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RESEARCH ARTICLE

The effects of leaf traits on litter rainfall interception with consequences for runoff and soil conservation

Pedro Henrique Medeiros Rajão¹  | Matty P. Berg^{2,3}  | Johannes H. C. Cornelissen²  | André Tavares Corrêa Dias^{1,4} 

¹Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, Brazil

²Department of Ecological Science, Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

³Conservation and Community Ecology Group, Groningen Institute for Evolutionary Life Sciences, Groningen University, Groningen, The Netherlands

⁴Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro, Brazil

Correspondence

Pedro Henrique Medeiros Rajão
Email: pedrorajao@yahoo.com.br

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Abstract

1. During rainfall, plant litter interception regulates overland flow with an impact on water runoff generation and sediment displacement. Besides the rainfall characteristics, the effects of litter mass, thickness, storage and drainage properties on rainfall interception are reasonably well understood. In contrast, less is known about the influence of leaf traits, which we hypothesized to affect interception, soil hydrology and conservation via litter structure assembly.
2. We measured the runoff and soil loss generation as determined by litter layer structural and hydraulic properties of 16 coexisting tropical woody species with wide-range morphological leaf traits in a rainfall simulator experiment.
3. Our results show that litter produced by coexisting species can differ in precipitation interception, thereby influencing runoff and soil loss. This is because there is important interspecific variation in litter water storage and drainage, which are negatively affected by leaf area (LA). Leaf water repellency positively affected litter water storage. Moreover, LA also negatively affected litter layer density. Litter density, in turn, increased runoff, but decreased soil loss, possibly due to protection against splash erosion.
4. These results can be used to predict the effects of plant traits on the soil water balance and soil integrity protection through ecohydrological interception by the litter layer. The next research steps will be to extend our model to multiple-species litter layers, and to validate and calibrate our model in different field situations in different ecosystems.
5. *Synthesis:* We revealed the direct and indirect effects of species leaf size and hydraulic traits on litter rainfall interception, runoff and soil loss. We propose a new litter-soil ecohydrological model, by using structural equation models, which can be used as a tool to predict ecosystem functioning, and guide management and restoration actions with water and soil conservation targets.

KEYWORDS

leaf litter hydrological traits, leaf litter size and shape, litter interception, rainfall interception, soil erosion, water runoff

1 | INTRODUCTION

The precipitation partitioning by vegetation is an important step in the terrestrial hydrological cycle and influences subsequent hydrological and related ecological processes. Vegetation redirects water flows, modulating water runoff and infiltration and preventing part of the precipitation from reaching the soil (Keim et al., 2005). Such effects have consequences both at local (Savenije, 2004; Yan et al., 2021) and global scales (Porada et al., 2018; van der Ent et al., 2014). To date, studies have focused mostly on understanding the effects of different vegetation types on rainfall interception (Gerrits & Savenije, 2011), but we still poorly understand the role of leaf traits of plant species in this process. Species traits are among the major drivers of ecosystem functioning (Cornwell et al., 2008; de Bello et al., 2010; Díaz & Cabido, 2001; Levine, 2016), but most of the knowledge about the effects of plant traits on ecosystem functioning is based on detailed studies of few processes (e.g. productivity, decomposition and flammability; Cornelissen et al., 2017; Cornwell et al., 2008; Reich et al., 1992). Therefore, we still do not know which plant traits control some of the other key ecosystem processes, and how they may control these processes (Dias et al., 2017). This is certainly the case for soil hydrological and erosive processes, which are strongly influenced by plant communities (Helvey & Patric, 1965; Li et al., 2014; Walsh & Voigt, 1977; Wang et al., 2020) and are related to the provisioning of important ecosystem services, like soil protection, flood prevention and recharge of underground water (Wen et al., 2019; Zhu et al., 2020).

In most terrestrial ecosystems, the litter layer acts as an important interface between the soil and the atmosphere, influencing the exchange of water and energy between these two components of the ecosystem (Pitman, 1989; Sayer, 2006). Rainfall is first intercepted by the canopy, which retains part of the precipitation. The remaining precipitation that crosses the canopy (throughfall) largely differs from rainfall in many properties, such as drop sizes, kinetic energy and timing (Keim et al., 2005). Throughfall interception by litter is a dynamic and continuous process that modifies the amount and behaviour of overland water flows (Coelho Netto, 1987; Li et al., 2021; Putuhena & Cordery, 1996). By intercepting and redirecting the precipitation, the litter layer can strongly regulate runoff and soil losses (Cerdà & Doerr, 2008; Gholami et al., 2013; Gomi et al., 2008; Li et al., 2014). This makes throughfall interception a highly relevant hydrological function of the litter layer (Bai et al., 2021; Zhu et al., 2020).

Litter interception shows large variation both between and within ecosystems, ranging from 1% to 50% of the precipitation being intercepted (Gerrits & Savenije, 2011). According to the classic deterministic model proposed by Walsh and Voigt (1977), the variation in litter interception is determined by climate, soil topography and vegetation structure and composition. For example, soil surface slope (Du et al., 2019; Li et al., 2013), rainfall characteristics, such as frequency, intensity and duration of raining events (Du et al., 2019; Guevara-Escobar et al., 2007; Li et al., 2013; Sato et al., 2004), litter layer thickness (Bai et al., 2021; Li et al., 2013; Liu et al., 2017; Sato

et al., 2004; Walsh & Voigt, 1977) and structure (Dunkerley, 2015; Ilek et al., 2015; Li et al., 2021; Park et al., 2010) can modulate litter interception. But we still do not know how species, through their traits, differentially determine litter interception and its consequences for water runoff and soil erosion.

Plant species composition determine two important hydraulic properties of the litter layer—that is, water storage capacity and lateral drainage or litter flow (Guevara-Escobar et al., 2007; Li et al., 2020; Sato et al., 2004; Walsh & Voigt, 1977). Litter water storage capacity (also called water retention in Walsh & Voigt, 1977) is the amount of water held in the litter layer, which, in the upper litter layer, is lost only by evaporation (Guevara-Escobar et al., 2007; Putuhena & Cordery, 1996). Litter flow represents the water that flows within the litter layer (Coelho Netto, 1987; Guevara-Escobar et al., 2007; Sato et al., 2004, see also Box 1 for the definition of litter flow and related concepts). The structure of the litter layer, by the combined fallen leaves, may form a temporary horizontal flow path for water within the litter layer, thereby contributing to lateral downslope litter flow during and following a rainfall event. In this way, the interaction between water storage capacity and litter flow is a key driver of surface runoff and infiltration processes (Guevara-Escobar et al., 2007; Li et al., 2013; Sato et al., 2004; Walsh & Voigt, 1977; Zhao et al., 2019) with consequences for soil loss (Li et al., 2014; Liu et al., 2017; Miyata et al., 2009).

