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PERTURBAÇÕES ANTRÓPICAS E A PRODUTIVIDADE PRIMÁRIA NA CAATINGA, PERNAMBUCO, BRASIL

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutora em Biologia Vegetal. Área de concentração: Ecologia e Conservação. Linha de pesquisa: Ecologia de Populações e comunidades

Orientador: Prof. Dr. Marcelo Tabarelli Co-orientadora: Dra. Sílvia Rafaela Machado Lins

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À minha mãe Suzana (in memoriam), que me
ensinou como se reerguer diante das
adversidades da vida.
Dedico

Ao meu marido Cristiano, pelo amor,
companheirismo e cumplicidade em todos os
momentos.
À minha filha Isabela, que ilumina minha vida de
maneira sublime e mágica.
Ofereço

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> “Se quisermos ter sucesso em conservação da natureza, precisamos de uma outra lógica diferente da nossa lógica econômica atual”.
>
> O Poema imperfeito – Fernando Fernandez

RESUMO

A produtividade primária líquida busca compreender a dinâmica dos ecossistemas através da produção e decomposição da serapilheira, sendo extremamente importante nas Florestas Tropicais Secas. O processo de decomposição é importante como fonte de nutrientes para comunidades florestais, pois determinam o fluxo de carbono e nutrientes (N, P, K, Ca e Mg) no solo. No entanto, a produção e decomposição da serapilheira são afetadas negativamente em ambientes antropizados com aumento da taxa de decomposição e diminuição do estoque final de nutrientes que retornarão ao solo. Portanto, este trabalho teve como objetivos: i) estimar a produção de serapilheira da Caatinga e estimar os fluxos de carbono e nutrientes relacionando-a com o uso da terra, condição climática e idade de regeneração florestal e ii) investigar como a precipitação e os distúrbios crônicos influenciam na decomposição foliar e alterações químicas da serapilheira através da dinâmica de C, N e P. O estudo foi realizado em 28 parcelas no Parque Nacional do Catimbau, na rede de parcelas permanente do PELD (Projeto de Extensão de Longa Duração), Catimbau, onde 13 parcelas com diferentes idades (10 a 76 anos) de regeneração e histórico de uso agrícola semelhante e 15 parcelas ao longo de um gradiente de precipitação de 510 a 940 mm e sem histórico de uso agrícola e classificadas num índice de perturbação antropogênica que varia de 0 a 100. A deposição de serapilheira foi registrada mensalmente a partir de cinco armadilhas de 0,5 m2 colocadas a 0,5 m acima do solo em cada parcela durante quatro anos. Para a velocidade de decomposição de serapilheira foram utilizadas amostras de folhas senescentes e utilizou-se a técnica *litter bags.* Foram estimadas para todas as amostras a perda de massa no início e após 360 dias de decomposição (coletas mensais). A média anual de serapilheira foi de 0,193 Mg ha-1 ano-1, variando entre 0,0035 e 0,564 Mg ha-1 ano-1. As diferenças na deposição de serapilheira foram significativas ao longo da cronossequência, mas o valor médio foi semelhante nas florestas maduras. Para a decomposição, os resultados evidenciam que a massa remanescente do experimento em 35,7% das parcelas em florestas maduras foi abaixo de 50% após 150 dias. Por outro lado, 57,1% das parcelas destas florestas maduras apresentaram massa remanescente abaixo de 50% após 210 dias, com padrão semelhante para as florestas em regeneração. Nosso estudo confirmou que a produção de serapilheira na Caatinga foi influenciada pela sazonalidade e pelos estágios sucessionais. Os distúrbios antrópicos afetaram negativamente a concentração de C, N e Mg nas florestas maduras. Já nas florestas em regeneração houve aumento na concentração de N e Ca quanto maior a cronossequência. No entanto, quanto mais avançado o processo de regeneração da floresta, menor a retenção de P na massa remanescente da serapilheira. Assim, este tema merece grande atenção, principalmente o escoamento de nutrientes pelas atividades humanas.

Palavras-chave: produção de serapilheira; precipitação; sazonalidade; decomposição; ciclagem de nutrientes.

ABSTRACT

Net primary productivity seeks to understand the dynamics of ecosystems through the production and decomposition of litter, being of utmost importance in the Tropical Dry Forests. The decomposition process is important as a source of nutrients for forest communities, as it determines the flux of carbon and nutrients (N, P, K, Ca and Mg) in the soil. However, the production and decomposition of litter is negatively affected in anthropized environments with an increase in the rate of decomposition and a decrease in the final stock of nutrients that will return to the soil. Therefore, this study had the following objectives: i) to estimate Caatinga litter production by relating it to land use, climatic condition and forest regeneration age and ii) investigate how precipitation and chronic disturbances influence leaf decomposition and chemical changes in litter through C, N, and P dynamics. The study was carried out in a total of 28 forest stands, located in the Catimbau National Park, within the permanent plot network of the LTER (Long-Term Ecological Research Project), Catimbau, using 13 forest stands of different successional ages (10 to 76 years old) with similar agricultural use history as well as 15 plots along a precipitation gradient ranging from 510 to 940 mm, with no agricultural use history and ranked on an anthropogenic disturbance index ranging from 0 to 100. Litter deposition was monthly recorded over four years using five traps of 0,5 m2 placed 0,5 m aboveground in each plot. In order to determine litterfall decomposition rates, senescent leaf samples were used by applying the litter bags technique. Mass loss was estimated in the beginning and after 360 days of decomposition for all samples (through monthly samplings). The mean annual litterfall was 0.193 Mg ha-1 yr-1, varying between 0.0035 and 0.564 Mg ha-1 yr-1. The differences in litter deposition were significant along the chronosequence, but the mean value was similar to the old-growth forest areas. For decomposition, the results show that the remaining mass of the experiment in 35.7% of the stands in mature forests was below 50% after 150 days. On the other hand, 57.1% of the plots in these mature forests showed a remaining mass below 50% after 210 days, with a similar pattern for the regenerating forests. Our study confirmed that litterfall production in Caatinga was influenced by seasonality and successional stages. Anthropogenic disturbances have negatively affected the concentration of C, N, and Mg in mature forests. In the regenerating forests, the longer the chronosequence, the higher the concentration of N and Ca. However, the more advanced the forest regeneration process, the lower the retention of P in the remaining litter mass. Thus, this topic deserves great attention, particularly nutrient drainage by human activities.

Keywords: litter production; precipitation; seasonality; decomposition; nutrient cycling

LISTA DE ABREVIATURAS E SIGLAS

ANPP	Aboveground Net Primary Production
C	Carbon
CAD	Chronic anthropogenic disturbance
Ca	Calcium
GIS	Geographic information system
GLM	Generalized linear model
ICP- OES	Inductively coupled plasma optical emission spectroscopy
Mg	Magnesium
NCf	Nutrient concentration in mass remaining
NCI	Nutrient concentration before mass decay
NPP	Net primary productivity
OF	Old-growth forests
N	Nitrogen
PARNA	Catimbau National Park
P	Phosphorus
RG	Regenerating forest
SDTF	Seasonally Dry Tropical Rainforests
VIF	Variance inflation factor
VPD	Vapor pressure deficit
TDF	Tropical dry forests

SUMÁRIO

1 INTRODUCTION

Land use activities such as agrosilvopastoral, urbanization and grazing are responsible for habitat destruction and fragmentation and, consequently, for the decrease in biodiversity (MELO et al., 2010; TABARELLI et al., 2010; MALHI et al., 2014; GARCÍA-VALDÉS et al., 2015). Habitat destruction and fragmentation affects the assembly patterns of biological communities and ecological processes in ecosystems, especially in tropical biotas (SALA et al., 2000). The Seasonally Dry Tropical Rainforests (SDTF) are particularly exposed to chronic anthropogenic disturbances, such as biomass loss, fuelwood extraction for domestic purposes, logging, overgrazing, and so forth (Singh, 1998), along with over-exploitation of natural resources (MARTORELL; PETERS, 2005; 2009; MILLES et al., 2006).

Among the SDTF, the Caatinga has been drastically modified by human activities since the beginning of European colonization during the 16th century (COIMBRA-FILHO; CÂMARA, 1996). In the Caatinga, acute anthropogenic disturbance is characterized by the removal of vegetation over large areas. Chronic anthropogenic disturbances, on the other hand, are subsistence agricultural cycles, overgrazing by livestock (especially goats), fuelwood extraction for domestic and commercial purposes, logging, mainly for use on farms and for the collection of plants for food, medicinal purposes or as a source of raw material (i.e., Non-Timber Forest Products (RAMOS et al., 2008). Thus, acute and chronic anthropogenic disturbances are responsible for changes in primary productivity.

Net primary productivity (NPP), that is, the total amount of carbon (C) taken up by photosynthesis minus the carbon lost through plant respiration, is a key flux of the forest carbon cycle, representing total carbon inputs over time and the energy base for heterotrophic organisms (BECKNELL et al., 2021). NPP estimation primarily includes direct measurement of aboveground net primary productivity (ANPP – Aboveground Net Primary Production) (FIELD et al., 1998)), often accessed by the correlation of litter production (SCHILLING et al., 2016), with biomass increase based on allometry (CLARK, 2002), or through annual litter production (LEBAUER; TRESEDER, 2008; STOCKER et al., 1995). Assessments of this character are important for the SDTF's, in which analyzing its productivity is seen as one of the priorities of research in ecology (SÁNCHEZ-AZOFEIFA et al., 2005), since they account for nearly half of the world's tropical and subtropical forests (MURPHY; LUGO 1986), and directly support the livelihoods of many of the world's poorest people (CAMPBELL, 1996; WAEBER et al., 2012). Moreover, they provide a wide range of ecosystem services, thus playing an important and complex role in providing support for the agricultural systems on which millions of subsistence farmers rely up on (CHIDUMAYO; GUMBO, 2010).

Litter has a direct impact on the soil fertility recovery during the fallow period of shifting cultivation (READ; LAWRENCE 2003). Therefore, the study of nutrient cycling as a way to understand the SDTF dynamics is important for the conservation and management of degraded areas, favoring the fast recovery of the ecosystem, avoiding the loss of species (MOURA, 2010). Therefore, understanding nutrient dynamics broadens sustainable activities of fundamental importance to curb desertification and conserve the Caatinga. The Caatinga presents an opportunity to study the mechanisms of the ecosystem processes operating in the SDTF, such as the production of litter (ARNAN et al., 2018; MENEZES et al., 2012) and decomposition, which is responsible for nutrient dynamics. Information related to the dynamics of essential nutrients such as nitrogen (N) and phosphorus (P) is still incipient in the SDTF (MENEZES et al., 2012; SAMPAIO, 1995; TIESSEN et al., 2001). However, empirical evidence indicates that N and P are the limiting elements for vegetation growth (MENEZES et al., 2012; SAMPAIO, 1995; TIESSEN et al., 2001). In some cases, nutrient availability may even be a determinant of the aboveground NPP (LA PIERRE et al., 2016). Despite this, nutrient dynamics are often ignored in productivity models (ANAV et al., 2015). However, studies on understanding these changes and the sustainability of production systems have received little attention in the context of dry forests (SINGH, 1998; FERREIRA et al., 2007; SALGADO et al., 2015; AGUIAR et al., 2014).

The majority of the population in the semiarid region depends on slash-and-burn agriculture and the sustainability of this agriculture depends on the forest regeneration process, making it fundamental to understand the factors that affect the productivity of this ecosystem. In the SDTF, primary productivity is mostly controlled by the amount and duration of rainfall, such that seasonal variations in rainfall constrain and control the productivity and nutrient dynamics of these ecosystems (LUGO; MURPHY, 1986; DIRZO et al., 2011). In arid and semiarid environments, variations in vegetation structure, caused by edaphic factors and rainfall distribution, can also lead to spatial changes in litter production (ARCHER et al., 1988; FACELLI; PICKETT, 1991; ALVAREZ et al., 2009; BISIGATO et al., 2009).

In the Caatinga, the vegetation cover and the litterfall are important for soil protection, since the soil is generally shallow, with low infiltration capacity, high surface runoff and reduced natural drainage (SAMPAIO et al., 1981; LOPES et al., 2009). Studies about production and accumulation of litter in the Caatinga are lacking (ANDRADE et al., 2008; COSTA et al. 2010; SANTOS et al. 2011; SILVA et al., 2015b),as well as its degradation rate (SAMPAIO, 1995; DANTAS, 2003; ALVES et al., 2006; LOPES et al., 2009; SANTANA; SOUTO 2011; MENEZES et al., 2012; BAUER et al., 2016). Within this context, the general objective of this study was to estimate the productivity of the Caatinga through litter production and the correlation with conditioning factors, such as aerial biomass, human disturbance and age of forest regeneration. We also assessed how precipitation rates and chronic disturbances influence leaf decomposition and chemical changes through C, N, and P dynamics.

We have tested the following hypotheses: (1) litter production increases along the chronosequence and is positively related to forest structural parameters and soil nutrients; (2) the seasonal variation in litter production is greater in the early stages of forest regeneration; (3) decreased precipitation directly influences the reduction of leaf mass, accelerating the rate of decomposition and consequently limiting the efficiency of nutrient re-translocation due to lixiviation; (4) the chronic anthropic disturbances directly influence the decrease of the ecosystem productivity, accelerating the rate of decomposition and decreasing the final stock of nutrients that will return to the soil. It is expected due to decreased precipitation in the region and the high degree of anthropogenic disturbance, a reduction in ecosystem productivity and an increase in the rate of decomposition will occur. Our findings are discussed in light of dry forest functioning in human-modified landscapes, including resilience over the long-term as ecosystem service provision.

2 THEORETICAL BASIS

2.1 ANTHROPIC DISTURBANCES

Human-induced disturbance is one of the most significant threats to tropical biodiversity (PEREIRA et al., 2010; TILMAN et al., 2017). In forest ecology, the concept of disturbance refers to phenomena that in some way disturbs the stability of a community or an ecosystem (ALBUQUERQUE et al., 2018). In recent decades, increasing levels of anthropogenic disturbance have been a major driver of biodiversity loss at local, regional, and global scales (SALA et al., 2000; FAHRIG, 2003; FISCHER; LINDENMAYER, 2007; CHAZAL; RONSEVELL, 2009). Despite habitat loss as the greatest threat to biodiversity (Fahrig 2003), the chronic disturbances also compromise the different dimensions of diversity (taxonomic, functional and phylogenic) and, consequently, the ecological processes (LEAL et al., 2014; REDFORD, 1992; RIBEIRO, 2015; 2016; 2019; SABATER, 2008).

Ecologists seek to understand how human actions can affect biodiversity (ALBUQUERQUE et al., 2018). According Singh (1998), in contrast to intense forest disturbances (total vegetation removal causing habitat loss), there are different chronic anthropogenic disturbances, some types of these disturbances are small-scale harvesting of forest biomass (fuel wood, forage, non-timber forest products). There have been few explicit tests that point to the long-term ecological consequences of such human actions (ALBUQUERQUE et al., 2018). However, some studies on forest resources use patterns to provide evidence of such consequences, e.g. wood harvesting for fuelwood demands large amounts of plant biomass (MEDEIROS et al., 2011; RAMOS et al., 2008; SPECHT et al., 2015). These resources are utilized on a daily basis among low-income rural populations in developing countries (ALBUQUERQUE et al., 2018). Thus, some studies have suggested that this activity, if practiced in the long term, can alter the species composition and decrease the population density and total basal area of trees, hence, decreasing the productivity of the ecosystem (LUNG; ESPIRA, 2015; RÜGER et al., 2008; SPECHT et al., 2015).

Chronic anthropogenic disturbances are especially prevalent in dry areas of the tropics, which have denser human populations and are more dependent on the forest resources of the ecosystem (SINGH, 1998; SPECHT et al., 2015). Thus, it is of fundamental importance to understand how chronic anthropic disturbances can impair ecosystem stability and consequently compromise the future use of these ecosystem resources by humans (CÂMARA et al., 2019).In areas of strong anthropic pressure, ecological communities are in a constant process of secondary succession, and species colonization and extinctions can occur continuously (LEHTILÄ et al., 2016) and consequently decreasing the stability of the ecosystem. In dry tropical areas, aridity is a major factor that affects ecosystem stability, where adverse environmental conditions harbor more dynamic communities than more humid areas, on which environmental conditions are more stable (DIAMOND et al., 2016). Moreover, aridity is able to interact with disturbances and intensify ecosystem instability (PULLA et al., 2015; PUIG-GIRONÈS et al., 2017).

