



PRECIPITATION DEFICITS AND HIGH TEMPERATURE INCREASE LEAF LITTERFALL IN OPEN RESTINGA VEGETATION, IN SOUTHERN BRAZIL

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Abstract: Climate is an important driver of litterfall along different ecosystems. However, little is known about how climate affects litter production in plant communities of Restinga. The aim of this study is to characterize the temporal variation in leaf litter production in an Open *Clusia* Formation in Restinga de Jurubatiba National Park, from 2001 to 2018, and assess how local variability in litter production reflects the local climatic conditions and its variability. We tested the hypothesis that monthly leaf litterfall increases in dry months and in drier and warmer than average months; we also evaluated if annual leaf litterfall increases in wetter and warmer years following leaf production patterns, that increases in these conditions. We found that litterfall peaks in the drier months. This pattern is consistent for many tropical ecosystems, even evergreen ecosystems, and may have evolved as a strategy that result in reduced water stress by plants, during drier and warmer periods, or may simply be a stress symptom. However, we also found that decreases in monthly rainfall and increases in monthly Δ Temperature (temperature observed minus estimated based on 1970-2000 interval) stimulate leaf litter production. Hot and warmer than average years also seem to stimulate leaf litterfall. It suggests that annual leaf litterfall and leaf production are less affected by precipitation regimes than variations in temperature (or radiation, which is directly related to temperature). It may result from the fact that *Clusia hilariana*, the dominant species in this ecosystem which accounts to 80 % of leaf litterfall, is a CAM photosynthesis species, a characteristic commonly associated with avoidance of water stress by plants. Although leaf litterfall seems to be predominantly driven by climate at annual scale, only 15 % of its variation

was associated to climate at seasonal scale, suggesting that local factors control litterfall at lower temporal scales in Open *Clusia* Formation.

Keywords: Climatic variability; coastal sand dune vegetation; litter production; open *Clusia* formation.

INTRODUCTION

On forests worldwide, litterfall is the main via of nutrient transfer from plants to the soil since about 90 % of net primary production are not consumed by herbivores and are converged to soil as litter (Cebrian 1999). The deposition of litter to the soil plays an important role in the dynamics of natural ecosystems once it affects nutrient cycling rates, respiration and organic matter incorporation in the soil, water retention and maintenance of soil integrity and temperature conditions (Chen *et al.* 2017, DeForest *et al.* 2009, Hobbie 2015), ultimately affecting its biodiversity (Sayer 2006). Therefore, quantifying litterfall pools is essential to understand the structure and function of tropical forests (Vitousek 1984).

Leaves represent the most important plant component for litter, being the largest source of soil organic matter, both in tropical (Barnes *et al.* 1998, Chave *et al.* 2010) and in most of the world's ecosystems (Berg & Laskowski 2005, Zhang *et al.* 2014). Leaves are also the largest component of net primary production (NPP) in tropical forests, what makes litterfall a good proxy for NPP estimates (Clark *et al.* 2001, Malhi *et al.* 2011). Leaf production and abscission are sensitive to exogenous intra- and inter-annual variability in climate (Chave *et al.* 2010, Wagner *et al.* 2016). As a result, litterfall dynamic are highly seasonal and its contribution to soil organic matter changes considerably within and between years in tropical forests (Chave *et al.* 2010, Wagner *et al.* 2016). So, litterfall production provides important information about the phenological cycles of plants and their influence on the return of nutrients to the soil (Proctor *et al.* 1983).

Understanding how variations in climate affect or regulate the temporal patterns in litterfall is an important step to predict resource availability in soil and the magnitude in plant productivity cycles. In tropical forests, when rainfall is smaller than evapotranspiration, soil moisture is depleted, increasing tensions in the xylem sap that can eventually trigger stomatal closure and other

physiological responses (Nepstad *et al.* 2002). So, either low water availability or a lack of rain along with temperature increases could limit tree growth and promote litterfall peaks (Lawrence 2005). Solar radiance also affects litterfall, and seasonal changes in daily insolation leads to production of new leaves and synchronous abscission of old ones (Chave *et al.* 2010, Wagner *et al.* 2016, Wright & Cornejo 1990, Zhang *et al.* 2014). Solar radiance is directly linked to temperature, an easily measurable variable and much more common explored in the literature. So, either low water availability or a lack of rain along with temperature increases could limit tree growth and promote litterfall peaks (Wagner *et al.* 2016, Wagner *et al.* 2012). This seems critical to South American ecosystems, for which long-term climate change scenarios predict increases in temperature and drought frequency and magnitude (Duffy *et al.* 2015, Fu *et al.* 2013). So, changes in climatic factors that affect the water and temperature balance may have considerable effects on the environmental quality and ecosystems functioning and severely affect tropical forests (Villela *et al.* 2012).

It should be noted that some ecosystems may be more sensitive to climate change, such as coastal sand dune vegetation known as *restingas*, particularly because it grows on sandy well-drained soils, subject to recurrent droughts and high temperature conditions (Hay & Lacerda, 1984). Restinga vegetation also produces a low quality litter (Villela *et al.* 2020), with low decomposition rates and, consequently, low nutrient availability for plant consumption (Brito *et al.* 2018, Moraes *et al.* 1999, Rosado & de Mattos 2010). So, plant community composition in these systems may be regulated by nutrients and water use efficiency, mainly during the dry season (Rosado & de Mattos 2007, 2010). The few species achieving high leaf water potentials, strong stomatal control and deep roots to access humid regions in the soil profile may become more abundant (Rosado & de Mattos 2010), which explains the strong oligarchic structure in open restinga vegetation dominated by *Clusia hilariana* and other few species (Pimentel *et al.* 2007, Scarano, 2002).

However, the effect of precipitation and temperature variability (deficits or excess) in plant components production and abscission is still not understood and rarely explored in these systems (Marques & Oliveira 2004, Rodarte 2008, Talora & Morellato 2000). Seasonal variations in climate may influence restinga productivity pattern, such that biomass production tends to be higher in wetter and warmer seasons, when plants produce more branches and leaves in general (Wagner *et al.* 2016, Wagner *et al.* 2012). Afterwards, in the dry season, a greater amount of leaves may be lost. Then, the production of leaf litterfall may be higher as more intense is the dry season. This variability may also have repercussions on plant community equilibrium, abiotic conditions and landscape dynamics such as fire incidence, affecting important environmental services to coastal inhabitants. Part of the difficulty in understanding the importance of these phenomena is due to the small time scale of most of the studies and, mainly, the lack of integrated approaches to evaluate these cyclical processes.

This work consists of a first effort to synthesize a series of data regarding the variations in litterfall in an Open *Clusia* Formation, a common vegetation in restinga ecosystems in Southeast Brazil, over a time lapse of 18 years, relying on multiple re-surveys of leaf litterfall. Here we aim to characterize the temporal variation in leaf litterfall in this ecosystem and assess how local variability in litter production reflects the local climatic conditions and its variability. We hypothesize that: 1) leaf litterfall increases in the dry months; 2) monthly leaf litterfall is associated to precipitation and temperature variability, being positively associated with precipitation deficits and extreme temperatures. Once leaf litterfall is a proxy of leaf production, we also evaluated if leaf litterfall increases in wet and warm years.

MATERIAL AND METHODS

Study Area

We concentrated efforts on the evaluation of leaf litterfall (hereafter, litterfall) trends in an Open *Clusia* Formation, in the Restinga de Jurubatiba National Park (22°00' - 22°23'S; 41°15' - 41°45'N). This is the most common physiognomy in the area, covering up to 32 % of the ca. 14,000 ha of this park

(Caris *et al.* 2013, Oliveira-Galvão *et al.* 1990). This type of vegetation is common in the sandy chords that interpose the arms and canals of coastal lagoons. Open *Clusia* Formation is dominated by shrubs and tree species organized in hemispheric vegetation islands surrounded by a sandy matrix, sparsely distributed and whose size varies from less than 1 to greater than 1,000 square meters (Araujo & Henriques 1984).

