# Litter decomposition in the Atlantic Rainforest of Brazil

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# Erklärung

Ich versichere, dass ich meine Dissertation mit dem Titel

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Marburg, den 31.05.2011

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# Chapter 1

# General Introduction

## Tropical forests

Covering only some 7 % of earths land surface, tropical rainforests are supposed to provide habitat for more than two third of earths species, most of them still unknown (Wilson, 1992). Beside their importance for sustaining earth's biodiversity, tropical rainforests play a crucial role in global carbon cycling and hence climate stability (IPCC, 2001). Nevertheless between 35 % to 50 % of the original tropical closed-canopy forest has already been removed and transformed into farmland, pasture, plantation or secondary forests (Wright, 2005). During the 1990s the estimated net loss of tropical forests was somewhere between 50,000 and 120,000 $km^2$ $yr^{-1}$ (Wright and Muller-Landau, 2006), with still increasing deforestation rates in Asia and the Brazilian Amazon (Fearnside and Barbosa, 2004; Hansen and DeFries, 2004). Hence, tropical rainforests are among the worlds most threatened ecosystems.

In South America the Atlantic Forests hold an eminent position, in terms of biodiversity as well as in terms of endangerment by human impact. These forests are known to maintain an extraordinary number of species with a very high degree of endemism. For example, of an estimated 20,000 plant species about 8000 are thought to be endemic to the Atlantic Rainforest. There are 261 mammal species (73 endemic ), 620 bird species (181 endemic ), 200 reptile species (60 endemic ), 280 amphibian species (253 endemic) and a vast number of invertebrates undescribed yet (Myres et al., 2000). Silva and Casteleti (2003) suggested, that the Atlantic Rainforest may harbour 1-8 % of the world's total species. These extraordinary high values of biodiversity are supposed to be due to environmental heterogeneity as caused by strong latitudinal, longitudinal and altitudinal differences among biogeographical sub-regions of the Atlantic Forest (Silva and Casteleti, 2003). Myres et al.

(2000) named the Atlantic forest among the eight “hottest hotspots” of biodiversity on earth.

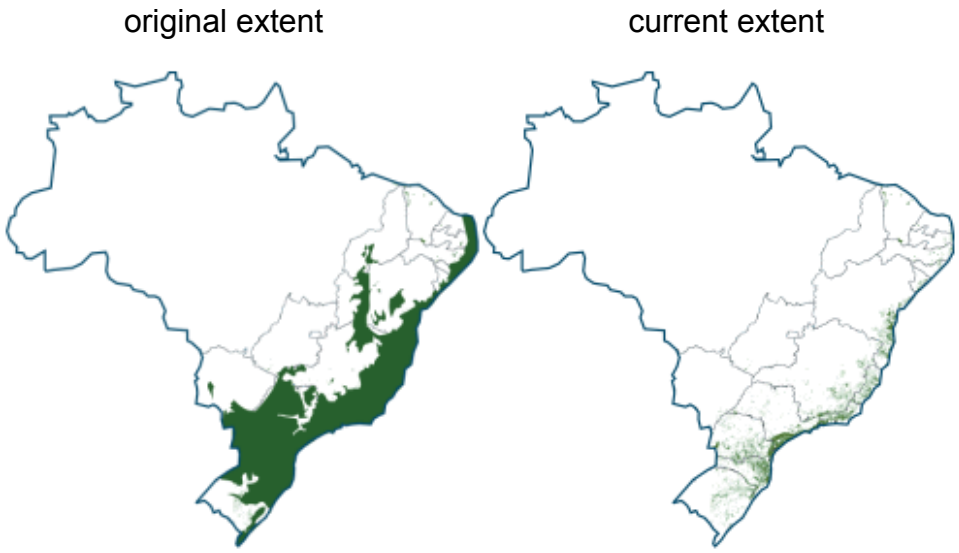


**Figure 1:** Original and current extent of the Atlantic Forest. (Adopted from the SPVS (Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental - Society for Wildlife Research and Environmental Education - www.spvs.org.br)).

Following Galindo-Leal and Câmara (2003) the Atlantic Forest holds another record as the “[…] arguably most devastated and most highly threatened ecosystem on the planet”. A recent study estimates the amount of remaining Atlantic forest somewhere between 11 % and 16 % of the original 150 million ha (Ribeiro, 2009; Figure 1). This estimate includes intermediate secondary forests and small forest fragments (<100 ha), which corresponds to some 30 % - 40 % of the remaining forest. The value of these secondary forest fragments for conservation of biodiversity is still questionable (Bihn et al., 2008). Many species require relatively large fragments of pristine forest to maintain viable populations. Thus, destruction of such habitats is likely to be associated with a serious loss of species in tropical forests, particularly in the Atlantic Forest (Dirzo and Raven, 2003; Hansen et al., 2008; Metzger, 2009).

## Diversity and ecosystem functioning

Species loss due to human impact may also lead to a loss of functional diversity possibly with strong consequences for ecosystem functioning (Petchey and Gaston, 2002). Tilman (2001) defined functional diversity as

"[…] the value and range of those species and organism traits that influence ecosystem functioning". Hence, as species become extinct their specific functional traits get lost. Such loss in turn may have strong unpredictable consequences for the functioning of ecosystem processes (Naeem et al., 1994; Tilman, 1999). The importance of biodiversity as a key determinant for ecosystem processes and the underlying mechanisms are still a matter of debates (McCann, 2000). The *rivet hypothesis* (Ehrlich and Ehrlich, 1981) assumes a certain degree of redundancy among functionally similar species within a community (Figure 2 a2 ). The theoretical extremes of this hypothesis are represented in the *redundancy hypothesis* (Walker, 1992) on the one hand and the *equal importance hypothesis* (Vitousek and Hooper, 1993) on the other hand. The *redundancy hypothesis* suggests a high degree of functional similarity between species resulting in a curvilinear relationship between diversity and ecosystem functioning (Figure 2 a1 ). By contrast, the *equal importance hypothesis* suggests that all species are unique in their functional traits resulting in a linear relationship between diversity and ecosystem functioning (Figure 2 a3 ). In the former loss of species have no mentionable effect on ecosystem functioning whereas in the latter each

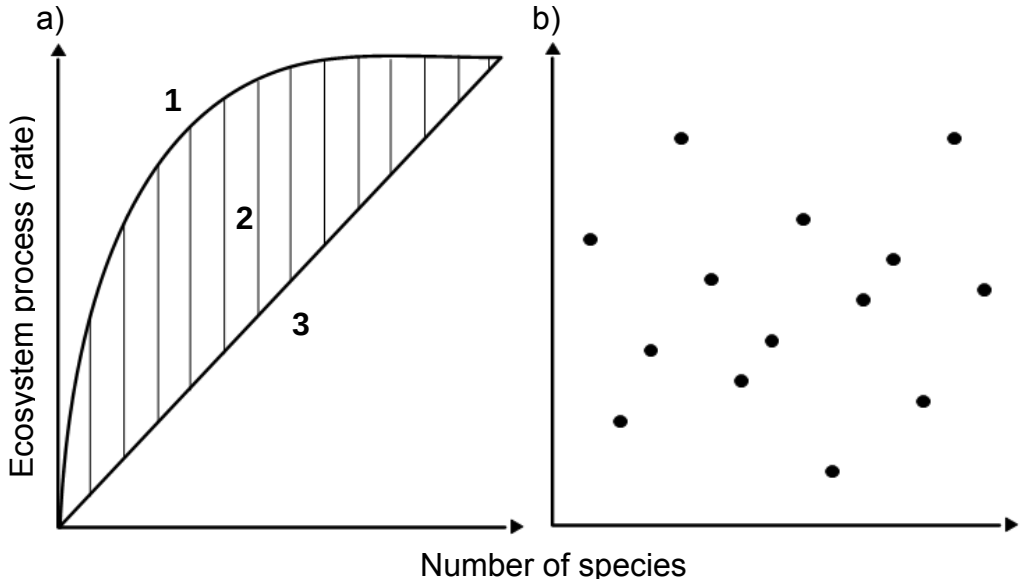


**Figure 2:** Possible relationships between ecosystem processes and the number of species following the a1) redundancy hypothesis, a2) rivet hypothesis, a3) equal importance hypothesis, b) idiosyncratic response hypothesis. (adapted from Johnson et al., 1996)

extinction of a species leads to a decrease in functional diversity with potential effects on ecosystem processes. All these hypotheses rest on the number of species. The *idiosyncratic response hypothesis* (Lawton, 1994) represents a contrasting view. It assumes that because of the complex and varied influences of individual species the relationship between ecosystem functioning and species diversity becomes unpredictable (Figure 2 b) (Mikola and Setälä, 1998). In contrast to the *redundancy* and the *equal importance hypothesis* the *idiosyncratic response hypothesis* rests on the importance of single species i.e. species identity. An understanding of the relationship between important ecosystem processes and species diversity is crucial for conservation and restoration management (Palmer et al., 1997). If the *rivet hypothesis* is more applicable, restoration efforts should concentrate on the number of species, which should depend on the degree of redundancy. The identity of species would be of minor interest. By contrast, if the *idiosyncratic response hypothesis* is more appropriate, the main focus would be on the selection of particular species.

## Litter decomposition

Decomposition of dead organic matter is one of the most important ecosystem processes (Swift et al., 1979). Depending on the ecosystem about 60 % – 100 %, of the net primary production enters the decomposition pathway, mainly as plant litter (Cebrian, 1999). In general, plants are unable to utilize complex organic compounds. Thus, essential nutrient elements such as P, S, K, Ca, Mg and in particular N bound in organic compounds have to be mineralised i.e. converted into inorganic forms which could be utilized by plants. Mineralization is performed by the decomposer community. The recycling of essential nutrient elements is vital for the maintenance of primary production because plants depend in their nutrient uptake on the continuous replenishment of the soil nutrient pool. In particular in tropical regions were nutrient uptake by plants is very high and nutrient storage capacity of soils mostly very low optimal functioning of the decomposition process is mandatory. The

decomposition process represents the link between the above- and the belowground part of the ecosystem. Mediated by the decomposer organisms complex interactions between plants and their nutrient pool the so called plant-soil feedback (Ehrenfeld et al., 2005) have been developed. It has been suggested that besides other factors, such interactions account for the high plant species diversity in high productive ecosystems like tropical forests (Bever et al., 1997; Mazzoleni et al., 2007; Miki et al., 2010).

## Dissertation Outline

The intention of my dissertation is to gain insights into litter decomposition dynamics in the Atlantic Forest of Brazil. I performed three studies on different topics related to litter decomposition. They deal with the diversity of litter mixtures as a potentially important factor that influences the decomposition process (Chapter 2), the diversity and successional dynamics of litter dwelling fungi, an important group of decomposers (Chapter 3) and the relationship between litter quality and the decomposer community (Chapter 4).

### *Diversity and ecosystem functioning: Litter decomposition dynamics in the Atlantic Rainforest*

Climate, litter quality i.e. decomposability and the decomposer community are the most important factors for decomposition (Cadish and Giller, 1997; Coleman et al., 2004). Other probable factors are plant species diversity and the composition of litter (reviewed by Hättenschwiler et al., 2005). That is, plant species diversity may influence decomposition dynamics in terms of plant species richness and / or plant species composition. Effects of plant species richness on decomposition dynamics in litter mixtures may arise from direct or indirect interactions between component species. They are independent of the identity of the component plant species and lead to non-additive decomposition dynamics of litter mixtures (Ball et al., 2008). By contrast, plant species composition may affect litter

decomposition in two different ways. First compositional effects may arise from the interactions of certain plant species leading to non-additive decomposition dynamics. Second, the presence/absence of certain plant species leads to additive decomposition dynamics. In both cases, the identity of the plant species is important. With regard to the relationship between diversity and ecosystem functioning a plant species richness effect would point to the *rivet hypothesis* and a plant species composition effect would point to the *idiosyncratic response hypothesis* (see above). The first study of this thesis (Chapter 1) refers on the influence of litter diversity on decomposition in the highly species-diverse Atlantic Rainforest in Brazil. In particular, I analyse whether litter decomposition is affected by species richness or species composition of the litter or both. Because these effects might be largely attributed to the soil biota involved, I also examine the effect of invertebrate exclusion. I intend to draw conclusions on the relationship between the decomposition subsystem and plant species diversity in the Atlantic Rainforest. The results of the study also provide valuable implications for conservation or reforestation management in this highly endangered ecosystem.

### *Succession of litter dwelling fungi along a forest successional gradient in the Atlantic Rainforest of Brazil*

Fungi are able to shift their community structure during decomposition which is known as micro-scale succession (Suzuki, 2002). Such flexibility ensures a highly effective recycling of essential nutrient elements (Swift, 1979). By contrast, so called macro-scale succession, describes changes in the fungal community following changes in the plant community after large scale disturbances, such as forest fires or deforestation (Suzuki, 2002). Here, the recovery of fungi communities may take several years until initial conditions are regained (Horikoshi et al., 1986). The succession of fungi strongly depends on the succession of plant communities and *vice versa*. Hence, changes in plant species richness or composition caused by disturbance may also have severe impacts on the diversity of decomposing fungi communities which in turn may influence the

decomposition process. The aim of Chapter 3 of this thesis is to provide a first assessment of litter dwelling fungi diversity, its successional dynamics and its relationship to tree species succession in two nature reserves of the Atlantic Forest along a successional gradient. I analyse if species richness and species diversity of litter dwelling fungi and trees increase with successional age and if the community composition of fungi and trees differ among successional stages. Further, I investigate if species richness of litter dwelling fungi increase with increasing tree species richness and if sites with similar tree communities are also characterized by similar fungi communities. The study focuses on litter dwelling fungi because of their substantial impact on the decomposition process by breaking down organic matter.

### *Lack of home-field advantage in the decomposition of leaf litter in the Atlantic Rainforest of Brazil*

Factors that influence decomposition rather act in concert than on their own (Lavelle et al., 1993; Aerts, 1997; Gartner and Cardon, 2004). This is in particular true for litter quality and the decomposer community. It has been suggested, that decomposer communities may be strongly adapted to the decomposition of litter of a certain plant species or more precisely on the decomposition of litter from the plants above them (Ayres et al., 2009a). This suggests that the decomposer community should decompose litter from its home site faster than litter from any other site. Such strong dependence between the decomposer community and their litter substrate has been referred to as home-field-advantage or in short HFA (Gholz et al., 2000). Two important preconditions must be fulfilled for the formation of HFA. First, litter quality should be relatively low due to decomposition inhibiting secondary compounds or recalcitrant tissues. Litter material of high quality or rather good decomposability without such constraints is likely to be decomposed in the same efficiency by different decomposer communities. No specific adaptations are necessary (Hunt et al., 1988; Strickland et al., 2009 a,b). Second, the capability of the decomposer community to adjust quickly to different substrates should be

low. A highly adjustable decomposer community is expected to decompose different litters at equal rates after short time of incubation. Microbial decomposer communities are known to be able to adjust quickly to various substrates by shifting their community structure (Goddard and Bradford 2003; Hanson et al. 2008). Hence macro- and meso-invertebrate decomposers are possibly more important for the formation of HFA than microbial decomposer communities. Despite these preconditions it has been suggested, that HFA is more rule than exception (Ayres, 2009b). However, this suggestion based solely on studies that examine monospecies litter. Whether HFA could also be supported for multispecies litter mixtures such as tropical forests litter, is still questionable.

