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Are litterfall and litter decomposition processes indicators of forest regeneration in the neotropics? Insights from a case study in the Brazilian Amazon

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ABSTRACT

Litterfall plays an important role in nutrient cycling and maintenance of soil fertility in terrestrial ecosystems. We gauged the effects of anthropogenic impacts on the production, decomposition and seasonality of litterfall in primary and secondary forests within a tropical landscape of the Brazilian Amazon. We hypothesized that leaf litter quantity and quality would differ in line with forest disturbance and that these changes would translate into dissimilar decomposition rates. If proved, these processes could be used as surrogates for indentifying the ecological status of forest habitats. The obtained results have shown that, in the study area litterfall is reduced and litter decomposition is braked in disturbed habitats when compared with primary and recovered secondary forests. Also, within similar climatic conditions, the litter production and decomposition rates begin to stabilize in mature secondary forests. Our results represent a useful contribution to understand the dynamics of the litterfall and litter decomposition processes in the neotropics. Both processes were correlated and sensitive to disturbance gradients and should used as forest recovery indicators in ecological monitoring and ecological restoration studies.

1. Introduction

Litterfall in forest ecosystems are composed of organic material, including leaves, twigs, flowers, fruits, bark, and other plant parts that have fallen to the forest floor (Celentano et al., 2011; Scoriza et al., 2012; Camargo et al., 2015). This material functions primarily as a route for the transfer of nutrients from vegetation to the soil, maintaining soil fertility which is essential for the sustainability of forest systems (Silver et al., 2014; Camargo et al., 2015; Erfani et al., 2017). In the Amazon region, litter is essential for the ecosystem functioning because of the low soil fertility and litter decomposition that allows for nutrient release from the plant biomass to the ecosystem (Martius et al., 2004; Quesada et al., 2011; Almeida et al., 2015). Litter layer also acts as a thermal insulator (microclimatic soil control) and water retainer. It mitigates erosive effects and has a significant effect on the hydrologic cycle, acting mainly as a filter and storing water from the atmosphere in the soil (Caldeira et al., 2013). In addition to all the ecological services mentioned above, litter is also a shelter and habitat for oviposition and larval development for many invertebrate species in soil (Cajaiba et al., 2017a) as well as an important feeding area and breeding grounds for many other animals, including vertebrates (Paudel et al., 2015).

Several biotic and abiotic factors affect litter production, such as vegetation type, altitude, latitude, precipitation, temperature, luminosity, relief, deciduousness, successional stage, water availability, and soil characteristics (Scoriza and Rodrigues, 2014; Holanda et al., 2017). Depending on the characteristics of each ecosystem, one factor may prevail over the others (Figueiredo Filho et al., 2003). Therefore, each soil type supports different plant species which are adapted to specific nutritional conditions. The factors affecting decomposition include substrate chemical composition, particularly the amount of leachate and water-soluble substances, environmental conditions such as temperature, precipitation, real evapotranspiration, humidity, aeration,

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and soil structure, as well as anatomical characteristics and energy levels (Silva et al., 2014; Pinto et al., 2016). Another factor to be considered is the composition of the detritivore community and its affinity for the substrate.

Tropical forests play an important role in global nutrient cycling (Lanuza et al., 2018). Although a vast amount of tropical forests has been cleared (FAO, 2015) and their nutrient cycling services have been significantly disrupted (Lanuza et al., 2018), the cover of tropical secondary forests has increased in some regions as a result of changing land uses (Aide et al., 2013; Chazdon, 2014). Moreover, there has been a dramatic increase in large-scale forest restoration (Chazdon et al., 2017; Lanuza et al., 2018). Regenerating secondary forest is an increasingly common forest type in the tropics, creating a patchy distribution of disturbance histories and stand ages across the landscape (Schilling et al., 2016). In conserved tropical forest ecosystems, there is a continuous production of litter throughout the year (Werneck et al., 2001). The total amount of produced litter at different periods depends on the type and composition of the studied vegetation (Schumacher et al., 2011), the biotic and abiotic characteristics of the areas, and the degree of disturbance and connectivity of the areas (Nascimento et al., 2015). Therefore, the contribution of litter in disturbed areas can be used as an indicator to evaluate the vegetation recovery process (Nascimento et al., 2015). The vertical and horizontal structure of the plant community and the species composition and distribution may also interfere with the litter distribution and production (Vidal et al., 2007). Thus, the litter can be classified as an environmental indicator because it responds to changes in the ecosystems through changes in its deposition processes (Gessner et al., 2010; Nascimento et al., 2015).

Our study examined the patterns of litterfall and litter decomposition processes in primary and increasingly common disturbed secondary forests in a landscape of the Brazilian Amazon. The following specific hypotheses were tested: (1) leaf litter quantity and quality decrease in line with forest disturbance; (2) these trends are highly correlated with litter decomposition rates; (3) forest disturbance gradients could be identified using litterfall production and litter decomposition processes. If proved, these hypotheses could support our main objective that is the use of litterfall and litter decomposition processes to assess the recovery status of secondary forests in the neotropics.

