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Litterfall and leaf decomposition in forest fragments under different successional phases on the Atlantic Plateau of the state of Sao Paulo, Brazil

Litterfall and leaf decomposition in forest fragments under different successional phases on the Atlantic Plateau of the state of Sao Paulo, Brazil

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Abstract: Litterfall and litter decomposition are vital processes in tropical forests because they regulate nutrient cycling. Nutrient cycling can be altered by forest fragmentation. The Atlantic Forest is one of the most threatened biomes in the world due to human occupation over the last 500 years. This scenario has resulted in fragments of different size, age and regeneration phase. To investigate differences in litterfall and leaf decomposition between forest successional phases, we compared six forest fragments at three different successional phases and an area of mature forest on the Atlantic Plateau of Sao Paulo, Brazil. We sampled litter monthly from November 2008 to October 2009. We used litterbags to calculate leaf decomposition rate of an exotic species, *Tipuana tipu* (Fabaceae), over the same period litter sampling was performed. Litterfall was higher in the earliest successional area. This pattern may be related to the structural properties of the forest fragments, especially the higher abundance of pioneer species, which have higher productivity and are typical of early successional areas. However, we have not found significant differences in the decomposition rates between the studied areas, which may be caused by rapid stabilization of the decomposition environment (combined effect of microclimatic conditions and the decomposers activities). This result indicates that the leaf decomposition process have already been restored to levels observed in mature forests after a few decades of regeneration, although litterfall has not been entirely restored. This study emphasizes the importance of secondary forests for restoration of ecosystem processes on a regional scale.
Keywords: biomass, nutrient cycling, secondary forest, tropical forest.

Resumo: A produção e a decomposição de serrapilheira são processos vitais nas florestas tropicais, uma vez que determinam a ciclagem de nutrientes. O processo de ciclagem de nutrientes pode ser alterado pela fragmentação florestal. A Floresta Atlântica é um dos biomas mais ameaçados mundialmente devido à ocupação humana nos últimos 500 anos. Este cenário resultou em fragmentos de diferentes tamanhos, idades e estádios de regeneração. Para explorar as diferenças na produção de serrapilheira e na decomposição foliar de acordo com o estádio sucessional da floresta, comparamos seis fragmentos florestais em três diferentes estádios sucessionais e uma área de floresta primária no Planalto Atlântico de São Paulo, Brasil. Coletamos a serrapilheira mensalmente de novembro de 2008 a outubro de 2009. Utilizamos bolsas de confinamento de serrapilheira para calcular a taxa de decomposição foliar de uma espécie exótica, *Tipuana tipu* (Fabaceae), durante o mesmo período de coleta da serrapilheira. A deposição de serrapilheira foi maior na área de estádio sucessional mais inicial. Esse padrão pode estar relacionado com as características estruturais dos fragmentos florestais, especialmente com a maior abundância de espécies pioneiras, que possuem uma maior produtividade e são espécies típicas de fragmentos em estádios iniciais de sucessão. Por outro lado, não encontramos diferenças significativas nas taxas de decomposição entre as áreas estudadas, o que pode ocorrer devido à rápida estabilização do ambiente de decomposição (efeito combinado das condições microclimáticas e das atividades dos decompositores). Estes resultados indicam que o processo de decomposição foliar foi restabelecido aos níveis das florestas maduras após algumas décadas de regeneração, embora a produção de serrapilheira ainda não tenha sido totalmente restaurada. Este estudo destaca a importância das florestas secundárias em um cenário regional de restauração de processos ecossistêmicos.
Palavras-chave: biomassa, ciclagem de nutrientes, floresta secundária, floresta tropical.

Introduction

Deforestation and forest fragmentation are major threats to biodiversity in the tropics (Laurance 1999), particularly in South America, where forest land has been continuously converted to agriculture, urbanization (Food... 2011) and industrial uses. An example of this network is the Brazilian Atlantic Rain Forest, whose exploitation dates back to the time of European colonization, 500 years ago, when the trade of forest resources in conjunction with the pressure from economic cycles in the followed centuries (Dean 1996) culminated in a fragmented and threatened biome. This exploitation resulted in isolated forest fragments of different sizes and successional phases (Ribeiro et al. 2009).

Forest fragmentation is known to alter the microclimate, as a result of a higher insolation and wind penetration, which increases temperature and decreases humidity along forest edges (Kapos et al. 1997). Moreover, fragmentation elevates the rates of tree mortality (Laurance et al. 1998), which influence forest diversity and species composition (Laurance et al. 1998). In addition to altering the ecosystem structure, forest fragmentation can lead to changes in ecological processes such as litter production (Werneck et al. 2001) and nutrient cycling (Laurance 2008).