The interest in the role of plant traits in water movements within soils is developing rapidly (Holder & Gibbes, 2017; Yan et al., 2021), but we still miss a proper identification and quantification of litter

BOX 1

The water fluxes within the litter layer have received different names in the scientific literature and their definitions often overlap in great extent. This makes it difficult to find comparative data and understand general patterns. Litter flow was defined as the water flowing mostly within the undecomposed portion of the litter, predominantly composed of leaf litter (Coelho Netto, 1987; Sato et al., 2004). Sidle et al. (2007) defined biomat flow as the water flow within the leaf litter layer, which is typically associated with the decomposing portion of the litter layer, the upper portion of the soil permeated by fine and dense roots, and the mixed horizon of well-decomposed organic materials and mineral soil. Finally, drainage flow was defined by Guevara-Escobar et al. (2007) as the water flow after the saturation of the water storage capacity of the litter layer during and after a rainfall event. Because of the large overlap in their definitions, these terms are often used in an interchangeable way. In our study we used the term litter flow because our experiment used only undecomposed leaf litter. We also refer more generally to runoff as the water that do not infiltrate in the soil running downhill.

traits that may determine specific species effects on litter interception and redistribution. Leaf size and shape have been mentioned as important traits mediating litter hydraulic properties (Dias et al., 2017; Li et al., 2013, 2021; Sato et al., 2004; Zhao et al., 2019). However, such claims are based on studies comparing few species or different vegetation types, which also differ in other properties, for example, litter layer thickness and leaf wax cover (Li et al., 2021; Sato et al., 2004; Wang et al., 2014). Additionally, leaf hydraulic traits are important determinants of canopy interception. For instance, the ability of the leaf surface to repel water (Rosado & Holder, 2013) decreases canopy storage (Wang et al., 2014; Yan et al., 2021), while the ability of the leaf surface to retain water drops (Holder, 2013; Holder & Gibbes, 2017; Wang et al., 2014) and to absorb water increases canopy storage (Cavallaro et al., 2022). The legacy of such leaf traits when they become litter to litter layer hydrological properties remains unknown.

In this paper, we revisit and advance the classical model of litter interception by adding the effect of leaf litter traits on litter hydrological properties and its consequence to runoff and soil conservation. This is a proof-of-concept study, where we used a functional approach with standardized measurements of litter effects on hydrological and erosive processes to compare 16 co-occurring tropical woody species comprising a wide range of leaf morphological and hydrological traits. We hypothesized that interspecific variation in leaf litter traits plays a key role in determining litter layer structural and hydrological properties, thereby, in turn, affecting hydrological and erosive processes (Figure 1). More specifically, we expected leaf size to have a prominent role in litter hydrological processes (Dias et al., 2017), with a larger leaf area (LA) reducing litter layer density, and, therefore, promoting horizontal flow paths for rainwater within the litter layer with a consequent increase in lateral litter flow (runoff) and reduction in storage on hillslopes. Additionally, and in line with evidence for rainfall interception by tree canopies (Holder, 2013; Holder & Gibbes, 2017), we expected leaf water repellency (Lrep), in contrast to leaf water-droplet retention (Lret) and leaf water-holding capacity (WHC), to increase lateral litter flow and decrease litter storage, with a consequent increase in soil loss. To our knowledge, this is the first quantification of leaf trait effects on litter hydrological processes. Our work is a first step in identifying

traits relevant to litter interception and its consequences for hydrologic and erosive processes. Our findings should subsequently be confronted with a wide range of conditions (e.g. slope, rainfall intensity and drop size) and more realistic natural conditions.

2 | MATERIALS AND METHODS

2.1 | Species selection and litter collection

We selected 16 woody species belonging to different families and comprising a broad range of leaf litter size, shape and hydrological traits (Table 1). To standardize across species, and because the fresh litter layer properties driven by undecomposed litter were expected to affect hydraulic properties most strongly, we hand-collected intact, virtually undecomposed leaves from the top of the litter layer at the National Park of Floresta da Tijuca, in Rio de Janeiro, Brazil (22°57' S and 43°17' W). Litter leaves were taken to the laboratory in large plastic bags with care to not compress and pack the leaves. On the same day, leaves were laid out to air-dry on a bench at room temperature.

2.2 | Leaf litter traits

We identified five key leaf traits to litter hydraulic properties according to previous evidence (Guevara-Escobar et al., 2007; Kim et al., 2014; Li et al., 2013, 2021; Sato et al., 2004; Zhao et al., 2019): LA, leaf curliness (CUR), leaf water-holding capacity (WHC), Lrep and Lret. LA and CUR (representing the degree of three-dimensional space occupied by leaves in the litter layer) are descriptors of the size and shape spectrum (SSS, Dias et al., 2017), which can affect litter layer porous structure and compaction (Burton et al., 2020; Cornelissen et al., 2017; Cornwell et al., 2015; Fujii et al., 2020) with potential effects on water storage (Liu et al., 2017; Sato et al., 2004; Walsh & Voigt, 1977) and drainage direction (Li et al., 2013; Sato et al., 2004; Sidle et al., 2007; Walsh & Voigt, 1977). Additionally, hydraulic traits indicate how leaf tissue and its surface interact with water. WHC reflects the capacity of the leaf tissue to absorb water

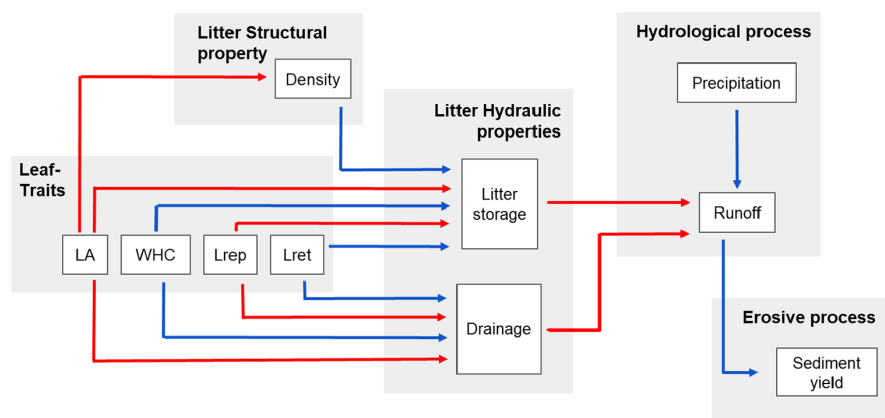


FIGURE 1 Ecohydrological model of rainwater interception by litter. Diagram shows a path model representing the hypothesis that leaf litter traits determine water runoff and erosion via shifts in litter layer hydraulic and structural properties. Red line, negative effects; blue line, positive effects.

