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Epiphyte influence on stemflow and nutrient cycling in a subtropical mixed ombrophilous forest

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ABSTRACT

Epiphytes play a fundamental role in rainfall redistribution and nutrient fluxes, particularly through stemflow modulation. Although stemflow represents a small fraction of total precipitation compared to throughfall, it is ecohydrological as it concentrates water and solutes at the tree base. This study quantifies the influence of the epiphytes *Aechmea* sp., *Hypnum cupressiforme* Hedw., and *Campyloneurum phyllitidis* (L.) C. Presl on stemflow dynamics and nutrient cycling in a Mixed Ombrophilous Forest (Araucaria Forest) in Southern Brazil. Monitoring was conducted between July 2022 and July 2023, measuring gross precipitation, throughfall, and stemflow across thirteen host trees before and after experimental epiphyte removal. Canopy characteristics and nutrient fluxes were also analyzed and statistically evaluated. Results indicated that stemflow volume was higher in the presence of epiphytes and decreased after their removal, demonstrating that the magnitude of this hydrological effect is species-specific. The association between *C. phyllitidis* and *H. cupressiforme*, as well as the isolated presence of *H. cupressiforme*, promoted higher stemflow yields, whereas the removal of *Aechmea* sp. and *H. cupressiforme* led to a reduction in volume. Regarding nutrient dynamics, calcium (Ca^{2+}) and potassium (K) exhibited the highest mean concentrations. Following epiphyte removal, a substantial increase in the concentration of most nutrients was observed, particularly for K (exceeding 70%), while sodium (Na^{+}) was the only element to show a reduction across both study periods. It is concluded that epiphytes regulate nutrient retention in the canopy and influence forest hydrology, potentially increasing or reducing stemflow.

Keywords: araucaria forest, ecohydrology,epiphytism, nutrient flux, rainfall partitioning.

Influência de epífitas no escoamento pelo tronco e na ciclagem de nutrientes em uma floresta ombrófila mista subtropical

RESUMO

As epífitas desempenham papel fundamental na redistribuição da chuva e no fluxo de nutrientes, especialmente por meio do escoamento pelo tronco. Embora o escoamento pelo tronco represente uma pequena parcela da precipitação total quando comparado à chuva interna, ele é importante do ponto de vista eco-hidrológico, pois concentra água e solutos na base das árvores. Este estudo teve como objetivo quantificar a influência das epífitas *Aechmea* sp., *Hypnum cupressiforme* Hedw. e *Campyloneurum phyllitidis* (L.) C. Presl na dinâmica do escoamento pelo tronco e na ciclagem de nutrientes em uma Floresta Ombrófila Mista (Floresta com Araucária), no sul do Brasil. O monitoramento foi realizado entre julho de 2022 e julho de 2023, com medições de precipitação total, chuva interna e escoamento pelo tronco em treze árvores hospedeiras, antes e após a remoção experimental das epífitas. As características do dossel e os fluxos de nutrientes também foram analisados e avaliados estatisticamente. Os resultados indicaram que o volume de escoamento pelo tronco foi maior na presença de epífitas e diminuiu após sua remoção, mostrando que a intensidade desse efeito hidrológico varia conforme a espécie. A associação entre *C. phyllitidis* e *H. cupressiforme*, assim como a presença isolada de *H. cupressiforme*, resultou em maiores volumes de escoamento pelo tronco, enquanto a remoção de *Aechmea* sp. e *H. cupressiforme* levou à redução desse volume. Em relação aos nutrientes, cálcio (Ca^{2+}) e potássio (K) apresentaram as maiores concentrações médias. Após a remoção das epífitas, observou-se aumento significativo na concentração da maioria dos nutrientes, com destaque para o potássio (superior a 70%), enquanto o sódio (Na^{+}) foi o único elemento que apresentou redução nos dois períodos avaliados. Conclui-se que as epífitas regulam a retenção de nutrientes no dossel e influenciam a hidrologia da floresta, podendo aumentar ou reduzir o escoamento pelo tronco.

Palavras-chave: eco-hidrologia, epifitismo, floresta com araucária, fluxo de nutrientes, partição da precipitação.

1. INTRODUCTION

The exchange of matter and energy at the Earth's surface is altered by forest cover. Leaves, branches, bark, and epiphytes distinctly modify the quantity, spatio-temporal patterns, and concentration of precipitation reaching the soil (Van Stan II and Pypker, 2015). Consequently, the presence of epiphytes enhances the effect of canopy structure on both vertical and horizontal rainfall redistribution, diversifying nutrient pathways and modifying water availability across space and time (Mandieta-Leiva *et al.,* 2020). Generally, epiphytes reduce throughfall and stemflow while increasing interception loss (Van Stan II and Pypker, 2015; Sheng *et al.*, 2022).

Epiphytes are plants that grow upon other plants, primarily on the trunks and branches of trees and shrubs—hence their name; from the Greek epi, meaning "upon," and phyte, meaning "plant" (Granados-Sánchez *et al.*, 2003). The host tree, or "phorophyte," serves solely as a structural support without being harmed; thus, epiphytes are structurally dependent plants that do not derive nutrients directly from their hosts (Granados-Sánchez *et al.*, 2003; Krömer and Gradstein, 2016; Mandieta-Leiva *et al.,* 2020). Epiphytes can be divided into non-vascular forms (e.g., mosses and lichens), which occur worldwide, and vascular forms (e.g., orchids and bromeliads), largely confined to tropical regions (Mandieta-Leiva *et al.,* 2020).

Rainfall interception can be substantially increased by epiphytes, particularly by bryophytes and bromeliads (Mandieta-Leiva *et al.,* 2020). These groups operate through distinct ecohydrological mechanisms: while bryophytes act as biological sponges with high capillary absorption capacity, tank bromeliads function as discrete reservoirs that provide detention storage, altering the timing and magnitude of water release to the forest floor. In forests with high precipitation, non-vascular vegetation consistently influences moisture dynamics by modifying interception, storage, and evaporation processes in both canopy and understory layers (Porada *et al.*, 2018). While forest components such as stems and branches intercept rainwater, canopy water storage capacity tends to be markedly lower in forests with sparse epiphyte biomass (Ah-Peng *et al.*, 2017).