In forests fragments, aboveground live biomass increases with succession (Vitousek & Reiners 1975) as a result of the recruitment of old growth species (characterized by a larger diameter and height (Clark 1996) and canopy development (Clark 1996, Songwe et al. 1988). Thus, litter production is expected to increase with forest development (Vidal et al. 2007). The amount of litter input, in turn, influences the composition of the decomposer community and associated with the drier microclimate conditions, typical of early successional forest fragments, can reduce the activity of decomposers (Bradford et al. 2002), resulting in a less efficient nutrient cycling.

Litterfall and leaf decomposition represent the main pathway for nutrient cycling in forest ecosystems (Montagnini & Jordan 2002). These ecosystem processes are of key importance on tropical forests, where the vegetation is generally sustained by soils with low fertility (Lavelle et al. 1993). Therefore, forest productivity depends on efficient nutrient cycling mechanisms that ensure rapid turnover of litter nutrients (Montagnini & Jordan 2002). In tropical montane forests, nutrient cycling mechanisms are especially relevant, since their leaf litter is composed by lower nutrient concentrations than those from lowland forests (Bruijnzeel & Veneklaas 1998) and the lower temperatures reduces the decomposition rate and nutrient release (Röderstein et al. 2005), making their soils extremely poor in nutrients (Bruijnzeel & Veneklaas 1998).

Although different aspects of forest fragmentation have been studied in the last decades in the tropics (Dixo et al. 2009, Banks-Leite et al. 2010, Bieber et al. 2011, Lira et al. 2012), its consequences on ecosystem processes are still poorly understood (Vasconcelos & Luizão 2004, Vidal et al. 2007, Ostertag et al. 2008). Thereby, this study aimed to evaluate how litterfall and nutrient cycling are affected by the structure of forest fragments at different successional phases under similar climatic conditions on the Atlantic Plateau of the state of Sao Paulo, Brazil. We hypothesized that forest fragments of later successional phases would have higher litterfall input and leaf decomposition than early successional fragments under similar climatic conditions, as a result of the major biomass and the more favorable environmental conditions (which represent the combined effects between microclimate and decomposers activities), respectively.

Materials and Methods

1. Study site

The study area is located in the municipalities of Ibiúna, Piedade and Tapiraí, state of Sao Paulo, southeastern Brazil at an altitude of 800 to 1100 m a.s.l. (Ponçano et al. 1981). The climate is temperate humid with temperate summer, Cfb (Köppen 1948). The average annual temperature is of 20 °C and an average annual precipitation is of 1808 mm (CIIAGRO/IAC 2012). The three soil classes of the region are Cambisol, Latosol and Argisol (Oliveira et al. 1999) with slopes ranging from 20 to 30% (Ponçano et al. 1981). The original vegetation is dense montane ombrophilous forest (*sensu* Veloso et al. 1991), which is considered a transition forest between the Atlantic coastal forests and the mesophilous semi-deciduous forests from inland Sao Paulo (Aragaki & Mantovani 1998).

In the municipalities of Piedade and Tapiraí, a landscape of 10,000 ha (23° 50' 00" S and 47° 20' 00" W) was bounded by the BioCAPSP II project (2000), and consists in forest fragments at different successional phases, surrounded by agricultural fields, cattle pasture and degraded areas. In this landscape, we selected six forest fragments of different land use history, size (26.7 to 167.1 ha) and age (25 to > 65 years) (Table 1). We adopted a classification of the successional phase of these fragments that was based on a combination of structural and floristic variables (basal area, density, basal area of pioneers, number of multiple trunks and maximum canopy height) (Table 1, see Jurinitz 2010 for details), which resulted in three phases: late secondary (1-2), intermediate (1-2) and early (1-2) (Table 1). The numbers after each phase refer to the increasing order of successional phases within each group, and lower figures indicate fragments at an earlier regeneration state. It is important to note, however, that this classification allows forest fragments of different ages to be classified in the same successional phase, e.g. Intermediate Secondary 1 and 2 (Table 1). This occurs because the successional phase of a fragment cannot be interpreted

Table 1. Characteristics of forest fragments on the Atlantic Plateau of the state of Sao Paulo, Brazil. Forest fragments are ordered by decreasing order of successional phase.