2. Material and methods

2.1. Study area

The study was developed in the municipality of Uruará, southwestern Pará state, northern Brazil (−03°43′27″S; −53°44′8″W, Fig. S1). The region is located approximately 1000 km away from Belém, the capital of Pará state, and is crossed by the Transamazon Highway (official designation BR-230). Uruará was part of the Altamira PIC (Integrated Colonization Project), one of the first official settlements in the Amazon, created to resettle families from the south, southeast and northeast of Brazil (Perz and Walker, 2002).

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Land cover is characterized by large deforested areas radiating from the main road (TransAmazon) to the feeder roads (travessões), and spreading westward over time from the area of initial settlement in the east. The area has unevenly distributed patches of high-fertility soils known as "terra roxa". Extensive livestock production, exploitation of timber at a large scale (mostly illegal) and cacao production are the main agro-pastoral strategies, but are usually complemented by annual crops and horticulture. In some parts of the study area, sandy soils predominate and pasture and annual crop production are favoured (Cajaiba et al., 2017b).

The climate is characterized as hot-humid (Köppen's classification), with annual average temperature and precipitation of 26 °C and 2000 mm respectively (Peel et al., 2007). The studied areas make up representative habiats of the region, such as Primary Forest (PF); Secondary Forest with 25, 15 and 5 years of regeneration (denominated of SF-25, SF-15 and SF-5, respectively). In each of the studied habitats, four areas were selected, thus totaling sixteen sampling areas (see Table S1 supplementary material, for details of the sampling effort).

2.2. Environmental conditions monitoring

In order to evaluate the environmental complexity of each study site (four per habitat and sixteen in total), an area of 10 m × 10 m (100 m^2) was delimited around each collector. The following parameters were measured: density, given by the average number of arboreal individuals with diameter at breast height (DBH) > 5 cm, measured with a measuring tape directly on the stem (1.3 m); canopy cover (through the following scales: 0–5%, 6–25%, 26–50%, 51–75%, 76–95% and 96–100%) measured with a convex spherical densitometer; pH of the soil, according to the Manual of soil analysis methods proposed by Embrapa (1997).

The data of air temperature, pluvial precipitation, relative humidity (monthly average values) were provided by the Meteorological Station at Ceplac (Comissão Executiva do Plano da Lavoura Cacaueira). The meteorological data obtained for the study period confirm the classification of the climate of the region as being of Aw type of Köppen - tropical humid, presenting only two well defined seasons: rainy season, which starts in January until mid June; and dry season, starting in July through December. The total rainfall in the study period was 1912.65 mm. The highest values were recorded in the months of March (283.75 mm) and April (275.12 mm) and the lowest values, in the months of September (35.1 mm) and November (34.71 mm). The average value of the air temperature for the period was 25.09 °C. The highest average temperature occurred in September (28.5 °C) and the lowest in May (23.1 °C). Relative air humidity in the region remained above 57%, with November and December having the lowest values (57%) and April, the highest (98.01%) month (Fig. S2, Supplementary material).

2.3. Litterfall production

In each sampling area, 10 collectors made of 2 mm nylon mesh measuring 1.0 × 1.0 × 0.15 m, installed 30 cm above the soil surface were randomly distributed to avoid litter mass loss due to microbial activity. To avoid the edge effect, the collectors were installed at a minimum distance of 100 m from the edge. The litter was collected monthly, over a period of 12 months, from August 2016 to July 2017. Each sample collected was divided into fractions: leaves, thin branches (diameter ≤ 2 cm), reproductive material (flowers, fruits and seeds) and residues (unidentified plant material and parts of animals and/or waste). The latter was excluded from the analysis because this fraction is composed of material from different origins and that cannot be identified (Vidal et al., 2007). In the laboratory, the materials were packed in paper bags and submitted to forced circulation at 65 °C for 72 h. Each fraction was weighed separately on a 0.001 g high precision digital scale to determine its contribution to total litterfall. The total production was obtained through the sum of the four fractions, which represents the monthly production of litter per collector. The annual production of litterfall was obtained through the sum of the monthly production of the collectors and was recorded in mg ha^{-1} $year^{-1}$ to allow comparison with other studies (Almeida et al., 2015).

2.4. Litter decomposition

For estimating litter decomposition, portions of 10 g of leaves previously dried in an oven at 65 °C until constant weight, were packed in litter bags with 1 mm^2 mesh and measuring 20 × 20 cm and were randomly distributed on the surface of the forest floor, simulating the natural fall of the materials from which litter originates.

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The litter bags (28 per site study and 448, in total; see Table S1 supplementary material) were installed at the beginning of August and collected at 30, 60, 90, 120, 150, 180 and 210 days. At each period, four bags were removed in each settlement. After collection, the material contained in each decomposition bag was cleaned with a brush to remove soil particles and possible organisms attached to the leaves. Subsequently, the material was oven dried at 60 °C for 72 h and weighed to obtain the remaining mass.

