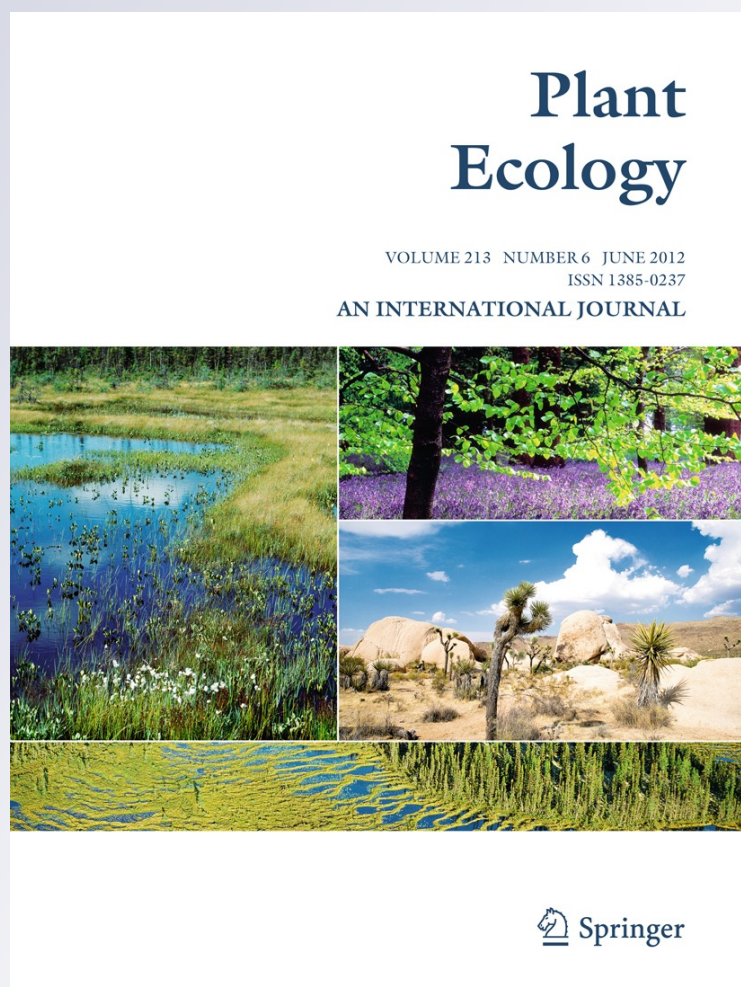# *The importance of mesofauna and decomposition environment on leaf decomposition in three forests in southeastern Brazil*

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The importance of mesofauna and decomposition environment on leaf decomposition in three forests in southeastern Brazil

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Abstract We examined the effects of soil mesofauna and the litter decomposition environment (above and belowground) on leaf decomposition rates in three forest types in southeastern Brazil. To estimate decomposition experimentally, we used litterbags with a standard substrate in a full-factorial experimental design. We used model selection to compare three decomposition models and also to infer the importance of forest type, decomposition environment, mesofauna, and their interactions on the decomposition process. Rather than the frequently used simple and double-exponential models, the best model to describe our dataset was the exponential deceleration model, which assumed a single organic compartment with an exponential decrease of the decomposition rate. Decomposition was higher in the wet than in the seasonal forest, and the differences between forest types were stronger aboveground. Regarding litter decomposition environment, decomposition was predominantly higher below than aboveground, but the magnitude of this effect was higher in the seasonal than in wet forests. Mesofauna exclusion treatments had slower decomposition, except aboveground into the Semi-deciduous Forest, where the mesofauna presence did not affect decomposition. Furthermore, the effect of mesofauna was stronger in the wet forests and belowground. Overall, our results suggest that, in a regional scale, both decomposers activity and the positive effect of soil mesofauna in decomposition are constrained by abiotic factors, such as moisture conditions.

Keywords Aboveground · Belowground · Brazil · Exponential models · Leaf decomposition · Soil mesofauna

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Introduction

Decomposition is a key process that defines soil fertility through the mineralization and humification of organic materials (Lavelle et al. 1993). It is especially important in tropical forests, which mostly grow on weathered, low-fertility soils (Jordan and Herrera 1981; Montagnini and Jordan 2002; Vitousek and Sanford 1986). Decomposition is determined by the interaction of physical parameters (climatic and soil conditions), the quality of the decomposing materials and the soil organisms (Epstein et al. 2002; Lavelle et al. 1993; Seastedt 1984; Swift et al. 1979). Biological factors gain importance as decomposition determinants when the abiotic conditions are favorable, for example under warm temperatures or no limited moisture conditions. Indeed, in the tropics,

biotic factors have been described as the best predictors of decomposition rates (Aerts 1997; Lavelle et al. 1993; Wall et al. 2008). Because most conceptual frameworks and models of decomposition have been based on temperate forest data, a main goal of forest ecosystem research is to understand how these factors interact and vary in importance to the decomposition rates in tropical forests (Powers et al. 2009).

In tropical areas, the temperature is quite constant, and precipitation patterns define mesoclimatic constraints, which are mostly related to the length and intensity of the dry seasons (Lavelle et al. 1993). The effect of moisture on microbiota activity (Salimon et al. 2004) can lead to different decomposition rates among tropical forests with distinct moisture conditions. Lower decomposition rates in seasonal versus aseasonal tropical forests (Castanho and Oliveira 2008; Powers et al. 2009) support this idea.