The mean annual rainfall in PNRJ varies between 1,100 to 1,250 mm (Alvares *et al.* 2013), being mostly concentrated between November and January, while precipitation deficits occur from June to August. The mean annual temperature varies between 21.3 to 22.4 °C, with small oscillations between the minimum and maximum temperatures, but January to March tends to be slightly hotter and June to August slightly colder than the average values. It is characterized as an *Aw* climate type (Tropical with dry winters) according to Köppen classification (Alvares *et al.* 2013).

The dominant species in this physiognomy is *Clusia hilariana* Schlttdl. (Clusiaceae) (Pimentel *et al.* 2007), a CAM photosynthesis species (Franco *et al.* 1996) that has the highest importance value (defined as the sum of the relative frequency, density and basal area) and that nucleates most of the vegetation islands in the area (Dias & Scarano 2007, Pimentel 2002). It is a physiognomy with a typically oligarchic structure (Dias & Scarano 2007, Monteiro *et al.* 2014), in which only 6 of the 62 tree species accounts for about half of the importance value of the vegetation; however, it shows a high diversity (Dias & Scarano 2007, Pimentel 2002). For this study, a representative area of Open *Clusia* Formation was selected for the evaluation of the objectives presented above (Figure 1).

Data sampling

In the study site, litterfall was monitored in clumps dominated by *Clusia hilariana* at three distinct time intervals: from October-2001 to October-2008, from May-2012 to April-2014 and from April-2016 to April-2018. Litterfall was sampled using litterfall traps (Rapp *et al.* 1999). But distinct approaches were considered on each of these sampling intervals, varying the number and size of litterfall traps and the sampling frequency. On the first interval, 12 clumps were monitored with a frequency varying from bi-weekly to monthly, with 0.25 m² litterfall

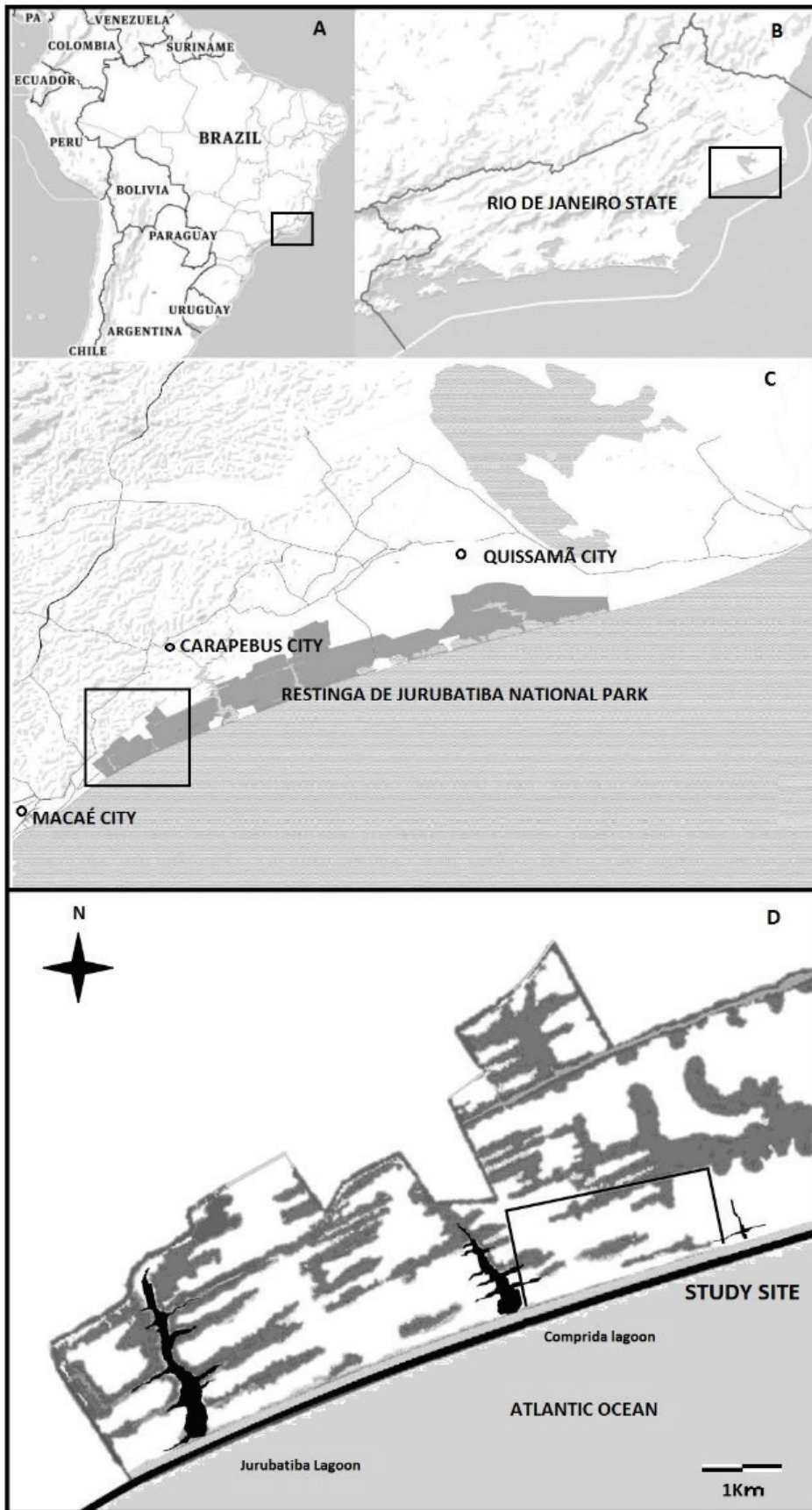


Figure 1. Study site in Restinga de Jurubatiba National Park, in Rio de Janeiro, Brazil. Open *Clusia* Formations are represented in white color within the square in Panel D, while grey color indicates other formations, mainly seasonally dry forest.

traps; on the second interval, 15 clumps were monitored bi-weekly with 0.25 m² litter-fall traps; in the last interval, 16 clumps were monitored with a frequency varying from bi-weekly to monthly, with 0.135 m² litterfall traps.

Trap content was collected and taken to the laboratory, where leaves were separated from other constituent parts and oven-dried at 60 °C until reaching a constant weight. Afterwards, they were weighed to the nearest 0.1 g. In order to standardize the sampling efforts and make the results comparable, we previously evaluated if the sampling (month of each period) achieved the minimum sample size necessary to accurately and precisely detect litterfall and its variation in the study area, according to Finotti *et al.* (2003). This was the case for all the months; then, we estimated the mean dry biomass (g.m⁻²) of litterfall per month, dividing the summed litter content by the total number of traps on each month.

Data Analysis

To test the first hypothesis that litterfall increases in the dry months, a linear regression was used to evaluate the relation between monthly litterfall and precipitation. To address the second hypothesis, that litterfall are positively associated with precipitation deficits and extreme temperature, we analyzed the linear relationship between monthly litterfall to precipitation and temperature departure from average values (Δ Precipitation and Δ Temperature), respectively. Δ Precipitation and Δ Temperature were estimated based on the difference between precipitation and temperature of a specific month and the average value of that respective month along the 1970 - 2000 intervals, respectively. By the way, monthly litterfall data was also related to monthly temperature. A Kolmogorov-Smirnov's test was used to test the normality of each variable, and whenever necessary, the variables were transformed to meet specific test assumptions. Data were interpreted as significant when $p < 0.05$. Climatic data was obtained from INMET, station 83698 - Campos dos Goytacazes.

We also evaluated if there were lagged correlations between monthly litterfall and climatic variables, by using a cross-correlation analysis (ccf function in R) to identify the optimum time lag - from zero to 12 months - in the litterfall response to each variable. Because the time series may be

auto-correlated, what gives a misleading indication of the relationship between the variables (Wei & Davidson 1998), we included litterfall data lagged by 1 month as an independent variable and used ACF plots to check and ensure that autocorrelation was removed from these seasonal relationships (Rowland *et al.* 2018). In this analysis, only the time series of litterfall data from the first interval (October - 2001 to October - 2008) were considered once it is the larger and have regular consecutive data records.

