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ORIGINAL ARTICLE

The legacy of forest logging on organic matter inputs and storage in tropical streams

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Abstract

Riparian forests play an important role in stream ecosystems, as they support biodiversity, reduce water erosion, and provide litter that fuels aquatic biota. However, they are affected by great array of anthropogenic threats (e.g., fire, logging, and organic pollution), which alter species composition and their physical structure. Although forest recovery after disturbance such as logging can take decades, the legacy of forest clear-cut logging on key processes in tropical riparian ecosystems is mostly unknown. Here, we investigated how litter inputs (leaves, twigs, and reproductive parts) and storage, key processes for carbon and nutrient recycling and for forest and stream biota, are influenced by riparian vegetation undergoing succession (after 28 years from logging) through the comparison of reference and logged forest sites in the Cerrado biome. Litterfall was overall similar between forest types, but litterfall of twigs was twofold higher at logged than reference sites. Similarly, litter inputs from the bank to the stream (i.e., lateral inputs) and streambed storage were 50–60% higher at logged than reference sites. The higher litterfall observed in logged forests could be related to higher proportion of tree species that are characteristic of primary and secondary successional stages, including fast-growing and liana species, which often are more productive and common in anthropogenic areas. Our results showed that the legacy impact of clear-cut logging, even if residual woody vegetation is maintained in riparian buffers, can shift the type, quantity, and seasonality of litter subsidies to tropical streams. This knowledge should be considered within the context of management and conservation of communities and ecosystem processes in the forest-stream interfaces.

Abstract in Portuguese is available with online material.

KEYWORDS
carbon fluxes, Cerrado savanna, forest clearing, forest productivity, litter decomposition, plant species richness

1 | INTRODUCTION

Forest harvesting is a widespread disturbance that significantly reduces forest cover and impairs fresh waters. The impacts of logging in forest streams can include changes in their natural hydrological pattern, water chemistry, and biological communities (Paul & Meyer, 2001; Snyder et al., 2003). The loss of riparian woody vegetation surrounding streams often shifts the dominant basal resource of aquatic food webs from plant litter to algal sources (Sweeney et al., 2004). Such consequences are ameliorated as forests recover from disturbances, although this may take decades of successional phases, including a diversity of plant species life forms (Boyero et al., 2021). Despite decades of research on how forest disturbances affect riparian ecosystems (that is, both riparian forest and streams), there is no consistent general effect because responses tend to be context-dependent (Richardson & Béraud, 2014).

The consequences of altered riparian forests to stream ecosystems and communities have been extensively studied in temperate areas (see Abelho, 2001; Acuña et al., 2007; Hoover et al., 2011; Pozo et al., 1997; Webster et al., 1990). However, this kind of information is scarce in the tropics (Rezende, Sales, et al., 2017; Santos et al., 2019), where most studies have been restricted to preserved forests (e.g., Bambi et al., 2017; Tonin et al., 2017, 2020). Although it is expected that forests with lower tree density—as a result of tree logging—reduce their litter production (Kiffney & Richardson, 2010; Richardson et al., 2012), studies have found contrasting results (Delong & Brusven, 1994; Londe et al., 2016). For instance, litterfall tends to be similar or even smaller in mature forests than in disturbed forests (Hagen et al., 2010). Litter production might increase with the proportion of early-successional tree species (Berry et al., 2008), exotic species (Hagen et al., 2010; Londe et al., 2016; Nunes & Pinto, 2007) and lianas—which are key components and common in tropical forests—as well as in disturbed areas, which are able to allocate a higher proportion of biomass to leaves compared to trees (Ingwell et al., 2010).

The rapid and ongoing conversion of natural forests into plantations and pastures threat biodiversity and ecosystem functions of the Cerrado biome, which is the world's most species-rich savanna and one of the largest biomes of South America (Strassburg et al., 2017, Eiten, 1994). Despite the relatively small area that riparian forests of Cerrado occupy, they hold one third of the plant species diversity, representing the greatest number of species per unit area within this biome (Paiva et al., 2015; Silva et al., 2008). Riparian forests also produce twice as much biomass as the adjacent Cerrado vegetation (Paiva et al., 2015), which makes them particularly important for nutrient cycling and carbon storage (Silva et al., 2008). Riparian forests of the Cerrado provide habitat to a variety of wildlife and plant litter to soils and riverine ecosystems, where litter is a major source of organic matter that often fuels the aquatic food web (Fischer & Fischenich, 2000). In this context, plant litter entering riverine ecosystems through litterfall or laterally from the banks establish a connection between terrestrial and aquatic environments (Gregory et al., 1991; Wallace et al., 1997). However, we still lack consistent evidence on the effects forest clear-cut logging on plant litter subsidies of tropical riparian ecosystems.

Our aim here was to investigate how clear-cutting and subsequent riparian forest regrowth and succession influenced litterfall to the forest, and litter inputs and accumulation (storage) in streams, by sampling two reference and two clear-cut logged sites at monthly intervals for two years in the Cerrado biome. We predicted (1) lower litterfall to the forest and lower litter inputs and storage in logged sites due to lower tree density and plant species richness in clear-cut forests (Kiffney & Richardson, 2010; Richardson et al., 2012); and (2) different timing of litter inputs and storage in reference—where peaks often occur in drier seasons (Tonin et al., 2017, Tonin et al., 2020)—and logged sites, although we could not a priori predict when peaks of inputs would occur in logged sites, given unknown phenology of new species found.

2 | METHODS

2.1 | Study area

We conducted a field study in four stream sites and their surrounding riparian forests within the Cerrado biome: two sites with naturally preserved vegetation (reference sites) and two sites with clear-cut vegetation ca. 30 years ago and undergoing natural recovery (logged sites) (Figure 1, Table 1). Reference sites had natural, dense, and perennial riparian vegetation along the streams, while logged sites had riparian buffers (minimum of 0–10 m from the stream) with some amount of residual woody vegetation along stream edges (often trees 5–10 m far from each other), and lots of herbs and grasses typical of agriculture abandoned areas undergoing passive restoration (Wallace et al., 1997). Clear-cutting in the logged sites occurred in the 1980s (ca. 30 years since the study starts) and reduced large (20–30 m) corridors of native vegetation to patches of 0–10 m wide. After logging, clear-cut areas were used for cattle, family agriculture, and fruit crops, but were abandoned and followed natural recovery for >15 years before the start of the study.

