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Research article

Divergent litter traits of riparian plant species between humid and drier biomes within the tropics

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Riparian forests provide abundant plant litter – mostly in the form of dead leaves (hereafter litter) – for both forest soils and adjacent stream ecosystems, supporting terrestrial and aquatic detritus-based food webs. Although the fate of litter is predominantly dependent on its chemical and physical traits, there is limited availability of data on those traits over large spatial scales or empirical comparisons of traits across tropical biomes. We filled this gap by exploring the differences and similarities of nine litter traits and their dependence on phylogenetics for 68 plant species from riparian forests across three continental-scale, South American biomes: Amazon, Atlantic Forest and Cerrado. All three biomes produced litter with similar percentages of carbon (C) and phosphorus (P), C:P mass ratios, specific leaf area and toughness. However, litter from the driest biome (Cerrado) was better defended chemically (higher phenolic content) and had lower nutritional quality (higher C:nitrogen [N] mass ratio) but showed lower nutritional limitation (lower N:P mass ratio) than litter from more humid biomes. We found no phylogenetic signal for traits after constructing a phylogenetic tree across all biomes, suggesting that trait differences across biomes were environmentally determined. However, a strong phylogenetic signal was observed for P in the Atlantic Forest, which indicates that closely related species have similar %P in that biome. Our

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findings suggest that litter from more humid biomes was higher in nitrogen, although more phosphorus-limited, than litter produced in drier climates such as that of the Cerrado biome.

Keywords: ecosystem functioning, litterfall, litter decomposition, neotropical, nutrient cycling, plant detritus

Introduction

Plant litter from riparian forests feeds heterotrophic communities of stream ecosystems, and its decomposition influences carbon and nutrient cycles in aquatic and terrestrial ecosystems (Marks 2019, Pausas and Bond 2020). This important process is controlled by a series of biological and environmental factors, but leaf litter (hereafter litter) traits are often considered the most important factors for predicting decomposition in terrestrial and aquatic ecosystems (Cornwell et al. 2008, Zhang et al. 2019). Litter traits refer to a set of intrinsic chemical and morphological attributes of litter, quantified in terms of palatability, toxicity and nutritional value for detritivorous animals and microbial decomposers (Gessner et al. 1999). This set of attributes is commonly referred to as 'litter quality', in which litter of higher quality (e.g. higher nutrient concentrations and lower phenolic and lignin contents) are generally more attractive and sustains higher activity of detritivores and decomposers than litter of lower quality (García-Palacios et al. 2015, Graça et al. 2015).

Leaf traits may indicate trade-offs between available resources, plant metabolism and plant-influenced ecosystem processes (Weiher et al. 1999, Craine et al. 2001). Several leaf traits co-vary, producing a trait spectrum: at one extreme are the traits associated with resource acquisition, and at the other are traits associated with resource maintenance (Wright et al. 2004), resulting in overall litter trait syndromes (Boyero et al. 2017). While previous studies pointed to a strong influence of edaphic factors on traits of green leaves (McGroody et al. 2004, Reich and Oleksyn 2004), some of these traits are conserved in senescent leaves (Killingbeck 1996). Climate also drives the distribution and composition of plant species across terrestrial ecosystems (Reich and Oleksyn 2004, Wright et al. 2004), resulting in a latitudinal gradient of riparian plant litter traits at a global scale, with high recalcitrance toward tropical zones (Boyero et al. 2017). This global spatial variation can influence the traits that affect forest soils and/or end up in streams (Ordoñez et al. 2009, Marks 2019). In this context, litter from the tropics tends to be tougher, more chemically defended (e.g. high phenolic content) and more P-limited (higher N:P ratio) than litter from other regions (Boyero et al. 2017). However, litter traits may also be driven by species' phylogenetic relatedness, which means closely related species are expected to be more similar in terms of litter traits than distantly related species due to the conservation of traits during the evolution of species lineages (Cadotte et al. 2017, LeRoy et al. 2020).

Riparian forests of neotropical biomes such as Amazon, Atlantic Forest and Cerrado produce large amounts of litter annually, which are subsequently decomposed in soils and streams (Tonin et al. 2017). However, the lack of a comparison of litter traits for riparian tree species from different tropical biomes has led to generalizations that tropical litter is of lower quality (García-Palacios et al. 2015, Boyero et al. 2017) despite the diversity of climates, plant species and biomes within the tropics. For example, the litter traits most relevant to carbon and food web dynamics, such as the content of nutrients in plant litter, were not comprehensively reported at the biome level. However, this information is essential to understanding ecosystem functions across and within regional scales.

