Forest Systems
31 (3), e019, 12 pages (2022)
eISSN: 2171-9845
https://doi.org/10.5424/fs/2022313-18791
INIA-CSIC

RESEARCH ARTICLE

OPEN ACCESS

Litter decomposition in a remnant of Atlantic Rain Forest and bamboo dominance

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Abstract

Aim of study: We compared the decomposition rate of the accumulated litter, the stock, and the return of nutrients to the soil, between an area dominated by bamboos in the understory and an area where this dominance does not occur.

Area of study: Fontes do Ipiranga State Park, an Urban Fragment of Atlantic Forest at the Municipality of São Paulo, Southeastern Brazil.

Materials and methods: The decomposition rates were measured over one year (0, 3, 6, 9, and 12 months), avoiding litter addition through nylon nets over the soil. The collected material was separated into the following fractions: bamboo leaves and branches (bamboo material); other leaves and branches (other material); very decomposed material not identifiable (unidentifiable). The content of macro (N, P, K, Ca, Mg, and S) and micronutrients (B, Cu, Fe, Mn, and Zn) were determined.

Main results: The litter accumulated was significantly higher in the mature area than in the bamboo area. The decomposition rates did not differ significantly between the two areas. Except for K and Mn, the concentrations of macro and micronutrients were equal to or greater in the mature forest.

Research highlights: Unlike reported in other areas, there is no greater litter accumulation in the bamboo-dominated understory nor a slower decomposition rate. The nutrient content is lower in the bamboo-dominated disturbed area.

Additional key words: *Aulonemia aristulata*; ecosystem processes; necromass; nutrient cycling; super-dominant species; forest understory; urban forest.

Abbreviations used: CienTec (Science and Technology Park of the University of São Paulo); FISP (Fontes do Ipiranga State Park); GBLS (Ground Bamboo Litter Stock); IAG (Institute of Astronomy and Geophysics); Mature (Mature Forest).

Citation: Vieira, MS; dos Santos, AR; Lopes, MIMS; Gomes, EPC (2022). Litter decomposition in a remnant of Atlantic Rain Forest and bamboo dominance. Forest Systems, Volume 31, Issue 3, e019. https://doi.org/10.5424/fs/2022313-18791

Received: 27 Aug 2021. **Accepted:** 24 Oct 2022.

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Funding agencies/institutions	Project / Grant
CNPq	475831/2012-08
CAPES	

Competing interests: The authors have declared that no competing interests exist.

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Introduction

The growth and establishment of bamboos in forests can interfere with the dynamics and structure of vegetation, reducing the production and the decomposition rate of biomass (Liu *et al.*, 2000; Budke *et al.*, 2010; Larpkern *et al.*, 2011). In general, the decomposition of bamboo species material is slower in relation to phanerogamous plants (Liu *et al.*, 2000; Montti *et al.*, 2011; Watanabe *et al.*, 2013), leading to a lower return of nutrients and carbon to the soil (Shanmughavel, 2004; Zaninovich *et al.*, 2017). The lignin:N, lignin:P and N:P relationships are higher (Liu *et al.*, 2000) than those generally found. In addition, the accumulation of material can delay or prevent the emergence of seedlings (Guilherme *et al.*, 2004; Taylor *et al.*, 2004, 2006; Young & Peffer, 2010) or cause damage to those al-

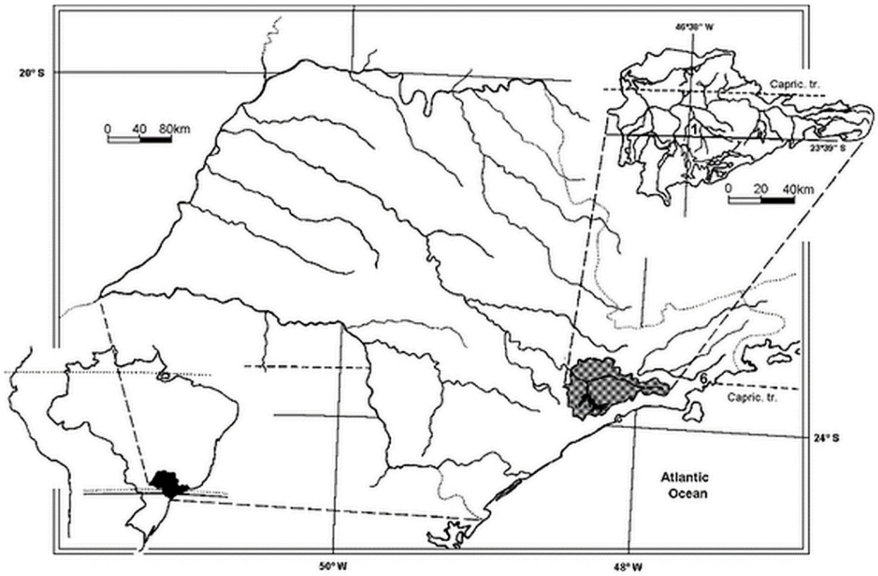

Figure 1. Location of Fontes do Ipiranga State Park (FISP), in the metropolitan area of São Paulo, SP.

ready established (Griscom & Ashton, 2006; Larpkern *et al.*, 2011).

Brazil has the greatest diversity in bamboo species in the Americas, where 89% of the genera and 65% of the species in the New World are present (Filgueiras & Santos-Gonçalves, 2004). The dominance of the understory by bamboo species has been documented in several forest types in Brazil (Lima *et al.*, 2012; de Carvalho *et al.*, 2013) and in other parts of the world (Taylor *et al.*, 2004; Soto *et al.*, 2019).

