

Relative effect of litter quality, forest type and their interaction on leaf decomposition in south-east Brazilian forests

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Abstract: Decomposition was studied in a reciprocal litter transplant experiment to examine the effects of forest type, litter quality and their interaction on leaf decomposition in four tropical forests in south-east Brazil. Litterbags were used to measure decomposition of leaves of one tree species from each forest type: *Calophyllum brasiliense* from restinga forest; *Guapira opposita* from Atlantic forest; *Esenbeckia leiocarpa* from semi-deciduous forest; and *Copaifera langsdorffii* from cerrado. Decomposition rates in rain forests (Atlantic and restinga) were twice as fast as those in seasonal forests (semi-deciduous and cerrado), suggesting that intensity and distribution of precipitation are important predictors of decomposition rates at regional scales. Decomposition rates varied by species, in the following order: *E. leiocarpa* > *C. langsdorffii* > *G. opposita* > *C. brasiliense*. However, there was no correlation between decomposition rates and chemical litter quality parameters: C:N, C:P, lignin concentration and lignin:N. The interaction between forest type and litter quality was positive mainly because *C. langsdorffii* decomposed faster than expected in its native forest. This is a potential indication of a decomposer's adaptation to specific substrates in a tropical forest. These findings suggest that besides climate, interactions between decomposers and plants might play an essential role in decomposition processes and it must be better understood.

Key Words: Atlantic forest, cerrado, *Copaifera langsdorffii*, leaf decomposition, local adaptation, restinga forest, semi-deciduous forest, substrate quality, tropical forest

INTRODUCTION

Litter decomposition is an important component of nutrient cycling in terrestrial ecosystems (Aber & Melillo 1991). It makes nutrients available for growth of primary producers and it releases carbon dioxide to the atmosphere. Any change in the decomposition rate may thus change the nutrient availability, plant growth and carbon budget of ecosystems. Decomposition rates are influenced by environmental conditions, substrate quality and soil organisms (Berg & McClaugherty 2003, Swift *et al.* 1979, Vitousek *et al.* 1994).

Environmental conditions include both climate and soil characteristics. Climate has a direct effect on litter decomposition due to the effects of moisture and temperature on the metabolism of soil organisms (Austin 2002, Liski *et al.* 2003, Wieder & Wright 1995). In the tropics, temperature and moisture conditions are near the optimum for biological activity most of the time. However

some variation may be attributed to differences in length and intensity of the dry season (Lavelle *et al.* 1993). Microbial activities also depend on edaphic characteristics such as fertility (Vitousek & Sanford 1986), soil texture (Epstein *et al.* 2002) and pH (Chapin *et al.* 2002).

Litter quality defines how beneficial the litter is to the microbial community as a nutrient or energy source. Litter nutrient and carbon fractions (e.g. lignin) concentrations have been identified as indicators of litter quality due to their influence on microbial activity and consequently litter decay rates. Among nutrients, nitrogen concentration or C:N ratio and phosphorus concentration or C:P ratio are of critical importance (Aerts 1997, Tanner 1981, Taylor *et al.* 1989, Vitousek *et al.* 1994). Other studies have found limitation of decay rates by lignin concentration or initial ratios of lignin:nitrogen (Aerts 1997, Meentemeyer 1978, Melillo *et al.* 1982, Moore *et al.* 1999, Murphy *et al.* 1998, Vitousek *et al.* 1994). On the other hand, several studies have found no evidence for a strong correlation between litter quality indices and decomposition rates (McClaugherty *et al.* 1985, Moore 1984) showing that, despite the fact that

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Table 1. Study areas, their location and site characteristics. All sites are located in São Paulo State, Brazil. Soil classification is according to Soil Survey Staff (1999). Tree species richness is from 10-ha plots, where all trees with dbh \geq 4.8 cm were identified.