Direct quantification of the epiphyte effect on net precipitation remains under-explored. This is largely due to the challenges of canopy access and the difficulties of *in situ* interception measurements, which often involve placing epiphyte bundles in mesh bags, weighing them at regular intervals, and subsequently laboratory-drying them for comparison (Van Stan II and Pypker, 2015; Ah-Peng *et al.*, 2017; González *et al.*, 2017). Despite these challenges, previous studies highlight the role of epiphytes in rainfall partitioning and the alteration of canopy-derived stemflow reaching the soil (Pypker *et al.*, 2006; González *et al.*, 2017; Ah-Peng *et al.*, 2017; Chen *et al.*, 2019; Mandieta-Leiva *et al.,* 2020). Furthermore, epiphytes do not merely act as physical barriers; they function as active biogeochemical filters, where increased water residence time within the epiphytic biomass facilitates the leaching of organic compounds and the capture of atmospheric dry deposition, fundamentally enriching the chemical signature of stemflow. However, research evaluating the role of epiphytes in the micro-hydrological cycle, soil water distribution, and nutrient flux within Brazilian forest environments remains incipient.

Recent studies have primarily focused on the influence of the forest canopy on the chemical properties of water reaching the soil, frequently neglecting the nutrient contributions from stemflow and the forest structure itself (Sheng *et al.*, 2022; Antoine *et al.*, 2025). This research gap emphasizes the need for a comprehensive approach that considers all potential nutrient sources within the interaction between vegetation and the hydrological cycle.

The Mixed Ombrophilous Forest (MOF) is a unique subtropical ecosystem characterized by the presence of the 'Paraná Pine' (*Araucaria angustifolia*), a conifer whose distinct architecture provides a singular template for investigating epiphyte-stemflow interactions. Despite the recognized importance of epiphytes in tropical ecosystems, there is still a lack of experimental data regarding their influence on the ecohydrology of urban MOF remnants. Most studies are observational, leaving a gap in understanding how the selective removal of specific epiphytic functional groups alters water and nutrient distribution. This study addresses this gap by employing an experimental biomass removal approach to investigate how different epiphytes alter stemflow regimes and water quality. We hypothesize that: (i) epiphytic removal will lead to a species-specific reduction in stemflow (SF) efficiency; and (ii) the chemical signature of the eluted solution will shift from a biologically regulated flow to a physically driven leaching process following the removal of the epiphytic buffer. Understanding these interactions is essential for assessing the impacts of environmental disturbances on forest ecohydrology and for guiding urban forest conservation practices.

2. MATERIAL AND METHODS

2.1. Study Site

The study was conducted in a 76.6-hectare remnant of mixed rainforest within the Araucárias Municipal Natural Park (Figure 1), located in Guarapuava, Paraná State, Southern Brazil (25°21'53"–25°23'01" S; 51°17'21"–51°18'49" W). The region is characterized by a humid subtropical forest with abundant rainfall; the mean annual precipitation (1995–2026) is 1,861.0 ± 300.7 mm (IAT, 2026). According to the Köppen climate classification, the climate is Cfb-type (temperate), characterized by the absence of a distinct dry season, fresh summers, and moderate winters, with a mean annual temperature of 17.5°C (Thomaz and Vestena, 2003). Sub-zero temperatures are frequent during winter, while summer temperatures remain mild due to the regional altitude.

The Araucárias Municipal Natural Park is a Conservation Unit (CU) with a high vegetation density, hosting approximately 1,397 individuals per hectare. The flora comprises 100 woody species distributed across 73 genera and 41 botanical families. The most species-rich families include Solanaceae (12 species), Myrtaceae (9), Bignoniaceae and Fabaceae (5 each), and Asteraceae, Euphorbiaceae, Lauraceae, Rubiaceae, Rosaceae, Rutaceae, Salicaceae, and Sapindaceae (Cordeiro, 2007).

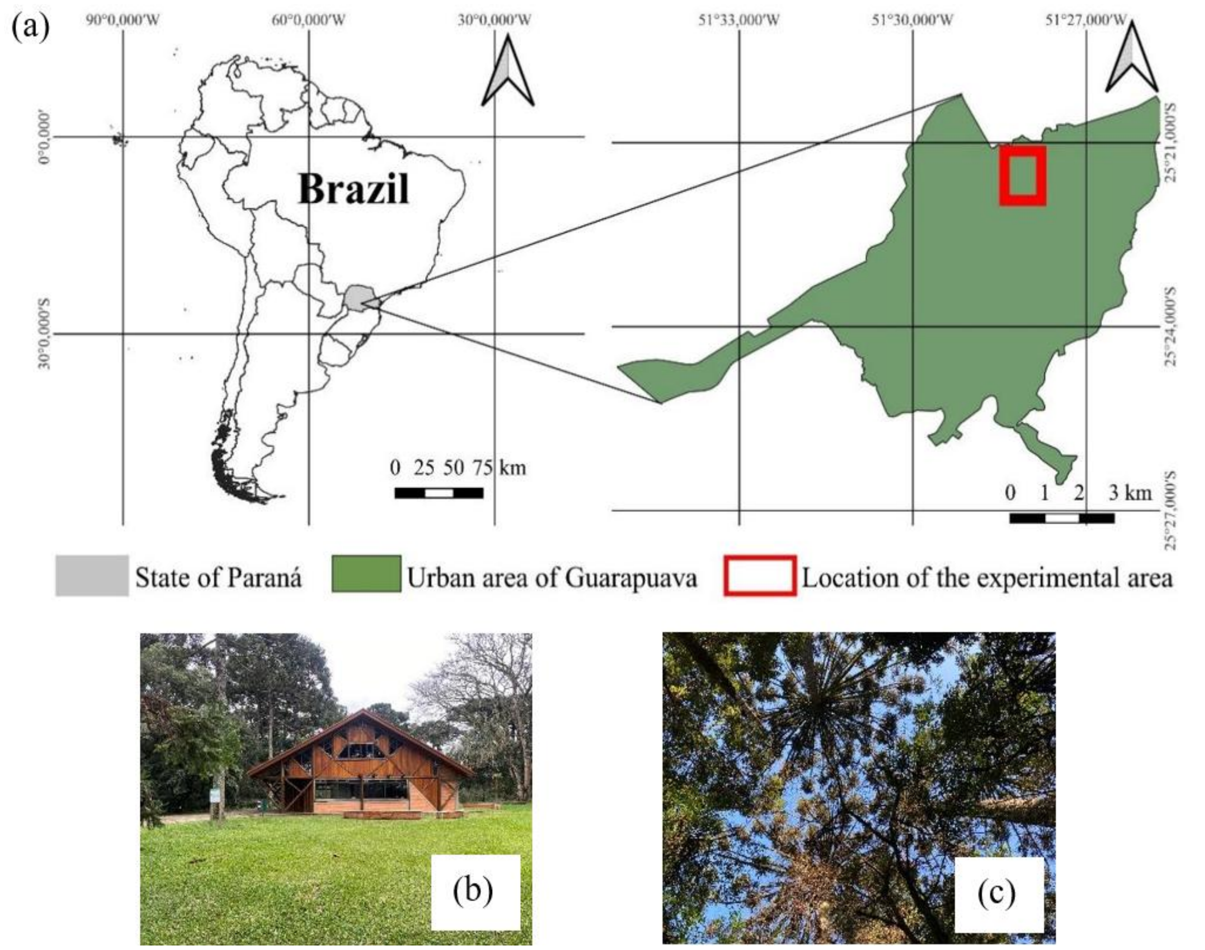

Figure 1. Geographic location of the study area in the Araucárias Municipal Natural Park, Guarapuava, Southern Brazil. The maps indicate the regional setting within the Mixed Ombrophilous Forest biome and the specific experimental plot location. (a) Environmental Education Center João Luiz Toledo (b), Diversity of the forest tree cover.

