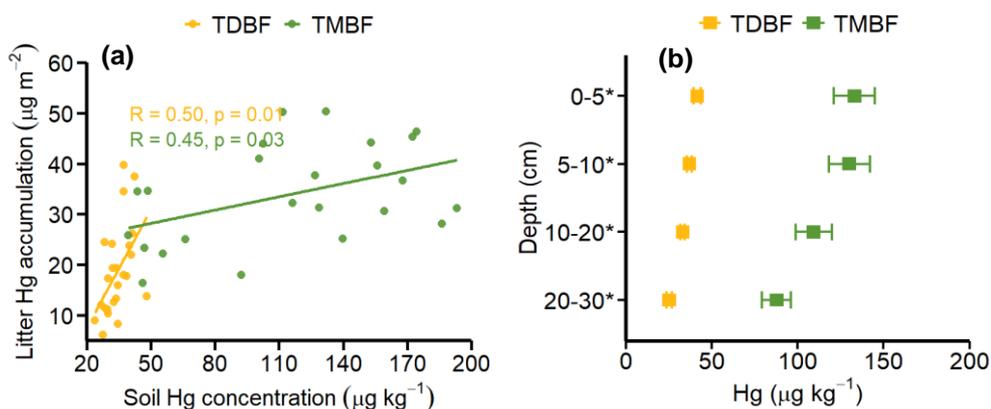
3.4.1 Role of litter in Hg accumulation in tropical soils

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 and soil Hg concentrations (0-30 cm depth-averaged) in both tropical forests (Fig. 6a).

590

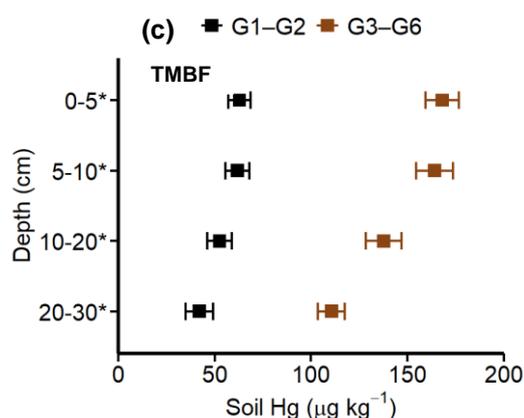


595



600

605



610

615 **Figure 6:** (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 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 (\pm standard error) concentrations of Hg at different depths in the TDBF and TMBF. (c) Mean (\pm 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 $p < 0.05$).

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



Despite TDBF and TMBF exhibiting, on average, similar foliar Hg concentration in mature leaves (50 vs. 53 $\mu\text{g kg}^{-1}$), soils in TMBF contained substantially more Hg. This difference is likely driven by sustained litter-mediated Hg inputs in TMBF, where litter Hg concentrations remained stable between seasons (~ 61 dry vs. ~ 59 wet $\mu\text{g kg}^{-1}$) when comparing the ratio of Hg inputs ($\mu\text{g m}^{-2}$) to litter accumulation (kg m^{-2}). In contrast, TDBF had lower litter Hg concentrations (44 and 35 $\mu\text{g kg}^{-1}$ in dry and wet seasons, respectively) and marked seasonal variability in litter mass driven by deciduous leaf shedding, as explained in the litter section. Thus, the combined effects of lower litter-Hg inputs, lower species density, and strong seasonal dependence likely explain the lower soil Hg concentrations in TDBF compared to TMBF. Different forests' Hg-soil dynamics are also shown in Fig. 6a, where contrasting slopes in the soil–litter Hg relationship between forests indicate distinct long-term Hg accumulation. In TMBF, consistent foliar Hg concentrations and frequent rainfall likely promote steady Hg inputs but also increase leaching potential. In TDBF, episodic yet intense dry-season litter Hg inputs, combined with reduced leaching under drier conditions, may favour more efficient Hg retention over time.

3.4.2 Anthropogenic disturbances affecting Hg sequestration dynamics in tropical forests

The depth-averaged Hg concentration (0–30 cm) in soils from plots G1 and G2 (55 $\mu\text{g kg}^{-1}$) was 2.6 times lower than in plots G3 – G6 (Fig. 6c). This difference is most likely due to human disturbance. Although plots G1 and G2 were also deforested, similar to plots G3 – G6, they were subsequently grazed and reforested mainly with *Theobroma cacao* for ~ 33 years (since approximately 1993), resulting in lower species diversity compared to G3 – G6. Thus, plots G1 – G2 received on average 1.5 times lower litter-derived Hg inputs ($25 \pm 3 \mu\text{g Hg m}^{-2}$, $n = 16$) than G3 – G6 ($38 \pm 11 \mu\text{g Hg m}^{-2}$, $n = 32$), likely due to cacao monoculture with a foliar Hg concentration of $\sim 61 \mu\text{g kg}^{-1}$, which is similar to Hg content in soil. 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 $\mu\text{g kg}^{-1}$, 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 TDBF, the area was also reforested; however, soil Hg concentrations were consistent across plots, 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 $\mu\text{g kg}^{-1}$) by Liu et al. (2023). Our results for TMBF fall within the range reported for less disturbed near primary forest areas (128 – 225 $\mu\text{g kg}^{-1}$) (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



660 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.