Forest type	Coordinates	Mean annual temperature ($^{\circ}$ C)	Mean annual precipitation (mm)	Dry season length (mo)	Elevation (m)	Soil	Tree species richness
Atlantic	24 $^{\circ}$ 00'S; 48 $^{\circ}$ 10'W	21	2800	0	480	Inceptisol	217
Restinga	25 $^{\circ}$ 03'S; 47 $^{\circ}$ 53'W	21	2100	0	5	Spodosol	117
Semi-deciduous	22 $^{\circ}$ 41'S; 49 $^{\circ}$ 16'W	21	1400	4	670	Ultisol	150
Cerradão	22 $^{\circ}$ 33'S; 50 $^{\circ}$ 22'W	21	1200	4	540	Oxisol	118

some patterns have been described, there is no universally accepted litter quality variable to predict decomposition rates.

In addition to the influence on microbial activity, litter quality affects the biomass and composition of microbiota and soil fauna (Elmer *et al.* 2004, Rantalainen *et al.* 2004, Scheu *et al.* 2003). There is some evidence that certain plant species may select the soil biota that facilitate decomposition of their own residues (Cookson *et al.* 1998, Elliott *et al.* 1993, Gholz *et al.* 2000, Hansen 1999, Hunt *et al.* 1988, McLaugherty *et al.* 1985). However, this interaction between original ecosystem (site) and litter type has never been reported in tropical forests.

In this study we examined the effects of the environment (forest type), litter quality (plant species) and their interaction on leaf decomposition rates. We hypothesized that: (1) the effect of forest type will be related to the amount (mean annual precipitation) and distribution (length of dry season) of rainfall, with sites experiencing higher rainfall with less-seasonal distribution having higher decomposition rates; (2) the effect of plant species will be due to substrate quality parameters like C:N, C:P, lignin concentration and lignin:N, with larger values of these parameters leading to lower decomposition rates; (3) interactions between forest type and substrate quality will be positive due to a relative increase in litter decomposition in its native forests, i.e. a 'home-field advantage'.

STUDY SITES

The Brazilian south-east is notable for the presence of fragments of different forest types occurring very close to each other in a small latitudinal extent. Remains of at least four forest types occur in the state of São Paulo, between latitudes of 25 $^{\circ}$ and 22 $^{\circ}$ south (Veloso 1992).

This study was conducted in four sites inside conservation units, each one representing one of the four forest types in São Paulo State (Table 1). Two of them are typical rain forests: restinga forest at Ilha do Cardoso State Park and Atlantic ombrophilous dense forest (referred to as Atlantic forest) at Carlos Botelho State Park. In these sites rainfall is well distributed along the year and there is no dry season (months with less than 100 mm of rain).

Furthermore, temperature remains relatively constant throughout the year, with similar values for both sites. Nevertheless, restinga and Atlantic forests have several unique characteristics. The restinga forest grows on poor sandy soil along the Brazilian coast. The vegetation is characterized by a continuous canopy 12 m high and abundant bromeliads in the ground layer. Despite the poor sand soil this forest shows a high diversity, with 117 species of tree in a 10-ha plot. On the other hand, the Atlantic forest occupies slopes along the Brazilian coast. This forest is characterized by dense vegetation with a canopy 15–20 m tall and high tree diversity, around 217 species in a 10-ha plot.

The other two forests are typically seasonal forests: semi-deciduous forest at Caetetus Ecological Station and cerradão at Assis Ecological Station. Both forests show irregular precipitation distribution with two distinct seasons. A dry season (months with less than 100 mm of rain) occurs from June to September with an average 70% less rainfall than during wet season months (45 vs. 150 mm mo $^{-1}$). During this study, March was an atypically dry month in both forests with 58% less rainfall than usual. Although these forests occur in the same climate region they show clear distinction concerning their soil properties. The semi-deciduous forest is typically more fertile than cerradão soil, showing higher percentages of clay, higher values of base saturation and lower values of aluminium saturation in the soil (Ruggiero *et al.* 2002). Semi-deciduous vegetation is characterized by deciduous species that represent approximately 40% of tree individuals and abundant climbing plants. Cerradão is the forest physiognomy of the Brazilian savanna, which is characterized by dense vegetation with trees 8–15 m tall and much reduced herbaceous vegetation.

METHODS

Litterbags and experimental design

Decomposition was determined using the litter bag technique. We chose one species from each forest type (Table 2) and collected recently fallen leaves from the soil surface in September 2003.