TABLE 1 Mean and standardized deviation (SD) of leaf litter traits of 16 collected woody species.

Traits	Size and shape		Hydraulic		
	CUR (cm)	LA (cm ²)	WHC (%)	Lret (°)	Lrep (°)
<i>Alchornea triplinervia</i> (Spreng.) Müll.Arg.	3.9±0.9	35.0±13.5	77.2±26.6	56.6±19.8	86.4±14.2
<i>Artocarpus heterophyllus</i> Lam.	2.8±1.3	78.4±32.6	64.2±29.1	36.6±13.6	75.6±12.7
<i>Bambusa</i> sp. Schreb.	1.4±0.6	21.3±5.6	89.7±25.4	16.2±3.5	78.6±12.4
<i>Centrolobium tomentosum</i> Guillem. ex Benth.	1.7±0.4	33.2±15.5	61.9±23.9	24.4±4.7	90.2±18.4
<i>Eucalyptus robusta</i> Sm.	2.7±1.3	38.1±7.1	61.5±12.8	36.3±3.8	74.6±7.1
<i>Eugenia brasiliensis</i> Lam.	0.8±0.3	34.9±15.7	20.1±6.3	55.3±11.1	79.6±10.4
<i>Ficus insipida</i> Willd.	4.1±0.8	62.5±10.6	22.9±8.3	24.8±5.8	97.9±10.4
<i>Hyeronima alchorneoides</i> Allemão	3.5±1.5	39.9±18.9	75.8±8.1	32.5±7.5	101.7±9.9
<i>Inga vera</i> Willd.	1.2±0.4	73.6±26.4	61.6±9.1	37.3±15.2	91.4±15.6
<i>Joannesia princeps</i> Vell.	2.3±0.9	25.7±10.3	17.3±12.3	37.6±8.2	93.0±8.1
<i>Lafoensia glyptocarpa</i> Koehne	1.6±0.4	10.1±2.2	17.7±6.2	22.8±3.4	86.4±5.9
<i>Myrcia spectabilis</i> DC.	3.2±1.4	108.7±27.8	84.7±12.4	38.5±8.6	71.7±10.1
<i>Ophthalmoblaptan macrophyllum</i> Allemão	6.7±1.9	220.2±80.5	42.3±15.4	42.1±12.3	70.8±9.2
<i>Sterculia striata</i> A.St.-Hil. & Naudin	4.0±1.8	83.5±40.1	56.3±12.9	29.3±6.9	106.2±12.3
<i>Pleroma granulosum</i> (Desr.) D. Don	2.4±0.5	25.2±5.8	63.8±13.2	34.3±8.5	108.3±5.9
<i>Vochysia laurifolia</i> Warm.	0.9±0.4	14.7±5.3	9.8±2.6	68.9±15.2	69.2±18.9

Abbreviations: CUR, leaf curliness (cm); LA, leaf area (cm²); Lrep, leaf water repellency (°); Lret, leaf water-droplet retention (°); WHC, leaf water-holding capacity (%).

(Makkonen et al., 2013), leading to a potential increase in litter water storage capacity. Lrep and Lret reflect the capacity of the leaf surface to repel and retain water respectively (Matos & Rosado, 2016; Rosado & Holder, 2013); these traits were shown to impact canopy storage and the heterogeneity of canopy drainage (Holder, 2013).

We measured the above-mentioned traits in leaf litter using modifications of standard protocols whenever necessary. CUR of dry leaf litter was measured as the maximum height of a leaf placed on a flat surface (after Engber & Varner, 2012). Leaf curliness represents the propensity to occupy the three-dimensional space, with low values indicating flat leaves and large values indicating more curled leaves. For each species, 10 air-dried leaves were randomly selected. Each leaf was placed on a bench and turned in several positions to find all its equilibrium points. Height was measured in all equilibrium points of the leaf and the average value was considered the curliness of the leaf. For measuring LA, 10 leaves per species were wetted in plastic bags with saturated paper towels overnight, allowing them to flatten without breaking. Leaves were scanned and LA was measured using the ImageJ software (following Pérez-Harguindeguy et al., 2013). WHC was measured after 1 h of submersion, reflecting the capacity and speed of leaf tissue to absorb water (Makkonen et al., 2013; Zhou et al., 2018). Ten leaves per species were submerged in ziplock bags filled with tap water and no air for 1 h. After this, leaves were carefully surface-dried with a paper towel, weighed and placed on a bench for air-drying. WHC was calculated as the difference between dry and wet weight, expressed as a percentage of dry weight. For measuring Lrep and Lret, leaf litter was wetted in plastic bags

with a soaked paper towel for allowing them to be cut and flattened without breaking. From each leaf, a 3×3 cm strip of the central part of the leaf was cut and horizontally fixed with pins onto a styrofoam block. A 5 µL drop of distilled water was tapped on the leaf strip surface with the aid of an automatic micropipette. A digital photo from the side of the drop on the leaf surface was taken and the angle formed between the drop and the leaf surface was measured using ImageJ software. The same procedure was repeated for the abaxial and adaxial surfaces and the Lrep was calculated as the average value of both leaf surfaces (Matos & Rosado, 2016). For measuring Lret, using an automatic micropipette, a 50 µL drop of distilled water was tapped on the leaf strip surface on the styrofoam block initially in a horizontal position. The styrofoam block was inclined progressively from 0° to 90°. The angle of inclination at the moment the drop begins to move represents the measure of water retention. Lret was calculated as the average of the values of the abaxial and adaxial surfaces (Matos & Rosado, 2016).

2.3 | Rainfall simulation

Rainfall simulations were performed at the experimental unit at Fiocruz Mata Atlântica, in Rio de Janeiro (22°56' S and 43°24' W). We used a rainfall simulator consisting of a 50,000L water tank connected to a water pump that directed the flow of water with constant pressure through a 12.7 mm (PVC) pipe to a FULLJET GG-30W spray nozzle (Sprayng Systems Co.). This nozzle sprayed drops of

water of approximately 3 mm diameter, producing a full cone covering an area of about 15 m². This rainfall simulator is cheap and simple to operate (Gemlack Ngasoh et al., 2020). The input pressure was set at approximately 2.0 kPa, with the nozzle at 1.70 m in height from the flume. This setting generated uniform precipitation with an intensity between 90 and 110 mm h⁻¹. For each experimental round, the rainfall simulator was turned on for 15 min, totalling precipitation of about 25 mm.