Chapter 3 of this thesis deals with the relationship between the decomposer community and associated leaf litter on forest sites of different successional age. I intend to ascertain whether HFA occurs in multispecies litter mixtures. To my knowledge, this is the first study that examines HFA in a tree species rich ecosystem using natural litter mixtures. I expect HFA between successional sites because of considerable differences in tree species composition and general litter quality along the successional chronosequence. I further argue that the strength of HFA should increase with increasing difference in successional age. Using a litterbag approach, I aim to investigate the role of invertebrate decomposers for HFA and their relative importance along a successional gradient. I expect valuable insights into the successional dynamics of the function of the decomposer subsystem of an Atlantic Rainforest and its resilience after deforestation and pasturing.

## The study area

The presented studies took place in two nature reserves in the Atlantic Forest in Brazil. The experimental studies (Chapter 2 and Chapter 4) were carried out in the Rio Cachoeira Nature Reserve near the city of Antonina in the coastal region of the Brazilian State of Paraná (approx. 25.25° S, 48.68° W). The assessment of litter dwelling fungi diversity (Chapter 3) was additionally conducted in the Serra do Itaqui Nature Reserve (approx.

25.29° S, 48.32° W) some 25 km off the Rio Cachoeira Nature Reserve. Both reserves are owned and managed by the Society for Wildlife Research and Environmental Education (SPVS - Sociedade de Pesquisa em Vida Selvagem e Educação Ambiental). Following Köppen`s classification the climate in both study regions is characterised as *Cfa* (mesothermic humid subtropical). Mean temperature varies between 16°C and 26°C and annual precipitation between 2000 and 3000 mm. The climate shows seasonality with lower precipitation and temperature during autumn and winter (March – August). The topography of the study region is variable and ranges from littoral plains to the “Serra do Mar” mountain range with altitudes between 0 and 600 m above sea level. All study sites were located on well-drained Cambisols (FAO, 1998). Independently of successional stage, for the depth of 0-5 cm, the soil was classified as a clayey (44,5 % of clay, 17,1 % of silt, 38,4 % of sand), acidic ($pH_{CaCl2}$ = 3,9) and with a low level of basic cations ($K^+$= 0,2 $cmol_c$ $dm^{-3}$, $Ca^{2+}$= 0,8 $cmol_c$ $dm^{-3}$, $Mg^{2+}$= 0,5 $cmol_c$ $dm^{-3}$). The average level of Total N was of 0,3 mg $dm^{-3}$, and P-Mehlich equal to 8,3 mg $dm^{-3}$, characterizing a low availability of nutrients for all sites. The original vegetation is characterised as *submontane ombrophilous dense atlantic forest* (IBGE, 1992). However, most of the original forests have been converted into pasture and now regenerate under the management of the SPVS. Thus, the study regions comprise old-growth forest patches, secondary forests in differing stages of succession and pastures.

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# Chapter 2

# Diversity and ecosystem functioning: Litter decomposition dynamics in the Atlantic Rainforest

with Kelly Geronazzo Martins, Martin Brändle, Martin Schädler, Renato Marques, Roland Brandl

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## Abstract

The relationship between ecosystem functioning and species diversity is important for conservation and restoration management of endangered ecosystems. Here we experimentally analysed the effects of tree species richness and composition on the fundamental ecosystem process of leaf litter decomposition in the Brazilian Atlantic Rainforest. We measured the decomposition rates of leaf litter of eight broad-leaved, native tree species either individually or in mixtures of two, four, or six species. Additionally, we analysed the effect of macro- and meso-invertebrate exclusion using coarse- and fine-meshed litter bags. Species composition, but not species richness, significantly influenced litter decomposition rates. Invertebrate exclusion also influenced litter decomposition, although this effect varied between species and mixtures. Overall, litter decomposition dynamics was non-additive, i.e. observed decomposition rates of litter mixtures differed from what would be expected from the decomposition rates of their component species. However, there were also differences between mixtures, which could be at least partly attributed to the varying influence of invertebrates. We conclude that the relationship between the decomposition subsystem and species diversity in the Atlantic Rainforest follows the idiosyncratic response hypothesis and not the rivet hypothesis. For conservation or reforestation management, our results emphasise the need to maintain or restore the composition of locally native tree species communities rather than to maintain only a high tree species richness.

## Introduction

The relationship between biodiversity and ecosystem processes is of central interest to assess the effect of global change on ecosystem functioning (Hooper et. al., 2005; Cardinale et al., 2006; Balvanera et al., 2006). Ecosystem processes may dramatically change as species become extinct, often with unpredictable consequences (Naeem et al., 1994; Tilman, 1999). A great number of species will be lost especially in species-rich tropical rainforests owing to human activity (Dirzo and Raven, 2003; Hansen et al., 2008). Nearly 50 % of the tropical closed-canopy forest has already been transformed into farmland, pasture, plantation or secondary forest (Wright, 2005). Hence, the accompanying loss of species may have severe impacts on tropical ecosystem functions, but more experimental investigations are needed.

The recent debate on the importance of biodiversity as a key determinant for ecosystem processes and stability prompted a flood of experimental and theoretical studies on the underlying mechanisms and patterns (McCann, 2000). The early hypotheses — the rivet hypothesis (Ehrlich and Ehrlich, 1981) and the idiosyncratic response hypothesis (Lawton, 1994) — provide a conceptual basis for the interpretation of observed patterns. Their basic difference lies in the importance placed on species identity and species richness. The rivet hypothesis assumes a certain degree of redundancy between functionally similar species within a community, whereas the idiosyncratic response hypothesis assumes the unpredictability of the relationship between ecosystem functioning and species diversity because of the complex and varied influences of individual species (Mikola and Setälä, 1998). Thus, species richness has a greater relevance in the rivet hypothesis, and species identity has a greater impact in the idiosyncratic response hypothesis. The former hypothesis has been further modified according to the assumed degree of redundancy of species (see redundancy hypothesis, Walker, 1992; and equal importance hypothesis, Vitousek and Hooper, 1993).

An understanding of the relationship between important ecosystem processes and species diversity would provide valuable implications for conservation and restoration management (Palmer et al., 1997). If the

relationship follows the rivet hypothesis, the main focus of restoration would be on the number of species, depending on the degree of redundancy. Which species are present would be of minor interest. If the relationship follows the idiosyncratic response hypothesis, the main focus would be on the actual species used for restoration.

The decomposition of plant litter is an essential process in terrestrial ecosystems, resulting in carbon and nutrients being recycled for primary production (Swift et al., 1979). Given that most of the plant material produced is in this way returned to the ecosystem, the importance of plant species richness and composition for ecosystems may be largely determined by their impact on litter decomposition (Wardle et al., 1997; Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Species richness effects on decomposition dynamics in litter mixtures arise from direct or indirect interactions between component species, independent of their identity, which leads to non-additive decomposition dynamics of litter mixtures (Ball et al., 2008). Compositional effects arise from the interactions or the presence/absence of certain species. Interactions between certain species lead to non-additive decomposition dynamics. If there are no interactions, but species differ in their decomposability, presence/absence of certain species leads to additive decomposition dynamics .In both cases, the identity of the species is important. A pure species richness effect would point to a relationship between diversity and litter decomposition following the rivet hypothesis, whereas a compositional effect would indicate an idiosyncratic relationship.

In previous studies on the effect of species richness and composition of litter mixtures on decomposition rates, non-additive effects of combining different litter types dominated, whereas the species richness of litter assemblages did not seem to be an important driver of decomposition processes (for reviews, see Gartner and Cardon, 2004; Hättenschwiler et al., 2005). The non-additive effects of mixing different litter types on decomposition dynamics are mostly attributed to the activity of the decomposer fauna (Hättenschwiler and Gasser, 2005; Schädler and Brandl, 2005). Thus, an effect of species richness and/or species composition on litter decomposition should be mediated by changes in the

activity of soil biota involved in decomposition. A plant-species-rich litter mixture may support a species-rich invertebrate fauna because of (i) differences in the attractiveness of certain litter types to different species of invertebrates and (ii) increased microhabitat diversity. Such a complementary use of resources by the decomposers may lead to an increased decomposition rate. Evidence for these effects is, however, scarce, and most studies point to the overwhelming importance of litter type identity and quality rather than the plant species richness of the litter for faunal diversity (Wardle et al., 2006; Zhang et al., 2008).

Litter decomposition is particularly important in the tropics because of the low nutrient storage capacity and the high turnover and uptake of nutrients in tropical soils. Furthermore, invertebrate fauna contribute comparatively more to decomposition in the tropics than in lower or higher latitudes because of the more favourable and stable climatic conditions (Heneghan et al., 1998; Lavelle et al., 1993; Beck, 2000; Gonzalez and Seastedt, 2001; Wall et al., 2008; Schmidt et al., 2008; Yang and Chen, 2009). Thus, invertebrate fauna may play a much greater role as agents of non-additive litter mixing effects in the tropics.

We investigated the influence of litter species richness, litter mixture composition, and invertebrate activity on litter decomposition in the highly species-diverse Atlantic Rainforest in Brazil. This rainforest is highly endangered: only 11.7 % of the original 150 million ha remain (Ribeiro et al., 2009). Of these remnants, 32–40 % are small fragments (<50 ha) or less-species-rich secondary forests. This trend of forest destruction, fragmentation and transformation into secondary forests causes a serious loss of biodiversity at the local and regional scales (Laurance, 2007; Barlow et al., 2007; Bihn et al., 2008; Metzger, 2009). Hence, it is important to investigate whether this loss of biodiversity causes a change in ecosystem functioning, e.g. in litter decomposition and consequently in nutrient and carbon cycling. In this context, we investigated whether litter decomposition is affected by species richness or species composition of the litter or both. Because these effects might be largely attributed to the soil biota involved in the decomposition, we also examined the effect of invertebrate exclusion. Our results allow us to

draw conclusions on the relationship between the decomposition subsystem and plant species diversity in the Atlantic Rainforest.

## Materials and methods

### *Study site*

As a part of the MATA ATLANTICA Project, a German–Brazilian cooperation, this study was initiated in the Atlantic Rainforest in the Brazilian state of Paraná, in the Cachoeira nature reserve (25.25° S, 48.68° W, 147 NN). The study area consists of secondary rainforest sites of different successional age (5 to >100 years) after usage as pasture. A forest site of medium successional age (35–50 years) was chosen for our experiment as it provides sufficient tree species on a small local scale and represents an achievable aim for reforestation.

### *Experimental set-up*

The eight most abundant broad-leaved tree species on the study site were chosen for the experiment (Table 1). Mature leaves were sampled directly from trees in July/August 2007. Leaves were air-dried, and a sub-sample of each type was oven-dried to determine dry weight. Air-dried leaves (4 ± 0.1 g) of each tree species were placed in litter bags (25 cm × 25 cm). In addition, air-dried leaves of two randomly chosen species (2 ± 0.08 g each; four different mixtures), four randomly chosen species (1 ± 0.06 g each; four different mixtures), and six randomly chosen species (0.66 ± 0.04 g each; four different mixtures) were placed in litter bags (Table 1). In this way, component species as well as species composition were replicated, and effects of species composition and of species richness could be separated (Schmid et al., 2002). Each litter bag set-up was replicated 20 times. The nylon litter bags used for half of the replicates were of a coarse mesh size (5 mm × 5 mm) to allow passage of soil macro- and meso-invertebrates. The other nylon litter bags were of a fine mesh size (20 µm × 20 µm) to exclude macro- and meso-fauna, but to allow access by bacteria, fungal hyphae, nematodes and protozoa. We are aware, that litter bags, especially fine-meshed bags, have the potential

to alter the microclimate within the bags by influencing moisture and temperature (Bradford et al., 2002). As this effect is greater for fine-meshed bags, differences between decomposition rates within fine and coarse-meshed bags might be due to microclimatic differences rather than invertebrate exclusion. Nevertheless, due to the favourable and stable climatic conditions on our study site, microclimatic differences should be less important than invertebrate exclusion.

**Table 1:** Plant species used, Mixture composition and *k*-values after 6 months

| Species No. | Species | Family | *k*-value | |
|---|---|---|---|---|
| | | | fine-meshed litter bag | coarse-meshed litter bag |
| 1 | *Alchornea glandulosa* (Ag) | *Euphorbiaceae* | 2.13 | 3.93 |
| 2 | *Alchornea triplinervia* (At) | *Euphorbiaceae* | 2.92 | 4.34 |
| 3 | *Cabralea canjerana* (Cc) | *Meliaceae* | 2.23 | 3.76 |
| 4 | *Marliera tomentosa* (Mt) | *Myrtaceae* | 0.92 | 0.78 |
| 5 | *Matayba guianensis* (Mg) | *Sapindaceae* | 1.44 | 1.57 |
| 6 | *Pera glabrata* (Pg) | *Euphorbiaceae* | 1.12 | 2.90 |
| 7 | *Inga edulis* (Ie) | *Fabaceae* | 1.24 | 1.35 |
| 8 | *Sloanea guianensis* (Sg) | *Elaeocarpaceae* | 1.52 | 1.89 |
| Mixture No. | Mixture | | | |
| 9 | Mt, Pg | | 0.94 | 1.31 |
| 10 | Ie, Pg | | 1.04 | 1.81 |
| 11 | Mt, Sg | | 1.27 | 1.40 |
| 12 | At, Mg | | 1.77 | 2.60 |
| 13 | Sg, Pg, Mt, Cc | | 1.40 | 2.01 |
| 14 | Pg, Mg, Cc, At | | 1.60 | 2.49 |
| 15 | Mg, Ag, Sg, At | | 1.91 | 2.68 |
| 16 | At, Mt, Mg, Sg | | 1.40 | 1.68 |
| 17 | Cc, Mt, Sg, Ag, At, Pg | | 1.68 | 2.27 |
| 18 | At, Mt, Ag, Cc, Pg, Ie | | 1.59 | 2.35 |
| 19 | Mg, Pg, Cc, Ag, Mt, Sg | | 1.62 | 1.93 |
| 20 | At, Mt, Sg, Cc, Pg, Mg | | 1.64 | 2.24 |

In August 2007, the litter bags were placed in five blocks (about five meters apart) using a randomised block design (two replicates per mesh size within each block). The forest floor was cleared of litter cover to avoid an artificial increase in litter diversity. Litter bags were placed on the bare soil and secured with wire hooks. Half of the litter bags were collected after 3 months, and the other half after 6 months. Thus, the total number of litter bags was 400 with 20 mixtures (including single species) x 2 mesh sizes x 5 blocks x 2 sampling dates. The leaf material remaining in the bags was oven-dried, cleaned (by carefully removing adhesive dirt with a

paintbrush) and weighed. The remaining leaf mass of all samples was incinerated at approx. 600°C to obtain ash-free dry weight to account for inorganic contamination. The decomposition rate was defined as the percent dry-weight loss. As a measure for decomposability we calculated *k*-values after 6 months of decomposition according to Olson (1963) for each of the litter types.