4 Conclusions and implications

Our study demonstrates that Hg sequestration in TDBF is strongly driven by seasonality, which influences plant water availability and, consequently, leaf phenology. In both forests, 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 rapid foliar Hg uptake, 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. Litter-derived Hg transfer to soils was also driven by seasonality, particularly in TDBF, with peak litter-derived Hg inputs occurring during the dry season. A similar dry-season peak in litter Hg was observed at a few TMBF sites, reflecting heterogeneous species distribution, with some of them increasing litter production under drier conditions. In this regard, 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 highlight the need to refine global Hg estimates by accounting for high species diversity, strong seasonal dynamics, and substantial in situ variability in tropical forests. When sampling in tropical forests, composite leaf sampling is essential, as foliar Hg concentrations varied considerably even within individual trees due to canopy position and light exposure.

Foliar Hg concentrations in both forest types exceeded global estimates and values reported for temperate, boreal, and deciduous temperate forests, highlighting their importance as Hg sequestration hotspots. Although soil Hg concentrations in TDBF were lower than in TMBF, the sequestration potential in undisturbed 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 soil Hg stocks, and recovery likely requires long-term ecosystem stability and native species diversity.



Data availability

Data will be made available on request.

690 **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-
695 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.

Disclaimer

700 Copernicus Publications adds a standard disclaimer: “Copernicus Publications remains neutral with regard to jurisdictional claims made in the text, published maps, institutional affiliations, or any other geographical representation in this paper. While Copernicus Publications makes every effort to include appropriate place names, the final responsibility lies with the authors. Views expressed in the text are those of the authors and do not necessarily reflect the views of the publisher.”
Please feel free to add disclaimer text at your choice, if applicable.

705 **Acknowledgements**

The authors acknowledge Petra Schmidt, José Andrés Herra Araya, and Antonia Schmidtke for their assistance in the field, and Malkin Gerchow for developing the Python script used to determine leaf area. We also thank Adelina Caezan, Sanaz



Arianmesh, André Dörrrie, Amelie Rother, and Alexandra Mayer for their laboratory support, as well as the workers at the Horizontes Experimental Research Station and La Gamba Tropenstation.

710 **Financial support**

The study was supported by the German Science Foundation (DFG) by a grant to M.P-R (PE 3026/3-1).

Review statement

The review statement will be added by Copernicus Publications listing the handling editor as well as all contributing referees according to their status anonymous or identified. {Citation}

715 **References**

Almeida, M. D., Lacerda, L. D., Bastos, W. R., and Herrmann, J. C.: Mercury loss from soils following conversion from forest to pasture in Rondônia, Western Amazon, Brazil, *Environ. Pollut.*, 137, 179–186, <https://doi.org/10.1016/j.envpol.2005.02.026>, 2005.

720 Anderson, Y. O.: Seasonal Development in Sun and Shade Leaves, *Ecology*, 36, 430–439, <https://doi.org/10.2307/1929579>, 1955.

10 chemicals of public health concern: <https://www.who.int/news-room/photo-story/photo-story-detail/10-chemicals-of-public-health-concern>, last access: 29 October 2024.

725 Ávila-Lovera, E., Urich, R., Coronel, I., and Tezara, W.: Seasonal gas exchange and resource-use efficiency in evergreen versus deciduous species from a tropical dry forest, *Tree Physiol.*, 39, 1561–1571, <https://doi.org/10.1093/treephys/tpz060>, 2019.

Bonan, G. B.: Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests, *Science*, 320, 1444–1449, <https://doi.org/10.1126/science.1155121>, 2008.

Borchert, R.: Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees, *Ecology*, 75, 1437–1449, <https://doi.org/10.2307/1937467>, 1994.

730 Bothwell, L. D., Selmants, P. C., Giardina, C. P., and Litton, C. M.: Leaf litter decomposition rates increase with rising mean annual temperature in Hawaiian tropical montane wet forests, *PeerJ*, 2, e685, <https://doi.org/10.7717/peerj.685>, 2014.

Brienen, R. J. W., Zuidema, P. A., and Martínez-Ramos, M.: Attaining the canopy in dry and moist tropical forests: strong differences in tree growth trajectories reflect variation in growing conditions, *Oecologia*, 163, 485–496, <https://doi.org/10.1007/s00442-009-1540-5>, 2010.

735 Bullock, S. H., Mooney, H. A., and Medina, E. (Eds.): Seasonally Dry Tropical Forests, Cambridge University Press, Cambridge, <https://doi.org/10.1017/CBO9780511753398>, 1995.