In the understory of the forest of the Fontes do Ipiranga State Park (FISP), a fragment of the Atlantic Forest, six species of bamboos are relatively common: *Aulonemia aristulata* (Doell) McClure, *Parodiolyra micrantha* (Kunth) Davidse & Zuloaga, *Chusquea bambusoides* Rupr. E.g. Döll, *Chusquea capituliflora* Trin., *Chusquea meyeriana* Ekman, and *Merostachys pluriflora* Munro ex E.G. Camus (Shirasuna & Filgueiras, 2013). *A. aristulata* occurs from the south to the northeast of Brazil extra-amazon, forms clusters in forest gaps, and propagates using amphipodial rhizomes (Soderstrom & Ellis, 1988). It belongs to the group of lignified bamboos, and its epidermis is formed by long and narrow cells (Ellis, 1979). It has a cylindrical, thick, reduced lumen, culms from 0.5 to 8.5 m in length, decumbent to scandent, forming dense thickets on the vegetation (Shirasuna & Filgueiras, 2013).

As a result of disturbances, some species, even those native to the area, may become super dominant, such as bamboos (Montti *et al.*, 2011; Zaninovich *et al.*, 2017; Liu *et al.*, 2019; Soto *et al.*, 2019), generating the need to develop recovery and management programs that meet conservation objectives. To this end, the soil-vegetation interactions must be well known, which can be understood by studying nutrient cycling through litter, allowing a quantitative comparison of the flow of matter between ecosystems (Vitousek, 1984).

Most of the bamboo species that occur in southern and southeastern Brazil do not present lignification as pronounced as the Asian species (Soderstrom & Ellis, 1988; Judziewicz *et al.*, 1999), and it is not clear whether the litter accumulation and the lignin:nutrient ratio found in decomposing material in forests understories dominated by bamboo is different from the surrounding areas in which bamboo represents only minor understory cover.

In this study, in a large Atlantic Forest fragment, we compared the decomposition rate of the accumulated litter, the stock, and the return of nutrients to the soil, between an area dominated by bamboos in the understory and an area where this dominance does not occur.

Material and methods

Study area

Fontes do Ipiranga State Park is located between the latitudes 23º38’08”S and 23º40’18”S and longitudes 46º36’48”W and 46º38’00”W, in the southeast zone of the city of São Paulo (Petri *et al.*, 2018), in the Paulistano Plateau on rocks of crystalline foundation and sedimentary rocks. Hills characterize the relief with convex tops ranging from 759 m to 837 m (Kondrat *et al.,* 2020). In 2013, part of its area was reduced from 526 to about 495 ha (Fig. 1).

The predominant soil types in the area are the Inceptisols and the Oxisols under a subtropical climate classified as Cwa in the Koppen system, with an average annual tem-

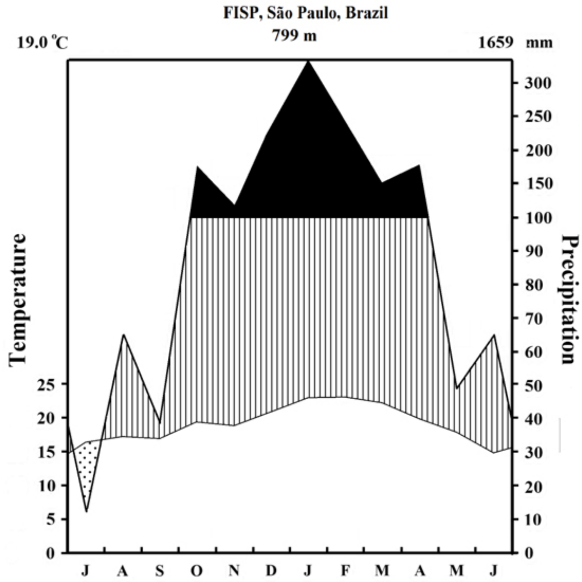

Figure 2. Climatic diagram of Walter-Lieth for study area (FISP) during the study period. Data was provided by the meteorological station of the Institute of Astronomy, Geophysics, and Atmospheric Sciences (IAG), University of São Paulo (USP).

perature of 18.7ºC and total annual rainfall of 1412.3 mm (data from 1933 to 2017; Kondrat *et al.,* 2020).

Fontes do Ipiranga State Park is the third largest State Park in the Metropolitan Area of São Paulo, and although it is immersed in an urban matrix, it is the largest in the metropolis with an isolated Atlantic Forest remnant. The park's native forest area covers about 340 ha, and its predominant vegetation is characterized as Atlantic Rain Forest in various stages of succession (Shirasuna & Filgueiras, 2013). There are 129 families, 543 genera, and 1,159 species recorded for the park's phanerogamic flora (Petri *et al*., 2018).