### *Data analysis*

The percent dry-weight loss was arcsine square-root transformed prior to all statistical analyses to approximate the normal distribution of residuals and to reduce variance heterogeneity. A nested general linear model (GLM) type III sum of squares was used to test the effects on decomposition rates of species richness, species composition (leaves of single species and mixtures; nested in richness), invertebrate exclusion, and time. Blocks were considered as a random factor in the analysis. The effect of invertebrate exclusion for each species and mixture was additionally tested by ANOVA.

Another approach was used to examine additive and non-additive effects of species loss following the method suggested by Ball et al. (2008). For this, a GLM (type I) sum of squares with litter disappearance as the dependent variable was used. We sequentially included time, block and the presence/absence of each single species as factors in the model. Time had two levels, and block had five levels. The species presence/absence terms had two levels each. As we used type I sum of squares, the order in which the presence/absence terms were included was important. We calculated omega square effect size from a GLM with type III sum of squares with percentage dry-weight loss as dependent variable and all single species as independent variables and included them into the former model in ascending order. We also included the interactions between presence/absence terms and time. Then we included a species interaction term with 20 levels, each representing one of the litter mixtures. A significant species interaction term would indicate non-additivity owing to species richness and/or composition of litter mixtures. Next, we included a species richness term with four levels (1, 2, 4, and 6

species) instead of the species interaction term to explore whether species richness is responsible for non-additive effects. If the richness term was significant, we again included the species interaction term representing the effect of composition into the model and retained the richness term. Significance of both terms would indicate the co-occurrence of non-additive richness and composition effects. Additionally we included an invertebrate exclusion term (two levels) to test whether additive or non-additive effects could be attributed to the activity of the decomposer fauna. We dealt with this term as with the richness term above.

To explore whether additivity or non-additivity was consistent throughout the mixtures, we used the method of Wardle et. al. (1997) and investigated whether the decomposition rates of each leaf litter mixture can be predicted from the decomposition rates of individual leaf litter types. For this, the expected amount of dry weight remaining in leaf mixtures ($R_e$) was calculated by using the observed mass loss of individual leaf litter types, assuming no diversity effects. We used the formula: [$R_e = \sum m_i \times p_{mi}$], with $m_i$ = initial mass of leaves of species *i* in the mixture and $p_{mi}$ = decomposition rate of leaves of species *i* without leaves of other species (Schädler and Brandl, 2005). This equation takes into account differences in initial leaf masses of component species. The observed litter masses remaining in mixtures ($R_o$) in relation to expected values were calculated as [$100 \times (R_o - R_e)/R_e$] per block. Deviations from zero indicate non-additive effects of litter mixing and were tested using 95 % confidence intervals. Additionally, another GLM (type lll sum of squares) was used to test the influence of species richness, species composition (nested in richness), invertebrate exclusion and time on the deviation of the remaining litter mass from the expected litter mass (see first analysis). Furthermore, we used an approach similar to that of Wardle et al. (1997) to investigate whether non-additive effects were generated by the presence/absence of invertebrates. For this, we calculated the expected influence of macro- and meso-invertebrates on the decomposition of leaf litter mixtures using the observed invertebrate effect on the component litter type when decomposing alone. This effect was

defined as the difference between remaining proportions of litter dry weight in fine- and coarse-meshed bags containing one leaf litter type. The expected remaining litter mass of mixtures in course-meshed bags ($Re_c$) was calculated as [$Re_c = Ro_{fj} + \sum m_i e_i$ ], with $Ro_{fj}$ = observed remaining litter mass of mixture $j$ in fine-meshed bags, $e_i$ = effect of invertebrates on decomposition of litter of species $i$, and $m_i$ = initial mass of component species $i$. Again we calculated the observed litter masses remaining in coarse-meshed bags ($Ro_c$) in relation to expected values as [$100 \times (Ro_c – Re_c)/Re_c$] per block and tested for significant deviations from zero as an indication of non-additivity using 95 % confidence intervals. All analyses were done using Statistica, version 6. For more information on the statistical procedures see Supplementary Table S1.

## Results

We found a great variation in $k$-values of the different litter types when decomposing alone in the presence (0.78–4.34) and absence (0.92–2.92) of invertebrates (Table 1).

**Table 2:** The effects of presence/absence of macro- and meso-invertebrates, tree species richness of the litter, mixture composition, and decomposition time on the decomposition rate of litter. The effects were tested using a nested GLM with type III sum of squares.

| Source | Decomposition rates | | | |
|---|---|---|---|---|
| | *df* | *MS* | *F* | *P* |
| Constant | 1 | 228.05 | 677.19 | < 0.001 |
| Fauna [F] | 1 | 0.90 | 32.74 | < 0.001 |
| Species richness$^{A}$ [S] | 3 | 0.18 | 0.55 | 0.653 |
| Mixture(species richness)$^{a}$ [M] | 16 | 0.33 | 12.09 | < 0.001 |
| Time [T] | 1 | 2.47 | 635.49 | < 0.001 |
| F × S$^{B}$ | 3 | 0.00 | 0.03 | 0.989 |
| F × M(S)$^{b}$ | 16 | 0.03 | 6.94 | < 0.001 |
| T × F | 1 | 0.04 | 14.29 | < 0.001 |
| S × T$^{C}$ | 3 | 0.01 | 1.40 | 0.278 |
| M(S) × T$^{c}$ | 16 | 0.00 | 0.97 | 0.521 |
| F × S × T$^{D}$ | 3 | 0.00 | 0.20 | 0.893 |
| F × M(S) × T$^{d}$ | 16 | 0.00 | 1.01 | 0.441 |
| Block | 4 | 0.01 | 2.31 | 0.06 |
| Residual | 307 | 0.00 | | |

Each term indicated by an upper case letter was tested against the term with the same letter in lower case; all other terms were tested against the residual. The factor M includes leaf litter mixtures as well as leaf litter of single tree species.

The amount of remaining litter mass was insufficient for a quantitative assessment of faunal activity during the decomposition process. However, in several cases we found diplopods and isopods which are important decomposers in our study region (Schmidt et al., 2008) within coarse-meshed litter bags. In contrast, within fine-meshed bags we did not find macro- or meso-invertebrates in any case (Gießelmann, pers. obs.). Thus, differences in decomposition rates between coarse- and fine-meshed bags could be attributed to the exclusion of macro-and meso-invertebrates.

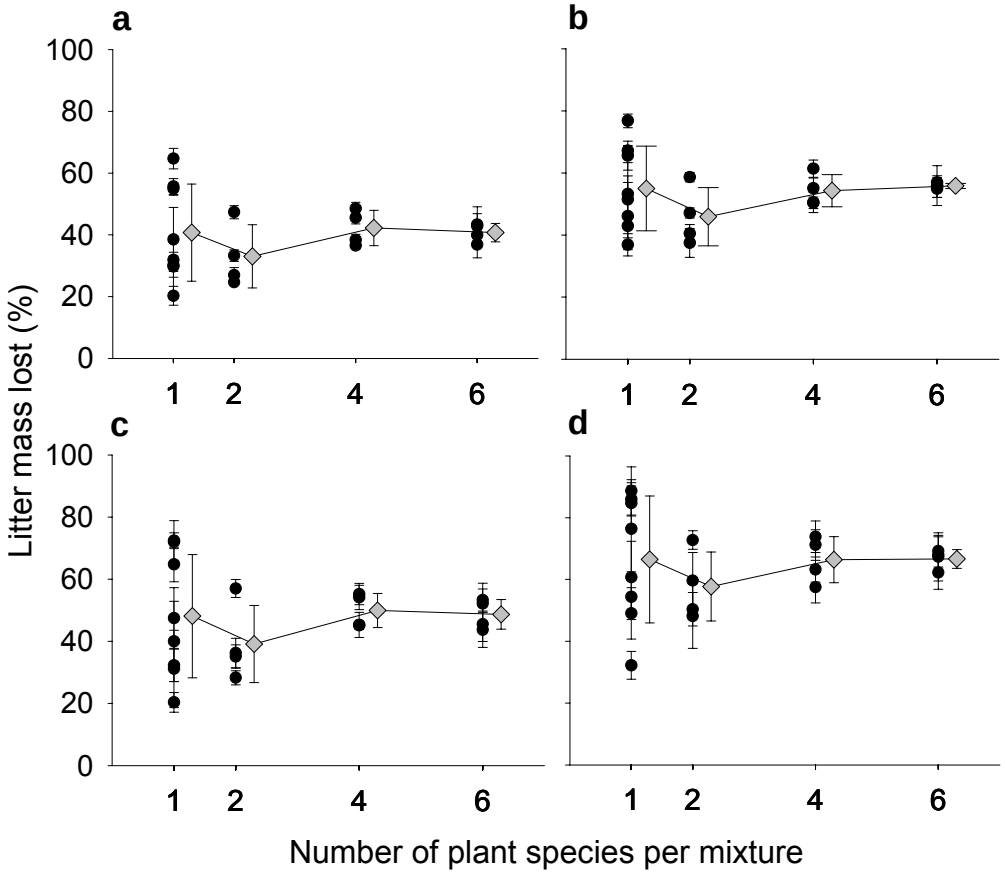


**Figure 1:** Percentage of the initial leaf litter mass lost for all tree species and mixtures (black circles; mean ± standard error, five replicates) and richness levels (grey diamonds; mean ± standard error, with species and mixtures as replicates), eight replicates for single species and four replicates for mixtures (a) after 3 months from fine-meshed bags, (b) after 6 months from fine-meshed bags, (c) after 3 months from coarse-meshed bags and (d) after 6 months from coarse-meshed bags.

The decomposition rates of leaf litter in our experiments were not influenced by the species richness of the mixtures (Table 2). In contrast, we found a significant effect of litter composition. These effects were consistent over the 6 months of decomposition as neither the number of

species nor the species composition interacted with time (Table 2). We also found a decrease in the variability of litter decomposition across litter assemblages with increasing species richness (Figure 1). The GLM to test for additivity and non-additivity revealed that all except one *(Sloanea guianensis)* of the litter types used significantly influenced decay dynamics (Table 3). This was consistent over time for all species (no significant interactions). Furthermore, the species interaction term had a significant influence on litter decomposition (Table 3). When the interaction term was replaced with the richness term, the richness term had no influence on litter decomposition (*P*=0.064). The observed and predicted values of the remaining litter mass of half of the mixtures significantly deviated in at least one case, which indicated non-additive effects (Figure 2). These deviations could not be explained by any of the main factors. However, the species composition interacted significantly with time and invertebrate exclusion (Table 4).

**Table 3:** Additive and non-additive effects of leaf litter mixing on leaf litter decomposition. The effects were tested using a GLM with type I sum of squares.

| Source | Decomposition rates | | | |
|---|---|---|---|---|
| | *df* | *MS* | *F* | *P* |
| Time | 1 | 2.60 | 523.26 | <0.001 |
| Block | 4 | 0.01 | 1.25 | 0.291 |
| *Sloanea guianensis* | 1 | 0.01 | 1.92 | 0.166 |
| *Pera glabrata* | 1 | 0.12 | 24.67 | <0.001 |
| *Alchornea glandulosa* | 1 | 0.85 | 170.68 | <0.001 |
| *Matayba guianensis* | 1 | 0.05 | 9.16 | <0.001 |
| *Inga edulis* | 1 | 0.42 | 85.18 | <0.001 |
| *Cabralea canjerana* | 1 | 0.80 | 160.31 | <0.001 |
| *Alchornea triplinervia* | 1 | 0.74 | 149.38 | <0.001 |
| *Marliera tomentosa* | 1 | 1.47 | 295.12 | <0.001 |
| Species interaction term | 11 | 0.12 | 24.66 | <0.001 |
| Fauna | 1 | 1.00 | 201.24 | <0.001 |
| Time*_Sloanea guianensis_ | 1 | 0.0014 | 0.27 | 0.602 |
| Time*_Pera glabrata_ | 1 | 0.0086 | 1.73 | 0.189 |
| Time*_Alchornea glandulosa_ | 1 | 0.0012 | 0.24 | 0.625 |
| Time*_Matayba guianensis_ | 1 | 0.0019 | 0.38 | 0.535 |
| Time*_Inga edulis_ | 1 | 0.0017 | 0.34 | 0.562 |
| Time*_Cabralea canjerana_ | 1 | 0.0185 | 3.72 | 0.054 |
| Time*_Alchornea triplinervia_ | 1 | 0.0001 | 0.03 | 0.867 |
| Time*_Marliera tomentosa_ | 1 | 0.0000 | 0.01 | 0.929 |
| Time*Species interaction term | 11 | 0.0040 | 0.81 | 0.632 |
| Time*Fauna | 1 | 0.07 | 13.50 | <0.001 |
| Residual | 345 | 0.01 | | |

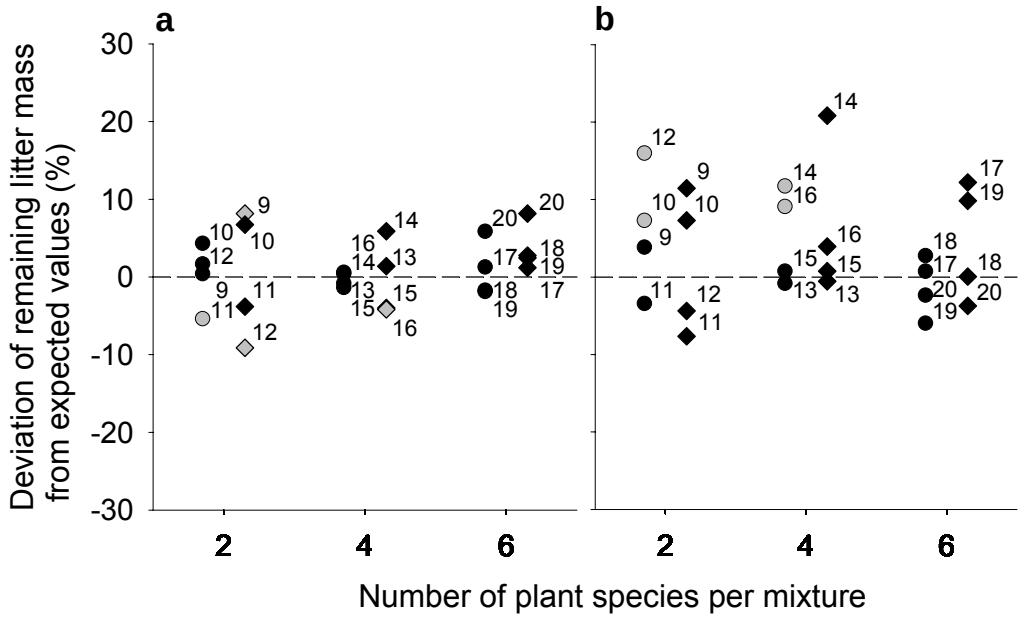


**Figure 2:** Percent deviation of observed litter mass remaining from expected values calculated from the leaf litter of one species decomposing alone, in the presence (diamonds) and absence (circles) of macro- and meso-invertebrates after (a) 3 months and (b) 6 months. Grey symbols indicate significant deviation from zero (95 % confidence interval). Each symbol refers to the mean of a mixture over all blocks (five replicates). Numbers indicate the mixtures (see Table 1). Positive deviations indicate antagonistic effects (i.e. decreased decomposition rates) and negative deviations indicate synergistic effects (i.e. increased decomposition rates).