Table 2. Tree species for which leaves were used in litter bags, their respective family, original forest type and their relative abundance among trees in their original habitat. Relative abundance was calculated as the percentage of individuals of each species tree in relation to the total individuals in a 10-ha plot (including only trees with dbh \geq 4.8 cm).

Species	Family	Forest type	Relative abundance (%)
<i>Calophyllum brasiliense</i> Camb.	Clusiaceae	Restinga	2.7
<i>Guapira opposita</i> (Vell.) Reitz	Nyctaginaceae	Atlantic	3.8
<i>Esenbeckia leiocarpa</i> Engl.	Rutaceae	Semi-deciduous	1.5
<i>Copaifera langsdorffii</i> Desf.	Leguminosae	Cerradão	18.4

The species were chosen due to their abundance (determined from previous inventories) and the feasibility of identifying their leaves on the forest floor. Detailed descriptions of the tree species are provided online at <http://www.lerf.esalq.usp.br/matbanc.php>. Approximately 2 g of air-dried leaves were placed in each 2-mm-mesh bag measuring 10 × 15 cm. This mesh prevents the loss of litter fragments and allows access by mesofauna (Swift *et al.* 1979), animals that generally have important effects on decomposition (Chapin *et al.* 2002). Each bag contained leaves from only one of the tree species. Fifteen bags were oven dried at 55 °C to establish the relationship between air-dry and oven-dry mass. In October 2003, at the beginning of the wet season, 80 litter bags were arranged in four randomized blocks at each site (each block containing all four species) and collected after 1, 3, 5, 7 and 9 mo ($n = 4$ bags per species per site per date). Bags harvested on the same date were tethered together with nylon fishing-line that was 2 m long and anchored to a plastic stake. Each bag was placed on mineral soil surface and pinned to the ground with wire staples to minimize movement. In the laboratory the substrate from litter bags was removed, transferred to Petri dishes, oven dried at 50–55 °C for 48 h and weighed to measure dry mass remaining. Mass losses were corrected for moisture content of air-dried samples.

Litter quality

Triplicate 5-g samples of fresh litter from each of the four species were ground in a Wiley mill and used for all subsequent analyses. The litter was analysed colorimetrically for total P following nitro-perchloric digestion in a block digester (Malavolta *et al.* 1997). Lignin was determined by digestion in hot sulphuric acid (Effland 1977). N and C were analysed by dry combustion on an automated elemental analyser Carlo Erba (CHN-1110).

Statistical analysis

Daily decomposition rates (k) were calculated using a single negative exponential decay model (Jenny *et al.* 1949, Olson 1963). Although this model is not always the most accurate fit to decomposition data (Ezcurra & Becerra 1987), it is widely used because it produces a single decomposition rate constant, which facilitates comparison between data from different treatments (Harmon *et al.* 1999, Wieder & Lang 1982). The model was fitted to the data by least-squares non-linear regression of the per cent mass remaining over time in each block. This produced four estimates of decay (k) for each litter species in each site. These data were tested for homogeneity of variance using Cochran's test, with log-transformations employed to meet the assumptions for homogeneity of variance. Split-plot analysis of variance (ANOVA) was used to determine the significance of the two main factors (forest type and litter species) and their interaction on daily decomposition rate. This layout is an extension of the randomized block design of two treatments, in which one of the treatments is applied to the entire block (forest type), and the other is applied to replicates within blocks (species; Gotelli & Ellison 2004). The Tukey's HSD (Honestly Significant Difference) test was used to compare treatment means ($\alpha = 0.05$).

ANOVA followed by Tukey's test also was applied for %C, %N and C/N to compare these quality parameters between the four species. For the other parameters this was not possible because we had only one sample for chemical analysis. To investigate the relationship between substrate quality and decay rates we regressed the following litter-quality parameters: percentage lignin, C:N ratio, C:P ratio and lignin: nitrogen ratio to rate decomposition at each forest type and to rate decomposition of species in their original forests.