2.2. Target Species and Experimental Design

The experiment followed a completely randomized design within a 1,750 m² (50 x 35 m) plot. The study area was delineated based on the presence of dominant trees harboring epiphytic communities on their trunks, following the sampling criteria established by Pypker *et al.* (2006). González *et al.* (2017), Ah-Peng *et al.* (2017), Chen *et al.* (2019), and Mandieta-Leiva *et al.* (2020).

Three representative epiphytic species were identified in the study area: *Aechmea* sp. (Bromeliaceae), *H. cupressiform* (Hypnaceae), and *C. phyllitidis* (Polypodiaceae) - Figure 2. These species are common epiphytes in the Atlantic Forest biome, specifically within MOF formations in Southern Brazil, and were selected for their high representativeness and abundance at the study site.

Aechmea is a botanical genus within the Bromeliaceae family, subfamily Bromelioideae. Bromeliads of this genus are widely distributed across the Brazilian territory and the state of Paraná (Zimolong and Krupek, 2019). *C. phyllitidis* is characterized by a horizontal, short-creeping rhizome covered with brown, strictly oval scales (Rocha, 2008).

Hypnum cupressiforme typically grows on tree trunks, walls, rocks, and other substrates, showing a preference for acidic environments and exhibiting tolerance to pollution (Vujičić *et al.*, 2011).

(a) Aechmea sp. *(b) Campyloneurum phyllitidis* (L.) C. Presl

(c) *Hypnum cupressiforme* Hedw.

Figure 2. Target epiphytic species investigated in this study: (a) *Aechmea* sp., (b) *Hypnum cupressiforme* Hedw., and (c) *Campyloneurum phyllitidis* (L.) C. Presl.

2.3. Stemflow, Throughfall and Precipitation Monitoring

Stemflow was collected from thirteen trees selected for their representativeness of the local forest structure. These trees are widely distributed within the study area and play an ecological role in local forest dynamics. Five host species were monitored: *Sebastiania commersoniana* (Baill.) L.B.Sm. and Downs, *Ocotea porosa* (Nees and Mart.) Barroso, *Myrcia guianensis* (Aubl.) DC., *Araucaria angustifolia* (Bertol.) Kuntze, and *Casearia decandra* Jacq. The Diameter at Breast Height (DBH) of the host trees ranged from 3.25 to 11.71 cm (mean: 4.91 ± 0.65 cm), with mean canopy area and tree height of 22.89 ± 7.51 m² and 7.22 ± 0.45 m, respectively.

The study was conducted over a one-year period, divided into two distinct monitoring phases to account for seasonal variations and environmental responses. The first phase, spanning from July 2022 to January 2023, involved monitoring trees in their natural state, with both vascular and non-vascular epiphytes present on the trunks (e.g., *M. guianensis* harboring *Aechmea* sp. and *H. cupressiforme* – Figure 3). Following this period, an experimental manipulation was performed: all epiphytic biomass was removed from the trunks, and stemflow was monitored for an additional five months, from February 2023 to July 2023. This comparative "before-and-after" experimental design allowed for the isolation and evaluation of the epiphytic role in stemflow dynamics, regarding both water quantity and chemical quality.

Figure 3. Comparative view of the *M. guianensis* trunk under two experimental conditions: with the natural presence of epiphytes (*Aechmea* sp. and *H. cupressiforme* - Figure a, and following their complete removal for stemflow evaluation - Figure b.

Vascular epiphytes in this study were relocated to nearby trees, while non-vascular epiphytes were removed from the trunks and placed on the forest floor. Non-vascular epiphytes possess high self-regeneration capacity on tree trunks; thus, this procedure was adopted to ensure the conservation of epiphytic biomass either on alternative host trees or the forest floor.

Based on the sampling protocols of Johansson (1974) and González *et al.* (2017), epiphytes located up to Zone II (approximately 2 meters height) were removed from the trunks. This height was deemed sufficient to represent the dominant epiphytic influence on stemflow in the MOF while maintaining experimental feasibility.

Stemflow (SF) was collected using either spiral-type collectors (PVC hoses) or collar-type funnels, depending on the trunk size. Spiral collectors were installed on trees with a DBH greater than 30 cm, while collar funnels were used for smaller individuals. These collectors were sealed around each trunk, and the resulting stemflow was directed into 5-L storage containers. Data from high-intensity events that resulted in container overflow were excluded from the analysis to prevent underestimation of the fluxes. These overflow events were rare, occurring in only 4 out of 41 monitored events, and did not compromise the overall annual water balance. Although four extreme rainfall events were excluded from the final analysis due to collector overflow, these represented less than 10% of the total recorded events. To ensure that nutrient flux calculations remained representative, a sensitivity analysis was performed, suggesting that while these high-magnitude events contribute to total hydraulic load, the observed patterns of nutrient concentration (particularly for K^+ and Ca^{2+} were consistently driven by the antecedent dry periods and canopy contact time rather than solely by discharge volume.

Throughfall (TF) was measured using galvanized iron troughs. Troughs provide a larger sampling area and their rectangular geometry allows for more accurate TF integration in areas with varying canopy overlap (Llorens *et al.*, 1997; Rowe *et al.*, 1999). A total of six troughs (2.00 m x 0.13 m each) were distributed across the plot, each connected to a 20-L plastic container. Additionally, four manual rain gauges were installed within the plot to capture spatial variability and ensure a representative measurement of precipitation partitioning. Gross precipitation (PG) was monitored continuously by an automated weather station, which recorded total rainfall (0.2 mm resolution), air temperature, relative humidity, solar radiation, and wind speed and direction at five-minute intervals.

2.4. Stemflow Nutrient Cycling and Chemical Analysis

Stemflow samples were collected monthly from July 2022 to July 2023 for the chemical analysis of K^+, Ca^{2+}, Mg^{2+}, and Na^+, encompassing periods both with and without epiphytic cover. Samples were retrieved within 48 hours following the cessation of rainfall events, maintaining consistent collection times and locations within the experimental plot. To prevent cross-contamination, sub-samples were stored in 300-mL polyethylene bottles that had been previously decontaminated in a 5% nitric acid bath for 24 hours. Following collection, samples were immediately refrigerated and stored at 4°C (Chen *et al.*, 2019). Laboratory analyses were performed at the Trace Analysis Laboratory of the Center for Molecular Sciences and Nanotechnology at the Midwestern State University.