We explored a dataset of litter traits – C, macronutrients (N, P and their mass ratios), and physical and chemical defenses – of the most representative litter entering streams at multiple sites across three continental-scale South American biomes: Amazon, Atlantic Forest and Cerrado. We aimed to assess the dissimilarity of litter traits from these three tropical biomes and their influences on litter decomposition. We hypothesized that 1) litter from the Amazon and Atlantic Forest biomes would be richer in nutrients than those from the Cerrado biome because the high humidity year-round in the former biomes stimulates and enhances the recycling of soil nutrients (Luizao 1989, Boeger et al. 2005, Grau et al. 2017); 2) litter from the Cerrado biome (those from riparian forests) would be more refractory (higher C:N and C:P mass ratios and with tougher tissues) than those from the Amazon and Atlantic Forest biomes due to the harsh climatic and edaphic factors for plants found in the Cerrado, such as low pH, low fertility and reduced water availability in some periods of the year (Kraus et al. 2004, Haridasan 2008, Miatto et al. 2016); 3) variations in such plant litter traits should be driven by environmental variation, not being a result of phylogenetic relatedness of species occurring in different biomes or in the same biome (Boyero et al. 2017).

Methods

Study sites

We studied riparian forests of low-order streams located inside preserved areas (1st–3rd order reaches; hereafter sites) in three South American biomes (Fig. 1): 1) Amazon (2 sites), 2) Cerrado (3 sites) and 3) Atlantic Forest (6 sites). Sites in the Amazon were located in nonflooded forests in the central and northern Amazon with equatorial climate, tall trees and evergreen canopy. Cerrado sites were located in the Brazilian Central Plateau with a tropical wet–dry climate, where streams drain through dense corridors of evergreen forests known as gallery forests. Atlantic Forest sites were located in inland and coastal areas of Brazil, spanning a large latitudinal gradient in climate (~ 30 degrees of latitude), from