Even though the importance of soil fauna was recognized more than 20 years ago (see Seastedt 1984), most decomposition models do not include it as a parameter (Wall et al. 2008). The effects of soil mesofauna on decomposition rates are relatively well known in temperate forest and arid ecosystems, but there is little information about tropical forests. Mesofaunal effects are pronounced in wet and humid climates, but they are less important where the temperature or moisture constrains biological activities, such as in temperate or dry tropical forests (Gonzalez and Seastedt 2001; Wall et al. 2008). However, in a pantropical decomposition comparison, no relationship between climate and mesofaunal effects was found (Powers et al. 2009). Therefore, it is still not clear how the environmental conditions influence the effect of mesofauna on litter decomposition.

Global experiments have shown that decomposition rates are generally higher below than aboveground, except in ecosystems where belowground environmental conditions impose strong constraints to soil organisms, as it is in tundra and wetlands (Adair et al. 2008; Cusack et al. 2009; Gholz et al. 2000; Smith et al. 2011). Decomposition processes may differ because micro-environmental conditions, as direct solar radiation on the forest floor leads to higher temperature oscillations aboveground (Gholz et al. 2000). Also, water availability is more stable belowground because water is retained among the soil particles (Paul and Clark 1989). Hence, belowground can be considered a buffered environment when compared with

aboveground, and it may provide more favorable living conditions to soil biota. The more stable environment belowground can explain the reported narrow variation of root compared to litter decomposition rates (Gholz et al. 2000). However, it is not clear how climatic constraints and decomposition environment interact in forests with different moisture conditions into the same tropical region. On one hand, the abiotic constraints imposed to soil organisms by temperature and moisture oscillations may result in a stronger influence of those conditions on the decomposition rates aboveground. On the other hand, the effects of soil fauna may be stronger belowground, as weak environmental constraints lead to higher biological activity (Gonzalez and Seastedt 2001; Wall et al. 2008).

We examined the effects of the soil mesofauna (present and excluded) and decomposition environment (above and belowground) on the leaf decomposition rates in three different forest types in the same tropical region. We predicted that (1) the decomposition rates would be higher in forest types with more favorable moisture conditions (defined by mean annual precipitation, length of the dry season, and differences in the soil texture). Furthermore, the differences between forest types would be smaller belowground, where the environmental conditions are buffered. (2) Regarding the litter environment decomposition, the decomposition would be higher belowground, where environmental conditions are more stable. Furthermore, we expected smaller differences between aboveground and belowground treatments in wetter forests. Finally, we also expected (3) slower decomposition in fauna exclusion treatments. Moreover, we expected smaller mesofauna effects at drier forests and aboveground, where moisture conditions may constraint biological activities.

Materials and methods

Study sites

Forest fragment remnants of at least four vegetation types occur between 22 and 25° S in the State of São Paulo (Veloso 1992) where this study was conducted. Each one of our study sites represents a forest type: Atlantic Forest, Restinga, and Semi-deciduous Forest. Although the temperature is quite constant among

Table 1 Description of the three forest sites in southeastern Brazil

Forest type	Location	MAT (°C)	MAP (mm)	Dry season (months)	Soil type	Sand (%)	Loam (%)	Clay (%)	Altitude (m)	Tree richness
Atlantic	24°00′S;48°10′W	21	2800	0	Inceptsol	50	15	35	480	217
Restinga	25°03′S;47°53′W	21	2100	0	Spodsol	90	5	5	5	117
Semi-deciduous	22°33′S;50°22′W	21	1400	4	Ultisol	81	8	11	670	118

Dry season is the number of months with <100 mm of rain. Soil texture was defined based on the 0–5 cm soil layer. Tree species richness from 10-ha plots, where all trees DBH $\geq$4.8 cm were identified

MAT mean annual temperature, *MAP* mean annual precipitation

them, moisture conditions change from one to another, because of mean annual precipitation, dry season length, and soil properties (Table 1).

The Atlantic Forest at Carlos Botelho State Park and Restinga Forest at Ilha do Cardoso State Park have high precipitation, with no dry season (months with <100 mm of rain). Nevertheless, these two forest types differ in moisture conditions because of their soil properties. The Atlantic Forest occupies slopes along the Brazilian coast and occurs on relatively young, poorly developed soils, with clay content ranging from 25 to 60 % and high water retention (Table 1). The Restinga Forest grows on poor sandy soils along the Brazilian coast, where water retention is very low because of its coarse-textured soils (Table 1). The Semi-deciduous Forest at Caetetus Ecological Station has irregular rainfall distribution throughout the year: the dry season occurs from June to September, with an average 70 % less precipitation than the rainy season months (45 vs. 150 mm per month). The soil is mesotrophic, with medium texture (Ruggiero et al. 2002). There is clay accumulation and water retention on the subsurface horizons down to 1 m of soil depth. Deciduous species represent approximately 40 % of the trees.

Experimental approach

We used a full-factorial experimental design to assess the effects of forest, soil mesofauna and decomposition environments on litter decomposition ($3 \times 2 \times 2$ factorial design). In order to evaluate decomposition experimentally we used litterbags method (Harmon et al. 1999). We placed standard material, described below, in litterbags with two different mesh sizes (mesofauna treatment) and placed them above and belowground (litter decomposition environment treatment) in the three forest sites, one from each type.