Study area	Study area acronym	Area (ha)	Age (yr)[a]	% Basal area of pioneers[b]	% Canopy opening[b]
Control	C	>26,000	-	-	-
Late Secondary 2	LS-2	97.6	≥65	0	3.7
Late Secondary 1	LS-1	26.7	≥65	0	3.7
Intermediate Secondary 2	IS-2	167.1	25	9.6	4.1
Intermediate Secondary 1	IS-1	85.3	≥65	2.2	8.2
Early Secondary 2	ES-2	39.9	25	13.9	6.4
Early Secondary 1	ES-1	41.3	25	36.8	8.2

[a]Lira et al. (2012). [b]Jurinitz (2010).

only as a chronosequence, but also as a consequence of many factors (such as the ones mentioned previously). The control area was located in the Jurupará State Park, municipality of Ibiúna (23° 57' 13" S and 47° 24' 31" W) and contained over 26,000 ha of preserved mature forest (Table 1).

2. Litterfall

Nine 0.5 × 0.5 m litter collectors were installed 1.5 m above the surface of the soil in each area. Collectors were arranged along three parallel transects 100 m apart, except for the Late Secondary 1 fragment; due to the small size of this fragment (Table 1), the distance between the transects was 50 m. Three collectors were installed at 40 m intervals along each transect (Figure 1a). We collected the deposited material monthly from November 2008 to October 2009, dried at 60 °C to a constant weight and weighed on a digital scale that was precise to the thousandth of a gram. Branches larger than 0.5 cm in diameter were discarded.

3. Litter decomposition experiment

Leaf decomposition rates were estimated using the litter confinement method in decomposition bags (Bocock & Gilbert 1957). Although this method may underestimate actual decomposition rates, it is recommended for comparative purposes (Wieder & Lang 1982). To avoid having any area be favored by the presence of soil microbiota that was locally specialized in decomposition of a particular substrate, as suggested in an earlier study performed in the Cerradão (Castanho & Oliveira 2008), which is a forest-like Brazilian savanna, we standardized the substrates in this experiment using an exotic species (*Tipuana tipu* (Benth.) Kuntze, Fabaceae). Decomposition bags were 0.2 × 0.2 m and made with 0.4 cm² nylon mesh filled with approximately 3 g of *T. tipu* leaves dried at 60 °C to a constant weight. In each forest fragment, 60 litterbags were distributed in 10 random blocks within a 50 × 100 m plot located at least 20 m from the forest edge (Figure 1b). We placed the bags on the soil surface with a minimum distance of 20 m between blocks. This experiment was conducted near the areas used for the litterfall. In the control area, we arranged the blocks along two litter sampling transects with five blocks per transect and a distance of 20 m between adjacent blocks. The experiment was set up at the beginning of the rainy season in October 2008. Sampling was performed after 30, 90,

150, 210, 300 and 390 days. In each period, we collected one litter bag per block, totaling 10 bags per study area. In the laboratory, we removed and transferred the material inside each bag to Petri dishes, dried at 60 °C to a constant weight and weighed. Due to trees falling in March and May 2009, three fragments (LS-1, IS-1 and ES-1) lost one decomposition block each.

4. Data analyses

We used the Monte Carlo permutation method to test for differences in litterfall between successional phases by calculating the modulus of the sum of the differences between average annual litter production from all areas ($X_{general}$) and the annual average from each area (X_j): $\Sigma \mid X_{general} - X_j \mid$. One thousand permutations were generated from monthly data, which was blind to the identity of the sampled areas. To check for differences between fragments, we calculated 95% confidence intervals (CI) by bootstrap resampling (1000 permutations of annual data with the identity of each area known). Areas were considered distinct when maximum or minimum values of the confidence interval from one fragment did not overlap the average from another area. In addition, the coefficient of variation (CV) was calculated to determine the variability of the dataset.

In the leaf decomposition experiment, we applied a simple model of exponential decay (Jenny et al. 1949, Olson 1963) to calculate decomposition rates: $-X_t/X_0 = e^{-kt}$, where X_0 is the initial dry mass, X_t is the dry mass at time t and k is the decay constant. The model was fit to the data using linear regression of the natural logarithm of leaf mass remaining in each decomposition block over time. Therefore, the slope coefficient of the linear equation represents the decomposition rate in each block. We used Analysis of variance (ANOVA) to test for effects of successional phase on the decomposition rate. The estimated decomposition rate for each block in each area served as the response variable, and the forest (with seven levels) served as the explanatory variable.

