Litterfall dynamics along a successional gradient in a Brazilian tropical dry forest

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Abstract

Background: This study aimed to determine the influence of soil traits, vegetation structure and climate on litterfall dynamics along a successional gradient in a tropical dry forest (TDF) in southeastern Brazil. We used a chronosequence design consisting of three successional stages (early, intermediate, and old-growth) defined based on forest age and vertical and horizontal structures.

Methods: Litterfall was recorded monthly for three years in 12 plots of 50×20 m (four plots per stage) where vegetation parameters (species richness, basal area, density and height for trees with diameter at breast height ≥ 5 cm) and soil chemical and physical traits were previously obtained. We placed eight 0.5-m^2 litter traps in each plot, totalling 96 traps. Samples were sorted into leaves, twigs, reproductive parts, and debris.

Results: Litterfall mass was composed mainly of leaves and varied slightly among years (4 to 4.5 Mg·ha^{-1}), within the range observed for other TDFs. Annual litterfall mass was higher at the old-growth forest than at the early and intermediate forest stages and this successional pattern was driven by vegetation characteristics (forest structural parameters and plant functional groups) and soil traits related to water-holding capacity. Litter amount in the intermediate stage was lower than expected for its forest structure (and similar to the early stage), possibly because its higher soil clay content increased the water holding capacity and leaf retention during the dry season. Seasonal variations in monthly litterfall were strongly driven by forest deciduousness and affected by climatic factors related to water availability. This pattern was consistent across the successional gradient, although differences for each litterfall component were observed.

Conclusions: Our results suggest that litter production in the studied TDF is influenced by multiple factors along succession, such as above-ground biomass and the degree of leaf retention mediated by soil water-holding capacity. Further studies on community phenological patterns can allow a better understanding of successional changes on litterfall and how fast this fundamental function recovers in secondary forests.

Keywords: Litterfall, Tropical dry forest, Secondary succession, Soil characteristics, Forest structure, Ecosystem functioning

Background

The timing and amount of litterfall (i.e., the above-ground senescent biomass that periodically falls to the soil surface; Ewel 1976) are strongly regulated by abiotic conditions, such as water, temperature, photoperiod and soil nutrients (Martínez-Yrízar and Sarukhán 1990; Lopes et al. 2015). Litterfall seasonality is tightly related to plant vegetative phenology (i.e., leaf emergence, development, ageing and abscission) because most of the litterfall mass is composed by leaves (Chave et al. 2009). Temporal patterns of leaf abscission that drive litter production vary across and within ecosystems, being unimodal, bimodal or irregular along the year (Zhang et al. 2014). In tropical dry forests (TDFs, Sanchez-Azofeifa et al. 2005), the litter production represents a more synchronized pulse of nutrient input to the soil system than in many other tropical forests (Jaramillo and Sanford 1995). The strong water deficit in the onset

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of the dry season is a crucial trigger of leaf shedding of the dominant drought-deciduous species, which compose at least 50% of TDF trees (Sanchez-Azofeifa et al. 2005). Indeed, TDFs occur in regions with mean annual precipitation between 700 and 2000 mm, and a marked dry season with at least three dry months (i.e., in which rainfall is lower than 100 mm; Sanchez-Azofeifa et al. 2005).

In TDFs, leaf loss in the dry season can reach up 95% (Pezzini et al. 2014), causing a massive accumulation of litter mass on the soil surface (Murphy and Lugo 1986; Lopes et al. 2015). At coarser spatial scales (i.e., regional or global), above-ground biomass and decomposition rates in TDFs increase with mean annual precipitation (Martínez-Yrízar 1995; Becknell et al. 2012; Gei and Powers 2014). The amount of litterfall is directly related to above-ground biomass accumulation (Lawrence 2005; Chave et al. 2009; Feng et al. 2019) and therefore affected by soil traits involved in forest growth (Peña-Claros et al. 2012; Yazaki et al. 2016) and vegetative phenology (Holbrook et al. 1995; Giraldo and Holbrook 2011). Usually, litter production is lower for vegetation types growing on nutrient-poor soils, especially those limited in phosphorus (P) (Alvarez-Clare et al. 2013; Alvarez-Clare and Mack 2015). P use-efficiency is generally high (i.e., biomass production is P-limited) and up to 65% of plant P is acquired through retranslocation (Jaramillo and Sanford 1995). In TDFs, the nutrients retranslocated from leaves during the dry season are used for growth at the next rainy season (Gei and Powers 2014). Furthermore, litterfall is affected by the available water in the soil (Holbrook et al. 1995; Jaramillo et al. 2011) which depends, in part, on soil texture (Pastor and Post 1986).

The amount of litterfall is also related to vegetation characteristics, such as floristic composition (Lowman 1988; Schilling et al. 2016) and forest structure (Ewel 1976; Celentano et al. 2011), which are influenced by forest age (Lebrija-Trejos et al. 2011; Nunes et al. 2014; Norden et al. 2015). During regeneration, forest structure components (e.g., plant height, density and basal area) usually increase (Quesada et al. 2009; Becknell and Powers 2014), positively affecting litter production (Ewel 1976; Celentano et al. 2011; Schilling et al. 2016). In turn, the increase in litterfall and changes in litter physical and chemical composition can affect successional pathways. Dominant life forms and functional groups change along forest succession (Ostertag et al. 2008; Nunes et al. 2014; Feng et al. 2019) and related shifts in plant carbon allocation patterns can alter leaf chemistry (Endara and Coley 2011) and, consequently, decomposition rates (Aerts 1997). Litter decomposition on the forest floor can accelerate the potential return of N and P in the soil (Yang et al. 2004; Feng et al. 2019; Froufe et al. 2019) and mediate plant competitive interactions,

usually favoring the replacement of pioneer species by intermediate- and late-successional species (Chazdon 2008). Litterfall can also change plant recruitment rates, acting as an insulating layer and reducing soil evaporation and the density of weeds (Facelli and Pickett 1991).