We recognize that throughfall can show significant heterogeneity in drop size, volume and kinetic energy, and that such throughfall properties change with the species present in the canopy (Levia et al., 2017). However, we decided to use a rainfall simulator that produces a homogeneous precipitation because our main objective was to quantify species' leaf trait effects on litter interception. Standardized and homogeneous experimental conditions are better to control other sources of variation, enabling species effects to be properly quantified. A recent review on throughfall drop size distributions showed that many tree species generate throughfall median drop size ranging from 1.5 to 5.7 mm, indicating that the drop size produced by our rainfall simulator (3 mm) is within the range of natural throughfall observed beneath many tree species (Levia et al., 2017). Nevertheless, maximum values for drop size can be as high as 8 mm; such large drops should have much more erosive kinetic energy. Because of this, future studies should validate our results under these conditions, evaluating how traits effects shown here are modulated by throughfall characteristics.

We used high precipitation intensity because of its relevance to erosion processes. Therefore, under heavy precipitation plant species effects on soil hydrological fluxes and soil erosive processes should be more relevant. Additionally, short-intensity precipitation bursts are highly relevant to erosion and are more common than those usually reported because most precipitation data are aggregated to the hourly level (Dunkerley, 2019). These short and intense rainfall simulation events were able to generate runoff without exceeding the infiltration capacity of the soil, preventing other types of runoffs due to overflow, and allowing us to have replicates for our 17 experimental treatments. In this way, short and intense precipitation events allow for a better quantification of litter interception and is commonly used in simulation experiments (Guevara-Escobar et al., 2007; Sato et al., 2004; Seitz et al., 2015; Walsh & Voigt, 1977). The influence of different precipitation intensities on the effects of leaf litter traits on hydrological and erosive processes should be investigated in future studies.

2.4 | Flume

We used a flume consisting of a wooden box (60×40×10 cm, length×width×height). To prevent overflow due to soil saturation in cases of high infiltration, holes of 1.5 cm in diameter were drilled in the bottom and lower part of the walls allowing the drainage of infiltrated water. The downstream wall of the flume was 5 cm lower than the other

walls, where an aluminium gutter was placed to direct the runoff water to a plastic container. At the entrance of the plastic container, we used a filter consisting of a fine nylon cloth (0.5 mm mesh size) for retaining the coarse soil particles transported by runoff water. During rain simulations, a sediment box was placed at an inclination of 20°. This inclination was chosen because it was reported to promote downslope litter water flow without reducing litter storage capacity (Du et al., 2019).

The soil, composed mostly of clay with about 20% sand, was collected near the experimental unit at Fiocruz Mata Atlântica (22°56' S and 43°24' W). Soil macro-aggregates were broken up with a hammer and sieved (in 0.5 mm mesh size) for removing stones and coarse organic matter. For each rain simulation run, the sediment box was filled with new soil with a moisture content ranging from 11% to 14% dry weight. The soil layer was standardized to a depth of 6 cm, that is 1 cm above the level of the gutter. Before placing the air-dried leaf litter, the soil was compressed using a wooden board, with standard gentle force, covering the whole area of the flume. On top of the soil, a leaf litter layer of 4 cm was placed, filling the remaining volume of the box. The litter layer with 4 cm depth was chosen because for some large-leaf species, the litter layer formed with only one layer of leaves, or with very little overlap, down to almost 4 cm depth. Therefore, to standardize our experimental units by the litter layer volume, we chose to build litter layers with 4 cm depth for all species. For this, leaves were randomly dropped from 40 cm above the flume, mimicking the natural litter packing. We used litter of only one species each time we ran the rain simulation. We performed five replicates for each species, totalling 85 experimental rounds (16 species plus control without litter cover). A PVC plate was placed on top of the gutter, preventing water from directly entering the gutter by experimental precipitation. Three rain gauges were placed next to the flume to record the rainfall input (see Supplementary Information, Figure S1).

Each rainfall simulation lasted 15 min and we recorded the rainfall inlet in the rain gauges. After stopping the rain, we waited for all the water to drain and drip through the gutter. This took no longer than 1 min. The drained volume was then recorded using the plastic container. The sediment filter was dried at 40°C and the difference between initial and final mass was used to quantify sediment yield. The sediment yield is a measure of potential erosive processes since we did not use structured soil in our experiment.

2.5 | Litter layer properties, hydrology and soil erosion

As response variables, we measured (i) litter layer density, (ii) litter water storage capacity and (iii) time to start water runoff (drainage proxy), (iv) runoff and (v) sediment yield (potential for soil erosion). For measuring litter water storage capacity, after a rain simulation event the litter layer was carefully transferred to a plastic bag to avoid the water dripping out. Litter was immediately weighed and dried at 50°C until constant weight. Litter storage capacity was calculated as the difference between wet and dry weight and expressed in mm (volume)

and % of precipitation (coefficient). We recorded the time to start water runoff as a drainage proxy, indicating the direction of water flow within the litter. For measuring the time to start runoff, we recorded the time until the first drop appeared from the gutter after starting the simulated rain. The shorter the time, the more laterally litter flow drains the incoming rainwater. More lateral water litter flow promotes a downslope flow faster as compared to more vertical water litter flow (Bai et al., 2021; Kim et al., 2014; Sidle et al., 2007). We also measured litter layer density as the total dry litter mass divided by the litter layer volume. Water runoff was measured as the final volume drained by the gutter and was expressed in mm (volume) and % of precipitation (coefficient). Sediment yield was measured as the dry weight, in grams, of soil particles trapped in the nylon cloth filter in the plastic container.

2.6 | Data analyses and litter ecohydrological model (SEM)

All data management and statistical analyses were performed using the R language and environment with RStudio (RStudio Team, 2016).

First, we tested if water runoff and sediment yield differed in the presence and absence of litter using a Kruskal–Wallis test ($\alpha=0.05$), since these variables did not follow a normal distribution. We also tested whether there was a difference in water runoff, sediment yield, water storage and time to start runoff between litter from different species. For this, we used a Kruskal–Wallis test, followed by a posthoc Dunn test. For Kruskal–Wallis tests, we used the *PMCMR*, an R package, and for Dunn tests, we used the *FSA* package.