The topography of both reference and logged sites varied from flat to irregular and the soil was predominantly well drained, although there were some areas with poorly drained soils, which is common for the region. Soils in the riparian forests were mostly hydromorphic and fluvic neosols, according to the Brazilian soil classification system (Reatto & Martins, 2005; Vendrame et al., 2010). The regional climate is seasonal—Aw according to the Köppen classification—with a rainy season from October to April and a dry season from May to September (Figure 2). Annual precipitation is ca. 1650 mm, with 8 mm of precipitation in the driest month (June) and 284 mm in the wettest month (December). Annual mean air temperature is ca. 20.7°C, ranging from 18.5°C in the coldest month (June) to 21.9°C in the hottest month (September) (Hijmans et al., 2005).

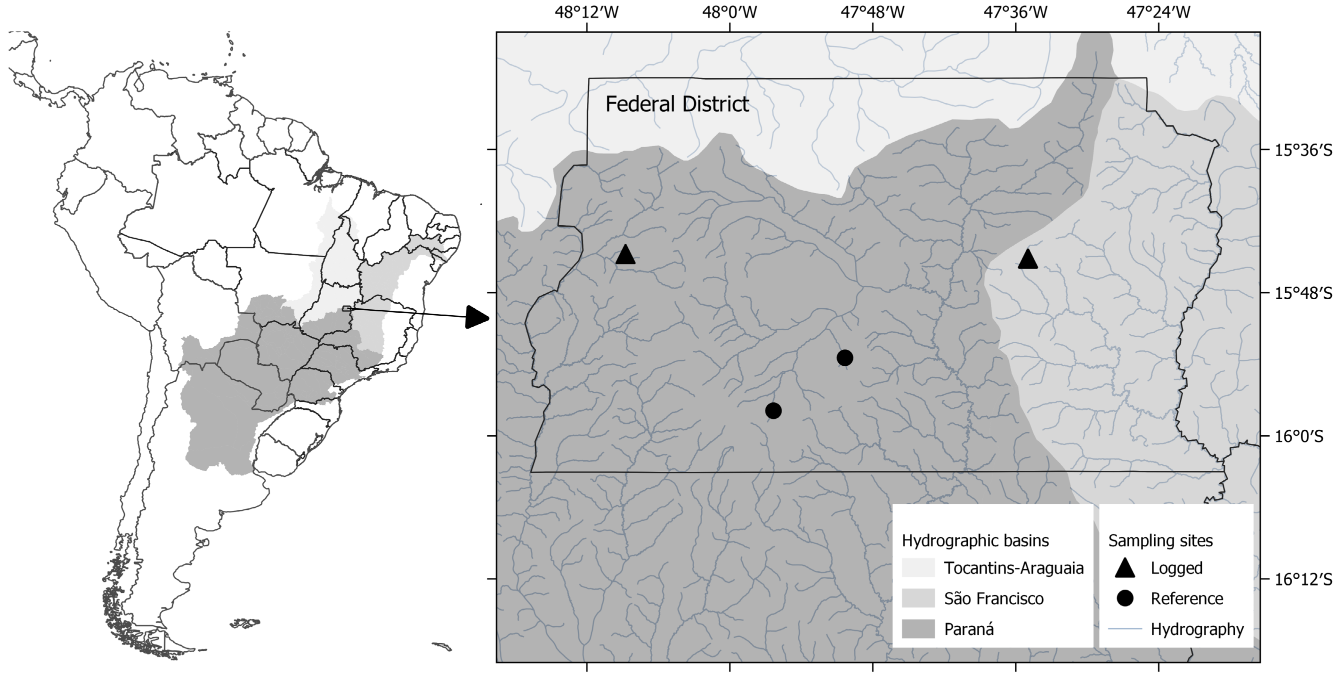

FIGURE 1 Location of the four studied sites in preserved areas (reference) and clear-cut logged areas (logged) within the Cerrado of the central plateau of Brazil

TABLE 1 Characteristics of watersheds, stream reaches and riparian buffers for reference and logged sites for the four study streams. Stream width, depth, and water flow are averages ± standard errors across all sampling events

	Reference sites		Logged sites	
	CAP	CVE	JAR	COM
Watershed				
Distance from the stream source (km)	1.8	2.4	3.1	2.6
Total drainage area (ha)	581	1630	1800	1420
Stream				
Altitude (m. a.s.l.)	1089	1079	989	1063
Latitude	15°57′43.68″S	15°53′22.15″S	15°56′14.77″S	15°44′35.05″S
Longitude	47°56′37.86″W	47°50′34.10″W	47°53′12.59″W	48°8′57.99″W
Stream order	Third	Third	Third	Third
Width (m)	3.00 ± 0.31	2.70 ± 0.45	2.50 ± 0.60	3.20 ± 0.40
Depth (m)	0.22 ± 0.19	0.33 ± 0.05	0.35 ± 0.10	0.25 ± 0.06
Water flow ($m\,s^{-1}$)	0.51 ± 0.48	0.10 ± 0.60	0.75 ± 0.54	1.17 ± 0.70
Streambed substrate	Silt, clay and gravel	Silt, stones	Clay, sand, stones	Silt, clay, stones
Canopy cover (%)[b]	70	95	28	8
Riparian buffers[a]				
Slope (degrees)	8	5	8	7
Natural vegetation (%)	94.6	94.7	46.8	66.5
Converted areas (agriculture/pasture) (%)	5.4	5.3	53.2	33.5

[a] Riparian buffers of 60-m wide. Watershed and land use variables were obtained using freely available QGIS software.

[b] Canopy cover, measured when standing in the center of the stream using fisheye camera lens after image analysis with ImageJ software.