- Bunyavechewin, S., Baker, P. J., and Davies, S. J.: Seasonally dry tropical forests in continental Southeast Asia: structure, composition and dynamics, in: *The Ecology and Conservation of Seasonally Dry Forests in Asia*, Smithsonian Institution Scholarly Press, 9–35, 2011.
- 740 Chave, J., Navarrete, D., Almeida, S., Álvarez, E., Aragão, L. E. O. C., Bonal, D., Châtelet, P., Silva-Espejo, J. E., Goret, J.-Y., von Hildebrand, P., Jiménez, E., Patiño, S., Peñuela, M. C., Phillips, O. L., Stevenson, P., and Malhi, Y.: Regional and seasonal patterns of litterfall in tropical South America, *Biogeosciences*, 7, 43–55, <https://doi.org/10.5194/bg-7-43-2010>, 2010.
- Chen, L., Zhou, J., Guo, L., Bian, X., Xu, Z., Chen, Q., Wen, S.-H., Wang, K., and Liu, Y.-R.: Global Distribution of Mercury in Foliage Predicted by Machine Learning, *Environ. Sci. Technol.*, 58, 15629–15637, <https://doi.org/10.1021/acs.est.4c00636>,
745 2024.
- Chidumayo, E. N.: Stem water monitoring reveals an association with rainfall and leaf flush timing in a tropical dry forest of Zambia, *Tree Physiol.*, 45, tpa084, <https://doi.org/10.1093/treephys/tpaf084>, 2025.
- Cusack, D. F., Reed, S., Andersen, K. M., Cinoğlu, D., Craig, M. E., Dietterich, L. H., Hogan, J. A., Holm, J. A., Nottingham, A. T., Ostertag, R., Soper, F. M., Wood, T. E., and Wong, M. Y.: Tropical forests and global change: biogeochemical responses and opportunities for cross-site comparisons, an organized INSPIRE session at the 108th Annual Meeting, Ecological Society of America, Portland, Oregon, USA, August 2023, *New Phytol.*, 241, 1922–1926, <https://doi.org/10.1111/nph.19511>, 2024.
- 750 Denzler, B., Eugster, W., Bogdal, C., Bishop, K., Buchmann, N., Hungerbühler, K., and Osterwalder, S.: Uptake of Gaseous Elemental Mercury by a Rainforest: Insights from a Tropical Glasshouse Used as a Dynamic Flux Chamber, *Environ. Sci. Technol.*, 59, 18675–18686, <https://doi.org/10.1021/acs.est.5c05823>, 2025.
- 755 Durner, W., Iden, S. C., and von Unold, G.: The integral suspension pressure method (ISP) for precise particle-size analysis by gravitational sedimentation, *Water Resour. Res.*, 53, 33–48, <https://doi.org/10.1002/2016WR019830>, 2017.
- Eamus, D.: Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics, *Trends Ecol. Evol.*, 14, 11–16, [https://doi.org/10.1016/S0169-5347\(98\)01532-8](https://doi.org/10.1016/S0169-5347(98)01532-8), 1999.
- Escobar-Camacho, D., Rosero-López, D., Ruiz-Urigüen, M., Barragán, K. S., Carpintero-Salvador, N., Daza, J. R., Aldous, A., Benítez, S., Tear, T., and Encalada, A. C.: Mercury in aquatic ecosystems of two indigenous communities in the Piedmont Ecuadorian Amazon: evidence from fish, water, and sediments, *Ecotoxicol. Lond. Engl.*, 33, 440–456, <https://doi.org/10.1007/s10646-024-02764-w>, 2024.
- Feinberg, A., Dlamini, T., Jiskra, M., Shah, V., and E. Selin, N.: Evaluating atmospheric mercury (Hg) uptake by vegetation in a chemistry-transport model, *Environ. Sci. Process. Impacts*, 24, 1303–1318, <https://doi.org/10.1039/D2EM00032F>, 2022.
- 765 Feng, C., Wang, Z., Ma, Y., Fu, S., and Chen, H. Y. H.: Increased litterfall contributes to carbon and nitrogen accumulation following cessation of anthropogenic disturbances in degraded forests, *For. Ecol. Manag.*, 432, 832–839, <https://doi.org/10.1016/j.foreco.2018.10.025>, 2019.
- Fostier, A., Melendez-Perez, J., and Richter, L.: Litter mercury deposition in the Amazonian rainforest., *Environ. Pollut.*, 2015.
- 770 Gei, M. G. and Powers, J. S.: Do legumes and non-legumes tree species affect soil properties in unmanaged forests and plantations in Costa Rican dry forests?, *Soil Biol. Biochem.*, 57, 264–272, <https://doi.org/10.1016/j.soilbio.2012.09.013>, 2013.
- Gerson, J. R., Szponar, N., Zambrano, A. A., Bergquist, B., Broadbent, E., Driscoll, C. T., Erkenwick, G., Evers, D. C., Fernandez, L. E., Hsu-Kim, H., Inga, G., Lansdale, K. N., Marchese, M. J., Martinez, A., Moore, C., Pan, W. K., Purizaca, R. P., Sánchez, V., Silman, M., Ury, E. A., Vega, C., Watsa, M., and Bernhardt, E. S.: Amazon forests capture high levels of