We used structural equation models (SEMs) to evaluate the direct and indirect effects of leaf traits on litter hydraulic and structural properties, and their consequences on water runoff and sediment yield. By using SEM, we could assess the relative importance of traits related to the SSS and hydrological traits in determining litter hydraulic properties and runoff and sediment yield.

Our SEM tested our main hypothesis that leaf traits, especially LA, directly affect litter layer structural and hydrological properties, which, in turn, affect water runoff and soil loss. More specifically, our model tested if (i) a larger litter LA favours the lateral flow of water through litter and reduces water storage in hillslopes; (ii) Lrep, in contrast to leaf water-droplet retention and leaf water-holding capacity, increases lateral litter flow and decreases litter storage which, in turn, (iii) should increase runoff with consequent enhancement in soil loss. We fitted SEM using Shipley's *d-sep* test due to our low number of replicates. For that, we used the *piecewiseSEM* R package (Lefcheck, 2016).

3 | RESULTS

3.1 | Interspecific variation in leaf litter traits

Species showed a large variation in leaf traits from the SSS (Table 1). LA varied by one order of magnitude, ranging from 10 to 220 cm². CUR varied from 0.8 to 6.7 cm and showed a high

correlation with LA ($r=0.77$; $p<0.05$). Because of this high correlation, we only used LA in further analyses. Species also showed a large variation in hydraulic leaf traits. Leaf repellency (Lrep) varied from 69.2° to 108.3°. Leaf retention (Lret) varied from 16.2° to 68.9°, while Leaf water-holding capacity (WHC) varied from 9.8% to 89.7%. Except for CUR and LA, no other trait was significantly correlated with any other (see Supplementary Information, Figure S2).

3.2 | Interspecific variation in hydraulic properties, water runoff and soil loss

Both runoff and sediment yield showed a strong difference between the control, that is, soil without litter and treatments of soil with a litter cover ($\chi^2=13.9$, $p=0.0002$; and $\chi^2=13.9$, $p=0.0002$ respectively).

We found differences in runoff between the leaf litter species ranging by one order of magnitude ($\chi^2=54.5$, $p<0.0001$; Figure 2), from 0.11 to 0.16 mm (or 0.4% to 0.6% of total rainfall) in *Vochysia* and *Lafoensia*, respectively, to 2.81 mm (11% of rainfall) in *Sterculia*. Sediment yield also showed a wide interspecific variation ($\chi^2=38.1$, $p=0.0009$; Figure 2), ranging from 0.71 g (or 2.98 g m⁻²) in litter layers from *Vochysia* to 5.67 g (or 23.8 g m⁻²) in litter layers from *Inga*.

We also found differences in hydraulic properties of litter layers between species: WHC ($\chi^2=59.7$, $p<0.0001$; Figure 2) and time to start water runoff ($\chi^2=55.5$, $p<0.0001$; Figure 2). *Lafoensia* had the largest WHC with 0.95 mm (4.0% of rainfall), while *Artocarpus* had 0.13 mm (0.5% of rainfall). *Artocarpus*, with approximately 15.2 s, was the species where water runoff started quicker, that is, the species with the most lateral litter flow. When the flume was covered with *Lafoensia* litter, runoff only started 300 s after starting the simulated rainfall, representing the lowest lateral litter flow. For more details, see Supplementary Information, Table S1.

3.3 | Ecohydrological litter interception model

We found no significant effect of initial soil moisture on runoff ($F=0.36$, $p=0.55$), sediment yield ($F=0.27$, $p=0.60$), litter storage capacity ($F=0.58$, $p=0.45$) and time to start runoff ($F=0.04$, $p=0.84$), showing that small variations in initial soil moisture between experimental runs did not affect our results. Therefore, initial soil moisture content was not included in our models.

Our original model, predicting that traits affect runoff and sediment yield only indirectly, via shifts in the litter layer properties (Figure 3), was rejected (Fisher's $C=67.213$; $p=0.005$; $df=40$). By evaluating the conditions of direct separation from our model, which were not corroborated by the data, we built an alternative model including both indirect and direct effects of leaf litter traits on water runoff and sediment yield. The alternative model showed