To test if litterfall increases in wet and warm years, we also used a linear regression to evaluate the relation between total annual litterfall and climatic variables (precipitation, temperature, Δ Precipitation and Δ Temperature), following the same criteria as described above. We estimated total annual litterfall by summing data from November of a specific year to October of the year after (12-month). So, basically, we estimated annual litterfall from the beginning of the warm and wet season (November) of one year to the cold and dry season of the following year (October). We also correlated monthly litterfall (from November of a specific year to October of the following year) between the years to evaluate temporal coherence between the same months along the years. For this analysis, we considered non-parametric Spearman rank correlation because some groups of years for all data sets didn't meet the assumptions for parametric analysis.

Multiple linear regressions were carried out to investigate the relationship between monthly and annual litterfall based on precipitation, temperature, Δ Precipitation and Δ Temperature, considering full time series of available litterfall data. For monthly litterfall data, multiple regressions were done considering both real synchronicity and the lags in responses to climatic variables identified in the cross-correlation analysis, and the differences were discussed. A Stepwise Regression was used to select the models with the highest likelihood using the least number of variables that better explain the relationship between predictors (climatic variables) and litterfall, based on Akaike Information Criterion (AIC). Multiple regressions were calculated considering the "lm" function and the selected models were chosen using the "stepAIC" function, that performs backward model selection, from the package 'MASS', available in R v.

3.5.2 (R Core Team 2018). For each selected model, the variance inflation factor (VIF) was estimated using the “vif” function from the package ‘car’. For monthly *Total* and *Clusia* litterfall data, all models presented VIF scores smaller than 2, what indicates that predictors are not redundant and therefore, should not be removed from the model. However, for annual litterfall data, only one variable was selected on the models, and VIF could not be calculated. All graphs were done using the GraphPad Prism 7.0 software for Windows. For a visual interpretation of climatic variability, 95 % confidence intervals were estimated for monthly data from the 1970 - 2000 intervals, and plotted on Δ Precipitation and Δ Temperature graphs.

RESULTS

The study site experienced a considerable seasonality in rainfall and temperature, both increasing substantially during the wet season, which starts between November and December and finish between April and May (Figure 2a and 2c). Accumulated annual precipitation on the monitored period varied from 676 mm in 2014 to 1,594 mm in 2008, with mean values of about 992 ± 332 mm (Figure 2a). This period can be considered wetter than average, once mean annual precipitation is a little bit larger than the average for 1970 – 2000 (955 mm), and some months presented consistent higher precipitation than average while it almost never dropped 97mm below the average (95 % CI; Figure 2b). Mean annual temperature varied from 24.01 °C in 2004 to 25.26 °C in 2015, and mean values of 24.64 ± 0.34 °C (Figure 2c). The period we evaluated can be considered warmer than average, once mean annual temperature is higher than average for 1970 – 2000 (24.00 °C), and higher temperature than average was common along the period, while temperature never dropped 0.29°C below the average (95 % CI), except for some winter months (Figure 2d).

In *Clusia hilariana* dominated clumps, litterfall seems to vary considerably along the more than 12-years monitored (Figure 2e). In this period, the mean total litterfall was 27.3 ± 14.7 g.m⁻², being *Clusia hilariana* leaves responsible for the largest contribution to litter layer: 18.5 ± 11.9 g.m⁻² (about 67.0 ± 15.7 % of total). Leaf production as litterfall

varied between 2.50 (in October, 2004) and 94.68 g.m⁻².month⁻¹ (in May, 2013). Mean annual litterfall corresponds to 328.5 ± 63.0 g.m⁻².

There was considerable seasonal variability in litterfall production, such that its peaks occurred generally during the dry season, mainly from May to October, except for a litterfall peak in March 2007 (Figure 2e). But only a few significant correlations of total monthly litterfall between years were detected (Supplementary Material), indicating a low temporal coherence in litterfall dynamics and a considerable inter-annual variability.

The strong seasonality of leaf litterfall resulted in significant correlations with most of the meteorological drivers evaluated. The total monthly litterfall is negatively related to precipitation and Δ Precipitation, and positively correlated with Δ Temperature, but is not related to temperature (Figure 3). Cross-correlations indicated that a lag of 2 months increases the correlation between litterfall and Δ Temperature, but no lags were detected in response to the other climatic variables.

Monthly litterfall was better predicted by precipitation and Δ Temperature (Table 1). Precipitation came out as the best predictor of leaf litterfall, explaining 12 %, and Δ Temperature being the other major contributor, explaining 4.6 %. Adjusted R² value was 0.15. So, 15 % of the variation in litterfall can be explained by the model, about 3 to 5 % more than the models containing individual climatic drivers. When stepwise multiple regression analysis was performed using lags identified in the cross-correlation analysis for climatic data, monthly litterfall were still better predicted by precipitation and Δ Temperature (Table 1), with only slightly changes in variables contribution to model explanation.

Despite evidences of seasonal effects of water limitations on monthly litterfall, no significant relation was found between accumulated annual precipitation nor Δ annual precipitation and annual litterfall (Figure 4). However, there was a consistent increase in annual litterfall due to increases in mean annual temperature and Δ annual temperature (Figure 4). Stepwise multiple regression showed that Δ Temperature was the single best predictor of annual leaf litterfall (Table 1).