Few studies investigated differences in litterfall seasonality among successional stages in tropical forest (Lawrence 2005; Kalácska et al. 2005; Chave et al. 2009; Aryal et al. 2015). In TDFs of Southern Mexico, Lawrence (2005) observed that seasonal variations in litter production were more pronounced in old secondary and mature forests. The author hypothesized that young secondary forests are subjected to lower drought stress because their smaller biomass, total leaf area and transpirational demand would reduce plant requirements for water. In a study conducted in a semi-evergreen forest in the same region, Aryal et al. (2015) related successional differences in litterfall seasonality to changes in plant composition during forest regeneration. Thus, it is expected that TDFs at different successional stages will vary in the amount and timing of litter production. Considering that most TDFs regenerate naturally after ceasing anthropogenic impacts (Chazdon 2008), unraveling temporal and spatial patterns of litterfall along successional gradients is fundamental for a better understanding of ecosystem functional recovery.

Despite the recent increasing scientific interest in TDFs (Portillo-Quintero et al. 2015), few studies have investigated the effects of vegetation, soil and climate variables on litterfall dynamics (i.e., changes in litterfall mass and constituents over time) in these ecosystems. The present study aimed to determine the synergistic influence of soil (texture and fertility), vegetation characteristics (forest structure and plant functional groups) and climate on successional and seasonal variations on litterfall mass in a TDF using a chronosequence design. We compared the seasonal deposition of different components of litter (leaves, twigs, flowers, fruits, and animal debris) along three consecutive years in a TDF in southeastern Brazil. We tested the following hypotheses: (1) litterfall mass increases along a successional gradient and is positively related to forest structural parameters and soil nutrients, and is negatively related to soil water-holding capacity; (2) the seasonal variation in litter deposition is more pronounced in advanced successional stages due to their higher amount of leaf area and above-ground biomass.

Methods
Study site
This study was conducted in Mata Seca State Park (MSSP; 15,360 ha), located in the São Francisco River valley, between 14°48′36′′–14°56′59′′S and 43°55′12′′–44°04′12′′W, in the municipality of Manga, north of Minas Gerais state, Brazil. The MSSP was created in the

year 2000 after the expropriation of four farms where the main economic activity was extensive cattle ranching. In 2000, approximately 1,525 ha of the MSSP were covered with abandoned pasture fields at an early regeneration stage, whereas the remaining area of the park was a mosaic of old-growth and secondary dry forests and riparian forests. The climate in the region is 'Aw' according to the Köppen's classification system, and is characterized by wet summers and dry winters. The average annual temperature in the region is approximately 24 °C, whereas the average minimum temperature is 21 °C in July, and the average maximum temperature is 33 °C in October (Nunes et al. 2012). The annual average precipitation is around 871 mm and is concentrated in the short rainy season (November–January). The dry season extends from May to October (Nunes et al. 2012), whereas transition periods are represented by 4 months, between the rainy and dry season (February–April) and between the dry and rainy season (October) (see Additional files 1 and 2). The soil types in the study site are typically eutrophic red Latosol and Petroplinthic Haplic Cambisol originated from the Bambuí Group and from colluvial-alluvial deposits of the Quaternary (Nunes et al. 2014). Soil texture ranges from moderate to loamy and relief ranges from flat to slightly undulating. Soils are fertile with moderate pH and nutrient availability and low aluminum levels (Nunes et al. 2014; Espírito-Santo et al. 2014).

In the MSSP, TDFs at different successional stages occur on flat, non-karst soils (Nunes et al. 2014; Pezzini et al. 2014). The vegetation of the area is composed mainly of deciduous vegetation and is dominated by species of the families Fabaceae and Bignoniaceae (Madeira et al. 2009; Nunes et al. 2012). This study was conducted along a chronosequence of secondary and old-growth forest sites situated along a 5-km transect, aiming to minimize differences in topography, soil characteristics and microclimatic conditions (Madeira et al. 2009). Litterfall deposition was investigated in three areas at different successional stages (early, intermediate and old-growth forests), which were defined according to the vertical (i.e., canopy height and the number of tree crown layers in the vertical profile of the forest) and horizontal (i.e., tree density and basal area) structural characteristics of the forest, as well as the time since the last disturbance and previous land use. Information on forest age and use history was tracked back to the 1970's and 1980's through interviews with former farm employees and the MSSP manager. The early-successional forest was used as pasture for 20 years and is regenerating since the year 2000, when the park was created and pastures were no longer managed (8 years old when the litterfall sampling started), although free-ranging cattle occasionally entered this area until 2006. In 2008, early successional plots were mainly composed of sparse trees

approximately 4 m in height (shrubs and herbs). The intermediate stage forest was also used as pasture for an undetermined period and abandoned in the early 1970s (approximately 38–40 years old). It has two vertical strata: the first is composed of fast-growing trees, 10–12 m in height, and a few emergent trees up to 15 m in height. The second stratum is composed of a dense understory with many lianas and juvenile trees. The old-growth forest patches have no records of clear-cutting and present three strata: the first consists of large trees forming a relatively closed canopy; the second consists of juvenile trees of different ages and sizes; and the third contains typical understory herbaceous and shrub species. Old-growth forests were protected as "legal reserves" (according to the Brazilian forest code, 20% of the natural vegetation of each farm in this region must be preserved) of one of the farms that was expropriated to create the park. Despite this protection status, we cannot consider them as intact because illegal logging of single trees (not clear cutting) occurred occasionally, and cattle from nearby pastures occasionally entered both intermediate stage and old-growth forests for very short periods. We considered that the effect of these events on forest dynamics was negligible because their frequency was very low along decades.