The degree of disturbance of a habitat fragment is expected to vary widely depending on its proximity to different disturbance vectors, with sites closer to vectors suffering more from anthropogenic disturbance (ANTONGIOVANNI et al., 2020). Forest fragments located near human settlements and pastures are more susceptible to chronic disturbance due to logging, grazing, poaching and fire (RIBEIRO et al., 2015; TAVARES et al., 2016). Roads are also important sources of chronic disturbance due to access in these previously remote areas (LAURANCE et al., 2009; REIJNEN et al. 1995; WILKIE et al., 2000). Proximity to other infrastructure, such as dams and transmission lines, is also correlated to disturbances (DECKER et al., 2017; RIBEIRO et al., 2015). Therefore, different fragments are expected to exhibit different levels of disturbance because it depends on the context in which they are located, their area and how they modulate edge effects - defined as the modification of ecological patterns and processes in adjacent ecosystems (FONSECA; JONER, 2007).

However, CAD (Faculty Evaluation Committee) field assessment is too expensive and time-consuming to be done on a macro-geographic scale. A cost-effective alternative is the use of remote indexes that integrate different chronic disturbance vectors (ARNAN et al., 2018; MARTORELL; PETERS, 2005). As such, it allows a quick diagnosis on the degree of integrity of the fragments over large territories and assists in strategic decisions for biodiversity conservation through the creation of protected areas, habitat restoration efforts, and sustainable resource management.

2.2 PRODUCTIVITY IN THE ECOSYSTEM

Net primary productivity (NPP) is a key process within ecosystems, particularly in tropical forests (CLARK et al., 2001b; ARAGÃO et al., 2009; MALHI et al., 2009). NPP is determined by the total amount of C that remains after part of the organic matter produced in photosynthesis is used for respiration, growth and maintenance of the plant (AMTHOR; BALDOCCHI, 2001). In forest ecosystems, NPP is usually assessed through the production of litter, since it is the main source of organic C, plant nutrient cycling, and one of the most important and measured components in tropical forests (VITOUSEK, 1982; CLARK et al., 2001a). Therefore, quantifying the litter reservoirs is essential to properly understand the structure and function of tropical forests (BRAY; GORHAM; 1964; VITAL et al., 2004), estimate productivity and evaluate phenology, carbon dynamics, biogeochemical cycles, and the capacity of forests to recover from natural and human disturbances (DE JONG, 2013). Moreover, identifying the factors that govern litterfall production can help us to better understand the response of forest ecosystems to climate change (SCHEER et al., 2011; THUILLE et al., 2006). Thus, understanding the dynamics of litterfall production can provide insight into nutrient cycling, forest growth, successional patterns, carbon fluxes, ecological disturbances and the interactions among environmental variables in forest ecosystems (VASCONCELOS; LUIZÃO, 2004; ZHOU et al., 2007; GONZÁLEZ-RODRIGUEZ et al., 2011).

Most studies on litterfall production in tropical forests have been conducted in humid forests, while fewer have addressed tropical dry forests (TDF) (SÁNCHEZ-AZOFEIFA et al., 2013), although the SDTF cover a greater extent and are more threatened by human activities (SÁNCHEZ-AZOFEIFA et al., 2013; BANDA et al., 2016). In TDF, seasonal variations in precipitation constrain and control nutrient productivity and dynamics (LUGO; MURPHY, 1986; DIRZO et al., 2011). Litterfall production in TDF occurs mainly in the dry season, as a strategy to avoid water loss through transpiration and to cope with water stress - low soil water availability and high vapor pressure deficit (VPD) (HUECHACONA-RUÍZ, 2016; ARYAL et al., 2015; VALENTINI et al.; 2008; MARTINS; RODRIGUES, 1999). Therefore, TDF litterfall production is negatively correlated with annual production, seasonal production, and monthly precipitation (ARYAL et al., 2015; ZHANG et al., 2014; CUBA et al., 2013; LAWRENCE, 2005; KELLY et al., 1988; MURPHY; LUGO, 1986).

However, most studies conducted to date on litterfall production in TDF have been short-term (PARSONS et al., 2014; SUNDARAPANDIAN; SWAMY, 1999), which limit the possibility of evaluating, modeling, and predicting the effects of climate change (SÁNCHEZ-SILVA et al., 2018; MARTÍNEZ-YRÍZAR et al., 1990; WHIGHAM et al., 1990). The few multi-year studies of litterfall production in TDF and its relationship with precipitation (TANG et al., 2010) have documented several patterns of monthly litterfall production at different times of the year (ARYAL et al., 2015; ZHANG et al., 2014), mostly with low or null precipitation (ARYAL et al., 2015; ZHANG et al., 2014; WAGNER et al., 2016). Most TDFs regenerate naturally after ceasing anthropogenic impacts (CHAZDON, 2008) and unraveling temporal and spatial patterns of litterfall along successional gradients is fundamental for a better understanding of ecosystem functional recovery (SOUZA et al., 2019).

2.3 DRY FORESTS AND THE CAATINGA

Tropical forests have been considered a key ecosystem in terms of providing valuable ecosystem services relevant for global sustainability (FERRAZ et al., 2014; POWERS et al., 2018). It is important to mention carbon sequestration, climate regulation and clean water, and the persistence of biodiversity (BRANDON, 2014). Due to the exploitation of *commodities,* such as timber, tropical forests are extremely important to the economy, particularly influencing the quality of life of thousands of people who depend on a huge array of forest products and services, both for subsistence and for trade (CARRASCO et al., 2014; BROCKERHOFF et al., 2017). This scenario is even more prevalent in seasonally dry tropical forests (SDTF), which account for 42% of the world's forests (SANTOS et al., 2011). The Caatinga represents the Brazilian SDTF and is home to a very dense human population that depends on natural resources for its subsistence (RITO et al., 2017).

The SDTF are widely recognized as the most threatened tropical forest biome (PENNINGTON et al., 2009), chronic disturbances being one of the main threats due to the history of colonization and utilization of natural resources (SAGAR; SINGH, 2004). Continuous biomass extraction compromises a natural region into a mosaic of areas with different degrees of disturbance (SINGH 1998; MARTORELL; PETERS, 2005). These disturbances include decreases in canopy cover and tree density, as well as reductions in basal area and tree height on disturbed sites (KUMAR; SHAHABUDDIN, 2005), negatively influencing the species composition and diversity (KUMAR; SHAHABUDDIN, 2005; RIBEIRO et al., 2015).

The Caatinga has historically been converted into successional mosaics due to shifting agriculture and cattle ranching (SOUZA et al., 2019) and inadequate management over time accelerates the desertification process (LIRA et al., 2006). Therefore, it is urgent to develop conservation and environmental recovery programs. Furthermore, the remaining Caatinga forests (both primary and secondary forests) represent a key source of various subsistence products, such as areas of livestock forage, wood extraction and medicinal plants that generate chronic disturbance (ARNAN et al., 2018). Thus, it must be thoroughly understood the dynamics of soil-vegetation interactions in these ecosystems (BORÉM; RAMOS, 2002).

2.4 ECOSYSTEM FUNCTIONING: NUTRIENT CYCLING AND LEAF DECOMPOSITION

Deforestation compromises the natural nutrient cycle and alters the quality and quantity of organic matter in the soil, with a decrease in microbial biomass activity (primarily responsible for nutrient cycling and energy flow in soil), which influences both the transformation of organic matter as well as mineral and C storage (ALVES, 2011). Thus, the maintenance and regeneration of forest ecosystems depend on the nutrient cycling through litterfall production and decomposition (SOUTO, 2006; ARAÚJO et al., 2019).

Litterfall production is considered one of the main routes of nutrient transfer from the vegetation to the soil (VITOUSEK, 1984; BÚRQUEZ et al., 1999; VITAL et al., 2004). Therefore, quantifying litterfall pools is essential to properly understand the structure and function of tropical forests (BRAY; GORHAM, 1964; VITAL et al., 2004). In semiarid terrestrial ecosystems, 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). Thus, understanding the dynamics of litterfall production can provide insight into nutrient cycling, forest growth, successional patterns, carbon fluxes, ecological disturbances and the interactions among environmental variables in forest ecosystems (VASCONCELOS; LUIZÃO, 2004; ZHOU et al., 2007; GONZÁLEZ-RODRIGUEZ et al., 2011).

Nutrient cycling in forest ecosystems comprises several biogeochemical nutrient cycles by which the transfer of elements in and/or out of the ecosystem occurs. Inputs are originated fromair, precipitation, weathering of the rocks, biological nitrogen fixation and also artificial fertilization. The vegetation returns nutrients to the soil through the circulation of matter, which is represented by the deposition of litter, composed of branches, trunks and leaves. Outputs are represented by losses due to erosion, leaching, volatilization and the export of nutrients, mostly represented by the removal of vegetation (PRITCHETT, 1986). The main mechanisms by which the cycling of nutrients occurs between the phytomass and the soil are the absorption of nutrients by the plants, retention in the biomass, internal translocation in the plant, fall of residues from the aerial part that will form the litter and decomposition of this material (PRITCHETT, 1979).

The nutrient cycling process is dynamic, as it can pass both from the abiotic to the biotic environment, or otherwise (SELLE, 2007) composed of a cyclic trajectory of elements that are essential to life, which are produced from several interconnected processes, and subsequently reused successive times, with some nutrient loss (DELITTI, 1995). It is an essential cycle for the maintenance of life on Earth and one of the main mechanisms involved is the deposition of burlap for its subsequent and gradual decomposition. The primary goal of cycling is to regulate and assist the development of ecosystems (DELITTI, 1995), this process varies with a number of factors such as temperature and precipitation, and between ecosystem types (CUNHA et al., 1993).

The pattern of nutrient cycling in the humid tropics is different from that in dry areas. The speed at which nutrients move between and within compartments is much faster in a tropical rainforest, where there is a great diversity of plant species, this way, the litterfall has a varied composition and a more stable nutrient cycle, establishing a large community of microorganisms that accelerate the decomposition process, directly influencing the nutrient cycling (SANCHES et al., 2008).

Different land uses and climate change can impact nutrient fluxes and stocks (MENEZES, 2012). The consequences of these impacts on the structure and functioning of productive systems deserve attention from researchers (MENEZES, 2012), given that nutrient cycling plays an essential role in maintaining the productivity of forest ecosystems. The necessity of efficient cycling is even greater in tropical soils, which are characterized by low fertility and high weathering (SANCHEZ; LOGAN, 1992).

Within this context, understanding productivity is an important approach to understanding the dynamics of the ecosystem (MOURA et al., 2016). The presence of forest-dependent rural populations is predominant in the tropics, which makes the Caatinga a unique opportunity to investigate regeneration in the context of multiple forest use. Here, we evaluate the regeneration of a Caatinga dry forest in the context of chronically disturbed forest stands (i.e. firewood gathering, logging, and foraging by cattle) to evaluate both its recovery rate and trajectory. We first examined the relative contribution of the ecosystem through its productivity in the face of chronic anthropic disturbances, along a precipitation and regeneration gradient. We expected productivity to be lower in areas of greater disturbance, lower precipitation, and at an early regeneration age.

We also investigated ecosystem functioning through nutrient cycling and leaf decomposition along regenerating and old growth forest stands. We expected Caatinga to show higher nutrient concentration in areas with less disturbance and at more advanced ages. Finally, we expected that the chronic disturbance imposed on regeneration of forest stands would alter the concentration, nutrient flux and leaf decomposition and consequently reduce the primary productivity of the Caatinga.

3 CHAPTER 1

Forest productivity and nutrients dynamics in a Caatinga dry forest: The role played by precipitation and human disturbances

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Abstract

This work aimed to estimate the productivity of the Brazilian dry forest (Caatinga), through the production of litter and estimate carbon and nutrients' fluxes, identifying conditioning factors such as land use, climatic condition and forest regeneration age. Litter deposition was monthly recorded over four years from five traps of 0.5 m2 placed 0.5 m above the ground in using 13 forest stands of different successional ages with agricultural use history and in 15 plots along a precipitation gradient, with no agricultural use history. The mean annual litterfall was 0.193 Mg ha-1 yr-1. The differences in litter deposition were significant along the chronosequence. The nitrogen (N) and carbon (C) fluxes, both the successional stage areas (Nflux 4.5 kg ha-1 yr-1, Cflux 105.54 kg ha-1 yr-1) and the old-growth forest areas (Nflux 4.8 kg ha-1 yr-1, Cflux 110 kg ha-1 yr-1) had higher fluxes in September. The lowest values in the old-growth forest areas occurred in December (Nflux 0.95 kg ha-1 yr-1, Cflux 28.74 kg ha-1 yr-1) and in the successional stage areas, the lowest value for carbon fluxes occurred in March (Cflux 41.44 kg ha-1 yr-1) and for N in December (Nflux 1.34 kg ha-1 yr-1). The litter was composed mainly of leaves, both in the forest areas in different successional stages and old-growth forest areas. Litterfall in Caatinga was influenced by seasonality and successional stages, with leaf deciduousness occurring in the beginning of the dry season in all successional stages.

Keywords: Litterfall, Regeneration Gradient, Seasonality, Litter production, Anthropic disturbance, Seasonally dry rainforest.

1 INTRODUCTION

Tropical forests represent unique habitats in terms of conserving and providing ecosystem services on global scale, such as the fixation of C from the atmosphere and its accumulation in plant biomass and soil (Van Veen et al., 1991; Onti et al., 2012). Although tropical forests cover a small part of the earth's surface (7 to 10%), they account for 35% of the land's net primary productivity (Poorter et al., 2015; Alamgir et al., 2016). Thus, besides stocking C, the aboveground biomass of these ecosystems is directly related to their productivity and several other relevant ecological services, as the provision of forest products for the livelihoods of rural/traditional populations (Maass et al., 2005; Beer et al., 2010; Houghton et al., 2015; Poorter et al., 2015; Portillo-Quintero et al., 2015).

In seasonally dry tropical forests (SDTF), primary productivity is controlled by time and amount of rainfall, causing a seasonal control in productivity and, consequently, in the nutrient dynamics of these ecosystems (Lugo & Murphy, 1986; Dirzo et al., 2011). Litter production is considered one of the main routes of nutrient transfer from vegetation to soil (Vitousek, 1984; Búrquez et al., 1999; Vital et al., 2004), which makes it extremely important to quantify the reservoirs of this litter to correctly understand the function and structure of tropical forests (Bray & Gorham 1964b; Vital et al., 2004). In semi-arid terrestrial ecosystems, litter 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). Therefore, understanding the dynamics of litter production can provide information not only about nutrient cycling but also ecological disturbances, successional patterns, forest growth, ecological disturbances, and the interactions between environmental variables in forest ecosystems (Vasconcelos & Luizão, 2004; Zhou et al., 2007; González-Rodriguez et al., 2011).

Estimating the productivity of an ecosystem is essential to answering ecological questions at the ecosystem level (Rosenzweig, 1968). Litter production assessment is also important in dry tropical forests (DTF), where productivity analysis is seen as one of the ecology research priorities (Sánchez-Azofeifa et al., 2005). However, tropical forests have been rapidly converted into human-modified landscapes (Arroyo-Rodríguez et al., 2017).

In the Americas, Mexico and Brazil harbor the largest areas of DTF ecosystems, where 73% (Maass et al., 2005) and 46% (MMA, 2011) of vegetation, respectively, was already altered or converted to other land uses (Arroyo-Rodríguez et al., 2017). As most of the oldest DTFs are characterized by highly fragmented landscapes at different levels of succession (Quesada et al., 2009), improving our understanding of the functioning of these ecosystems is very important to achieve conservation policies (Moura et al., 2016), and maintenance of ecosystem services.

In Brazil, Caatinga represents the SDTFs and has been converted into human-modified landscapes, with the predominance of family farming and extensive livestock farming that relies on native vegetation as the main source of forage (Sampaio, 1995; Silva et al., 2017). The remaining vegetation of the Caatinga suffers from some types of chronic anthropogenic disturbances (Silva et al., 2017). Consequently, more than 90% of the Caatinga that still covers the Brazilian Northeast lands represents secondary forest vegetation under regeneration, as part of the slash and burn agriculture fallow cycle and the regrowth cycle of fuel wood production (Gariglio et al., 2010). The disturbances can eliminate large useful trees and alter the relative contribution of traits and, consequently, the functional composition of plant assemblages by the proliferation of species adapted to the disturbance (Ribeiro et al., 2016; Sfair et al., 2018), thus altering productivity of forest and the return of nutrients that it provides to the ecosystem. However, despite this relevance, there are few studies available reporting fluxes of carbon and nutrients in this ecosystem (Ferreira et al., 2007).