We used two different litterbag mesh sizes to assess the effects of the soil mesofauna through the selective exclusion of different components of the decomposer community. The fine mesh (52 μm mesh nylon cloth) permits access by bacteria, fungal hyphae, nematodes, and protozoa, while it restricts access by meso- (100 μm–2 mm) and macrofauna (>2 mm) (Swift et al. 1979). The coarse mesh (2 mm mesh nylon netting) permits access by mesofauna, such as Acari, Collembola, and some Nematoda.

The litterbags were placed above and belowground to evaluate changes between the leaf and root decomposition environments. The aboveground bags were placed on the mineral soil surface, and the belowground bags were buried to a depth of 10 cm. To evaluate the effect of the decomposition environment alone (isolated from the chemical quality effect), we buried a standard material composed of bay leaves (*Laurus nobilis* L, Lauraceae), which is native to the Mediterranean region and is not found in either of the studied forests. Bay leaves were selected on the basis of its carbon (C) fractions and nitrogen (N) concentrations, which are similar to those found in the litter in tropical forests, with a C:N ratio of 35 (Aerts 1997). Furthermore, the use of standard non-native substrates is useful to access the soil mesofauna and environmental controls on decomposition (Harmon et al. 1999), as it eliminates the differences caused by initial substrate quality or by specially adapted decomposers (see "home-field advantage" in Ayres et al. 2009).

Regarding the effect of forest type, our experimental design does not permit to generalize our results to the all Atlantic, Restinga, and Semi-deciduous Forests from southeastern Brazil because we sample at one site per forest type. Therefore, the conclusions and implications of our results are limited to the three studied forest sites. Furthermore, the climate, quality of the surrounding litter and soil, and decomposer

community were not isolated in the experiment; thus, we evaluated the effects of these parameters together when we compare forests. However, we expected that any differences observed in the decomposition rates among the three studied forests might be mostly caused by differences in the moisture conditions, an essential determinant of decomposition process (Lavelle et al. 1993; Salimon et al. 2004). The three studied forests represent a humidity gradient defined by different values of mean annual precipitation, dry season lengths, and soil texture; according to the following order: Atlantic > Restinga > Semi-deciduous Forest. At this point, it is important to remark that temperature conditions are homogeneous into the three studied forests, therefore, any climatic constraints to decomposers metabolism may be imposed by moisture conditions. Hence, biotic factors, like microbial diversity and abundance, may change together in the humidity gradient, favoring decomposition in wet than moisture-limited forests.

The litterbags (10×15 cm) were filled with 1.00 ± 0.01 g air-dried, sterilized bay leaves, sealed and tied with nylon lines for a total of 60 strings (3 bags each). There were three replicates per treatment and retrieval date, for a total of 180 litterbags. The field experiment began in October 2003, at the start of the rainy season. Two large staples were placed approximately 10 m apart on level ground at each study site. Around each staple, ten strings were arranged in a radial pattern interspersing the above and belowground treatments. Two strings (one above and the other belowground) per staple were retrieved at 1, 3, 5, 7, and 9 months after placement. Following retrieval, the litterbags were opened, and their contents removed. The samples were gently washed in tap water to remove adhering soil particles, dried at 50–55 °C until constant weight and reweighed to ±0.01 g. Prior to the experiment, some extra litterbags were weighed before and after oven drying at 55 °C, for later correction of the mass loss for the moisture content of air-dried samples used to fill the litterbags.

Decomposition models

To describe the decomposition process, we first selected the model that best described all data, using full models with all main factors (forest type, litter decomposition environment, and mesofauna) and their interactions. We used three decomposition models: (i)

single exponential (Jenny et al. 1949; Olson 1963); (ii) double exponential (Lousier and Parkson 1976); and (iii) exponential deceleration (Rovira and Rovira 2010). The single exponential is the most widely used approach to describe decomposition processes in comparing differences between treatments (Harmon et al. 1999; Wieder and Lang 1982). It describes the process with a single value that can be directly compared and interpreted as the rate of mass decay (Wieder and Lang 1982).

$$X_t = X_0 e^{-kt} \text{ Single exponential} \tag{1}$$

where X_t is the amount of litter at time t, X_0 is the initial amount, and k is the decomposition rate. The double-exponential model considers two litter compartments, each one with its own constant decomposition rate (Lousier and Parkson 1976; Wieder and Lang 1982).

$$X_t = a e^{(-k_1 t)} + (1-a) e^{(-k_2 t)} \text{ Double exponential} \tag{2}$$

where a is the initial amount of the labile pool, k_1 is its decomposition rate, $1-a$ is the initial amount of the recalcitrant pool, and k_2 is its decomposition rate. A limitation of this approach is the difficulty in defining a priori the proportion of each compartment. When there is information about the components of the decomposing litter, the compartments can be defined based on, for example, the proportion of cellulose and lignin as the recalcitrant pool. When this information is not available, labile mass fraction (a) can be a parameter estimated by the model. In any case, as the process is described by two or more different rates, it is hard to decide what factors influenced each k. If all factors affect both rates, it complicates the interpretation of multiple designs and compromises the degrees of freedom of the model. In our case, we model only k_1 and we estimate the labile component (a) as a model parameter because we do not have information about the substrate components.