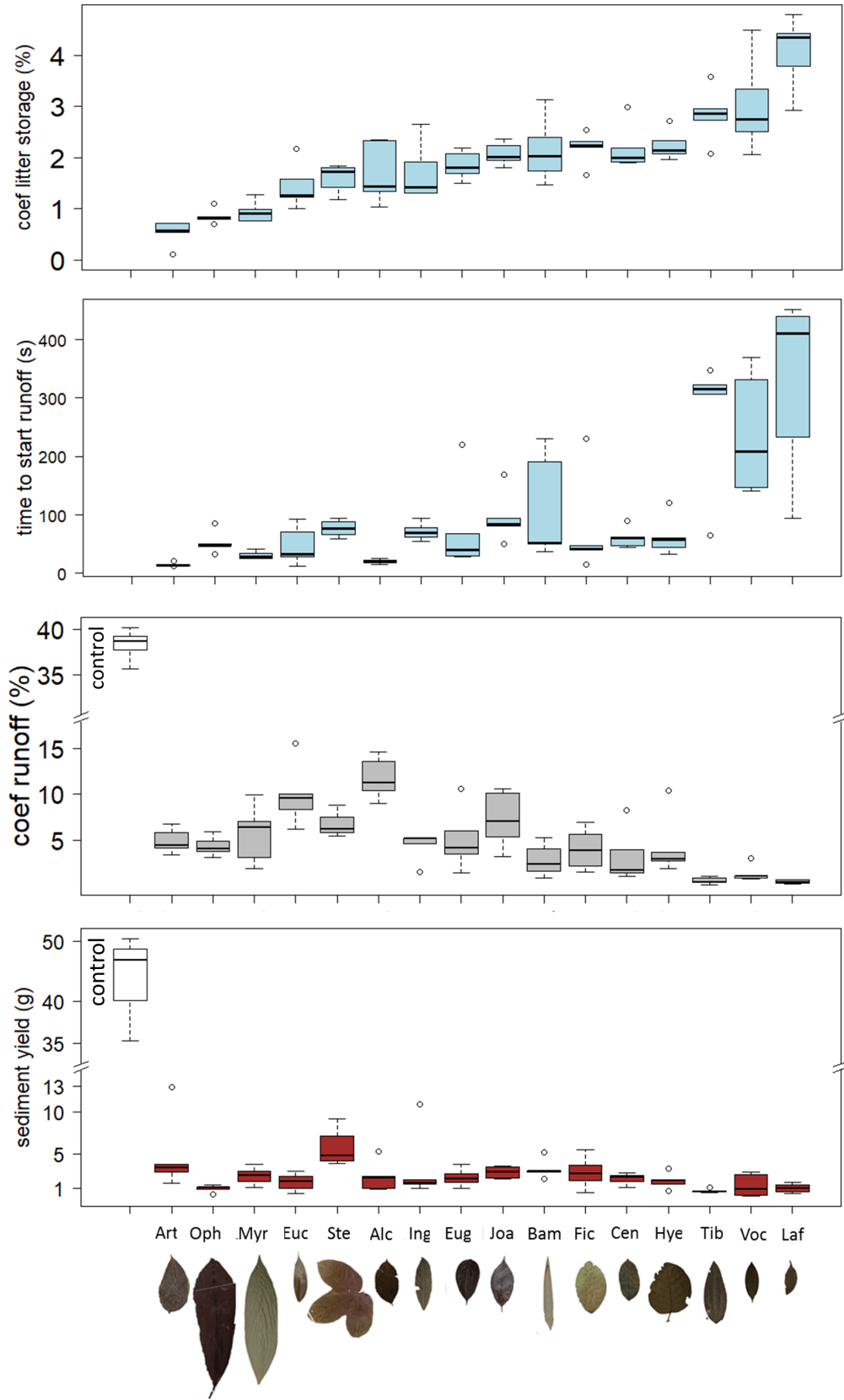


FIGURE 2 Boxplot showing litter hydraulic properties (coefficient of litter storage capacity and time to start runoff), coefficient of runoff and soil loss (sediment yield) for litter layers from 16 plant species. Coefficient of runoff (%) and sediment yield (g) were significantly different between control and all treatments of litter cover pooled together. ALC, *Alchornea triplinervia*; ART, *Artocarpus heterophyllus*; BAM, *Bambusa* sp.; CENT, *Centrolobium tomentosum*; EUC, *Eucalyptus robusta*; EUG, *Eugenia brasiliensis*; FIC, *Ficus insipida*; HYE, *Hyeronima alchorneoides*; ING, *Inga vera*; JOA, *Joannesia princeps*; LAF, *Lafoensia glyptocarpa*; MYR, *Myrcia spectabilis*; OPH, *Ophthamoblapton macrophyllum*; STER, *Sterculia striata*; TIB, *Tibouchina granulosa*; VOC, *Vochysia laurifolia*.

a good fit with the data (Fisher's $C=26.418$; $p=0.654$; $df=30$). The relationships between single traits and litter properties and hydraulic processes can be seen in Figure 4. Except for the effect of WHC on runoff (std.estimate=0.19; $p<0.05$), no other direct effects of litter traits were found. In general, the model showed that the effects of leaf litter traits on hydrology and erosion were mostly due to changes in the litter layer's structural and hydraulic properties. The model highlighted the importance of leaf traits in determining interspecific differences in species effects on soil hydrology and erosion (Figures 3 and 4): (i) leaf traits affect litter hydraulic and structural properties, where LA has negative effects on litter storage capacity (std.estimate=-0.73; $p<0.001$), Time to start runoff (std.estimate=-0.65; $p<0.001$) and litter density (std.estimate=-0.48; $p<0.001$), while Lrep has positive effects on time to start runoff (std.estimate=0.28; $p<0.001$). (ii) The litter hydraulic properties determine runoff, with negative effects of litter storage capacity (std.estimate=-0.31; $p<0.01$) and time to start runoff (std.estimate=-0.45; $p<0.001$) on runoff. Additionally, litter density showed negative effects on sediment yield (std.estimate=-0.25; $p<0.01$) and positive effects on runoff (std.estimate=0.18; $p<0.05$). In turn, (iii) runoff positively affected sediment yield (std.estimate=0.51; $p<0.001$).

4 | DISCUSSION

Litter interception is an important determinant of soil water balance and soil erosion under high rainfall intensity (Du et al., 2019; Li et al., 2013; Walsh & Voigt, 1977). Here, we showed that leaf litter from coexisting plant species can strongly differ in their litter interception with consequences for runoff and soil loss. While previous studies investigated the effects of plant traits on litter interception focusing on comparisons between contrasting vegetation types (e.g. needle- vs. broad-leaf, deciduous vs. evergreen; Guevara-Escobar et al., 2007; Li et al., 2013; Liu et al., 2017; Puthena & Cordery, 1996; Sato et al., 2004), or compared litter of a few species for their effects on hydrological properties (Jourgolami et al., 2022; Zagyvai-Kiss et al., 2019), our multi-species experiment is the first to show comprehensively how certain key leaf traits are important drivers of surface litter storage and drainage properties and of runoff and soil loss processes. These findings contribute to our understanding of the spatial variation in rainfall interception and redirection by litter, both at fine spatial scale (within a vegetation, Ilek et al., 2015; Park et al., 2010; Rosalem et al., 2019; Zhu et al., 2020) and large spatial scale (within an ecosystem; Bai et al., 2021; Du et al., 2019). In this way, our study

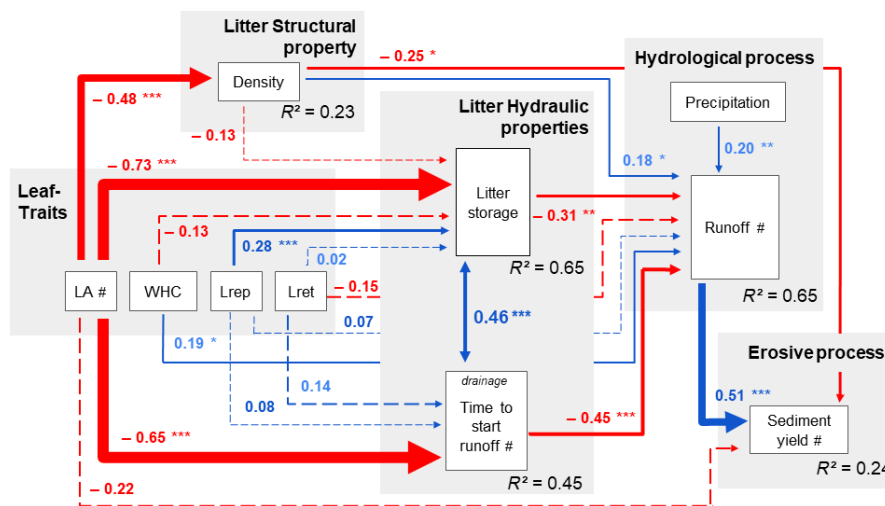


FIGURE 3 Structural equation model (SEM) showing the effects of leaf traits on structural and hydraulic properties and its consequences to runoff and soil loss (Fisher's $C=26.418$; p -value=0.654; $df=30$). Based on results from the original model (Figure 1), the (minor) direct effect of leaf traits on sediment yield is included. Path diagrams show standardized coefficients. Positive effects are depicted in blue and negative effects in red. Significant effects are represented by solid lines. The thickness of the arrow is proportional to the magnitude of the coefficient. LA: leaf area (cm^2); WHC: leaf water-holding capacity (%); Lrep: leaf water repellency ($^\circ$); Lret: leaf water-droplet retention ($^\circ$); density: litter density (kg m^{-2}); litter storage: volume of litter water storage capacity (mm); time to start runoff (s); precipitation: volume of simulated rainfall (mm); runoff (mm); soil loss as sediment yield (g) dragged through the flume. #, transformed (log) variables. ***, p -value <0.001 ; **, p -value <0.01 ; *, p -value <0.05 ; without *, p -value >0.05 .