**Table 4:** The deviation of the remaining leaf litter mass from expected values. The effects of presence/absence of macro- and meso-invertebrates, tree species richness of the litter, mixture composition, and decomposition time were tested using a nested GLM with type III sum of squares.

| Source | Deviation from expected values | | | |
|---|---|---|---|---|
| | *df* | *MS* | *F* | *P* |
| Constant | 1 | 967.30 | 1.55 | 0.249 |
| Fauna [F] | 1 | 7.50 | 0.03 | 0.866 |
| Species richness$^{A}$ [S] | 2 | 11.17 | 0.03 | 0.971 |
| Mixture(species richness)$^{a}$ [M] | 9 | 379.57 | 0.98 | 0.492 |
| Time [T] | 1 | 471.49 | 2.76 | 0.131 |
| F × S$^{B}$ | 2 | 149.96 | 0.60 | 0.569 |
| F × M(S)$^{b}$ | 9 | 249.95 | 7.11 | 0.004 |
| T × F | 1 | 0.08 | 0.00 | 0.964 |
| S × T$^{C}$ | 2 | 164.47 | 0.96 | 0.418 |
| M(S) × T$^{c}$ | 9 | 171.02 | 4.86 | 0.014 |
| F × S × T$^{D}$ | 2 | 79.98 | 2.27 | 0.159 |
| F × M(S) × T$^{d}$ | 9 | 35.19 | 0.33 | 0.966 |
| Block | 4 | 358.38 | 3.31 | 0.012 |
| Residual | 182 | 108.32 | | |

Each term indicated by an upper case letter was tested against the term with the same letter in lower case; all other terms were tested against the residual. The factor M includes leaf litter mixtures as well as leaf litter of single tree species.

In general, the exclusion of invertebrates considerably decreased the litter decomposition rate. However, this effect varied between litter type and mixtures (significant interaction; Table 2). After 3 months as well as after 6 months, the decomposition of the litter of half of the individual leaf types as well as of the litter of mixture 11 did not significantly differ in the presence and absence of invertebrates. Mixture 9 also showed no significant effect of invertebrate exclusion but only after 6 months (Figure 3).

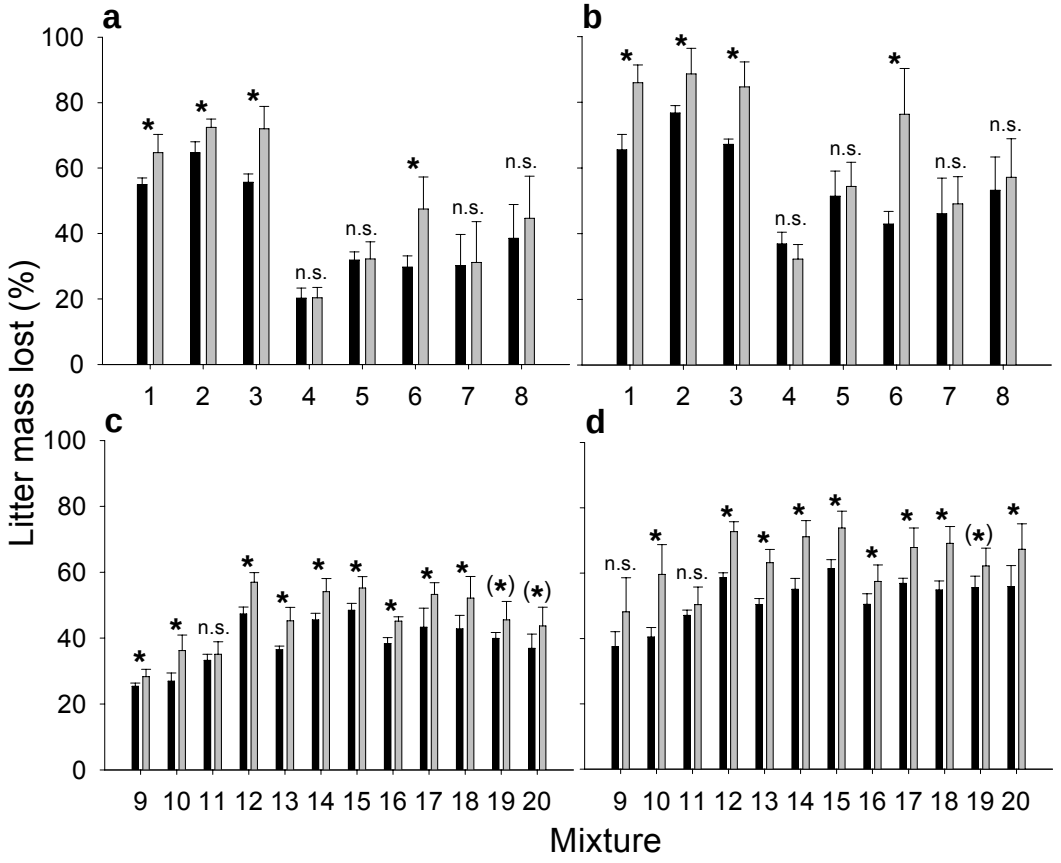


**Figure 3:** Percentage of the initial leaf litter mass lost in the presence (grey bars) and absence (black bars) of macro- and meso-invertebrates for single species after (a) 3 and (b) 6 months and for mixtures after (c) 3 and (d) 6 months, averaged over blocks; error bars are standard deviation. Asterisks indicate significant differences. Numbers indicate the mixtures (see Table 1).

The invertebrate exclusion treatment also interacted with time, which suggested a change in the contribution of invertebrates with ongoing decomposition (Table 2). In the test for additivity and non-additivity, invertebrate exclusion as well as its interaction with time showed a significant influence (Table 3). Furthermore, invertebrate presence/absence interaction with species composition had a significant

influence on the deviation of observed and expected decomposition rates (Table 4). However, significant deviations from expected values in the presence of invertebrates occurred only after 3 months (Figure 2). After 6 months, all significant deviations occurred in the absence of invertebrates, though some mixtures including invertebrates also strongly deviated from zero without being significant (Figure 2). These findings were supported by a comparison of the observed and expected influence of invertebrates. The same mixtures that showed significant deviations from expected decomposition rates (Figure 2) showed non-additivity regarding invertebrate influence after 3 months. However, after 6 months, only mixture 12 showed a highly significant non-additive effect in the presence of invertebrates (Figure 4).

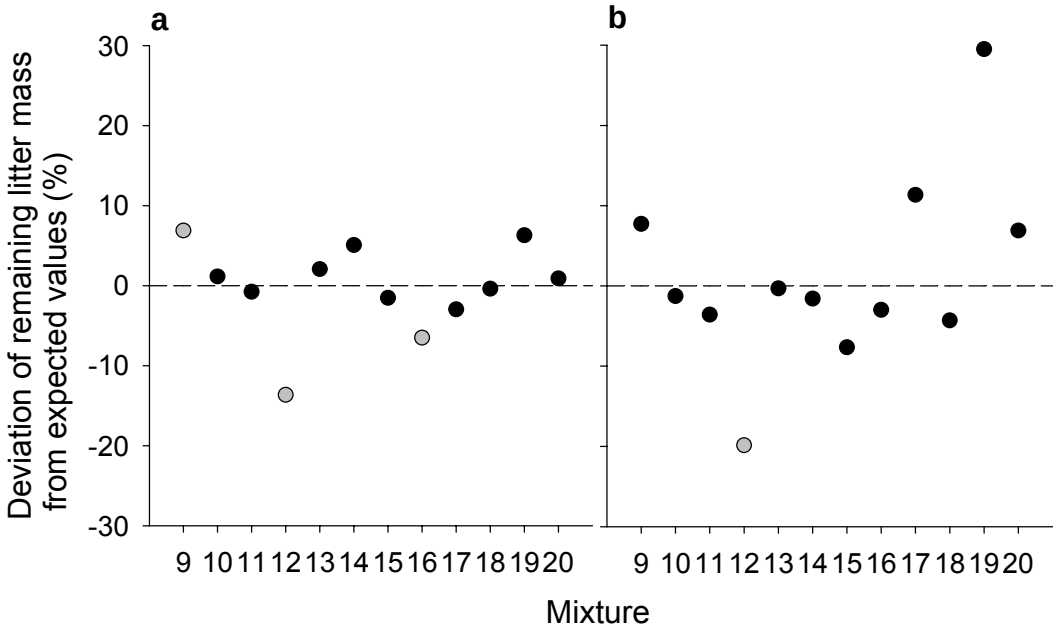


**Figure 4:** Percent deviation of observed litter mass remaining from expected values. The deviation was calculated from the influence of macro- and meso-invertebrates on the decomposition of the leaf litter of one species for all mixtures after (a) 3 and (b) 6 months, averaged over blocks. Grey symbols indicate significant deviation from zero (95 % confidence interval). Positive deviations indicate antagonistic effects (i.e. observed decomposition rates decreased compared to expected decomposition rates) and negative effects indicate synergistic effects (i.e. observed decomposition rates increased compared to expected ). Numbers indicate the mixtures (see Table 1).

## Discussion

Our study adds to the growing body of studies that do not report a direct relationship between species richness of leaf litter types and the decomposition rate (Hättenschwiler et al., 2005; Schindler and Gessner,

2009). Unlike the number of leaf litter types, leaf litter identity and mixture composition had a striking influence on litter decomposition (Table 2). The importance of the species identity of the leaf litter and therefore the low degree of functional redundancy was further confirmed by the significant influence of the presence of all but one species on the decomposition rate in leaf litter mixtures (Table 3). However, the significant non-additive effects in our results indicate that differences in litter decomposition cannot be explained exclusively by differences in litter decomposability, but can be explained also by interactions between certain leaf litter types within mixtures. These interactions lead to unpredictable decomposition dynamics. As expected, our test for additivity or non-additivity following the approach of Ball et al. (2008) showed that the non-additive effects observed were due to species composition rather than species richness (Table 3) (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Ball et al., 2008).

In accordance with several other studies, our results demonstrate the importance of invertebrates for decomposition in a tropical rainforest (Beck, 2000; Gonzalez and Seastedt, 2001; Wall et al., 2008; Yang and Chen, 2009), although this effect could have been overestimated because of microclimatic differences between fine and coarse-meshed bags. Additionally, differences in litter mass loss between fine and coarsed-meshed bags could be due to an increased loss of fragmented litter material from coarse-meshed bags. However, fragmentation of leaves is part of the litter degradation process and mainly performed by larger invertebrates (Swift et al., 1979; Coleman et al., 2004). Therefore, we agree with Bradford et al., (2002) and consider the breakdown and loss of small litter fragments from the sample as a functional role of decomposing invertebrates. However, the effect of invertebrates on decomposition varied considerably among leaf litter types and mixtures (Figure 3). This variation is probably caused by differences in litter chemistry and consequently palatability of the different litter types for invertebrates (Seastedt, 1984; Loranger, 2002; Schädler et al., 2003). We further showed that the non-additive effects of litter mixing were largely attributable to the activity of invertebrates involved in decomposition

(Table 3; Figure 2). Therefore, the varying effect of invertebrates on the decomposition of various types of leaf litter may also account for differences in non-additivity between mixtures. For example, the decomposition rate of mixture 9 in the presence of invertebrates was significantly lower than expected values after 3 months and was even lower after 6 months, even if not significant. This mixture includes leaves of *Marlieara tomentosa,* which decompose slowly when not mixed with leaves of other tree species, irrespective of the presence or absence of invertebrates (Figure 3). By contrast, leaves of *Pera glabrata,* the other species in the mixture, decompose rapidly in the presence of invertebrates. The genus *Marlieara* belongs to the family *Myrtaceae*. Members of this family contain many polyphenols and essential oils, which can be expected to prevent invertebrate feeding (Rosenthal and Berenbaum, 1991; Hättenschwiler and Vitousek, 2000). Thus, it seems likely that antagonistic effects of this mixture are due to the influence of *M. tomentosa* on invertebrate decomposers. As another example, mixture 12 consists of easily decomposable (*Alchornea triplinervia*) and poorly decomposable (*Matayba guianensis*) leaves; this mixture showed a significant synergistic effect after 3 months in the presence of invertebrates and a significant antagonistic effect in the absence of invertebrates after 6 months. A rather similar pattern was found for mixture 16, which contained leaves of three species with low decomposability (*M. tomentosa, M. guianensis, Sloanea guianensis*) and leaves of one species with high decomposability (*A. triplinervia)*. The non-additive effects of these examples were due to the influence of invertebrates, as confirmed by these mixtures also having congruent significant deviations between the observed and expected invertebrate effect (Figure 4). However, the influence of invertebrates on non-additivity is restricted to the earlier decomposition phase. In the later phase, significant non-additive effects occurred solely in the absence of invertebrates. Thus, other members of the decomposer community, such as micro-invertebrates or fungi, must be responsible for these non-additive effects. As an exception, mixture 12 showed a significant negative deviation from the expected invertebrate effect after 6 months. However,

there was no significant deviation between the observed and expected overall decomposition values in the presence of invertebrates but significant positive deviations in the absence of invertebrates. Thus, the synergistic non-additivity caused by invertebrates seemed to be masked by antagonistic non-additive effects caused by other members of the decomposer community, leading to “pseudo-additivity” (Schindler and Gessner, 2009). This exception suggests that a lack of deviation between observed and expected decomposition values do not ultimately rule out non-additive effects. Additionally, we found relatively strong but non-significant deviations between observed and expected decomposition values for some mixtures in the presence of invertebrates after 6 months (Figure 2). The fact, that they were not significant might be attributed to a high variability in the invertebrate effect among blocks. This points to a patchy distribution of invertebrates on our study site. Thus, the effect of invertebrates on decomposition also varies spatially. The findings presented highlight the high degree of idiosyncrasy of decomposition dynamics in our study owing to species identity and specific interactions enhanced by invertebrate decomposer activity (see also Chapman et al., 1988; Blair, 1990; Wardle et al., 1997; Bardgett and Shine, 1999).

Although we found no direct effect of species richness on decomposition, the number of tree species might nevertheless influence the decomposition process in other ways. In accordance with other studies (Schädler and Brandl, 2005; Lecerf et al., 2007; Keith et al., 2008), we found a decreasing variability in decomposition rates with increasing tree species richness of the litter (Figure 1). Lecerf et al., (2007) and Keith et al. (2008) interpret such a reduction of variability in the decomposition rate as a component of higher ecosystem stability concerning ecosystem processes (e.g. decomposition). Following the “variance reduction effect” postulated by Huston (1997), this reduction is just due to the increasing similarity of mixtures drawn from a limited species pool. Studies of larger species pools are necessary to evaluate whether there might be a stabilizing effect of litter diversity on the decomposition rate across litter mixtures with a limited overlap in species composition.