- 775 atmospheric mercury pollution from artisanal gold mining, *Nat. Commun.*, 13, 559, <https://doi.org/10.1038/s41467-022-27997-3>, 2022.
- Giweta, M.: Role of litter production and its decomposition, and factors affecting the processes in a tropical forest ecosystem: a review, *J. Ecol. Environ.*, 44, 11, <https://doi.org/10.1186/s41610-020-0151-2>, 2020.
- 780 Graydon, J. A., St. Louis, V. L., Lindberg, S. E., Sandilands, K. A., Rudd, J. W. M., Kelly, C. A., Harris, R., Tate, M. T., Krabbenhoft, D. P., Emmerton, C. A., Asmath, H., and Richardson, M.: The role of terrestrial vegetation in atmospheric Hg deposition: Pools and fluxes of spike and ambient Hg from the METAALICUS experiment, *Glob. Biogeochem. Cycles*, 26, <https://doi.org/10.1029/2011GB004031>, 2012.
- Guentzel, J. L., Landing, W. M., Gill, G. A., and Pollman, C. D.: Mercury and major ions in rainfall, throughfall, and foliage from the Florida Everglades, *Sci. Total Environ.*, 213, 43–51, [https://doi.org/10.1016/S0048-9697\(98\)00071-0](https://doi.org/10.1016/S0048-9697(98)00071-0), 1998.
- 785 Gustin, M. S., Huang, J., Miller, M. B., Peterson, C., Jaffe, D. A., Ambrose, J., Finley, B. D., Lyman, S. N., Call, K., Talbot, R., Feddersen, D., Mao, H., and Lindberg, S. E.: Do We Understand What the Mercury Speciation Instruments Are Actually Measuring? Results of RAMIX, *Environ. Sci. Technol.*, 47, 7295–7306, <https://doi.org/10.1021/es3039104>, 2013.
- Gustin, M. S., Dunham-Cheatham, S. M., Harper, J. F., Choi, W.-G., Blum, J. D., and Johnson, M. W.: Investigation of the biochemical controls on mercury uptake and mobility in trees, *Sci. Total Environ.*, 851, 158101, <https://doi.org/10.1016/j.scitotenv.2022.158101>, 2022.
- 790 Gworek, B., Dmochowski, W., and Baczewska-Dąbrowska, A. H.: Mercury in the terrestrial environment: a review, *Environ. Sci. Eur.*, 32, 128, <https://doi.org/10.1186/s12302-020-00401-x>, 2020.
- Hasnat, G. N. T. and Hossain, M. K.: Global Overview of Tropical Dry Forests:, Book Title: Practice, Progress, and Proficiency in Sustainability DOI: 10.4018/978-1-7998-0014-9.ch001, 1–23, <https://doi.org/10.4018/978-1-7998-0014-9.ch001>, 2020.
- 795 Hasselquist, N. J., Allen, M. F., and Santiago, L. S.: Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence, *Oecologia*, 164, 881–890, <https://doi.org/10.1007/s00442-010-1725-y>, 2010.
- Höbinger, T., Schindler, S., Seaman, B. S., Wrška, T., and Weissenhofer, A.: Impact of oil palm plantations on the structure of the agroforestry mosaic of La Gamba, southern Costa Rica: potential implications for biodiversity, *Agrofor. Syst.*, 85, 367–381, <https://doi.org/10.1007/s10457-011-9425-0>, 2012.
- Holzman, B. A.: Tropical Forest Biomes, DOI: 10.5040/9798216027669, <https://doi.org/10.5040/9798216027669>, 2008.
- 800 Huber, W. and Weissenhofer, A.: The La Gamba Research Station in Costa Rica – History, Nature and Research., in: Research at the Tropical Field Station La Gamba in Costa Rica., vol. 156, *Verl. der Zoologisch-Botanischen Ges. in Österreich*, Wien, 3–11, 2019.
- Huber, W., Weissenhofer, A., Zamora, N., and Weber, A.: Plant diversity and biogeography of the Golfo Dulce region, Costa Rica / Diversidad vegetal y biogeografía de la región de Golfo Dulce, Costa Rica, in: Natural and cultural history of the Golfo Dulce Region, Costa Rica, edited by: Weissenhofer, A., *Biologiezentrum*, Linz, 97–103, 2008.
- 805 Jiménez, L., Ramón, P., Sarango, J., Burneo, J. I., Gusmán, J., and Gusmán-Montalván, E.: Long-term grazing exclusion enhances soil carbon and nitrogen stocks in tropical dry forests of southern Ecuador, *Front. Soil Sci.*, 5, <https://doi.org/10.3389/fsoil.2025.1617798>, 2025.



- 810 Jiskra, M., Wiederhold, J. G., Skyllberg, U., Kronberg, R.-M., Hajdas, I., and Kretzschmar, R.: Mercury Deposition and Re-emission Pathways in Boreal Forest Soils Investigated with Hg Isotope Signatures, *Environ. Sci. Technol.*, 49, 7188–7196, <https://doi.org/10.1021/acs.est.5b00742>, 2015.
- 815 Jiskra, M., Sonke, J. E., Obrist, D., Bieser, J., Ebinghaus, R., Myhre, C. L., Pfaffhuber, K. A., Wängberg, I., Kyllönen, K., Worthy, D., Martin, L. G., Labuschagne, C., Mkololo, T., Ramonet, M., Magand, O., and Dommergue, A.: A vegetation control on seasonal variations in global atmospheric mercury concentrations, *Nat. Geosci.*, 11, 244–250, <https://doi.org/10.1038/s41561-018-0078-8>, 2018.
- Kearsley, E., Verbeeck, H., Stoffelen, P., Janssens, S. B., Yakusu, E. K., Kosmala, M., De Mil, T., Bauters, M., Kitima, E. R., Ndiapo, J. M., Chuda, A. L., Richardson, A. D., Wingate, L., Ilondea, B. A., Beeckman, H., van den Bulcke, J., Boeckx, P., and Hufkens, K.: Historical tree phenology data reveal the seasonal rhythms of the Congo Basin rainforest, *Plant-Environ. Interact.*, 5, e10136, <https://doi.org/10.1002/pei3.10136>, 2024.
- 820 Klock, A. M., Vogt, K. A., Vogt, D. J., Gordon, J. G., Scullion, J. J., Suntana, A. S., Mafune, K. K., Polyakov, A. Y., Gmur, S. J., and Gómez de la Rosa, C.: See the forest not the trees! Ecosystem-based assessment of response, resilience, and scope for growth of global forests, *Ecol. Indic.*, 140, 108973, <https://doi.org/10.1016/j.ecolind.2022.108973>, 2022.
- 825 Koenig, A. M., Magand, O., Laj, P., Andrade, M., Moreno, I., Velarde, F., Salvatierra, G., Gutierrez, R., Blacutt, L., Aliaga, D., Reichler, T., Sellegri, K., Laurent, O., Ramonet, M., and Dommergue, A.: Seasonal patterns of atmospheric mercury in tropical South America as inferred by a continuous total gaseous mercury record at Chacaltaya station (5240 m) in Bolivia, *Atmospheric Chem. Phys.*, 21, 3447–3472, <https://doi.org/10.5194/acp-21-3447-2021>, 2021.
- Laacouri, A., Nater, E. A., and Kolka, R. K.: Distribution and Uptake Dynamics of Mercury in Leaves of Common Deciduous Tree Species in Minnesota, U.S.A., *Environ. Sci. Technol.*, 47, 10462–10470, <https://doi.org/10.1021/es401357z>, 2013.
- 830 Larcher, W.: *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups*, Springer Science & Business Media, 540 pp., 2003.
- Lima, F. R. D., Pereira, P., Silva Junior, E. C., Vasques, I. C. F., Oliveira, J. R., Windmöller, C. C., Inda, A. V., Weindorf, D. C., Curi, N., Ribeiro, B. T., Guilherme, L. R. G., and Marques, J. J.: Geochemistry signatures of mercury in soils of the Amazon rainforest biome, *Environ. Res.*, 215, 114147, <https://doi.org/10.1016/j.envres.2022.114147>, 2022.
- 835 Lindberg, S., Bullock, R., Ebinghaus, R., Engstrom, D., Feng, X., Fitzgerald, W., Pirrone, N., Prestbo, E., and Seigneur, C.: A Synthesis of Progress and Uncertainties in Attributing the Sources of Mercury in Deposition, *AMBIO J. Hum. Environ.*, 36, 19–33, [https://doi.org/10.1579/0044-7447\(2007\)36%255B19:ASOPAU%255D2.0.CO;2](https://doi.org/10.1579/0044-7447(2007)36%255B19:ASOPAU%255D2.0.CO;2), 2007.
- Liu, Y.-R., Guo, L., Yang, Z., Xu, Z., Zhao, J., Wen, S.-H., Delgado-Baquerizo, M., and Chen, L.: Multidimensional Drivers of Mercury Distribution in Global Surface Soils: Insights from a Global Standardized Field Survey, *Environ. Sci. Technol.*, 57, 12442–12452, <https://doi.org/10.1021/acs.est.3c04313>, 2023.
- 840 Lu, Z., Wang, X., Zhang, Y., Zhang, Y.-J., Luo, K., and Sha, L.: High mercury accumulation in two subtropical evergreen forests in South China and potential determinants, *J. Environ. Manage.*, 183, 488–496, <https://doi.org/10.1016/j.jenvman.2016.08.073>, 2016.
- 845 Lucchini, R. G., Basta, P. C., Crespo-Lopez, M. E., Gastañaga, M. del C., O’Callaghan-Gordo, C., Olivero-Verbel, J., Vega, C., Moncada Barbosa, S. M., Espinal, C., Felty, Q., and Deoraj, A.: Mercury Contamination and Co-exposures in the Amazon Basin: At the Center of the Planetary Environmental Crisis, *Ann. Glob. Health*, 91, 42, <https://doi.org/10.5334/aogh.4817>, n.d.