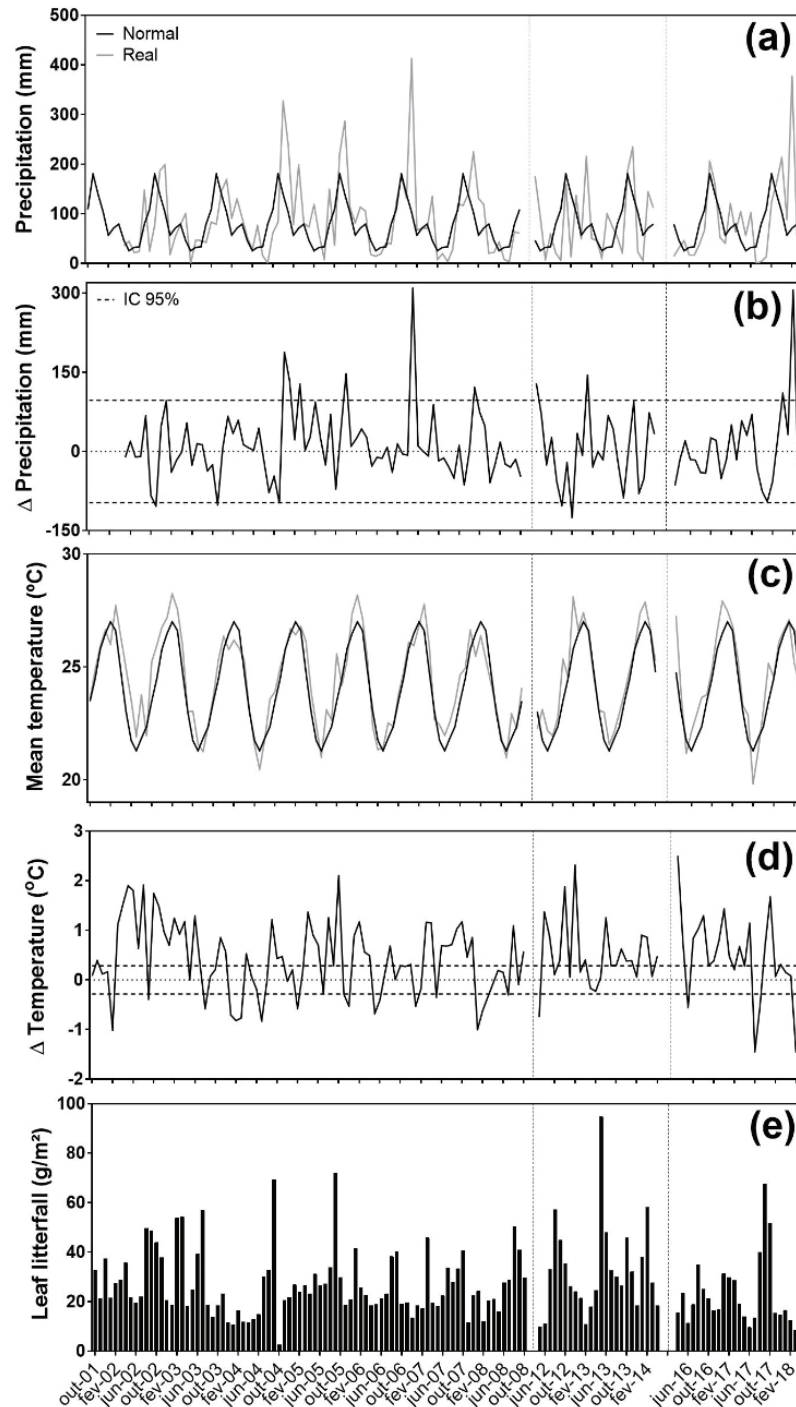


Figure 2. Climatic variables (*a* to *d*) and leaf litterfall (*e*) monthly variation from October-2001 to October-2008, from May-2012 to April-2014 and from April-2016 to April-2018. For *a* and *c*, the grey line indicates monthly accumulated precipitation and mean temperature, respectively, and the black line indicates the monthly average values of these variables estimated from the 1970 – 2000 period. On *b* and *d* are depicted the monthly accumulated precipitation and mean temperature departure from the average values (Precipitation and Temperature, respectively) and dashed lines indicate the 95 % confidence interval (95 % CI) around historical average values (1970 – 2000). Positive values indicate higher than the historical average. On *e*, columns represent the monthly litterfall, in $\text{g}\cdot\text{m}^{-2}$.

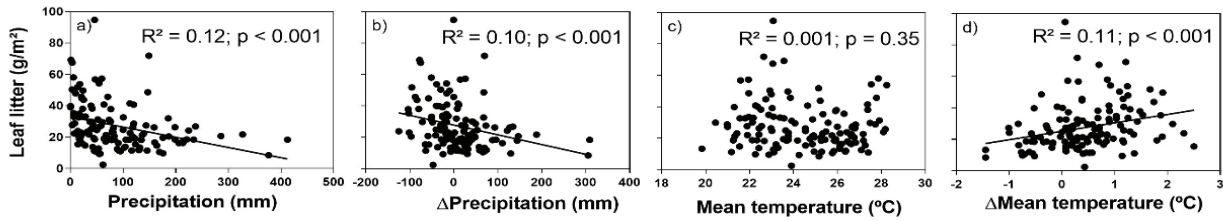


Figure 3. Monthly litterfall as a function of monthly Precipitation (a), Δ Precipitation (b), Mean Temperature (c) and Δ Temperature (d). R^2 and p values are presented in the top of the graph. Black lines are depicted for significant regressions, at the $p < 0.05$ level.

Table 1. Results of Multiple regression analysis for predicting Monthly and Annual litterfall from climatic variables and from lags in these variables. Only selected variables are depicted in the table. % R^2 indicates the contribution of each selected variable to model R^2 . AIC indicates the Akaike's Information Criterion value for the selected model, while Δ AIC indicates the difference between the selected models from the model containing all climatic variables.

Variable	Coefficient	Std Error	t value	p value	% R^2	AIC	Δ AIC
Model - Monthly litterfall							
$(R^2 = 0.164; Ad R^2 = 0.150; F(2, 120) = 11.77; p < 0.001)$						-17.03	2.75
Precipitation	-0.003	0.001	-2.657	0.009	11.8		
Δ Temperature	0.311	0.122	2.558	0.012	4.6		
Intercept	0.148	0.163	0.912	0.363			
Model Lag - Monthly litterfall							
$(R^2 = 0.155; Ad R^2 = 0.140; F(2, 118) = 10.8; p < 0.001)$						-15.34	3.04
Precipitation	-0.004	0.001	-3.775	< 0.001	12.0		
Δ Temperature	0.260	0.118	2.205	0.029	3.5		
Intercept	0.275	0.142	1.933	0.056			
Model - Annual litterfall							
$(R^2 = 0.618; Ad R^2 = 0.554; F(1, 6) = 9.71; p = 0.021)$						57.52	3.1
Δ Temperature	171.12	54.9	3.117	0.021	61.8		
Intercept	266.58	23.51	11.341	< 0.001			

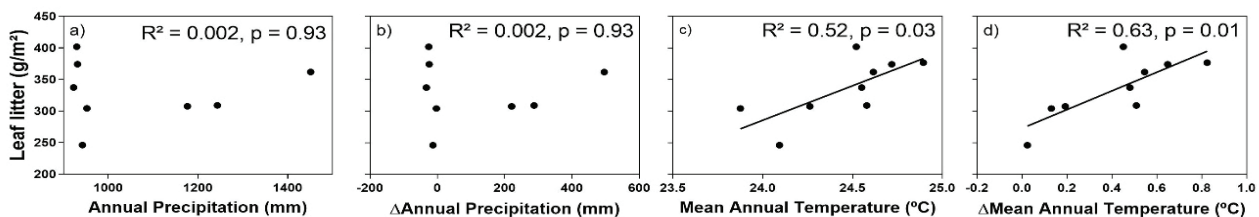


Figure 4. Annual litterfall as a function of Annual Precipitation (a), Δ Annual Precipitation (b), Mean Annual Temperature (c) and Δ Mean Annual Temperature (d). R^2 and p values are presented in the top of the graph. Black lines are depicted for significant regressions, at the $p < 0.05$ level.

DISCUSSION

Restinga litterfall production and seasonality

The amount of leaf litterfall found in this study ($3.29 \pm 0.63 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) is within the previously recorded ranges for open areas in restinga ecosystems (2.58

and $8.20 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; Table 2). To this comparison, litterfall was converted to $\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, according to the equation:

$$\text{Litterfall} = (\text{AL} \times 10,000) / 1,000,000,$$

where AL = annual average of litterfall ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$).

Table 2. Estimates of annual leaf litter production, leaf contribution to total litterfall, months of peak production and total duration of study in some restinga ecosystems and their respective sites. Restinga ecosystems are divided in flooded and non-flooded and classified according to the vegetation physiognomy in Patchy, Shrubby and Arboreal, mentioning the domination of a specific species or the arboreal stratum (low or high) when necessary.

Restinga Ecosystem	Site	Total Annual leaf litterfall (Mg.ha ⁻¹)	Mean leaf contribution to total annual litterfall (%)	Month(s) of largest contribution	Time interval (months)	Study
<i>Non-flooded</i>						
Shrubby - <i>C. hilariana</i> dominated clumps	Jurubatiba, RJ	3.29 ± 0.63	80.0	May - October	134	This study
Shrubby - clumps without <i>C. hilariana</i>	Jurubatiba, RJ	2.58	64.8	October/January	24	Brito et al., 2015; 2018
Patchy - Allagoptera arenaria dominated	Marambaia, RJ	8.20	-	-	12	Carvalho et al., 2014
Arboreal - low	Ilha do Mel, PR	3.79	74.6	November	12	Pires, 2006
Arboreal - low	Ilha do Mel, PR	3.36	61.5	November/December	24	Brietz, 1994
Arboreal - low	Ilha do Cardoso, SP	2.93	75.0	December	12	Moraes et al., 1999
Arboreal - high	Marambaia, RJ	4.95 ± 0.8	75.0	January	24	Camara et al., 2018
<i>Periodically Flooded</i>						
Arboreal - high	Ilha do Mel, PR	4.62	59.3	November/December	24	Brietz, 1994
Arboreal - high	Marambaia, RJ	7.45 ± 0.5	67.3	January	12	Paula et al., 2009
Arboreal - high	Marambaia, RJ	4.42	57.9	September	12	Pereira et al., 2012
Arboreal - high	Jurubatiba, RJ	5.84	57.7	October/December	24	Brito et al., 2015; 2018

The litterfall production recorded in non-flooded restinga forested areas tends to vary between 2.93 to 4.95 Mg.ha⁻¹.yr⁻¹ and can reach values between 4.42 to 7.45 Mg.ha⁻¹.yr⁻¹ in more humid areas (Table 2). Our results show that the amount of leaf litterfall found in this study are also within the previously recorded ranges for non-flooded dense restinga forests, but slightly lower than that found for periodically flooded restinga forests (Table 2). In open restinga, vegetation cover is not

homogeneous and this litter amount can be even lower if we consider the proportion of clump cover; in the study site, clumps cover from ~20 % (Dias *et al.* 2006) to 40 % of the area (Oliveira-Galvão *et al.* 1990), and litterfall would correspond to about 0.66 ± 0.13 to 1.32 ± 0.26 Mg.ha⁻¹.yr⁻¹, considerably less than that recorded for flooded and non-flooded dense restinga forests.