Large part of the semiarid population, such as the population of the Caatinga, depends on slash-and-burn agriculture and the sustainability of this agriculture. The soil fertility recovery in Caatinga is achieved with shifting cultivation and fallow with forest regrowth (Menezes et al., 2012), being directly coupled to litter productivity (Read & Lawrence, 2003). As for nutrients' fluxes, litterfall is highly influenced by the distinct biomass and species composition of early successional stages (Guariguata & Ostertag, 2001; Read & Lawrence, 2003; Barlow et al., 2007; Campo et al., 2007). Although the responses of the productivity of the ecosystems have already been well documented for tropical forests exposed to habitat loss and fragmentation (Leal et al., 2005; Ramos et al., 2008), the same responses are expected to be present in the Caatinga, even if associated with other conditions.

The main objective of this study was to estimate the productivity of the Caatinga through litter production and estimate carbon and nutrients' fluxes, identifying and analyzing the relationship with conditioning factors, such as aboveground biomass, human disturbance and age of forest regeneration. We tested the following hypotheses: (1) litter production increases along the chronosequence and is positively related to forest structural parameters and soil nutrients; (2) seasonal variation in litter production is more pronounced in the early stages of forest regeneration. Our uncovered findings are discussed in the light of drivers affecting dry forest functioning in human-modified landscapes, including long-term resilience as provision of ecosystem services.

2 METHODS

2.1 Study area

The study was carried out within the Catimbau National Park (hereafter, "PARNA Catimbau") (between 8º4'00" and 8º36'35" S and between 37º09'30" and 37º14'40" W), covering an area of about 62,000 ha and located between the municipalities of Buíque, Tupanatinga and Ibimirim, in the state of Pernambuco, Brazil (Fig. 1). Approximately 70% of PARNA Catimbau has Latosol soil (Rito et al., 2017). The climate is predominantly semi-arid BSh with distinct areas of tropical rainy climate As' according to the Köppen scale (Peel, Finlayson & Mcmahon, 2007). The temperature varies between 21°C and 25°C and annual rainfall varies between 650 and 1100 mm, with great irregularity in the inter-annual regime (Rito et al., 2017). Generally, about 60 to 75% of rainfall occurs over three months, from March/April to June/July, which corresponds to the rainy season and the coldest period. The predominant vegetation is dry forest where trees and shrubs of Fabaceae, Euphorbiaceae, Boraginaceae and Burseraceae predominate (Rito et al., 2017).

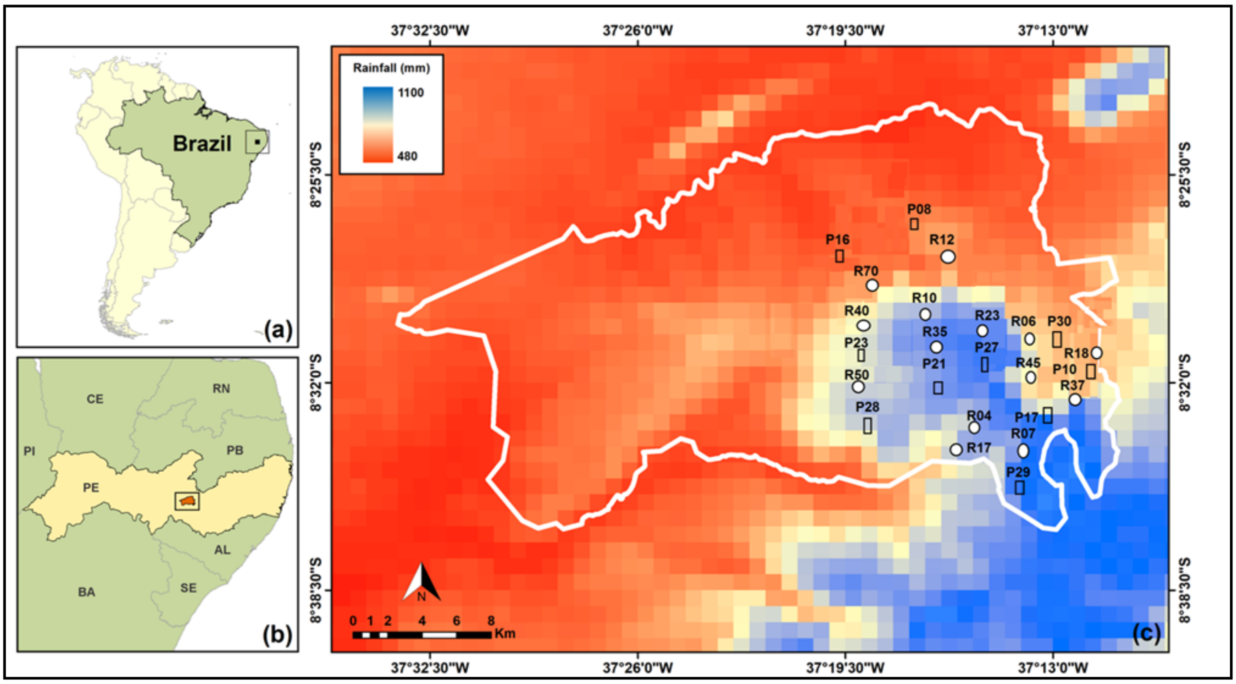

Figure 1. Map of the Catimbau National Park, in Pernambuco state, northeastern Brazil (a-b) and showing (c) regenerating forest stands (R) (white circles) and old-growth forests (P)A (open squares; with no recent history of agricultural use).

PARNA Catimbau was created in 2002 and throughout these years, residents have never been compensated and continue to live within this conservation unit area. There are small urban centers, small farmers, mythical-religious communities, areas of archaeological importance, in addition to small private tourist developments. The historic presence of these residents has given rise to a huge mosaic in terms of land use and human pressure on the biota (i.e. anthropic landscapes), which makes PARNA Catimbau an excellent opportunity to examine how agriculture, livestock, logging, and hunting, among other chronic disorders, affect the Caatinga biota and the establishment of emerging or new ecosystems.

2.2 Sampling design

We selected 28 forest stands (20 x 50 m each) from the Long-Term Ecological Research Project network (LTER-Catimbau), where 13 of them represent a chronosequence ranging from 10 to 76 years old, with a similar history of slash-and-burn agriculture as main land use. The remaining 15 forest stands follow a precipitation gradient, ranging from 510 to 940 mm, and are considered preserved areas, with no historical agricultural use (Fig. 1). These 15 areas also contain an anthropogenic disturbance index, which was previously measured using the global GMDI index (Global Multimetric Disturbance Index) (Arnan et al., 2018).

The index ranges from 0 to 100 and is derived from 3 sub-indexes (human presence, herbivory by domestic herbivores and collection of timber and non-timber materials). Each sub-index was calculated based on several measurements, through: (1) remote sensing according to the geographic information system (GIS), to estimate the distance of access to the forest areas; (2) semi-structured interviews to assess, as example, the abundance of goats and the amount of firewood used per day and (3) in situ surveys in the plots (e.g. quantification of shallow cut and feces trails of domestic herbivores) (Arnan et al., 2018).

2.3 Litterfall, carbon and nutrients annual fluxes estimation

Litterfall was estimated through monthly samplings from permanent traps over a four-years period in all the 28 forest stands, from September 2016 to August 2020. Each trap consists of a square-shaped PVC structure that has four vertical rods at the base to serve as a support. The collector has an area of 0.5 x 0.5 cm (0.5 cm^2) that supports a nylon mesh of 2 mm (Wright et al., 2011). The standard of the summation symbol (Σ) was adopted for the location of the traps. The establishment of a standard distribution for all areas gives a random model of location in the areas without favoring any environmental factor (Edwards, 1977). In the laboratory, the samples were sorted, weighed and oven-dried at 60 °C and chemically analyzed.

The weighed material was divided by the collector area and the values were divided by the number of days of each collection interval and extrapolated to 1 hectare. The results were multiplied by 30 days to estimate the monthly litter production in each plot and then added the 12 months and divided by 4 to obtain the annual litter production.

To estimate the annual fluxes of carbon (C), nitrogen (N), phosphorus (P), calcium (Ca) and magnesium (Mg), the annual litter mass was multiplied by the average concentrations of C, N and P in the leaves (Vitousek, 1982).

2.4 Chemical Analysis

The litter samples were dried at 60°C and grounded to fine powder to pass through a 2 mm sieve. Sub-samples of leaf material were weighed (2 to 3 mg) and sealed in tin capsules. The capsules were introduced into the elemental analyzer EuroVectorModel EA3000 for the determination of total C and N concentrations. Gases are generated following the samples' combustion, then, purified in a chromatography column and introduced into the mass spectrometer for isotopic ratios determinations (IRMS Delta Plus, Finnigan Matt, San Jose, CA, USA). Sugarcane leaves were used as standard material for vegetation material. Theδ15N and δ13C natural abundance is expressed in parts per thousand (‰) as a result of a standard internationally recognized equation:

$$\delta^{15}N \text{ or } \delta^{13}C = (R_{sample} / R_{standard} - 1) \times 1000$$

where, R is the molar ratio in the sample and standard between 13C and 12C or 15N and 14N. The standard used for C isotope was Peedee Belemnite (PDB; limestone of the Grand Canyon region, USA) and atmospheric air for N isotope. The analytical errors accepted were ± 0.3%, 0.1%, 0.3 ‰ and 0.5 ‰ for C, N, $\delta^{13}C$ and $\delta^{15}N$, respectively.

Phosphorus (P), calcium (Ca) and magnesium (Mg) in litter concentration was determined through a wet digestion method, using nitric acid and perchloric acid (4:1 ratio), where 10 mL of the mixture of acids was added to 0.5 g of each sample (Sarruge & Haag, 1974). After that, the digests were diluted to 25 mL and the P, Ca e Mg concentration determined Inductively Coupled Plasma Optical Emission spectroscopy (ICP- OES; Perkin Elmer Modelo Optima 8300 DV).

2.5 Data analysis

To compare litter production, nutrient concentration and fluxes across forest stands, we used one-way ANOVA test. We fitted a generalized linear model (GLM) to test the effect of chronic anthropogenic disturbance, precipitation, aboveground biomass and forest type (i.e. old-growth forest and regenerating forest stands). After checked residuals and evaluation of error distributions adequacy (Crawley 2007), we log-transformed data (response variable) that did not meet homoscedastic criteria. We adopted the variance inflation factor (VIF) using the “car” package for R to assess if there was collinearity among predictors. All variables could be maintained in the models since none of them showed VIF < 2.0, meaning independence among predictors (Jou, Huang & Cho 2014). All analyses were performed in R software (R Development Core Team, 2017).

3 RESULTS

Across the regenerating forest stands, the average annual litter production ranged from 0.0035 Mg ha^{-1} yr^{-1} to 0.564 Mg ha^{-1} yr^{-1}, averaging 0.193 ± 0.016 (mean ± SE) Mg ha^{-1} yr^{-1} with regenerating forest stands exhibiting significant variation (ANOVA F=10.92, P < 0.001; Fig. 2). In fact, litter production decreased in the early-successional stands, with the highest scores across middle and late-successional forest stands (Fig. 2). Finally, regenerating forest stands supported similar litter production (mean ± SE 0.193 ± 0.016 Mg ha^{-1}yr^{-1}) as compared to old-growth forests (mean ± SE 0.168 ± 0.01 Mg ha^{-1}) (ANOVA F= 1.86, P=0.17).

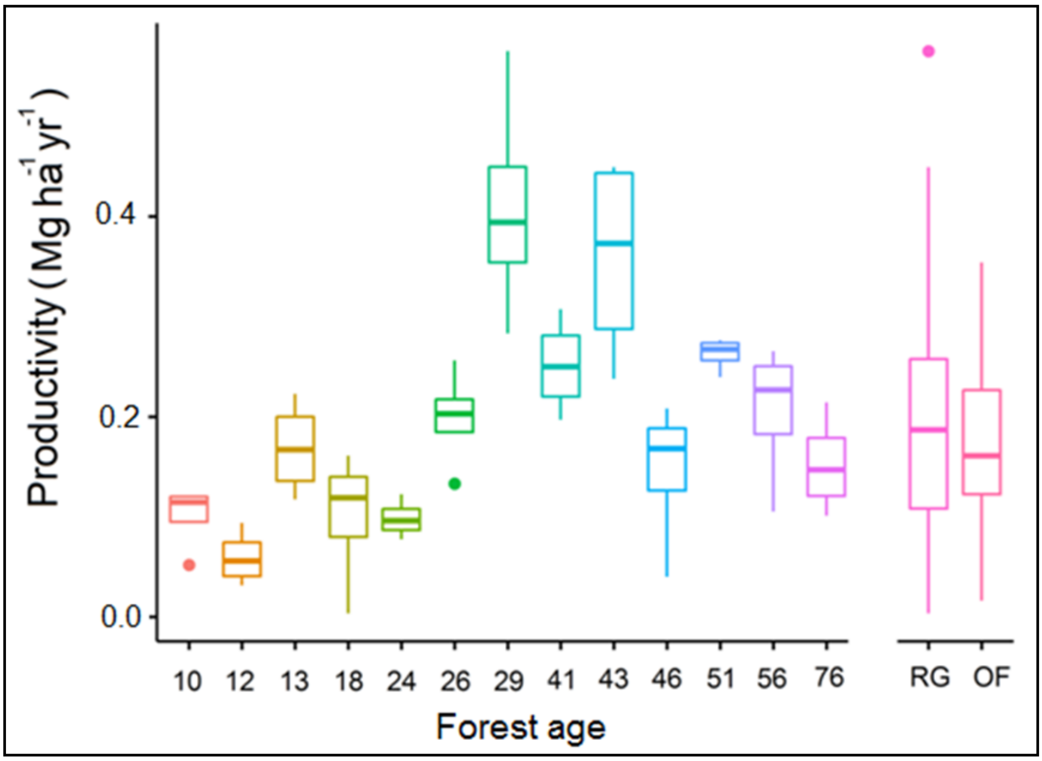

Figure 2. Mean ± SE of productivity (i.e. litter production) across regenerating forest stands (RG) and old-growth forests (OF) in Catimbau National Park, Pernambuco state, northeastern Brazil.

As expected, litterfall production changed significantly across seasons both regenerating and old-growth forest stands (Fig. 3), with litter production being greater during the dry season. The August-February interval accumulated 0.26 Mg ha^{-1} mo^{-1}; i.e.16.0 % of the total annual deposition. Rainy season (March-July) accumulated 0.05 Mg ha^{-1} yr^{-1}; i.e. only 3% of the total annual deposition (Fig. 3). In this perspective, precipitation positively influenced monthly litter production (Table 1, Fig. 4a), although aboveground biomass and chronic anthropogenic disturbance were also important predictors (Table 1). In fact, litter production increased across those forest stands supporting higher aboveground biomass but decreased across the stands exposed to high levels of chronic anthropogenic disturbance (Fig. 4b and c).

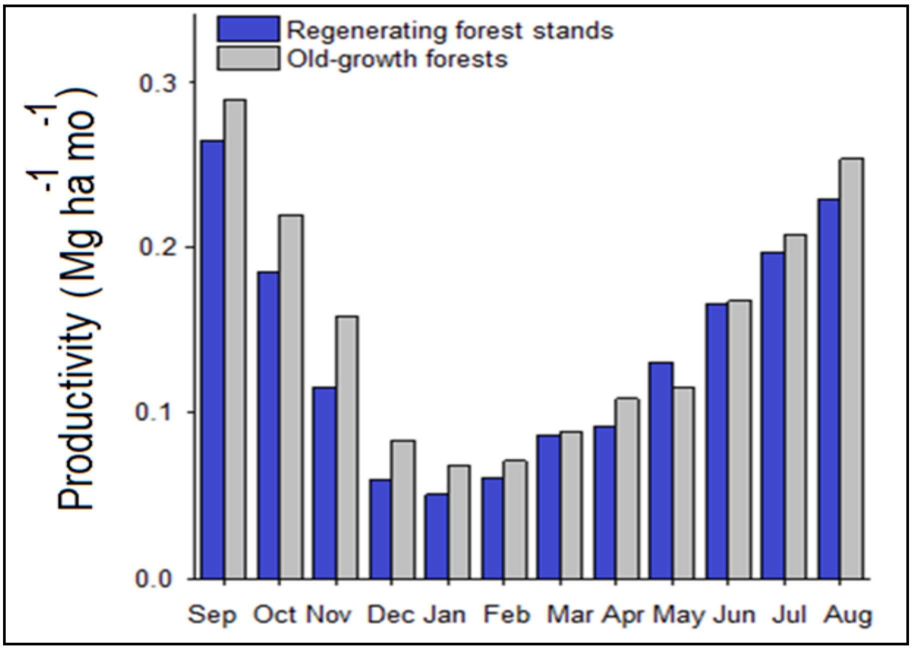

Figure 3. Mean monthly litter production over 48 months in areas with different ages of regeneration and old growth forest areas in Catimbau National Park, Pernambuco state, northeastern Brazil.