The enrichment ratio and Volume-Weighted Mean (VWM) concentrations were calculated to evaluate the influence of canopy and epiphytic processes on nutrient enrichment relative to gross precipitation. Enrichment ratio values > 1.0 indicate that the stemflow is enriched with nutrients compared to incident rainfall (Tonello *et al.*, 2021). To quantify nutrient input via stemflow and gross precipitation, VWM concentrations per event were calculated as follows Equation 1:

$$VWM = \frac{\sum_{n=1}^{i} Ci * Vi}{\sum_{n-1}^{i} Vi} \quad (1)$$

Where: VWM is the volume-weighted mean concentration of the ion (mg/L^{-1}), Ci is the ion concentration in stemflow or gross precipitation (mg/L^{-1}), and Vi is the corresponding volume (mm) of stemflow or gross precipitation for each sampling period (Sun *et al.*, 2021).

2.5. Statistical Analysis

The data on interception, precipitation, throughfall, and stemflow were tabulated and statistically analyzed. Descriptive statistics were calculated, including mean, median, standard deviation, standard error, and coefficient of variation. Data normality was assessed prior to statistical testing. When assumptions of normality were met, comparisons were performed using parametric tests, including Student's t-test (at a 5% significance level) and one-way analysis of variance (ANOVA), followed by Tukey's post hoc test when appropriate. Non-normally distributed data were analyzed using non-parametric approaches. Spearman's rank correlation was applied to assess relationships between stemflow volumes among the different epiphytic groups. Simple linear regression was used to evaluate relationships between variables and to develop predictive models. Nutrient data were analyzed using pairwise comparisons with Bonferroni-adjusted p-values. All statistical analyses were performed using Microsoft Excel, IBM SPSS Statistics, and SigmaPlot 14.0 (Systat Software Inc.).

3. RESULTS AND DISCUSSION

A total of 41 rainfall events were monitored during the study period, accumulating a gross precipitation of 2,078.9 mm. On average, interception loss, throughfall, and stemflow accounted for 21.5%, 78.4%, and 0.1% of the total precipitation, respectively (Table 1). These partitioning values for interception, throughfall, and stemflow are consistent with the ranges reported in previous studies for similar forest ecosystems (Suescún *et al.*, 2019; Santos *et al.*, 2022; 2023; 2024; León-Pelaéz *et al.*, 2023).

Table 1. Summary of mean rainfall partitioning components in a Mixed Ombrophilous Forest (MOF) remnant, Southern Brazil.

Year	Gross Precipitation (P_G)	Throughfall (TF)		Stemflow (SF)		Interception loss (I)	
	(mm)	(mm)	(% of P_G)	(mm)	(% of P_G)	(mm)	(% of P_G)
Total	2078.90 ±5.30	1619.90 ±4.30	78.40	1.93 ±0.0	0.10	457.10 ±1.60	21.50
Mean	159.92	124.61	-	0.15	-	35.16	-

Total mean stemflow volumes for *S. commersoniana*, *C. decandra, M. guianensis O. porosa*, and *A. angustifolia* were 1,621.1 L, 0,613, 0.555 L, 0.183 L, and 0.017 L, respectively. Regarding the cumulative stemflow volume at the Araucárias Municipal Natural Park (2,991 L), *S. commersoniana* accounted for 54.2% of the total generated flow, followed by *C. decandra* (20.5%), *M. guianensis* (18.6%), *O. porosa* (6.1%), and *A. angustifolia* (0.6%). The disproportionate stemflow volume observed in *S. commersoniana* compared to other species, such as *A. angustifolia*, suggests a highly efficient funneling mechanism. This 'phenomenon' can be attributed to its specific canopy architecture, characterized by acute branch angles that prioritize the centripetal drainage of intercepted rainfall toward the main stem. Furthermore, the smoother bark texture of *S. commersoniana* likely minimizes bark water storage capacity, allowing for rapid saturation and subsequent translation of intercepted water into stemflow. In contrast, the thick, deeply fissured bark of *A. angustifolia* acts as a important hydrological sink, where most intercepted water is stored or evaporated before reaching the base of the trunk.

When comparing periods with and without epiphytic cover (Table 2), higher stemflow rates were observed during the epiphytic phase for the analyzed trees. This increase corresponds to 30.9% of the total stemflow volume. It is important to note, however, that the total gross precipitation during the post-removal period (850.21 ± 38.50 mm) was lower than during the pre-removal phase (1,228.69 ± 31.90 mm).

Table 2. Comparative analysis of throughfall (TF) and stemflow (SF) during the pre-removal (with epiphytes) and post-removal (epiphytes removed) experimental phases.

	Gross Precipitation (P_G)	Throughfall (TF)	Stemflow (SF)	
	(mm)	(mm)	(L)	(mm)
With Epiphytes (Pre-removal phase)	1228.69	973.90	202.95 ± 6.22	1.25 ± 0.42
Without Epiphytes (Post-removal phase)	850.21	646.02	93.77 ± 4.77	0.68 ± 0.12
Total	2078.90	1619.92	296.73 ± 1.90	1.93 ± 0.58

A total of 25 rainfall events were recorded during the pre-removal phase (with epiphytes), while 16 events occurred during the post-removal phase (epiphytes removed). Despite the difference in the number of events, *S. commersoniana* consistently exhibited the highest stemflow volumes in both periods, whereas *Araucaria angustifolia* showed the lowest values. In the pre-removal phase, *S. commersoniana* recorded 52.20 L (± 0.446), while *A. angustifolia* recorded 0.434 L (± 0.54). In the post-removal phase, *S. commersoniana* yielded 14.30 L (±

0.236), and *A. angustifolia* produced 0.280 L (± 0.42).

The analysis of forest stemflow before and after epiphyte removal indicated that the presence of these plants was associated with higher stemflow volumes. It is important to emphasize that this behavior reflects the overall average of the three investigated epiphytes (*Aechmea* sp., *C. phyllitidis*, and *H. cupressiforme*) rather than individual species results. Consequently, stemflow was higher during the period when epiphytes were present on the trees compared to the subsequent period following their removal (Table 3).

Table 3. Comparative stemflow dynamics across different epiphytic groups during pre-removal (With Epiphytes) and post-removal (Without Epiphytes) phases.