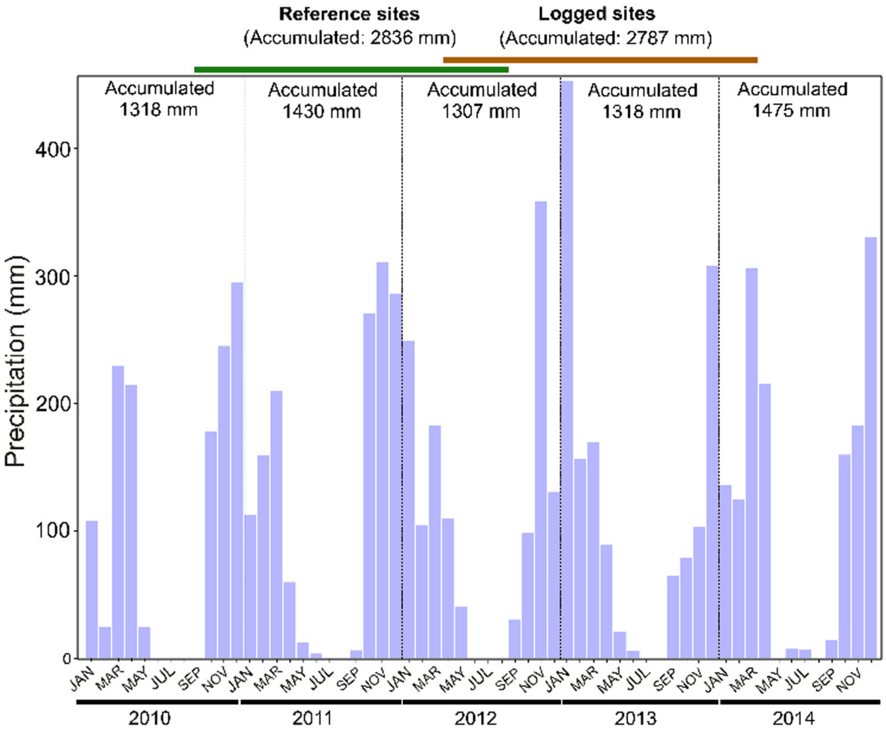

FIGURE 2 Monthly precipitation for the study period (2010–2014) showing seasonal dry-wet periods typical of Cerrado savanna climate and, accumulated precipitation for each year and, for reference (horizontal green bars) and logged sites (horizontal brown bars). Data from automatic meteorological station (A001, Brasília) of National Institute of meteorology (INMET). Note the similar seasonal precipitation trends and accumulated precipitation for reference and logged sites.

2.2 | Phytosociological survey

The phytosociological survey was performed in the riparian forests of each site to record tree density and species composition. The survey consisted of sampling nine 10 × 10 m plots, parallel to the stream margin, at each site, following Felfili et al. (2011). All individual trees with a diameter equal or greater than 5.0 cm, measured at 1.30 m above the ground, were sampled (Felfili, 1995). All individuals within the above criteria were counted and identified (Moro & Martins, 2011). Species identifications were confirmed by consulting the databases of the Tropics projects (http://www.tropicos.org), the Flora do Brazil species list (http://floradobrasil.jbrj.gov.br/reflora), and the Link species network (http://www.splink.org.br), based on the APG III classification system (Souza & Lorenzi, 2012).

2.3 | Experimental design and procedure

Each site consisted of three equally distanced sampling sections within a 100–150 m long stream. At each section, we sampled (i) litterfall to the forest (organic material that accumulates in the riparian forest soil), as a proxy of riparian forest production (Clark et al., 2001), with one suspended net (1 m^2, 1-mm mesh, 1 m above the soil level and 3–5 m distant from the stream channel) at each stream margin; (ii) litterfall to the stream, with 18 plastic buckets (26-cm diameter, with small holes at the bottom to allow rainwater to drain and placed 2 m above the streambed); (iii) lateral inputs (organic matter accumulated in the soil of the forest that enters the stream laterally), with 2 lateral traps (50 × 25 × 50 cm, with a 1-mm mesh) fixed to the soil at each margin; and (iv) benthic litter storage (hereafter storage) within the stream, with three Surber samples (0.10 m^2, 250-μm mesh) taken haphazardly in pool and riffle areas that were further sieved through a 1-mm mesh.

Samples were collected once a month over 2 years (September 2010 to August 2012 in reference sites and April 2012 to March 2014 in logged sites), comprising a total of 24 sampling events. Although reference and logged sites were sampled in different years, interannual variability is often minor (Tonin et al., 2020), especially when accumulated precipitation and precipitation seasonality are similar between years or periods (Tonin et al., 2017), as occurred in reference and logged sites.

Samples were transported to the laboratory, washed to remove inorganic particles (only in the case of benthic samples and lateral inputs, which may have adhered soil that can overweight litter components parts), oven-dried (60°C for at least 72 h), sorted into four categories of litter—that is, leaves, twigs, reproductive parts (fruits, flowers, and seeds) and unidentified parts—and weighed to the nearest 0.001 g. Litterfall and lateral inputs were estimated as litter dry mass (DM) per m^2 per day (d) at each sampling reach, and storage as litter DM per m^2 on each occasion, further details were provided by Tonin et al. (2020).

2.4 | Data analyses

All analyses were performed in R v. 4.0.1 (R Core Team, 2020) using the packages boot (Canty & Ripley, 2016; Davison & Hinkley, 1997), nlme (Pinheiro et al., 2020), and mgcv (Wood, 2011), while figures were drawn with ggplot2 (Wickham 2016). To test our first hypothesis (i.e., logged sites showed lower litterfall to the forest and lower litter inputs, and storage), we calculated non-parametric bootstrapped 95% confidence intervals (BCa method based on 1000 bootstrap replicates) for each litter flux (litterfall to the forest, litterfall to the stream, lateral inputs, and storage within the stream) separately for reference and logged sites for each litter fraction (leaves, twigs, reproductive parts, and total litter). This is a simple and straightforward method that facilitates the interpretation of results (i.e., overlapping confidence intervals indicate non-significant differences) and obviates the need to meet the assumptions of parametric models (e.g., normal distribution and homogeneity of variances), which are seldom met in complex field data such as ours (Efron & Tibshirani, 1994; Wood, 2005). We tested whether confidence intervals for each response variable differed between sites.