Results

1. Litterfall

Litter production was seasonal. All areas studied exhibited a similar pattern (Figure 2), and the highest production was during the
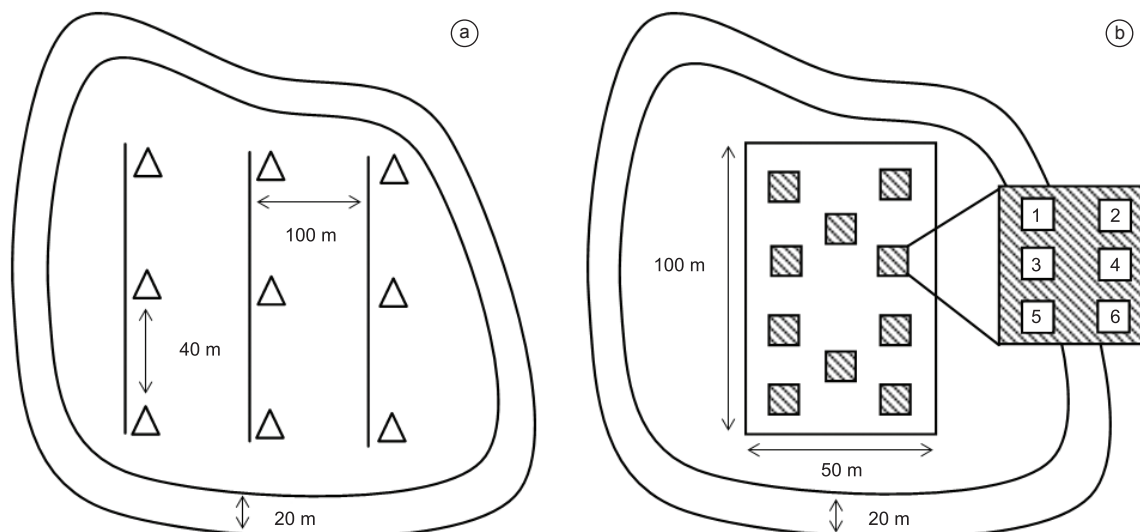
Figure 1. Design of the litterfall traps (a) and the decomposition experiment (b) in the studies areas on the Atlantic Plateau of the state of Sao Paulo, Brazil. The triangles represent the litterfall traps of 0.25 m²; the hatched squares represent the decomposition plots and the numbers, each litterbag.

rainy season (509.1 ± 112.5 kg/ha from November 2008 to January 2009) and was the lowest during the dry season (178.3 ± 56.5 kg/ha from March to June). The early secondary fragment 1 (ES-1) exhibited two higher litterfall peaks than the other forest fragments, which were in the middle of the rainy season and at the end of the dry season (Figure 2).

The comparison of average litterfall between areas showed that production in fragment ES-1 was significantly higher than other areas studied (p < 0.05), except for fragment ES-2 (Table 2). The latter did not show any differences compared to late phase fragments or the control area; however, it did differ from the intermediate secondary fragments (Table 2). The other areas showed no significant differences between them (Table 2). The coefficients of variation indicated a broad range in litter production values for the study areas, which were between 60.3 to 72.3% (Table 2).

2. Litter decomposition experiment

Leaf decomposition was rapid, and almost 70% of the initial mass was lost in the first 30 days (Figure 3). The fitted simple exponential model had a p-value that was less than 0.05 in over 70% of the cases (blocks). The coefficient of determination (R^2) ranged from 0.21 to 0.99 and was equal to or greater than 0.70 in 73% of the cases (n = 67). Decomposition blocks showed high variation in decomposition rates over time in each study area. However, the average decomposition rates did not differ between areas (p = 0.238, Figure 4).

Discussion

1. Litterfall

Studies in tropical forests have identified a seasonal pattern in litter production. Litterfall may peak in dry periods in forests with higher water restriction (Dantas & Phillipson 1989, Sanchez & Alvarez-Sanchez 1995, Barlow et al. 2007) or alternatively in wetter period in forests with lower water restriction as in the Atlantic Forest (Leitão-Filho et al. 1993, Pinto & Marques 2003, Vidal et al. 2007). The pattern of higher deposition of litter in the rainy season may be

related to more favorable environmental conditions for leaf renewal in the rainy season, such as greater day length, relative humidity and precipitation (Jackson 1978). In the early secondary fragment 1 (ES-1), the second peak of litterfall coincided with the dry season (September 2009) and may be due to high precipitation, which was atypical for the period when compared with the 12 previous years (Figure 5, CIIAGRO/IAC). The mechanical action of the rain associated with wind may have contributed to an increase in plant material falling to the ground (Xiong & Nilsson 1997, Moraes 2002). In fact, significant amounts of green leaves and branches were found in collectors from this fragment for this period. In other areas, the increase in litter production in the drier period was not as significant, which was possibly due to the presence of a more closed canopy (Table 1) than the fragment ES-1 (Table 1), that can reduce the impact of rainfall on lower strata. Moreover, it could also be related to terrain slope; however, our samples were conducted on areas with less than 20 degrees of topographic inclination which reduces the impact of this factor.