2.5. Data analysis

Data was examined using univariate and multivariate two-tailed analyses. Data analyses were performed with the statistical program SPSS 17 for Windows and R v3.5.0 (R Development Core Team, 2016) using the packages *vegan* (Oksanen et al., 2013) and *glm2* (Marschner, 2011). Variables were tested for assumptions such as normality and homoscedasticity by inspecting residuals and using the Shapiro-Wilk test (Shapiro and Wilk, 1965).

2.6. Habitat-specific environmental conditions

We used One-way ANOVAs to gauge significant differences in environmental conditions among the studied habitats. Tukey post hoc tests were applied to check for pair-wise differences (Sokal and Rohlf, 1995). Additionally, a Non Metric Multidimensional Scaling (NMDS) was applied to collapse similarities/differences in litterfall production (total and fractions) between the different habitats, so that they could be easily visualized and interpreted.

2.7. Habitat-specific litterfall production and seasonality

Two-way ANOVA, followed by pair-wise comparisons (Tukey's test,) was applied to verify possible interactions between litterfall production (total and fractions), habitats and seasons. Before applying the ANOVA, the normality of the data was verified by the Shapiro-Wilk test.

2.8. Influence of environmental conditions on litterfall production

A generalized linear model (GLM) analysis was used to determine the variation in litterfall production (response variable) attributable to the environmental conditions considered (explanatory variables, see please *Measurement of environmental variables*), and which of them significantly contributed to explain such responses. We assessed the fit of each candidate model using the Akaike information criteria (AIC) value (Akaike, 1974; Hurvich and Tsai, 1989), by comparing all possible combinations using the Akaike weights (AICwi, Anderson et al., 2000). The equation with the lowest AIC and highest adjusted R^2 was selected in order to reduce complexity in statistical model selection (e.g. Santos et al., 2011). To deal with over-dispersion, we used the mean regression function and the variance function from the Poisson generalized linear model, leaving the dispersion parameter unrestricted (quasi-Poisson). This strategy results in the same coefficient estimates as the standard Poisson model; however, inference is adjusted for over-dispersion (O'Hara and Kotze, 2010). The tolerance values of explanatory variables were used to assess multicollinearity and remove redundant variables using Spearman's rho correlation coefficient (only predictors with correlation lower than 0.7, e.g. Elith et al., 2006).

2.9. Habitat-specific litter decomposition

The decomposition rate of the litter was quantified by means of mass loss measurements, with the following formula: Re% = (Po/Pr) × 100, where, *Re* is the percentage of mass remaining; *Po* is the initial dry weight of the leaf; *Pr* is the remaining weight (or final weight) of the leaflet, observed at the end of each month of study.

After the calculation of the remaining mass over the period, the decomposition constant k was calculated, according to Thomas and Asakawa (1993), according to the exponential model: $Xt = Xo \cdot e^{-kt}$, where, *Xt* weight of the dry material remaining after *t* days; *Xo* is weight of the dry material placed in the bags at time zero ($t = 0$), and *k* is the decay constant (unit: year^{-1}). Possible differences between decay rates were tested by analysis of covariance (ANCOVA), using habitat as covariate.

3. Results

3.1. Habitat-specific environmental conditions

The variables canopy cover, diameter at breast height and density were significantly different among all habitats, with higher values for primary forest - PF ($P < 0.05$). The secondary forest SF-5 (5 years of regeneration) was hotter and significantly different from PF and SF-25 ($P < 0.05$), but not significantly different when compared to SF-15 ($P > 0.05$). Relative air humidity was higher in PF and SF-15, while SF-5 was less humid ($P < 0.05$). There was no statistically significant difference between the habitats regarding monthly precipitation ($P > 0.05$). Regarding soil pH, SF-5 had more acidic soils, while PF had more alkaline soils (see Table S2, Supplementary material for associated variable differences between habitats).

3.2. Habitat-specific litterfall production and seasonality

The average annual litterfall production of the four areas, for the period studied, was 9.095 mg ha^{-1} year^{-1}. The total annual litter production was significantly different among the studied habitats (ANOVA, $F_{3,957} = 5.37$, $P < 0.0001$). The primary forest - PF, presented higher annual production of litter (10.86 mg ha^{-1} year^{-1}), significantly higher than the other habitats ($P < 0.0001$). On the other hand, the secondary forest with five years of regeneration (SF-5) produced the smallest annual amount of litter (7.41 mg ha^{-1} year^{-1}) and was significantly lower in relation to the other habitats ($P < 0.01$). The total litter production in the secondary forests (SF-25 and SF-15) did not differ among themselves ($P > 0.05$) (Fig. 1) (see Material Suplementar, Table S3, for details of the associated diferences and Tukey post-hoc values).