To explore our second hypothesis (i.e., timing of peak litter inputs and storage would be different between reference and logged sites), we examined temporal dynamics of litter inputs and storage over the 2 years at reference and logged treatments separately with generalized additive mixed models (GAMMs) with time (number of each sampling event) as a continuous predictor and site as a random term for each litter input/storage and fraction separately. Additive rather than linear models were preferred because they allowed non-linear relationships over time, which were observed after initial data exploration using scatterplots with the residuals of linear models. GAMMs were fitted with a normal distribution of response data, the identity-link function, restricted maximum likelihood method and with time as a smooth term. Cross-validation was used to estimate the optimal amount of smoothing, which was represented by the effective degrees of freedom (edf) of GAMMs with higher edf indicating greater non-linearity (Zuur et al., 2009). We further visually compared patterns of each response variable between reference and logged sites. Seasonality was attested using the edf and *p*-values, with higher edf values (and *p*-values <0.05) indicating a higher seasonality. Different residual spread among sampling events (with a constant variance function structure, VarIdent) was allowed to meet homogeneity assumption as its need was detected while structuring the models (Zuur et al., 2009). Spatial and temporal correlation (within and among streams, and between subsequent sampling events) were inspected using variograms and autocorrelation function of normalized residuals of models, and none were detected.

3 | RESULTS

3.1 | Riparian plants in reference and logged sites

We recorded 549 trees in total, with average numbers (and 95% confidence intervals) of individuals per square meter as follows: 0.26 (0.22–0.30) at reference sites and 0.14 (0.10–0.17) at logged sites. Thus, reference sites had on average 86% higher tree density than logged sites, a difference that was statistically significant as shown by non-overlapped confidence intervals. Trees sampled belonged to 137 species, with 104 species at reference sites and 72 species at logged sites (Table S1). Thirty-nine species were shared by reference and logged sites, which correspond to 40–50% of similarity between forest types in terms of species composition. Dominant tree species (i.e., those that represented more than half of individuals in the riparian forest) comprised 20 and 16 species in reference and logged sites, of which 8 of them were shared by both forest types (Figure 3). Although tree species composition differed among the four sites, there were a very clear differences between reference and logged sites (Figure 3).

3.2 | Differences in litter fluxes between reference and logged sites

Litterfall to the forest, when including all litter fractions (leaves, twigs, and reproductive parts), was similar between reference and logged sites. Litterfall to the stream and lateral inputs were more than twofold higher in logged than reference sites and storage in the stream was 60% higher in logged than reference sites. When different litter fractions were analyzed separately, litterfall to the forest was twofold greater in logged than reference sites for twigs, but did not differ for leaves and reproductive parts. Litterfall to the stream was 2.2 and threefold higher in logged than reference sites for leaves and twigs, respectively, but not for reproductive parts. Lateral inputs were 2.4 and 14-fold higher in logged than reference sites for leaves and twigs, respectively, but not for reproductive parts and storage was twofold and 18-fold higher in logged than reference sites for leaves and twigs, respectively, and sevenfold higher in reference than logged sites for reproductive parts (Figure 4, Table S2).

3.3 | Seasonal patterns of litter fluxes

Seasonal patterns were evident in both reference and logged sites for litterfall to the forest, litterfall to the streams, lateral inputs, and storage in streams, mostly for leaves (Figures 5–7). When considering different litter types separately, litterfall to the forest was seasonal at reference sites, peaking mostly at the end of the dry season (September–October), but non-seasonal at logged sites, in all cases (Table S2). At reference sites, storage within the stream had a consistently similar pattern as litterfall to the forests and to the streams (for leaves and reproductive parts). In contrast, twigs storage was uniform (i.e., non-seasonal) at reference sites and seasonal at logged sites, where it increased in drier periods. Seasonal patterns as litterfall to streams and lateral inputs were remarkably similar between reference and logged sites (except for lateral twigs inputs) (Figures 5–7).

4 | DISCUSSION

Our observational study in preserved (reference) and clear-cut riparian forests surrounding streams allowed us to assess relevant and previously unexplored legacy impact of forest logging on key processes in riparian ecosystems over 2 years. The results indicated that riparian vegetation undergoing succession (after decades of