Table 2. Average annual litterfall (kg/ha) in forest fragments on the Atlantic Plateau of the state of Sao Paulo, Brazil.

| Study area	Average annual litterfall (kg/ha)	95% CI		% CV
		Min.	Max.	
Control	344.5[ac]	301.2	393.5	70.1
Late Secondary 2	346.1[ac]	301.7	392.9	71.6
Late Secondary 1	362.3[ac]	322.7	404.6	60.6
Intermediate Secondary 2	323.1[ab]	279.6	368.3	72.3
Intermediate Secondary 1	324.5[ab]	286.6	364.7	64.5
Early Secondary 2	371.0[cd]	329.4	415.5	63.0
Early Secondary 1	405.2[d]	352.4	462.4	72.1

Minimum and maximum values of the 95% confidence interval (CI) and coefficient of variation (CV) are shown as percentages. Different letters represent significant differences based on the bootstrap test (α = 0.05). Forest fragments are ordered by decreasing order of successional phase.
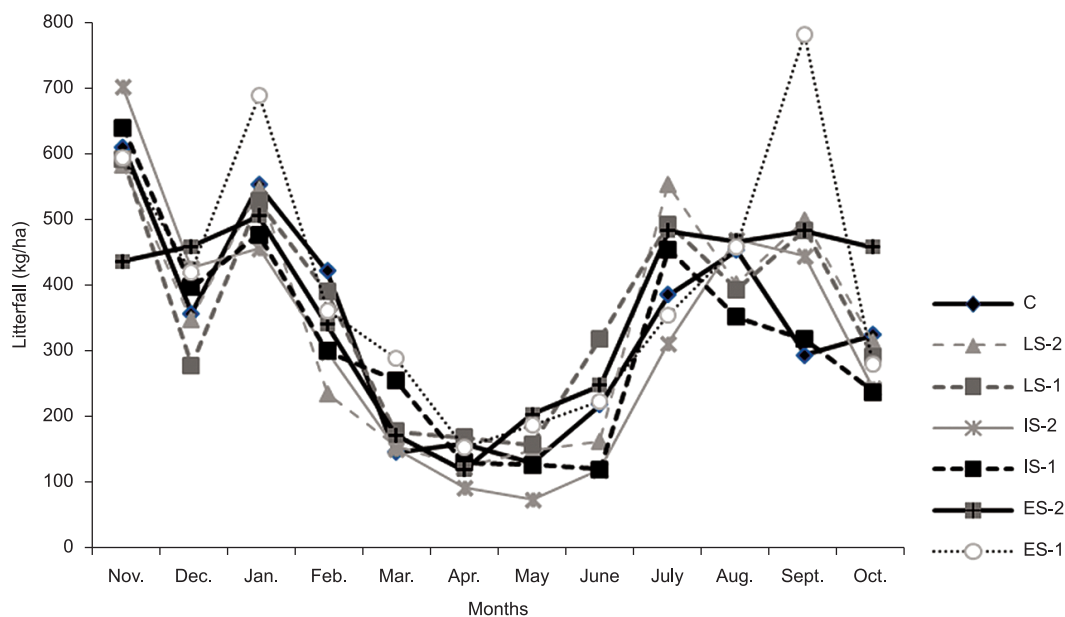
Figure 2. Monthly average litterfall biomass (kg/ha) over 12 sampling months (sampling started in 2008) in forest fragments on the Atlantic Plateau of the state of Sao Paulo, Brazil. Control (C), Late Secondary 2 (LS-2), Late Secondary 1 (LS-1), Intermediate Secondary 2 (IS-2), Intermediate Secondary 1 (IS-1), Early Secondary 2 (ES-2) and Early Secondary 1(ES-1).