The third decomposition model, recently proposed by Rovira and Rovira (2010), is based on a generalized approach where the decomposition rate is an integral function of time:

$$X_t = X_0 e^{-\left(\int_0^t f(t) \, dt\right)} \tag{3}$$

A particular case of this generalized approach is when the decomposition rate decreases with time following an exponential curve:

$$f(t) = a + be^{-mt} \qquad (4)$$

where m represents the decreasing rate of k, a is the basal rate, and b is the range of the rate variation, such that $a + b$ is the maximum rate. Rovira and Rovira (2010) have integrated this formula relative to t and obtained:

$$\int_0^t f(t)\mathrm{d}t = at - \frac{b}{m}(e^{-mt} - 1) \qquad (5)$$

To obtain the exponential decrease of the decomposition rate described in Rovira and Rovira (2010), the eq. 5 is inserted into eq. 3

$$X_t = X_0 e^{-\left(at - \frac{b}{m}(e^{-mt} - 1)\right)} \text{ Exponential deceleration} \qquad (6)$$

The resulting model, hereafter called the "exponential deceleration," seems simpler than the double exponential because it considers a single organic compartment, whose decomposition rate decreases with time.

One important matter that was not addressed by any of the three models presented is that the variation in mass through time is not homogeneous. The litterbag approach has a fixed initial mass that has no typical random variation associated with it, excepting the measurement error. During the decomposition process, the mass loss variation increases with time, as decomposition is an intrinsically accumulative process. Thus, to accommodate this feature, we modeled the mass standard deviation as the inverse to the mass remaining and compared these models with fixed variance models (see details in Online Resource 1).

Statistical analysis

We used a model selection approach to find the best model to describe our data (Burnham and Anderson 2002) and infer factors that influenced the decomposition process. To make decisions about the model comparison, we used Akaike Information Criterion (AIC) and considered models with different support when the AIC difference between the models (ΔAIC) was more than two units (Burnham and Anderson 2002).

First, the model selection was applied to select, among the three concurrent decomposition models presented above, the one that best described our data.

After that, the selected model was used to understand how the following factors affected the decomposition process: (i) forest type; (ii) mesofauna presence; (iii) litter decomposition environment; and (iv) their interactions. Regardless of decomposition model selected, we also estimated the coefficients of the three decomposition models, using all main factors and interactions, to provide decomposition values (k or m) and permit comparisons with previous studies that have used them. In the single- or double-exponential model, the factors were modeled to affect the decomposition rate (k). Conversely, in the case of the exponential decelerated model, the factors were modeled to affect the k-decreasing rate (m).

To understand the effect of the forest type, the mesofauna presence, and litter decomposition environment on decomposition, we used a hierarchical approach from a full selected model and compared it with simpler models, first taking off the third-order interaction, followed by the second-order interactions and then by each factor. As long as the simplest model was not a better solution to explain the data than a previous, more complex one, we stopped the procedure and defined the previous complex model as the better solution. Because corrections for small sample size are needed for more complex models, we used the AICc (Burnham and Anderson 2002) to correct that bias. As long as the AICc converges to the AIC as the sample size increases, we used AICc for all the comparisons. We used the R environment (version 2.15.0, R Development Core Team 2012) with the bbmle package (Bolker and R Development Core Team 2012) for all statistical analyses.

Results

Decomposition models

Each of the decomposition models was better fitted when using a standard deviation that grew as the inverse of the mass loss (Table 2). Although the double-exponential model had a better fit when compared to the single exponential, the exponential deceleration model was the most plausible model to describe the mass loss over time (Table 2). Therefore, our base model to test for factors affecting the decomposition process was the exponential deceleration model with growing variance.

Effects of forest type, litter decomposition environment, and mesofauna

The best model under the exponential deceleration decomposition model includes all main effects (forest type, litter decomposition environment, and the fauna presence) as well as all the second-order interactions (model 2.ar in Table 3). The model that includes the same terms as well as the third-order interaction was equally plausible (model 1.ar in Table 3), indicating that there is no certainty about the importance of this last term. In addition, the selected models considered Restinga and Atlantic as one forest type (wet forests), indicating that the Atlantic and Restinga Forests had indistinguishable decomposition rates, and mesofauna exclusion and litter decomposition environment had the same effect on the mass decay in these two forests. Because the Restinga and Atlantic Forests were affected in the same way by the factors analyzed, the results hereafter were considered with respect to only two of the forest types: wet forests and Semi-deciduous Forest.

As predicted, the k deceleration rate (m) was strongly affected by forest type and the magnitude of this effect depended on the litter decomposition environment (Fig. 1). Aboveground, the k deceleration rate (m) was smaller in wet forests (Table 4), indicating that the decomposition rate (k) decelerated more slowly and, consequently, the decomposition was faster in wet than Semi-deciduous Forest. Below-ground, the differences between forests were smaller and dependent on the presence of mesofauna (Fig. 1). There is no difference in belowground decomposition between wet and Semi-deciduous Forests when mesofauna was excluded (Fig. 1).

Regarding the litter decomposition environment, decomposition belowground was predominantly higher than aboveground (Fig. 1). However, the magnitude of this effect depended on forest type and the mesofauna presence (Table 4; Fig. 1). The difference between above and belowground decomposition was stronger in semi-deciduous than in wet forests, as well as in the presence of mesofauna than in its absence (Fig. 1).