The leaf fraction presented the highest contribution in total litter production in all studied habitats (annual average mg ha^{-1} year^{-1}, dp ± 0.944). ANOVA showed statistical difference in leaf production between the studied habitats ($F_{3,957} = 51.18$, $P < 0.001$), being higher

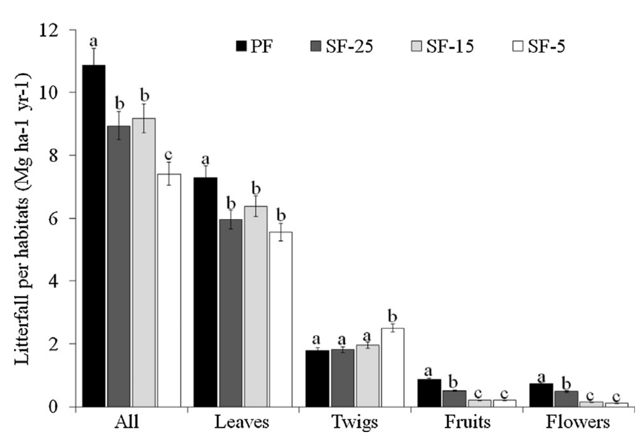

Fig. 1. Barplot expressing the annual average litterfall production and fractions per habitat. Error bars indicate 95% confidence intervals. The values followed by the same letters are not significantly different according to Tukey test. PF, Primary Forest; SF-25, Secondary Forest (with 25 years of regeneration); SF-15, Secondary Forest (with 15 years of regeneration); SF-5, Secondary Forest (with 5 years of regeneration).

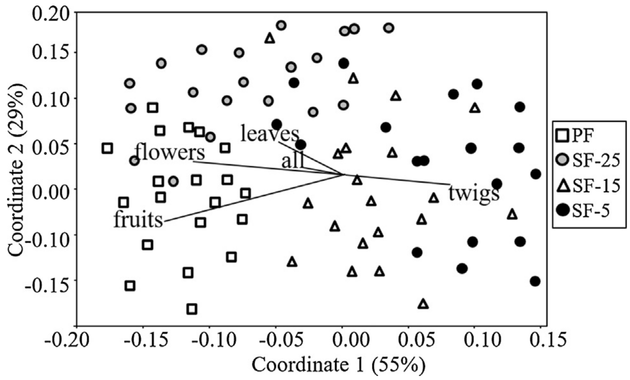

Fig. 2. Non-metric multidimensional scaling (NMDS) showing the annual litterfall production pattern (total and fractions) grouped in accordance with the habitats. PF, Primary Forest; SF-25, Secondary Forest (with 25 years of regeneration); SF-15, Secondary Forest (with 15 years of regeneration); SF-5, Secondary Forest (with 5 years of regeneration).

in PF ($P < 0.01$). Secondary forests did not show significant differences in leaf production ($P > 0.05$) (Fig. 1). The second largest fraction that contributed to total litter production was the twigs (annual average of 2.11 mg ha^{-1} $year^{-1}$, dp ± 0.334), being statistically different between the studied habitats (ANOVA, $F_{3,957} = 83.48$, $P < 0.001$). SF-5 was the habitat that presented the greatest contribution of twigs ($P < 0.01$). The other habiats did not differ ($P > 0.05$) (Fig. 1). Fruits and flowers were significantly different between habitats (ANOVA, $F_{3,184} = 281.51$, $P < 0.05$; $F_{3,266} = 164.49$, $P < 0.05$, respectively), with PF presenting higher values than the other habitats ($P < 0.05$) (Fig. 1) (see Material Suplementar, Table S3 for details of the associated diferences and Tukey post-hoc values). Regarding the annual litterfall production pattern (total and fractions), the NMDS results depicted significant similarities/differences between habitats: higher production of fruits and flowers in the primary forest (PF) and later secondary forest (SF-25), and the higher production of forest twigs in the early stages of regeneration (SF-5) (Fig. 2).

The total deposition of litter and its fractions followed a seasonal pattern throughout the analyzed period. During the dry season (September to November) there was an increase in total litter production, strongly influenced by the increase in leaf and branch production, a pattern observed in all the studied habitats (Fig. 3 and Fig. 4). There was a statistically significant difference in the production of leaves and branches, with higher values in the drier months for all habitats ($P < 0.05$) (Fig. 3 and Fig. 4). Flowers and fruits were higher in rainy periods in all the environments studied. However, no statistically significant difference was observed ($P > 0.05$), with the exception of PF that presented higher biomass in the rainy season for flowers and fruits ($P < 0.05$) (Fig. 3 and Fig. 4).

3.3. Influence of environmental conditions on litterfall production

The results of the generalized linear models (GLM) indicated that the total litterfall production and its fractions were explained by six variables: temperature, canopy cover, tree circumference, tree density, humidity and precipitation (Table 1). Total litterfall production was positively correlated with temperature and canopy cover and negatively correlated with humidity and tree circumference. Leaf fall was positively influenced by higher temperatures and negatively influenced by humidity. The production of twigs was influenced by the canopy cover. Canopy cover, tree density and precipitation were associated with an increase in fruit production, while the temperature negatively influenced the production of fruits (Table 1).