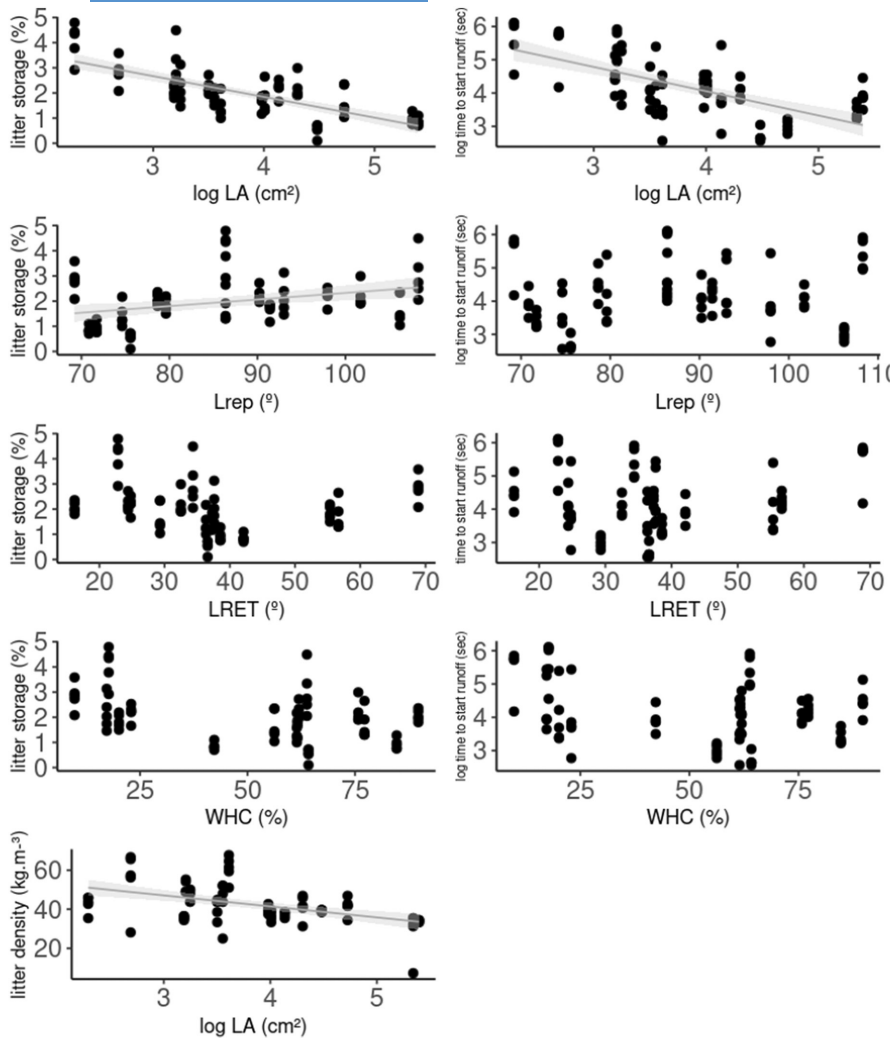


FIGURE 4 Relationships of leaf traits with litter hydraulic properties (litter storage (%) and time to start runoff [s]) and litter structural property (litter density [kg m^{-3}]) with regression line when $p < 0.05$. LA: leaf area (cm^2); Lrep: leaf water repellency ($^\circ$); Lret: leaf water droplet retention ($^\circ$); WHC: leaf water-holding capacity (%); litter density: litter density (kg m^{-3}); storage capacity: volume of litter water storage capacity (mm); time to start runoff (s).

opens new perspectives to a better understanding of the mechanisms behind the crucial role of interspecific variation in traits in soil water fluxes and soil conservation.

Our findings corroborated our main hypothesis, with leaf traits influencing the storage and flow of water through litter layers and soil erosion mostly through changes in the litter layer's structural and hydrological properties. Among the examined traits, LA showed an overruling effect, negatively influencing litter layer density and storage capacity and positively influencing lateral litter flow. Our study adds to the growing body of literature showing the importance of traits from the 'SSS' for a wide variety of ecosystem processes (Dias et al., 2017). Leaf size can influence many aspects of plant functioning, including thermoregulation, light capture strategy and hydraulic properties (Niinemets et al., 2007) and varies with climatic drivers (Moles et al., 2014; Wright et al., 2017). Although the role of leaf size for plant fitness is becoming well established (Niinemets et al., 2007), the afterlife consequences of this trait for ecosystem processes, and possible feedback to plant performance, are less understood. Leaf size and shape are major determinants of the litter layer density, which in turn, is an important driver of processes as distinct as litter fire propagation (Cornwell et al., 2015), provision of habitat for soil

fauna (Fujii et al., 2020) and erosion and runoff control as shown in this study. Future studies need to incorporate litter layer stratification as the decomposition process changes the size of litter fragments resulting in larger recently fallen leaves on the top of the litter layer and small litter fragments (of altered physico-chemical quality) on the soil surface (Fujii et al., 2020; Pitman, 1989).

Leaf traits are known to influence rainfall interception and water storage capacity of the tree canopy (Holder et al., 2020; Klamerus-Iwan et al., 2020; Rosado & Holder, 2013; Yan et al., 2021). Here, we showed that the overall role of leaf traits to precipitation partitioning is extended after leaf abscission by influencing litter hydrological properties. However, while Lrep reduces canopy storage capacity (Holder, 2013; Holder et al., 2020; Wang et al., 2014), we found the opposite effect of this trait on litter storage capacity. High Lrep (i.e. low surface wettability) promotes drops structured by water surface tension, which easily fall from the living leaves (Holder et al., 2020). When leaves are packed in a litter layer, however, the movement of structured drops can be impaired by other leaves increasing storage. These contrasting effects of Lrep on canopy and litter storage highlight the importance of integrating both canopy and litter compartments when investigating the precipitation partitioning by vegetation.

