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Effects of forest structure on litter production, soil chemical composition and litter–soil interactions

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ABSTRACT

Litter production in forest ecosystems is a major indicator of primary productivity because litter helps incorporate carbon and nutrients from plants into the soil and is directly involved in plant–soil interactions. To our knowledge, few studies have investigated the relationship between species diversity and ecosystem processes in subtropical forest fragments. In this work, we determined forest structural parameters and assessed seasonal leaf litter input, leaf decomposition rate, litter quality and soil characteristics in two subtropical Atlantic Forest fragments. Litter production was greater in the native fragment with the higher species diversity (FN1). The two native fragments (FN1 and FN2) differed in basal area, volume and dominance in the upper stratum, which were positively correlated with litter production in FN1 but negatively correlated in FN2. Soil in FN1 exhibited higher contents of organic C, available phosphorus and exchangeable calcium, and the leaf litter had a higher C:N ratio. Although these results are consistent with a plant–soil feedback, which suggests the presence of a complementary effect, the dominance of certain families in subtropical forest fragments results in a selection effect on litter productivity and decomposition.

Keywords: biodiversity, carbon, decomposition, phosphorus, selection effect

Introduction

Productivity in terrestrial ecosystems is directly linked to nutrient cycling among the various components of the plant–soil system (Vitousek 1984; Terror *et al*. 2011). In forest ecosystems, primary production is usually evaluated through litter production because litter is the main source of soil organic C and plant nutrient cycling (Vitousek 1982); in addition, it can also usually be evaluated from tree diameter and height measurements, using an allometric equation (Chambers *et al*. 2001). The close relationship between forest structure, climate and soil makes this system an ideal model for evaluating the relationship between litter production and decomposition, nutrient cycling and abiotic factors (Aerts & Chapin 2000).

Litter decomposition results in the incorporation of organic C into soil and in the cycling of plant nutrients, which provide readily available resources for plant growth (Austin & Vivanco 2006; Cheng *et al*. 2010). In addition, the release of secondary metabolites by plants may affect ecological interactions and the soil microbial community (Niro *et al*. 2016; Schuman *et al*. 2016). The decomposition rate of litter varies with the quality of the substrate, and also with the amount and activity of decomposers (Xiaogai *et al*. 2013), which are closely associated (Wardle *et al*. 2006). Litter decomposition can also influence soil properties and

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alter the stability of soil organic C and cation exchange processes in plant–soil interactions (Sausen *et al*. 2014).

Forest decomposition systems have been the focus of several studies in recent years (Pimenta *et al*. 2011; Terror *et al*. 2011; Wang *et al*. 2013; Sausen *et al*. 2014). However, the influence of species richness and litter composition on nutrient cycling remains a topic of hot debate (Szanser *et al*. 2011). The biochemical quality of litter is crucial for proper ecosystem functioning (Hättenschwiler *et al*. 2011); in fact, the higher tree species richness is, the greater is the diversity of the microbial communities involved in decomposition processes (Wardle *et al*. 2006; Manzoni *et al*. 2012; Prescott & Grayston 2013).

Most studies on nutrient cycling and litter decomposition have focused on only one or two species of trees in the dominant vegetation structure (Jacob *et al*. 2010). However, this commonly used model does not reflect the decomposition dynamics in native forest ecosystems, where tree diversity is usually very high (Fuqiang *et al*. 2010; Xiaogai *et al*. 2013). Several studies using bags of mixed litter from species constituting the forest stratum suggest that litter in forests with a high tree diversity decompose rapidly, especially when nutrient concentrations differ between species (Quested *et al*. 2002; Wickings *et al*. 2012; Ge *et al*. 2013; Xiong *et al*. 2014).