In this study, it was recorded the highest proportion of leaves (~ 80 %) compared with other

restinga ecosystems (Table 1), and with the Atlantic forest and worldwide evergreen forests, averages of 67 % (Martinelli, Lins & dos Santos-Silva 2017) and ~ 70 % (Zhang *et al.* 2014), respectively. Leaves are the most important source of organic matter to the soil (Barnes *et al.* 1998, Berg & Laskowski 2005, Zhang *et al.* 2014) and are particularly relevant in nutrient poor ecosystems, such as restingas. In these coastal evergreen forests, leaf abscission tends to be a continuous process, but variable in magnitude within and between years; as a result, litterfall display an irregular pattern throughout the year. In Open *Clusia* Formation, leaf litter do not input to the soil in a synchronous manner, it means, the amount of litterfall produced in each month is not similar along years. This imposes limitations on the ability to predict the temporal variations on litterfall during the year. It may also suggest a certain decoupling between climatic predictability - which presents a unimodal regime (Figure 2) - and leaf litter production.

However, fluctuations in the amount of rainfall and in thermal amplitudes also vary between years, which may explain such decoupling. In fact, in evergreen forests, seasonal peaks are not uncommon due to plant phenological responses to multiple drivers, mainly climatic seasonality (Chave *et al.* 2010, Wagner *et al.* 2016). In Open *Clusia* Formation, leaf litterfall showed little change across the 12-years, tending to peak in winter or spring, what corresponds to the dry season as found across some other restinga sites (Table 2). This is also a common pattern in tropical forests (Araújo *et al.* 2019, Chave *et al.* 2010, Martinelli *et al.* 2017, Rowland *et al.* 2014, 2018, Wagner *et al.* 2016, Zhang *et al.* 2014), even in sites where the seasonal drought is not so strong (Morellato *et al.* 2000). This pattern may have evolved as a plant strategy that results in reduced water stress during drier and warmer periods (Nepstad *et al.* 2002, Wright & Cornejo 1990), and sometimes it is associated to a simultaneous leaf production process, using nutrients re-captured from senescent leaves before abscission (Jackson 1978). It may explain the great variation among the month of litterfall peaks in distinct restinga ecosystems (Table 2), even though rainfall and temperature seasonal patterns didn't change much between sites.

Also, restinga species possess a distinct ability to retain or lose leaves, once individual species

phenology respond to climatic variability in a very diverse way (Rosado 2006, Rosado & de Mattos 2007), what may affect the temporal coherence in litterfall between distinct patches/sites and years. As a result, litter production is a considerably variable process, both in spatial and temporal scales. For example, while we found a significant effect of meteorological drivers on litterfall in *Clusia* dominated clumps in Open *Clusia* Formation, Brito *et al.* (2018) reported no relation between litterfall and temperature or accumulated precipitation nor in patches without *Clusia* neither in the same vegetation nor in a neighbor periodically flooded forest. Also, *C. hilariana* is the main source of organic matter and nutrients to restinga soils in Restinga de Jurubatiba National Park (Silva 2003, Villela *et al.* 2020) and is probably the main driver of significant relations between climatic variables and leaf litterfall we detected. Litter production in this system is related to the characteristics of this dominant species in the clumps. But its contribution to total leaf litterfall production in those clumps may also vary with its senescence stage from 50 % to 70 % (Villela *et al.* 2020). However, the effect of climate on *Clusia* with distinct characteristics remains to be evaluated.

Effect of climatic variability on litterfall

We hypothesized that leaf litterfall in Open *Clusia* formation would respond to drought conditions and historical variations in temperature and water availability, such that litterfall would increase in the dry months, being negatively related to precipitation and positively related to precipitation deficits and extreme temperatures. In fact, the sole effect of reductions in monthly precipitation and Δ precipitation and increases in Δ temperature seems to enhance monthly litter production. This seems to confirm that longer and more intense dry seasons can lead to dry-season increases in litterfall. Seasonal character of the local rains has an important effect on the structure of the vegetation, which is associated with soil water deficit conditions (Brito *et al.* 2018).

When those three variables and the time lag - that indicates the time the vegetation takes to respond to changes in environmental factors - are considered as predictors, the power of the model to predict tendencies in litterfall increases. The results we report suggest that both temporal variations

in precipitation and in the amplitude of droughts and warm periods act together to determine the amount of leaf litter inputs to the soil. This also reinforces the notion that climatic variables have direct effects - mainly related to water balance - and indirect effects - affecting the endogenous rhythm - on restinga plants, that ultimately affect production rates and biomass loss, corroborating our first and second hypothesis.

We also expected that litterfall would increase on wetter and warmer years as a result of the increased leaf production in these periods (Rodrigues 2014). In fact, annual litterfall tended to increase in warmer and, mainly, warmer than expected years (Δ temperature). But, contrary to that, no clear trends of increase or reduction on annual litterfall were associated with annual precipitation and Δ Precipitation. So, our expectations were only partially met. A similar response of litterfall and leaf production to temperature and temperature increases in relation to historical records have been registered by Guerreiro *et al.* (2018) in an Amazonian evergreen forest, who discussed these processes as an effect of abnormal or brusque changes in temperature after a long time of adaptation of tree species to low levels of variation in these factors. In restinga ecosystems, temperature variations can be even stronger due to low sandy soil specific heat.

Although it has been demonstrated that water availability is a major climate driver of litterfall production on annual basis across the tropics (Wagner *et al.* 2016), many studies reported that litterfall is better explained by variations in temperature than in rainfall (Chave *et al.* 2010, Ferreira *et al.* 2014, Guerreiro *et al.* 2018, Martinelli *et al.* 2017). First, the relation between water availability and precipitation for plants is not straightforward and is determined by soil and plant characteristics, such as field capacity, root distribution, extractable water, etc (Wagner *et al.* 2012). Second, the temperature is linked to solar radiation, and both can affect plant responses in multiple ways, affecting their succulence, stomatal opening, transpiration, photosynthesis and growth rates (Fauset *et al.* 2018, Niinemets 2001). These factors also have been demonstrated to trigger the flushing of new leaves and leaf abscission during the dry season (Chave *et al.* 2010), being a key driver of litterfall patterns, even in drier tropical forests (Borchert *et al.* 2015, Girardin *et al.* 2016). Also, the

dominant species in this ecosystem - *C. hilariana* - is a CAM photosynthesis species, a characteristic commonly associated with the avoidance of water stress by plants. Increases in litterfall in warmer periods can result from the fact that the production and maintenance of *C. hilariana* leaves are less resilient to cold and dry periods (Rodrigues 2014), consequently with better performance in the summer periods, when high radiation and greater water availability are recorded. *C. hilariana* also tends to respond to accumulated climatic variations from previous periods. So, the leaves dropped in colder months (when lower thermal averages are recorded) were those produced in previous warmer and/or with moderate radiation incidence months. Therefore, knowing the accumulated conditions in previous periods makes it possible to predict *C. hilariana* phenological responses and so, *Clusia* dominated clumps response.

Although our results suggest that annual leaf production - estimated by leaf litterfall - may be less affected by water stress than variations in temperature or radiation, we may not ignore the possibility that the effect of seasonality in litterfall confuses the effect of the annual precipitation and/or temperature in litterfall. In this case, even with greater leaf production due to a wet year, if the dry season is less dry or colder than usual, we may have less leaf abscission. Perhaps, the effects of such variations on litterfall on dry periods do not allow us to properly estimate annual leaf production; neither detects the effects of climatic conditions on annual leaf production.