3.4. Habitat-specific litter decomposition

An exponential regression model adequately described decomposition rates for all habitats studied, with R^2 values varying from 0.83 to 0.97 (Fig. 5, see model equations for all habitats in Table S4, supplementary material). The average litter decomposition rate for all habitats

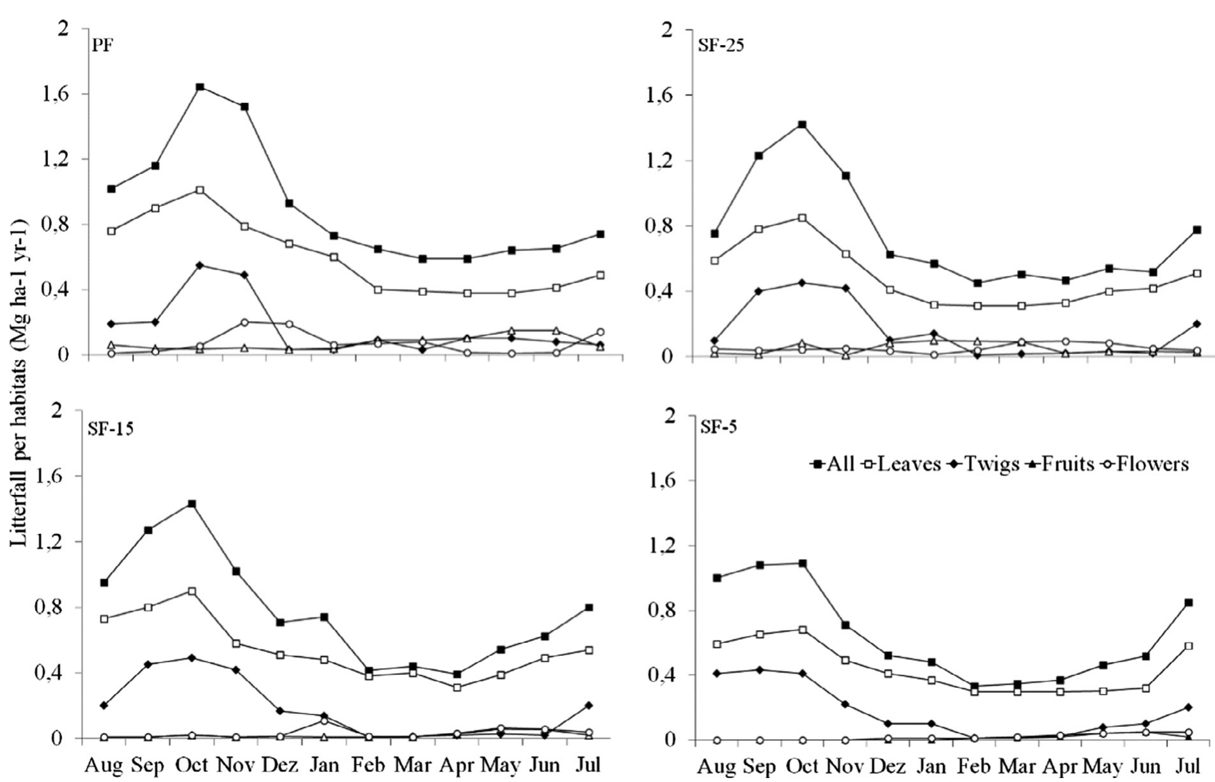

Fig. 3. Mean monthly litter fall and fraction per habitat. PF, Primary Forest; SF-25, Secondary Forest (with 25 years of regeneration); SF-15, Secondary Forest (with 15 years of regeneration); SF-5, Secondary Forest (with 5 years of regeneration).

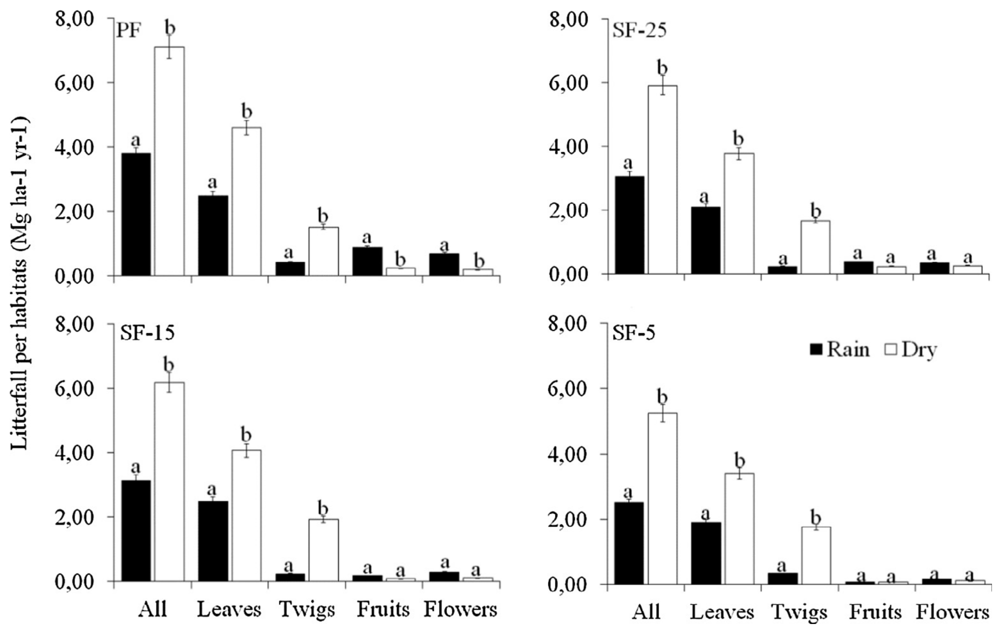

Fig. 4. Seasonal litterfall production (total and fractions) for the rainy season (corresponding january to june) and dry period (corresponding july to december) for all the studied habitats. The values followed by the same letters are not significantly different according to Tukey test.