Although structure in subtropical forest fragments has been the subject of several studies (Budke *et al*. 2010; Müller *et al*. 2012; Mélo *et al*. 2013), few have examined the relationship between the structural characteristics of vegetation (particularly species diversity) and ecosystem functioning processes. Litter production provides important information on ecosystem functioning; in fact, it relates nutrient cycling, decomposition dynamics and soil organic carbon incorporation according to species diversity and structural parameters of vegetation to tree size and abundance in a forest community (Hack *et al*. 2005; Gilliam 2007; Aragão *et al*. 2009).

The primary purposes of this work were (1) to relate the structural characteristics of vegetation with litter production, and (2) to examine the dynamics of litter decomposition and litter–soil interactions, in two Atlantic Forest fragments in southern Brazil. The working hypotheses were that forest fragments with an increased species diversity will have also increased basal area and volume leading to differences between lower and upper strata, and that such differences are associated with increased litter production and with soil and litter chemical composition.

Materials and methods

Study areas

Two subtropical Atlantic Forest fragments were studied. Both are bordered by 3rd order streams and located in southern Brazil. One of the native fragments (FN1) is located at 27º28'39''S 52º31'45''W and 27º39'40''S 52º20'24''W, and the other (FN2) at 27º30'21''S 52º11'10''W and 27º40'43''S 52º02'15''W. The study was conducted over a period of 12 months, and measurements made on a monthly basis from January to December 2013. The mean rainfall for the period was 175 mm (range 90–316 mm) and the mean monthly temperatures ranged from 13 to 22 °C.

The target forest fragments were representative of the typical Atlantic Forest vegetation, where the native forest is highly fragmented and degraded, and the sites with the greatest cover are located where steep slope factors such as ground, shallow soils and the presence of rocky outcrops make soil difficult or impossible to use for agricultural purposes (Decian *et al*. 2009). A total of 20 plots 10 × 10 m in size were established in each fragment, with 10 units on each side of the stream, totalling a sample area of 0.2 ha.

Litter production

Litter produced in the two study areas was collected monthly by using 1 m long × 1 m wide × 0.15 m deep wood collectors furnished with a fine nylon mesh screen 1 mm thick. A total of 10 collectors were randomly distributed in each of the study areas (five on each side of the streams). Samples were collected on a monthly basis from January to December 2013 and transferred to the Plant Ecology and Systematics Laboratory of the Universidade Regional Integrada do Alto Uruguai e das Missões for drying to a constant weight in an oven at 60 °C and weighing. Seasonal litter productivity for the winter, spring, summer and autumn seasons was calculated from the combined monthly masses, and seasonal means were expressed in t ha^{-1}.

Vegetation structure

Vegetation structure was characterized in a phytosociological survey of the lower and upper strata in 10 sampling units in the target areas. All species were identified *in loco*. Plants less than 0.3 m high and having a diameter at breast height (DBH) not greater than 15 cm were assigned to the lower stratum, whereas those with DBH > 0.15 m were assigned to the upper stratum. The phytosociological parameters for the two strata were estimated by using the software Fitopac 2 (Shepherd 2010) to calculate basal area, absolute dominance and volume for each species in two forest fragments.

Litter decomposition

Decomposition rate was evaluated in the leaf fraction (viz., the main component of litter), using the mixed litter bag method (Berg *et al*. 1993; Xiong *et al*. 2014). Bags were prepared according to the following criteria: (i) species from the most abundant families in the study areas; (ii) the most abundant species from each family in each forest fragment;

and (iii) leaf size for bag incubation for 12 months. The most abundant families in the study areas were Myrtaceae, Lauraceae, Sapindaceae and Euphorbiaceae. Detailed information about the species survey is provided as Table S01 in Supplementary Material.

The species meeting the selection criteria were *Nectandra megapotamica* (Spreng.) Mez. (Lauraceae), *Cupania vernalis* Cambess. (Sapindaceae), *Allophylus puberulus* (Cambess.) Radlk. (Sapindaceae), *Sebastiania brasiliensis* Spreng. (Euphorbiaceae) and *Myrcianthes pungens* (O.Berg) D. Legrand (Myrtaceae) in FN1; *N. megapotamica*, *C. vernalis*, *A. puberulus*, *S. brasiliensis* and *Campomanesia xanthocarpa* O.Berg (Myrtaceae) in FN2. All were evergreen species.