The area is subject to anthropogenic influences from the surrounding area, such as edge effect, pollution, fires, and urban heat island influence (Gomes *et al.*, 2003; Petri *et al.*, 2018; Kondrat *et al.*, 2020). During the study period, the average annual air temperature was 19.0ºC, the coldest month was June (14.8ºC), and the hottest month was February (23.1ºC). The total annual precipitation was 1659 mm, concentrated between December and March. The driest month was July with 12.2 mm of precipitation and the rainiest month was January with 332.8 mm (Fig. 2). The metropolitan area of São Paulo has experienced a great change in climate over the past 80 years. There was a 1.7 °C increase in the average annual temperature in that period, an increase of approximately 30% in the annual rainfall, and a 3.8 °C increase in the maximum temperatures for the FISP's IAG weather station (de Lima & Rueda, 2018). This station presents a complete (no missing data) and long data series which justifies its use as a reference station in climate studies (de Lima & Rueda, 2018).

The study was carried out in two FISP sites. In the first one, at the boundaries of the Institute of Botany, a patch of an old-growth forest without bamboo dominance (Fig. 3a) was selected as a control area (mature). It comprises a large and mature heterogeneous forest with no changes in physiognomy for at least 60 years (Petri *et al.*, 2018; Kondrat *et al.*, 2020), where the bamboo represents only 4% of the understory cover (Shirasuna & Filgueiras, 2013). This area was identified from analyses of aerial photographs and satellite images taken on four dates (1953/1955, 1962/1965, 1977 and 1994) and with on-site inspections (Shirasuna & Filgueiras, 2013). The other area is in CienTec (Science and Technology Park of the University of São Paulo). It has a homogeneous and dense canopy, and is in a secondary medium stage of succession (Shirasuna & Filgueiras, 2013), with 60% of the understory area covered by bamboos (unpublished data), here called "bamboo" site (Fig. 3b, Fig. 4.).

a) b)

Figure 3. View of the understory dominated by bamboo (a) and the understory of mature forest (b) in Fontes do Ipiranga State Park (FISP), Brazil.

Table 1. Average concentration of macronutrients in the "total" litter (every 90 days) and its fractions ± standard error (g kg^{-1}), in June 2011 and June 2012, in two areas in the Fontes do Ipiranga State Park: the understory dominated by bamboo ("bamboo") and the understory of mature forest ("mature").

Month/ year	N		P		K		Ca		Mg		S	
	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature
Other material												
Jun/2011	17.8+0.3	19.0+0.4	0.4+0.1	0.5+0.1	1.4+0.1	1.3+0.1	7.8+0.3***	9.1+1.3	1.1+0.1	0.9+0.1	1.0+0.1**	1.3+0.1
Jun/2012	14.8+0.9	16.7+0.4	0.4+0.1	0.4+0.1	1.1+0.3	0.8+0.1	8.3+0.8 *	11.7+0.1	0.7+0.1	0.6+0.1	0.9+0.1*	1.1+0.1
Bamboo material												
Jun/2011	17.9+0.1	17.9±0.1	0.5+0.1	0.4+0.1	1.3+0.5	0.8±0.1	4.0+0.9 *	5.0±0.1	0.4±0.1	0.5±0.1	1.0+0.1*	1.3±0.1
Jun/2012	13.5+0.1	16.2+0.1	0.5+0.1	0.5+0.1	1.3+0.3	0.8±0.1	2.3+0.2	3.3±0.1	0.4+0.2	0.4±0.1	1.0+0.1	1.3+0.1
Unidentifiable												
Jun/2011	18.8+0.7	20.1+0.7	0.6+0.1*	0.5+0.1	1.4+0.1	1.1+0.1	4.1+0.8	5.4+1.6	0.8+0.2	0.4+0.1	1.5+0.1*	1.9+0.1
Jun/2012	16.4+0.5*	19.3+0.7	0.5+0.1	0.6+0.1	0.9+0.1	0.8+0.1	3.0+0.5*	5.1+0.5	0.4+0.1	0.4+0.1	1.5+0.1	1.8+0.1
Total												
Jun/2011	18.3+0.1*	19.8+0.6	0.5+0.1	0.5+0.1	1.5+0.1	1.3+0.2	5.3+0.2*	6.5+1.0	0.8+0.1	0.6+0.1	1.2+0.1*	1.6+0.2
Sep/2011	15.7+0.6	17.7+0.8	0.6+0.1	0.6+0.1	1.8+0.4	1.9+0.7	4.0+0.7	6.0+1.3	0.9+0.1	1.1+0.1	1.1+0.2	1.8+0.3
Dec/2011	15.8+0.8	17.6+1.8	0.6+0.1	0.6+0.1	1.6+0.4	1.5+0.4	4.5+1.0	6.4+1.4	0.7+0.1	0.9+0.1	0.6+0.1*	1.6+0.1
Mar/2012	13.7+0.5	18.2+2.4	0.5+0.1	0.6+0.1	1.6+0.3	1.5+0.4	3.9+0.8	7.5+1.6	0.7+0.1	0.8+0.1	0.4+0.1*	1.6+0.3
Jun/2012	15.0+0.5**	17.5+0.1	0.5+0.1	0.5±0.01	1.3+0.2	1.1+0.1	4.5+1.0	7.2+0.1	0.6+0.1	0.6±0.01	1.2+0.1	1.7±0.01

*, **, and *** on the line indicate significance level at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively, for comparison between sites within the same period (T-test).

The two areas have acidic soils (pH < 4.3) presenting saturation in aluminum greater than 50% and dystrophy, with the sum of bases less than 50%. They differ in the contents of organic matter (63 *vs.* 17 g dm^{-3}), nitrogen (3.5 *vs.* 1.5 g dm^{-3}), sulphur (35 *vs.* 8 mg dm^{-3}), potential acidity (33 *vs.* 15 cmol dm^{-3}), and zinc (3.6 *vs.* 1.5 mg dm^{-3}) for the "mature" and the "bamboo" areas, respectively. Both areas present soil with clay texture and a low C:N ratio (<11), indicating a high decomposition of organic matter for the two areas (unpublished data).