## Conclusions

The differences in decomposition rate of the leaf litter, the significant influence of the presence/absence of almost all single species on the decomposition and the specific interactions between certain species, which leads to unpredictable non-additive effects in some cases, highlight the importance of leaf litter identity and the low degree of redundancy of leaf litter type in our experiment. This, combined with the specific and varying effect of macro- and meso-invertebrates, involved in the decomposition points to a relationship between the decomposer subsystem and plant species diversity in the Atlantic Rainforest following the idiosyncratic response hypothesis.

For conservation or reforestation management, our results accentuate the need to keep or restore the composition of locally native tree species communities rather than to maintain only a high tree species richness. Our study complements theoretically the practical reforestation experiences that were made during the last 30 years in the Brazilian Atlantic Forest (for a review, see Rodrigues et al., 2009).

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# Supplementary Material

**Table S1:** Guide for statistical procedures

| Method | Factor(s) | Variable | Appearance |
|---|---|---|---|
| GLM type III | Fauna = mesh size; species richness = number of litter types; mixture = all used mixtures and species; Time = decomposition time; Block = replicate block | litter mass disappearance | Table 1 |
| ANOVA (for each mixture) | Mesh size | litter mass disappearance | Figure 3 |
| GLM type I | Time = decomposition time; Block = replicate block; "*Tree species name*" = presence/absence of each tree species; Species interaction term = all used mixtures and species | litter mass disappearance | Not shown |
| GLM type I | Time = decomposition time; Block = replicate block; "*Tree species name*" = presence/absence of each tree species; Species richness = number of litter types | litter mass disappearance | Not shown |
| GLM type I | Time = decomposition time; Block = replicate block; "*Tree species name*" = presence/absence of each tree species; Fauna = mesh size | litter mass disappearance | Not shown |
| GLM type I | Time = decomposition time; Block = replicate block; "*Tree species name*" = presence/absence of each tree species; Species interaction term = all used mixtures and species; Fauna = mesh size | litter mass disappearance | Table 2 |
| GLM type III | Fauna = mesh size; species richness = number of litter types; mixture = all used mixtures and species; Time = decomposition time; Block = replicate block | deviation of the remaining litter mass from the expected litter mass | Table 3 |
| One sample t-test | observed litter mass remaining – expected litter mass remaining<br>Test for significant deviations from zero for all mixtures | | Figure 2 |
| One sample t-test | observed invertebrate effect – expected invertebrate effect<br>Test for significant deviations from zero for all mixtures | | Figure 4 |

# Chapter 3

## Succession of litter dwelling fungi along a successional gradient of forests in the Atlantic Rainforest of Brazil

with Kelly Geronazzo Martins, Martin Brändle, Jochen Bihn, Gustavo Pacheco, Renato Marques, Roland Brandl

in preparation

### Abstract

Fungi play an important role for essential ecosystem functions such as litter decomposition and a loss of fungi diversity may decrease ecosystem functionality. The objective of this study was to assess the resistance or resilience of the community of litter dwelling fungi along a chronosequence of forest succession. We used a genetic fingerprinting technique to estimate species richness, diversity and species turn-over of litter dwelling fungi and compared it to species richness and species turn-over of trees. While tree species richness increased with increasing successional age, species richness of fungi showed no differences. Species composition between successional stages, however, differed in trees and fungi and was even correlated. We suggest, that the community of litter dwelling fungi comprise several sub-communities of which the mayor part are so called latent species which act as a seed bank for fungal succession. Therefore the communities of fungi are able to react to environmental change leading to a high flexibility of these communities.

## Introduction

The ongoing destruction of natural habitats and their transformation into secondary ecosystems causes considerably loss of biodiversity in the tropics. This has been well documented for plants, vertebrates and some groups of insects (Barlow et al., 2007; Bihn et al, 2008; Feeley and Silman, 2009; Pimm, 2009) and should also be true for microbial organisms such as fungi (Carney et al., 2006; Bastias et al., 2007; Carson et al., 2010). Fungi play an important role for several essential ecosystem functions like decomposition (Hawksworth, 1992; Swift et al., 1979). Hence, changes in fungal diversity due to habitat disturbances may have severe impacts on ecosystem processes and ecosystem services (McGuire et al., 2010). However, knowledge of the resilience of fungi communities after disturbances is still scarce.

The recycling of organic materials such as plant litter is crucial for ecosystems, in particular in tropical regions that are often characterised by low capacity of nutrient storage in the soil and a high nutrient uptake and turnover (Jordan, 1985; Vitousek and Sandford, 1986; Lewis, 2006). Species diversity and functional flexibility of the assemblages of microbial decomposers leads to a complete mineralization of nutrients (Hanson et al., 2008). In turn, the variability of litter quality influences the composition and diversity of the decomposers. A litter mixture with a high variability in litter quality promotes a diverse decomposer community (Lodge, 1997). From this we expect that decreasing tree diversity should be followed by a decline in the diversity of decomposers. Such cascading effects (Koh, 2004) should be especially pronounced for specialised organisms like saprophytic fungi (Lodge et al., 1995). Single species in the community of saprophytic fungi decompose particular substrates, i.e. the litter of one or few tree species in a certain stage of decomposition (Hansgate et al., 2005; Kubartová et al., 2009). Overall the community is able to degrade the litter of many different tree species in all stages of decomposition by rapidly shifting its richness and community composition (Goddard and Bradford, 2003; Hanson et al., 2008). This has been referred to as micro-scale succession (Suzuki, 2002). The magnitude of this flexibility depends on the phylogenetic and functional diversity of saprophytic fungi. The

higher the fungal diversity, the broader the potential to decompose a wide range of substrates (McGuire, 2010). If diversity of fungal decomposers declines because of the reduction of plant species diversity due to human impact, the functional diversity of the fungal community may also decline (Carney et al., 2006; de Castro et al., 2008). Nevertheless the recovery of the saprophytic fungal community during forest regeneration depends on its resilience. Hence, to understand the importance of secondary forests in comparison to primary forests (Corlett, 1995), knowledge about the successional dynamics and the degree of resilience of saprophytic fungi is important.

The aim of this study is to provide an assessment of the diversity of litter dwelling fungi along a gradient of forest succession within two nature reserves of the Mata Atlântica. These rainforests are highly endangered and less than 12 % of the originally extent of 150 million ha are left (Ribeiro et al., 2009). Of these remnants 32-40 % are small fragments of primary forests with an area of less than 100 ha, or secondary forests. This trend of forest destruction, fragmentation and transformation into secondary forests might cause a serious loss of biodiversity (Laurance, 2007; Gardner et al., 2007; Metzger et al., 2009). The studied reserves provide several sites with secondary forests of different successional age covering young (ca. 10 years after usage as pasture) up to old stages of more than a hundred years. We focus on litter dwelling fungi because of their substantial impact on nutrient cycling. Because plant and fungi communities are known to be closely related (He et al., 2005; Carney et al., 2006; Bastias et al., 2007; Eskelinen et al., 2009) we expected a strong relationship between successional patterns of trees and fungi. Therefore, we analysed the succession of the tree community in terms of species richness, diversity and community composition and compared it to the successional patterns of the associated fungi communities.

## Material and Methods

### *Study site*

As a part of the SOLOBIOMA Project, a German–Brazilian cooperation, this study was initiated in the Atlantic Rainforest in the Brazilian State of Paraná. It was conducted in two nature reserves approximately 25 kilometer apart: the Rio Cachoeira nature reserve (25.25° S, 48.68° W) and the Itaqui nature reserve (25.29° S, 48.32° W). Both regions provide sites covered by secondary forest of different successional age previously used as pastures. Twelve study sites were established in each region covering four successional stages, each one replicated three times (I = initial succession, ~10 years; A = advanced succession, 15-20 years; M = medium succession, 35 – 50 years and F = old growth forest, > 100 years. The old growth forest sites in both study regions showed the original vegetation which is characterised as *submontane ombrophilous dense atlantic forest* (IBGE, 1992) and served as reference for a primary forest.

### *Sampling of trees*

Each plot was divided in 10 sub-plots of 10 m x 10 m, where all trees with circumference diameter at breast height ≥15 cm were recorded. If possible, the taxonomic identification of trees was done *in situ*. If this was not possible, leaves were collected and determined by comparison with herbarium specimens from the UPCB Herbarium of the Universidade Federal do Paraná, or collected material was sent to specialists. The taxonomic identification of angiosperms followed the Angiosperm Phylogeny Group (APG II 2003).

### *Sampling of fungi*

We collected on each site in both reserves ten samples of fine leaf litter every five meter along a 45 meter transect. Litter of each 0.25m$^2$ sample plot was sieved using a 5 mm metal sieve. From each plot we sampled approximately 10 g of fine leaf litter that were immediately placed in plastic bags. The samples were deep-frozen as soon as possible and stored

frozen for further processing. The sieve was cleaned after each sampling to avoid cross-contamination.

***ARISA***

We extracted total DNA from approximately 0.3 g of each sample using the FastDNA® SPIN Kit for Soil and the FastPrep® Instrument (MP Biomedicals, Santa Anna, CA) following the instructions of the manufacturer. PCR was performed in a 25 µl reaction containing 1µl template DNA, 0.2 mM (2.5 µl) dNTP, 1.5 mM (1.5 µl) $MgCl_2$, 1 U (0.4 µl) Jumpstart Taq (Sigma Aldrich), 2 µl Jumpstart Buffer without $MgCl_2$ (Sigma Aldrich), 2,5 µl BSA, 0.2 µM (0.5 µl) forward primer ITS-1F (5`-CTT GGT CAT TTA GAG GAA GTA A-3`) labelled with DY-781 (Biomers), 0.2 µM (0.5 µl) reverse primer ITS-4 (5`-TCC TCC GCT TAT TGA TAT GC-3`) and 14.1 µl sterile water. These primers are specific to the internal transcribed spacer (ITS) region of genomic DNA of fungi (White et al. 1990, Gardes and Bruns 1993). PCR conditions included an initial denaturising step of 5 min at 95°C, followed by 35 cycles of 30 s at 95°C, 30 s at 55°C, and 1min 72°C. The final annealing step was set to 10 min at 72°C. PCR products were diluted with water at a ratio of 1:10. We resolved ARISA fragments on 6.5 % polyacrylamide gels and analysed them under denaturing conditions for 3 h at 1500 V / 40 W on a LiCor® DNA sequencer (ScienceTec). We converted the resulting gel images into electrophoreograms using the Gel-Pro Analyzer Software (vers. 4.5, Media Cybernetics). Fragment size standardisation (lengths in base pairs) was obtained using the LiCor® 50-700 bp size standard. For further processing and management of the data we conducted using R (vers. 2.12.1). We identified and summarised peaks representing fragments of lengths between 300 bp and 900 bp for each sample in a presence/absence table. Based on a NCBI database (www.ncbi.nlm.nih.gov) analysis for ITS fragment lengths we expected that more than 99 % of all fungi species show ITS lengths within this range. Based on personal observations of all images we considered only peaks with a fluorescence intensity of at least 10 % of the intensity of the highest peak in the image (16 bit greyscale) for further analyses to avoid

false positive bands. Identified peaks were defined as OTUs (operational taxonomic units) and will in the following be referred to as species of fungi.

### *Statistical analysis*

We estimated tree and fungal species richness for each site using the Jack I estimator (Heltshe and Forrester, 1983). To calculate the completeness of our samples we used the formula adopted from (Paulus et al., 2006): *Completeness = observed species number x 100 / estimated species number.*

We used a GLM type III with region and successional stage nested within region as factors (Statistica vers. 6.1) to compare estimated species numbers between successional stages and study regions. We also calculated the Simpson`s index of Diversity (1-D) for each study site using the jackknife procedure suggested by Heltshe and Forrester (1985). We used the frequencies of occurrence i.e. the presence of a certain tree/ fungi species on the sample plots of a site as a measure of abundance. Thus, the maximum abundance of each species per site was 10. Again we tested for differences using a GLM type III with region and successional stage nested in region as factors (Statistica vers. 6.1).

To compare tree and fungal community composition and to analyse the species turnover between successional stages we used a MANOVA based on dissimilarity matrices with Bray-Curtis dissimilarity index (function ADONIS, vegan package; R vers. 2.12.1). As successional stage was nested within region, we used region as a constraining factor for permutations (999), i.e. permutations were performed only within regions.

We performed a CA (correspondence analysis) on the occurrence frequencies of species in all sites of both regions to investigate whether tree and fungal community composition followed a successional trend. To test for the effect of regions and successional stage we additionally performed a CCA (constrained correspondence analysis) with regions and successional stages as factors constraining the ordination. We used an ANOVA like permutation test to test for significance of the factors (function anova.cca; vegan package; R vers. 2.12.1).

To examine the relationship between the estimated richness of tree and fungi species for both regions a simple linear regression was used (function lm; stat package; R vers. 2.12.1). We compared tree and fungal community compositions within each region using Procrustes analysis on CCA ordinations of frequency of occurrence matrices for fungal and tree communities with successional stage as the constraining factor (protest; vegan package; R vers. 2.12.1). Additionally we compared Bray-Curtis dissimilarity matrices based on frequency of occurrence data of fungal and tree communities within each region using Mantel tests.

## Results

### *Species richness and diversity of trees and fungi*

*Trees*

On single sample plots across all study sites we found between 1 and 17 tree species in the Cachoeira nature reserve and between 1 and 22 in the Itaqui nature reserve. The pooled tree species numbers for the study sites across all age classes ranged between 5 and 45 in Cachoeira and between 4 and 56 in Itaqui (means per successional stage are presented in Table 1 and Figure 1).

**Table 1:** Trees species richness and diversity; Means ± standard deviation. Successional stages: I, ~10 years; A, 15–20 years; M, 35–50 years; F, >100 years.

| **Region** | **Cachoeira** | | | | **Itaqui** | | | |
|---|---|---|---|---|---|---|---|---|
| **Successional Stage** | **I** | **A** | **M** | **F** | **I** | **A** | **M** | **F** |
| Mean observed species number | 8.7 ± 3.2 | 22.7 ± 5.1 | 37.7 ± 6.0 | 42.0 ± 3.0 | 9.3 ± 5.5 | 30 ± 12.0 | 41.7 ± 4.2 | 50.3 ± 6.6 |
| Mean estimated species number | 12.3 ± 4.5 | 34.8 ± 9.2 | 53.9 ± 7.8 | 61.5 ± 7.1 | 12.0 ± 6.4 | 41.1 ± 14.9 | 56.0 ± 7.2 | 74.3 ± 14.6 |
| Completeness (%) | 70.5 | 65.2 | 69.9 | 68.3 | 77.5 | 72.9 | 74.5 | 67.7 |
| Simpson index (1-D) | 0.78 | 0.92 | 0.96 | 0.97 | 0.77 | 0.94 | 0.97 | 0.97 |

On average the observed tree species richness represented some 70 % of the estimated tree species richness suggesting reasonable sample completeness (Table 1). The estimated tree species richness differed significantly among successional stages (GLM, nested within region: $p < 0.01$) but not between study regions (GLM; $p = 0.19$). The Simpson`s index indicated a high degree of diversity for all successional

stages, although diversity was low for youngest sites (means per successional stage are presented in Table 2). The diversity indices significantly differed among successional stages (stage (region): p = 0.02) but not between regions (p = 0.94).