Table 1
Parameter values of the generalized linear models (GLM; selected by the highest Akaike weight and adjusted R^2) used to determine of the variation in litterfall production. Akaike Information Criteria (AIC), Akaike information criteria weights (AICw – values in parentheses), Adjusted R^2 ($AdjR^2$), Variance ratio (F), significance level ($^{**}P < 0.001$, $^{*}P < 0.01$). (T, Temperature; CC, Canopy cover; DBH, Diameter at breast height; D, Density; H, Humidity; P, Precipitation).

Equations	AIC (AICw)	$AdjR^2$	F
Litterfall production			
All = 27.051 + 0.207 * T + 0.314 * CC − 0.411 * DBH − 0.159 * H	51.932 (1.862)	0.74	28.01^{**}
Leaves = −2.342 + 0.31 * T − 0.029 * H	17.443 (0.821)	0.62	44.13^{**}
Twigs = −4.115 + 0.082 * CC	26.176 (0.516)	0.39	37.74^{*}
Fruits = 37.214 − 0.212 * T + 0.192 * CC + 0.501 * D + 0.092 * P	13.001 (0.759)	0.22	20.14^{*}

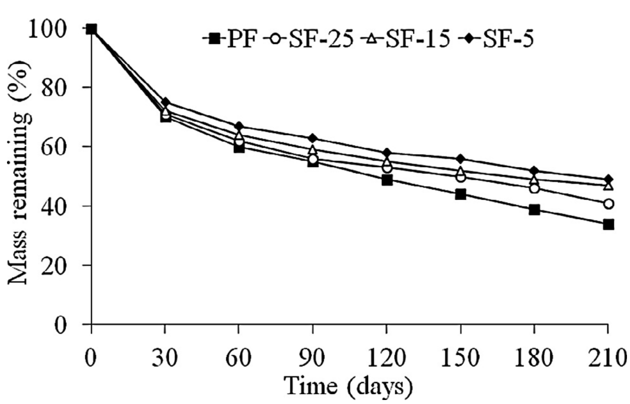

Fig. 5. Percent of initial dry-mass remaining as a function of incubation period in litter. The decomposition equations of the exponential regression model for all studied habitats are expressed in Table S4, supplementary material. PF: Primary Forest; SF-25: Secondary Forest (25 years of regeneration); SF-15: Secondary Forest (15 years of regeneration); SF-5: Secondary Forest (5 years of regeneration).

was approximately 55%. The most conserved habitats (PF and SF-25) attained highest rates of decomposition with (60% and 57%, respectively) (Fig. 5). The rate of decomposition was more intense in the first 60 days for all habitats (Fig. 5).

The habitat type had a significant effect on litter decomposition in the studied habitats (ANCOVA, $F = 19.54$, $P < 0.01$), and the process was hastened in PF in relation to disturbed habitats (SF-15 and SF-5, $P < 0.05$). However, PF was not different from SF-25 ($P > 0.05$). SF-15 and SF-5 also did not differ among themselves in the decomposition rates ($P > 0.05$) (Fig. 5).

The average decomposition rate K obtained for the period was 0.35. However, each environment had different rates: PF ($K = 0.49$), SF-25 ($K = 0.38$), SF-15 ($K = 0.28$) e SF-5 ($K = 0.26$).

4. Discussion

4.1. Litterfall production and habitats

The known values of litterfall production for tropical forests apparently demonstrate the varied character of this process, which must be analysed by including the interaction of climatic, edaphic, biological factors, and successional stages of forests (Cianciaruso et al., 2006). This study found a higher production of leaves among the litter fractions, followed by twigs, reproductive parts and miscellaneous. These results were consistent with the pattern observed in most tropical forests (Sousa Neto et al., 2011; Dickow et al., 2012). The specific separation of leaf fraction is of great importance as it can provide data on phenology, nutrition, and patterns of nutrient cycling system (Ferreira et al., 2014). Leaves are one of the most important components of litter and respond rapidly to climatic changes (Liu et al., 2004). On our study site, the proportion of leaf litterfall in relation to stems and reproductive structures was higher across all months. On the other hand, secondary forest with 5 years of regeneration presented a higher production of twigs. According to Almeida et al. (2015), areas with low plant density have simple vertical and horizontal vegetation structure, affecting litterfall production. This simplification of forest structure allows greater wind speed within the forest, which can cause the fall of branches and leaves (Almeida et al., 2015). The effect of wind combined with low air humidity and high temperatures increases evapotranspiration levels and accentuates the effects of water stress on litterfall production (Almeida et al., 2015). The number and density of mature trees in primary forests that regularly produce abundant flowers, fruits, and seeds during the year may result in a higher variation in reproductive parts compared to secondary forests. The higher litterfall in the primary forest compared to the secondary forests has corroborated our hypotheses that higher litterfall would be observed in the primary forest due to their superior biomass and closed canopy (Werneck et al., 2001; Vidal et al., 2007). The higher biomass produced in the primary forest may be associated with a high number of old and large tree species that present greater deposition of the leaf fraction, especially during the dry season. This process may be a response to water stress because abscission would reduce the water loss through transpiration (Londe et al., 2016).