The mesofauna effect was very important, but depended as much on the litter decomposition environment as the forest type. As predicted, the mesofauna effect was especially higher to decomposition below-ground and in wet forests. In the wet forests, the presence of mesofauna reduced the k deceleration rate, increasing decomposition in both the litter decomposition environments, but especially belowground (Fig. 1). On the other hand, in the Semi-deciduous Forest, the effect of mesofauna increased decomposition only belowground, with no effect aboveground (Fig. 1).

Discussion

Decomposition models

We found that the exponential deceleration model (Rovira and Rovira 2010) was the model that best described the mass loss over time in three southeastern Brazilian Forests. It has been suggested that exponential curves are often the most realistic models to explain decomposition datasets in terms of both mathematical and biological behavior (Wieder and Lang 1982). Therefore, since its proposal (Jenny et al. 1949, discussed by Olson 1963), the single-exponential model has been widely used to explain decomposition patterns (Castanho and Oliveira 2008; Gholz et al. 2000; Gonzalez and Seastedt 2001; Powers et al. 2009) because of its mathematical simplicity and easily compared results. However, decomposition

Table 2 Summary of the model selection results for the three candidate decomposition models

Model	Expression	AICc	AICc*	ΔAICc	ΔAICc*
Single exponential	$X_t = X_0 e^{-kt}$	−417.7	−455.4	254.7	217.0
Double exponential	$X_t = a e^{(-k_1 t)} + (1-a) e^{(-k_2 t)}$	−544.4	−669.4	128.0	3.0
Exponential deceleration	$X_t = X_0 e^{-\left(at - \frac{b}{m}(e^{-mt}-1)\right)}$	−546.6	**−672.4**	125.8	**0.0**

For comparisons we used the full models (including forest type, the mesofauna presence, and litter decomposition environment, and their interactions). Akaike Information Criterion corrected for small sample size (AICc) and distance from the base model (ΔAICc). The results for models with growing variance as the inverse of the mass remaining are marked (*). The selected model (ΔAICc < 2) is in *bold*

Table 3 Summary of the model selection results

Model #	Terms included							Selection criteria		
	for	lde	fau	for:lde	lde:fau	for:fau	for:lde:fau	AICc	ΔAICc	k
1	*	*	*	*	*	*	*	−672.4	8.0	16
2	*	*	*	*	*	*		−674.1	7.2	14
3	*	*	*	*	*			−667.1	14.2	12
4	*	*	*		*	*		−654.5	26.8	12
5	*	*	*	*		*		−665.6	15.7	13
6	*	*	*					−640.9	40.4	12
1.ar	*	*	*	*	*	*	*	**−680.5**	**0.8**	**12**
2.ar	*	*	*	*	*	*		**−681.3**	**0.0**	**11**
3.ar	*	*	*	*	*			−670.6	10.7	10
4.ar	*	*	*		*	*		−658.5	22.9	10
5.ar	*	*	*	*		*		−671.6	9.7	10
6.ar	*	*	*					−643.7	37.6	9
Null								−520.0	161.3	5

The model is the exponential deceleration decomposition, using the k-decreasing rate (m) as the response variable and the forests type (for), litter decomposition environment (lde), mesofauna (fau), and their interactions as the fixed predictor variables. The terms included in each candidate model are indicated by *asterisk*. Akaike Information Criterion corrected for small sample size (AICc), distance from the base model (ΔAICc), and the number of parameters (k) for each model. The models designed with *.ar* indicate that the levels *Atlantic* and *Restinga* under forest treatment are joined together. Selected models (ΔAICc < 2) are in *bold*

datasets often result in dynamics with strong curvatures that cannot fit well to a single-exponential equation (Adair et al. 2008; Rovira and Rovira 2010), as was the case with our study.

The double-exponential model fitted to our data much better than the simple exponential model did, indicating that assuming two decomposition stages characterized by different decomposition rates provided a better fit to our decomposition dataset than assuming one single compartment. The difference in decomposition rate between the labile and the recalcitrant fractions (Melillo et al. 1989) supports the idea of the two-step nature of decomposition dynamics (Wieder and Lang 1982). Even though the double-exponential model was useful to fit the data, it did not necessarily reflect what actually occurred in the decomposition process. The two main assumptions of the double-exponential model (i.e., independent compartments and constant decomposition rates) are not realistic from a biological point of view because: (i) the labile and recalcitrant fractions interact as decomposition proceeds (i.e., microbial mass formation implies the transfer of materials between both of the pools); and (ii) the chemical quality of the compartments changes over time (Rovira et al.

2008). The best model to explain our datasets was the Rovira and Rovira (2010) exponential deceleration, which assumes a single organic compartment with an exponential decrease of the decomposition rate. This result suggests that we do not need the assumption of an internal structure of the decomposing substrate (i.e., organic compartments) to describe leaf decomposition. In addition to simplicity, the exponential deceleration model maintains biological realism, indicating that the substrate quality changes with decomposition, from a more labile to a more recalcitrant organic matter composition.