RESULTS

Decomposition rates of four separate species were measured in each of the four forests. Patterns of mass loss for these are summarized in Figure 1. The data exhibited a good fit to the single negative exponential decay model indicated by the coefficients of determination (r^2). Coefficients of determination were higher than 0.83 in 81% of the cases and in only one of them r^2 was smaller than 0.5.

Daily decomposition rates varied significantly according to forest type and species, and there was a significant interaction between these factors (Table 3). According to Tukey's test, decomposition was significantly faster in rain forests than in seasonal forests. Atlantic and restinga forests showed decomposition rates twice as high as those of semi-deciduous forest and cerradão. Tukey's test also

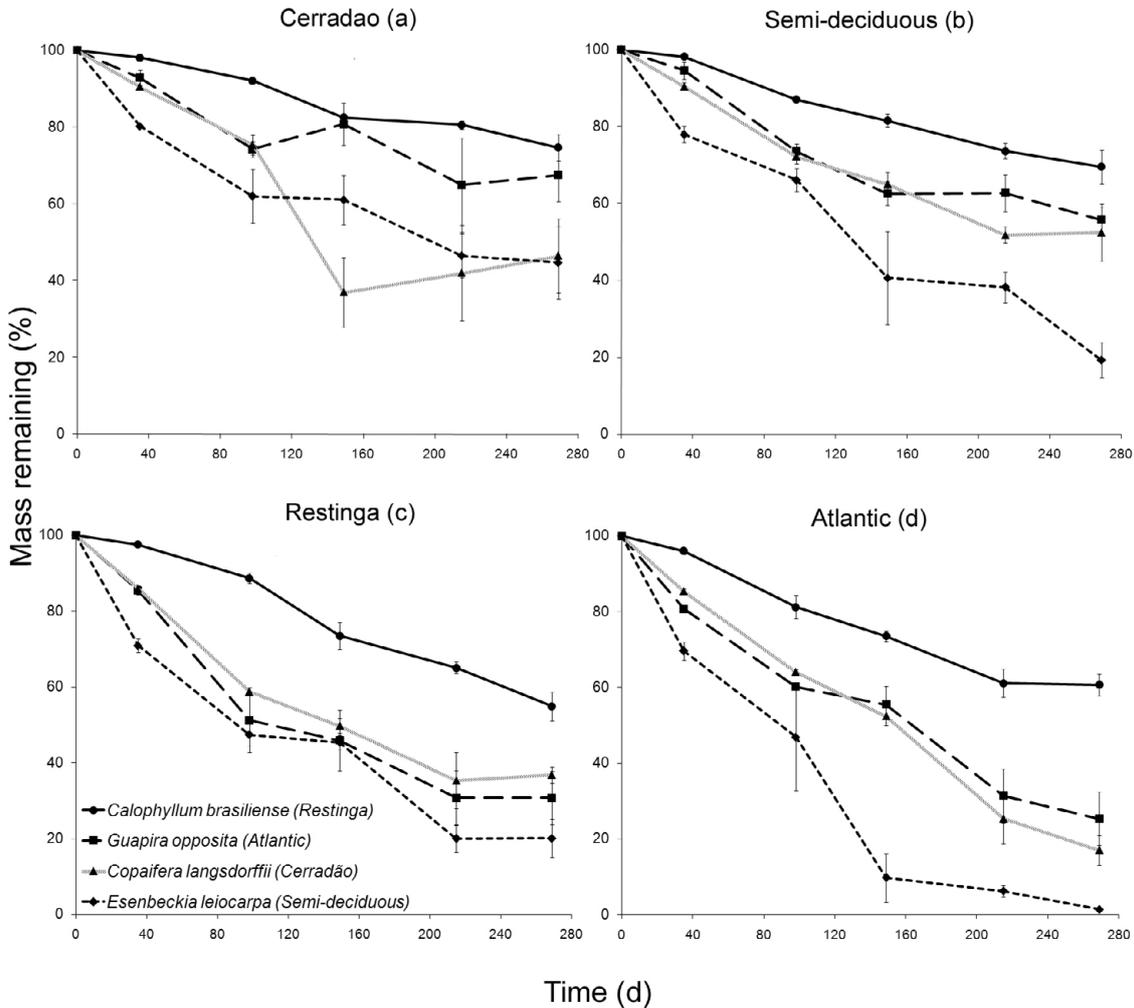


Figure 1. Per cent mass remaining (mean \pm SE) of four litter types in two seasonal forests (cerradão and semi-deciduous) (a, b) and two rain forests (restinga and Atlantic) (c, d), all located in south-east Brazil. The original forest of each species follows its name. The litter bags were placed out in the field in October 2003.