*Fungi*

We recorded for the Cachoeira reserve between 5 and 48 fungi species and for the Itaqui reserve between 4 and 46 fungi species on sampled plots. The pooled number of species per site ranged between 80 and 144 with a mean of 111 ± 19 for Cachoeira and between 69 and 138 with a mean of 99 ± 21 for Itaqui (± standard deviation; means per successional stage are presented in Table 2 and Figure 1).

**Table 2:** Fungal species richness and diversity; Means ± standard deviation. Successional stages: I, ~10 years; A, 15–20 years; M, 35–50 years; F, >100 years.

| **Region** | **Cachoeira** | | | | **Itaqui** | | | |
|---|---|---|---|---|---|---|---|---|
| **Successional Stage** | **I** | **A** | **M** | **F** | **I** | **A** | **M** | **F** |
| Mean observed species number | 119.0 ± 8.2 | 115.7 ± 32.6 | 94.0 ± 12.8 | 114.3 ± 8.5 | 105.7 ± 28.1 | 90.0 ± 27.4 | 99.3 ± 13.8 | 101.0 ± 29.6 |
| Mean estimated species number | 185.0 ± 13.0 | 186.8 ± 53.8 | 142.0 ± 16.6 | 183.6 ± 12.3 | 168.7 ± 44.6 | 142.8 ± 48.2 | 148.8 ± 21.1 | 155.3 ± 46.2 |
| Completeness (%) | 64.3 | 61.9 | 66.2 | 62.2 | 62.7 | 63.0 | 66.7 | 65.0 |
| Simpson index (1-D) | 0.98 | 0.97 | 0.97 | 0.98 | 0.97 | 0.96 | 0.97 | 0.99 |

The values of completeness indicated that we sampled on average some two third of the assemblages of fungi (Table 2). The GLM to test for differences of the estimated species richness between regions and successional stages showed neither an effect of region (p = 0.14) nor of successional stage (nested within region) (p = 0.67). Simpson`s index of diversity of all successional stages showed very high values (means of replicated sites are presented in Table 2). Estimated fungal diversity did not differ between regions and among successional stages (region: p = 0.5; stage (region): p = 0.2).

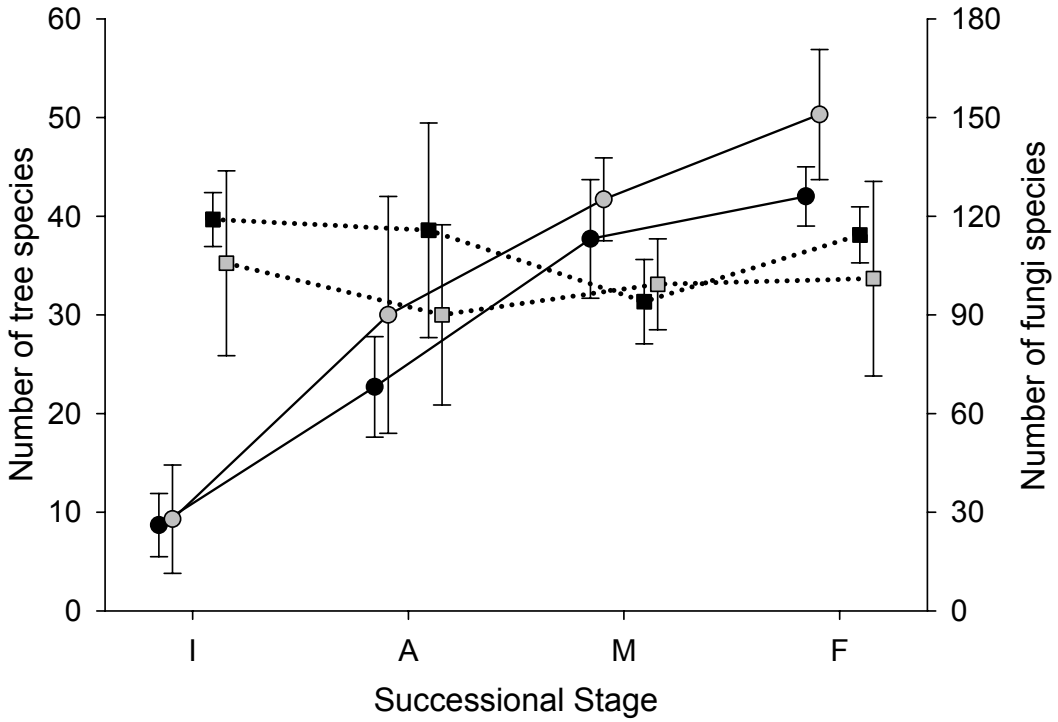


**Figure 1:** Species richness of trees and fungi along a successional gradient. Circles and solid lines: Mean number of tree species ±SD; three replicate sites per successional stage; black circles = Cachoeira; grey circles = Itaqui. Squares and dotted lines: Mean number of fungi species ± standard deviation; three replicate sites per successional stage; black squares = Cachoeira; grey squares = Itaqui. Successional stages: I, ~10 years; A, 15–20 years; M, 35–50 years; F, >100 years.

### *Community composition of trees and fungi*

*Trees*

The MANOVA analysis showed significant differences in tree species composition between both study regions ($p < 0.01$) and successional stages ($p < 0.01$). These results were confirmed by the permutational tests for significance of the CCA axes. Successional stages ($p < 0.01$) as well as regions ($p = 0.04$) differed significantly in their tree species composition. The CA ordination plot showed the successional development of the tree communities in the study regions (Figure 2). On the youngest successional sites (I) the tree species communities were relatively similar between regions but showed considerable heterogeneity within successional age. The vegetation in the advanced successional sites (A) already started to differentiate between the study regions. The heterogeneity of the tree species composition was still high. Especially in

the Serra do Itaqui Nature Reserve the advanced successional sites considerably differed in their tree species composition. While site A2 was still similar to the sites of the youngest successional stage, site A1 already showed a tree community typical for sites of medium successional age. With ongoing succession the study regions became increasingly distinct in their tree community. Whereas tree communities homogenised within successional age classes.

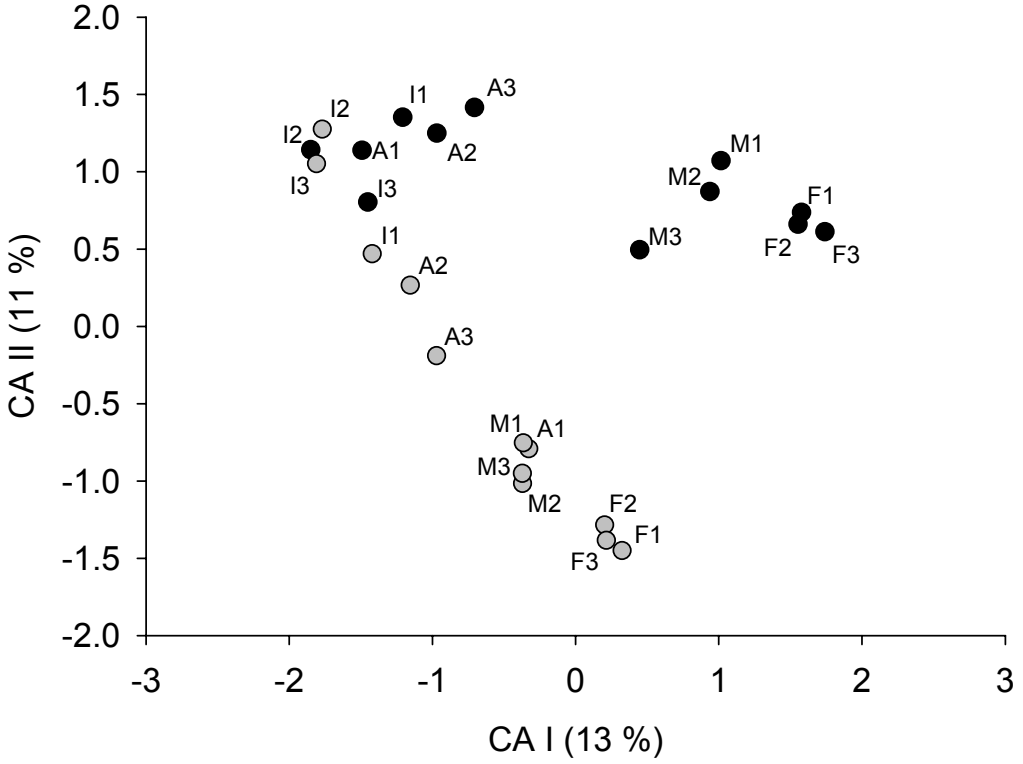


**Figure 2:** Ordination plot of correspondence analysis of tree communities for all sites in both regions; black circles = Cachoeira; grey circles = Itaqui;. CA I explains 13 % and CA II 11 % of total variance. Successional stages: I, ~10 years; A, 15–20 years; M, 35–50 years; F, >100 years.

*Fungi*

Fungal communities of Cachoeira and Itaqui differed significantly in their species composition ($p = 0.02$). We also found significant differences among successional stages ($p < 0.01$). The results of the CCA, however, partly differed from the former analysis. While the effect of successional stage on fungi composition was supported (permutation test, $p < 0.01$) we found no significant differences among regions (permutation test, $p = 0.18$). The ordination plot derived from the CA analysis showed a

successional trend along the second CA Axis (Figure 3). The youngest (I) and the oldest (F) sites were clearly separated although variability of the youngest sites was quite high. The medium successional sites (M) were located between both extremes as expected, whereas the advanced successional sites (A) showed a strong overlap with all other successional stages. There was also a strong outlier of stage A (A2_C). Exclusion of this outlier did not change the results.

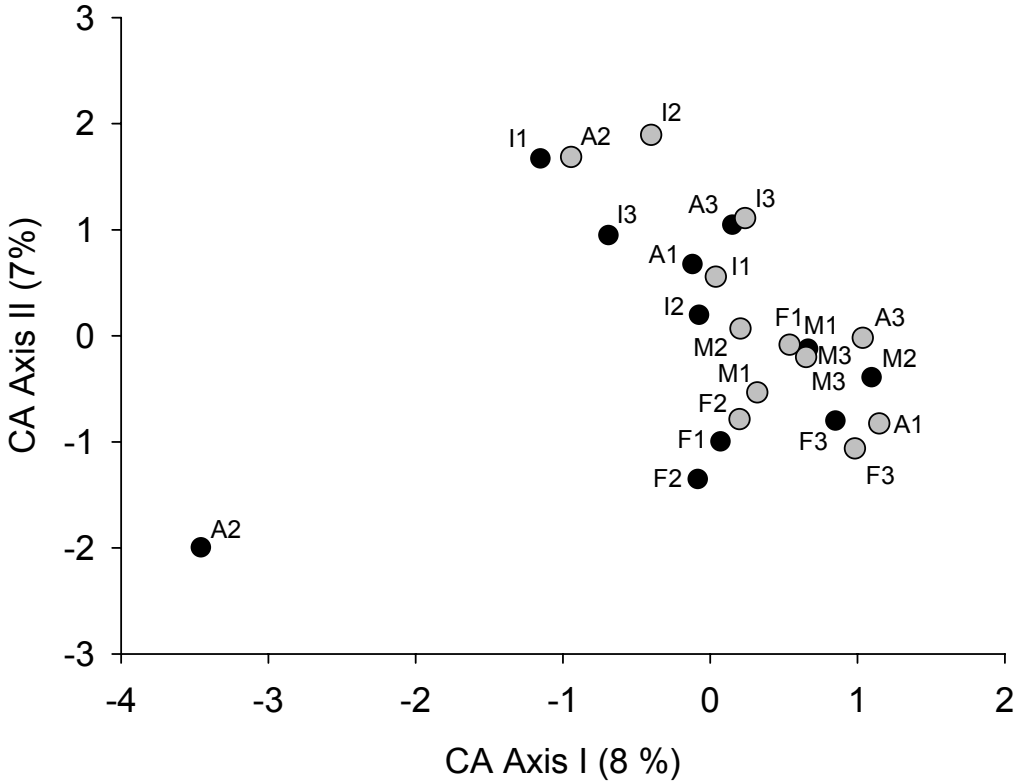


**Figure 3:** Ordination plot of correspondence analysis of fungi communities for all sites in both regions; black circles = Cachoeira; grey circles = Itaqui;. CA I explains 8 % and CA II 7 % of the total variance. Successional stages: I, ~10 years; A, 15–20 years; M, 35–50 years; F, >100 years.

### *Relationship between tree and fungi community*

Species richness of fungi and trees was not related (Cachoeira: $p = 0.34$; Itaqui = 0.75). The Procrustes test, however, revealed a significant relationship in the compositional change of fungal and tree communities for both regions (Cachoeira: Procrustes correlation $r = 0.62$, $p = 0.01$; Itaqui: Procrustes correlation $r = 0.77$, $p < 0.01$; both tests are based on 1000 permutations). Sites with similar tree communities also show similar

fungi communities. Matrix correlations of the Bray-Curtis distances confirmed these results (Cachoeira: $r = 0.23$, $p = 0.04$; Itaqui: $r = 0.46$, $p < 0.01$; mantel tests based on 1000 permutations).

## Discussion

Genetic fingerprinting techniques, like ARISA, are unable to provide an accurate assessment of absolute microbial diversity, because richness of rare species is generally overlooked (Bent and Forney, 2008). However, it has been repeatedly shown that these techniques are adequate for comparative analyses of microbial communities (Kennedy and Clipson, 2003; Thies, 2007). Especially the ARISA method was found to provide reproducible results with a high resolution (Gillevet et al., 2009; Okubo and Sugiyama, 2009; Slabbert et al., 2010; Banning et al., 2011). Nevertheless, our quantitative estimates of total fungi species richness and diversity should be interpreted with caution. Rare species may have been overlooked as we used a quite high intensity threshold for identification. However, our comparative interpretations, which are the main topic of this study, should be robust.