It is important to point out that future climate scenarios point to greater uncertainties in precipitation, with more concentrated rains in certain periods, and temperature increases in the southeast region, what was already registered during the period covered in this study. More concentrated rain events means an increase in the duration of dry periods. This, together with temperature increases, has been demonstrated to promote an increase in litter production in restinga ecosystems. Not only actual increases in duration of dry periods and temperatures but also relative changes to what restinga plants are adapted seem to be the mechanisms explaining variations in litterfall in the study site. It should be noted that prolonged droughts that characterize the changes in the seasonal patterns of rainfall

predicted for the future already affect the region and may have serious implications for the carbon and energy balance in restinga, since leaf litter is the main source of nutrients that subsidize new production cycles, and once it may have a severe impact on the risk of fire in this ecosystem. On the other hand, in a scenario of global climate change, the surrounding conditions can cause large amounts of water to be supplied in a short period of time, which, together with predicted sea level rise, could completely transform the dynamics of well drained and periodically flooded areas, changing the rhythms of plant production and nutrients cycling.

Finally, although climatic variability is determinant for litter production, its effects are dependent on temporal scale that data are evaluated. While leaf litterfall seems to be predominantly driven by climate at annual scale, thereby suggesting the process is controlled by exogenous drivers, only 15 % of variation in leaf litterfall were associated to climate at seasonal scale, suggesting both exogenous and endogenous processes controlling litterfall at lower temporal scales, what is consistent with what was previously reported by Wagner *et al.* (2016). It suggests that local factors may be better predictors of leaf production and litterfall. Future evaluations regarding restinga plants production cycles should also consider the effects of other local factors, such as species diversity, clump structure, water table variations, changes in the vegetation cover and the physiology of the plants in adjacent areas. Field measures, together with other mechanisms of spatial analysis of leaf production, senescence and abscission must also contribute to a better understanding of plant cycle and leaf litterfall dynamics (Guan *et al.* 2014).

ACKNOWLEDGEMENTS

We would like to thank Augusto Sulzer, Quezia Souza and Professor Marcos Paulo Barros for the support in field and laboratory. We would also like to thank Foundation Carlos Chagas Filho Research Support of the State of Rio de Janeiro (FAPERJ), the National Council for Scientific and Technological Development (PELD – CNPq 441610/2016-1) and the Coordination for the Improvement of Higher Education Personnel (CAPES). We also would like

to thank Chico Mendes Institute for Biodiversity Conservation (ICMBio / MMA), for the partnership over these years (licence number 505607).

REFERÊNCIAS

- Alvares, C. A., Stape, J. L., Sentelhas, P. C., de Moraes, G., Leonardo, J., & Sparovek, G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, 22(6), 711–728. DOI:10.1127/0941-2948/2013/0507
- Araujo, D. d., & Henriques, R. P. 1984. Análise florística das restingas do Estado do Rio de Janeiro. In: Lacerda, L.D., Araújo, D.S.D., Cerqueira, R. & Turcq, B. (Eds.). *Restingas: origem, estrutura e processos*. pp. 159–193. *Anais do Simpósio de Restingas Brasileiras*. Niterói: CEUFF.
- Araújo, V., Barbosa, M., Araújo, J., & Vasconcellos, A. 2019. Spatial-temporal variation in litterfall in seasonally dry tropical forests in Northeastern Brazil. *Brazilian Journal of Biology*, 1–12. DOI: 10.1590/1519-6984.192113
- Barnes, B. V., Zak, D. R., Denton, S. R., & Spurr, S. H. 1998. *Forest Ecology*. New York: John Wiley & Sons. p. 774.
- Berg, B., & Laskowski, R. 2005. Litter fall. *Advances in Ecological Research*, 38, 19–71. DOI:10.1016/S0065-2504(05)38002-0
- Borchert, R., Calle, Z., Strahler, A. H., Baertschi, A., Magill, R. E., Broadhead, J. S., Kamau, J., Njoroge, J., Muthuri, C. 2015. Insolation and photoperiodic control of tree development near the equator. *New Phytologist*, 205(1), 7–13. DOI:10.1111/nph.12981
- Brietz, R. M. D. 1994. *Ciclagem de nutrientes minerais em duas florestas da planície litorânea da Ilha do Mel, Paranaguá, PR*. Dissertação de Mestrado. Universidade Federal do Paraná, Curitiba. p. 256.
- Brito, L. S. 2015. *Avaliação do aporte e decomposição da serapilheira e lixiviação de nutrientes em duas fitofisionomias de uma restinga do Norte Fluminense*. Dissertação de Mestrado, Universidade Federal do Rio de Janeiro - Campus UFRJ-Macaé Professor Aloisio Teixeira, Macaé. p. 83.
- Brito, L. S., Irmiler, U., Forte, B. V. G., Xavier, T. P., & Martins, R. L. 2018. Matter turnover in the oligotrophic restinga ecosystem and the

- importance of the key species *Clusia hilariana*. *Biota Neotropica*, 18(4), 1–10. DOI:10.1590/1676-0611-bn-2018-0552
- Camara, R., Pereira, M. G., Menezes, L. F. T., Segall, A. B., & Castro, J. S. R. 2018. Litter Dynamics in a Forest Dune at Restinga da Marambaia, RJ, Brazil. *Floresta e Ambiente*, 25(2). 1–10. DOI:10.1590/2179-8087.004616
- Caris, E. A. P., Kurtz, B. C., Cruz, C. B. M., & Scarano, F. R. 2013. Vegetation cover and land use of a protected coastal area and its surroundings, southeast Brazil. *Rodriguésia*, 64(4), 747–755. DOI:10.1590/S2175-78602013000400006
- Carvalho, D. C. d., Pereira, M. G., & de Menezes, L. F. T. 2014. Aporte de biomassa e nutrientes por *Allagoptera arenaria* na Restinga da Marambaia, Rio de Janeiro, RJ. *Floresta*, 44(3), 349–358. DOI:10.5380/ufv44i3.28142
- Cebrian, J. 1999. Patterns in the fate of production in plant communities. *The American Naturalist*, 154(4), 449–468. DOI:10.1086/303244
- Chave, J., Navarrete, D., Almeida, S., Alvarez, E., Aragao, L., Bonal, D., Chatelet, P., Silva-Espejo, J. E., Goret, J.-Y., von Hildebrand, P., Jimenez, E., Patino, S., Penuela, M. C., Phillips, O. L., Stevenson, P. & Malhi, Y. 2010. Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences*, 7, 43–55. DOI:10.5194/bg-7-43-2010
- Chen, H. Y., Brant, A. N., Seedre, M., Brassard, B. W., & Taylor, A. R. 2017. The contribution of litterfall to net primary production during secondary succession in the boreal forest. *Ecosystems*, 20(4), 830–844. DOI:10.1007/s10021-016-0063-2
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., & Ni, J. 2001. Measuring net primary production in forests: concepts and field methods. *Ecological applications*, 11(2), 356–370. DOI:10.1890/1051-0761(2001)011[0356:MNPIF]2.0.CO;2
- DeForest, J. L., Chen, J., & McNulty, S. G. 2009. Leaf litter is an important mediator of soil respiration in an oak-dominated forest. *International journal of biometeorology*, 53(2), 127–134. DOI:10.1007/s00484-008-0195-y
- Dias, A. T., de Mattos, E. A., Vieira, S. A., Azeredo, J. V., & Scarano, F. R. 2006. Aboveground biomass stock of native woodland on a Brazilian sandy coastal plain: estimates based on the dominant tree species. *Forest Ecology & Management*, 226(1-3), 364–367. DOI:10.1016/j.foreco.2006.01.020
- Dias, A. T. C., & Scarano, F. R. 2007. *Clusia* as nurse plant. In: Lüttge, U. (Ed.). *Clusia: a woody neotropical genus with remarkable plasticity and diversity*. pp. 55–71. Springer.
- Duffy, P. B., Brando, P., Asner, G. P., & Field, C. B. 2015. Projections of future meteorological drought and wet periods in the Amazon. *Proceedings of the National Academy of Sciences*, 112(43), 13172–13177. DOI:10.1073/pnas.1421010112
- Fauset, S., Freitas, H. C., Galbraith, D. R., Sullivan, M. J., Aidar, M. P., Joly, C. A., Phillips, O. L., Vieira, S. A. & Gloor, M. U. 2018. Differences in leaf thermoregulation and water use strategies between three co-occurring Atlantic forest tree species. *Plant, Cell & Environment*, 41(7), 1618–1631. DOI:10.1111/pce.13208
- Ferreira, M. L., Silva, J. L., Pereira, E. E., & Lamano-Ferreira, A. P. N. 2014. Litter fall production and decomposition in a fragment of secondary Atlantic Forest of São Paulo, SP, southeastern Brazil. *Revista Árvore*, 38(4), 591–600. DOI:10.1590/S0100-67622014000400002
- Finotti, R., Freitas, S. R., Cerqueira, R., & Vieira, M. V. (2003). A Method to Determine the Minimum Number of Litter Traps in Litterfall Studies. *Biotropica*, 35(3), 419–421. DOI:10.1111/j.1744-7429.2003.tb00595.x
- Franco, A. C., Haag-Kerwer, A., Herzog, B., Grams, T. E., Ball, E., de Mattos, E. A., Scarano, F. R., Barreto, S., Garcia, M. A., & Mantovani, A. 1996. The effect of light levels on daily patterns of chlorophyll fluorescence and organic acid accumulation in the tropical CAM tree *Clusia hilariana*. *Trees*, 10(6), 359–365. DOI:10.1007/BF02185639
- Fu, R., Yin, L., Li, W., Arias, P. A., Dickinson, R. E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., & Fisher, R. (2013). Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences*, 110(45), 18110–18115. DOI:10.1073/pnas.1302584110
- Girardin, C. A., Malhi, Y., Doughty, C. E., Metcalfe, D. B., Meir, P., del Aguila-Pasquel, J., Araujo-Murakami, A., da Costa, A. C. L., Silva-Espejo, J. E., & Farfan Amezcua, F. 2016. Seasonal trends of Amazonian rainforest phenology, net