- Ma, H., Cheng, H., Guo, F., Zhang, L., Tang, S., Yang, Z., and Peng, M.: Distribution of mercury in foliage, litter and soil profiles in forests of the Qinling Mountains, China, *Environ. Res.*, 211, 113017, <https://doi.org/10.1016/j.envres.2022.113017>, 2022.
- 850 Mainville, N., Webb, J., Lucotte, M., Davidson, R., Betancourt, O., Cueva, E., and Mergler, D.: Decrease of soil fertility and release of mercury following deforestation in the Andean Amazon, Napo River Valley, Ecuador, *Sci. Total Environ.*, 368, 88–98, <https://doi.org/10.1016/j.scitotenv.2005.09.064>, 2006.
- McLagan, D. S., Mitchell, C. P. J., Huang, H., Lei, Y. D., Cole, A. S., Steffen, A., Hung, H., and Wania, F.: A High-Precision Passive Air Sampler for Gaseous Mercury, *Environ. Sci. Technol. Lett.*, 3, 24–29, <https://doi.org/10.1021/acs.estlett.5b00319>, 2016.
- 855 Mendes, K. R., Campos, S., da Silva, L. L., Mutti, P. R., Ferreira, R. R., Medeiros, S. S., Perez-Marin, A. M., Marques, T. V., Ramos, T. M., de Lima Vieira, M. M., Oliveira, C. P., Gonçalves, W. A., Costa, G. B., Antonino, A. C. D., Menezes, R. S. C., Bezerra, B. G., and Santos e Silva, C. M.: Seasonal variation in net ecosystem CO₂ exchange of a Brazilian seasonally dry tropical forest, *Sci. Rep.*, 10, 9454, <https://doi.org/10.1038/s41598-020-66415-w>, 2020.
- 860 Millstead, L., Jayakody, H., Patel, H., Kaura, V., Petrie, P. R., Tomasetig, F., and Whitty, M.: Accelerating Automated Stomata Analysis Through Simplified Sample Collection and Imaging Techniques, *Front. Plant Sci.*, 11, <https://doi.org/10.3389/fpls.2020.580389>, 2020.
- Monaci, F. and Baroni, D.: Leaves and Tree Rings as Biomonitoring Archives of Atmospheric Mercury Deposition: An Ecophysiological Perspective, *Plants*, 14, 1275, <https://doi.org/10.3390/plants14091275>, 2025.
- 865 Montañez-S. *, A., Avella-M., A., López-Camacho, R., Montañez-S. *, A., Avella-M., A., and López-Camacho, R.: Litterfall and nutrient transfer dynamics in a successional gradient of tropical dry forest in Colombia, *Rev. Biol. Trop.*, 71, <https://doi.org/10.15517/rev.biol.trop.v71i1.52278>, 2023.
- 870 Monteiro, L. C., Vieira, L. C. G., Bernardi, J. V. E., Recktenvald, M. C. N. do N., Nery, A. F. da C., Fernandes, I. O., de Miranda, V. L., da Rocha, D. M. S., de Almeida, R., and Bastos, W. R.: Mercury distribution, bioaccumulation, and biomagnification in riparian ecosystems from a neotropical savanna floodplain, Araguaia River, central Brazil, *Environ. Res.*, 252, 118906, <https://doi.org/10.1016/j.envres.2024.118906>, 2024.
- Mora-Chacón, F., Meza-Picado, V., Chinchilla-Mora, O., Gutiérrez-Leitón, M., Mora-Chacón, F., Meza-Picado, V., Chinchilla-Mora, O., and Gutiérrez-Leitón, M.: Curvas de altura dominante e índice de sitio locales para plantaciones de Samanea saman en Liberia, Guanacaste, Costa Rica, *Rev. Cienc. Ambient.*, 56, 63–80, <https://doi.org/10.15359/rca.56/2.4>, 2022.
- 875 Morffi-Mestre, H., Ángeles-Pérez, G., Powers, J. S., Andrade, J. L., Huechacona Ruiz, A. H., May-Pat, F., Chi-May, F., and Dupuy, J. M.: Multiple Factors Influence Seasonal and Interannual Litterfall Production in a Tropical Dry Forest in Mexico, *Forests*, 11, 1241, <https://doi.org/10.3390/f11121241>, 2020.
- 880 Oliveira de Morais, T. M., Berenguer, E., Barlow, J., França, F., Lennox, G. D., Malhi, Y., Chesini Rossi, L., Maria Moraes de Seixas, M., and Ferreira, J.: Leaf-litter production in human-modified Amazonian forests following the El Niño-mediated drought and fires of 2015–2016, *For. Ecol. Manag.*, 496, 119441, <https://doi.org/10.1016/j.foreco.2021.119441>, 2021.
- Peng, H., Zhang, X., Bishop, K., Marshall, J., Nilsson, M. B., Li, C., Björn, E., and Zhu, W.: Tree Rings Mercury Controlled by Atmospheric Gaseous Elemental Mercury and Tree Physiology, *Environ. Sci. Technol.*, 58, 16833–16842, <https://doi.org/10.1021/acs.est.4c05662>, 2024.