Sampling design

To compare litterfall at different successional stages, we used a sampling design with years and successional stages as treatments and plots as replicates. Sampling was performed monthly from May 2008 to April 2011 in 12 permanent plots of 20 m × 50 m (four plots per successional stage) (Madeira et al. 2009; Pezzini et al. 2014). Eight 0.5-m^2 litter traps were placed in each plot, totaling 32 litter traps per successional stage and 96 litter-traps in the study site. Traps were 20 cm in height off the ground, allowing the contribution of herbaceous vegetation, which is especially important in the earlier successional stages (Nassar et al. 2008). Litterfall was sampled monthly and sorted into leaves (whole leaves, leaflets and rachides), twigs (woody parts and bark), reproductive parts (flowers, fruits and seeds), and debris (insect parts and other unidentified material). Litterfall fractions were oven-dried (at 80 °C) until a constant weight was achieved, and were weighed using an analytical scale (0.0001 g).

Vegetation data (tree species richness, stem density, height, basal area and abundance of three functional groups - pioneer, light-demanding and shade tolerant species - for trees with diameter at breast height ≥ 5 cm) and soil nutritional (pH, P-Mehlich, K, Ca, Mg, Al, H + Al, sum of bases, cation exchange, aluminum saturation, base saturation and organic matter) and textural data (coarse sand, fine sand, silt and clay) from the study

plots were extracted from Madeira et al. (2009) and Nunes et al. (2014) (see Additional files 3 and 4). Climatic data (precipitation, average wind speed, actual evapotranspiration, insolation, number of days with rain, average temperature and relative humidity) were obtained from the National Institute of Meteorology weather station located in Mocambinho, 10 km away from the MSSP.

Data analyses

Annual litterfall mass of each plot was estimated in Megagrams per hectare ($Mg \cdot ha^{-1}$). We used a multivariate analysis of variance (MANOVA) to evaluate the annual variation in total litterfall mass (all components together) among years and successional stages (Zar 2010). Then, we used analyses of variance (ANOVA) to perform the same comparisons for total litterfall mass and each litter component (leaves, twigs, reproductive parts and debris) ($n = 12$ plots for each year). Total litterfall mass and each litterfall component were used as response variables in separate analyses, whereas year and successional stage were used as explanatory variables. Mean litterfall values for years and stages were compared using Tukey's post hoc tests conducted after the above-mentioned ANOVAs. The data were log-transformed to meet the requirements of normality and homoscedasticity (Zar 2010).

Mean monthly litterfall mass of each plot was estimated over 36 months, using averaged data from the eight litter traps placed per plot. We used linear mixed-effect models (LME; Crawley 2007) to compare monthly variations on litter deposition (total and for each component separately; response variables). We used these models because monthly samples were taken repeatedly in the same plots. To deal with this nested structure, data were grouped by plot and the resulting groups (month/plot measurements) were codified as a random variable to account for temporal pseudoreplication along the study period (36 months × 12 plots = 432 observations; $n = 36$ groups).

To summarize the edaphic and vegetation structure data for the 12 studied plots, three independent principal component analyses (PCAs) were performed: (i) with soil chemical properties (13 soil chemical variables) as indicators of soil fertility; (ii) with soil physical properties (coarse sand, fine sand, silt and clay) as indicators of soil water-holding capacity; and (iii) with the vegetation characteristics data. A fourth PCA was conducted with climatic data collected over 36 months regardless of the successional stage (i.e., data were not collected per plot but for a single climatic station). We used PCA scores instead of the raw data because the soil, vegetation and climatic parameters were not orthogonal (i.e., not independent), then the use of multiple regressions would not

be recommended (Peña-Claros et al. 2012). The scores of the first axes from each PCA were chosen to indicate environmental gradients because they summarized the patterns observed in the data and explained most of the data variation (see Additional files 5 and 6), being suitable for use in the multiple regression models described below.

We used multiple regression analysis through generalized linear models (GLMs) to determine the effect of chemical and physical soil properties, vegetation characteristics and climatic variables on litterfall deposition (Crawley 2007). We used mean annual litterfall mass per plot as response variable and the scores from the first axes of three PCAs (texture, fertility and vegetation) as explanatory variables ($n = 12$). In this model, we used stepwise comparisons (backward selection) with the removal of non-significant explanatory variables and an adjustment for orthogonal partitioning of variance (type III sum of squares), in order to verify the proportion of variance exclusively explained by each variable regardless of the sequential order in which the explanatory variables were inserted in the model. Additionally, we performed a simple regression analysis using the average monthly litter mass (regardless of the successional stage) as response variable and the scores of the first axis of the PCA of climatic data as the explanatory variable ($n = 36$). All GLMs were adjusted for the Gaussian distribution and all continuous response variables were log-transformed. All analyses were followed by residual analyses and evaluation of error distributions adequacy (Crawley 2007) and conducted in the R software (R Development Core Team 2014).