Field procedure

In order to evaluate the decomposition rate of the accumulated litter on the soil, the method of covering the material was used. It involves the comparison between the quantities of litter existing at time 0 (zero) and after regular time intervals (Δt), avoiding the addition of the material produced by the canopy of the trees using nylon mesh covers of 1 × 1.5 m (2 mm mesh size) (Olson, 1963; Chapman, 1976). In June 2011, 60 cover meshes were laid out on the ground, 30 in each area. From June 2011 to June 2012, a sample was taken from the area under the cover mesh every three months. On the day of installation, the first collection of material (t = 0) was carried out, taking two samples in the vicinity of each mesh.

Throughout the study, five samples had to be discarded in the mature area because they showed clear signs of interference by fauna, probably by nine-banded armadillo (*Dasypus novemcinctus*), which is very common in the site.

We quantified aboveground biomass of litter by harvesting a selected 0.0625 m^2 (25 × 25 cm) in the center of the mesh, and all material contained inside was separated into the fractions: i) bamboo leaves and branches (bamboo material); ii) other leaves and branches (other material), and iii) more decomposed and unidentifiable material (unidentifiable).

Immediately after the separation, each fraction was stored separately in labeled paper bags and dried at 60 ºC with forced air circulation until reaching a constant weight. Subsequently, each sample was weighed on an analytical scale to obtain the dry mass of the amount of accumulated material, and after reaching constant weight, the samples were mixed between the fractions and corresponding periods and specific plots, obtaining composite samples. After mixing, they were grounded in a knife mill and placed in plastic tubes for further chemical analysis of macronutrients (N, P, K, Ca, Mg, and S) and micronutrients (B, Cu, Fe, Mn, and Zn) in the plant nutrition laboratory of the Escola Superior de Agricultura "Luiz de Queiroz".

Data analysis

The decomposition coefficients k were calculated according to Jenny *et al*. (1949) and Olson (1963): $M_t = M_i e^{-kt}$,

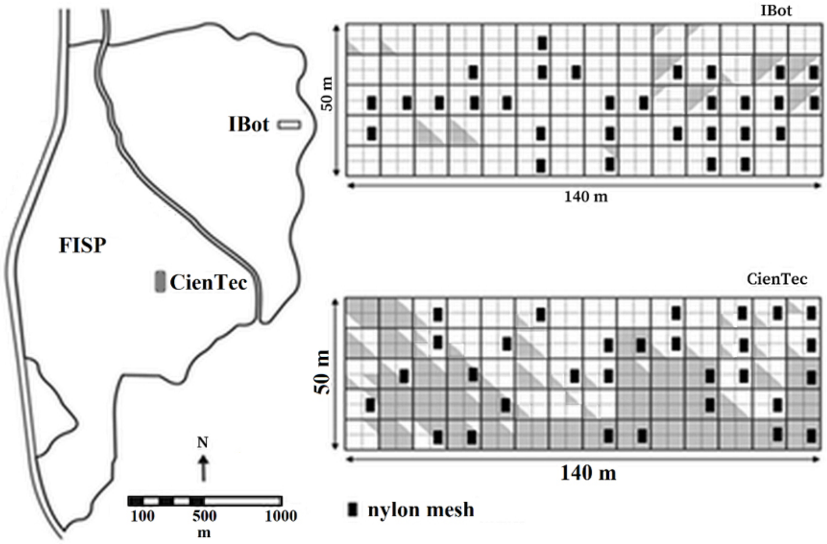

Figure 4. Distribution of the covering meshes for the sampling of the litter. Old-growth forest (IBot): "mature"; CienTec: "bamboo". The occurrence of bamboo species within the areas is represented in grey..

where M_t = mass at time t, M_i = initial mass, k = exponential decay coefficient, and t = time in days.

The normality of the distribution of the remaining mass data of the fractions and the nutrient concentration was verified by the Shapiro-Wilk normality test.

In order to compare the decomposition curves, it was tested whether the slopes of the regression lines (time *vs.* mass) differed between the areas using the transformed decay function $\ln(M_t) = \ln(M_i) - kt$. This comparison form allows the entire process to be analyzed simultaneously and not just the final result (t = 12 months). As a result, very different processes can converge, and significant differences in decomposition rates and initial stock can no longer be detected. The mass values of each sample were transformed by

Table 2. Average concentration of micronutrients in the "total" litter and its fractions ± standard error (mg kg^{-1}), in June 2011 and June 2012 in two areas in the Fontes do Ipiranga State Park: the understory dominated by bamboo (bamboo) and the understory of mature forest (mature).