- 885 Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., van der Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C., Aquino, S., and Cornelissen, J. H. C.: New handbook for standardised measurement of plant functional traits worldwide, *Aust. J. Bot.*, 61, 167–234, <https://doi.org/10.1071/BT12225>, 2013.
- 890 Pleijel, H., Klingberg, J., Nerentorp, M., Broberg, M. C., Nyirambangutse, B., Munthe, J., and Wallin, G.: Mercury accumulation in leaves of different plant types – the significance of tissue age and specific leaf area, *Biogeosciences*, 18, 6313–6328, <https://doi.org/10.5194/bg-18-6313-2021>, 2021.
- POORTER, H.: Larcher, W. *Physiological plant ecology*. 4th edn, *Ann. Bot.*, 93, 616–617, <https://doi.org/10.1093/aob/mch084>, 2004.
- 895 Rea, A. W., Lindberg, S. E., Scherbatskoy, T., and Keeler, G. J.: Mercury Accumulation in Foliage over Time in Two Northern Mixed-Hardwood Forests, *Water. Air. Soil Pollut.*, 133, 49–67, <https://doi.org/10.1023/A:1012919731598>, 2002.
- Reich, P. B., Uhl, C., Walters, M. B., Prugh, L., and Ellsworth, D. S.: Leaf demography and phenology in Amazonian rain forest: A census of 40 000 leaves of 23 tree species, *Ecol. Monogr.*, 74, 3–23, <https://doi.org/10.1890/02-4047>, 2004.
- Rodriguez-Pascual, M. J., Vega, C. M., Andrade, N., Fernandez, L. E., Silman, M. R., and Torrents, A.: Hg Distribution and Accumulation in Soil and Vegetation in Areas Impacted by Artisanal Gold Mining in the Southern Amazonian Region of Madre De Dios, Peru, <https://doi.org/10.2139/ssrn.4717633>, 6 February 2024.
- 900 Rowland, L., Hill, T. C., Stahl, C., Siebicke, L., Burban, B., Zaragoza-Castells, J., Ponton, S., Bonal, D., Meir, P., and Williams, M.: Evidence for strong seasonality in the carbon storage and carbon use efficiency of an Amazonian forest, *Glob. Change Biol.*, 20, 979–991, <https://doi.org/10.1111/gcb.12375>, 2014.
- 905 Ruangpanit, N.: Tropical seasonal forests in monsoon Asia: With emphasis on continental southeast Asia, 33, 31–40, https://doi.org/10.1007/978-94-011-0343-5_4, 1995.
- Rutter, A. P., Schauer, J. J., Shafer, M. M., Creswell, J. E., Olson, M. R., Robinson, M., Collins, R. M., Parman, A. M., Katzman, T. L., and Mallek, J. L.: Dry deposition of gaseous elemental mercury to plants and soils using mercury stable isotopes in a controlled environment, *Atmos. Environ.*, 45, 848–855, <https://doi.org/10.1016/j.atmosenv.2010.11.025>, 2011.
- 910 Sánchez-Azofeifa, G. A., Kalacska, M., Quesada, M., Calvo-Alvarado, J. C., Nassar, J. M., and Rodríguez, J. P.: Need for Integrated Research for a Sustainable Future in Tropical Dry Forests, *Conserv. Biol.*, 19, 285–286, https://doi.org/10.1111/j.1523-1739.2005.s01_1.x, 2005.
- Schneider, L., Fisher, J. A., Diéguez, M. C., Fostier, A.-H., Guimaraes, J. R. D., Leaner, J. J., and Mason, R.: A synthesis of mercury research in the Southern Hemisphere, part 1: Natural processes, *Ambio*, 52, 897–917, <https://doi.org/10.1007/s13280-023-01832-5>, 2023.
- 915 Selin, N. E.: Global Biogeochemical Cycling of Mercury: A Review, *Annu. Rev. Environ. Resour.*, 34, 43–63, <https://doi.org/10.1146/annurev.environ.051308.084314>, 2009.
- Silva do Nascimento, L., Abreu Pestana, I., Seidel, M., Marques da Silva Junior, J., Cherene Vaz de Oliveira, B., Ribeiro Gomes, P., Koschinsky, A., Dittmar, T., and de Rezende, C. E.: Mercury concentrations along the Amazon estuary and plume: Spatial trends and geochemical processes, *Environ. Res.*, 271, 121129, <https://doi.org/10.1016/j.envres.2025.121129>, 2025.