Results

Annual and successional variations in litterfall amount and composition

In the studied TDF, litterfall was primarily composed by leaves ($4.30 \pm 0.01 \; Mg \cdot ha^{-1}$), followed by twigs ($0.94 \pm 0.08 \; Mg \cdot ha^{-1}$), reproductive parts ($0.29 \pm 0.02 \; Mg \cdot ha^{-1}$), and debris ($0.12 \pm 0.01 \; Mg \cdot ha^{-1}$). Total litterfall mass varied significantly among years (MANOVA - *Wilks* = 0.279, $F = 5.37$, $P < 0.001$, $n = 36$) and successional stages (MANOVA - *Wilks* = 0.138, $F = 10.2$, $P < 0.01$, $n = 36$). Mean annual litterfall mass (regardless of the successional stage) was higher in the Year 3 ($F_{2,33} = 7.33$, $P < 0.01$) and in the old-growth forest (regardless of the year) ($F_{2,33} = 7.22$, $P < 0.01$), but there was no interaction between years and successional stages ($F_{2,33} = 1.16$, $P > 0.05$). Total litterfall mass was higher at the old-growth forest in the Years 1 and 2, whereas no difference was found among successional stages in the Year 3 (Fig. 1). In addition, the mass of each litter component also varied among successional stages within each year, except for the Year 3 (Table 1). In general, in the Years 1 and 2, the mass of each litter
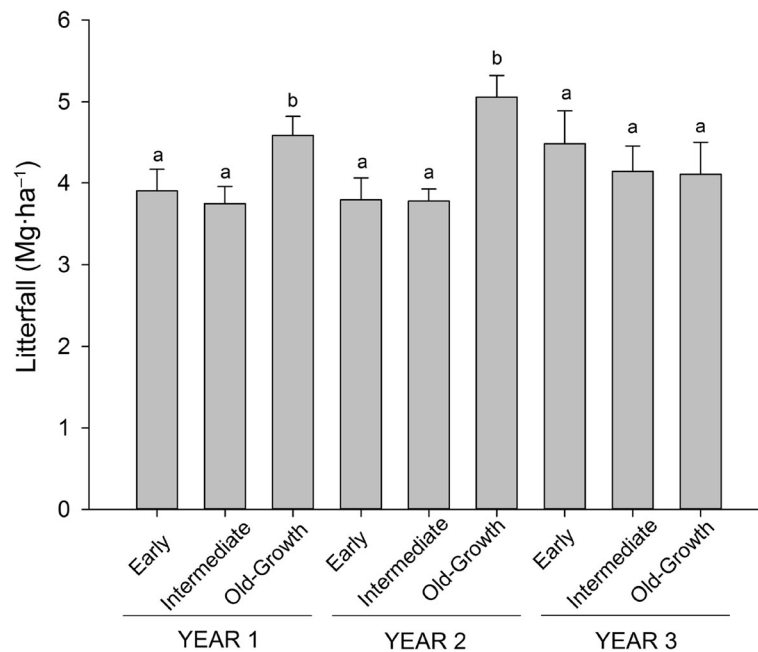
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Fig. 1 Mean (± SE) annual litterfall (Mg·ha^{-1}) per plot for (a) sampling years (May 2008 to April 2011) and (b) successional stages (early, intermediate and old-growth) in a tropical dry forest at Mata Seca State Park, northern Minas Gerais, Brazil (*n* = 12 plots for each year). Different letters represent statistically different means (*P* < 0.05) among stages within each year.

component tended to increase along the successional gradient, except for reproductive parts in the Year 1 and debris in the Year 2, which showed no significant differences among successional stages (Table 1).

Litterfall seasonality
As expected for a TDF, monthly total litterfall mass showed strongly seasonal variations for the three successional stages (*n* = 36, *F* = 4.58, *P* < 0.001; Fig. 2), peaking in the beginning of the dry season (in June in the Years 1 and 2 and May/June in the Year 3), when approximately 40% of the annual litter deposition occurred. The lower litter deposition (20%) was observed from September

to December, in the end of the dry season (when most plants were already leafless), and in the beginning of the rainy season, when new leaves are produced. Small peaks of litterfall were observed in the end of the rainy season, in March–April, as a consequence of short dry spells that usually occur in January and February (Fig. 2 and Additional file 2).

The deposition of each litter component also varied seasonally and showed different peaks across sampling years. The variation in leaf mass within successional stages ($F_{2,33}$ = 4.54, *P* < 0.001) showed a similar pattern to that observed for total litterfall mass, with peaks in the beginning of the dry season in June (Years 1 and 2)

Table 1 Mass of annual litterfall components (mean ± SE, Mg·ha^{-1}) during three consecutive years at three successional stages (early, intermediate and old-growth) of a tropical dry forest in northern Minas Gerais, Brazil (*n* = 12 plots for each year)

Years/Stages		Leaves	Twigs	Reproductive parts	Debris
Year 1	Early	3.43 ± 0.40 [a]	0.22 ± 0.03 [a]	0.16 ± 0.03 [a]	0.09 ± 0.03 [a]
	Intermediate	2.86 ± 0.14 [b]	0.55 ± 0.08 [b]	0.22 ± 0.03 [a]	0.12 ± 0.01 [b]
	Old-Growth	3.64 ± 0.18 [a]	0.54 ± 0.08 [b]	0.23 ± 0.02 [a]	0.17 ± 0.01 [c]
Year 2	Early	3.30 ± 0.40 [a]	0.27 ± 0.03 [a]	0.10 ± 0.02 [a]	0.12 ± 0.03 [a]
	Intermediate	2.76 ± 0.11 [b]	0.76 ± 0.08 [b]	0.16 ± 0.03 [b]	0.10 ± 0.01 [a]
	Old-Growth	3.84 ± 0.18 [c]	0.91 ± 0.08 [b]	0.18 ± 0.02 [b]	0.13 ± 0.01 [a]
Year 3	Early	3.51 ± 0.40 [a]	0.29 ± 0.03 [a]	0.32 ± 0.07 [a]	0.06 ± 0.03 [a]
	Intermediate	3.31 ± 0.11 [a]	0.40 ± 0.08 [a]	0.34 ± 0.07 [a]	0.08 ± 0.01 [a]
	Old-Growth	3.41 ± 0.18 [a]	0.34 ± 0.05 [a]	0.29 ± 0.06 [a]	0.06 ± 0.01 [a]