An amount of approximately 2.5 ± 0.1 g dry matter (60ºC, 24 h) of senescent leaves was weighed and placed in a nylon mesh bag (mesh 10 mm, size 10 × 10 cm). A total of 25 litter bags were placed on the soil surface near the litter collectors in each forest fragment. Five litter bags in each fragment were placed on the soil surface and collected after 1, 2, 4, 6 and 12 months. Leaf decomposition rate was expressed as the percent of leaf mass remaining in the bags after each time.

The decomposition rate was calculated as $M_t = M_0e^{-kt}$ (Olson 1963), where M_t denotes leaf mass at time t, M_0 the initial mass and k the decomposition rate. The rate was used to estimate the mean time needed for the leaf litter fraction to decompose, in days.

Chemical composition of the soil and quality of the leaf litter

Individual soil samples for analysis were collected by using a cutting blade in a 0.5 × 0.5 m area from the 0–10 cm layer at six different locations in each fragment and combined to obtain composite samples. Each composite sample was split into three subsamples for analysis for organic C by dry combustion on Shimadzu (VCSH TOC instrument), macronutrients (N, P, K, Ca, Mg and S) and micronutrients (Cu, Zn, Fe, Mn and B) in the leaf litter fraction each season. The samples were dried at 60 °C for 24 h and ground in a porcelain mortar, a 10 g subsample being stored for chemical analysis. For soil and leaf litter nutrient analyses, 10 g of each sample was sent to the Soil Analysis Laboratory of the Federal University of Rio Grande do Sul School of Agronomy. Leaf litter nutrients were quantified according to Tedesco *et al.* (1995) and expressed in g kg^{-1} or mg kg^{-1}.

Data analysis

Seasonal litter productivity was assessed via a two-way analysis of variance (two-way ANOVA) for comparison of mean total productivity between seasons and study areas. A two-way ANOVA was also used to evaluate differences in seasonal leaf litter productivity between areas and seasons. All data were subjected to logarithmic transformation to reduce the homoscedasticity of the data.

Seasonal litter productivity was related to species richness in the upper and lower tree strata via Pearson's correlation coefficient, and so were structural parameters (absolute dominance, basal area and volume) in the two strata to total litter productivity. Correlation was assumed when $r \geq 0.30$. Differences in parameters between the structured areas for each stratum (upper and lower) were assessed via a *t*-test. Differences in decomposition dynamics between the study areas were also evaluated via a *t*-test, with $p \leq 0.05$ being considered significant.

Differences in soil characteristics between the study areas were evaluated via a *t*-test for each soil component (organic C, macronutrients and micronutrients). Differences in macro- and micronutrients contents, and in C:N ratio, between areas and seasons were assessed by two-way ANOVA, and those in leaf litter nutrients via a *t*-test. All analyses were performed in the statistical environment R (R Core Team 2013).

Results

Seasonal litter production

Total and leaf litter production changed seasonally in both forest fragments ($p \leq 0.0001$ in FN1 and $p = 0.005$ in FN2), with differences in autumn and spring (Fig. 1A-B). Litter production was greatest in spring in both fragments, and greater in FN1 than in FN2.

Relationship between vegetation structure and litter production

In the upper stratum, FN1 exhibited an increased higher basal area ($p = 0.004$), volume ($p = 0.04$) and dominance $p = 0.004$) relative to FN2. This was also the case with basal area ($p = 0.02$) and absolute dominance ($p = 0.02$) in the lower stratum, but not with volume, which was similar in the two areas ($p = 0.13$).

Relating litter production to structural parameters revealed a positive correlation between dominance, basal area and volume in the upper stratum in FN1 ($r > 0.4$, Tab. 1), and also a negative correlation between dominance, basal area and volume in the same stratum in FN2 ($r = 0.3$, Tab. 1). On the other hand, the structural characteristics of the lower stratum in FN1 and FN2 were uncorrelated with litter production.