Epiphyte Group	Experimental Phase	Gross Rainfall (mm)	Stemflow (L)	Stemflow (mm)
Aechmea sp. / *H. cupressiforme*	With Epiphytes	1,228.69	109.06 ± 1.089	7.60 ± 0.80
	Without Epiphytes	850.21	26.55 ± 2.65	1.63 ± 0.09
	Total	2,078.90	135,62 ± 13.08	9.23 ± 0.81
C. phyllitidis / *H. cupressiforme*	With Epiphytes	1,228.69	7.74 ± 2.674	0.09 ± 0.01
	Without Epiphytes	850.21	7.31 ± 0.895	0.12 ± 0.01
	Total	2,078.9	15.05 ± 3.543	0.21 ± 0.02
H. cupressiforme	With Epiphytes	1,228.69	86.14 ± 5.295	8.27 ± 0.60
	Without Epiphytes	850.21	59.90 ± 3.244	5.74 ± 0.34
	Total	2,078.9	146.05 ± 8.428	14.0 ± 0.94

Stemflow behavior was directly influenced by the presence of the epiphytic association *Aechmea* sp./ *H. cupressiforme* (Table 4). During the study, a 62.7% reduction in mean stemflow was observed following the removal of these epiphytes. This decrease demonstrates that the *Aechmea* sp./ *H. cupressiforme* association played a determinant role in stemflow patterns, being primarily responsible for the overall reduction in flow averages, even when the other two epiphytic groups were present.

Table 4. Statistical summary of annual mean stemflow (SF, L) according to epiphytic group.

	Standard Error (SE)	p-value (Shapiro-Wilk test)	Coefficient of Variation
Aechmea sp./ H. cupressiforme	149.53	0.19	0.71
C. phyllitidis/ H. cupressiforme	51.17	0.01	0.84
H. cupressiforme	78.40	0.80	0.52

In contrast to *Aechmea* sp./ *H. cupressiforme*, the groups *C. phyllitidis*/*H. cupressiforme* and *H. cupressiforme* (isolated) exhibited distinct dynamics (Table 4). For these groups, stemflow volumes increased 32.2% and 15.1%, respectively, after the epiphytes were removed. These results suggest a functional dynamic opposite to that observed with *Aechmea* sp.. Specifically, the removal of *C. phyllitidis* and *H. cupressiforme* led to an increase in stemflow, indicating that these epiphytes initially acted as barriers or storage sinks, whereas *Aechmea* sp. appears to have facilitated or funneled the flow toward the collectors.

The observed reduction in stemflow volume following epiphyte removal challenges the traditional view of epiphytes solely as interceptive surfaces that increase evaporative loss. Instead, our findings suggest that species such as *H. cupressiforme* and *C. phyllitidis* act as biological conduits. By capturing atmospheric moisture and directing it along the bark micro-topography, these epiphytes may effectively reduce the 'threshold' rainfall depth required to initiate stemflow, thereby enhancing localized soil moisture patches at the tree base during low-intensity events.

A difference was observed between the *C. phyllitidis* / *H. cupressiforme* and the isolated *H. cupressiforme* groups. Notably, the *C. phyllitidis* / *H. cupressiforme* association exhibited a lower stemflow volume compared to the isolated *H. cupressiforme*. When epiphytes were present on the trunks, trees harboring *H. cupressiforme* showed a remarkable 91% increase in stemflow compared to those without epiphytic cover. Interestingly, following the removal of the epiphytes, the trees previously hosting *H. cupressiforme* continued to generate a substantial 88% increase in stemflow. These results highlight not only the differences in water retention capacity between *C. phyllitidis* / *H. cupressiforme* and *H. cupressiforme* but also the persistence of enhanced stemflow patterns even after biomass removal.

The results indicate that epiphytes interfere with stemflow (Tables 4 and 5), with data following a non-normal distribution. The coefficients of variation (CV) indicate differences in stemflow variability depending on the epiphyte type. The value (CV = 0.71), referring to the *Aechmea* sp./ *H. cupressiforme* combination, shows lower variability, suggesting a more stable flow pattern. The second (CV = 0.84), for the *C. phyllitidis* / *H. cupressiforme* pair, points to greater variation. Finally, the third value (CV = 0.52), obtained for isolated *H. cupressiforme*, reveals higher dispersion, indicating that in the absence of other epiphytes, the stemflow pattern becomes more erratic.

Table 5. Spearman's rank correlation matrix between stemflow volumes of the studied epiphytic groups.

	Aechmea sp./ *H. cupressiforme*	*C. phyllitidis/H. cupressiforme*	*H. cupressiforme*
Aechmea sp./ H. cupressiforme	1.00	0.07	0.34
C. phyllitidis/ H. cupressiforme	0.07	1.00	0.80
H. cupressiforme	0.34	0.80	1.00

Correlation analysis indicated that the *Aechmea* sp./*H. cupressiforme* association showed a weak relationship with the other epiphytic groups, whereas *C. phyllitidis*/ *H. cupressiforme* and isolated *H. cupressiforme* exhibited a strong correlation. This suggests that the latter two groups follow similar interception and storage patterns.

Regarding hydrological thresholds, during the *Aechmea* sp./ *H. cupressiforme* phase, stemflow (SF) was only recorded in rainfall events exceeding 36 mm, while in the post-removal phase, the threshold dropped to 16 mm. *H. cupressiforme* generated SF during higher magnitude events in both pre-removal (≥ 40 mm) and post-removal (≥ 38 mm) periods. Conversely, *C. phyllitidis* / *H. cupressiforme* triggered SF in smaller events, starting at 11 mm (pre-removal) and 16 mm (post-removal). These distinct storage capacities suggest that while Aechmea sp. facilitates rapid release after an initial storage peak, *C. phyllitidis* and *H. cupressiforme* act as sinks, delaying SF initiation.

The host tree also influences these dynamics. While *Aechmea* sp. showed initial storage followed by rapid funneling, *H. cupressiforme* retained water for prolonged periods. *C. phyllitidis* / *H. cupressiforme* exhibited the highest retention capacity, indicating that epiphytic morphological traits and host tree conditions (such as bark rugosity) jointly govern stemflow dynamics.

3.1. Nutrient input and enrichment

Ca^{2+} showed the highest annual concentration in stemflow (Table 6), ranging from 48.65 to 171.90 mg L^{-1}. This pattern is consistent with results reported for Amazonian forests by Lima *et al.* (2026). K^+ also showed high concentrations, reaching a peak of 228 mg L^{-1}, mainly associated with *Ocotea porosa*. Similar patterns were reported in a Cerrado forest by Tonello *et al.* (2021). This species has a wide canopy (107.64 m²) and a highly rugose bark, which likely enhanced K^+ leaching and indicates that its structural traits influenced nutrient cycling dynamics.

Table 6. Volume-weighted mean (VWM) of ion concentrations in gross precipitation (P_G) and stemflow (SF) across the studied species during the pre-removal (with epiphytes) and post-removal (epiphytes removed) phases.