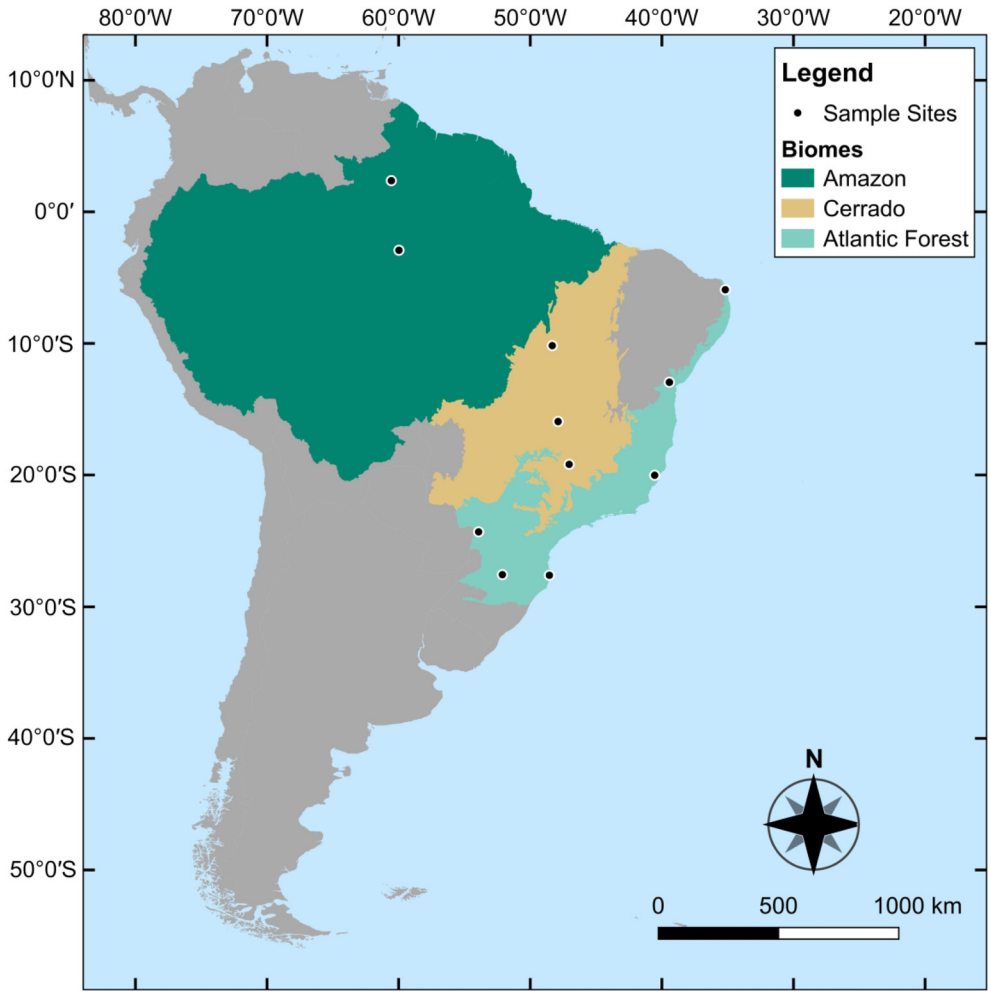

Figure 1. Location of litter collection sites at 11 riparian forests distributed across three biomes: Amazon, Atlantic Forest and Cerrado.

subtropical to equatorial, comprising tropical and subtropical rainforests, Araucaria forests and seasonal tropical forests.

The dataset analyzed comprises information from litter for 68 plant species collected across 11 riparian forests within preserved areas (reference conditions) of three neotropical biomes within the tropics: the Amazon (Cantá and Manaus), the Cerrado (Patrocínio, Brasília and Palmas) and the Atlantic Forest (Erechim, Florianópolis, Varzedo, Parnamirim, Palotina and Santa Leopoldina). We analyzed seven chemical traits (%C, %N, %P, %Phenols, C:N, C:P and N:P ratios) and two physical traits of the litter (toughness and specific leaf area).

Field sampling protocol

The sampling sites consisted of a 100 m stretch of each forest stream with the most extensive vegetation cover and without apparent anthropogenic impact. Litterfall was sampled using suspended litter traps (1 m^2, 10 mm mesh) fixed 1.5 m high on both streambanks to optimize the sampling effort. Fallen leaves were collected every 15 days to avoid leaching or decomposition. Recently fallen leaves were sampled during the period of maximum litterfall in the year, which was defined according to recent literature (Tonin et al. 2017) and/ or the expertise of local researchers. Litter was transported to the laboratory and oven-dried (60°C, 72 h) for chemical analyses; litter used to determine specific leaf area (SLA) and toughness was air-dried only. All litter samples from the same site were pooled and homogenized. Then, the litter for the 5 to 10 most representative tree species in terms of dry mass were separated and identified to the lowest possible taxonomic level.

Physical and chemical characterization of litter traits

Twenty grams of litter from each was ground in a vibratory ball mill (Fritsch Pulverisette, Model 0, Idar-Oberstein, Germany) for the chemical analyses. The C and N concentrations (% of dry mass) were analyzed by total combustion (950°C) in an elemental analyzer (Leco Instruments Ltda, Model Truspec CHN628). The P concentration was quantified spectrophotometrically (measuring absorbance at 882 nm) using the ascorbic acid method after combustion (550°C

for 4 h) and digestion (with hydrochloric acid) of litter samples (Flindt et al. 2020). Total phenols were determined using the Folin–Ciocalteau method (Bärlocher and Graça 2020). All chemical analyses were run using triplicates of 100-mg portions of litter powder from each species. Entire leaves were used for the determination of SLA and toughness. SLA, a proxy for litter toughness (that is, higher SLA values are usually found for softer litter; Boyero et al. 2017), was estimated using between 10 to 20 leaf discs (12 mm diameter) from different parts of the leaves and from different leaves of the same species. Each leaf disc was then weighed (0.01 mg) to determine its mass. SLA was obtained through the quotient of leaf disc area to leaf dry mass (in grams). Litter toughness was estimated with a penetrometer, which measures the pressure (in kgF cm^{-1}) necessary to pierce the tissue of a leaf with a steel rod (1.55-mm diameter) (Boyero et al. 2011). The litter toughness of a species was the average of 10 to 20 measurements made on different leaves.

Data analysis

We analyzed the physical and chemical litter traits of plant species from biomes using principal component analysis (PCA; 'factoextra' and 'FactoMineR' packages) on standardized data (*scale* function). To explore how litter traits differed among biomes (Amazon, Atlantic Forest and Cerrado), we calculated the nonparametric 95% confidence intervals (CI) for litter traits from each biome (based on 1000 resamples with the BCa method) using the *boot* function and package (Davison and Hinkley 1997, Canty and Ripley 2021). In addition to providing information about data variability/dispersion, CIs can express the statistical significance of tests regarding comparisons of means (Wood 2005). This technique avoids meeting the assumptions for parametric models (for example, normal distribution and homogeneity of variance) and facilitates interpretation (Carpenter and Bithell 2000, Wood 2005).