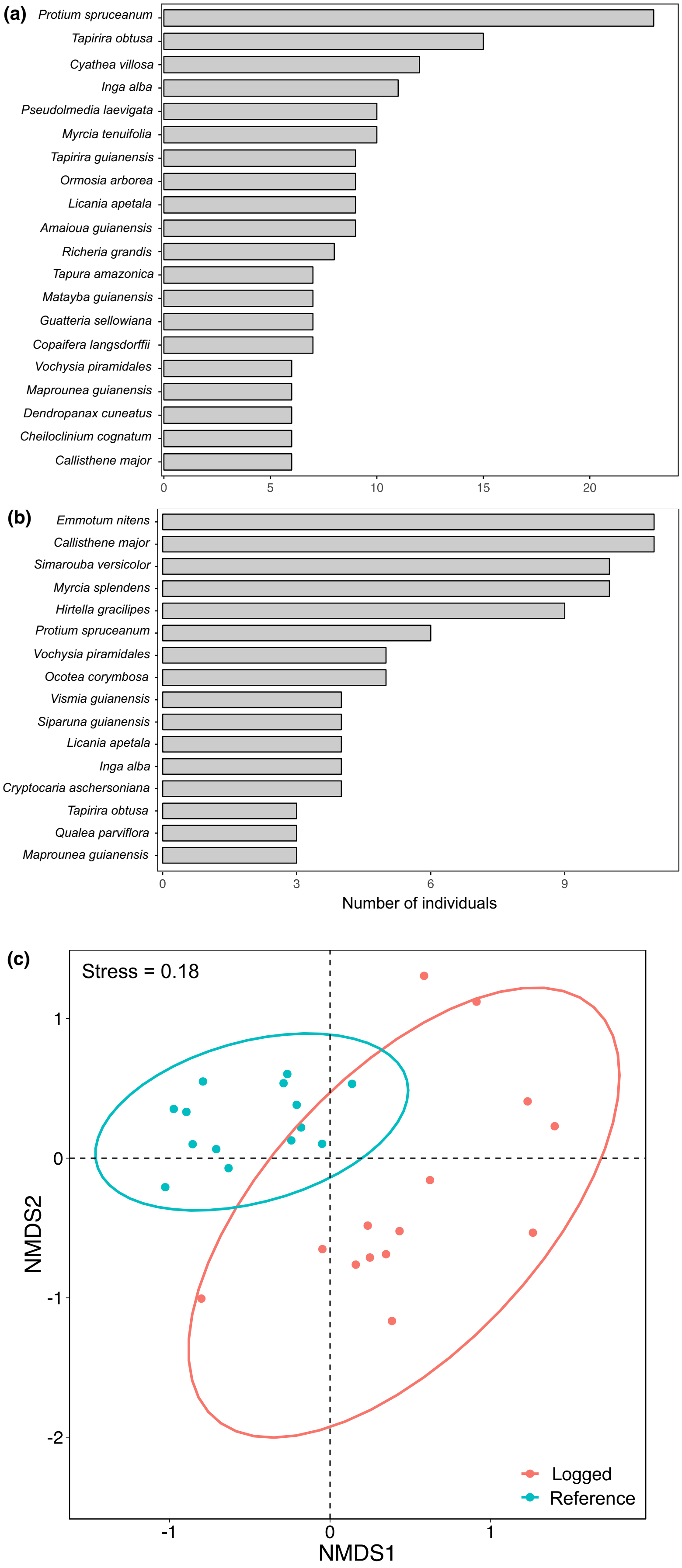

FIGURE 3 Most abundant species representing 50% of total sampled trees at (a) reference and (b) logged riparian forests sites, and (c) biplot of non-metric multidimensional scaling (NMDS) analysis of tree species composition in riparian forests; blue and red dots represent sampling plots at reference and logged sites, respectively.

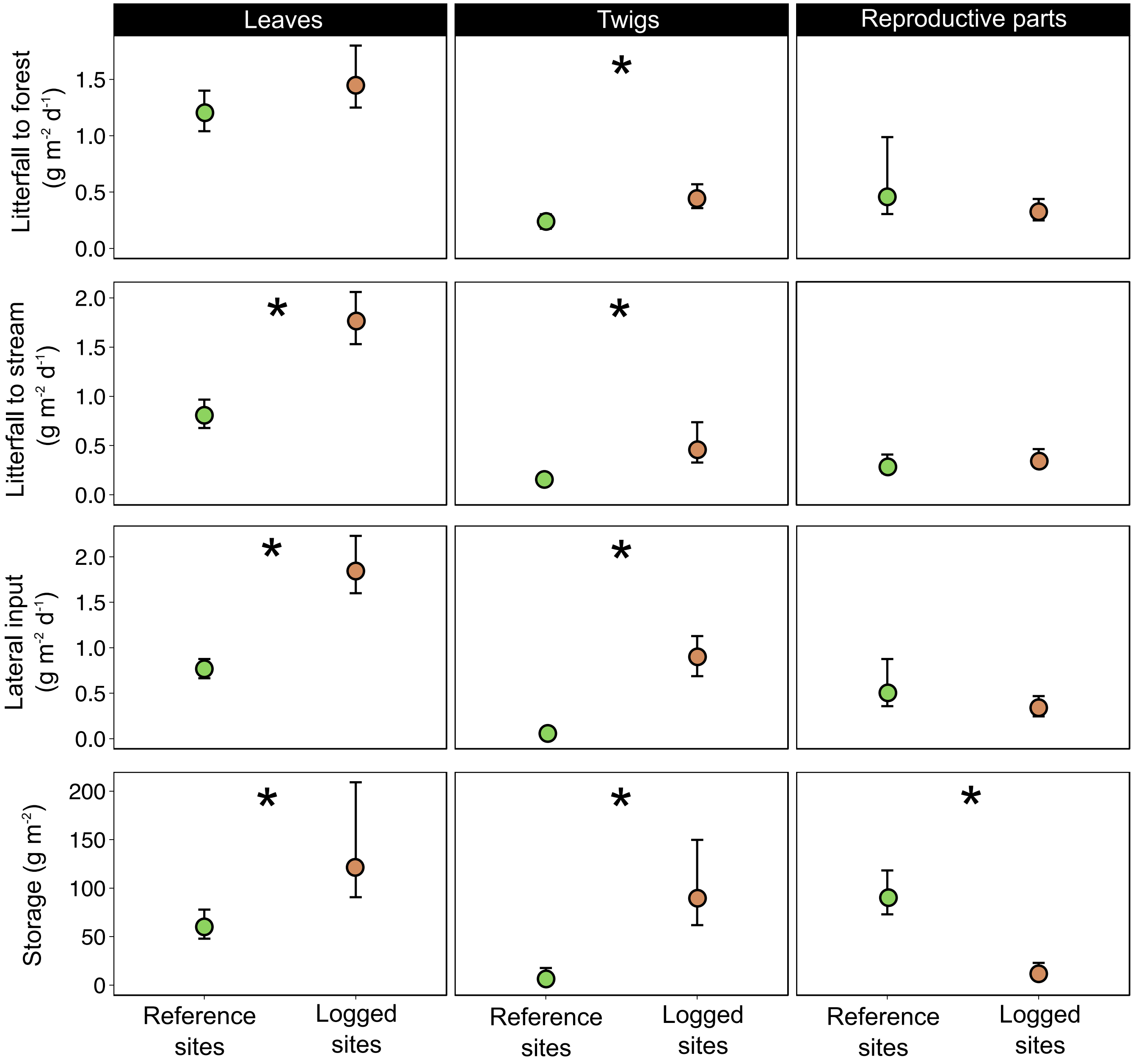

FIGURE 4 Litterfall to forest, litterfall to stream, lateral inputs and storage of leaves, twigs and reproductive parts at natural (green circles) and logged forest sites (brown circles). Circles are means and lines denote upper and lower limits of 95% confidence intervals; non-overlapped intervals (i.e., those that were statistically significant) were indicated with an asterisk.

clear-cutting) increases litterfall to streams but conserve similar seasonal litterfall patterns from those observed for reference sites. However, the seasonality of litterfall to the forest and organic matter storage within streams are changed.