Nutrient concentrations (mg L⁻¹)				
		Annual	With epiphytes (Pre-removal phase)	Without epiphytes (Post-removal phase)
Ca^{2+}	P_G	7.65 ± 2.64	17.09 ± 4.67	2,47 ± 0,50
	SF	7.91 ± 2.11	8.48 ± 3.22	7,23 ± 2,86
K^+	P_G	4.45 ± 1.41	8.58 ± 2.11	2,19 ± 1,30
	SF	5.03 ± 1.95	1.81 ± 0.32	8,79 ± 3,80
Na^+	P_G	4.19 ± 0.60	4.16 ± 0.88	4,20 ± 0,90
	SF	2.38 ± 0.43	1.87 ± 0.32	2,97 ± 0,85
Mg^{2+}	P_G	1.47 ± 0.58	3.45 ± 0.97	0,38 ± 1,14
	SF	1.06 ± 0.28	0.95 ± 0.30	1,18 ± 0,53
Overall Mean P_G		4.44 ± 1,26	8.32 ± 3.13	2.31 ± 0.78
Overall Mean SF		4.09 ± 1,52	3.27 ± 1.74	5.04 ± 1.78

Mg^{2+} recorded the lowest stemflow concentrations, ranging between 3.18 and 26.00 mg L⁻¹. This result agrees with Dick *et al.* (2018), who likewise reported Mg^{2+} as the nutrient with the lowest concentration in stemflow. Despite variations among individual trees, Mg^{2+} showed a total accumulation of 121.02 mg L⁻¹ over the study period, indicating lower availability or mobility compared to Ca^{2+} and K^+. Stemflow remains a critical component for nutrient leaching, as it enhances ion availability at the soil-tree interface (Lima *et al.*, 2023).

During the pre-removal phase (with epiphytes), Ca^{2+} concentrations in stemflow were notably higher, ranging from 22.79 mg L⁻¹ to 134.96 mg L⁻¹. Additionally, Na^+ emerged as a major nutrient during this period, totaling 46.69 mg L⁻¹. These results suggest that epiphytic presence may influence interception and elution dynamics, potentially retaining and releasing nutrients differentially across precipitation events. In the post-removal phase (epiphytes removed), nutrient dynamics shifted, with K^+ becoming the dominant nutrient (21.98 to 162.21 mg L⁻¹, totaling 212.93 mg L⁻¹). Mg^{2+} consistently maintained the lowest concentrations in both periods, reflecting its low susceptibility to leaching in the stemflow pathway, regardless of epiphyte presence.

Regarding cumulative input (gross precipitation + stemflow), Ca^{2+} was the dominant nutrient, following the overall trend: $Ca^{2+} > K^+ > Na^+ > Mg^{2+}$ (Table 4). Ca^{2+} also provided the highest input during the pre-removal phase for both gross precipitation and stemflow.

The results of this study are comparable to those reported by Yang *et al.* (2024) in a mixed broadleaf forest in northeastern China, where *Tilia amaurensis* and *Quercus mongolica* were the species that contributed most to Ca^{2+} input, with values of 16.68 g tree⁻¹ and 39.75 g tree⁻¹, respectively. However, this trend shifted during the post-removal phase (epiphytes removed). In this period, stemflow exhibited higher K^+ concentrations, while Na^+ was the predominant ion in gross precipitation. The following nutrient trends were observed: $K^+ > Ca^{2+} > Na^+ > Mg^{2+}$ for stemflow and $Na^+ > Ca^{2+} > K^+ > Mg^{2+}$ for gross precipitation.

Ca^{2+} emerged as the nutrient with the highest mean annual concentration in stemflow. Nevertheless, comparing the phases with and without epiphytic cover revealed contrasting behaviors. During the pre-removal phase (with epiphytes), all nutrients showed a decline in concentration, particularly K^+ and Mg^{2+}, with reductions exceeding 70%. Conversely, following epiphyte removal, only Na^+ concentrations decreased, while K^+ levels increased by more than 70%.

Na^+ was the only nutrient to consistently decline across all periods. Given its prevalence in gross precipitation, this suggests that Na^+ is actively absorbed by branches, trunks, and epiphytes. Both Na^+ and Mg^{2+} are primarily of marine origin (Backes, 2007), and their relatively lower concentrations at the study site can be attributed to the distance from the coast. This trend was also reflected in the annual balance, characterized by reduced Na^+ and Mg^{2+} concentrations and enriched K^+ and Ca^{2+} levels.

On an annual scale, enrichment was higher in SF only for Ca^{2+} (3.2%) and K^+ (11.5%). Conversely, Na^+ and Mg^{2+} concentrations decreased by -43.0% and -27.9%, respectively. During the pre-removal phase (with epiphytes), all ions showed reduced enrichment, with declines of -50.3% (Ca^{2+}), -78.9% (K^+), -50.0% (Na^+), and -72.4% (Mg^{2+}). Following epiphyte removal, however, enrichment increased for all ions except Na^+. Data analysis was performed using the Kruskal-Wallis test, which revealed significant differences between the groups ($p < 0.001$). A post hoc test with Bonferroni correction was then applied, revealing differences primarily between the Mg^{2+} – K^+ and Mg^{2+} – Ca^{2+} groups (Figure 4).