- Silva-Filho, E. V., Machado, W., Oliveira, R. R., Sella, S. M., and Lacerda, L. D.: Mercury deposition through litterfall in an Atlantic forest at Ilha Grande, Southeast Brazil, *Chemosphere*, 65, 2477–2484, <https://doi.org/10.1016/j.chemosphere.2006.04.053>, 2006.
- 925 Siwik, E. I. H., Campbell, L. M., and Mierle, G.: Fine-scale mercury trends in temperate deciduous tree leaves from Ontario, Canada, *Sci. Total Environ.*, 407, 6275–6279, <https://doi.org/10.1016/j.scitotenv.2009.08.044>, 2009.
- Siyum, Z. G.: Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives, *Ecol. Process.*, 9, 25, <https://doi.org/10.1186/s13717-020-00229-6>, 2020.
- 930 Souza, S. R., Veloso, M. D. M., Espírito-Santo, M. M., Silva, J. O., Sánchez-Azofeifa, A., Souza e Brito, B. G., and Fernandes, G. W.: Litterfall dynamics along a successional gradient in a Brazilian tropical dry forest, *For. Ecosyst.*, 6, 35, <https://doi.org/10.1186/s40663-019-0194-y>, 2019.
- Sprovieri, F., Pirrone, N., Ebinghaus, R., Kock, H., and Dommergue, A.: A review of worldwide atmospheric mercury measurements, *Atmospheric Chem. Phys.*, 10, 8245–8265, <https://doi.org/10.5194/acp-10-8245-2010>, 2010.
- Stamenkovic, J. and Gustin, M. S.: Nonstomatal versus Stomatal Uptake of Atmospheric Mercury, *Environ. Sci. Technol.*, 43, 1367–1372, <https://doi.org/10.1021/es801583a>, 2009.
- 935 Stivanello, S., Lai, H. R., Hill, T., and Chapman, H. M.: Discordant changes in foliar and reproductive phenology of tropical dry-forest trees under increasing temperature and decreasing wet-season rainfall, *BioRxiv Cold Spring Harb. Lab.*, <https://doi.org/10.1101/2024.03.24.585819>, 2024.
- Stork, N. E., Goosem, S., and Turton, S. M.: Australian Rainforests in a Global Context, Book Title: Living in a Dynamic Tropical Forest Landscape DOI: 10.1002/9781444300321.ch1, 4–20, <https://doi.org/10.1002/9781444300321.ch1>, 2008.
- 940 Teixeira, D. C., Lacerda, L. D., and Silva-Filho, E. V.: Mercury sequestration by rainforests: The influence of microclimate and different successional stages, *Chemosphere*, 168, 1186–1193, <https://doi.org/10.1016/j.chemosphere.2016.10.081>, 2017.
- Teixeira, D. C., Lacerda, L. D., and Silva-Filho, E. V.: Foliar mercury content from tropical trees and its correlation with physiological parameters *in situ*, *Environ. Pollut.*, 242, 1050–1057, <https://doi.org/10.1016/j.envpol.2018.07.120>, 2018.
- 945 Tiwari, R., Hegde, B., Hegde, S., Bandaru, P., Ramesh Babu, M., Somashekhara Achar, K. G., Greiser, C., Muscarella, R., Barua, D., Galbraith, D., and Gloor, E.: Contrasting Seasonal Variation of Photosynthesis in Evergreen and Deciduous Tree Species From a Tropical Forest, *Physiol. Plant.*, 177, e70410, <https://doi.org/10.1111/ppl.70410>, 2025.
- Tonin, A. M., Lima, L. S., Bambi, P., Figueiredo, M. L., Rezende, R. S., and Gonçalves, J. F.: Litterfall Chemistry Is Modulated by Wet-Dry Seasonality and Leaf Phenology of Dominant Species in the Tropics, *Front. For. Glob. Change*, 4, <https://doi.org/10.3389/ffgc.2021.666116>, 2021.
- 950 Wang, X., Bao, Z., Lin, C.-J., Yuan, W., and Feng, X.: Assessment of Global Mercury Deposition through Litterfall, *Environ. Sci. Technol.*, 50, 8548–8557, <https://doi.org/10.1021/acs.est.5b06351>, 2016.
- Wang, X., Yuan, W., Lin, C.-J., Zhang, L., Zhang, H., and Feng, X.: Climate and Vegetation As Primary Drivers for Global Mercury Storage in Surface Soil, *Environ. Sci. Technol.*, 53, 10665–10675, <https://doi.org/10.1021/acs.est.9b02386>, 2019.
- 955 Wang, X., Yuan, W., Lin, C.-J., and Feng, X.: Mercury cycling and isotopic fractionation in global forests, *Crit. Rev. Environ. Sci. Technol.*, 52, 3763–3786, <https://doi.org/10.1080/10643389.2021.1961505>, 2022.