Litter decomposition

The study areas exhibited no difference in final mass loss (percent weight lost at $t = 12$ months) or decomposition

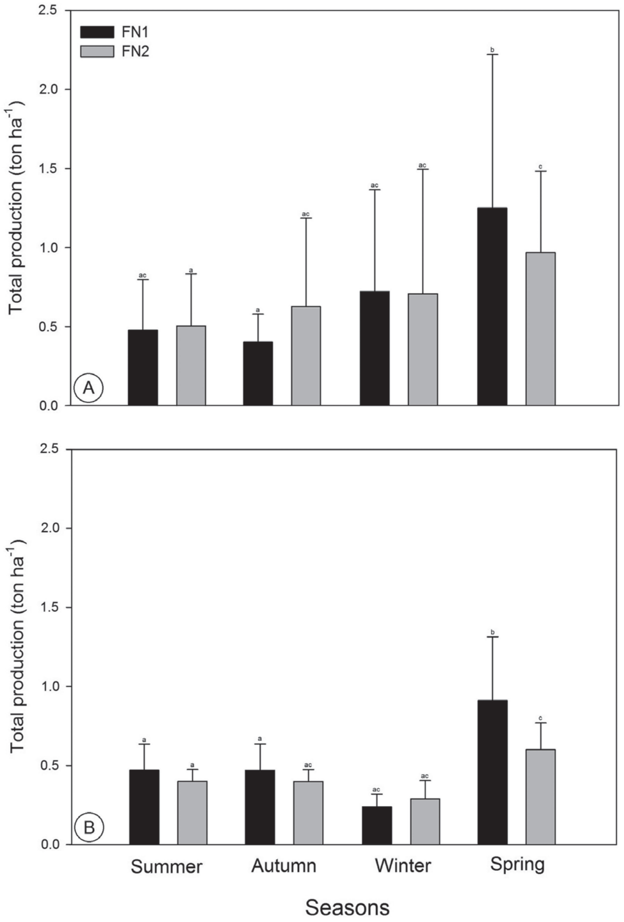

Figure 1. A) Seasonal production of total litter and B) leaf litter in the two forest fragments. Different letters indicate differences between study areas and seasons. (*n* = 8–10).

Table 1. Relationship of litter production with absolute dominance (ADo), basal area (BA) and volume (vol.) in the lower and upper stratum of the two forest fragments (FN1 and FN2).

Fragment	Stratum	ADo (m^2 ha)	BA (m^2 ha^{-1})	Vol. (m^3)
FN1	Lower	0.05	0.03	0.01
	Upper	0.48*	0.48*	0.49*
FN2	Lower	-0.08	-0.05	-0.02
	Upper	-0.30	-0.30	-0.30

The values in the table are Pearson's correlation coefficients (*r*).
* Significant correlation ($r \geq 0.30$).

rate of the leaf litter fraction ($p = 0.47$). The reduction in leaf litter mass after 12 months (365 days) of incubation in litter bags was 74.8% in FN1 and 73.9% in FN2. The decay constant was 1.27 ± 0.55 (mean ± standard error) in FN1 and 1.05 ± 0.63 in FN2; therefore, total decomposition of litter would require a long time in both areas (463 days in FN1 and 383 days in FN2). The weight loss in FN1 was greatest within the first month (22.7%) and from the tenth to the twelfth (12.5%); and that in FN2 maximal within the first month (27.7%) and from the fourth to the sixth (19.4%) (Fig. 2).