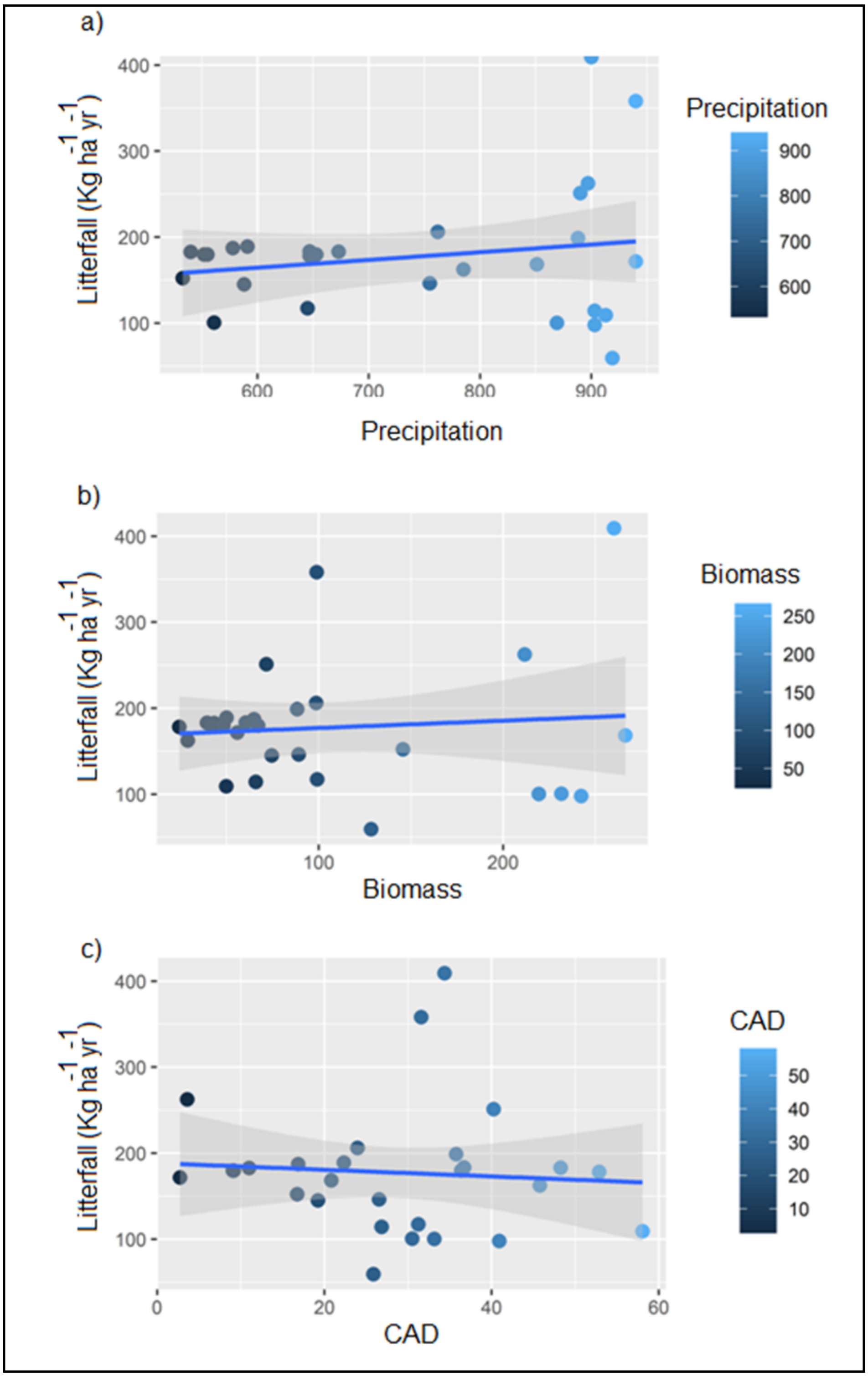

Figure 4. Significant effect of precipitation (a), aboveground biomass (b) and chronic anthropogenic disturbance – CAD (c) on litter production over 48 months in Catimbau National Park, Pernambuco state, northeastern Brazil.

Table 1. Results of the Generalized Linear Models (GLMs) with the effects of forest biomass, chronic disturbance, precipitation, and forest type on litter production over 48 months in Catimbau National Park, Pernambuco state, northeastern Brazil.

	Estimate	**SE**	**z value**	**p**
Litter				
Intercept	4.97	8.05×10^{-1}	61.6	**<0.001**
Biomass	7.52×10^{-4}	2.75×10^{-4}	2.73	**0.006**
Precipitation	3.82×10^{-4}	$1.1 \times 10\text{-}^{4}$	3.44	**<0.001**
CAD	-3.24×10^{-3}	1.04×10^{-3}	3.01	**0.001**
Forest type	1.9×10^{-1}	4.3×10^{-2}	4.35	**<0.01**

Overall litter nutrient concentration was highly variable across forest stands with little responses to our explanatory variables. Briefly, nutrient concentration varied from 19 to 28 g Kg^{-1} (N), 0.6 to 1.2 g Kg^{-1} (P), 404 to 540 g Kg^{-1} (C), 4.2 to 11.5 g Kg^{-1} (K), 7.1 to 28 g Kg^{-1} (Ca) and 2.3 to 5.0 g Kg^{-1} (Mg). Accordingly, no significant differences were detected for N (ANOVA F=0.94, P=0.51), C (ANOVA F=0.19, P=0.99) and P (ANOVA F=0.89, P=0.55) across regenerating forest stands (Fig. 5a), including those suggesting any linear relationship with forest age. Similarly, litter concentration of C, P and Mg was similar in both regenerating (C 484 ± 20 ; P 0.8 ± 0.03; Mg 3.17 ± 0.17) and old-growth forests (C 504 ± 70 g kg^{-1}; P 0.83 ± 0.03 g kg-1; 3.2 ± 0.1 g kg^{-1}). However, old-growth forests produced a litterfall with higher concentration of Ca (mean ± SE, 14.3 ± 0.8) and K (mean ± SE 6.9 ± 0.4) as compared to regenerating forest stands (Ca mean ± SE 11.6 ± 0.6, K mean ± SE 5.8 ± 0.4; Fig. 6). In general, all explanatory variables played a small role on litterfall nutrient concentration (Table S1). Precisely, aboveground biomass correlated negatively with C concentration while CAD positively affected K litter concentration.

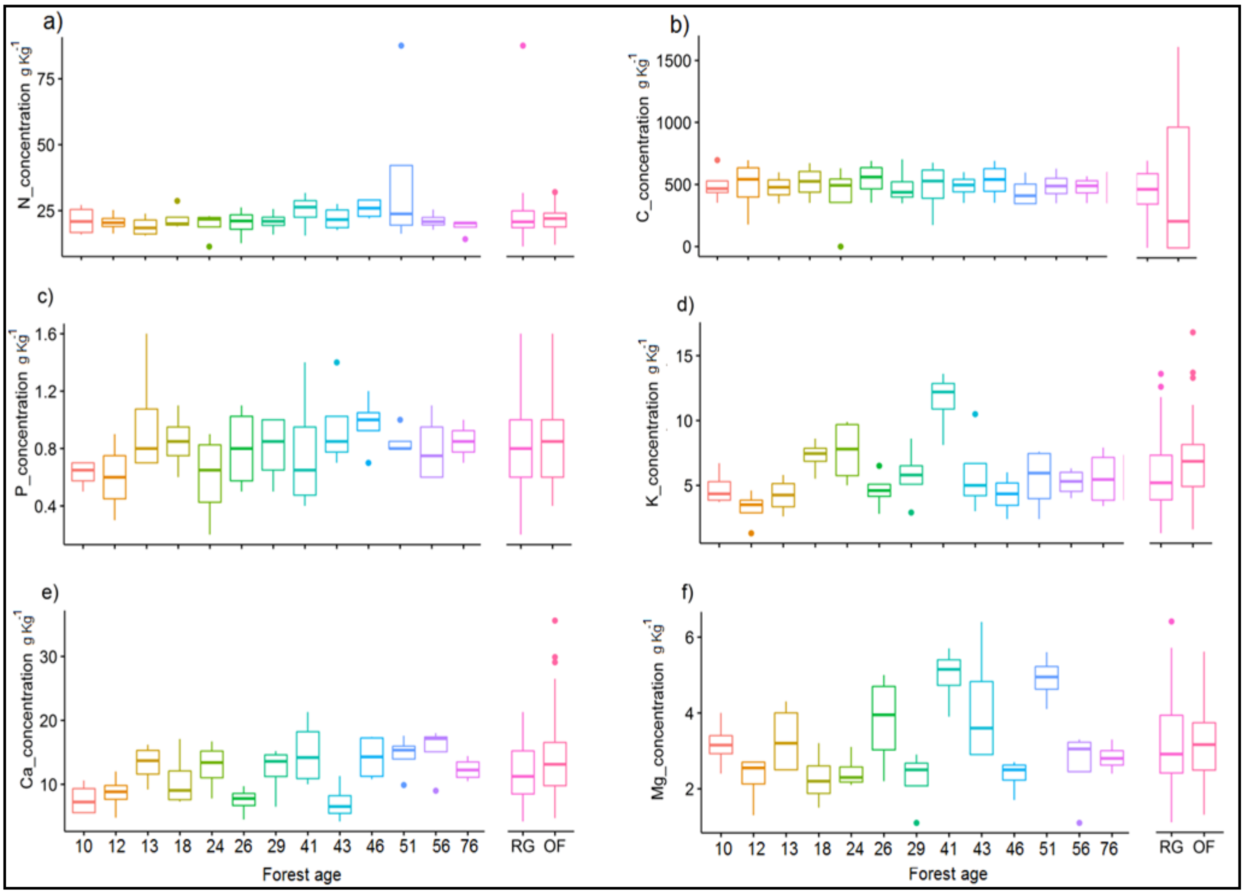

Figure 5. Mean ± SE of foliar concentrations for N (a), C (b), P (c), K (d), Ca (e) and Mg (f) over the 48 months across regenerating forest stands (RG) and old-growth forests (OF) in Catimbau National Park, Pernambuco state, northeastern Brazil.

N (ANOVA F=2.49, P=0.01), C (ANOVA F=1.98, P=0.04) and P (ANOVA F=2.41, P=0.01) fluxes varied across forest regenerating stands, with middle and late-successional forest stands showing higher scores than early-successional forests (Fig. 6), although there was no evidence of variation correlated to forest age; i.e. linear changes as forest regeneration proceeds. Moreover, regenerating forest stands showed lower fluxes of C and P than old growth forests, with the opposite pattern regarding N flux (Fig. 6), although the average scores were slightly different; i.e. little biological differences. Finally, precipitation positively affected C flux (Table S2).

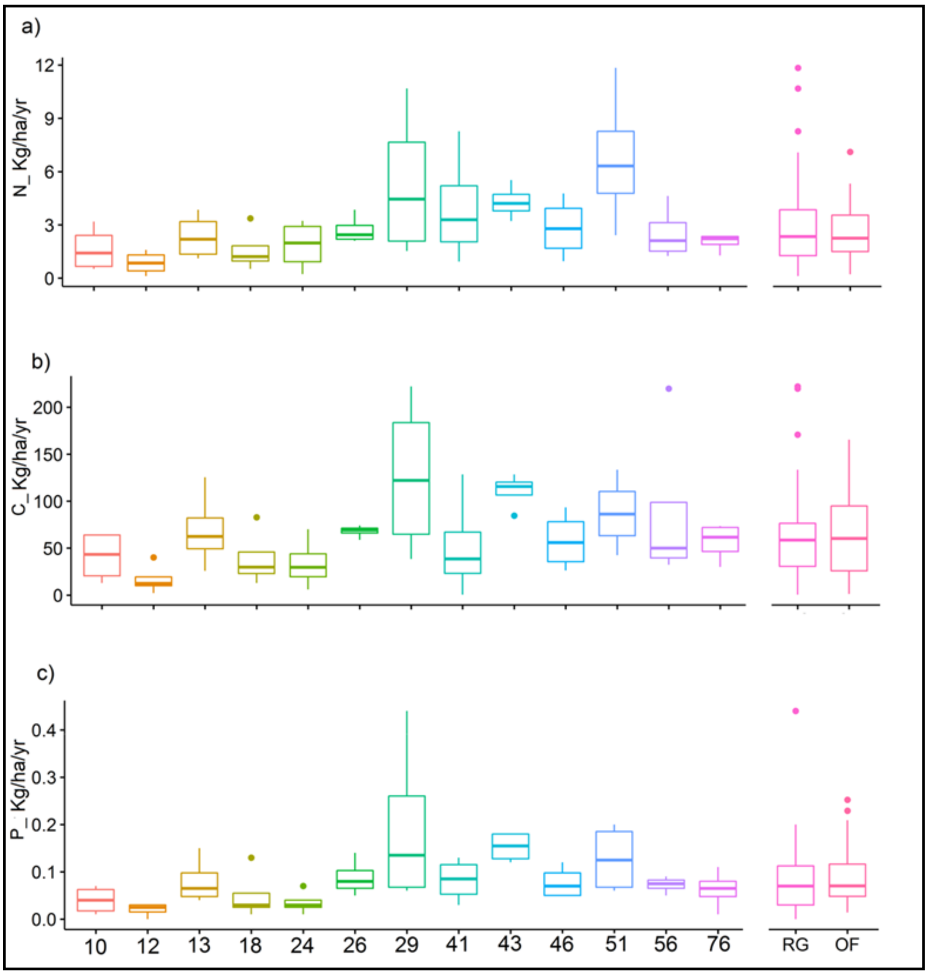

Figure 6. Fluxes of C (a), N (b) and P (c) over 48 months across regenerating forest stands (RG) and old-growth forests (OF) in Catimbau National Park, Pernambuco state, northeastern Brazil.

4 DISCUSSION

Our results suggest that the Caatinga dry forest is a low productivity ecosystem as the annual litter production represents only a small fraction of the aboveground biomass and contain little reproductive plant material. Moreover, litterfall production is highly seasonal, with production varying across forest stands but with no differences relative to forest succession status; i.e. regenerating and old-growth forest stands producing in average similar amounts of litterfall. However, litter production is affected by a combination of precipitation, aboveground biomass and chronic disturbance. Although litter nutrient concentration is highly variable across forest stands it apparently does not respond to forest successional status, precipitation, aboveground biomass and disturbance, with few exceptions. In contrast to concentration, nutrient fluxes are more predictable across successional mosaics, particularly considering forest sucessional status. In synthesis, Caatinga forest productivity and nutrient dynamics respond more intensively to environmental variables, aboveground biomass and chronic disturbance rather than forest stand age or successional status.

Our findings reinforce the notion that in tropical dry forest litterfall is highly seasonal or concentrated in the dry season (Martínez-Yrízar & Sarukhán, 1990; Read & Lawrence, 2003; Campo & Vázquez-Yanes, 2004), with litter production positively associated with aboveground biomass and precipitation (Lawrence, 2005; Chave et al., 2009; Becknell et al., 2012; Feng et al., 2019). However, we offer evidence suggesting that human chronic disturbance negatively impacts litter production across forest mosaics in human-modified landscapes. In contrast to literature, forest stand age or forest successional status play a minor role on litter production and other related attributes (Coleman & Crossley, 1996). We particularly refer to the lack of a clear trend between forest stand age, forest successional status and the following ecosystem-level attributes: litter production, nutrient concentration and fluxes via litterfall. In fact, predictable changes by ecosystem-levels attributes along forest regeneration such as those examined here are plausible due to trends relative to aboveground biomass but also due to the balance between acquisitive vs. conservative plant strategies along forest regeneration (Powers & Marín-Spiotta, 2017). Finally, our uncovered patterns reinforce the notion that dry forest are less productive ecosystem as compared to humid forests. Briefly, litterfall production in dry forests ranges from 1.5 up to 12.6 (Martínez-Yrízar, 1995; Morffi-Mestre et al., 2020), while it ranges from 8 up to 19.3 in humid forests (Martinelli et al., 2017).