- primary productivity, and carbon allocation. *Global Biogeochemical Cycles*, 30(5), 700–715. DOI:10.1002/2015GB005270
- Guan, K., Wood, E. F., Medvigy, D., Kimball, J., Pan, M., Caylor, K. K., Sheffield, J., Xu, X., & Jones, M. O. 2014. Terrestrial hydrological controls on land surface phenology of African savannas and woodlands. *Journal of Geophysical Research: Biogeosciences*, 119(8), 1652–1669. DOI:10.1002/2013JG002572
- Guerreiro, Q., Oliveira Junior, R., Ruivo, M., Silva, K., Beldini, T., Guedes, M., Mota, A. F. L., Moraes, B. L. T., Santos, P. R. B., & Duin, I. (2018). Litter production in a natural stand of Brazil nut trees (*Bertholletia excelsa* Bonpl.). *African Journal of Agricultural Research*, 13(5), 228–238. DOI:10.5897/AJAR2017.12856
- Hay, J. D., & Lacerda, L. D. 1984. Ciclagem de Nutrientes no Ecossistema de Restinga. In: L. D. Lacerda, Araújo, D.S.D., Cerqueira, R. & Turq, B. (Ed.), *Restingas: Origem, Estrutura, Processos*. pp. 459–473. Niterói: CEUFF.
- Hobbie, S. J. 2015. Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends in Ecology and Evolution*, 30(6), 357–363. DOI:10.1016/j.tree.2015.03.015
- Jackson, J. F. 1978. Seasonality of flowering and leaf-fall in a Brazilian subtropical lower montane moist forest. *Biotropica*, 38–42. DOI:10.2307/2388103
- Lawrence, D. 2005. Regional-Scale Variation in Litter Production and Seasonality in Tropical Dry Forests of Southern Mexico. *Biotropica*, 37(4), 561–570. DOI:10.1111/j.1744-7429.2005.00073.x
- Malhi, Y., Doughty, C., & Galbraith, D. 2011. The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1582), 3225–3245. DOI:10.1098/rstb.2011.0062
- Marques, M. C., & Oliveira, P. 2004. Fenologia de espécies do dossel e do sub-bosque de duas Florestas de Restinga na Ilha do Mel, sul do Brasil. *Revista Brasileira de Botânica*, 27(4), 713–723.
- Martinelli, L. A., Lins, S. R., & dos Santos-Silva, J. C. 2017. Fine litterfall in the Brazilian Atlantic forest. *Biotropica*, 49(4), 443–451. DOI:10.1111/btp.12448
- Monteiro, M. M., Giaretta, A., Pereira, O. J., & Menezes, L. F. T. 2014. Composição e estrutura de uma restinga arbustiva aberta no norte do Espírito Santo e relações florísticas com formações similares no Sudeste do Brasil. *Rodriguésia*, 65(1), 61–72. DOI:10.1590/S2175-78602014000100005
- Moraes, R., Delitti, W. B. C., & Struffaldi-de Vuono, Y. 1999. Litterfall and litter nutrient content in two Brazilian Tropical Forests. *Brazilian Journal of Botany*, 22(1), 09–16. DOI:10.1590/S0100-84041999000100002
- Morellato, L. P. C., Talora, D. C., Takahasi, A., Bencke, C. C., Romera, E. C., & Zipparro, V. B. 2000. Phenology of Atlantic rain forest trees: a comparative study. *Biotropica*, 32(4b), 811–823. DOI:10.1111/j.1744-7429.2000.tb00620.x
- Nepstad, D., Moutinho, P., Dias-Filho, M., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., & Ray, D. 2002. The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *Journal of Geophysical Research: Atmospheres*, 107(D20), LBA 53 - 1–18. DOI:10.1029/2001JD000360
- Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, 82(2), 453–469. DOI:10.1890/0012-9658(2001)082[0453:GSCCO L]2.0.CO;2
- Oliveira-Galvão, A., Galvão, W., & Carvalho, V. 1990. Monitoramento da cobertura vegetal da restinga de Carapebus-Macaé (RJ), a partir de imagens orbitais. In: S. Watanabe (Ed.), *II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira: Estrutura, função e manejo*. pp. 442–454. São Paulo: ACIESP.
- Parsons, S., Valdez-Ramirez, V., Congdon, R., & Williams, S. 2014. Contrasting patterns of litterfall seasonality and seasonal changes in litter decomposability in a tropical rainforest region. *Biogeosciences*, 11(18), 5047–5056. DOI:10.5194/bg-11-5047-2014
- Paula, R. R., Pereira, M. G., & Menezes, L. F. T. 2009. Aporte de nutrientes e decomposição da serapilheira em três fragmentos florestais periodicamente inundados na Ilha da Marambaia, RJ. *Ciência Florestal*, 19(2), 139–148. DOI:10.5902/19805098405
- Pereira, M. G., Silva, A. N., Paula, R. R., & Menezes, L.