To our knowledge, this is the first study that includes the increment of variance with time as decomposition proceeds. Such consideration notably improved the model fitting for all the three tested equations: the single, double, and exponential deceleration models. The mass loss standard deviation increasing with time may have reflected cumulative spatial differences on the decomposition process between sample units. Those differences can be the result of the interaction of multiple decomposition control factors (Aerts 1997), which has been described as operating on different scales of time and space (Bardgett et al. 2005; Lavelle et al. 1993).
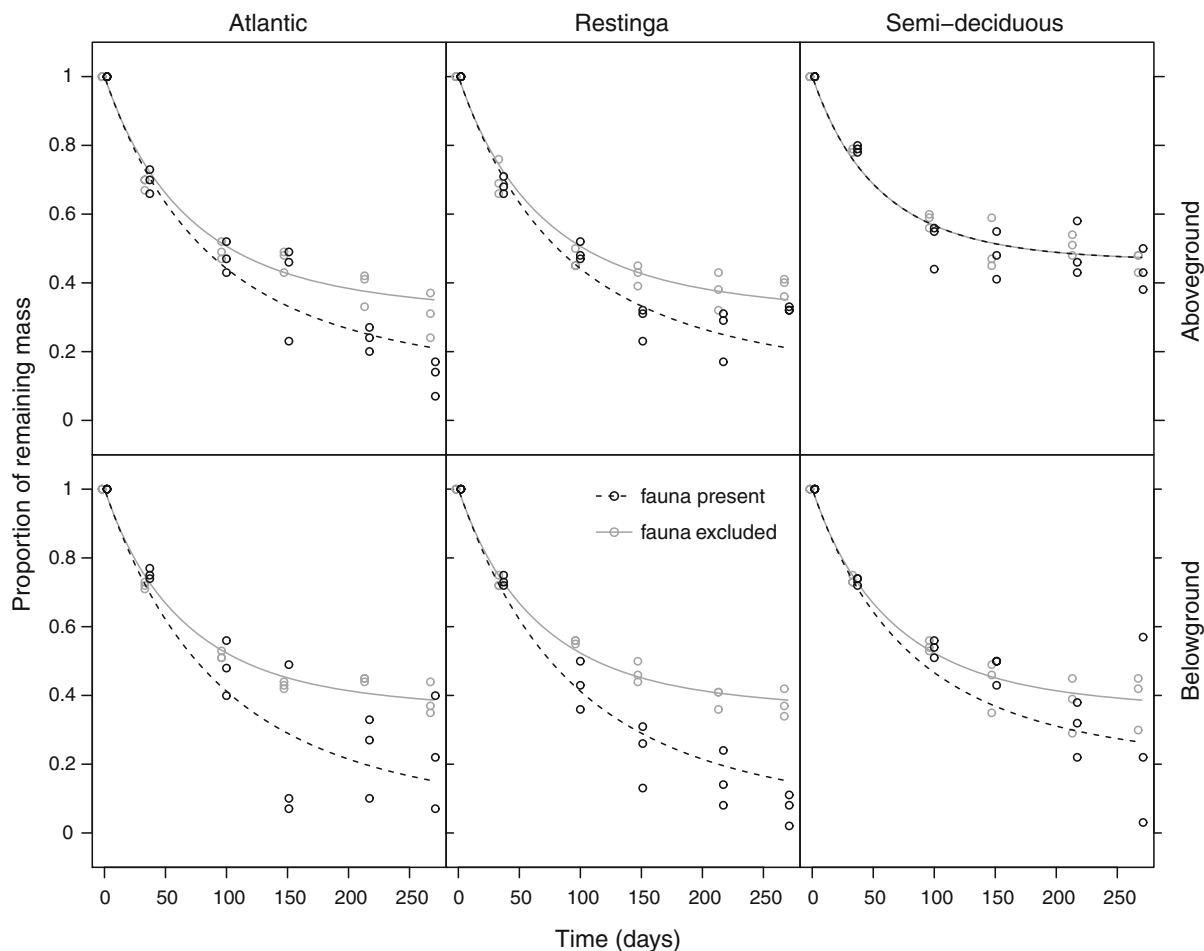
Fig. 1 Observed and predicted proportion of the remaining mass of *Laurus nobilis* in three forests of southeastern Brazil following two treatments: with and without mesofauna, and above and belowground. The *lines* represent the proportion of the remaining mass predicted by the selected model, which includes the effect of forest type, litter decomposition environment, the mesofauna presence, and their second-order interactions (model 2.ar in Table 3). *Dots* from different mesofauna treatment (present and excluded) were separated at the *x* axis by ±2 days for better visualization

The effect of the forest type

The results regarding the effect of forest type corroborated our first prediction that the aboveground decomposition would be faster in the forests with more favorable humidity conditions. The importance of moisture conditions for the decomposition process, as indicated by the faster decomposition in wet forests than in seasonal forest, has been reinforced by other studies performed in tropical regions (Castanho and Oliveira 2008; Cusack et al. 2009; Powers et al. 2009) and can be explained by the fact that water availability affects decomposition, primarily through its effects on the community of decomposers (Fragoso and Lavelle 1992). Both the wet forests, Restinga and Atlantic,

present similar precipitation regime, but great differences in soil water retention, which could make them distinct regarding humidity condition. Although the aboveground decomposition was faster in wet than Semi-deciduous Forest, there were no differences between the Atlantic and Restinga Forests. These results suggest that the length of dry season exerts a more consistent control on decomposition than MAP and soil texture. However, our experiment was not designed to disentangle that question and we cannot draw definitive conclusions about the specific factors defining differences among the three studied forests.