- Werden, L. K., Alvarado J., P., Zarges, S., Calderón M., E., Schilling, E. M., Gutiérrez L., M., and Powers, J. S.: Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of degraded Vertisols, *J. Appl. Ecol.*, 55, 1019–1028, <https://doi.org/10.1111/1365-2664.12998>, 2018.
- 960 Wohlgemuth, L., Osterwalder, S., Joseph, C., Kahmen, A., Hoch, G., Alewell, C., and Jiskra, M.: A bottom-up quantification of foliar mercury uptake fluxes across Europe, *Biogeosciences*, 17, 6441–6456, <https://doi.org/10.5194/bg-17-6441-2020>, 2020.
- 965 Wohlgemuth, L., Rautio, P., Ahrends, B., Russ, A., Vesterdal, L., Waldner, P., Timmermann, V., Eickenscheidt, N., Fürst, A., Greve, M., Roskams, P., Thimonier, A., Nicolas, M., Kowalska, A., Ingerslev, M., Merilä, P., Benham, S., Iacoban, C., Hoch, G., Alewell, C., and Jiskra, M.: Physiological and climate controls on foliar mercury uptake by European tree species, *Biogeosciences*, 19, 1335–1353, <https://doi.org/10.5194/bg-19-1335-2022>, 2022.
- Wolfe, B. T., Sperry, J. S., and Kursar, T. A.: Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis, *New Phytol.*, 212, 1007–1018, <https://doi.org/10.1111/nph.14087>, 2016.
- Wood, T. E., Cavaleri, M. A., and Reed, S. C.: Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes, *Biol. Rev.*, 87, 912–927, <https://doi.org/10.1111/j.1469-185X.2012.00232.x>, 2012.
- 970 Wright, L. P., Zhang, L., and Marsik, F. J.: Overview of mercury dry deposition, litterfall, and throughfall studies, *Atmospheric Chem. Phys.*, 16, 13399–13416, <https://doi.org/10.5194/acp-16-13399-2016>, 2016.
- Xu, Z., Wang, Z., and Zhang, X.: Mapping the forest litterfall mercury deposition in China, *Sci. Total Environ.*, 839, 156288, <https://doi.org/10.1016/j.scitotenv.2022.156288>, 2022a.
- 975 Xu, Z., Chen, L., Zhang, Y., Han, G., Chen, Q., Chu, Z., Zhang, Y., Li, C., Yang, Y., and Wang, X.: Meteorological Drivers of Atmospheric Mercury Seasonality in the Temperate Northern Hemisphere, *Geophys. Res. Lett.*, 49, e2022GL100120, <https://doi.org/10.1029/2022GL100120>, 2022b.
- Yang, Y., Yanai, R. D., Driscoll, C. T., Montesdeoca, M., and Smith, K. T.: Concentrations and content of mercury in bark, wood, and leaves in hardwoods and conifers in four forested sites in the northeastern USA, *PLOS ONE*, 13, e0196293, <https://doi.org/10.1371/journal.pone.0196293>, 2018.
- 980 Yavitt, J. B., Wright, S. J., and Wieder, R. K.: Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama, *Austral Ecol.*, 29, 177–188, <https://doi.org/10.1111/j.1442-9993.2004.01334.x>, 2004.
- 985 Yuan, W., Sommar, J., Lin, C.-J., Wang, X., Li, K., Liu, Y., Zhang, H., Lu, Z., Wu, C., and Feng, X.: Stable Isotope Evidence Shows Re-emission of Elemental Mercury Vapor Occurring after Reductive Loss from Foliage, *Environ. Sci. Technol.*, 53, 651–660, <https://doi.org/10.1021/acs.est.8b04865>, 2019.
- Yuan, W., Wang, X., Lin, C.-J., Song, Q., Zhang, H., Wu, F., Liu, N., Lu, H., and Feng, X.: Deposition and Re-Emission of Atmospheric Elemental Mercury over the Tropical Forest Floor, *Environ. Sci. Technol.*, 57, 10686–10695, <https://doi.org/10.1021/acs.est.3c01222>, 2023.
- 990 Die Tropenstation La Gamba: <https://www.yumpu.com/de/document/read/4245416/die-tropenstation-la-gamba>, last access: 28 October 2025.
- Zhang, H., Yuan, W., Dong, W., and Liu, S.: Seasonal patterns of litterfall in forest ecosystem worldwide, *Ecol. Complex.*, 20, 240–247, <https://doi.org/10.1016/j.ecocom.2014.01.003>, 2014.

<https://doi.org/10.5194/egusphere-2026-1354>

Preprint. Discussion started: 26 March 2026

© Author(s) 2026. CC BY 4.0 License.



Zhou, J. and Obrist, D.: Global Mercury Assimilation by Vegetation, *Environ. Sci. Technol.*, 55, 14245–14257, <https://doi.org/10.1021/acs.est.1c03530>, 2021.

995 Zhou, J., Wang, Z., and Zhang, X.: Deposition and Fate of Mercury in Litterfall, Litter, and Soil in Coniferous and Broad-Leaved Forests, *J. Geophys. Res. Biogeosciences*, 123, 2590–2603, <https://doi.org/10.1029/2018JG004415>, 2018.

Zhou, J., Obrist, D., Dastoor, A., Jiskra, M., and Ryjkov, A.: Vegetation uptake of mercury and impacts on global cycling, *Nat. Rev. Earth Environ.*, 2, 269–284, <https://doi.org/10.1038/s43017-021-00146-y>, 2021.