Overall, the successional patterns of tree species richness and community composition of our study are in line with other studies in the tropics (Guariguata and Ostertag, 2001; Chinea, 2002; Libsch et al., 2008). Furthermore, the strong differences between our study regions regarding the composition of late successional tree communities underline the high regional tree species diversity in the Atlantic Rainforest. The numbers of fungi species we found correspond to those found in other, similar studies (Bills and Polishook, 1994; Polishook et al., 1996; de Castro et al., 2008). There were no differences in species richness and diversity among successional stages. Thus, species richness of fungi seems to be independent of tree species richness (Figure 1). The high species richness of litter dwelling fungi in young successional forests may be due to different reasons. First, fungal communities remain unchanged, because they are not seriously affected by disturbance (Allison and Martiny, 2008). This implies a high degree of resistance of litter fungi

communities. Second, the original fungal community has already recovered after 10 to 15 years, implying a high degree of resilience. Many groups of organisms in tropical forests need decades for recovery of former conditions after severe disturbance (Dunn, 2004; Liebsch et al., 2008; Bihn et al., 2008). However, due to high growth rates and physiological flexibility of microbial communities a rapid recovery within few years appears to be feasible (Allison and Martiny, 2008). Both, high resistance and resilience, would predict that if species richness does not differ, fungal communities should be more or less identical across successional stages. However, we found considerable differences in fungal species composition among sites along a successional gradient. As fungal species richness did not differ between successional sites and old growth forest, it appears that original fungal communities only in part resisted or recovered from disturbance. The resistant or resilient part of the fungal community, i.e. those species all successional sites have in common, should be mostly generalistic. Such species may not be strongly restricted to certain tree litter but able to utilize a variety of litter such as grass, herbs or shrubs of the understorey of younger successional forest sites. The other part of the fungal community, those fungi solely occurring on younger stages, may present species that have colonised from elsewhere or that are likely to have been already present in the original communities as so called latent species (Suzuki, 2002). These species are present only in very small abundances or as dormant spores in communities of old growth forest. After disturbance such species quickly increase in biomass as caused by the changed environmental conditions. At the same time the former high abundant fungi which are more specialised to certain tree species will become latent species. With ongoing succession and regeneration of the tree community the fungi community should shift again.

The ability of fungal communities to shift their structure during the decomposition process as a response to changes in the substrate composition and quality is well-known (Goddard and Bradford, 2003; Hansgate et al., 2005; Hanson et al., 2008). This has been referred to as micro-scale or substratum succession (Swift, 1979). A similar process has

been suggested on the macro-scale during secondary forest succession (Suzuki, 2002). Strong dependency on plant communities may also explain the high variability of the fungal communities of the young successional stages I and A. Here variation in plant species community composition was considerably higher than in older stages (Figure 2). This should be due to differences among sites regarding seed arrival and conditions for seed establishment in the early successional phases (Cheung et al, 2010). It has been shown that these factors strongly affect forest recovery in tropical regions (Aide et al., 1995; Guggenberg and Zech, 1999).

The successional patterns we found were consistent across both study regions. We found significant differences of fungi communities between our study regions although these differences were quite low (insignificant result of the cca analysis). These results point to a weak location effect that should also be due to differences in plant community compositions between our study regions. Nevertheless, the fungi community did not reflect the strong regional differences in tree species community composition. Thus, fungi may be more related to functional traits of trees associated to a certain successional stage than to species identity.

## Conclusions

Our results suggest that deforestation does not cause an enduring loss of fungi diversity in forest ecosystems of the Atlantic Rainforest of Brazil. The total fungi community seems to comprise several sub-communities of which the major part are so called latent species (Suzuki, 2002) which act like a seed bank for fungal succession. Hence, although we found considerable differences in fungal communities between successional stages the total litter dwelling fungal community should be highly resilient or resistant to deforestation. Recovery of the active fungal community should mainly depend on the recovery of the former plant communities. Due to its high species diversity the fungal community should also maintain its functional diversity. Thus, a loss of ecosystem functionality

due to a decrease in fungal diversity is less likely. Nevertheless, as for plant regeneration (Wijedeven and Kuzee, 2000) nearby old growth forest patches should be important as sources for the establishment and maintenance of the fungal “seed bank”. Thus, the protection of these forest patches is important to preserve the resistance and resilience of the fungal community.

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# Chapter 4

## Lack of home-field advantage in the decomposition of leaf litter in the Atlantic Rainforest of Brazil

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submitted

### Abstract

Experiments using litter monocultures have indicated that litter decomposes faster on its home site owing to specialised decomposers leading to a home-field advantage (HFA). However, most natural forests, in particular tropical rainforests, harbour more than one species of trees, all of which contribute to the local litter layer. Since interactions among different litter types that cause non-additive decomposition dynamics may prevent HFA, the occurrence of HFA in such multispecies ecosystems is still a matter of debate. Here we studied whether there is an HFA in a highly diverse forest ecosystem in the Atlantic Rainforest of Brazil. We used a litter decomposition experiment using natural litter mixtures with reciprocal transfers among three forest successional stages that differed in their tree species composition and general litter quality. We also investigated the role of soil macro- and meso-invertebrates for HFA and their relative importance along a successional gradient. Results of various statistical procedures failed to demonstrate HFA. A reason for this lack of a HFA may be rapid shifts in the composition of local microbial communities in response to local litter quality. Our experiments indicate a rapid resilience of the microbial decomposition during forest regeneration.

## Introduction

The physicochemical environment, litter quality, as well as abundance and composition of the decomposer community are the main drivers of decomposition in terrestrial ecosystems (Swift, 1979; Coûteaux et al., 1995; Cadish and Giller, 1997; Hättenschwiler et al., 2005; Schädler and Brandl, 2005). These factors often interact during litter decomposition (Lavelle et al., 1993; Aerts, 1997; Gartner and Cardon, 2004) and their strength and interactions vary among biomes and ecosystems (Aerts, 1997).

If there is a close specialisation of decomposers to the litter of certain plant species, the composition of plant communities should determine the composition of the associated communities of decomposers (Schädler et al., 2003; Negrete-Yankelevich et al., 2008a,b). Such a specialisation might lead to a decreased ability of the decomposer community to decompose foreign litter material. This effect has been referred to as “home-field advantage” (HFA) (Gholz et al., 2000).

As indicated by Ayres et al. (2009a), HFA seems to be widespread in forest ecosystems. However, to our knowledge, all studies that found evidence of HFA focused on the decomposition of a litter from a single plant species. Many natural forests, in particular tropical rainforests, however, harbour a larger number of tree species, all of which contribute to the local litter layer. Litter mixtures, however, have decomposition dynamics different from that of monocultures (Hättenschwiler et al., 2005; Chapman and Newman, 2010) and the decomposition of site-specific litter reflects the specific characteristics of all plant species in the community including transfer of substances between litter from different plant species with non-additive, complex consequences on decomposers and decomposition (Chapman et al., 1988; Blair et al., 1990; Schimel and Hättenschwiler, 2007; Ball et al., 2008). Hence, the validity of the HFA in natural mixed stands is still a matter of debate.

Two factors are important for the formation of HFA. Firstly, the litter material should be of low quality, i.e., containing recalcitrant or toxic compounds that constrain decomposition. In contrast, high-quality litter is decomposed by almost all decomposers because no specific adaptations

are necessary and therefore HFA is unlikely (Hunt et al., 1988; Ayres et al., 2009a,b; Strickland et al., 2009a,b). Secondly, the decomposer community should be conservative in its traits responsible for decomposition of certain chemical substances leading to some degree of specialisation of decomposer species (Hunt et al., 1988; Gholz et al., 2000; Ayres et al., 2009b). Nevertheless a community of specialised decomposers may adjust to different litter types by shifts in the abundance of individual decomposer species according to the demands of the litter as long as species occur at low abundances or species are able to reach a site. This argument may particularly apply to microorganisms. The short generation times of bacteria as well as the potential of fungi to react via a rapid growth of the mycelium are traits that allow microbial communities to adjust on short time scales to varying substrates leading to shifts in the composition of the communities (Suzuki, 2002; Goddard and Bradford, 2003; Hanson et al., 2008). Overall the importance of microbial decomposers for the formation of HFA is still poorly understood and inoculum experiments have yielded conflicting results (compare Strickland et al., 2009a with Ayres et al., 2006).

Here we investigated the importance of microbial decomposers *versus* macro- and meso-invertebrates for HFA during decomposition of mixtures of leaf litter on forest sites of different successional stages in the Atlantic Rainforest in Brazil, a hot-spot of biodiversity (Myres et al., 2000). To our knowledge, this is the first study that examines HFA in an ecosystem rich in tree species using natural litter mixtures. We expected HFA between successional sites because of considerable differences in tree species composition and general litter quality along the successional chronosequence (Fisk et al., 2002; Xuluc-Tolosa, 2003; Mayer, 2008; Mason et al., 2011). Further, we argue that the strength of HFA should increase with increasing difference in successional age. Such experiments promise insights into the successional dynamics of decomposers and the resilience of decomposer communities.

## Material and Methods

### *Experimental setup*

Our study was carried out in the Atlantic Rainforest in the southern Brazilian state of Parana. As part of the SOLOBIOMA project, a German–Brazilian cooperation (www.solobioma.ufpr.br ), the study was conducted in the Cachoeira Nature Reserve (25.25° S, 48.68° W, 147 NN), which provides secondary rainforest sites of different successional stage after clearance and having been used as pasture. Three different successional stages were chosen: A (advanced), 15–20 years old; M (medium), 35-50 years old; and F (forest), >100 years old. Each stage was replicated three times (three sites of each successional stage, i.e., nine sites total: A1, A2, A3, M1, M2, M3, F1, F2, F3). Sites were selected to form true replicates (for further details see Bihn et al., 2008). The sites selected for this study were located on well-drained Cambisols (FAO, 1998). Independently of successional stage and for the depth of 0-5 cm, the soil was classified as a clayey (45 % of clay, 17 % of silt, 38 % of sand), acidic ($pH_{CaCl2}$ = 3.9) and with a low concentrations of basic cations ($K^+$= 0.2 $cmol_c$ $dm^{-3}$, $Ca^{2+}$= 0.8 $cmol_c$ $dm^{-3}$, $Mg^{2+}$= 0.5 $cmol_c$ $dm^{-3}$). The average level of Total N P-Mehlich was of 0.3 mg $dm^{-3}$, respectively 8.3 mg $dm^{-3}$ indicating a low availability of nutrients for all sites.

The successional sites differ considerably in tree species richness and composition. Species richness of trees increased with increasing successional stage (mean number of tree species per 1000 $m^2$ ± SD; three replicate sites per successional stage: stage A, 23 ± 5; stage M, 38 ± 6; stage F, 42 ± 3; $p < 0.01$, ANOVA, Gießelmann, Martins et al. in preparation), and species composition differed between the successional stages (Figure S1). Additionally, the litter quality in terms of N content increased and C/N ratio decreased along the chronosequence (Figure S2; Balbinot, 2009). On this background we expected to find HFA when comparing successional stages A and F because of their clear differences in litter quality and tree species composition.

To test for HFA, we set up a reciprocal transplant experiment. First we collected natural mixtures of litter for each site. For this we placed four

litter traps of 0.75 m × 0.75 m on each of the nine replicated sites. Litter was sampled for 8 months (September 2007 until April 2008). Litter traps were emptied every 2 weeks. Collected leaf litter was oven dried and stored under dry conditions. Thirty-six nylon litter bags with a coarse mesh size (5 mm × 5 mm) and 36 with a fine mesh size (20 µm × 20 µm; size of bags 25 cm × 25 cm) were filled with 3 ± 0.1 g of randomly chosen air-dried leaf litter from one of the nine sites. Coarse litter bags allowed the passage of soil macro- and meso-invertebrates; fine litter bags excluded these animals but allowed access by bacteria, fungal hyphae, nematodes, and protozoa. In April 2008 four replicates of each site-specific mixture (A1, A2, A3, M1, M2, M3, F1, F2, F3) and mesh size (coarse and fine) were placed randomly on top of the litter layer at each site and secured with wire hooks. For example, at site A1, 36 coarse and 36 fine litter bags were placed; each set contained four replicates of leaf litter from one of the nine sites. Thus, 72 litter bags were placed on each site leading to a total of 648 litter bags. Litter bags were gathered after 6 months. The leaf material remaining in each bag was oven-dried, cleaned (by carefully removing adhesive dirt with a paintbrush), and weighed. The remaining leaf mass was corrected by the ash-free dry weight to account for inorganic contaminants. The percent loss of ash-free dry weight was defined as the decomposition rate.

### *Data analysis*

As a first simple test for HFA, we calculated a general linear model (GLM) with type I sum of squares. We used the above defined decomposition rate as the dependent variable, mesh size as the first factor (two levels: coarse and fine mesh size), home vs. away as the second factor (three levels: 1, plant material from the home site: home; 2, plant material from different site of the same successional stage: away; same stage; and 3, plant material from a different site of a different successional stage: away; different stage), and the interaction of the two factors. To analyse whether there are differences between the home vs. away factor levels, we calculated three linear contrasts: between levels 1 (home) and 2 (away; same stage), between levels 1 (home) and 3 (away; different stage), and

between levels 1 (home) and 2 + 3 (away; in general). To analyse the effect of macro- and meso-fauna exclusion on litter mixtures in more detail, we also compared the decomposition rates with and without invertebrates averaged over mixtures and sites using ANOVA.

A simple GLM is, however, not a sufficient test for HFA as it disregards general differences between sites that possibly influence decomposition rates (Ayres et al., 2009a,b). Hence, we additionally used a method originally developed for calculating home-site effects in sports by Clarke and Norman (1995), which has been recently used to test for HFA in litter decomposition experiments (Ayres et al., 2009b). This method allows the HFA to be calculated for each of the four replicates per litter mixture separately. It measures the additional decomposition at home (ADH) for each mixture, with a positive value of ADH indicating HFA (home-field advantage) and a negative value of ADH indicating HFD (home-field disadvantage):

$$ADH_{a1\_1} = (HDD_{a1\_1} – ADD_{a1} - H) / (N - 2) \quad (1)$$

with HDD being the home decomposition difference, ADD the away decomposition difference, H the mean home performance for all mixtures, and N the total number of mixtures. Lower-case letters indicate different litter mixtures (e.g. a1 = litter mixture sampled on site A1), and upper-case letters indicate the site on which the mixture is decomposed (e.g. $D_{a3A1}$ = decomposition of litter mixture a3 on site A1).

HDD is calculated as the sum of the differences between the decomposition rates (D as the percentage ash free dry weight loss) of a certain mixture on its home site and all other mixtures on the home site of that certain mixture:

$$HDD_{a1\_1} = (D_{a1\_1A1} – D_{a2A1}) + (D_{a1\_1A1} – D_{a3A1}) + … + (D_{a1\_1A1} – D_{f3A1}) \quad (2)$$

ADD is the sum of the differences between the decomposition rates of a certain mixture on its away sites and the decomposition rates of the mixtures associated with these sites:

$$ADD_{a1} = (D_{a1A2} – D_{a2A2}) + (D_{a1A3} – D_{a3A3}) +...+ (D_{a1F3} – D_{f3F3}) \quad (3)$$

and H is calculated as the sum of HDD for all mixtures divided by the number of mixtures minus one.

$$H = (HDD_{a1\_1} + HDD_{a1\_2} + HDD_{a1\_3} +…+HDD_{f3\_3}) / (N - 1) \quad (4)$$

ADH was calculated for each litter mixture replicate, i.e. four replicates per site. A significant deviation from zero was tested for each site using one-sample t-tests.