Several factors affect the production of litterfall, such as succession stage, tree age, and dominant plant or tree species (Barlow et al., 2007; Celentano et al., 2011). Quantitative changes in the litter layer affect the population dynamics and community structure of soil animals that in turn affect the breakdown of organic matter and its incorporation into the soil (Sayer, 2006; Santos et al., 2008). In disturbed areas, the litterfall composition may have a great importance to understand ecological properties because the diversity of plant species is related to biomass production and availability of nutrients to the soil. Moreover, litterfall composition provides information regarding the relationships between living beings and the ecosystem (Ferreira et al., 2014).

4.2. Litterfall seasonality and environmental conditions

Litterfall may be affected by physical factors such as the mechanical action of wind and rain and plant physiological responses to environmental changes (Santiago and Mulkey, 2005; Valenti et al., 2008). On a regional scale, precipitation and temperature are the most important climatic factors controlling ecological processes (Liu et al., 2004) related to the litterfall (Cianciaruso et al., 2006; Valenti et al., 2008). The pattern of temporal variation in litterfall production found in our study, with a peak in dry periods, has been recorded in most studies in the Amazon and other tropical regions (Barlow et al., 2007; Silva et al., 2011). Leaf aging, caused by photoinhibition, stomatal closure, and subsequent leaf overheating, might lead to leaf shedding at the end of the dry season (Sanches et al., 2009; Almeida et al., 2015). As a side effect, trees are prepared for the upcoming season of highest net primary production. By contrast, the peaks during the rainy season are the result of strong winds and thunderstorms (Dawoe et al., 2010; González-Rodríguez et al., 2011). This finding explains the observed increase in peaks of branch and deposition inactivity during wet months.

The production pattern of the fractions that compose the litterfall, in relation to the dry and rainy period, corroborates several studies (Silva et al., 2007; Sanches et al., 2008). The mechanical action of rain (during rainy season) associated with wind may have contributed to an increase in the reproductive material of plants (flowers and fruits) in primary and late secondary forests and the highest number of twigs in the forest in the early stages of regeneration (Vendrami et al., 2012). The pattern observed for the reproductive material fraction may be related to the adaptation of many species to the local climatic seasonality. Flowering and/or fruiting occur at the end of the dry season and beginning of the rainy season when more favourable conditions for seed germination and seedling development are present (Muniz, 2008; Almeida et al., 2015). In addition, forests in early stages of regeneration have few species of flowering plants, probably because they have not reached reproductive age yet (Londe et al., 2016). The highest production of reproductive parts during the highest precipitation period may emerge due to the increased investment of plants in reproduction because the environmental conditions are less limiting. Barlow et al. (2007) found a higher production of fruit during the wet season in a secondary forest in the Amazon. Sanches et al. (2009) examined data indicating that the fraction of reproductive parts (i.e. flowers) was observed only in the rainy season. The production pattern observed in the fraction the twigs, mainly fine twigs, is possibly associated with the mechanical energy imposed by the wind during rains, allied to the weight gain of the twigs by watering, thus facilitating its fall and, consequently, increasing its production at the beginning of rains (Martins and Rodrigues, 1999; Almeida et al., 2015). Drying and dying of smaller branches during the dry season can also contribute to their fall at the beginning of the rainy season.

4.3. Litter decomposition, habitats and environmental conditions

The litter decomposition process has a fundamental role in the nutrient flux to the soil (Patricio et al., 2012). Its significance increases in degraded sites where the recovery of self-determining functions strengthens their existence (Horodecki and Jagodziński, 2017). In our study, the hypothesis that decomposition rates would differ between habitats was supported. Gradients of forest recovery/disturbance were associated with trends in decomposition. Primary forests and late secondary forests presented faster decomposition rates compared to secondary forests at the initial regeneration stages. This result counteracts studies on tropical forest succession showing that environmental conditions for litter decomposition at the early successional phases were as favourable as those at the late successional phases (Xuluc-Tolosa et al., 2003; Vasconcelos and Laurance, 2005). On the other hand, higher temperatures and lower soil moisture in younger forests under a developing canopy may contribute to slower decomposition rates (Martius et al., 2004), which reinforce the hypothesis of higher soil moisture and higher decomposition rate found in this study during the litterbag exposition. According to Uma et al. (2014), the processes of leaf decay are largely controlled by soil microorganisms and are, therefore, influenced by temperature, moisture, and pH.