Month/ year	B		Cu		Fe		Mn		Zn	
	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature
Other material										
Jun/2011	28.8+1.6	34.8+2.6	30.3+3.8**	37.2+2.9	1609.3+158.9	1861.7+331.3	870.3+164.1	603.5+52.2	95.0+3.6**	131.3+11.7
Jun/2012	17.9+2.2	16.5+1.9	21.7+1.1**	28.2+0.7	1290.8+146.3	1505.3+35.1	1499.2+154.5	1097.8+156.6	103.0+11.4	133.3+8.8
Bamboo material										
Jun/2011	34.3+6.1	29.9+0.1	25.2+1.2***	32.0±0.1	980.5+43.0	1388.0+0.1	893.8±21.25	860±0.1	86.5+15.0	133.5±0.1
Jun/2012	18.1+0.1	20.1+0.1	22.0+1.5	37.5±0.1	1773.2+324.2	2397.5+0.1	1658.8±285.2	2035.0±0.1	89.8+13.2	140.5±0.1
Unidentifiable										
Jun/2011	21.6+1.8	25.8+2.8	39.2+5.1*	63.5+4.1	2652.2+580.6	3395.2+81.1	823.0+75.1	565.0+62.5	97.7+8.7	147.3+19.2
Jun/2012	12.4+1.1	15.6+2.5	31.2+1.9**	48.8+1.7	2984.2+49.6**	3499.3+72.9	1563.2+104.6	1402.7+111.8	97.2+14.7*	154.2+10.48
Total										
Jun/2011	27.6+0.7	31.7+2.4	33.2+0.9*	48.7+5.2	1880.6+95.4	2498.6+318.2	801.4+26.0	615.4+44.5	94.6+1.3***	147.7+12.1
Sep/2011	26.1+2.5	32.6+3.1	28.7+3.5	39.5+6.0	2371.5+311.2	2593.9+305.3	1841.8+261.9	1717.8+178.0	103.5+24.1	168.4+18.6
Dec/2011	21.2+1.2	22.8+0.7	24.7+2.2	33.6+4.3	2278.5+255.5	2716.8+213.6	1700.8+108.6	1480.1+277.9	110.1+2.4	147.8+11.6
Mar/2012	17.2+0.7	19.2+0.7	25.0+3.8	39.2+5.3	2173.8+423.0	2563.2+434.2	1373.9+182.1	1303.8+175.1	100.6+7.5	180.2+21.5
Jun/2012	16.1+1.2	17.4+0.2	25.8+1.7	40.0+0.1	2122.8+270.6	2569.4+5.3	1483.9+108.9	1325.1+ 8.1	100.2+6.6**	154.6+0.8

*, **, and *** on the line indicate significance level at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively, for comparison between sites within the same period (T-test).

Table 3. Average amount of macronutrients in the "total" litter and its fractions ± standard error (kg ha^{-1}), in June 2011 and June 2012 in two areas in the Fontes do Ipiranga State Park: the understory dominated by bamboo (bamboo) and the understory of mature forest (mature).

Month/ year	N		P		K		Ca		Mg		S	
	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature
Other material												
Jun/2011	100.2±9.8*	170.6±8.1	2.5±0.3	4.2±0.1	7.7±0.9	11.3±0.6	43.5±2.2	84.0±12.0	5.9±0.7	7.8±0.5	5.9±0.7*	11.3±0.6
Jun/2012	13.8±1.0*	24.1±1.2	0.3±0.0*	0.6±0.0	1.0±0.3	1.2±0.0	8.0±1.7*	17.0±1.1	0.7±0.1	0.9±0.0	0.8±0.0*	1.6±0.1
Bamboo material												
Jun/2011	3.0±0.8	3.2±0.0	0.0±0.0	0.0±0.0	0.2±0.0	0.1±0.0	0.6±0.0	0.9±0.0	0.0±0.0	0.1±0.0	0.1±0.0	0.2±0.0
Jun/2012	0.7±0.0	0.5±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.0	0.1±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Unidentifiable												
Jun/2011	3.5±1.1	5.5±0.3	0.1±0.0	0.1±0.0	0.2±0.0	0.3±0.0	0.7±0.2	1.4±0.1	0.1±0.0	0.1±0.0	0.2±0.0	0.5±0.0
Jun/2012	34.2±2.5**	69.4±3.3	1.0±0.0 ***	2.0±0.0	1.9±0.0	3.1±0.2	6.5±0.9**	18.3±0.9	0.8±0.0*	1.5±0.0	3.0±0.0	6.6±0.3
Total												
Jun/2011	36.7±16.1	67.7±31.7	0.9±0.4	1.6±0.7	2.9±1.2	4.5±2.1	15.1±7.1	32.3±17.2	2.1±0.9	3.0±1.5	2.2±0.9	4.5±2.0
Sep/2011	22.8±17.8	44.1±36.6	0.7±0.5	1.1±0.9	2.0±1.2	3.0±1.8	8.3±7.2	21.0±19.1	1.3±1.0	2.2±1.6	1.7±1.4	3.4±2.4
Dec/2011	19.8±9.2	42.7±22.2	0.6±0.2	1.1±0.5	1.7±0.7	2.8±1.2	7.4±4.6	17.8±10.6	0.9±0.4	2.0±1.0	0.7±0.3	3.3±1.5
Mar/2012	13.0±4.4	37.3±9.9	0.4±0.1	1.1±0.2	1.3±0.4	2.7±0.3	4.4±2.0	16.3±5.4	0.7±0.2	1.5±0.0	0.4±0.1***	2.9±0.1
Jun/2012	17.0±4.8	37.0±10.0	0.5±0.1	1.1±0.2	1.1±0.2	1.9±0.4	5.0±1.3**	13.8±2.7	0.5±0.1*	1.0±0.1	1.4±0.4	3.5±0.9

*, **, and *** on the line indicate significance level at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively, for comparison between sites within the same period (T-test).

the Box-Cox method to allow the data's normal distribution and homoscedasticity in adjusting a linear regression model.