- E.T. 2012. Aporte e decomposição de serapilheira em floresta periodicamente inundável na restinga da Marambaia, RJ. *Ciência Florestal*, 22(1), 59–67.
- Pimentel, M. 2002. Variação espacial na estrutura de comunidades vegetais da formação aberta de *Clusia* no Parque Nacional da Restinga de Jurubatiba, RJ. Doctoral Thesis. Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, Rio de Janeiro.
- Pimentel, M. C., Barros, M. J., Cirne, P., Mattos, E. A. d., Oliveira, R. C., Pereira, M. C., Scarano, F. R., Zaluar, H. L. T., & Araujo, D. S. 2007. Spatial variation in the structure and floristic composition of "restinga" vegetation in southeastern Brazil. *Brazilian Journal of Botany*, 30(3), 543–551. DOI:10.1590/S0100-84042007000300018
- Pires, L. A., Britez, R. M. d., Martel, G., & Pagano, S. N. 2006. Produção, acúmulo e decomposição da serapilheira em uma restinga da Ilha do Mel, Paranaguá, PR, Brasil. *Acta Botânica Brasílica*, 173–184.
- Proctor, J., Anderson, J., Fogden, S., & Vallack, H. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. II. Litterfall, litter standing crop and preliminary observations on herbivory. *Journal of Ecology*, 71(1), 261–283.
- Rapp, M., Santa Regina, I., Rico, M., & Gallego, H. A. 1999. Biomass, nutrient content, litterfall and nutrient return to the soil in Mediterranean oak forests. *Forest Ecology & Management*, 119(1-3), 39–49. DOI:10.1016/S0378-1127(98)00508-8
- Rodarte, A. 2008. Caracterização espacial, temporal e biologia floral das espécies de restinga, com ênfase nos recursos florais. Doctoral Thesis, Universidade Federal do Rio de Janeiro - Museu Nacional, Rio de Janeiro.
- Rodrigues, R. F. C. 2014. Estudo da Variação dos Caracteres Estruturais, Anatômicos e Fisiológicos da Folha de *Clusia hilariana* Schlttdl. (Clusiaceae) Relacionados à Sazonalidade no PARNA Restinga de Jurubatiba. Master Thesis, Universidade Federal do Rio de Janeiro - Campus UFRJ-Macaé Professor Aloisio Teixeira, Macaé. p. 68.
- Rosado, B. H. P. 2006. A importância da inclusão de diferentes dimensões de variação de características morfo-fisiológicas e de crescimento para o entendimento dos padrões de dominância de plantas de restinga. Master Thesis, Universidade Federal do Rio de Janeiro, Rio de Janeiro. p. 100.
- Rosado, B. H. P., & de Mattos, E. A. 2007. Variação temporal de características morfológicas de folhas em dez espécies do Parque Nacional da Restinga de Jurubatiba, Macaé, RJ, Brasil. *Acta Botânica Brasílica*, 21(3), 741–752.
- Rosado, B. H. P., & de Mattos, E. A. 2010. Interspecific variation of functional traits in a CAM-tree dominated sandy coastal plain. *Journal of Vegetation Science*, 21(1), 43–54. DOI:10.1111/j.1654-1103.2009.01119.x
- Rowland, L., da Costa, A. C., Oliveira, A. A., Almeida, S. S., Ferreira, L. V., Malhi, Y., Metcalfe, D. B., Mencuccini, M., Grace, J., & Meir, P. 2018. Shock and stabilisation following long-term drought in tropical forest from 15 years of litterfall dynamics. *Journal of Ecology*, 106(4), 1673–1682. DOI:10.1111/1365-2745.12931
- Rowland, L., Malhi, Y., Silva-Espejo, J. E., Farfán-Amézquita, F., Halladay, K., Doughty, C., Meir, P., & Phillips, O. L. 2014. The sensitivity of wood production to seasonal and interannual variations in climate in a lowland Amazonian rainforest. *Oecologia*, 174(1), 295–306. DOI:10.1007/s00442-013-2766-9
- Sayer, E. J. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews*, 81(1), 1–31. DOI:10.1017/S1464793105006846
- Scarano, F. R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. *Annals of Botany*, 90(4), 517–524. DOI:10.1093/aob/mcf189
- Silva, A. 2003. Solos e produção de serrapilheira em moitas no Parque Nacional da Restinga de Jurubatiba, RJ. Master Thesis, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes. p. 78.
- Talora, D. C., & Morellato, L. P. C. 2000. Fenologia de espécies arbóreas em floresta de planície litorânea do sudeste do Brasil. *Brazilian Journal of Botany*, 13–26.
- R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>

- Villela, D., de Mattos, E., Pinto, A., Vieira, S., & Martinelli, L. 2012. Carbon and nitrogen stock and fluxes in coastal Atlantic Forest of southeast Brazil: potential impacts of climate change on biogeochemical functioning. *Brazilian Journal of Biology*, 72(3), 633–642. DOI:10.1590/S1519-69842012000400003
- Villela, D. M., Silva, A. P., Bonadiman, G. S. L., Silva, A., & Souza, R. 2020. *Clusia hilariana* a key species on nutrient cycling in sand dune vegetation thickets. *Oecologia australis*, 24(2):420–437.
- Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, 65(1), 285–298. DOI:10.2307/1939481
- Wagner, F. H., Hérault, B., Bonal, D., Stahl, C., Anderson, L. O., Baker, T. R., Becker, G. S., Beeckman, H., Souza, D. B., Botosso, P. C., Bowman, D. M. J. S., Bräuning, A., Brede, B., Brown, F. I., Camarero, J. J., Camargo, P. B., Cardoso, F. C. G., Carvalho, F. A., Castro, W., Chagas, R. K., Chave, J., Chidumayo, E. N., Clark, D. A., Costa, F. R. C., Couralet, C., Mauricio, P. H. S., Dalitz, H., Castro, V. R., Milani, J. E. F., Oliveira, E. C. O., Arruda, L. S., Devineau, J.-L., Drew, D. M., Dünisch, O., Durigan, G., Elifuraha, E., Fedele, M., Fedele, L. F., Filho, A. F., Finger, C. A. G., Franco, A. C., Júnior, J. L. F., Galvão, F., Gebrekirstos, A., Gliniars, R., Graça, P. M. L. A., Griffiths, A. D., Grogan, J., Guan, K., Homeier, J., Kanieski, M. R., Kho, L. K., Koenig, J., Kohler, S. V., Krepkowski, J., Lemos-Filho, J. P., Lieberman, D., Lieberman, M. E., Lisi, C. S., Santos, T. L., Ayala, J. L. L., Maeda, E. E., Malhi, Y., Maria, V. R. B., Marques, M. C. M., Marques, R., Chamba, H. M., Mbwambo, L., Melgaço, K. L. L., Mendivelso, H. A., Murphy, B. P., O'Brien, J. J., Oberbauer, S. F., Okada, Pélissier, R., Prior, L. D., Roig, F. A., Ross, M., Rossatto, D. R., Rossi, V., Rowland, L., Rutishauser, E., Santana, H., Schulze, M., Selhorst, D., Silva, W. R., Silveira, M., Spann, S., Swaine, M. D., Toledo, J. J., Toledo, M. M., Toledo, M., Toma, T., Filho, M. T., Hernández, J. I. V., Verbesselt, J., Vieira, S. A., Vincent, G., Castilho, C. V., Volland, F., Worbes, M., Zanon, M. L. B., & Aragão, L. E. O. C. 2016. Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests. *Biogeosciences*, 13(8). DOI:10.5194/bg-13-2537-2016
- Wagner, F., Rossi, V., Stahl, C., Bonal, D., & Hérault, B. 2012. Water availability is the main climate driver of neotropical tree growth. *PloS one*, 7(4), e34074. DOI:10.1371/journal.pone.0034074
- Wei, X., & Davidson, G. 1998. Impacts of large-scale timber harvesting on the hydrology of the Bowron River Watershed. Paper presented at the Proceedings of the CWRA 51th annual conference: mountain to sea: human interaction with the hydrologic cycle. Canadian Water Resource Association, Victoria, British Columbia.
- Wright, S. J., & Cornejo, F. H. 1990. Seasonal drought and leaf fall in a tropical forest. *Ecology*, 71(3), 1165–1175. DOI:10.2307/1937384
- Zhang, H., Yuan, W., Dong, W., & Liu, S. 2014. Seasonal patterns of litterfall in forest ecosystem worldwide. *Ecological Complexity*, 20, 240–247. DOI:10.1016/j.ecocom.2014.01.003

Supplementary material:

Table S1. Spearman's correlation coefficients (r_{Spearman}) for total monthly leaf-fall between years. A year was considered a period of 12-months from November of a specific year to October of the year after. Significant correlation coefficients are in bold and level of significance are depicted as follow: * $p < 0,05$; ** $p < 0,001$.

Submitted: 5 September 2019

Accepted: 21 April 2020

Published on line: 20 May 2020

Associate Editor: Pedro Villa