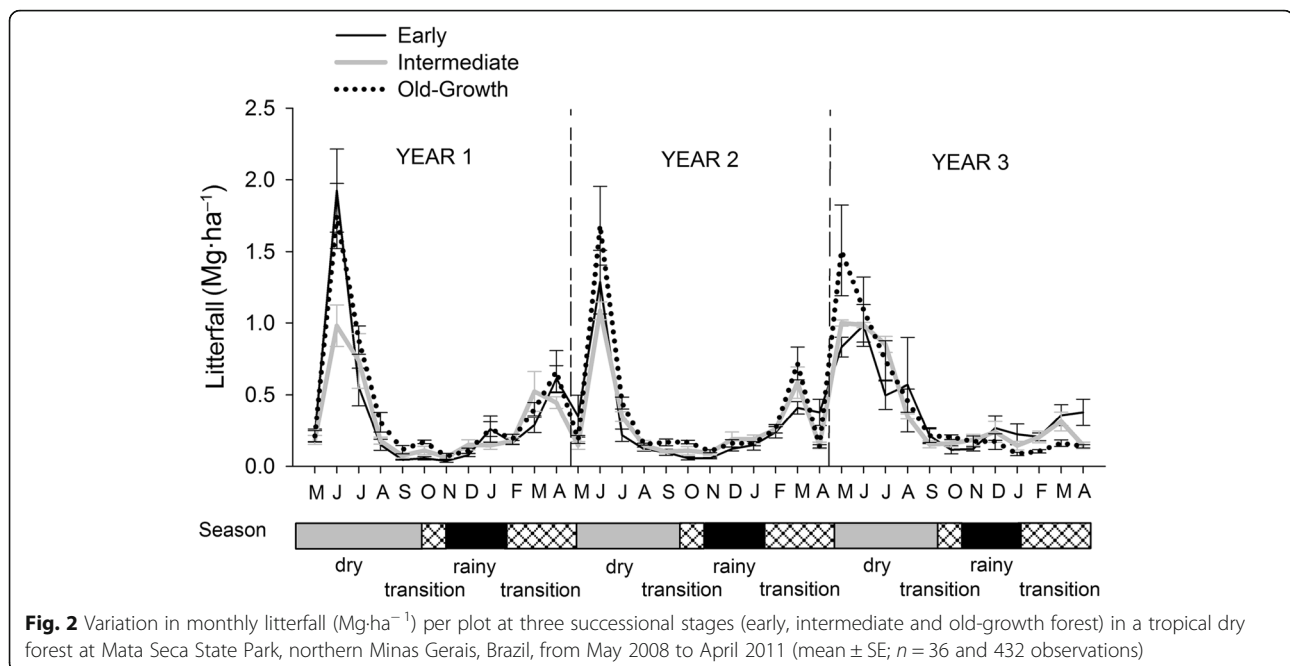Different letters in the same column indicate significant differences in a post-hoc Tukey test (*P* < 0.05)

Fig. 2 Variation in monthly litterfall (Mg·ha^{-1}) per plot at three successional stages (early, intermediate and old-growth forest) in a tropical dry forest at Mata Seca State Park, northern Minas Gerais, Brazil, from May 2008 to April 2011 (mean ± SE; $n = 36$ and 432 observations)

and May (Year 3) (Fig. 3a). Twig mass showed no clear pattern among successional stages across years ($F_{2,33} = 1.45$, $P < 0.01$) and peaked from January to May in different years (Fig. 3b). The mass of reproductive parts showed different patterns among stages and across sampling years ($F_{2,33} = 4.39$, $P < 0.001$). At the early- and late-successional stages, peak deposition of reproductive parts was observed during the dry season, from June to October in Years 1 and 2, and from August to December in the Year 3 (extending to the beginning of the rainy season in this year). At the intermediate stage, peak deposition showed no consistent inter-annual pattern, occurring at different months across the three years (Fig. 3c). Finally, the debris component showed a similar pattern in the three sampling years: higher biomass deposition from December to June, encompassing the whole rainy season and the beginning of the dry season, with slight inter-annual differences in peak deposition during this period ($F_{2,33} = 2.87$, $P < 0.001$) (Fig. 3d).

Drivers of litterfall deposition
The first axis of the PCA on soil texture explained 69% of the variation, correlating positively with clay and negatively with sand and silt contents (soil texture axis, see Additional file 5). The first axis of the PCA on soil fertility explained 87% of the variation, correlating positively with K$^+$, Ca^{++}, Mg^{++}, sum of bases and cation exchange, and negatively with aluminum saturation (soil fertility axis). The first axis of the PCA on vegetation characteristics explained 71% of the variation, correlating positively with basal area and tree height, and negatively

with the abundance of pioneer species (vegetation axis). Finally, the first axis of the PCA on climatic data explained 89% of variation, correlating positively with precipitation, number of days with rain and relative humidity (climatic axis) (see Additional file 6).

Mean annual litterfall mass was affected by the scores of all PCAs with the exception of the soil fertility axis (Table 2). The soil texture axis summarized the gradient in water-holding capacity of the soil and negatively affected the mean annual litterfall mass (Fig. 4a). Mean annual litterfall mass was positively related with the vegetation axis (Fig. 4b) and negatively related to the climatic axis (Table 2, Fig. 5).