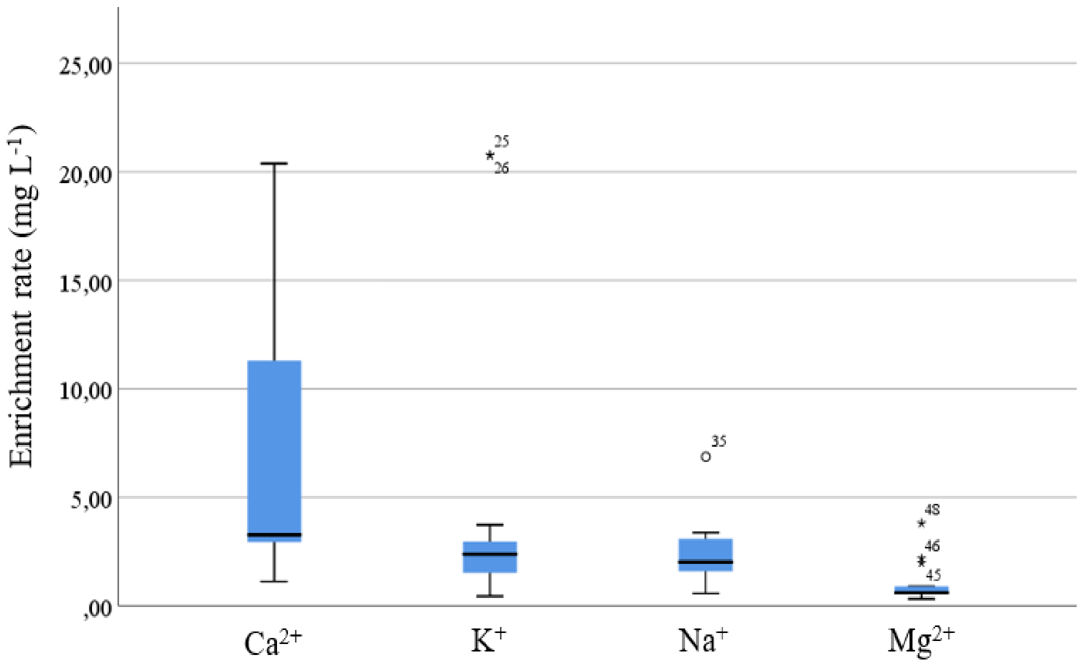

Figure 4. Enrichment rate in stemflow: a Kruskal–Wallis analysis

These findings contrast with Morais *et al.* (2021), who identified lower K^+ stocks in Lowland Dense Ombrophilous Forests in Northeastern Brazil. While those authors associated such patterns with the presence of epiphytes, our study did not reproduce this relationship in the Mixed Ombrophilous Forests (MOF) of Southern Brazil.

Our data demonstrate that interception loss (I) decreases exponentially as event volume increases, while throughfall (TF) and stemflow (SF) increase with rainfall depth. However, detailed observation reveals additional complexity; although a general upward trend exists, the relationship is non-linear, and variation in stemflow can be substantial. In other words, a high-volume rainfall event does not automatically guarantee a proportional increase in stemflow, underscoring the necessity of considering various environmental factors for a comprehensive understanding of runoff in natural systems (Levia *et al.*, 2011).

A relevant factor is that leaves with higher physical resistance tend to remain attached to the stem longer, favoring greater interception during high-intensity events. Furthermore, this type of foliage reduces the "splash effect," contributing to increased water retention by the canopy (Venkatraman, 2021). This mechanism helps clarify part of the interception losses observed in the Araucárias Municipal Natural Park. Consequently, generalizing conclusions regarding interception losses across specific forest types is inappropriate, as results are frequently conditioned by precipitation characteristics (intensity and duration) and meteorological variables, such as wind speed, air temperature, and relative humidity (Crockford and Richardson, 2000).

MOF occupy vast regions in Southern Brazil and play a fundamental role in atmospheric balance. The evaporation of large water volumes occurs from leaf surfaces, contributing to climate regulation globally (Lima and Tonello, 2023). Our results corroborate the findings of Sun *et al.* (2022), indicating that interception is sensitive to seasonal vegetation characteristics and climatic elements. The higher precipitation in July 2023 compared to July 2022 serves as an example where lower interception rates may indicate a differentiated ecosystem response to rainfall events over time-data that are vital for hydrological modeling projections.

Analysis of the annual mean stemflow in relation to precipitation highlights a direct relationship between rainfall volume and increased flow. This temporal variation reinforces the role of precipitation as a determinant factor in water redistribution within urban forests. According to some authors (Návar and Bryan, 1990; Lorenzon *et al.*, 2015), understory trees produce more stemflow than emergent trees with larger DBH, suggesting that some species have morphologically evolved to capture rainfall and direct a larger water volume toward their roots. In this study, we observed a notable absence of a uniform storage trend among species.

The *Araucaria angustifolia*, despite having a canopy area of only 8.29 m² compared to 72 m² for *O. porosa*, exhibited a high storage rate. In contrast, *O. porosa*, with its wider canopy and rugose bark, recorded a lower storage rate than *A. angustifolia*. This occurs because, besides reaching the forest floor directly, part of the precipitation may initially strike the trunks, intensifying the flow. Moura *et al.* (2009) noted that forest cover is essential to the local water balance and can alter the mechanisms of water entry into the soil surface, where the intertwining of branches among different species can intensify stemflow.

Beyond absolute volumes, the hydrological impact of epiphytes is best understood through the stemflow efficiency ratio, which normalizes the data against the variability of rainfall events across experimental phases. Our results reveal a distinct functional dichotomy between 'funnelers' and 'sinks.' The association *Aechmea* sp./ *H. cupressiforme* functioned as a hydrological facilitator; even with higher total rainfall in the pre-removal phase, the drastic 62.7% reduction in stemflow following its removal indicates that this bromeliad enhances the tree's catchment efficiency. Once the *Aechmea* sp. tanks reach their storage capacity, they trigger a rapid overflow mechanism that directs water toward the trunk, effectively bypassing the bark's initial abstraction.

In contrast, a scale-dependent 'sponge effect' was observed for the *C. phyllitidis* / *H. cupressiforme* and isolated *H. cupressiforme* groups. For these epiphytes, the removal led to an increase in SF efficiency (32.2% and 15.1%, respectively). This suggests that at the event scale, these bryophytes and ferns act as storage sinks, sequestering a high percentage of low-to-medium intensity rainfall. The persistence of high stemflow volumes (88%) in trees previously hosting *H. cupressiforme* even after removal suggests that the epiphytic cover may have altered the bark's hydraulic properties over time or that these phorophytes possess intrinsic morphological traits (e.g., preferential flow paths) that favor high SF generation regardless of biotic cover.

These findings underscore that the "scale of influence" of epiphytes on the forest water balance is species-specific. While tank epiphytes potentially increase the volume of water reaching the soil-tree interface during large events, mat-forming bryophytes act as a regulatory buffer, delaying stemflow initiation and reducing the total volume delivered to the root zone during smaller, more frequent events.

Nutrient dynamics in stemflow were directly linked to physical tree characteristics, such as bark roughness and canopy extent. Ca^{2+} and Mg^{2+} represented the extremes of the concentration gradient (highest and lowest, respectively). These results may be related to bark thickness, while K^+ concentrations are linked to storage and transport cells, such as parenchyma (Oka *et al.*, 2021). Enrichment ratios (ER) confirmed that gross precipitation (P_G) was enriched upon interaction with the forest canopy, reinforcing SF as a critical nutrient source at the soil-plant interface, consistent with previous findings (Hofhansl *et al.*, 2012; Germer *et al.*, 2012; Lima *et al.*, 2024).

While Zhao *et al.* (2023) suggest that Ca^{2+} and Mg^{2+} have low affinity with structural tissues and show little interference in canopy biological exchange, our study identified Ca^{2+} as the most leachable nutrient. This high Ca^{2+} concentration may be linked to the park's urban location near industrial areas and construction sites. As noted by Dowtin *et al.* (2021), Ca^{2+} is a primary component of concrete and asphalt, and high atmospheric concentrations are often associated with resuspended urban dust. This urban influence contrasts with more remote sites, such as those studied by Oka *et al.* (2021), where Cl^- predominated due to low anthropogenic influence, or by Morais *et al.* (2021), where high Na^+ concentrations were driven by marine aerosols.