We performed a hierarchical agglomerative clustering analysis to assess trait similarity from different species across sites and biomes using a Euclidean distance matrix calculated with the average method. We used the k-means method to define the number of clusters, minimizing a criterion known as inertia or within-cluster sum-of-squares (Steinley 2006). Traits were standardized before the analysis. All analyses were performed using R ver. 4.2.1 (<www.r-project.org>).

Finally, we tested the phylogenetic signal of each litter trait to investigate whether such traits might be determined by the species' phylogenetic relationship. The phylogenetic signal has been commonly used to investigate the tendency for related species to have more similar trait values with each other than with random species drawn from a phylogenetic tree (Blomberg and Garland 2002). Therefore, we used the most complete dated mega-tree (i.e. GBOTB.extended.tre) available as a backbone to generate the phylogenetic relationships for the 62 species of our dataset using the R package 'V.Phylomaker' (Jin and Qian 2019) (Supporting information). We also reconstructed phylogenetic trees separately for each biome (Amazon, Atlantic Forest and Cerrado). The mega-tree found in GBOTB.extended.tre is a combination of GBOTB (GenBank taxa with a backbone provided by Open Tree of Life) for seed plants (Smith and Brown 2018) and the pteridophyte clade of phylogeny found in Zanne et al. (2014). This mega-tree includes 74 533 species of vascular plants from 479 families. The *phylo.maker* function generates phylogenetic hypotheses under three scenarios depending on how the new tips are bonded to nodes. Here, we used scenario 1, in which a new tip is bonded to the genus basal node (details in Jin and Qian 2019). To maximize species match, we checked our species list and standardized the spelling and nomenclature of species with GBOTB.extended.tre tips. We determined the presence of a phylogenetic signal (i.e. a significant result) and quantified the strength of the phylogenetic signal (i.e. the effect size, Nakagawa and Cuthill 2007) of litter traits using Pagel's λ in the R package 'phytools' (Revell 2012). We calculated the Pagel's λ index for all species and for each biome (Amazon, Atlantic Forest and Cerrado). Pagel's λ indicates the correlation between species traits and phylogeny. Under a Brownian motion model (BM), species traits diverge from their ancestors at a continuous rate and randomly throughout the evolution time (Felsenstein 1985); Pagel's λ is expected to be equal to 1 (strongly influenced by phylogeny), whereas values of 0 imply phylogenetic independence (Pagel 1999). However, Pagel's λ can also adopt values > 1 in cases in which traits are more similar than predicted by BM (Freckleton et al. 2002).

Results

Sixty-one percent of the variability in litter traits was retained in the first two components of the PCA (33% of PC1 and 28% of PC2, Fig. 2). The C:N mass ratio (r = 0.91), phenols (r = 0.62) and toughness (r = 0.59) were positively correlated with PC1, while N (r = −0.92) and SLA (r = 0.82) were negatively correlated with PC1 (Fig. 2). C:P (r = 0.94) and N:P (r = 0.76) mass ratios were positively correlated with PC2, while P (r = −0.20) was negatively correlated with PC2. Litter from the Amazon tended to be positively associated with N, C:P, N:P and SLA; litter from the Cerrado tended to be positively associated with C, P, C:N, phenols and toughness, while litter from the Atlantic Forest presented much greater variability than litter from other biomes and tended to be positively associated with several traits (Fig. 2).

When we analyzed each litter trait individually, we found that the litter samples from the three biomes had similar concentrations of C and P, C:P mass ratio, SLA and toughness, as supported by confidence intervals (Fig. 3A, C, E, H). However, litter from the Amazon and the Atlantic Forest showed 87% more N and higher N:P mass ratios than litter from the Cerrado (1.21–177, 14.2–48.3 confidence intervals; 1.17–1.54, 20–40; 0.81–1.05, 12.6–18.7, respectively)