Table 3. Results of split-plot ANOVA for the effects of species and forest type on the daily decomposition rate (k).

Source	df	F	P
Forest type	3	49.9	< 0.00001
Species	3	115	< 0.00001
Forest type \times Species	9	4.1	0.001
Block	12	0.97	0.49
Error	36		

indicated significant differences among decomposition rates of all species; *Esenbeckia leiocarpa* decomposed faster than *Copaifera langsdorffii* followed by *Guapira opposita* and then *Calophyllum brasiliense*.

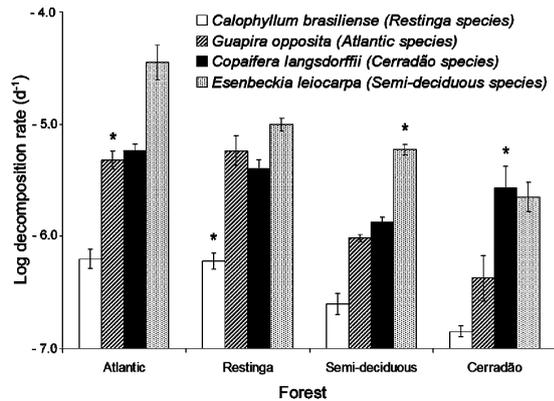
The interaction between forest type and litter species was significant in part because *C. langsdorffii* decomposed faster than expected in its native forest, cerradão. In the Atlantic, restinga and semi-deciduous forests, *G. opposita* and *C. langsdorffii* showed intermediate decomposition rates that did not differ statistically. However in cerradão

these differences were significant and *C. langsdorffii* showed median rates 89% greater than *G. opposita* (Figure 2).

In order to confirm the accelerated decomposition of *C. langsdorffii* in its native forest (cerradão) we performed a complementary analysis. The other three species had a higher decomposition rate in semi-deciduous than cerradão forest, while *C. langsdorffii* showed an inverse pattern (Figure 2). This difference, however, was not significant according to a post hoc Tukey's HSD test. Although this pairwise test reveals differences among particular pairs of treatments, it may be slightly conservative with a potential risk of a Type II error (Gotelli & Ellison 2004). For this reason we conducted another analysis to answer the following question: what is the probability that *C. langsdorffii* exhibits a higher decomposition rate in cerradão than in semi-deciduous forest by chance? In order to calculate the probability that the observed increase in decomposition rate in

Table 4. Initial concentrations of major litter chemical parameters for each of the four litter species. Values are mean \pm SE (n = 3). For %P and %lignin there are only unique values. Different letters in a column indicate that mean values are significantly different at $\alpha = 0.05$ (ANOVA/Tukey HSD).

Litter	%C	%N	%P	%lignin	C/N	C/P	lignin/N
<i>Calophyllum brasiliense</i>	49.4 \pm 0.2 ^a	0.77 \pm 0.06 ^a	0.03	47.9	64.6 \pm 4.6 ^a	1650	62.7
<i>Guapira opposita</i>	44.6 \pm 0.7 ^b	3.52 \pm 0.09 ^d	0.13	36.8	12.7 \pm 0.5 ^c	343	10.4
<i>Copaifera langsdorffii</i>	48.6 \pm 2.3 ^a	1.23 \pm 0.07 ^b	0.13	44.5	39.4 \pm 0.6 ^b	810	36.2
<i>Esenbeckia leiocarpa</i>	49.7 \pm 0.7 ^a	1.49 \pm 0.02 ^c	0.06	41.9	33.3 \pm 0.2 ^b	829	28.1

**Figure 2.** Logarithm of daily decomposition rate (k) of four species in four forest types in south-east Brazil. Error bars indicate 1 SE. Asterisk indicates in situ rate for each species.