4.1 | Higher litterfal to the streams but similar litterfall to the forests at logged sites

Logged sites—which had lower tree density, mostly restricted to the stream edge—showed similar litterfall to the forest soil, and higher litterfall to streams (Figures 2b and 3). This was true for leaves and twigs, which are the main fractions of litter that enter streams in general (Hagen et al., 2010) and in the Cerrado biome in particular (Rezende et al., 2016; Tonin et al., 2017). These results suggest that a narrow band (ca. 10 m wide) of riparian vegetation is sufficient to provide litter to riparian systems. Logged stream sites received two-fold higher quantities of litterfall than reference streams, possibly because individual trees along the logged stream sites contributed larger quantities of litter inputs than individual trees along the reference stream sites. Widely spaced trees tend to grow larger and produce more litter due to reduced competition for essential resources such as water, nutrients, and light, with other trees (Delong & Brusven, 1994; Pinkard & Neilsen, 2003). Thus, the greater tree

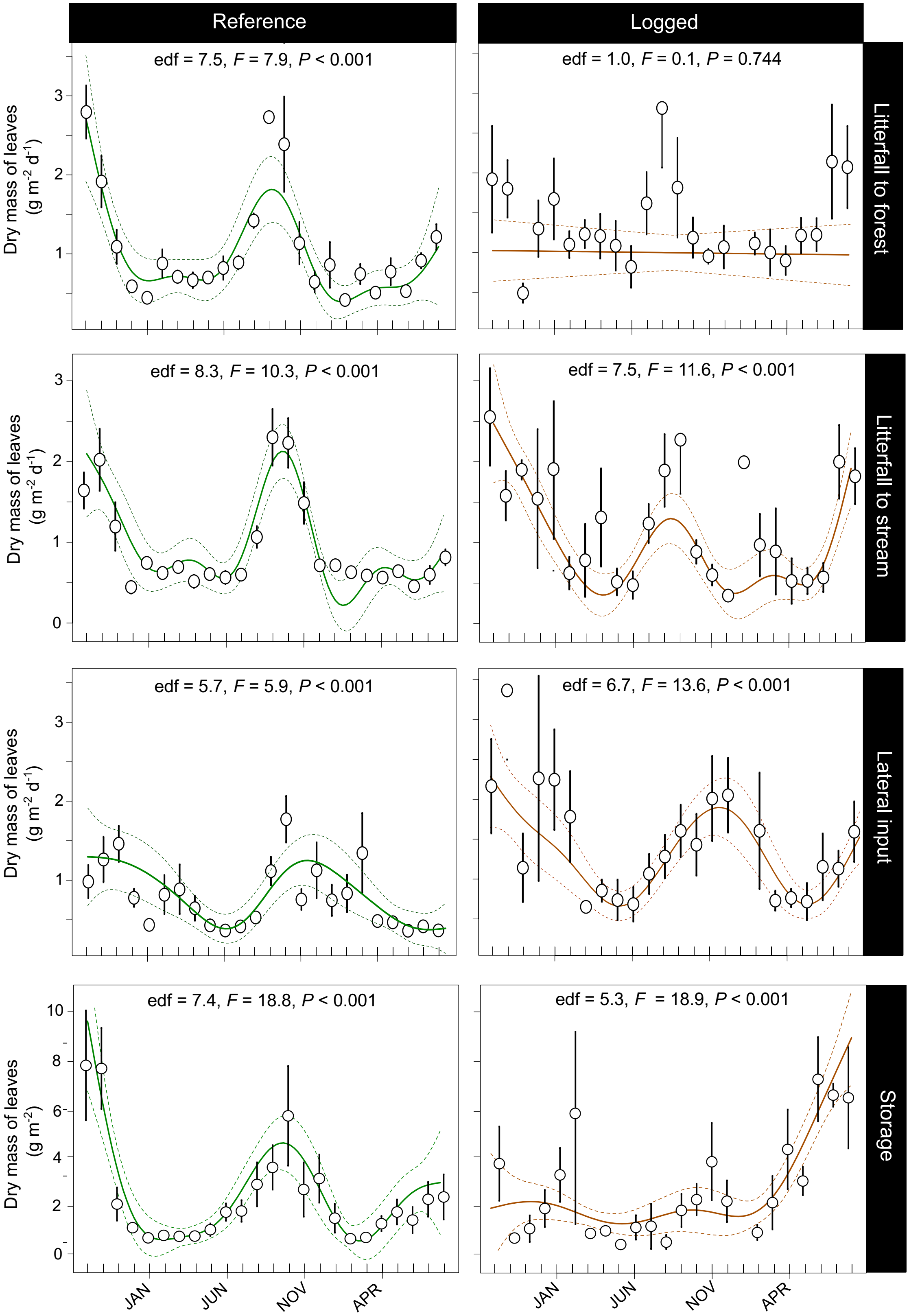

FIGURE 5 Temporal dynamics of litterfall to the forest, litterfall to the stream, lateral input and storage of leaf litter at reference (natural) and logged riparian forests sites over 2 years. Effective degrees of freedom (edf), *F*- and *p*-values are from generalized additive mixed effects models (GAMM). Continuous lines (green or brown) are the smoothers from GAMM and, upper and lower dotted lines the 95% confidence intervals from each model. Circles are means, and vertical lines denote upper and lower limits of standard errors from data of multiple sampling sites within streams.