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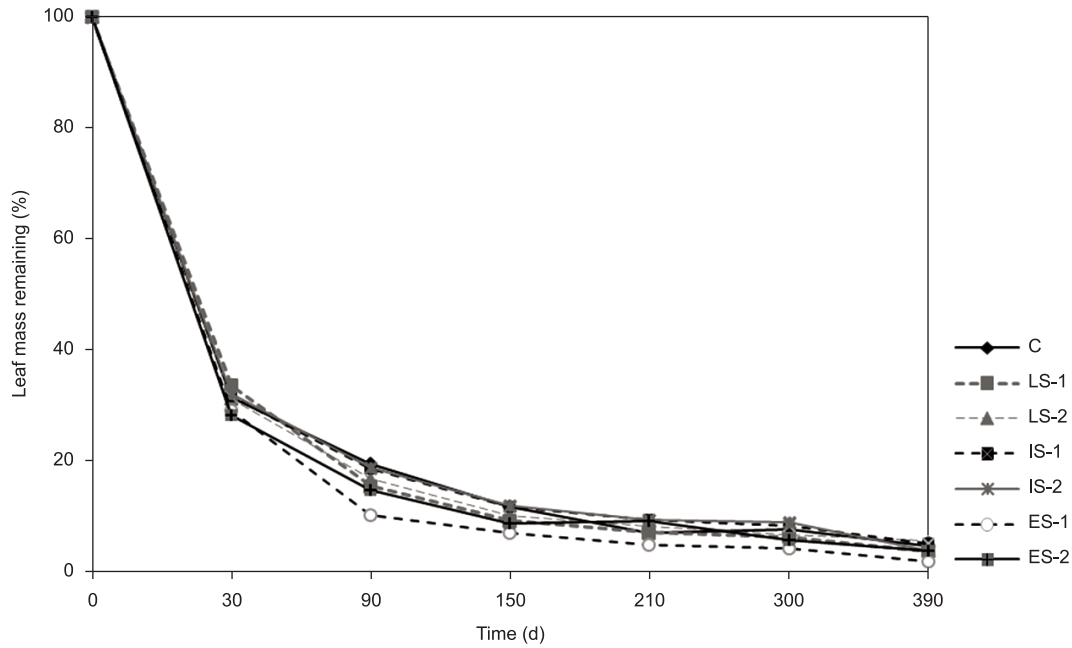
Figure 3. Leaf mass percentage remaining over 390 days in forest fragments on the Atlantic Plateau of the state of Sao Paulo, Brazil. Control (C), Late Secondary 2 (LS-2), Late Secondary 1 (LS-1), Intermediate Secondary 2 (IS-2), Intermediate Secondary 1 (IS-1), Early Secondary 2 (ES-2) and Early Secondary 1(ES-1).
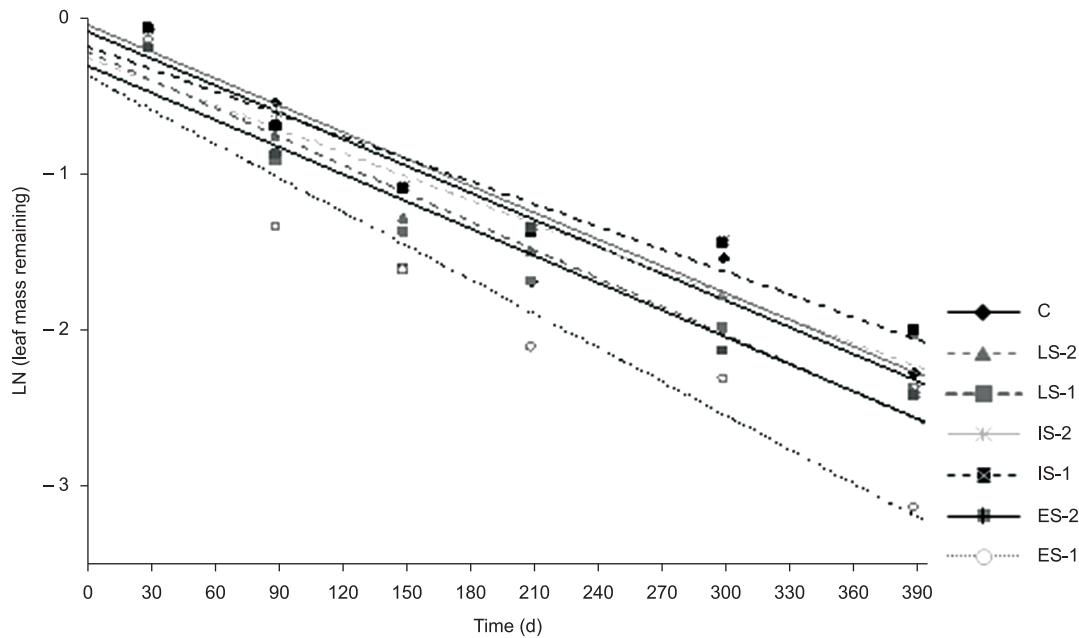

Figure 4. Natural logarithm of leaf mass remaining over time in forest fragments on the Atlantic Plateau of the state of Sao Paulo, Brazil. Mean decomposition blocks over time with fitted lines for each study area. Late Secondary 2 (LS-2), Late Secondary 1 (LS-1), Intermediate Secondary 2 (IS-2), Intermediate Secondary 1 (IS-1), Early Secondary 2 (ES-2) and Early Secondary 1(ES-1).