In this context, Caatinga dry forest emerges as a low-productivity ecosystem (i.e Barbosa et al., 2007) by producing in average < 2 Mg ha-1 yr-1 (around 5% of the standing aboveground forest biomass; 38.8 ± 25.1 Mg ha−1; Souza et al., 2019), with litter nutrient concentration, and consequently flux, among the lowest values by tropical forests, including dry forests (see Lugo & Murphy, 1986; Kauffman et al., 1993; Campo et al., 2000, 2007; Jaramillo et al., 2003; Souto et al., 2009; Rentería & Jaramillo, 2011; Moura et al., 2016), particularly P. Most of the forest stands produced litter with reduced concentration of P (< 0.8%), resulting into less than 0.2 kg of P ha^{-1} yr^{-1} potentially added to the soil; please note that P is a key element regarding tropical forest productivity (Pett-Ridge, 2009).

We already know that water and nutrients availability are the main drivers of tropical forest productivity (Malhi, 2012) and these variables probably explain our uncovered patterns. In fact, the Caatinga dry forest in our focal landscape covers highly-impoverished sandy soils with precipitation ranging from 480 to 1100 mm (Rito et al., 2017). Precipitation has proved to positively affect forest aboveground biomass (Souza et al., 2019), but also the taxonomic/functional composition of plant assemblages (Rito et al., 2017; Pinho et al., 2019). Additionally, nutrient-impoverished ecosystems tend to favor plant strategies associated with nutrient preservation, including the reabsorption previous to leaf abscission (Aerts, 1997), what could explain litter low nutrient concentration as we documented here. However, nutrient and water supply are not completely regulated by natural phenomena. Caatinga remaining forest is constantly submitted to slash-and-burn agriculture and the exploitation of forest products, including foliage removal by free-raging livestock, particularly goats (Lins et al., 2022). Exotic goats in the Caatinga vegetation operates as generalist herbivores by consuming even litter during the dry season (Jameli et al., 2021). In our focal landscape firewood monthly consumption can achieve 154 kg per family (Specht et al., 2019). All these activities are expected to export nutrients in addition to soil physical degradation and thus explain the negative relationship we documented between chronic disturbance and litter production. Among the disturbance-adapted species thriving in our focal landscapes, we shall mention resource-conservative strategists such those from the Croton genus, suggesting plant functional composition might affect nutrient concentration and flux.

These disturbance package associated with forest dependent people, including forest nutrients for crop production via slash-and-burn agriculture (Silva et al., 2017) has also been proposed to affect Caatinga regeneration dynamics by favoring woody plant species able to resprout (Vanderlei et al., 2021), while they disfavor seed-based recruitment (Vanderlei et al., 2022). Such leading role via resprouting woody plant explains why Caatinga forest regeneration does not proceed via directional changes in plant assemblage attributes (e.g. taxonomic and functional changes), with regenerating and old-growth stands supporting in average similar scores (Barros et al., 2021) like we observed here relative to most litter-related attributes; i.e. no directional changes related to forest age and forest successional status or stand-specific profiles. We refer to patterns of litterfall, nutrient and concentration in some extent uncorrelated with forest regeneration. Finally, our findings are consistent to but also explain the low scores of aboveground forest biomass in the Caatinga dry forest as compared to other dry forests, including the occurrence of regenerating forest stands with reduced resilience (see Souza et al., 2019). Precisely, litter nutrient concentration and fluxes indicate little amounts of nutrients returning to soil via litter mineralization, which is likely to feedback into ecosystem productivity (Tabarelli et al., 2017).

In synthesis, the Caatinga dry forest covering sandy soils is a low-productivity ecosystem probably due to a combination of natural and human-related drivers. Precisely, patterns of ecosystem functioning tend to respond directly to nutrient/water availability mediated by natural conditions plus human-related disturbances rather than to forest stand age or forest successional status as these former variables are not strictly correlated to forest aboveground biomass. A combination of reduced productivity, litter low nutrient concentration and low rates of plant-soil nutrient flux via litter fall is likely to not only feedback into low productivity but also result in a relative fragile/sensitive ecosystem, particularly to those land uses not able to return the nutrients removed via agropastoral production but also the exploitation of forest products as predominate in the Caatinga dry forest and most of dry forests globally. Regardless of the pattern, the Caatinga ecosystem services associated with forest productivity play a key role for local populations (fodder, firewood, nutrients for agropastoral production) but also globally such as C sequestration, climate regulation, biodiversity persistence (Silva et al., 2017). Both climate change and increased demand for forest products can further depress Caatinga productivity but also forest resilience (i.e. low recovery rates or even arrested succession). Thus, this topic deserves high attention, particularly the nutrient drain by human activities.

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CONFLICT OF INTEREST

The authors declare there are no conflicts of interest.

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SUPPLEMENTARY MATERIAL

Table S1. Results of the Generalized Linear Models (GLMs) exhibiting the effects of aboveground biomass, chronic disturbance, forest type and precipitation on the concentration of C, N, P, K, Ca, and Mg in Catimbau National Park, Pernambuco state, northeastern Brazil.

	Estimate	**SE**	**z value**	**P**
C				
Intercept	6.27	4.81×10^{-2}	134.4	**<0.001**
Biomass	-6.41×10^{-4}	1.73×10^{-4}	3.708	**<0.001**
Precipitation	-4.27×10^{-5}	6.73×10^{-5}	0.636	0.52
CAD	-7.08×10^{-4}	6.29×10^{-4}	-1.126	0.26
Forest type	6.65×10^{-2}	2.71×10^{-2}	2.451	**0.01**
N				
Intercept	3.04	0.22	13.54	**<0.001**
Biomass	-1.42×10^{-4}	7.99×10^{-4}	-0.17	0.85
Precipitation	2.08×10^{-4}	3.11×10^{-4}	0.66	0.50
CAD	-3.05×10^{-3}	2.91×10^{-3}	-1.04	0.29
Forest type	7.74×10^{-4}	0.12	0.06	0.95
P				
Intercept	3.68×10^{-2}	1.16	0.03	0.97
Biomass	-1.47×10^{-4}	4.24×10^{-4}	-0.03	0.97
Precipitation	-2.78×10^{-4}	1.63×10^{-3}	-0.17	0.86
CAD	-7.84×10^{-4}	1.54×10^{-2}	-0.05	0.95
Forest type	1.62×10^{-2}	0.67	0.02	0.98
K				
Intercept	2.11	0.42	5.01	**<0.001**
Biomass	-1.72×10^{-4}	1.55×10^{-3}	-0.11	0.91
Precipitation	-7.59×10^{-4}	6.1×10^{-4}	-1.24	0.21
CAD	1.13×10^{-2}	5.62×10^{-3}	2.02	**0.04**
Forest type	-3.33×10^{-2}	0.24	-0.13	0.89
Ca				
Intercept	2.96	0.29	10.2	**<0.001**

	Estimate	**SE**	**z value**	**P**
Biomass	4.21×10^{-4}	1.1×10^{-3}	0.38	0.70
Precipitation	-6.58×10^{-4}	4.16×10^{-4}	-1.58	0.11
CAD	3.92×10^{-3}	3.84×10^{-3}	1.02	0.30
Forest type	-0.15	0.17	-0.90	0.36
Mg				
Intercept	0.82	0.61	1.36	0.17
Biomass	-1.24×10^{-3}	2.14×10^{-3}	-0.58	0.56
Precipitation	-7.59×10^{-4}	8.21×10^{-4}	0.92	0.35
CAD	-3.99×10^{-3}	7.55×10^{-3}	-0.52	0.59
Forest type	2.09×10^{-2}	0.32	0.06	0.94

Table S2. Results of the Generalized Linear Models (GLMs) exhibiting the effects of chronic disturbance, forest type and precipitation on C, N and P fluxes in Catimbau National Park, Pernambuco state, northeastern Brazil.

Nutrient flux	**Estimate**	**SE**	**z value**	**p**	**R^2**
C					
Intercept	3.91	0.12	30.67	**<0.001**	
Precipitation	4.61×10^{-4}	1.81×10^{-4}	2.54	**<0.05**	
CAD	1.65×10^{-3}	1.63×10^{-3}	1.01	0.31	0.12
Forest type	2.29×10^{-1}	5.32×10^{-2}	4.31	**<0.001**	
N					
Intercept	0.69	9.59	1.15	0.24	
Precipitation	6.95×10^{-4}	8.36×10^{-4}	0.83	0.41	0.04
CAD	$39\text{-}1.05 \times 10^{-3}$	7.64×10^{-3}	0.18	0.85	
Forest type	8.41×10^{-2}	2.44 x 10-1	0.34	0.73	
P					
Intercept	2.85	3.33	0.86	0.39	
Precipitation	7.86×10^{-4}	4.64×10^{-3}	0.16	0.86	
CAD	1.57×10^{-3}	4.28×10^{-2}	0.03	0.97	0.08
Forest type	4.01×10^{-2}	1.34	0.03	0.97	

4 CHAPTER 2

Chronic anthropogenic disturbance alters litter mass decay and nutrient concentration patterns in a Brazilian tropical dry forest

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Abstract

The decomposition process is considered an important source of nutrients in forest communities, since they determine the flux of carbon and nutrients (N, P, K, Ca and Mg) in the soil. However, in anthropized environments the productivity of the ecosystem ends up being negatively influenced, increasing the decomposition rate and decreasing the final stock of nutrients that will return to the soil. Therefore, this work aimed to investigate how precipitation and chronic disturbances influence leaf decomposition and chemical changes in the litterfall by determining the dynamics of C, N, and P. The study was carried out within the Catimbau National Park, in the permanent plot network of the Long-Term Ecological Research Project network (LTER-Catimbau) – 26 plots – 12 plots are areas with different ages of regeneration (10 to 76 years old) which have a similar agricultural use history and, 14 plots are considered areas without agricultural use history, which are geographically situated in different precipitation profiles, following a gradient from 510 to 940 mm. These 14 plots were ranked on an anthropogenic disturbance index ranging from 0 to 100 and derived from 3 sub-indexes ((human presence, herbivory by domestic herbivores and collection of timber and non-timber materials). In order to determine litterfall decomposition rates, senescent leaf samples were used by applying the *litter bags* technique. Mass loss was estimated in the beginning and after 30, 60, 90, 120, 150, 180, 240, 270, 300, 330, 360 days of decomposition for all samples, totalizing one year of collection. The mass loss at each collection was determined from the initial dry mass minus the remaining dry mass inside each litter bag. Our results eshow that the remaining mass of the experiment in 35.7% of the stands in mature forests was below 50% after 150 days. On the other hand, 57.1% of the plots in these mature forests showed a remaining mass below 50% after 210 days, with a similar pattern for the regenerating forests. Our study confirmed that litterfall production in Caatinga was influenced by seasonality and successional stages. Anthropogenic disturbances have negatively affected the concentration of C, N, and Mg in mature forests. In the regenerating forests, the longer the chronosequence, the higher the concentration of N and Ca. However, the more advanced the forest regeneration process, the lower the retention of P in the remaining litter mass.

Keywords: Caatinga, productivity, nutrient cycling.

1 INTRODUCTION

Litter decomposition and nutrient release are important components of nutrient cycling in terrestrial ecosystems (Powers et al., 2009; Krishna & Mohan, 2017). The process of litter decomposition is a key factor mainly in terms of nutrients release to the soil (Cusack et al., 2009). The speed with which litter nutrients return to the soil depends on colonization by microorganisms that use it as an energy resource, releasing CO2 into the atmosphere and nutrients in the soil (Terror, 2009). The litter decomposition process influences the carbon flux and the cycling patterns of other nutrients (for example, phosphorus and nitrogen) (Facelli & Pickett, 1991; Aduan, Vilela & Klink, 2003), being the most important step of cycling of nutrients, as it represents a key process in the maintenance of soil fertility (Silver & Miya, 2001) and one of the limiting factors in the establishment and development of forest ecosystems (Vitousek & Sanford, 1986).

Soil structure and composition can vary spatially and influence the decomposition process (Chapin, Matson & Vitousek, 2011). The presence of soil organisms (e.g. micro, meso and macro fauna), litter quality and soil compaction can alter litter mass decay over the time. For example, soil compaction combined with accelerated loss of vegetation cover can decrease decomposition rates by establishing lower moisture content and aeration level which results in a decline in the decaying community (Oliveira et al., 2019). Decomposition rates also depend on the characteristics of the surrounding environment, such as the greater availability of nutrients in the soil, temperature and moisture (which tend to accelerate decomposition) (Fravolini et al., 2016; Gora et al., 2018). On regional scales, precipitation is considered to be the main predictor of decomposition rate mainly across arid and semi-arid ecosystems (Lieberman, 1982; Reich & Borchert, 1984; Bullock & Solis-Magallanes, 1990; Aerts, 1997).

Despite the role played by litter decomposition and nutrient release in terms of nutrient cycling, very little is known about this process mainly across seasonally dry tropical forests. These dry forests respond to 40% of tropical forest original cover (Miles et al., 2006), but most of the dry forest cover globally has been converted into human-modified landscapes (Arroyo-Rodríguez et al., 2017). Across these dry forests, a myriad of factors including climatic conditions (particularly precipitation and water availability), soil fertility, forest sucessional status and both natural and human disturbance regimes can alter decomposition rate and consequently nutrient cycling.

The Caatinga dry forest represent ones of the largest blocks of seasonally dry tropical forest globally (Silva et al., 2017). Since the Europeans arrived in the region (16th century), Caatinga old-growth forests have been converted into vegetation mosaics due to a combination of slash-and-burn agriculture and livestock production via free-ranging animals feeding on the native vegetation (Barros et al., 2021; Silva et al., 2017). Both activities rely on the nutrients offered by the forest ecosystem as external nutrient inputs via industrial fertilizers are not common. Accordingly, this socioecological system based on forest extractivism depends on forest regeneration able to produce biomass, accumulate but also transfer nutrients to soil via litterfall (Lawrence, 2005). It is reasonable in the long-run it is reasonable to expect the forest ecosystem experiments nutrient shortage due to an unbalance between nutrient output vs. input as suggested by forest stands exhibiting reduced growth (little resilience) and widespread desertification (Souza et al., 2019). However, little information is available on nutrient cycling in the Caatinga socioecological system and its drivers including the role played by crop/livestock production but also by the exploitation of forest products, such as firewood, in average, every single family consume over a 100 kg per month (Specht et al., 2019).

Here, we evaluate the litter decomposition (i.e. litter mass decay) in a human-modified landscape in the Brazilian Caatinga. More specifically, we compare patterns of mass loss, nutrient concentration and stock in remaining litter mass across dry forest plots. We also test if chronic anthropogenic disturbance, precipitation, aboveground biomass and forest type (i.e. old-growth forest and regenerating forest stands) affect litter decomposition as well as nutrient concentration during decay. Our hypothesis is that low precipitation directly influences the reduction of leaf mass, increasing the rate of decomposition and consequently limiting the efficiency of retranslocation of nutrients due to leaching mainly across regenerating forest stands, where vegetation is more sparse. We also hypothesized that chronic anthropogenic disturbances directly influence the decrease in ecosystem productivity, increasing the rate of decomposition and decreasing the final stock of nutrients that will return to the soil.

2 MATERIALS AND METHODS

2.1 Study area

The study was carried out within the Catimbau National Park (hereafter, ‘PARNA Catimbau”) (between 8º4'00" and 8º36'35" S and between 37º09'30" and 37°14'40" W) covering an area of about 62,000 ha and is located between the municipalities of Buíque, Tupanatinga and Ibimirim, in the state of Pernambuco, Brazil (Fig. 1). Approximately 70% of PARNA Catimbau has Latosol soil (Rito et al., 2017). The climate is predominantly semi-arid BSh with distinct areas of tropical rainy climate As' according to the Köppen scale (Peel, Finlayson & Mcmahon, 2007). The temperature varies between 21°C and 25°C and annual rainfall varies between 650 and 1100 mm, with great irregularity in the interannual regime (Rito et al., 2017). Generally, about 60 to 75% of rainfall occurs over three months, from March/April to June/July, which corresponds to the rainy season and the coldest period. The predominant vegetation is dry forest where trees and shrubs of Fabaceae, Euphorbiaceae, Boraginaceae and Burseraceae predominate (Rito et al., 2017).