Litter water storage capacity and lateral litter flow are important litter hydrological properties determining water runoff (Kim et al., 2014; Sidle et al., 2007; Xia et al., 2019) and were expected to increase with increasing LA according to the pioneering work by Sato et al. (2004). Here, we found the opposite pattern, showing that larger leaves reduced water storage capacity, but promote larger lateral litter flow as compared to smaller leaves. These contrasting results probably lie in the fact that we worked with a set of broad-leaf species showing a wide range of LA values, while Sato et al. (2004) compared broad-leaf species to needle-leaf species. The small area of needle leaves is also accompanied by the virtual absence of a flat surface, promoting low litter storage capacity (Guevara-Escobar et al., 2007; Klamerus-Iwan et al., 2020; Li et al., 2013; Sato et al., 2004). Contrarily, in tropical forests, small leaves create denser litter layers packed with small cup-like leaves increasing litter water storage capacity. This also suggests a non-linear relationship between leaf size and litter water storage capacity in the range of small leaf-area values and illustrates the importance of new comparative studies using a large number of species to properly quantify the effects of traits on ecosystem services (Eviner & Chapin III, 2003).

Runoff is considered an important driver of soil erosion in forests (Gerke et al., 2015; Li et al., 2013; Sidle et al., 2007), therefore, the positive effect of litter layer density on runoff but negative effect on sediment yield is contradictory at first sight. This is because soil erosion is the result of multiple mechanisms acting during the interaction between soil and precipitation (Li et al., 2013; Sidle et al., 2007; Weil & Brady, 2016). Low-density litter layers often have gaps, and, therefore, are less effective in protecting soil from the direct impact of raindrops and the resulting splash erosion (Gholami et al., 2013; Li et al., 2021; Yan et al., 2021). The combination of soil particles' detachment via splash erosion and runoff are key elements contributing to increased soil loss (Campbell et al., 2004; Cerdà & Doerr, 2008; Gholami et al., 2013; Weil & Brady, 2016). Interestingly, we showed that both runoff and litter layer density were determined by LA, evidencing different mechanisms by which traits of the SSS (Cornelissen et al., 2017; Dias et al., 2017) can modulate soil conservation in forest ecosystems.

4.1 | New perspectives

Here, we have shown how species traits modulate soil hydrological and erosive processes. These findings open new perspectives for understanding the role of plant species composition in regulating soil hydrology and erosion. For this, the next important steps are to up-scale the effects of these traits from species to communities, to calibrate our predictions under contrasting experimental conditions (e.g. slope, rain intensity and drop size), and to validate our model in real ecosystems differing in species and functional trait composition, soil properties, topography and climate and incorporating canopy effects.

Based on the mass-ratio hypothesis (Grime, 1998), where a dominant trait value drives the ecosystem properties and processes, we can expect a reduction of runoff in communities with the dominance of species with small leaves. However, increased infiltration during longer and intense rainfall events may promote runoff via soil saturation mechanisms. Additionally, communities containing species showing contrasting values of LA, that is, high functional diversity of LA (Dias et al., 2013), could result in low soil erosion due to soil protection by small leaves, while presenting intermediate to high water runoff due to the promotion of downhill path water flow by large leaves. Moreover, multi-species litter layers may show non-additive diversity effects on litter layer structure (Zhao et al., 2016), giving potential deviations of ecohydrological properties compared from those predicted based on the properties of the component species. The few available studies investigating diversity effects of plant species on erosion found contrasting results (e.g. Berendse et al., 2015; Seitz et al., 2015). Considering traits identified here as relevant to runoff and erosion can help to design new experiments evaluating how functional composition influences these important ecosystem processes.

Future experiments should also test if the traits' effects found here are modulated by environmental conditions, such as slope, rain intensity and drop size. By performing similar experiments under different conditions, it should be possible to build 'effect curves', as analogue to response curves (Skelton et al., 2015), describing how trait effects change along environmental gradients. This would allow to identify the conditions under which trait effects are more relevant. Specifically, simulations with larger drop size, resulting in increased kinetic erosive energy (Levia et al., 2017), would be particularly important to evaluate the effects of litter traits on soil erosion control.

Finally, we recommend research on possible relationships between the canopy branch and leaf traits of different tree species, as possible agents of throughfall properties, and their leaf litter traits as determinants of the subsequent fate of throughfall water. A better understanding of the effects of leaf litter traits on hydrological processes at the vegetation level will enable us to propose management and restoration strategies with functional targets (Felix et al., 2023; Laughlin, 2014); and to select species composition that maximizes desirable processes, such as soil infiltration and resulting services (e.g. groundwater recharge and soil conservation). In a world where rainfall patterns are changing quickly (Carvalho, 2020), our findings will also help to better model and predict the effects of climate change on the hydrological cycle by incorporating the effects of plant traits on precipitation partitioning.

AUTHOR CONTRIBUTIONS

Pedro Henrique Medeiros Rajão, Matty P. Berg, Johannes H. C. Cornelissen and André Tavares Corrêa Dias conceived the ideas. Pedro Henrique Medeiros Rajão and André Tavares Corrêa Dias designed the methodology, collected the data, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. Johannes H. C. Cornelissen is an Associate Editor of Journal of Ecology, but took no part in the peer review and decision-making processes for this paper.


PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.xOk6djr5> (Rajão et al., 2023).

ORCID

Pedro Henrique Medeiros Rajão  <https://orcid.org/0000-0003-0113-4417>

Matty P. Berg  <https://orcid.org/0000-0001-8442-8503>

Johannes H. C. Cornelissen  <https://orcid.org/0000-0002-2346-1585>

André Tavares Corrêa Dias  <https://orcid.org/0000-0001-8847-5753>

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SUPPORTING INFORMATION

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

Figure S1. Schematic figure of the experimental setup with rainfall simulator and flume.

Figure S2. Correlation matrix of leaf traits: (a) PCA with traits of the size and shape spectrum (SSS) and hydrological traits (HT) of the litter. Each dot represents one of the 10 species. (b) Pearson's correlation matrix (r) between traits of the size and SSS and HT of the litter. Correlations with an X are those with $p > 0.05$. The darker the colour, the higher the r .

Table S1. Mean, standardized deviation (SD) and results of Dunn test's groups of soil loss (g), runoff (%), litter storage capacity (%) and time to start runoff (s).

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