Aimed at determining if the nutrient concentrations differed between the areas in each collection, the T-test was performed after log transformation of data, and the non-parametric equivalent Mann-Whitney test for those that even transformed did not present normal distribution. The analysis was performed in the SigmaPlot 11.0 and Past 4.04 software (Hammer *et al.*, 2001).

Results

Accumulated litter and decomposition

The litter accumulated at the beginning of the study (T_0) was significantly higher in the mature area (9451 ± 324 kg ha^{-1}) than the bamboo area (5964 ± 117 kg ha^{-1}, T28 = 3.574, p = 0.0007). The initial stock of the "bamboo material" fraction did not differ between the areas (Man-Whitney test, U28 = 342, p = 0.3054). In "bamboo", the "bamboo material" fraction, mostly *A. aristulata*, represented an annual average of 131 kg ha^{-1} of accumulated litter, presenting relatively stable stocks until the sixth month and rapid decline after that (Fig. 5). Unlike the other fractions, the "unidentifiable" fraction presented increasing stocks during the year for the two areas, with a greater amount of accumulated litter for the last estimate. It artificially increased since it is more difficult to identify the parts as time progresses. The decomposition rates of total fractions (k = 1.79 in bamboo site and k = 1.81 in mature site) did not differ significantly between areas ($t_{>120}$ = 0.228, p = 0.819). The highest rates and decomposition constants k occurred from the sixth month (December 2011) of the experiment for the "total" litter and its fractions. The "bamboo material" fraction had higher decomposition rate in the bamboo area ($F_{4.144}$ = 13.62, p = 0.0003).

Concentration of nutrients in the accumulated litter

Except for K and Mn, the concentration of macro and micronutrients was equal to or greater in the mature area (Tables 1 & 2). Among the 26 significant differences in concentration, 25 were for higher concentrations in fractions collected in the mature forest.

Quantity of nutrients in the accumulated litter

The quantities of Ca, Mg, S, B, Cu, and Zn in the litter were significantly higher in the "mature" area, while quantities of P, K, Mg, Fe, and Mn were similar in both areas (Tables 3 & 4). At the end of the study, the "other material" fraction contained significantly higher amounts of N, P, Ca, S, B, Cu, Fe, and Zn in the "mature" area, and the "unidentifiable" fraction in the "mature" area had higher amounts for N, P, Ca, Mg, B, Cu, Fe, Mn, and Zn. All the nutrient amounts increased in the final period in both areas. The "bamboo material" fraction showed no significant difference (Tables 3 & 4) between the areas for any nutrient, indicating similar nutrient release from this fraction in both areas.

The highest transfer of macro and micronutrients to the soil occurred in the "mature" area. The "other material" fraction contributed the most to the transfer process, and N was the most abundant nutrient participating in the total nutrients with more than 50% in each area.

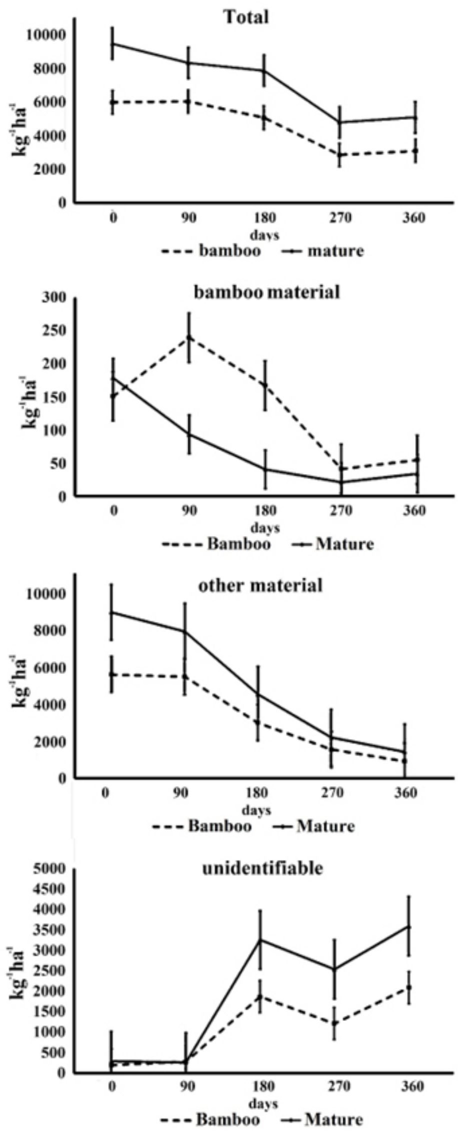

Figure 5. Average litter mass (+ SD) and its fractions throughout the year.

Discussion

Stocks and decomposition rate

The higher mass of leaf litter on the ground of old-growth forest area may be related to the higher production of litter in this location, greater closure of the canopy ("mature" 92% and "bamboo" 88%) (Vinha *et al.*, 2011), the greater richness of plant species and density of individuals (Kondrat *et al.*, 2020), and a late secondary successional stage with no longer disturbance history (Shirasuna & Filgueiras, 2013). In contrast, the smaller stocks in the forest understory covered by bamboo may be due to recent or recurrent disturbance, under which *A. aristulata* established and expanded in the understory with its consequences on the forest structure (Taylor *et al.*, 1991; Campanello *et al.*, 2007; Zaninovich *et al.*, 2017).