The high spatial heterogeneity in litterfall suggests there was considerable variation in the biotic and abiotic conditions within each area, and the highest coefficients of variation were in areas that were larger than 80 ha. In this context, smaller fragments were less heterogeneous, which was likely due to edge effects, such as wind and temperature, in a relatively higher proportion of the fragment when compared with larger fragments, once edge effects can propagate hundred meters into the forest (Laurance 2000). The exception to this

pattern was fragment ES-1, which had a high coefficient of variation despite its small area (41.3 ha), likely due to the presence of two bodies of water. This factor likely altered the local microclimate, which increased spatial variability. However, this effect could have been also overestimated due to the small sample size.

The higher litterfall in the early successional fragment 1 (ES-1) when compared with the fragments of later successional phases revealed a pattern contrary to our prediction that higher litterfall

Ecosystem processes in Atlantic Forest fragments
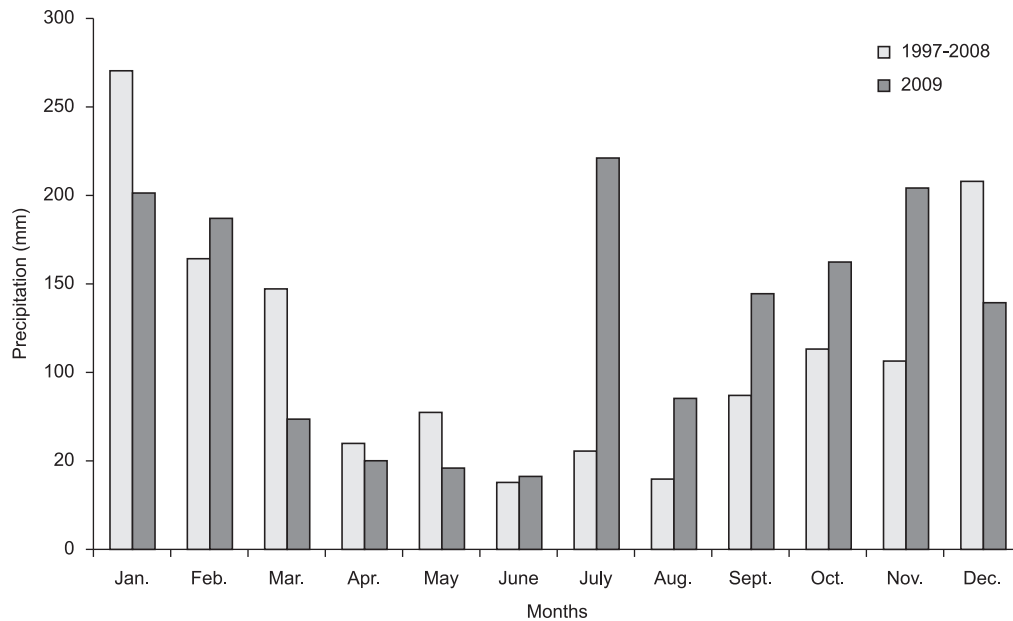
Figure 5. Average rainfall of the years 1997-2008 and 2009 of the municipality of Piedade, state of Sao Paulo, Brazil (CIAGRO/IAC).