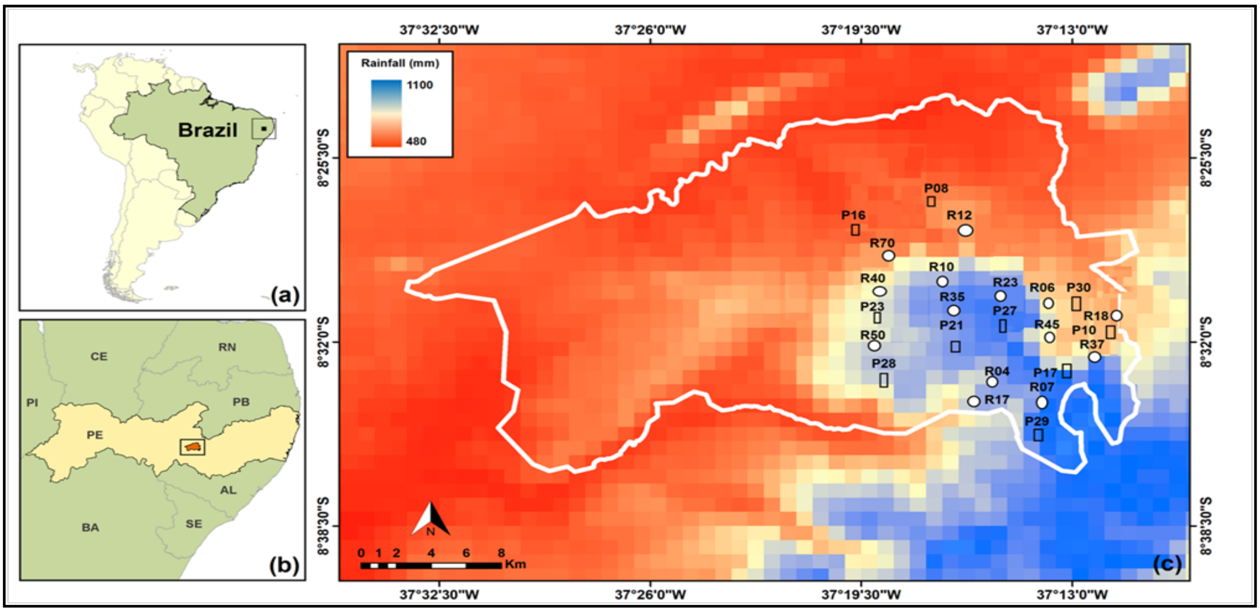

Figure 1. Map of the Catimbau National Park, in Pernambuco state, northeastern Brazil (a-b) and showing (c) regenerating forest stands (R) (white circles) and old-growth forests (P) A (open squares; with no recent history of agricultural use).

PARNA Catimbau was created in 2002 and throughout these years, residents have never been compensated and continue to live within this conservation unit area. There are small urban centers, small farmers, great owners, mythical-religious communities, areas of archaeological importance, in addition to small private tourist developments. The historic presence of these residents has given rise to a huge mosaic in terms of land use and human pressure on the biota (i.e. anthropic landscapes), which makes PARNA Catimbau an excellent opportunity to examine how agriculture, livestock, logging, and hunting, among other chronic disorders, affect the Caatinga biota and the establishment of emerging or new ecosystems.

2.2 Sampling design

We selected 26 forest stands (20 x 50 m each) from the Long Term Ecological Research Project network (LTER-Catimbau), where 13 of them represent a chronosequence ranging from 12 to 76 years old, with a similar history of slash-and-burn agriculture as main land use. The remaining 15 forest stands follow a precipitation gradient (Barros et al., 2021), ranging from 510 to 940 mm, and are considered preserved areas, with no historical agricultural use (Fig. 1). These 14 areas also contain an anthropogenic disturbance index, which was previously measured using the global GMDI index (Global Multimetric Disturbance Index) (Arnan et al., 2018).

The index ranges from 0 to 100 and is derived from 3 sub-indices (human presence, herbivory by domestic herbivores and collection of wood and non-wood materials). Each sub-index was calculated based on several measurements, through: (1) remote sensing according to the geographic information system (GIS), to estimate the distance of access to the forest areas; (2) semi-structured interviews to assess, as example, the abundance of goats and the amount of firewood used per day and (3) in situ surveys in the plots (e.g. quantification of shallow cut and feces trails of domestic herbivores) (Arnan et al., 2018).

2.3 Litter mass decomposition

To assess the rate of litter decomposition, samples of senescent leaves collected in each plot in September and October 2018 were used. These samples were homogenized, oven dried at 60°C and placed in litter bags (minimum of 12 per plot). The litter bag technique is widely used because of its easy replication and cost (Harmon et al., 1999).

Nylon mesh bags (20 x 25 cm), with a 2 mm mesh, were made, which allowed the access of microfauna (< 0.1 mm) and mesofauna (0.1 – 0.2 mm), according to the classification de Swift et al. (1979). Each litter bag was filled with 10 g of senescent leaves of the species existing in each plot. The litter bags were attached to wires, which in turn were tied to a rebar and placed on the ground, preserving the litter that already existed on the ground (Fig. S1). Each wire corresponded to a month of collection that was carried out during a year. After the collection of decomposing plant material, they were taken to the laboratory to be carefully sieved and sorted to remove debris and materials that had entered the bags over the time they were exposed. Subsequently, they were dried in an oven at 60°C until reaching constant weight and then the dry mass of the remainder inside each litter bag was determined.

The mass loss was determined in each collection from the initial dry mass minus the remaining dry mass inside each litter bag. Mass loss was estimated for all samples, at the beginning and after 0, 30, 60, 90, 120, 150, 180, 240, 270, 300, 330, 360 days of decomposition, totaling 1 year of collection.

2.4 Nutrient concentration and stock

We measure nutrient concentration following litter mass decay. For this, first litterfall was estimated through monthly samplings from permanent traps over a four-years period in all 28 plots, from September 2016 to August 2020. Each trap consists of a square-shaped PVC structure that has four vertical rods at the base to serve as a support. The collector has an area of 0.5 x 0.5 cm (0.5 cm^2) that supports a nylon mesh of 2 mm (Wright et al., 2011). The standard of the summation symbol (Σ) was adopted for the location of the traps. The establishment of a standard distribution for all areas gives a random model of location in the areas without favoring any environmental factor (Edwards, 1977). In this case, we regard this nutrient concentration from litter collected in traps, as initial nutrient concentration (i.e. before litter mass decay). Second, to measure nutrient concentration following decay process (1-360 days), we used the litter mass remaining from litter bags.

In the laboratory, the samples were sorted, weighed and oven-dried at 60 °C and chemically analyzed. The litter samples from both traps and litter bags were dried at 60°C and grounded to fine powder to pass through a 2 mm sieve. Sub-samples of leaf material were weighed (2 to 3 mg) and sealed in tin capsules. The capsules were introduced into the elemental analyzer EuroVector Model EA3000 for the determination of total C and N concentrations. Gases are generated following the samples' combustion, then, purified in a chromatography column and introduced into the mass spectrometer for isotopic ratios determinations (IRMS Delta Plus, Finnigan Matt, San Jose, CA, USA). Sugarcane leaves were used as standard material for vegetation material. Theδ15N and δ13C natural abundance is expressed in parts per thousand (‰) as a result of a standard internationally recognized equation:

$$\delta^{15}N \text{ or } \delta^{13}C = (R_{sample} / R_{standard} - 1) \times 1000 \ldots\ldots (1)$$

where, R is the molar ratio in the sample and standard between 13C and 12C or 15N and 14N. The standard used for C isotope was Peedee Belemnite (PDB; limestone of the Grand Canyon region, USA) and atmospheric air for N isotope. The analytical errors accepted were ± 0.3%, 0.1%, 0.3 ‰ and 0.5 ‰ for C, N, δ13C and δ15N, respectively.

Phosphorus, calcium and magnesium in litter mass remaining was determined through a wet digestion method, using nitric acid and perchloric acid (4:1 ratio), where 10 mL of the mixture of acids was added to 0.5 g of each sample (Sarruge & Haag, 1974). After that, the digests were diluted to 25 mL and the P, Ca e Mg concentration determined Inductively Coupled Plasma Optical Emission spectroscopy (ICP- OES; Perkin Elmer Modelo Optima 8300 DV).

Finally, we measure the nutrient stock in the litter mass remaining. For this, the nutrient concentration of C, N, P, Ca, K and Mg in the litter mass was multiplied by total litter mass remaining.

2.5 Data analysis

The percentage of litter mass loss (LML %) was estimated with the equation: LML (%):LMt/LM0 × 100, where LMt is the remaining litter mass at the sampling time, and LM0 is the initial litter mass for decomposition. Decay constants (k values) for each plot and different forest type (i.e. old-growth forests and regenerating forest stands) were estimated by fitting a single pool exponential decay function (Olson 1963):

$$LM_t=LM_{0e}^{-kt}$$

LMt is the litter mass at a given time t, LM0 is the initial litter mass, e is the exponential constant, k is the decay rate constant over the time t. We adopted a similar way to verify the changes in nutrient concentration (NC) following litter mass decay.

To compare mass loss, nutrient concentration and stock in remaining litter among dry forest plots, we use one-way ANOVA analyses. We used paired t-tests to compare nutrient concentration before and after litter mass decay. We fitted a generalized linear model (GLM) to test the effect of chronic anthropogenic disturbance, precipitation, aboveground biomass and forest type (i.e. old-growth forest and regenerating forest stands) on mass loss and nutrient concentration in remaining litter. Finally, we compare nutrient stock in remaining litter mass among dry forest plots using ANOVA one-way test. Data normality was analyzed using the Kolmogorov-Smirnov test. We log-transformed litterfall data (response variable) for the model for a better fit, to accomplish normality and to avoid heteroscedasticity in our models. We adopted the variance inflation factor (VIF) using the “car” package for R to assess if there was collinearity among predictors. All variables could be maintained in the models since none of them showed VIF < 2.0, meaning independence among predictors (Jou, Huang & Cho, 2014). All analyses were performed in R (R Development Core Team, 2017).

3 RESULTS

3.1 Litter mass decay and drivers

Litter mass decay along the time or simply litter decomposition rate was highly variable across forest stands particularly by considering forest sucessional status (Table 1, Fig. 2). Regenerating forest stands exhibited two peaks of litter mass decay: approaching the first 30 days by achieving a 20%-loss and around the 90th with a 40% of biomass loss. Moreover, nearly 65% of the regenerating forest stands exceed 50% of biomass loss around the 230th day (Fig. 2). At the end of the experiment 5.07% ± 0.47% of litter biomass still persisted. Old-growth forests achieved such a 50%-threshold at the 210th day (Fig. 2) and at the end of the experiment 4.6% ± 0.56% of litter biomass still persisted across old-growth forest stands; litter decomposition rate slower and more homogeneous across old-growth forest stands.

Table 1. Mass remaining (g) over 360 days of decay, mass loss (initial litter mass – final litter mass) and mass loss rate (LM_t/LM_0 x 100, where LM_t is the remaining litter mass at the sampling time, and LM_0 is the initial litter mass for decomposition) following mass decay process across regenerating forest stands (RG) and old-growth forests (P) in Catimbau National Park, Pernambuco state, northeastern Brazil. Value of initial litter mass = 10 g; k (decay constant).

Plot	Mass remaining (g)	Mass loss (g)	Mass loss rate	K
RG 10	3.84	6.16	38.4	-0.95
RG 12	4.95	5.05	49.5	-0.70
RG 13	5.42	4.58	54.2	-0.61
RG 18	5.15	4.85	51.5	-0.66
RG 26	2.95	7.04	29.6	-1.22
RG 29	6.79	3.2	68	-0.38
RG 41	9.27	0.72	92.8	-0.07
RG 43	4.31	5.68	43.2	-0.84

RG 46	3.75	6.25	37.5	-0.98
RG 51	5.05	4.95	50.5	-0.68
RG 56	4.93	5.07	49.3	-0.70
RG 76	4.44	5.56	44.4	-0.81
P2	10.59	0.59	105.9	0.06
P4	6.13	3.87	61.3	-0.49
P8	6.41	3.59	64.1	-0.44
P10	3.05	6.95	30.5	-1.18
P11	3.86	6.14	38.6	-0.95
P14	5.42	4.58	54.2	-0.61
P16	4.68	5.32	46.8	-0.76
P17	3.14	6.86	31.4	-1.15
P20	3.82	6.18	38.2	-0.96
P22	3.62	6.38	36.2	-1.01
P23	4.02	5.98	40.2	-0.91
P25	2.91	7.09	29.1	-1.23
P26	3.08	6.92	30.8	-1.17
P27	2.54	7.46	25.4	-1.37
P30	5.76	4.24	57.6	-0.55

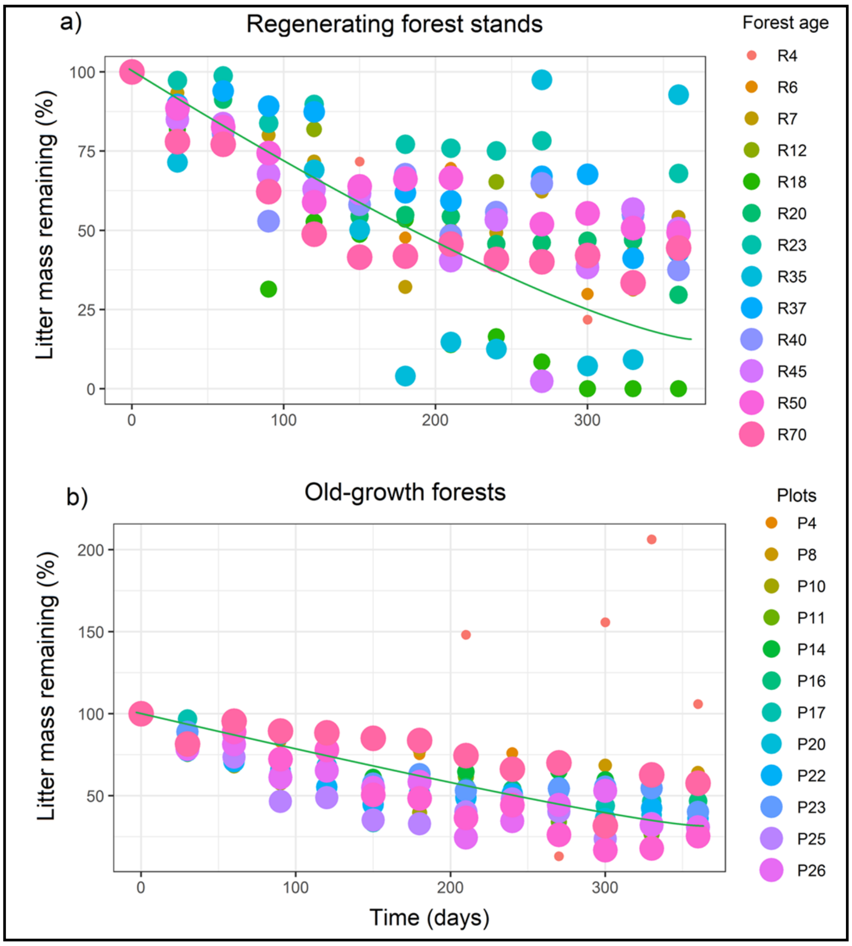

Figure 2. Litter decomposition curves for regenerating forest stands (a) and old-growth forests (b) over 360 days in Catimbau National Park, Pernambuco state, northeastern Brazil.

Considering total litter loss or decomposition it exhibited a significant variation across both regenerating (ANOVA F=2.04, P=0.02) and old-growth forest stands (ANOVA F=3.59, P<0.001) (Table 1, Fig. 3). Regenerating forest stands achieved 4.92 ± 0.47 (mean ± SE g) while old-growth forests achieved 5.47 ± 0.47 g, i.e. but no significant differences to compare these forest types (ANOVA F=0.41, P=0.52). A similar pattern was found for decay rate constants with no significant variation among forest types (ANOVA F=0.95, P=0.33), although old-growth forests exhibited highest values (Table 1, Fig. S2). Regarding mass decay drivers, chronic anthropogenic disturbance was the main predictor affecting positively litter mass loss mainly across regenerating forest stands (Table 2, Fig. 4), while other explanatory variables played a minor role (Table 2). A unexpected finding in our field decomposition experiment was the weak but negative effect by precipitation on litter mass decay (Table 2).