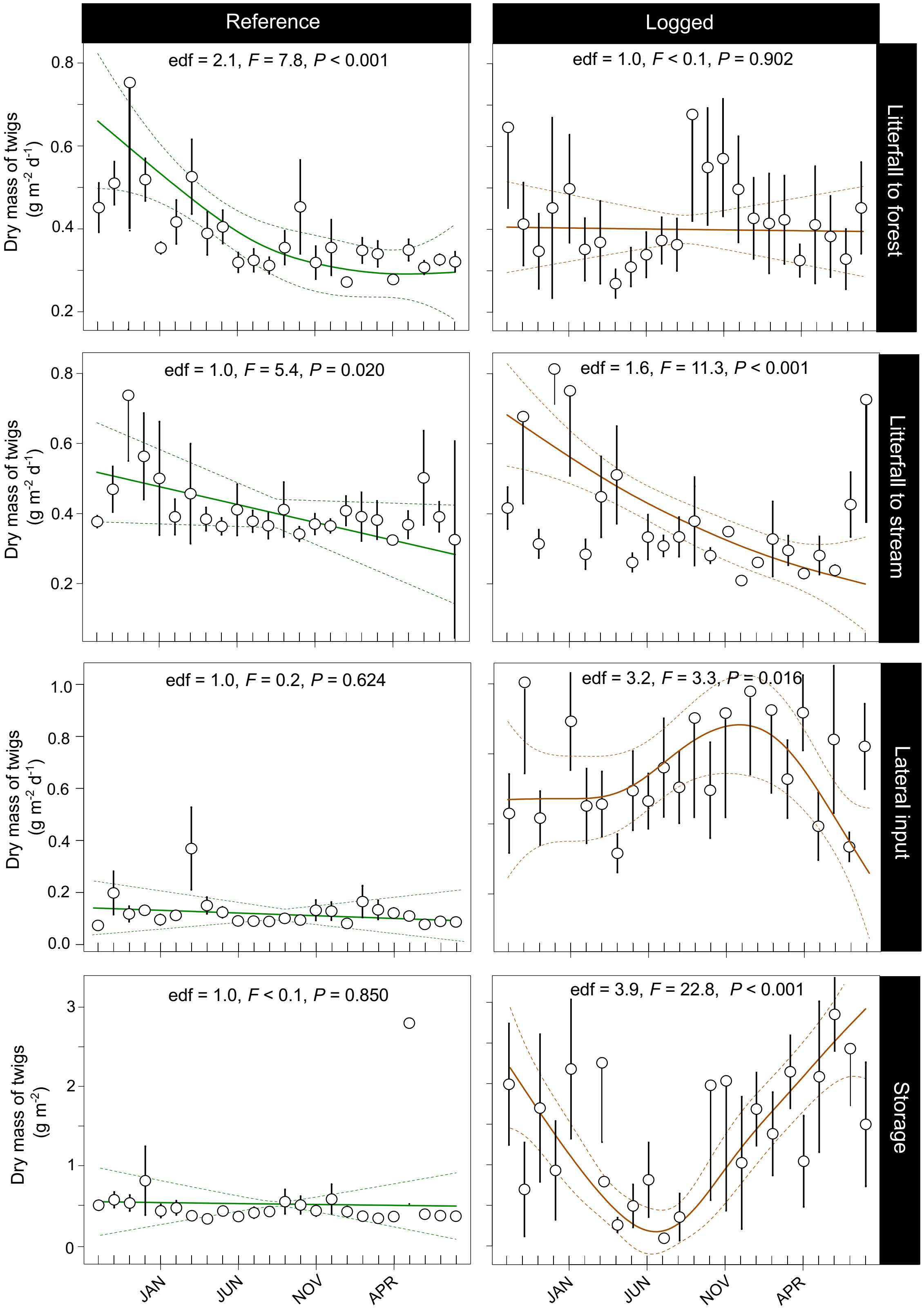

FIGURE 6 Temporal dynamics of litterfall to the forest, litterfall to the stream, lateral input and storage of twigs at reference and logged riparian forests sites over 2 years. Effective degrees of freedom (edf), *F*- and *p*-values are from generalized additive mixed effects models (GAMM). Continuous lines (green or brown) are the smoothers from GAMM and, upper and lower dotted lines the 95% confidence intervals from each model. Circles are means, and vertical lines denote upper and lower limits of standard errors from data of multiple sampling sites within streams.