would be observed in forests at an advanced successional phase due to their greater biomass and a more closed canopy (Werneck et al. 2001, Nascimento & Villela 2003, Vidal et al. 2007). The greater biomass produced in ES-1 may be associated to a high biomass of pioneer species, given the fact that in this fragment 36.8% of the total basal area corresponded to pioneer species, when compared with the others fragments where this proportion were quite smaller (Table 1). Pioneer species are characterized by rapid growth (Martins & Rodrigues 1999), have a higher investment in production of leaves and roots rather than timber (Leitão-Filho et al. 1993, Guariguata & Ostertag 2001) and higher leaf turnover than late successional trees (Coley 1983). Data from forests at early successional phases suggest that once the forest canopy is closed, which may be around 20 years, litter input, especially leaf production, stabilizes to the levels of mature forest (Barlow et al. 2007). Although fragment ES-1 is 25 years old, it has a high canopy openness percentage compared with late successional forests (Table 1), which implies in a higher litter production. Therefore, fragment age is not always a good indicator of litterfall or successional phase because during ecological succession, features of the landscape where the fragment is located influence its temporal dynamics. For example, proximity to preserved forest areas may speed up the successional process because the preserved forests may serve as a source of propagules for the fragment (Brown & Lugo 1990). In this context, the controversial pattern of litterfall in Atlantic forests (higher amounts of litter production in later successional phases (Vidal et al. 2007, Scheer et al. 2009), or alternatively higher litterfall in early succession phases (Leitão-Filho et al. 1993) or even the absence of differences in litterfall between fragments of different successional phases (Barlow et al. 2007, Dickow et al. 2012), may be related to the divergent structures and historical disturbance of the forest fragments studied. Fragments ES-1 and ES-2 showed no differences in litter production, which was likely due to their similar structure (Jurinitz (2010)).

2. Litter decomposition experiment

The selected litter for the decomposition experiment presented a rapid decay, being faster than the decomposition of a species from the Atlantic Forest (*Guapira opposita* (Vell.) Reitz, Nyctaginaceae),

which had lower C:N ratio (Castanho & Oliveira 2008). It is established that litter with low C:N ratios decompose faster than those with higher C:N ratio (Xuluc-Tolosa et al. 2003). Besides the composition of the material, the rapid mass loss in the study areas (70% after the first 30 days) may also be attributed to favorable climatic conditions of the tropics (high temperature and humidity) for decomposition activity (Brown & Lugo 1990). In general, weight loss during leaf decomposition can be divided into two phases: an initial rapid loss, which is attributed to the leaching of soluble components in the litter, such as sugars and proteins, and a period of slower mass loss, which is attributed to the breakdown of more recalcitrant components such as cellulose and lignin (Xu et al. 2004).

The hypothesis that decomposition rates would differ between forest fragments was not supported by the results of this study. Differences in the decomposition rate between the forests fragments studied would be expected to be lower in fragments of early successional phase, since those forests have a more open canopy which influences the microclimate conditions and consequently reduces the decomposers activity (Aerts 1997). Studies on tropical forest succession have showed that environmental conditions for litter decomposition on forests at early successional phase were as favorable as those on forests at late successional phase (Ewel 1976, Xuluc-Tolosa et al. 2003, Vasconcelos & Laurance 2005). Besides, Höfer et al. (2001) have found similarities in nutrient cycling efficiency by macrofauna communities between disturbed areas (agricultural fields and secondary forests) and mature forests in the central Amazon even though each area had different species. Additionally, studies of decomposition rates with natural litter comparing chronosequences have found a pattern similar to this study (Ostertag et al. 2008, Gießelmann et al. 2011). According to Gießelmann et al. (2011), the absence of difference in the decomposition rates between forests at different successional phases may be related to the ability of the microorganisms to quickly adjust their community structure to environmental variations through rapid population growth or growth of hyphae. Therefore, macrofauna activity and environmental conditions in the fragments may have been restored to similar levels observed in mature forest, which may explain the lack of differences in decomposition rates in this study.

Alternatively, the lack of significant differences in leaf decomposition among the areas may be attributed to the great spatial heterogeneity observed in each area. According to Lavelle et al. (1993), intra-area variation may be greater than inter-area variation, which emphasizes the importance of local soil and biological factors for decomposition on rain forests. Only severe changes in forest structure, such as total removal of vegetation, could affect decomposition as it was evaluated in this study (Ewel 1976).

In conclusion, the results indicate that an abundance of pioneer species in forest fragments is a determining factor for high litterfall in forest areas of the Atlantic Plateau of Sao Paulo. Nevertheless, the decomposition process of the standardized material was not affected by environmental changes after a few decades of secondary succession caused by forest fragmentation, which was likely due to rapid stabilization of the combined effect of microclimatic conditions and decomposers activities. However, it should be noted that actual decomposition rates from study areas may also be influenced by the local substrate and therefore may differ from the rates determined in this study. This study indicates that the decomposition environment in forest fragments may have been restored to similar levels observed in mature forests approximately two decades after fragmentation. Thus, the conservation of secondary forests is essential for restoration of ecological functions even though the local biodiversity is lower compared to mature forests.

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