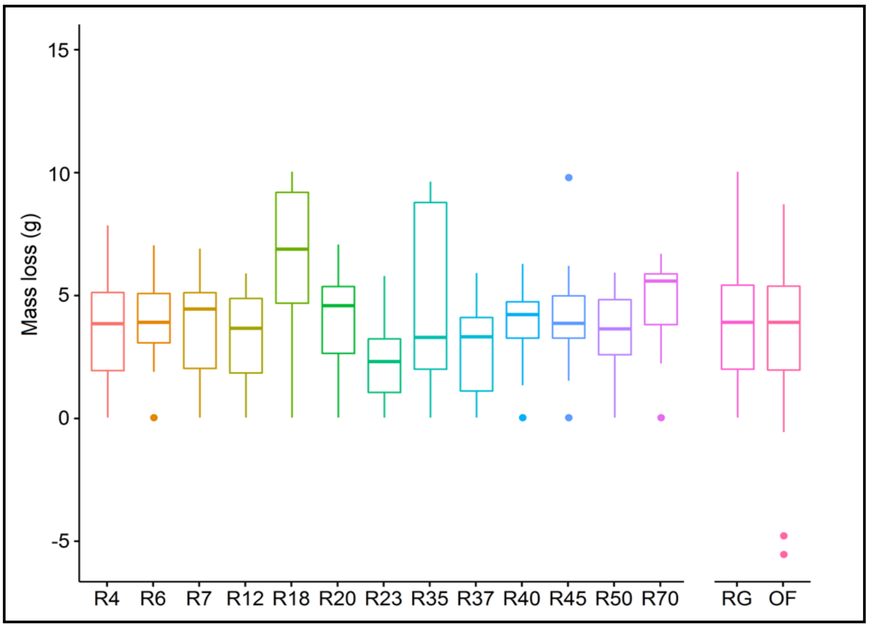

Figure 3. Mean ± SE of litter decomposition (mass loss) over 360 days across regenerating forest stands (RG) and old-growth forests (OF) in Catimbau National Park, Pernambuco state, northeastern Brazil.

Table 2. Results from Generalized Linear Models (GLMs) with the effects of aboveground biomass, chronic anthropogenic disturbance (CAD), rainfall and forest type on litter mass loss in Catimbau National Park, Pernambuco state, northeastern Brazil.

Explanatory variables	**Estimate**	**SE**	**z value**	**P**
Intercept	4.14	0.25	16.39	**<0.001**
Biomass	-2.72×10^{-3}	7.52×10^{-3}	-0.41	0.893
Rainfall	-4.9×10^{-4}	2.22×10^{-4}	-2.14	**0.032**
CAD	9.87×10^{-3}	2.12×10^{-3}	4.64	**<0.001**
Forest type	-1.73×10^{-3}	8.32×10^{-4}	-2.08	**0.037**

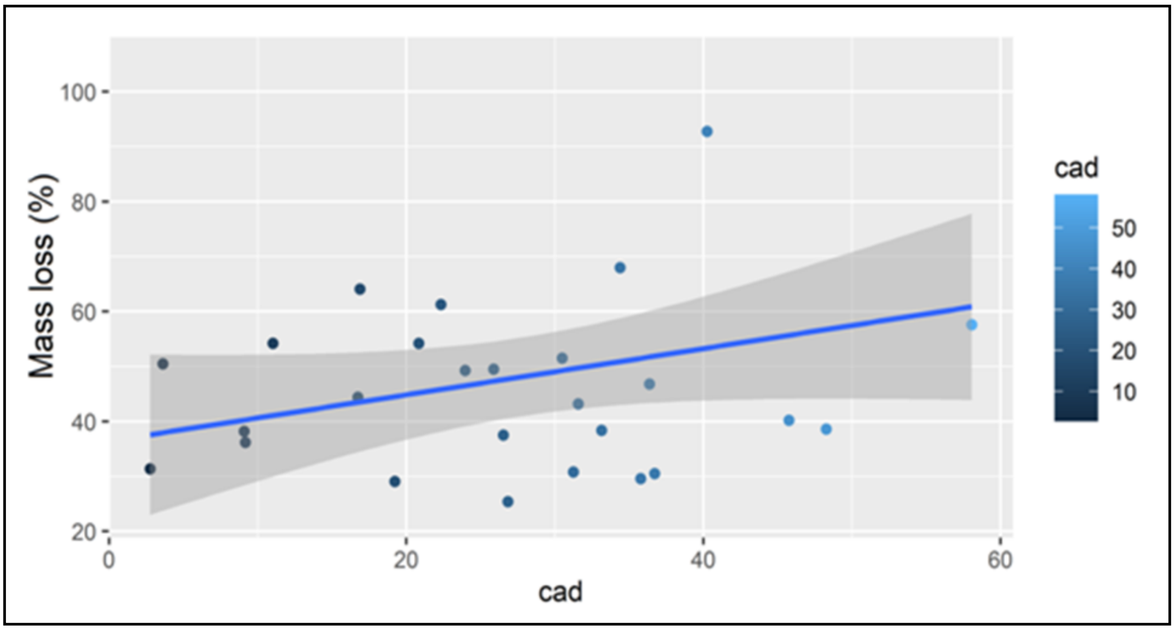

Figure 4. Positive effect of chronic anthropogenic disturbance (CAD) on mass loss over 360 days in Catimbau National Park, Pernambuco state, northeastern Brazil.

3.2 Nutrient concentration and drivers

Litter nutrient concentration was highly variables across forest stands with significant differences relative to initial vs. final nutrient concentration (Table 2, Fig. 5). Moreover, regenerating forest stands and old-growth forests exhibited a similar pattern with no significant variation relative to nutrient concentration elapsed the mass decay period (C concentration ANOVA F=0.02, P=0.87; N concentration ANOVA F=2.46, P=0.12; P concentration ANOVA F=2.74, P=0.11; Ca concentration ANOVA F=3.64, P=0.06; K concentration ANOVA F=0.05, P=0.81 and Mg concentration ANOVA F=1.62, P=0.21) (Table 3). Moving to drivers, nutrient concentration in the remaining litter mass was affected mainly by chronic anthropogenic disturbance (negatively) (Table 3, Fig. 6) and aboveground biomass (positively) (Table 3).

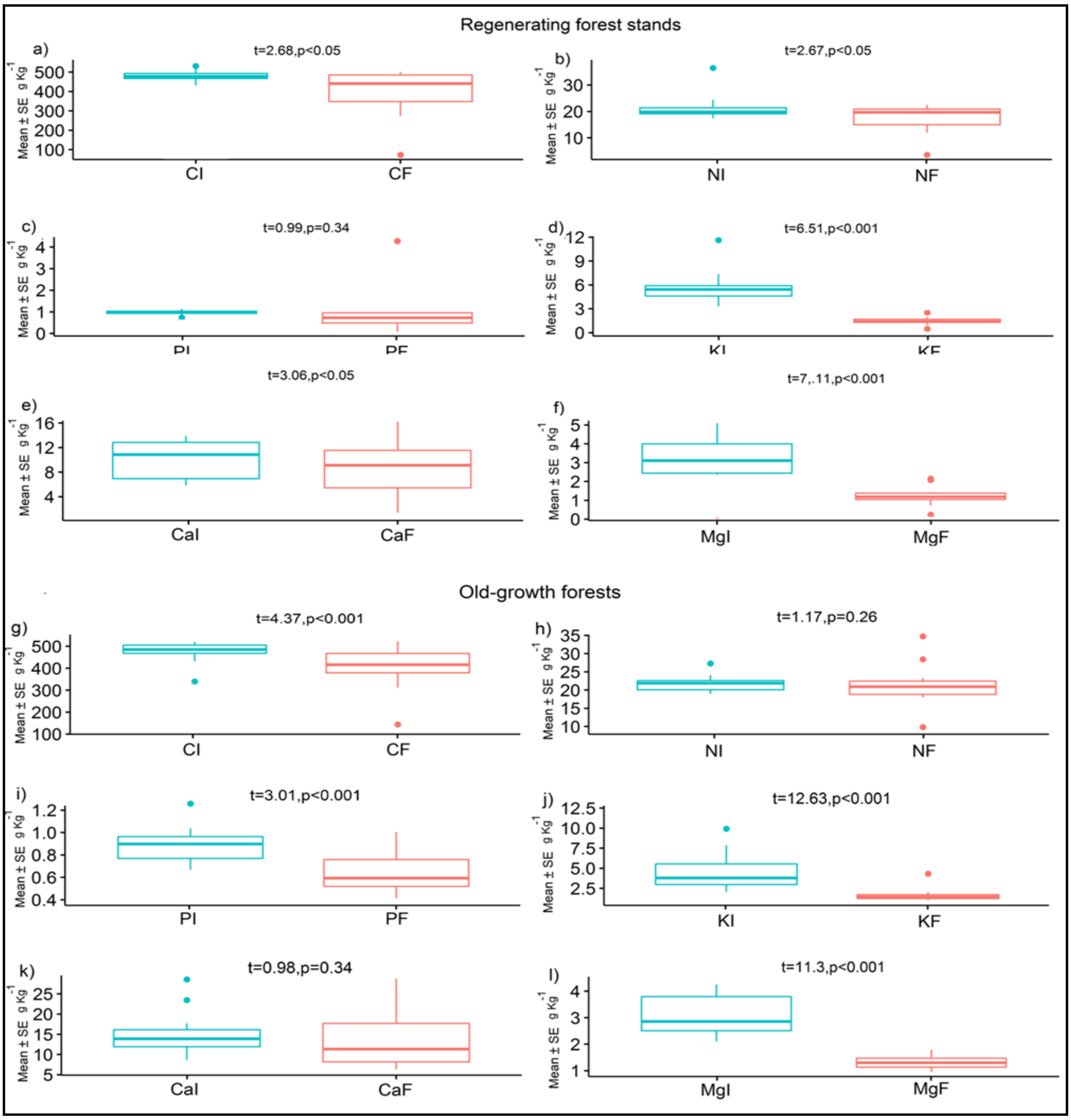

Figure 5. Paired comparisons of nutrients concentration (g Kg^{-1}) before (I) and after litter mass decay (F) across regenerating forest stands (RG) and old-growth forests (OF) in Catimbau National Park, Pernambuco state, northeastern Brazil. C- Carbon, N – Nitrogen, P – Phosporus, K – Potassium, Ca – Calcium, Mg – Magnesium.

Table 3. Nutrient concentration (g kg^{-1}) in litter mass regarding initial (I) (i.e. before litter mass decay) and final (F) values (i.e. concentration in litter mass over 360 days of decomposition) in Catimbau National Park, Pernambuco state, northeastern Brazil. C-Carbon, N – Nitrogen, P – Phosporus, K – Potassium, Ca – Calcium, Mg – Magnesium. R – Regenerating forest stands, P – Old-growth forests.

Plot	CI g kg^{-1}	CF g kg^{-1}	NI g kg^{-1}	NF g kg^{-1}	PI g kg^{-1}	P Fg kg^{-1}	KI g kg^{-1}	KF g kg^{-1}	CaI g kg^{-1}	CaF g kg^{-1}	MgI g kg^{-1}	MgF g kg^{-1}
R4	495.2	279.4	21.13	11.9	0.64	0.96	4.77	1.12	7.64	3.44	3.17	1.04
R6	489.0	273.2	20.56	12.0	0.58	0.78	3.22	0.98	8.60	4.53	2.26	0.65
R7	474.8	368.6	19.04	20.2	0.98	0.33	4.23	2.19	13.24	10.94	3.30	1.36
R12	517.6	397.4	21.96	19.5	0.84	0.09	7.25	1.55	10.64	8.32	2.28	1.29
R20	539.9	495.2	20.22	15.8	0.78	0.49	4.60	0.6	7.45	5.22	3.80	1.15
R23	481.1	475.7	20.83	18.8	0.82	0.49	5.77	1.02	12.23	9.29	2.25	0.77
R35	475.7	72.3	24.93	3.5	0.76	0.69	11.54	0.15	14.94	0.86	4.98	0.17
R37	485.2	473.7	22.05	22.4	0.96	0.97	5.89	1.24	7.13	5	4.15	2
R40	530.0	480.4	25.79	20.6	0.96	0.57	4.24	0.98	14.19	11.11	2.35	1.2
R45	439.3	406.2	37.81	21.8	0.83	0.86	5.48	1.26	14.52	15.47	4.90	2.07
R50	487.1	499.3	21.17	19.7	0.80	4.28	5.21	0.98	15.34	15.63	2.64	1.08
R70	473.0	495.9	18.79	21.4	0.85	4.29	5.55	1.6	12.35	8.85	2.84	1.08
OF	479.7	119.9	23.0	9.1	0.70	0.54	12.24	4.23	17.20	7.91	2.98	1.3
P4	533.1	376.8	22.20	20.2	0.98	0.98	6.12	1.12	13.44	19.07	2.86	1.1
P8	513.2	444.3	22.34	21.5	0.61	0.87	5.85	1.46	8.47	8.43	2.52	1.31

Plot	CI g kg^{-1}	CF g kg^{-1}	NI g kg^{-1}	NF g kg^{-1}	PI g kg^{-1}	P Fg kg^{-1}	KI g kg^{-1}	KF g kg^{-1}	CaI g kg^{-1}	CaF g kg^{-1}	MgI g kg^{-1}	MgF g kg^{-1}
P10	504.3	286.9	19.98	21.1	0.90	0.41	10.19	1.41	28.05	28.44	4.37	1.36
P11	485.8	332.5	19.28	21.8	0.90	0.58	8.24	1.34	14.98	15.6	2.60	1.4
P14	521.0	498.4	22.91	17.2	0.77	0.53	5.39	1.19	11.64	10.99	2.38	1.07
P16	483.7	371.9	24.38	19.0	0.72	0.93	7.48	1.13	13.55	10.36	2.92	1.13
P17	528.3	405.1	19.32	18.3	0.65	0.55	4.76	1.05	8.13	5.99	3.80	1.75
P20	523.5	490.9	21.14	19.0	0.66	0.57	5.17	1.15	11.17	7.73	4.16	1.54
P22	446.1	440.4	20.55	27.7	0.98	0.7	5.71	1.83	13.38	12.32	3.14	1.78
P23	516.8	445.5	23.52	21.6	0.91	0.77	4.38	0.97	12.76	11.64	2.66	1.13
P25	499.1	369.2	22.25	17.8	1.20	0.39	8.35	1.94	22.96	20.54	4.18	1.7
P26	353.4	340.9	22.54	22.5	0.84	0.39	7.36	1.74	12.75	7.02	2.23	1.25
P27	450.5	426.0	27.63	34,0	0.84	0.46	6.82	1.44	16.25	25.16	3.17	0.95
P30	490.2	391.6	20.32	17.5	0.76	0.6	5.08	0.93	9.17	6.36	4.04	1.25

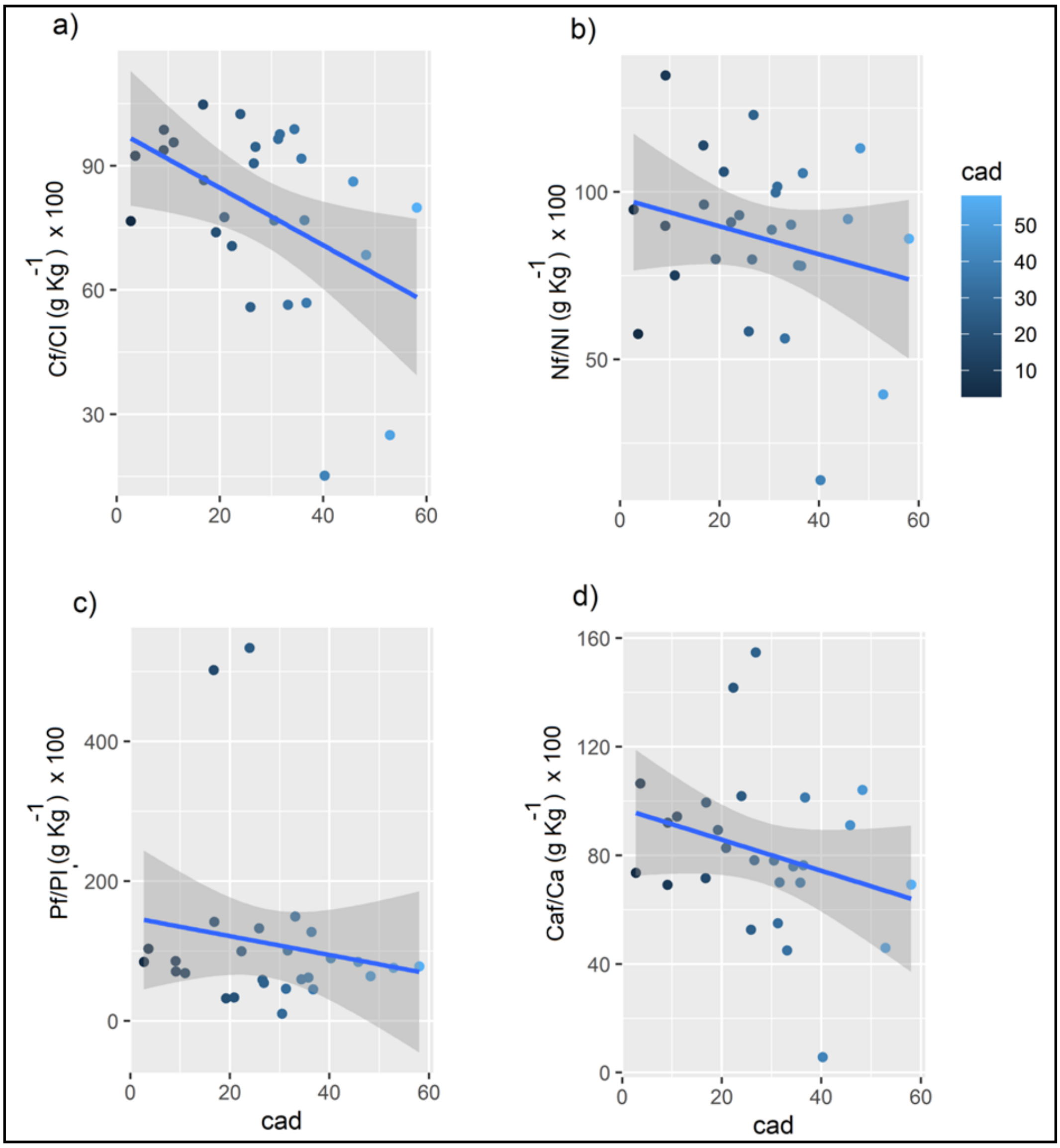

Figure 6. Negative effect of chronic anthropogenic disturbance (CAD) on changes in nutrient concentration following litter mass decay (NCf/NCI X 100, NCf nutrient concentration in mass remaining, NCI – nutrient concentration before mass decay) in Catimbau National Park, Pernambuco state, northeastern Brazil.