The material exposed to decomposition showed a marked decrease in the first months (average of approximately 28% in the first 30 days), which might be expected due to the great contribution of organic matter to the total litterfall. This finding can be attributed to favourable climatic conditions of the tropics (high temperature and humidity) for decomposition activity (Vendrami et al., 2012). At a regional scale with similar climatic conditions, litter decomposition rates are primarily controlled by litter quality (Pandey et al., 2007; Cornwell et al., 2008). In addition, leaf litter decomposition is a complex process affected by tree species, microclimate, and soil properties. Several authors indicated that the role of litter quality in enhancing decomposer activities is at least as important as abiotic factors (e.g. temperature and soil moisture) in tropical and temperate forests (Madritch and Cardinale, 2007; Cizungu et al., 2014; Veen et al., 2015). Tree species affect decay dynamics by supplying litter of a specific quality and generating species-specific micro-environmental conditions. Weight loss during leaf decomposition can be divided into two phases: an initial rapid loss due to the leaching of soluble components in the litter such as sugars and proteins and a period of slower mass loss due to the breakdown of more recalcitrant components such as cellulose and lignin (Xu et al., 2004).

4.4. Litterfall and litter decomposition as indicators of forest recovery

Anthropogenic disturbance such as deforestation for monocultures, forest fires, forest fragmentation, selective cutting of timber affects soil and litter characteristics as well as biodiversity (Erfani et al., 2017). Thus, sustainable management requires a detailed understanding of the complex relationships between disturbance levels and ecosystem functioning indicators (Cajaiba et al., 2018). Litterfall is a useful indicator of productivity and ecological functions and has been used to monitor site productivity and nutrient cycling (Khanna et al., 2009). The monitoring protocol requires frequent visits to litterfall traps for at least an entire year in tropical forests (Martinelli et al., 2017). Careful analysis of non-foliar fractions can reveal valuable additional information and guide management and restoration actions (Londe et al., 2016). An example is the fruit that composes the fraction of reproductive litterfall: a large fraction of fruit may indicate the relationship between large vertebrates and seed dispersal (Ferreira et al., 2014). Moreover, the fall of twigs may be an indirect indicator of community maturity because young plants tend to lose smaller twigs (Londe et al., 2016). In fact, the NMDS analysis demonstrated that the recovery of forests is associated with higher production of fruits and flowers, while the dominance of twigs and branches indicated disturbance. These functional characteristics must be selected according to land use, soil characteristics, and environmental circumstances (Cardoso et al., 2013; Erfani et al., 2017). In this way, understanding of litter dynamics in different stages of forest regeneration could be used as a proactive method to recommend restoration practices for landowners and public agencies (Celentano et al., 2011).

4.5. Implications for forest management and restoration in neotropical ecosystems

Secondary forests in the neotropics typically occur on land abandoned after few years of cultivation because of the characteristic low soil fertility (Gómez-Acata et al., 2016; Tian et al., 2018). Neotropical forests have been drawing more attention due to increasing intensity of anthropogenic disturbance because they may act as buffer zones, service providers, and habitats for endangered species displaced from destroyed primary forests (Brearley et al., 2004). Although secondary forests may replace some important ecosystem functions such as nutrient cycling and carbon storage (Ostertag et al., 2008), other attributes such as biodiversity may take a longer time to recover because they are highly depend on complex dispersion and habitat selection processes (e.g. Gardner et al., 2007; Barlow et al., 2007; Trumbore et al., 2015). It is therefore vital to understand which functions and services can be provided by secondary forests and to what extent ecosystem functioning is restored during forest recovery and regeneration (Lohbeck et al., 2015). This information will be fundamental to sustain functions and services in future tropical forest landscapes dominated by anthropogenic habitats (Lohbeck et al., 2015). Strategies to implement forest recovery are particularly needed in the tropics, given the rate of landscape change (Lamb et al., 2005) and the need to maintain essential ecosystem functioning (Celentano et al., 2011).

5. Conclusion

The obtained results represent a useful contribution to understand the relevance the dynamics of the litterfall and litter decomposition under very complex and variable regional conditions. In general, our results have shown that in Amazonia (1) the decomposition of litter is slower in in more disturbed environments than late primary and secondary forests, and (2) within similar climatic conditions, litterfall and litter decomposition rates begin to stabilize in 25-y-old secondary forests. However, previous studies have shown that not all nutrient cycling functions are restored in the long term (e.g. Martius et al., 2004). Therefore, litterfall and decomposition experiments in older secondary forests should be done to clarify if the effects of microclimatic patterns are consistent through the years. We consider the relation between these patterns and the potential effects of on decomposition under land-use change fundamental investigation. In addition, future work should also examine in detail the role of the diversity of decomposers (invertebrates, bacteria and fungi) for the magnitude and stability of litter decomposition in tropical forests. Nevertheless, since ecological integrity of the studied ecosystems can be only partly assessed by litterfall indicators, our results should be complemented with information from other indicators, interactions and interferences with precise applicability conditions. Despite the limitations inherent to a preliminary demonstration, the methodology proposed is applicable to other type of ecosystems affected by gradients of changes.

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