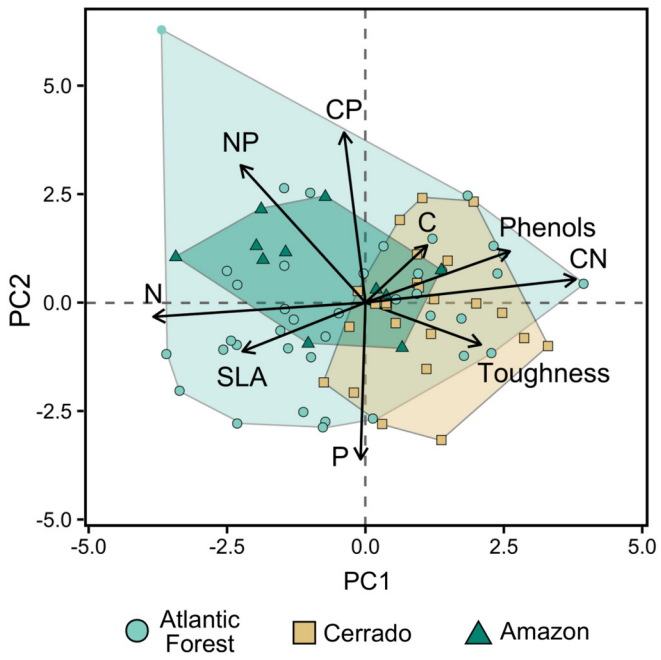

Figure 2. Principal component analysis (PCA) of litter traits (nitrogen (N); phosphorus (P) and carbon (C) and phenol concentrations; N:P, C:N, C:P ratios; toughness and specific leaf area (SLA)) and plant species litter from Amazon, Atlantic Forest and Cerrado.

(Fig. 3B, F), suggesting a higher P limitation in the former and in the most humid biomes (N:P mass ratio > 16; Fig. 3F). We found a higher C:N mass ratio and phenolic content in litter from the Cerrado (51.3–65.8, 30.5–45.0) than in litter from the Amazon (32–48, 12–23) and the Atlantic Forest (32–47, 14–22) (Fig. 3D, G).

The cluster analysis with the 62 species from different sites across biomes aggregated the species into five groups, which were related to different litter traits. The first group (red color in Fig. 4) was related to high N:P and C:P ratios and was composed of only one species from the Atlantic Forest (*Myrceugenia miersiana*) The second group (yellow color) was related to high SLA values and was composed of one species from the Cerrado (*Copaifera langsdorffii*). The third group (green color) was related to high P content and was composed of five species from the Atlantic Forest and three species from the Cerrado. The fourth group (blue color) was associated with high values of N, toughness and C:N ratio and was composed of two species from the Amazon Forest, seven species from the Atlantic Forest and 27 species from the Cerrado. Finally, the fifth group (pink color) was related to low phenolic and C contents and was composed of six tree species from the Amazon Forest and 16 species from the Atlantic Forest (Fig. 4).

No phylogenetic signals were found for most traits using the reconstructed tree for all three biomes or using one separate tree for each biome. However, P showed a strong