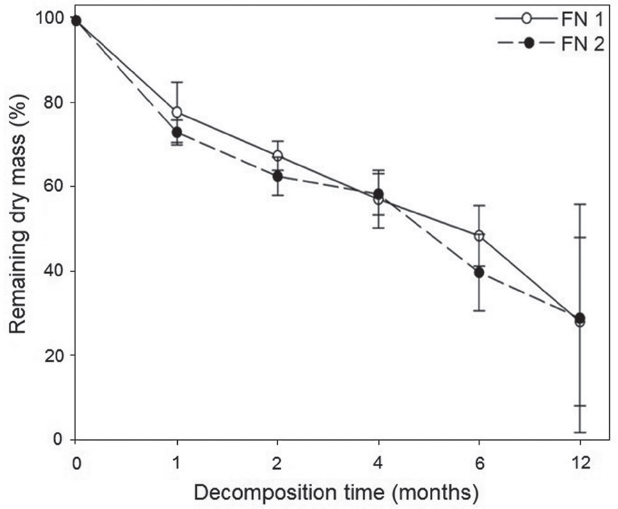

Figure 2. Leaf decomposition rate, expressed as the percent reduction in mass over the course of 12 months in the two forest fragments. Bars represent mean standard deviations (*n* = 5).

Soil chemical composition and leaf litter C:N ratio

As can be seen from Table 2, the chemical composition of the soil in the two areas differed except in the contents in potassium, magnesium and zinc, and in potential acidity (H+Al). The organic carbon, phosphorus and calcium concentration contents were significantly higher in FN1 than in FN2 ($p = 0.0001$). The contents in the micronutrients manganese and sodium differed between the two areas, and were higher in FN1. Finally, the C:N ratio differed between seasons and areas (Tab. 3), and was higher in FN1 throughout the year.

The chemical analyses of plant tissue revealed differences in nitrogen, phosphorus and iron contents of the leaf litter between the study areas in the summer, autumn and spring seasons. The contents in potassium and copper of leaf litter differed in summer, winter and spring; those in manganese and sulphur in summer and autumn; and that in zinc in all seasons except spring (see Tab. S02 in Supplementary Material). There were no differences in potassium, calcium, copper, manganese or boron between the study areas in autumn.

Discussion

The biodiversity influences ecosystem functioning via two different mechanisms (Ruiz-Benito *et al*. 2014). One, known as the "complementary effect", is associated with the partitioning and facilitation of niches where species diversity increases efficiency in resource use and nutrient retention. The other, known as the "selection effect", increases the probability of the more productive species to become the dominant species in a plant community. The influence of some species on ecosystem functioning has indeed been

Table 2. Contents in soil organic C, macronutrients and micronutrients in the two forest fragments ($n = 6$).

Fragment	P	K	Ca	Mg	S	Zn	Cu	B	Mn	OC
	mg dm^{-3}									g dm^{-3}
FN1	6.7 ± 1.8a	242.3 ± 53a	16.2 ± 17a	5.9 ± 0.5a	19.0 ± 1.2a	13.1 ± 2.5a	1.3 ± 0.2a	1.2 ± 0.08a	53.0 ± 7.6a	64.1 ± 8.2a
FN2	4.0 ± 0.6b	282.5 ± 36a	10.2 ± 1.1b	3.1 ± 0.3a	14.3 ± 1.2b	14.6 ± 0.8a	5.1 ± 0.5b	0.9 ± 0.05b	73.5 ± 3b	34.2 ± 2.2b

Different letters indicate significant differences in nutrient concentration between fragments as determined via a *t*-test

Table 3. *F*- and *P*-values obtained in two-way ANOVAs used to identify differences in C: N ratio of leaf litter between forest fragments (FN1 and FN2) and seasons.

	Df	Sum of squares	Mean Square	F	P
Forest fragments	3	72 634	24211	1135.02	2.00 10^{-16}
Seasons	3	717	239	11.21	1.45 10^{-6}
Interaction	8	2601	325	15.24	1.88 10^{-15}
Residuals	125	2666	21		

observed in several studies (Gaston 2010; Cardinale *et al.* 2012; Cadotte *et al.* 2013) where the losses in some species were offset by other species in the same functional group (Joner *et al.* 2011).