The total litter accumulated at the beginning of the study (9451 ± 324 kg ha^{-1} in the mature area and 5964 ± 117 kg ha^{-1} in the bamboo area) was higher than the other two sites of the same forest type (mature Atlantic Rain Forest), although under greater annual rainfall. The first site is in Cubatão, a municipality with 4088 kg ha^{-1} (Lopes *et al.*, 2009), and the other in the municipality of Santo André with 6615 kg ha^{-1} (Domingos *et al.*, 2000).

The average annual stock of the fraction "bamboo material" ("bamboo" 131 kg ha^{-1} and "mature" 74 kg ha^{-1}) was lower than those obtained in the bamboo savannas, which vary from 4100 to 7200 kg ha^{-1} (Tripathi & Singh, 1994). On the other hand, the annual percent decomposition in "bamboo" (61%) and "mature" (83%) areas was higher than those found in temperate forests in Japan (Watanabe *et al.*, 2013), in which, after one year, 35% of leaf decomposition and 31% of stem decomposition were recorded and similar to those in Northeast India (Nath & Das, 2011), where the decomposition constant *k* was higher than 1. A possible explanation for such large differences may be the very nature of bamboos in this study. As exposed above (see Introduction), *A. aristulata* is a small understory bamboo. In general, ground bamboo litter stock (GBLS) is included with standing dead parts (Kiyono *et al.*, 2007; Yuen *et al.,* 2017), and separate estimates for GBLS are rare.

The increasing stocks of the "unidentifiable" fraction (material that became unidentifiable after fragmentation) represented continuous decomposition of the other fractions since all the litter fractions that decomposed throughout the year are part of it, thus increasing the decomposing material and reducing the amount of other fractions' identifiable material. The most abundant bamboo species in the mature area was *M. pluriflora* rather than *A. aristulata*. It may also explain the higher decomposition rate of the "bamboo material" fraction in the mature area (81%) than the other (63%) as *A. aristulata* is slightly more lignified (Grombone-Guaratini *et al.*, 2011).

Similarly to this study, in which the greatest mass losses occurred in the months with higher precipitation (December/2011 to March/2012), Austin (2002) found that

Table 4. Average amount of micronutrients in the "total" litter and its fractions ± standard error (kg ha^{-1}), in June 2011 and June 2012 in two areas in the Fontes do Ipiranga State Park: the understory dominated by bamboo (bamboo) and the understory of mature forest (mature).

Month/ year	B		Cu		Fe		Mn		Zn	
	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature	Bamboo	Mature
Other material										
Jun/2011	0.1±0.0**	0.3±0.0	0.1±0.0	0.3±0.0	9.2±1.6	16.3±1.1	4.9±1.0	5.5±0.5	0.5±0.0**	1.1±0.0
Jun/2012	0.0±0.0*	0.1±0.0	0.0±0.0**	0.1±0.0	1.2±0.1*	2.1±0.1	1.3±0.1	1.5±0.1	0.1±0.0**	0.1±0.0
Bamboo material										
Jun/2011	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.0	0.2±0.0	0.1±0.0	0.1±0.0	0.0±0.0	0.0±0.0
Jun/2012	0.0±0.0	0.00±0.0	0.0±0.0	0.0±0.0	0.1±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
Unidentifiable										
Jun/2011	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.4±0.1	0.9±0.0	0.1±0.0	0.1±0.0	0.0±0.0	0.0±0.0
Jun/2012	0.03±0.0*	0.0±0.0	0.0±0.0**	0.1±0.0	6.1±0.3**	12.5±0.4	3.2±0.2*	5.0±0.1	0.2±0.0**	0.5±0.0
Total										
Jun/2011	0.0±0.0	0.1±0.0	0.0±0.0	0.1±0.0	3.4±1.5	6.6±3.0	1.7±0.8	2.1±1.0	0.2±0.1	0.4±0.2
Sep/2011	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	3.3±2.5	5.1±3.9	2.6±2.1	3.6±3.0	0.1±0.1	0.3±0.2
Dec/2011	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	2.8±1.2	5.7±2.7	2.1±1.0	3.1±1.6	0.1±0.0	0.3±0.1
Mar/2012	0.0±0.0*	0.1±0.0	0.0±0.0*	0.1±0.0	2.1±0.7	5.2±1.5	1.3±0.5	2.7±0.7	0.1±0.0**	0.3±0.0
Jun/2012	0.0±0.0*	0.1±0.0	0.0±0.0	0.1±0.0	2.6±0.9	5.9±1.9	1.6±0.4	2.6±0.7	0.1±0.0*	0.3±0.0

*, **, and *** on the line indicate significance level at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively, for comparison between sites within the same period (T-test).

the litter decomposition in Hawaiian forests increased linearly along a natural rainfall gradient ranging from 500 to 5500 mm average annual precipitation. The high weight loss between 6 and 9 months can be explained by the loss of low molecular weight molecules, such as amino acids, that are easily degraded or leached in the first phases of decomposition (Stout *et al.*, 1988), while the lower rates of decomposition from 9 months onwards can be explained by the increased contents of more recalcitrant cellular structures (Berg & McClaugherty, 2013; Gioacchini *et al.*, 2015).