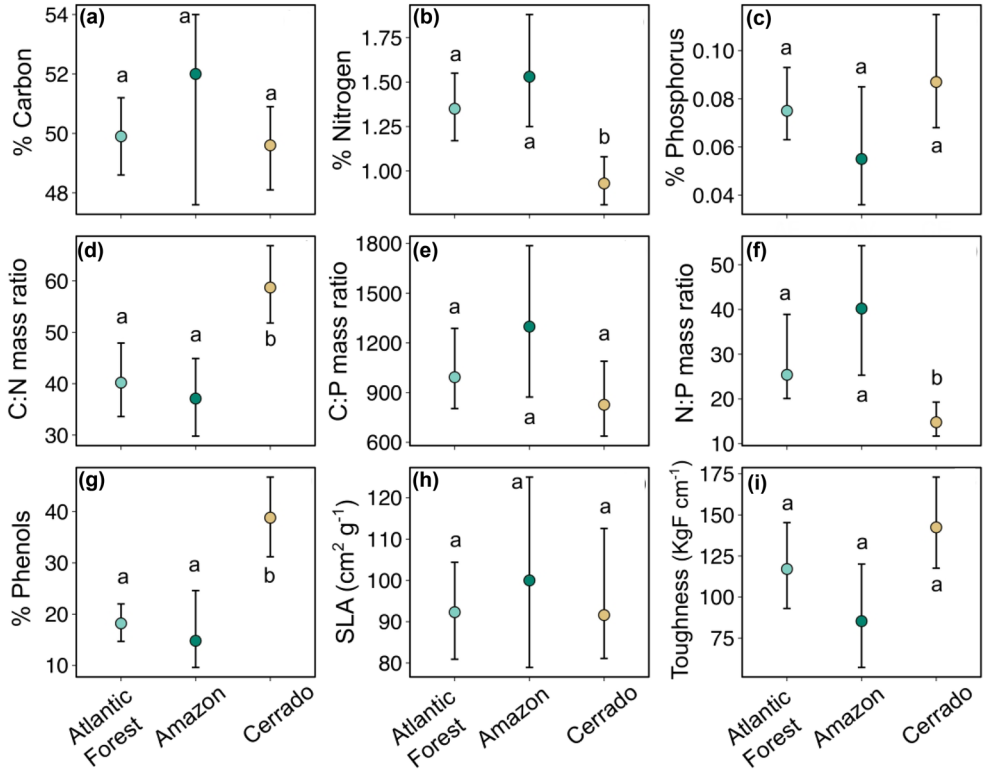

Figure 3. Concentration of (a) carbon (C); (b) nitrogen (N); (c) phosphorus (P); (d) N:P mass ratio; (e) C:N mass ratio; (f) C:P mass ratio; (g) specific leaf area; (h) toughness; and (i) phenolic concentration of litters from Amazon, Atlantic Forest and Cerrado. The circles are the means of different species and the vertical lines denote the upper and lower limits of 95% confidence intervals. Different letters indicate statistically significant differences among biomes.

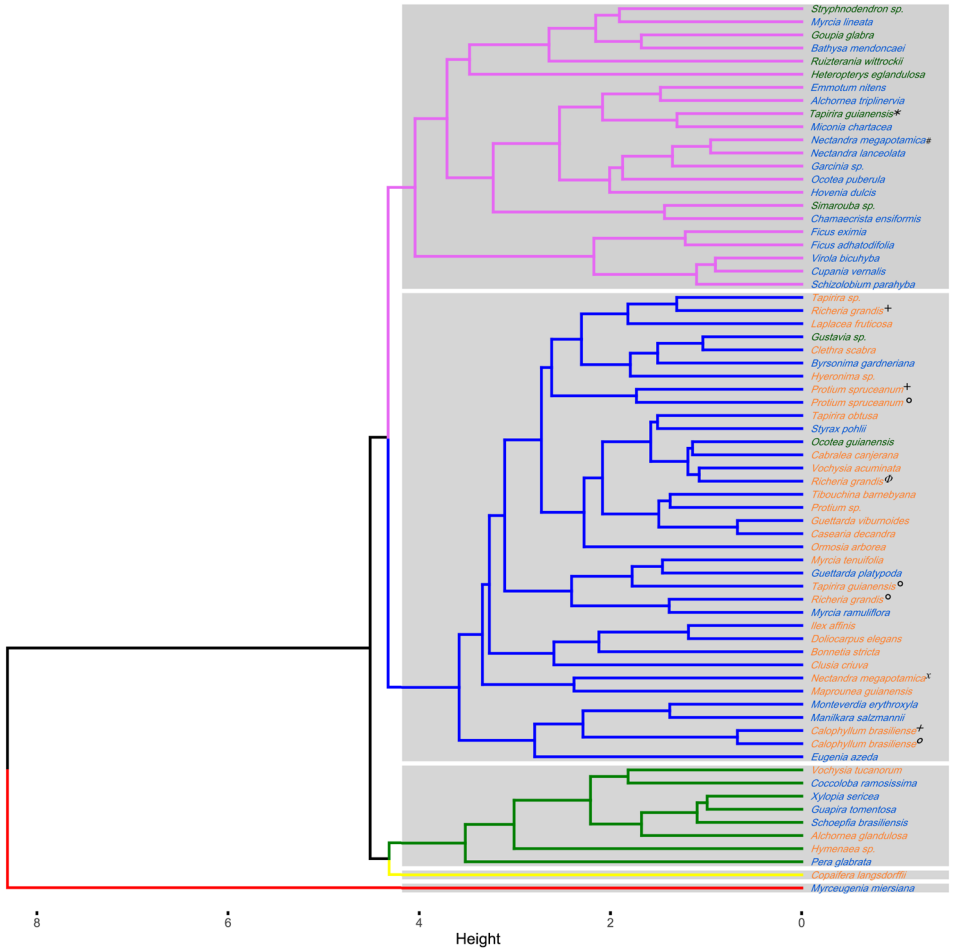

Figure 4. Hierarchical agglomerative clustering of litter traits for tree species from Amazon Forest (dark green), Atlantic Forest (light green) and Cerrado (light brown) biomes. Branches with same colors indicate more similar clusters in relation to the physical and chemical traits of litter. Cophenetic correlation coefficient of 0.75. Different symbols denote species from Cantá (*), Palmas (+), Brasília (°), Patrocínio (x), Erechim (#) and Mucugê (Φ).