As expected, the belowground differences in decomposition between the wet and Semi-deciduous Forests were less pronounced than the aboveground

Table 4 Daily mass decay rates (k) and daily decelerate coefficient (m) for decomposition process based on three exponential models with all factors and interactions, and growing variance

Forest type	Mesofauna present		Mesofauna excluded	
	Aboveground	Belowground	Aboveground	Belowground
	Single exponential (k)			
Atlantic	0.00763	0.00773	0.00720	0.00637
Restinga	0.00794	0.00803	0.00743	0.00566
Semi-deciduous	0.00553	0.00610	0.00461	0.00598
	Double exponential (k_1)			
Atlantic	0.00297	0.00382	0.00142	0.00088
Restinga	0.00276	0.00391	0.00133	0.00073
Semi-deciduous	0.00033	0.00192	0.00011	0.00094
	Exponential deceleration (m)			
Atlantic	0.00530	0.00318	0.00948	0.01129
Restinga	0.00596	0.00321	0.00950	0.01150
Semi-deciduous	0.01314	0.00757	0.01521	0.01083
	Model 2.ar (m)			
Wet forests	0.00479	0.00306	0.00890	0.01006
Semi-deciduous	0.01243	0.00629	0.01331	0.01006

We also presented the coefficients based on the selected model Model 2.ar (see Table 3). Double-exponential model: labile pool (a) = 0.471; k_2 = 0.0174. Exponential deceleration: a = 0.0003; b = 0.010

differences, and they were only significant in the presence of mesofauna. This can be explained by the higher stability of belowground environmental conditions, which are indeed, quite stable down to a depth of a few centimeters. Soil respiration, for example, is positively correlated to soil temperature at a 2-cm depth; however, below this depth, soil respiration is largely uncoupled from temperature (Jassal et al. 2008). Soil respiration is also correlated with soil moisture (Davidson et al. 2000) and water remains available to biota longer into the soil than on its surface. Thus, belowground may provide more favorable living conditions for decomposers than aboveground because lower temperature and moisture oscillations lead to similar decomposition rates belowground even among forests with distinct moisture conditions.

The effect of litter decomposition environment

As expected, the decomposition process was affected by the litter decomposition environment, with higher decomposition rates predominantly belowground. Furthermore, we found evidences that the magnitude of this effect depended on the forest type, as indicated by the higher differences between above and belowground in the semi-deciduous than in the wet forests. Despite global experiments demonstrating higher wood decomposition rates belowground (Smith et al. 2011), Gholz et al. (2000) have found higher decomposition rates aboveground in a tropical wet forest (above to belowground ratio of >1), whereas the inverse was true in a tropical dry forest (above to belowground ratio of <1). Those results suggest that litter decomposition belowground is higher on tropical forests with limiting humidity conditions to the biota. In those forests, higher decomposition rates are found belowground, probably because the higher water availability and higher stability in the environmental conditions few centimeters below soil surface increase the activity and abundance of the decomposer community. That could explain why the differences between above and belowground were smaller in the wet forests than in the seasonal forest. The differences in decomposition above and belowground may have implications for the importance of root decomposition in forests with strong abiotic constrains to soil biota activity.

The effect of soil mesofauna

Our results show the importance of the soil mesofauna in defining the decomposition process, as its exclusion had significant effects on decomposition in the three studied southeastern Brazilian Forests. However, the mesofauna effects depended on the forest type and litter decomposition environment being higher in the wet forests than in the Semi-deciduous Forest and belowground than aboveground. These results corroborated our third prediction, which stated that differences between mesofauna treatments would be smaller where moisture conditions constraint biological activities. This result suggests that the mesofauna effects depended on environmental limiting conditions, such as water deficit, an idea that has been stated by other authors. For example, Wall et al. (2008) found neutral effects of mesofauna exclusion in cold and dry forests, and Gonzalez and Seastedt (2001) reported disproportionally larger effects of soil mesofauna on litter decomposition rates in wet than dry tropical forests. However, in a pan-tropical study, it has been reported that the mean annual precipitation and effects of mesofaunal exclusion were not correlated (Powers et al. 2009). This discrepancy may be related to differences in regional biotic conditions, such as the richness or functional mesofauna component groups, which could differ among sites (Wall et al. 2008) due to the wide spatial scale of the study of Powers et al. (2009) (23 forests in 14 countries on 3 continents). In the absence of climatic constraints, fauna biomass is concentrated on the surface litter and rapidly decreases in the upper few centimeters of the underlying soil (Paul and Clark 1989). However, in water-limited ecosystems, the activities of the soil fauna may be so inhibited that the fauna exclusion has no impact on the decomposition process, thus, explaining the lack of effect of mesofauna treatment founded aboveground in the Semi-deciduous Forest. This result reinforces the idea of climatic constraints being the major decomposition-controlling factor aboveground (Cusack et al. 2009; Gholz et al. 2000).

In conclusion, our study showed that, rather than the simple or double-exponential models frequently used in decomposition studies, the model that assumed an exponential decrease on the decomposition rates in a single organic compartment with increasing variance along time was more plausible to describe the decomposition process. Considering the several computation tools available today, we have less limitation in exploring new decomposition models that, in addition to good model fits, maintain the biological realism and stimulate insights about the mechanisms behind the decomposition process. Regarding the factors that affect leaf decomposition, our study suggests that humidity conditions are important to decomposition process in the studied southeastern Brazilian Forests. Furthermore, the higher differences among the forests aboveground suggest that belowground decomposition is much less affected by moisture constraints than aboveground and provides more conductive conditions to soil biota. In consequence, decomposition process is enhanced there, especially in water-limited forests. Moreover, the smaller effect of mesofauna in the seasonal forest aboveground indicates that hazard environmental conditions, such as moisture deficit, can inhibit mesofauna activities and ultimately annul their effects on decomposition.