Discussion
The present study is one of the few to evaluate successional differences in litter deposition in TDFs using data collected monthly across three years. As expected, litterfall dynamics was strongly driven by vegetative phenology (leaf deciduousness) in all successional stages, and was very concentrated in a single month (June) in the beginning of the dry season, although slight interannual variations were observed. On average, the annual amount of litterfall was higher in the old-growth forest, and plot variation in litter deposition was directly related to forest characteristics and inversely related to soil retention capacity. The recovery of ecosystem functions related to litterfall along succession in TDFs may depend not only on the resilience of above-ground biomass but also on soil traits affecting water availability and leaf retention during the dry season.
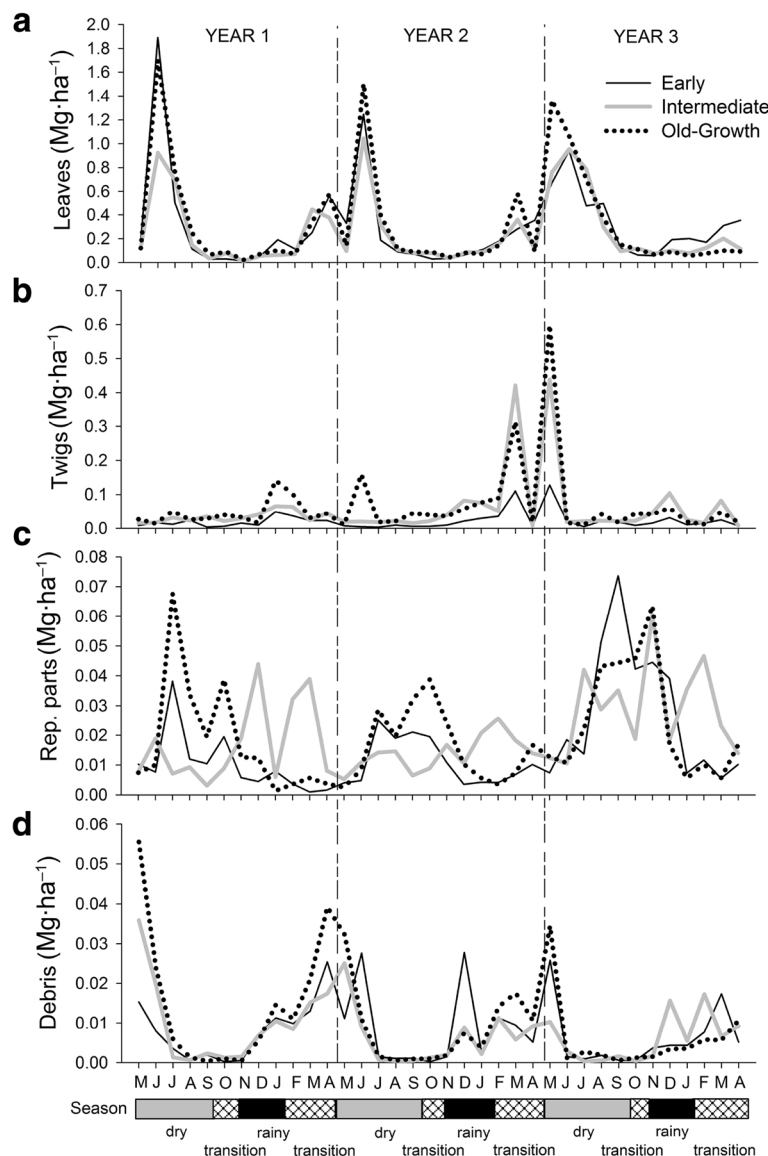
Fig. 3 Mean seasonality of litterfall fractions (Mg·ha^{-1}) per plot at three successional stages (early, intermediate and old-growth forest) of a tropical dry forest at Mata Seca State Park, northern Minas Gerais, Brazil, from May 2008 to April 2011. **a** leaves, (**b**) twigs, (**c**) reproductive parts and (**d**) debris (mean ± SE; *n* = 36 and 432 observations)

Annual and successional variations in litterfall deposition

Considering all successional stages together, litter biomass varied from 4 Mg·ha^{-1} in the first and second years to 4.5 Mg·ha^{-1} in the third year. This slight inter-annual variation (only 0.5 Mg·ha^{-1}; 12.5%) is within the range observed for other TDFs (Martínez-Yrízar 1995; Lawrence 2005; Cao et al. 2016; Rai et al. 2016) and may occur as a consequence of climatic factors (e.g., differences in the amount of rain between the studied years) or stochastic events (e.g., occurrence of windstorms that could cause tree fall and canopy opening, increasing litter deposition). Indeed, litterfall in year three peaked earlier (in May instead of June) and was less concentrated, with a

gradual decrease until August 2010. Total precipitation during the previous wet season was lower than the average (764 mm from September 2009 to May 2010; see Additional file 1), which could have increased water stress and leaf fall during the dry season of year three.

Mean annual litterfall mass was approximately 20% higher in the old-growth forest compared to the early and intermediate successional stages and this difference was related to vegetation characteristics, especially to basal area and height. Indeed, living above-ground biomass is more than six-fold higher in the old-growth forest compared to the early succession stages in the studied TDF (see Madeira et al. 2009; Espírito-Santo et al. 2014).

Table 2 Multiple regression through generalized linear models (GLM, type III sum of squares) showing the effects of the scores of the first axes from four principal component analyses: (i) soil texture, (ii) soil fertility and (iii) vegetation characteristics on the mean annual litterfall mass per plot ($n = 12$, adjusted $R^2 = 0.46$); and (iv) climate on the mean monthly litterfall mass ($n = 36$, adjusted $R^2 = 0.78$)

Response varhiable	Explanatory variables	DF	Deviance	Estimate	Standard Error	F	P
Mean annual litterfall mass ~ Axis1 from PCA texture + Axis1 from PCA fertility + Axis1 from PCA vegetation							
Annual litterfall mass	Null model (intercept)		0.839	1.404	0.031		
	Axis1 from PCA texture	1	0.126	−0.404	0.186	5.589	0.028[a]
	Axis1 from PCA fertility	1	0.016	0.009	0.035	0.709	0.409
	Axis1 from PCA vegetation	1	0.245	0.236	0.067	10.871	0.003[a]
Mean monthly litterfall mass ~ Axis1 from PCA climatic							
Monthly litterfall mass	Null model (intercept)		18.189	−1.103	0.168		
	Axis1 from PCA climatic	1	14.987	−0.013	0.002	4.71	0.041[a]

[a] Explanatory variable retained in the minimum adequate model ($P < 0.05$)
Estimates indicate intercepts and coefficient parameters. At both models, response variables were log-transformed

Similar results have been reported by Schlittler et al. (1993) and Lawrence (2005) for TDFs, reinforcing that there is a direct relationship between above-ground standing biomass and litter deposition. Despite that, litterfall amount varied considerably among plots from the same stage, and some intermediate plots with high basal area and height had lower litterfall than plots from early stages (see Fig. 4b). Indeed, some studies have reported higher litterfall at later successional stages (Martius et al. 2004; Lawrence 2005; Chave et al. 2009; Feng et al. 2019), whereas other studies have shown that litter mass is higher at early and intermediate stages because of the abundance of herbaceous, shrubby and small pioneer tree species that have high aerial biomass (Ewel 1976; Vendrami et al. 2012). In our study, litterfall was negatively correlated with the abundance of pioneer tree species in the plots, but our inclusion criteria (diameter at breast height ≥ 5 cm) underestimates the biomass of a vegetation layer (herbs and shrubs) that probably contributes substantially to litter deposition in early successional stages.