3.3 Nutrient stocks in the remaining litter mass

To compare nutrient stocks over 360 days of litter mass decay, there was no significant difference among dry forest plots (C stock ANOVA F=0.62, P=0.43; N stock ANOVA F=0.18, P=0.66; P stock ANOVA F=2.76, P=0.11; Ca stock ANOVA F=2.4,P=0.13; K stock ANOVA F=0.66, P=0.42 and Mg stock ANOVA F=0.36,P=0.55), although old-growth forests showed highest values regarding N (mean ± SE 87.6 ± 6.01, Ca (mean ± SE 55.42 ± 6.7 Kg ha^{-1}), K (mean ± SE 8.03 ± 2.65 Kg ha^{-1}) and Mg (mean ± SE 6.02 ± 0.66 Kg ha^{-1}) stocks, while regenerating forest stands exhibited highest values in terms of C (mean ± SE 1865.7 ± 193.34 Kg ha^{-1}) and P (mean ± SE 5.97 ± 1.95 Kg ha^{-1}) stocks (Fig. 7).

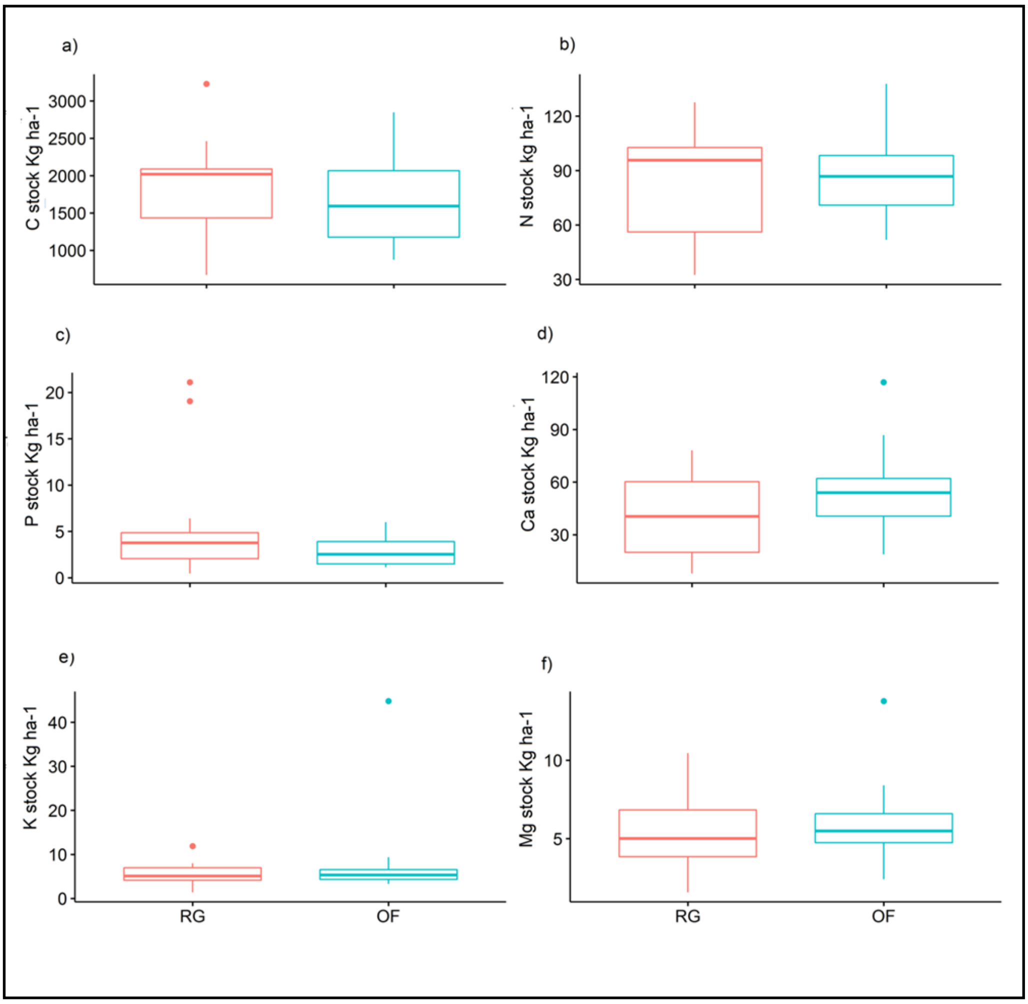

Figure 7. Nutrients stocks (Kg ha^{-1}) in litter mass remaining at 360 days across regenerating forest stands (RG) and old-growth forests (OF) in Catimbau National Park, Pernambuco state, northeastern Brazil.

Table 4. Results of Generalized Linear Models (GLMs) showing the effect of aboveground biomass, chronic disturbance, forest type and rainfall on nutrient concentration following litter mass decay in Catimbau National Park, Pernambuco state, northeastern Brazil.

Nutrient concentration	**Estimate**	**SE**	**z value**	**P**
C				
Intercept	4.62	0.12	38.46	**<0.001**
Biomass	1.31×10^{-4}	2.05×10^{-4}	1.01	0.28
Rainfall	-1.09×10^{-4}	7.41×10^{-5}	-1.47	0.14
CAD	-8.42×10^{-3}	7.24×10^{-4}	-5.27	**<0.001**
Forest type	-4.94×10^{-2}	3.06×10^{-2}	0.42	0.67
N				
Intercept	4.69	0.11	40.74	**<0.001**
Biomass	1.28×10^{-3}	9.52×10^{-4}	2.77	**<0.01**
Rainfall	-6.44×10^{-5}	3.33×10^{-4}	0.19	0.84
CAD	-5.84×10^{-3}	3.16×10^{-3}	-2.67	**<0.01**
Forest type	-2.09×10^{-1}	6.89×10^{-2}	-4.23	**<0.001**
P				
Intercept	6.55	0.11	65.28	**<0.001**
Biomass	-6.52×10^{-3}	3.93×10^{-4}	-16.05	**<0.001**
Rainfall	-2.27×10^{-3}	1.42×10^{-4}	-15.91	**<0.001**
CAD	-1.36×10^{-2}	1.61×10^{-3}	-8.39	**<0.001**
Forest type	1.59	0.05	29.11	**<0.001**
K				
Intercept	3.22	0.22	14.27	**<0.001**
Biomass	2.95×10^{-3}	8.35×10^{-4}	3.53	**<0.01**
Rainfall	-2.01×10^{-4}	3.07×10^{-4}	-0.65	0.51
CAD	-8.81×10^{-3}	3.01×10^{-3}	-1.92	0.05
Forest type	-0.27	0.13	-2.01	**0.04**
Ca				

Intercept	4.41	1.18 x 10^{-1}	38.79	**<0.001**
Nutrient concentration	**Estimate**	**SE**	**z value**	**P**
Biomass	1.15 x 10^{-3}	4.72 x 10^{-4}	2.44	**<0.01**
Rainfall	2.08 x 10^{-5}	1.61 x 10^{-4}	0.12	0.89
CAD	-6.58 x 10^{-3}	1.52 x 10^{-3}	-4.32	**<0.001**
Forest type	-3.92 x 10^{-1}	7.21 x 10^{-1}	-5.44	**<0.001**
Mg				
Intercept	4.25	0.16	25.36	**<0.001**
Biomass	1.21 x 10^{-3}	6.52 x 10^{-4}	1.85	0.06
Rainfall	-7.07 x 10^{-4}	2.33 x 10^{-4}	-3.02	**0.01**
CAD	-3.13 x 10^{-3}	2.23 x 10^{-3}	-1.39	0.16
Forest type	-0.17	0.11	-1.77	0.07

4 DISCUSSION

Our results suggest litter decomposition occurs slowly across Caatinga dry forest mosaics as ≈ 50% of litter mass persisted elapsed a year. However, litter decomposition rate and total biomass decay is highly variable across forest stands with little influence of forest successional status. Perhaps, old-growth forest stands support a slower and more homogeneous decomposition rate.

Such as site-specific profile result in part of a combination of chronic anthropogenic disturbance plus precipitation by affecting litter decomposition in opposite directions. Nutrient concentration change along the decomposition process with significant differences relative to initial vs final concentration mainly regarding high variation considering both initial vs. final concentration across forest stands exhibits. Nutrient concentration on the remaining litter is a combination of chronic disturbance and aboveground biomass. Accordingly, nutrient stocks/amounts delivered to soil across forest stands is highly variable (i.e. stand-specific) and no related to forest successional status. We refer to forest stands delivering relatively high amounts of P and C while other deliver relatively high scores of N, Ca, K and Mg, particularly across old-growth forests.

Our findings reinforce the notion that litter decomposition occurs slowly across dry forests as compared to humid forests (González & Seastedt, 2001; Powers et al., 2009); it is required more than a year to complete decomposing and total nutrient return to soil. Compared to other dry forests Caatinga fits in the range documented by this biota. However, we found evidence suggesting that across forest successional mosaics created by slash-and-burn agriculture plus the exploitation of forest products decomposition rate is highly variable and benefit from chronic disturbance while it is negatively affected by precipitation. Although all ecosystem-level attributes are expected to change predictably as forest regeneration proceeds (Guariguata & Ostertag, 2001), patterns in the Caatinga dry forest appears to be site-specific with little influence of forest successional status or the age by forest regenerating stands as already documented in terms of plant assemblages (Barros et al., 2021) and forest aboveground biomass, although in average aboveground biomass is higher across old-growth forest stands (Souza et al., 2019). Not only decomposition rate is site-specific but also nutrient concentration in the remaining litter mass and consequently the nutrient apport to the soil by resulting from a combination chronic disturbance and aboveground biomass rather than regeneration-related variables. These findings highlight chronic disturbances as key driver in tropical human-modified landscapes from population to ecosystem level (Singh, 1998). Finally, nutrient flux or amount transferred to the soil compartment via litter decomposition (i.e. kg per ha) fits in the lower range by tropical forests. We shall mention 5.9 kg ha^{-1} yr^{-1} of P and 87 kg ha^{-1} yr^{-1} of N received annually by some forest stands in our focal landscape, while other dry tropical forests receive up to 142 kg ha^{-1} yr^{-1} of N and 8.7 kg ha^{-1} yr^{-1} of P (Campo, Solís & Valencia, 2007).

The slow rates of litter decomposition exhibited by the Caatinga dry forest in our focal landscape may simply result from a combination of prolonged dry seasons plus reduced soil fertility as these conditions are expected to reduce microbial activity; note that the Caatinga in our focal landscape is covered by impoverished sand soils. The mechanisms behind the relationship between litter decomposition and chronicle disturbance is probably more complex as it may involve habitat desiccation, trampling and nutrient input by goat feces and urine. Chronic disturbance was also correlated to lower nutrient concentration in the remaining litter suggesting rapid mineralization. As already mentioned, goats represent a conspicuous element in our focal landscape, particularly across regenerating forest stands (Jamelli, Bernard & Melo, 2021), with a negative impact on herb assemblages (Menezes et al., 2020) and woody plant seedling survival (Lins et al., 2022). In fact, herbivores including livestock can speedup nutrient cycling across several ecosystems by for instance consuming plants (i.e. deposition of readily accessible nutrients in faeces) (Bakker et al., 2006), but the mechanisms operating in the Caatinga dry forest deserves investigation. By speeding up nutrient mineralization during the rainy season, chronic disturbance probably favor forest regeneration, while mineralization during the dry season probably results in nutrient leaching rather than plant absorption. Moreover, slow litter decomposition can favor litter consumption by goats, particularly in the dry season and thus contribute to nutrient output as most of goat feces concentrates in the husbandries. In fact, rapid litter decay during the rainy season following litter fall during former dry season apparently represent the best scenario for forest regeneration by limiting litter consumption by goats and nutrient mineralization outside the plant growth period. Finally, the relationship between precipitation, woody plant species richness and aboveground biomass (Souza et al., 2019), and precipitation and the functional profile by woody plant assemblages as documented in our focal landscape (Pinho et al., 2019) somehow affect litter decomposition as suggested here.

In synthesis, nutrient mineralization via litter decomposition appears to a complex process by responding to natural (precipitation and aboveground biomass) and human-related forces such as chronic disturbance. A combination of reduced nutrient concentration and litter production plus litter consumption by goats and nutrient mineralization during dry season probably limit forest regeneration or plant growth in a system marked by impoverished sandy soils and reduced aboveground biomass. This perspective highlight how complex, and still understood, nutrient cycling becomes as old-growth forests move towards human-modified forests through which land use occurs concomitantly such as slash-and-burn agriculture free-range livestock production and exploitation of forest products.

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CONFLICT OF INTEREST

The authors declare there are no conflicts of interest.

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SUPPLEMENTARY MATERIAL

Figure S1. Decomposition experiment with 12 litter bags across dry forest plots in Catimbau National Park, Pernambuco state, northeastern Brazil.

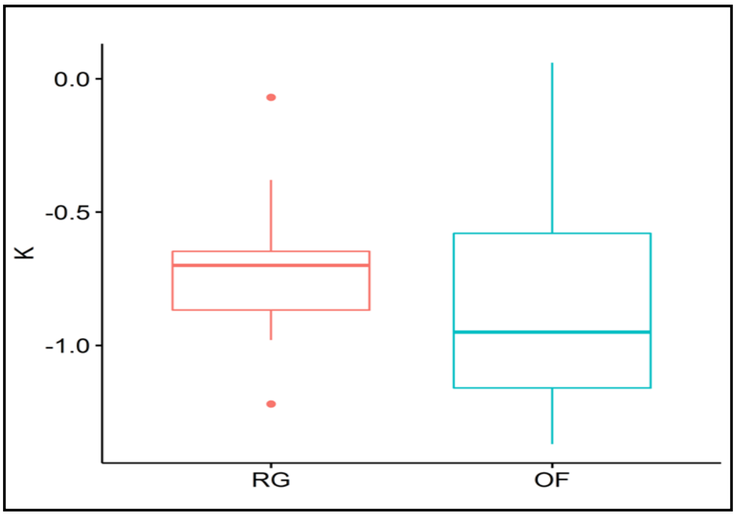

Figure S2. Decay rate constant (k) values across regenerating dry forest stands (RG) and old-growth forests (OF) in Catimbau National Park, Pernambuco state, northeastern Brazil.

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