phylogenetic signal for the Atlantic Forest, as indicated by significance tests for Pagel's λ (λ = 0.709, p = 0.045, Supporting information). We then reconstructed the ancestral P content in litter from the Atlantic Forest, which provides evidence that the evolution of this trait may have resulted in species with low P content but also species with intermediate to high P content (Fig. 5). For example, closely related species of the genera *Myrceugenia*, *Eugenia*, *Myrcia* and *Miconia* showed low P contents. In contrast, the genera *Nectandra*, *Ocotea*, *Virola* and *Xylopia* showed intermediate to high P contents.

Discussion

This study revealed striking similarities in the physical and chemical traits of litter from the Amazon and Atlantic Forest biomes. Although these biomes are spatially isolated, there is evidence of past connections between them during the expansion periods of rainforests (Fouquet et al. 2012, Ledo and Colli 2017). This finding corroborates the connection of floristic composition and functional traits among neotropical forests (Fouquet et al. 2012). Despite the importance of phylogenetic relatedness of species to determine species traits, we found no phylogenetic signals for the studied traits across biomes; however, within the Atlantic Forest biome, we found a strong phylogenetic signal for P (below). Consequently, litter traits seem to be driven by environmental differences among biomes, such as temperature, rainfall, edaphic conditions and topography.

We found higher N contents in litter from the Amazon and the Atlantic Forest than in litter from the Cerrado. However, there were similar P contents in litter across all three biomes, partially corroborating our first hypothesis that litter from the Amazon and Atlantic Forest biomes would be richer in nutrients than that from the Cerrado biome. According to Reich and Oleksyn (2004), N:P mass ratios < 14 would indicate N limitation. Thus, the higher N contents of litter from the Amazon and the Atlantic Forest led to higher N:P mass ratios, indicating that litter from the most humid biomes (that is, Amazon and Atlantic Forest) is more P-limited than

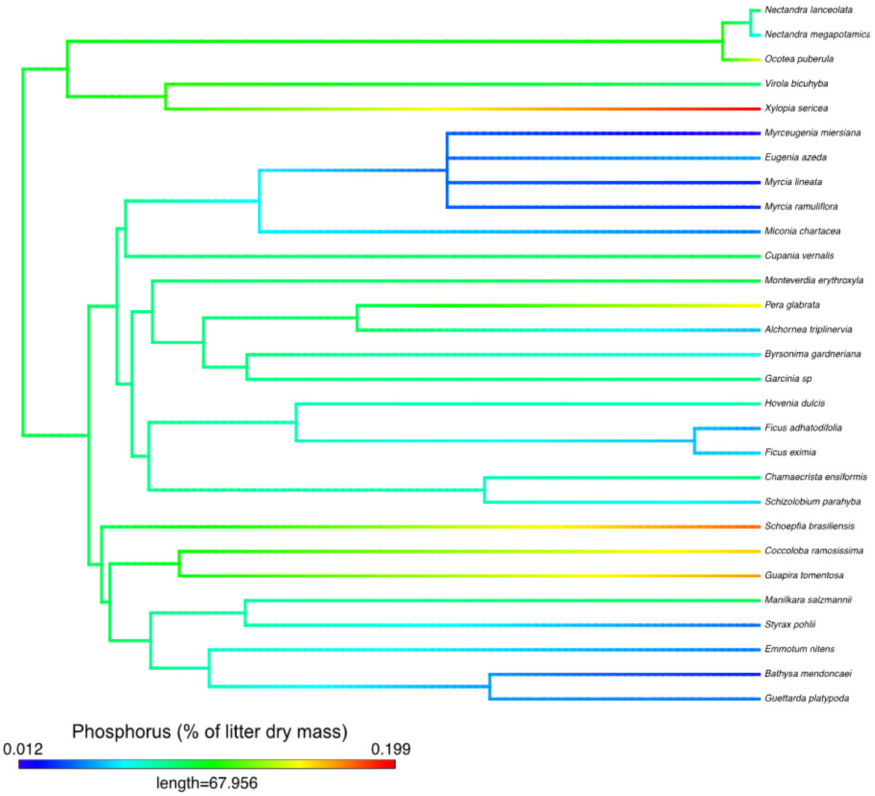

Figure 5. Observed phosphorus (P) content for litter of 29 plant species from the Atlantic Forest and the reconstructed estimation of the ancestral P content. The colored scale indicates the P content, which varies from low (blue) to high (red). The length of the legend gives a scale for the branch lengths in the Atlantic Forest phylogenetic tree.

that from the Cerrado. Considering that the P contents in litter were similar among the biomes, the observed difference in the N:P mass ratio suggests that P resorption rates are similar and that the variation in the N:P ratio was due to differences in N resorption rates before leaf senescence (Haridasan 2008, Grau et al. 2017). These different nutritional limitations of the litter may influence the nutrient availability for decomposers (Güsewell 2004, Sena et al. 2021).