C. langsdorffii is due to chance, we first calculated the index $\text{diff}k$ ($k_{\text{cerradão}} - k_{\text{semi-deciduous}}$) for each species, that indicates a relative high decomposition in cerradão for positive values. Then we contrasted the difference between *C. langsdorffii* mean $\text{diff}k$ with the mean for the other tree species together (diffmean). The null distribution that expresses the diffmean in a random world was created assigning $\text{diff}k$ to species by chance with randomization procedure without replacement using R software (<http://www.R-project.org/>). We reshuffled $\text{diff}k$ 1000 times calculating the random expected diffmean each time. The number of times that the randomization procedure gives diffmean equal or higher than the observed value, divided by the number of randomizations is the probability that the observed difference in decomposition rate for *C. langsdorffii* is due by chance. The results showed that *C. langsdorffii* mean $\text{diff}k$ is 2.4 times higher than the other tree species ($P < 0.001$). In order to exclude the possible effect of *E. leiocarpa* in its native forest (semi-deciduous forest), which could inflate the effect for *C. langsdorffii*, we performed the same analysis without *E. leiocarpa* data and the result did not change.

The greatest initial concentrations of % lignin, lignin:N ratio and C:N ratio were found in *C. brasiliense*, followed by *C. langsdorffii*, *E. leiocarpa* and *G. opposita*. For C:P ratio this sequence was altered due to an inversion between *C. langsdorffii* and *E. leiocarpa* (Table 4). None of the regressions between decomposition rate and litter quality parameters was significant (all $P > 0.11$).

DISCUSSION

Forest type effect

Our study demonstrates that Atlantic and restinga forests have decomposition rates twice those of semi-deciduous forest and cerradão. It is possible that differences between decomposition rates are mainly due to differences in climate. In hierarchical models of litter decomposition, climate is the primary factor controlling the decomposition process (Lavelle & Spain 2001, Lavelle *et al.* 1993), because it is the main regulator of bacterial and fungal metabolism.

The four forest types present very similar and relatively regular mean annual temperature (MAT) across years (20–23°C). However, there is a clear difference in precipitation. The Atlantic and restinga forests have a mean annual precipitation (MAP) higher than 2000 mm and a lack of distinct dry season. On the other hand, the semi-deciduous forest and cerradão have a MAP much lower (approximately 1400 mm) and a pronounced dry season from June to September. During the experiments Atlantic and restinga forests received amounts of rain twice as high as in seasonal forests (2200 vs. 1200 mm). When investigating the effects of water availability on litter decomposition along a natural rainfall gradient in Hawaii, Austin (2002) found that decomposition increases linearly across a range of MAP from 500 to 5500 mm. Beyond the total amount of rainfall, its seasonal distribution is an important control on decomposition rates. Wieder & Wright (1995) observed an increase in decomposition rates during the dry season in irrigated plots of tropical forests in Panama.

These forests also present differences in edaphic features. Among the studied forest types, semi-deciduous presents the more fertile soil, restinga forest has the poorest soil and Atlantic and cerradão present intermediate fertilities (Moraes *et al.* 1999, Ruggiero *et al.* 2002). These differences cannot explain the higher decomposition rates found in Atlantic and restinga forests compared to semi-deciduous forest and cerradão. However soil fertility can be a secondary factor explaining the tendency inside each group (rain vs. seasonal forests) to reduced decomposition in forest with less fertile soil.

Although the results make it possible to compare the effect of forest on decomposition rates we must be careful

in extrapolating them from individual species to the ecosystem-level litter decomposition. Several studies have shown decomposition rates of mixed foliage is often not predicted by the decomposition rates of the component species, a property known as non-additive effect (Gartner & Cardon 2004). Moreover the single species used in this study do not represent the litter quality of each forest. In general semi-deciduous forest presents the highest litter quality, restinga the poorest while Atlantic and cerrado present intermediate values (Meguro *et al.* 1979, Moraes *et al.* 1999, Peres *et al.* 1983), according to their soil fertility.