Based on our results, the studied forest fragments differ structurally and the differences are related to litter production, which affects the two fragments in opposite ways. Litter production in the two fragments exhibited seasonal variation (especially during spring). Pearse *et al.* (2014) point out that the phenological characteristics of the species are associated with the observed differences in litter production. Also, the strong presence of some species in our fragments was possibly related in a direct manner with the greater dominance and basal area of the tree strata, which were positively correlated with litter productivity in FN1. Thus, the structural pattern of the fragments was seemingly responsible for their differences in litter production in the absence of substantial differences in species composition between the two.

The relationship between forest structure and litter productivity in spring may also be associated with the presence or dominance of certain species through a selection effect (Ruiz-Benito *et al.* 2014). In fact, the presence of dominant species may have been responsible for most leaf fall in spring. Also, the absence of differences in litter production in the other seasons may also have resulted from the dominance of some species. The analysis of forest structure and litter composition revealed a strong presence of certain species such as *N. megapotamica*, *Allophylus edulis*, *A. puberulus*, *Matayba eleagnoides* and *Styrax leprosus* in both fragments. These species exhibited marked leaf loss throughout the year and may have been the greatest contributors to the similarity in litter production between the two areas in the summer, autumn and winter seasons.

The marked differences in forest structure did not reflect in the litter decomposition dynamics. In fact, both forest fragments exhibited similar weight losses throughout. Thus, mass loss at the end of the 12-month period was approximately 75% in FN1 and FN2, and suggestive of rapid decomposition of the leaf litter fraction. Litter in forest fragments is known to decompose more rapidly under a subtropical climate than under a tropical climate, which suggests an effect of climate (Scheer 2008; Terror *et al.* 2011; Oliveira *et al.* 2013) through precipitation seasonality in subtropical regions. However, leaf decomposition in exotic species from the same region was previously found to be slower than in this study (Sausen *et al.* 2014; Vieira *et al.* 2014).

It should be borne in mind that we used mixed litter (Wickings *et al.* 2012) containing evergreen and secondary species in both study areas. In addition, the areas were located in the same region, so no major differences in abiotic conditions (precipitation) potentially influencing the litter decomposition dynamics existed. However, given their close relationship (Vitousek & Sanford 1986; Berg & McClaugherty 2008), litter production and decomposition in forest fragments with a strong presence of certain species [e.g., Atlantic Forest fragments in southern Brazil with families such as Fabaceae, Myrtaceae and Lauraceae, and the presence of *Araucaria angustifolia* (Oliveira-Filho *et al.* 2013)] may be subject to a selection effect.

The contents in macro- and micronutrients of soil, and the C:N ratio of leaf litter, differed between the study areas, and the latter also between seasons. These results indicate that litter production in FN1 was markedly seasonal, evidenced by the production during the spring, as suggested by the increased C:N ratio of leaf litter and nutrient contents of soil (particularly phosphorus, calcium and organic C). The other fragment, FN2, exhibited increased micronutrient contents in the soil. These results suggest that litter–soil interactions may be subject not only to a selection effect, but also to a complementary effect. The structural differences between the fragments may be related to differences in resource use efficiency and explain the plant–soil feedback observed. Thus, the increased contents in soil macronutrients (especially calcium and phosphorus) and also increased leaf litter C:N ratio in FN1 may be responsible for the increased soil organic carbon content observed.

We can therefore conclude that productivity and leaf litter decomposition were similar in the two study areas, with vegetation structure and seasonality influencing litter production. These ecosystem processes are subject to selection mechanisms, whereas soil nutrient and organic C contents, and leaf litter quality, are subject to complementary effects. Interestingly, both types of effect may operate in the functioning processes of the target ecosystem, where everything has a specific role.

Conclusions

The dominance of certain families in subtropical forest fragments results in a selection effect on litter productivity and decomposition. However, plant–soil feedback in such fragments is seemingly governed by soil contents in organic C, phosphorus and calcium, which suggests the presence of a complementary effect.

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