Riparian forests of the Cerrado produced litter with higher phenolic content and higher C:N mass ratio than litter from the Amazon and the Atlantic Forest, but the content of C, P, C:P mass ratio and toughness values were similar among all the biomes, partially corroborating our second hypothesis that litter from the Cerrado would be more refractory than litter from the Amazon and the Atlantic Forest. The highest phenolic content was observed for litter from the Cerrado, supporting previous evidence that tree species from this biome produce more chemically defended litter (Haridasan 2008, Miatto et al. 2016). The low N content for litter from the Cerrado – and thus the high C:N ratio – is likely a strategy used by plants to conserve the limited and essential available N in the soils. Consequently, N-poorer litter may decompose at slower rates in both forest soils and in streambeds, as shown elsewhere (García-Palacios et al. 2015, Zhang et al. 2019). Although SLA is considered an opposite proxy for litter toughness (Boyero et al. 2017), these two litter traits did not differ among the three biomes, indicating that riparian species from these biomes produce tough and malleable litter. Although multiple traits were similar across the biomes, we showed the existence of relevant differences in terms of the C:N mass ratio and phenolic content between drier (Cerrado) and humid biomes (Amazon and Atlantic Forest), which possibly constrain litter decomposition in the Cerrado, reducing the turnover and availability of nutrients to aquatic and terrestrial food webs as well as for plant growth (Ordoñez et al. 2009).

Although no phylogenetic signal was observed for the studied traits using a tree for all biomes, we found a strong phylogenetic signal for P from the Atlantic Forest. This result indicates that closely related species have similar P contents in the Atlantic Forest and suggests that phylogeny is essential for determining P content within the Atlantic Forest biome. This finding contrasts with no phylogenetic signal observed for the Amazon and Cerrado biomes in the present study and with findings of a global survey (Boyero et al. 2017) but agrees with regional studies using green leaves, which reported a significant signal for P (Kraft and Ackerly 2010, Silva and Batalha 2010). However, differences among studies should be interpreted cautiously, as the phylogenetic signal can depend on the study scale, sample size, model, index and phylogenetic tree used (Münkemüller et al. 2012).

Several tree species were found across sites, which allowed us to examine differences between phenotypic plasticity and

environmental regulation. On the one hand, litter specimens of *Protium spruceanum* and *Calophyllum brasiliensis* were found in different areas of the Cerrado and clustered closely, suggesting that individuals of these two species produce litter with low phenotypic plasticity (Sultan 2000, Kroon et al. 2005). On the other hand, litter specimens of *Richeria grandis* were sampled at different sites of the Cerrado and did not cluster closely, suggesting some phenotypic plasticity (Sultan 2000, Kroon et al. 2005). A similar pattern occurred with the litter of *Nectandra megapotamica*, the only species sampled in more than one biome. *Nectandra megapotamica* litter showed greater trait similarity with litter specimens of other tree species from the same biome sampled, suggesting that functional responses of individual traits are induced by environmental conditions (Sultan 2000, Boyero et al. 2017). These plastic responses of riparian tree species may have important consequences for litter stoichiometry and influence nutrient availability in detritus-based ecosystems such as forest streams (Danger 2020).

Here, we demonstrated that litter traits for tree species from the Amazon and Atlantic Forest biomes of South America are remarkably similar, mainly in terms of C, P, C:P mass ratio, SLA and toughness. However, litter from the Cerrado was nutrient-poor and highly chemically defended (although similar in terms of toughness of litter tissues), traits which usually retard litter decomposition and biological activity. We showed that species phylogeny seems to have lower importance than environment in the determination of litter traits, at least at the biome scale. Finally, we demonstrate how the litter of riparian tree species from different South American biomes are physically and chemically characterized, providing evidence for their possible repercussions to carbon and nutrient dynamics.

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Author contributions

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Data are available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.20223537 (Sena et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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