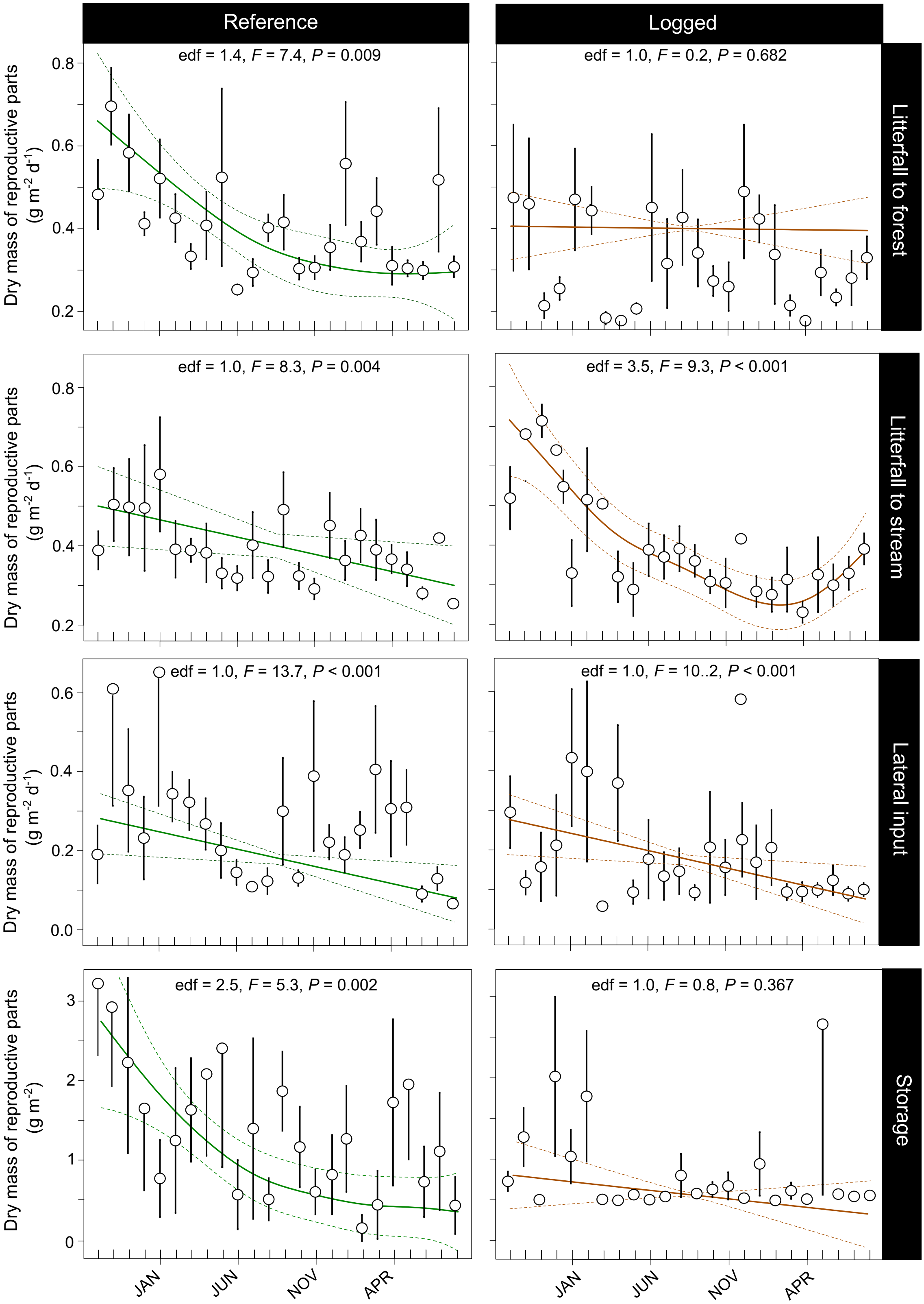

FIGURE 7 Temporal dynamics of litterfall to the forest, litterfall to the stream, lateral input and storage of reproductive parts (i.e., flowers, fruits, and seeds) at reference and logged riparian forests sites over 2 years. Effective degrees of freedom (edf), *F*- and *p*-values are from generalized additive mixed effects models (GAMM). Continuous lines (green or brown) are the smoothers from GAMM and, upper and lower dotted lines the 95% confidence intervals from each model. Circles are means, and vertical lines denote upper and lower limits of standard errors from data of multiple sampling sites within streams.

density in reference sites may not compensate for the lower litter production per individual tree. An alternative reason for the higher litterfall in logged stream sites is the increased presence of lianas species, which produce much large quantities of leaves than trees and are widespread in disturbed areas (Ingwell et al., 2010; Schnitzer & Bongers, 2011). Also, species of early and mid-development stages—commonly found in logged sites—often have rapid growth (Londe et al., 2016) and are able to allocate a higher proportion of carbon to leaf production than species of more advanced developmental stages (Ingwell et al., 2010).

The higher litterfall at logged compared to reference stream sites contrasts with the findings of other studies showing higher litter inputs to streams in more species-rich riparian ecosystems (Gonçálves et al., 2014; Rezende et al., 2016, 2017a; Wantzen et al., 2008). Litterfall, as a measure of ecosystem productivity, could be expected to be higher in ecosystems with greater diversity due to the positive effect of species diversity on ecosystem processes shown through experiments (Cardinale et al., 2007), modeling (Tilman et al., 1997) and meta-analyses (Grace et al., 2007; Hooper et al., 2012). However, our study agrees with findings showing that litterfall increases in sites altered by anthropogenic impact (Delong & Brusven, 1994; Hagen et al., 2010; Kiffney & Richardson, 2010).

4.2 | Seasonality of litter fluxes disappears at logged sites

Literfall to the forest was seasonal at reference sites, peaking at the end of the dry season (September–October), but it was aseasonal at logged sites. Clear seasonal patterns of litterfall in reference riparian zones of the Cerrado savanna biome are well established and supported by several studies (França et al., 2009; Rezende et al., 2016; Tonin et al., 2017, 2020). Seasonal patterns are the result of plant phenology, which indicate that most senescent leaves are lost as a result of precipitation variability within the year (Reich, 1995). However, although greater water stress, and thus seasonality, would be expected in logged sites—as a consequence of a more intense edge effect and drier conditions (Méndez-Toribio et al., 2014)—results indicated the absence of seasonal patterns in most response variables and litter types. In summary, the lack of seasonality in logged sites may be related to the identity of most of the new species found which may produce litter year-round and/or different species peak at different periods of the year proving a constant litter supply over the year.

Storage was higher at logged sites for leaves and twigs (albeit higher at reference sites for reproductive parts) and twig storage was uniform throughout the year at reference sites, but seasonal at logged sites. This pattern is opposite to that of litterfall, which was aseasonal at the logged sites, possibly related to greater flow variability, supporting our second hypothesis. Storage is highly dependent on flow, being enhanced in the dry season (with low flow) and reduced in the rainy season when flow and hence litter transport increases (Tonin et al., 2020). These patterns are highly relevant for stream communities because stored litter creates a variety of habitats for organisms, including flow refugia, and increases the nutrient retentive capacity of streams, which is especially true for twigs storage (Gurnell et al., 2002). Reproductive parts are more labile food resources to stream food webs than leaves, twigs, or other litter parts. However, reproductive parts are transient resources because they tend to be produced only in certain periods of the year and are easily consumed or decomposed given their high nutritional content (Elosegi & Pozo, 2005; Sabater et al., 2008).

5 | CONCLUSIONS AND INSIGHTS FOR RIPARIAN FOREST MANAGEMENT

Combined, our results point to important differences in stream litter dynamics between riparian vegetation undergoing succession and preserved reference sites, with potential consequences on stream communities and ecosystem processes. Thus, while increased litterfall to streams at logged sites may be initially interpreted as a positive effect, the higher temporal heterogeneity of litter inputs at logged sites and their different species composition (with higher contribution of lianas and species of early and mid-development stages plants compared to native trees) may have negative consequences for stream communities, which will face the scarcity and lower quality of resources. Understanding litter dynamics in riparian forests is of key importance if our interest is to preserve stream communities and ecosystems, and this knowledge should be considered within the context of forest management and conservation.

AUTHOR CONTRIBUTIONS

PB, RSR, and JFGJr designed the study; PB, FCV, FGGM, and AMT collected field data and did laboratory work; AMT analyzed the data, AMT and RSR constructed the figures; PB, RSR, and AMT wrote the manuscript with substantial inputs from JFGJr and LB. All authors contributed critically to the manuscript and gave the final approval for publication.

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CONFLICTS OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

All data used are available in the paper and in the FigShare online repository using the link: https://doi.org/10.6084/m9.figshare.20422128.v1.

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