However, our results suggest that vegetation characteristics are not the only factors driving successional differences in litterfall in TDFs. Soil traits, mostly related to water-holding capacity, also affected the variations in litterfall amount among plots. The PCA analysis indicated that clay content was the main factor involved in the negative relationship between mean annual litterfall mass and the texture axis (see Fig. 4a). The higher retention of water in clay soils (Pastor and Post 1986; Resende et al. 2002) would allow plants to hold their leaves for a longer period, decreasing litter deposition. Greater values for soil clay content were recorded at the intermediate stage and may have reduced litterfall to the levels observed in the early stage, despite their marked differences on the forest parameters considered in the present study. In the old-growth forest, where above-ground biomass is much higher and clay content is

similar to the early stage, litterfall remained higher than the other two stages. Thus, it is likely that the interplay between vegetation characteristics (i.e., forest structure and abundance of pioneer species) and soil physical characteristics influence the amount of litterfall along the secondary succession in TDFs. Anyway, our GLM model indicated that the vegetation axis-1 explained 30% of the mean annual litterfall mass, whereas 15% was explained by soil texture axis-1. Other variables not evaluated in the present study, such as species diversity associated with leaf lifespan and phenology and plant physiology, could provide additional information on the causes of differences in litter deposition among successional stages.

Seasonal variations in litterfall

As expected, the temporal litterfall dynamics was strongly determined by climatic factors that affect vegetative phenology, especially water availability (precipitation, air humidity and number of days with rain). Indeed, the model that tested the (negative) relationship between mean monthly litterfall mass and PCA climatic axis showed a high deviance value ($R^2 = 78\%$, see Fig. 5). The role of water stress in driving seasonal variation in litterfall, with peaks in the beginning of the dry season, was already reported in other studies with TDFs (Reich and Borchert 1984; Jaramillo and Sanford 1995; Xuluc-Tolosa et al. 2003; Lopes et al. 2015). However, the influence of climate on leaf abscission is complex (Holbrook et al. 1995) and the vegetation may show delayed responses, shifting the peak of leaf fall ahead of the maximum and/or minimum values of the climate variables (Martínez-Yrízar 1995; Becknell et al. 2012). Such variability was detected in our three-year study, as the litter deposition pattern was slightly different in the Year 3 (dry season of 2010). However, we did not detect a clear trend in monthly precipitation during the study period that could explain such variation (see Additional file 1).
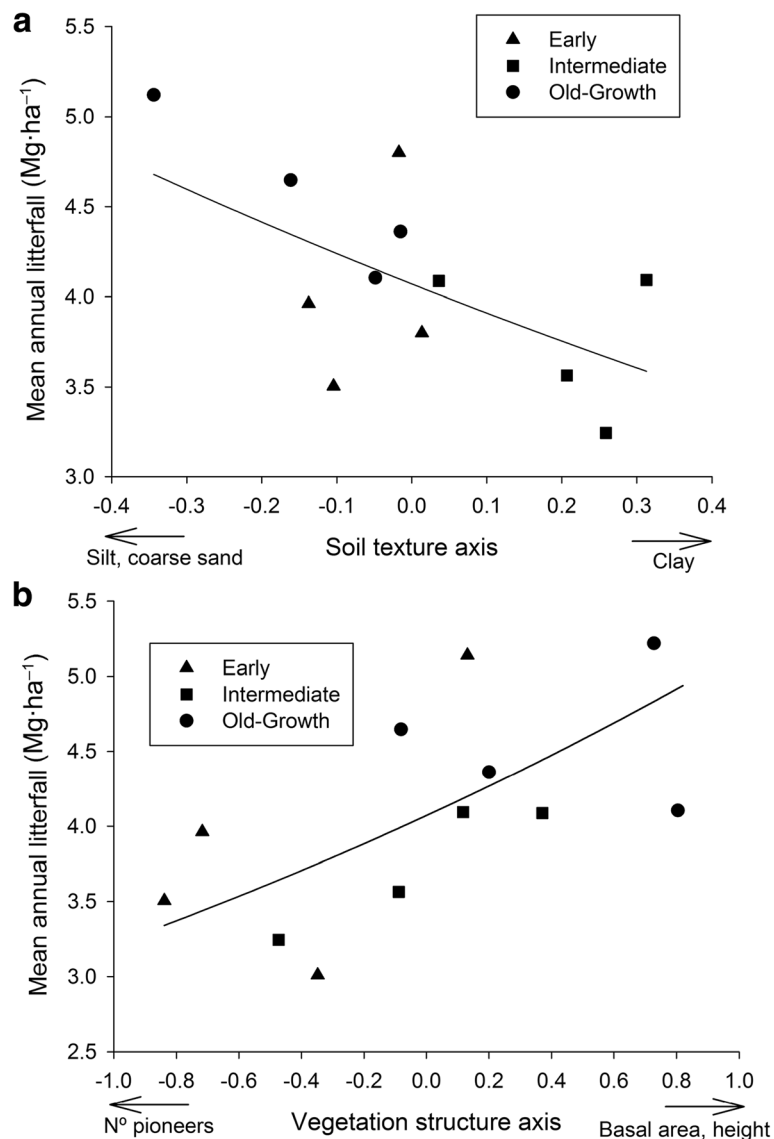
Fig. 4 Mean annual litterfall mass (Mg·ha^{-1}) in relation to (**a**) soil texture and (**b**) vegetation characteristics (summarized by the scores of the first axes of principal component analyses; mean ± SE; $n = 12$)