Our results demonstrate the effects of forest type on decomposition rates. The differences observed between forests suggest that precipitation intensity and distribution might be important predictors of decomposition rates at regional scales.

Substrate effect

In our regional-scale study, the species effect on decomposition rates was larger than the forest type effect, because it explained most of the variation found in percentage of mass remaining during the experiment (Table 3). However the decomposition rates are not predicted by quality parameters.

Although some studies have showed correlations between initial parameters of litter quality and decomposition rates (Alvarez-Sánchez & Enríquez 1996, Melillo *et al.* 1982, Moore *et al.* 1999) the initial indices exhibit some limitations in predicting decomposition. This occurs due to changes in the litter composition during the decomposition process (Heal *et al.* 1997). Some studies have shown a shift on litter quality parameters control according to stages of decomposition (Berg 1986, Loranger *et al.* 2002, Taylor *et al.* 1989). In tropical forests, where decomposition is generally accelerated, this effect can be very strong because the later the stage of decomposition the less important are the initial properties of the litter. Therefore, changes in the quality parameters controlling decomposition might have prevented the predictive power of simple measures of initial composition of litter. Another potential explanation for the lack of correlation might be the small sample size ($n = 4$).

Forest type and substrate interaction

Generally, soil microbial biomass varies across vegetation types. This reflects in part the quality of resource input from the dominant plant species to the soil (Wardle 2002). Elmer *et al.* (2004) and Scheu *et al.* (2003) found changes in the trophic structure and biomass of the soil fauna community in response to replacement of tree species in

monocultures. Both studies suggest that the litter quality is the most important factor influencing these changes. Furthermore, mutualisms between the producer and decomposer subsystems might involve selection by the plant for a community of soil organisms that is adapted for decomposing substrates produced by that species (Wardle 2002).

We found that *Copaifera langsdorffii* has accelerated decomposition in its original site. A possible explanation for this is that *C. langsdorffii* selects decomposer communities that preferentially break down its litter. Experiments with reciprocal litter transplant in different temperate forests arrived at similar conclusions since at least one studied species showed accelerated mass decay in its original site (Elliot *et al.* 1993, Hunt *et al.* 1988, McLaugherty *et al.* 1985). Other authors have found evidence of selection by the plants for the decomposer community (Cookson *et al.* 1998, Hansen 1999). As far as we are aware, this is the first time that accelerated decomposition in a native site has been observed in a tropical forest. Just one other study using reciprocal placement of rain-forest tree leaf litter showed no interaction between litter type and placement (Wiegert & Murphy 1970).

Recently the hypothesis that litter decomposes faster in the presence of biota derived from native soil was explicitly tested in laboratory conditions and it was rejected (Ayres *et al.* 2006). However, this study design had certain limitations, notably the exclusion of larger soil fauna and its relatively short duration (103 d over simulated temperate conditions), that encompassed only the early phase of decomposition.

Therefore, if it is a selective advantage for plant species to alter the soil community in ways that enhance decomposition of their litter and their ability to access nutrients, why is this pattern not observed in the other three species? In contrast to other studies, the forests in this study are extremely diverse, with minimal richness of 117 tree species in the restinga forest and maximum of 217 in the Atlantic forest in 10-ha plots. Despite being between the most abundant species, *C. brasiliense*, *G. opposita* and *E. leiocarpa* represent less than 4% of the trees in their respective forests. On the other hand, even with the high tree species richness present in the cerrado (118 species in a 10-ha plot), *C. langsdorffii* is a dominant species, representing 18% of tree individuals. In addition to higher density, this is a deciduous species, so we can presume that the leaves of *C. langsdorffii* were superior to other species in terms of its contribution to its original forest litter. This difference may explain the lack of accelerated decomposition in original site for the other three species.

Our findings reinforce the importance of climate on the decomposition process in tropical forests at regional scales and demonstrate the lack of correlation

between decomposition rates and initial substrate quality parameters. Beyond that, our data suggest that the relatively little studied interactions between plant and decomposer communities may play an essential role in decomposition processes as well as in related processes such as nutrient availability and ecosystem productivity.

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