The observed dichotomy between "funneling" and "sink" epiphytes has direct implications for the hydrochemical enrichment of the forest floor. In trees hosted by *Aechmea* sp., the rapid funneling mechanism not only increases water volume but also accelerates the transport of accumulated dry deposition and urban dust (rich in Ca^{2+}) from the canopy to the soil. This explains why Ca^{2+} concentrations were higher during the pre-removal phase; the bromeliad tanks act as "biogeochemical hotspots," capturing atmospheric particulates and releasing them in concentrated pulses when the tanks overflow.

Conversely, the "sponge effect" exerted by *H. cupressiforme* and *C. phyllitidis* during the pre-removal phase led to a notable reduction in nutrient enrichment ratios, particularly for K^+ and Mg^{2+} (reductions > 70%) - Figure 5. Because these epiphytes retain water for longer periods within their tissues, they likely promote the biotic uptake of mobile ions or physically trap solutes, preventing them from being eluted in the stemflow.

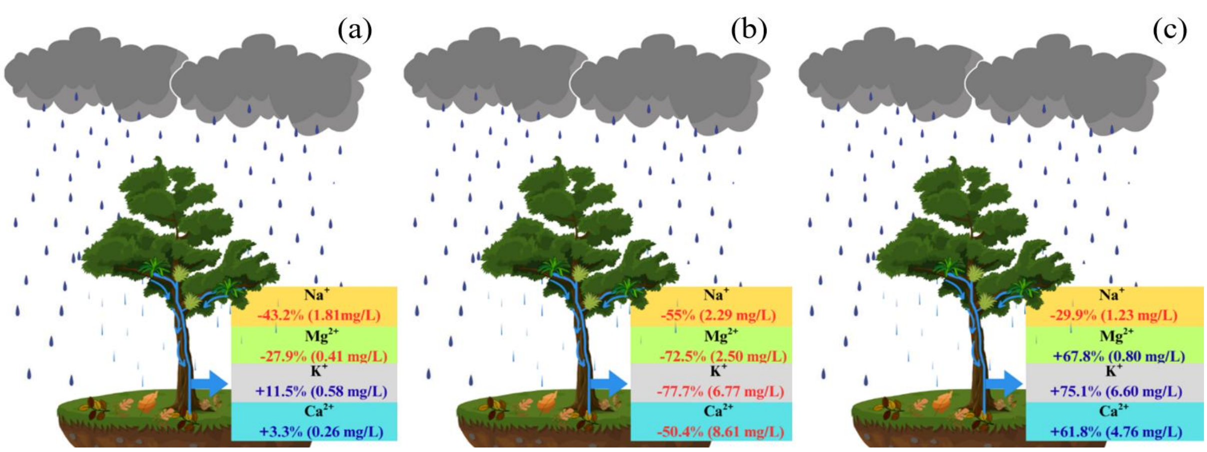

Figure 5. Effect of epiphyte removal on nutrient dynamics in stemflow in Mixed Ombrophilous Forest. (a) Annual total (period WITH epiphytes + WITHOUT epiphytes), (b) Period with epiphytes, and (c) Period without epiphytes.

Following epiphyte removal, the increase in K^+ concentrations (exceeding 70%) suggests that the bare bark becomes directly exposed to the leaching action of rainfall. Without the epiphytic "buffer," the rain interacts directly with the tree's bark parenchyma—which is rich in soluble potassium, leading to a "flushing effect" that was previously mitigated by the epiphytic biomass. This transition from a biologically regulated flow (with epiphytes) to a physically driven flow (without epiphytes) underscores the role of epiphytes as chemical regulators at the stem interface.

These results underscore the dual role of the epiphytic community as both a hydrological facilitator and a biogeochemical regulator in Subtropical MOF. The high retention of potassium within the canopy during the 'with-epiphyte' phase highlights a critical nutrient-cycling bypass, where epiphytes intercept leached solutes before they reach the forest floor. Consequently, the loss of epiphyte biomass, due to climate change or forest degradation, could lead to a decoupling of these nutrient pulses, potentially altering the spatial heterogeneity of soil fertility in Araucaria-dominated landscapes.

4. CONCLUSIONS

The investigation at the Araucárias Municipal Natural Park provided critical insights into rainfall interception, stemflow dynamics, and their interactions within the Mixed Ombrophilous Forest (MOF). Annual average results revealed an interception loss of 21.5%, throughfall of 78.4%, and stemflow of only 0.1%.

Stemflow in the MOF was higher during the pre-removal phase (with epiphytes) than in the post-removal phase, an effect primarily attributed to the *Aechmea* sp./ *H. cupressiforme* association. The removal of this group resulted in a reduction in stemflow. Conversely, the presence of *C. phyllitidis*/ *H. cupressiforme* and isolated *H. cupressiforme* led to increased stemflow upon removal. This indicates that while *C. phyllitidis* and *H. cupressiforme* act as storage sinks by intercepting and retaining water within their structures, *Aechmea* sp. serves as a facilitator, contributing to greater flow generation when present on the trunk.

Our findings suggest that once saturated, *Aechmea* sp./ *H. cupressiforme* contributes directly to increased stemflow by funneling excess water toward the trunk. This contradicts the traditional assumption that epiphyte removal would necessarily increase flow by eliminating physical barriers; in this urban MOF remnant, the opposite was observed. We demonstrated that tank epiphytes (*Aechmea* sp.) serve as facilitators that increase the volume of water delivered to the soil-tree interface.

Regarding nutrient fluxes, a clear dilution effect was identified: higher stemflow volumes were associated with lower nutrient concentrations. In the post-removal period, decreased flow volumes led to increased nutrient concentrations. Nutrient input trends during the epiphytic phase followed the order $Ca^{2+} > K^{+} > Na^{+} > Mg^{2+}$, shifting to $K^{+} > Ca^{2+} > Na^{+} > Mg^{2+}$ after removal. The transition from a biologically regulated flow (with epiphytes) to a physically driven flow (without epiphytes) underscores the role of epiphytes as chemical regulators. This understanding is fundamental for improving conservation strategies and forest management practices, particularly in predicting how biodiversity loss and changes in canopy structure may affect local hydrological cycles and soil nutrient availability under current climate change projections.

Ultimately, these results highlight the specific eco-hydrological dynamics of MOF remnants, showing that different epiphytic functional groups and host tree characteristics create unique interactions with rainfall. This understanding is fundamental for forest management and urban ecosystem planning, particularly in predicting how changes in canopy structure and biodiversity loss may impact local hydrological cycles.

5. DATA AVAILABILITY STATEMENT

Data availability not informed.

6. ACKNOWLEDGMENTS

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