The k values are among the values cited for tropical forests, from 1.1 to 3.8, while in temperate forests, this coefficient is between 0.4 and 1.4 (Zhang *et al.,* 2008; Waring, 2012). Similar decomposition rates in both areas and in the litter renewal time may be associated with the fact that they are under the same climatic regime (Aerts, 1997), and that over the years of regeneration, there may have been a change in the decomposition rate through the combination of microclimate factors and the activities of decomposers in the degraded site converging to the decomposition rate that occurs in the most preserved patch (Vendrami *et al.*, 2012). However, this comparison is only indicative since most of the k values of the meta-analyses cited were calculated from homogeneous material in litterbags, usually leaves, and not from material on the ground as in this study. In addition, the decomposition rate was negatively correlated with study length (Vendrami *et al.*, 2012).

Nutrient concentrations

Our results clearly show the higher concentration of nutrients in the litter of the old-growth forest area and the immobilization of some nutrients in both areas. The higher concentrations of nutrients in the mature site are because it is a more mature area, with higher species richness, higher density of individuals (Kondrat *et al.*, 2020), and in a late secondary successional stage without a history of disturbance for more than six decades (Shirasuna & Filgueiras, 2013). Different macro-nutrient contents in the litter may be correlated with the mobility of the elements in the plant (Berg & McClaugherty, 2013). For example, the great variability of potassium in the litter shows a relationship between the nutrient and the variation in rainfall due to its high leaching capacity by washing the leaves of the litter (Campo *et al.*, 2000) and by not being part of organic compounds occurring in soluble form (Marschner, 1997). It can be observed by the variation of potassium concentrations in the "total" fractions during the year and in the low concentrations in the last month (June 2012) in the "unidentifiable" and "other material" fractions. Calcium and magnesium, even being moderately washable (Caldeira *et al.*, 2019), presented smaller variations in the contents, a fact observed in the immobilization of Ca in the two sites for "other material" and immobilization of Ca and Mg only in the "mature" for the "unidentifiable" and "total". The tendency to immobilize Ca observed in the fractions "other material" in the two areas and "unidentifiable" and "total" is due to this being a structural component of plant tissue cells, thus tending to be one of the last to be released into the soil by the decomposition of the litter (Tian *et al.*, 1992).

The small variation in the concentration and amount of P throughout the year in all litter fractions was expected because the nutrient is highly recalcitrant and has little mobility in the systems (Townsend *et al.*, 2002). The highest levels of S can be observed in the colder months (Xiao *et al.*, 2014), a fact also observed in this study in all the accumulated litter fractions, where the S concentration increased in the final period (June 2012, winter in Southern Hemisphere). Their low mobility can explain the higher concentration of Fe and Zn. Iron mobility can also be reduced by increases in P and Mn, K deficiency (Loué, 1993), or by contamination with the soil when collecting litter.

Quantity of nutrients in the accumulated litter

The low nutrient transfer through bamboo can be explained by the high mechanical resistance of bamboo fibers formed by lignin and cellulose that resist impacts, traction, and decomposing microorganisms. In addition, external coating with silica and wax provides a protective layer for internal moisture retention and its structure (Liese, 1980). On the other hand, decomposition rates suggest that this may not be the case since *A. aristulata* does not present such marked lignification, especially regarding most Asian species (Soderstrom & Ellis, 1988). The nutrient contents presented by the "bamboo material" fraction agree with the results of a study conducted on a degraded mixed alluvial forest remnant (Galvão *et al.*, 2012), where it was found that local vegetation was suppressed by the Paraguayan bamboo species *Guadua* and there was a decrease in the transfer of nutrients and organic carbon by the leaves and canes from bamboo to the soil.

Other researchers reported the following stocks of nutrients in the litter: N, 18–296 kg ha^{-1}; P, 1–13 kg ha^{-1}; K, 4–61 kg ha^{-1}; Ca, 16–237 kg ha^{-1}; Mg, 3–25 kg ha^{-1}; and S, 7–29 kg ha^{-1} (Domingos *et al.*, 2000; Dickow *et al.*, 2012; Hayashi *et al.*, 2012), which, except for N, are all higher than those obtained in this study. However, nutrient stocks in the accumulated litter of natural tropical forests range from (kg ha^{-1}) 7 to 96 of N, 0.2 to 5 of P, 1 to 16 of K, 4 to 270 of Ca, and 0.7 to 14 of Mg (O'Connell & Sankaran, 1997), which are within the range for the macronutrient quantities obtained in the litter fractions accumulated in this study.

The high initial amount of nitrogen and its low release indicating its immobilization at the end of this study at both sites in the total litter and its fractions is because of this nutrient's importance in directing the decomposition by microorganisms and in its ability to bind the lignin and remain in the litter until the end of the process (Berg & McClaugherty, 2013; Fukuzawa *et al.*, 2015). Except for the "bamboo material" fraction, the higher amounts of nutrients in the total litter and its fractions in the "mature" litter showed higher nutritional conditions in the "mature" litter and higher nutrient transfer to the soil of this area.

Conclusions

Unlike in many areas with vegetation cover dominated by bamboos, the accumulated litter stock was not higher than in the undisturbed nearest area. There was no difference in the decomposition rate between the sites. In general, the concentration of macro and micronutrients and their total quantities were lower in the bamboo area. A potential limitation of our study is that it was restricted to comparing two areas. However, it shows a situation in which the bamboo-dominated understory differs from those normally found, and the results obtained here can be used to explore the issues further. Less lignified understory bamboos can play a very different role in the rate and return of nutrients than no shade-tolerant and/or more lignified bamboo species.

Authors' contributions

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