References

Adair EC, Parton WJ, Delgrosso SJ, Silver WL, Harmon ME, Hall SA, Burke IC, Hart SC (2008) Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. Global Change Biol 14:2636–2660

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449

Ayres E, Steltzer H, Simmons BL, Simpson RT, Steinweg JM, Wallenstein MD, Mellor N, Parton WJ, Moore JC, Wall DH (2009) Home field advantage accelerates leaf litter decomposition in forests. Soil Biol Biochem 41:606–610

Bardgett RD, Bowman WD, Kaufmann R, Schmidt SK (2005) A temporal approach to linking aboveground and belowground ecology. Trends Ecol Evol 20:634–641

Bolker B and R Development Core Team (2012) bbmle: tools for general maximum likelihood estimation. R package version 1.0.4.1. http://CRAN.R-project.org/package=bbmle

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretical approach. Springer-Verlag, New York

Castanho CT, Oliveira AA (2008) Relative effects of litter quality, forest type and their interaction on leaf decomposition in southeastern Brazilian forests. J Trop Ecol 24:149–156

Cusack D, Chou WW, Yang WH, Harmon ME, Silver WL, LIDET Team (2009) Controls on long-term root and leaf litter decomposition in neotropical forest. Global Change Biol 15:1339–1355

Davidson ED, Verchot LV, Cattânio JH, Ackerman IL, Carvalho JEM (2000) Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry 48:53–69

Epstein HE, Burke IC, Lauenroth WK (2002) Regional patterns on decomposition and primary production rates in the US great plains. Ecology 83:320–327

Fragoso C, Lavelle P (1992) Earthworm communities of tropical rain forests. Soil Biol Biochem 24:1397–1408

Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biol 6:751–765

Gonzalez G, Seastedt TR (2001) Soil fauna and soil litter decomposition in tropical and subalpine forests. Ecology 82:955–964

Harmon M, Nadelhoffer K, Blair J (1999) Measuring decomposition, nutrient turnover, and stores in plant litter. In: Robertson G, Bledsoe C, Coleman D, Sollins P (eds) Standard methods for long-term ecological research. Oxford University Press, New York, pp 202–240

Jassal RS, Black TA, Novak MD, Gaumont-Guay D, Nesic Z (2008) Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand. Global Change Biol 14:1–14

Jenny H, Gessel SP, Bingham FT (1949) Comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci 68:419–432

Jordan CF, Herrera R (1981) Tropical rain forests: are nutrients really critical? Am Nat 117:167–180

Lavelle P, Blanchart E, Martin A, Martin S, Spain A, Toutain F, Barois I, Schafer R (1993) A hierarchical model for decomposition in terrestrial ecosystems: applications to soils of the humid tropics. Biotropica 25:130–150

Lousier JD, Parkson D (1976) Litter decomposition in a cool temperate deciduous forest. Can J Ecol 54:419–436

Melillo JM, Aber JD, Linkins AE, Ricca A, Fry B, Nadelhoffer KJ (1989) Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant Soil 115:189–198

Montagnini F, Jordan C (2002) Reciclaje de nutrientes. In: Kattan GH, Guariguata MR (eds) Ecologia y conservación de bosques neotropicales. Ediciones LUR, Cartago, pp 591–623

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331

Paul EA, Clark FE (1989) Soil Microbiology and Biochemistry. Academic Press, San Diego

Powers JS et al (2009) Decomposition in tropical forests: a pantropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. J Ecol 97:801–811

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. ISBN 3-900051-07-0

Rovira P, Rovira R (2010) Fitting litter decomposition datasets to mathematical curves: towards a generalized exponential approach. Geoderma 155:329–343

Rovira P, Kurz-Besson C, Coûteaux MM, Vallejo VR (2008) Changes in litter properties during decomposition: a study by differential thermogravimetry and scanning calorimetry. Soil Biol Biochem 40:172–185

Ruggiero PGC, Batalha MA, Pivello VR, Meirelles ST (2002) Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, southeastern Brazil. Plant Ecol 160:1–16

Salimon CI, Davidson EA, Victoria RL, Melo AWF (2004) CO_2 flux from soil in pastures and forests in southwestern Amazonia. Global Change Biol 10:833–843

Seastedt TR (1984) The role of microarthropods in decomposition and mineralization processes. Annu Rev Entomol 29:25–46

Smith AC, Bhattib JS, Chenc H, Harmond ME, Arpa PA (2011) Modelling above- and below-ground mass loss and N dynamics in wooden dowels (LIDET) placed across North and Central America biomes at the decadal time scale. Ecol Model 222:2276–2290

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Blackwell, Oxford

Veloso HP (1992) Sistema fitogeográfico. In: Veloso HP (ed) Manual Técnico da Vegetação Brasileira. Séries Manuais Técnicos em Geociências, Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, pp 9–38

Vitousek PM, Sanford RL Jr (1986) Nutrient cycling in moist tropical forest. Ann Rev Ecol Syst 17:137–167

Wall DH, Bradford MA, ST Johnz MG et al (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biol 14:2661–2677

Wieder RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63:1636–1642