Seasonal variations were consistent across successional stages for total litterfall mass and for the leaf component, indicating that differences in the plant community (functional groups) and habitat conditions (soil traits and forest structure) are not as important as climatic factors for litterfall dynamics. A similar result was observed for temporal variations in leafing intensity, which did not differ among successional stages from 2007 to 2010 in the same plots (Lopezaraiza-Mikel et al. 2014), highlighting the tight, climate-controlled connection between litterfall seasonality and community vegetative phenology in TDFs. The other litterfall components showed less consistent temporal and successional patterns. Twig mass is composed by dead branches that

usually remain attached to the trees for a longer time due to the structure and architecture of the canopy (Maass et al. 2002). Their deposition can occur during the rainy season as a consequence of stochastic events such as hail, lightning, storms and strong winds. The mass of debris was mainly composed of insect faeces and body parts, and similar results have been reported by Martínez-Yrízar and Sarukhán (1990) and Martínez-Yrízar (1995). Peaks in this component of the litterfall were observed in the rainy season, when herbivorous insects are more abundant, and in the beginning of the dry season, when insect death is high due to the synchronization of their life cycle with leaf availability (Silva et al. 2012; but see Silva et al. 2017).
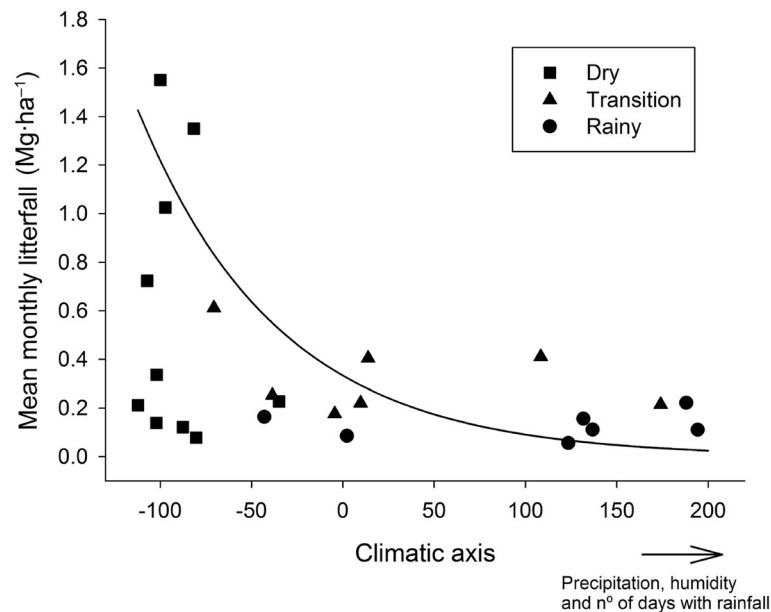
Fig. 5 Mean monthly litterfall mass (Mg·ha^{-1}) in relation to climatic variables (the climatic gradient was summarized by scores of the firs axis of a principal component analysis; mean ± SE; $n = 36$)

The mass of reproductive parts in the litterfall may be determined by the dispersal syndromes of the plant species, because flower and fruit falls are highly variable in time and reflect the reproductive phenology of the species. The deciduous, wind-dispersed species that dominate the studied TDF usually produce flowers during the dry season and fruits in the beginning of the rainy season (Nunes et al. 2012). Also, plant species dispersed by animals usually produce flowers and fruits in the middle of the rainy season (Pezzini et al. 2008, 2014). Thus, the deposition of reproductive parts in the litterfall occurs in peaks along the entire year. However, the reproductive phenology differs among successional stages (Pezzini et al. 2014, Lopezaraiza-Mikel et al. 2014), with consequences to litter deposition. Although the temporal patterns were similar for the early stage and the old-growth forest, this litterfall component was quite different for the intermediate stage, probably as a result of its much higher abundance of lianas, a life form with a contrasting reproductive phenology in relation to trees (Ramírez 2002).

Conclusion

Litterfall dynamics is a key process in ecosystem functioning and the long-term evaluation of litter components along successional gradients provides fundamental information on TDF regeneration, including productivity, nutrient and water cycling, seed germination and seedling recruitment, vegetative and reproductive phenology and fauna activity. Our three-year study showed consistent climatic effects on litterfall seasonality and interannual variations. Although temporal patterns of litter deposition did not differ among stages, total litterfall was 20% higher in the old-growth forest compared to the early and intermediate stages, a difference that is much lower than the observed for forest structural parameters (Madeira et al. 2009; Espírito-Santo et al. 2014). This result suggests that litterfall in the studied TDF is influenced by multiple factors along succession, such as the degree of leaf retention mediated by soil water-holding capacity. Further studies on community phenological patterns can allow a better understanding of successional changes on litter deposition and how fast this fundamental function recovers in secondary forests.

Additional files

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Additional file 5: Table S5. Loading of the first axes from three principal component analyses (PCA): soil texture, soil chemistry and vegetation characteristics. Significance levels are based on a Pearson's correlation between soil and vegetation properties and the scores of the first axes of the PCAs for 12 plots from three successional stages (early, intermediate and old-growth) in a tropical dry forest. Bolded correlations are significant at $P < 0.05$. (PDF 45 kb)

Additional file 6: Table S6. Loading of the first axis from a principal component analyses (PCA) using climatic data from the Mocambinho weather station, 10 km away from the Mata Seca State Park. Significance level are based on a Pearson's correlation between climatic properties collected during the 36 months of study and the scores of the first axis of the PCA. Bolded correlations are significant at $P < 0.05$. (PDF 627 kb)

Authors' contributions
Conceived and designed the study: MDMV, ASA, MMES and GWF. Collected data and samples in the field: SRS, MMES and MDMV. Processed samples in the lab: SRS and MDMV. Analyzed the data: SRS, JOS, BGSB and MDMV. Wrote the paper: SRS, MDMV, MMES, GWF, BGSB, JOS and ASA. All authors read and approved the final manuscript.

Availability of data and materials
The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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