To analyse the effects of the different successional stages on HFA, we used the above formula again but calculated ADH pair wise between all combinations of successional stages, which results in six comparisons of ADH for each mesh size (A-M, M-A, F-M, M-F, A-F, F-A,). Note that for each pair-wise comparison of successional stages, two tests of ADH are possible. We then averaged over mixture replicates (four) and site replicates (three) to get the mean ADH for each combination of successional stages. Again we used one-sample t-tests to test for significant deviations from zero.

## Results

The GLM did not indicate HFA: The home vs. away factor was not significant (Table 1). Furthermore, none of the tested linear contrasts showed significant differences in decomposition rates (1 (home) and 2 (away; same stage): p = 0.25; 1 (home) and 3 (away; different stage): p = 0.78; 1 (home) and 2 + 3 (away; in general): p = 0.61). As expected, the decomposition rates in litter bags with coarse and fine mesh sizes differed significantly, whereas the interaction between home vs. away and mesh

size was not significant (Table 1). Although overall significant, the exclusion of the macro- and meso-fauna had general weak effects (below 5 % in most cases; Figures 1 and 2). This difference between bags with macro- and meso-invertebrates and bags excluding these decomposers is due to the decomposition of litter sampled on the youngest successional stage A (Figure 1).

**Table 1:** The effects of mesh size (coarse and fine) and Home versus Away (1, decomposition at home; 2, decomposition at a different site of the same successional stage; and 3, decomposition at a different site of a different successional stage) and its interaction on decomposition rates. The effects were tested using a GLM with type I sum of squares.

| Source | Decomposition rates | | | |
|---|---|---|---|---|
| | *df* | *MS* | *F* | *P* |
| Meshsize | 1 | 0.07 | 9.97 | < 0.01 |
| Home vs. away | 2 | 0.02 | 1.25 | 0.11 |
| Meshsize x Home vs. away | 2 | 0.01 | 1.92 | 0.28 |
| Residual | 642 | 0.01 | | |

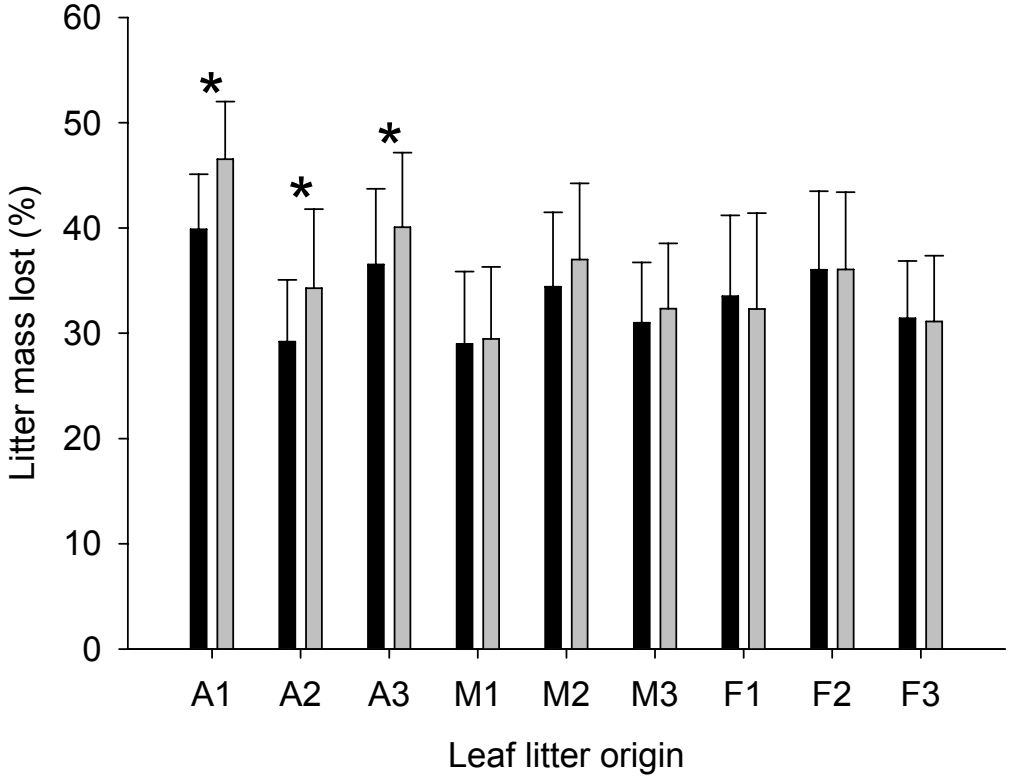


**Figure 1:** Difference between leaf litter decomposition with and without invertebrates for all mixtures averaged over sites. Mixtures A1–A3 originate from sites of successional stage A, mixtures M1–M3 originate from sites of successional stage M, and mixtures F1–F3 originate from sites of successional stage F. Black bars: without macro- and meso-invertebrates; grey bars: with macro- and meso-invertebrates; errors are standard deviation; asterisks indicate significance at $p < 0.05$. Successional stages: A, 15–20 years; M, 35–50 years; F, >100 years.

When we averaged the effects of macro- and meso-invertebrate exclusion across mixtures within sites, we found no significant effects (Figure 2). The overall decomposition rate of mixtures did not differ significantly between successional stages (Figure 1; ANOVA: with invertebrates: $p = 0.51$; without invertebrates: $p = 0.15$).

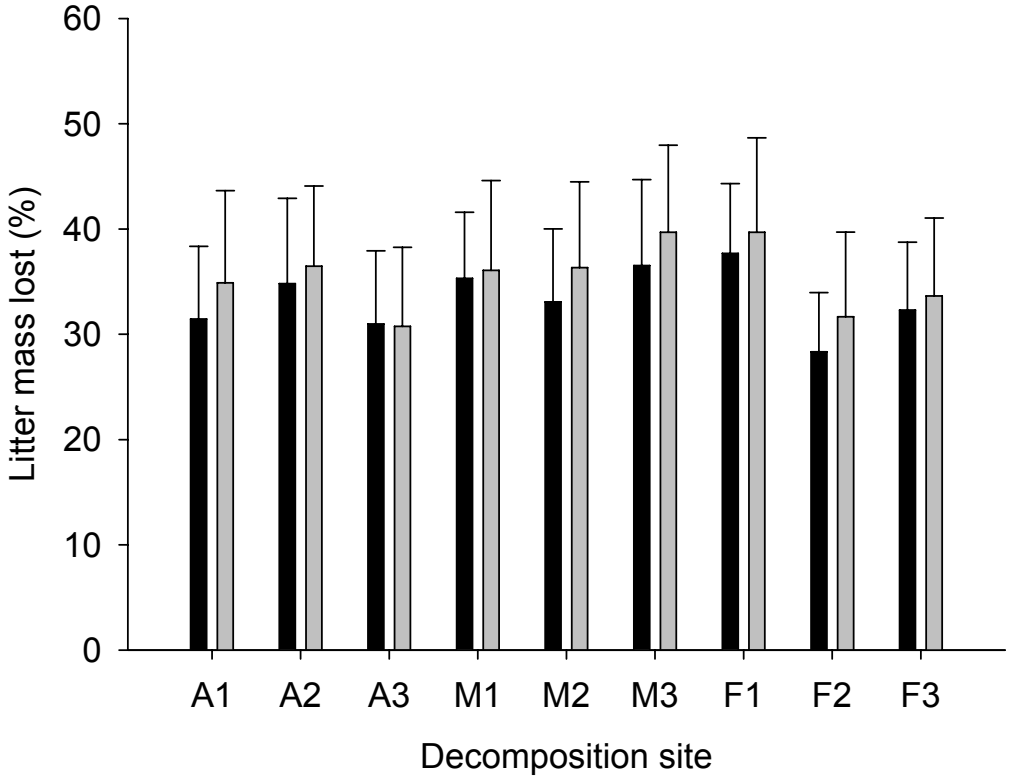


**Figure 2:** Difference between decomposition with and without invertebrates for all sites averaged over mixtures. Sites A1–A3 are in successional stage A, Sites M1–M3 are successional stage M, and sites F1–F3 are successional stage F. Black bars: without macro- and meso-invertebrates; grey bars: with macro-and meso-invertebrates; errors are standard deviation. Successional stages: A, 15–20 years; M, 35–50 years; F, >100 years.

Using the method suggested by Ayres et al. (2009b), we found a significant positive ADH (4.75 %) for only one site of successional stage A indicating HFA and even a significant negative ADH (−6.05 %) indicating HFD for one site of successional stage M. All other sites showed no significant deviation from zero (Figure 3). All pair-wise tests for HFA between successional stages revealed no significant deviation from zero. However, the standard deviation was high in most cases, which indicates a high variability in HFA among replicates (Figure 4).

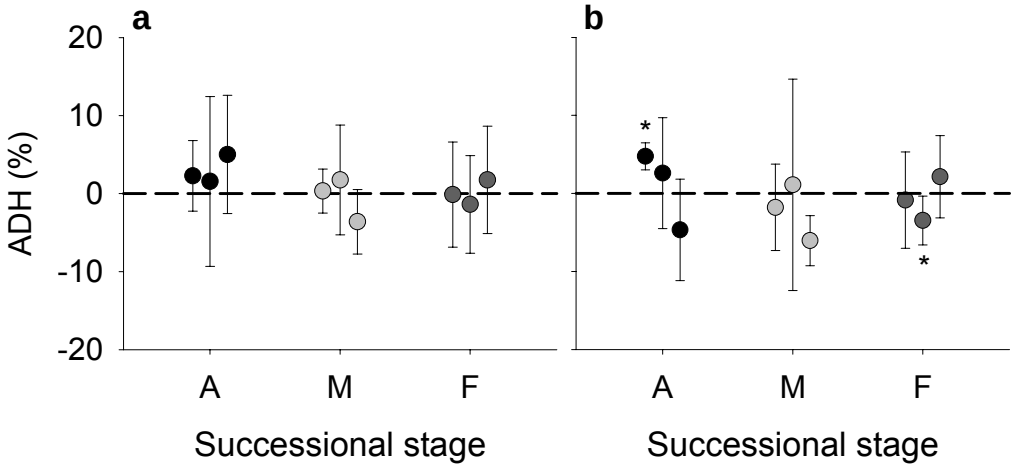


**Figure 3:** Mean additional decomposition at home (ADH) as a percentage of the initial litter mass for each site (4 replicates); a) with macro- and meso-invertebrates and b) without macro- and meso-invertebrates; errors are standard deviation; asterisks indicate significant deviation from zero. Successional stages: A, 10–15 years; M, 35–50 years; F, >100 years.

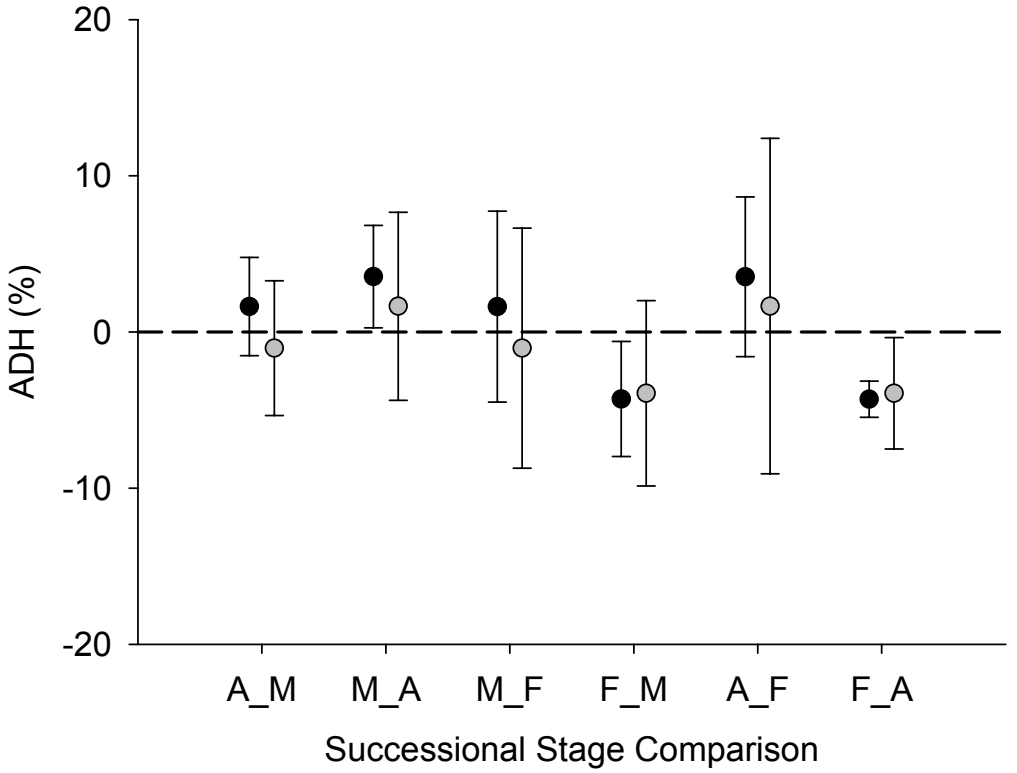


**Figure 4:** Additional decomposition at home (ADH) as a percentage of the initial litter mass between different successional stages, averaged over 3 sites with 4 replicates each, and with (black circles) and without (grey circles) macro- and meso-invertebrates. The first letter refers to the successional stage of the leaf litter in the litter bag and the second letter refers to successional stage of the site on which the litter bag was placed. For example, A_M indicates HFA of leaf litter of successional stage A on sites of successional stage M. Errors are standard deviation. Successional stages: A, 15–20 years; M, 35–50 years; F, >100 years.

## Discussion

Overall, our results do not suggest a common home-field-advantage for decomposition processes in a diverse rainforest and its successional stages. Even between stages A and F which showed clearest differences in litter quality and tree species composition we found no HFA.

During our study macro- and meso-invertebrates had a low effect on decomposition. Our experiment took place in winter and spring. During these seasons the mean temperature and precipitation are somewhat lower in the study region compared to summer and autumn (Figure S3). It is well known that the influence of the macro- and meso-fauna on decomposition depends on weather conditions (Wall et al., 2008) and the relatively cool and dry condition during our study might have led to an overall low effect of macro- and meso-invertebrates. Furthermore, within the bags with a fine mesh size favourable microclimatic conditions might have led to an increased decomposition within these bags by microorganisms, which all need high temperatures and moisture for their physiological processes. However, in a companion study using litterbags with the same mesh sizes as in the presented study we found considerable effects of macro- and meso-invertebrates (on average more than 11 % increased decomposition for mixtures with macro- and meso-invertebrates after 6 months of decomposition; see Gießelmann et al., 2010). Thus, microclimate differences due to mesh size seem to be of minor importance here. The only litter in our study that was significantly faster decomposed with the activity of the macro- and meso-fauna was the litter material from the youngest successional stage (Figure 1). This effect was consistent over sites (Figure 2), indicating that this effect relies on specific traits of the litter. Due to the low nutrient and high carbon content of the litter from early successional sites shredding and ingestion by macro- and meso-invertebrates may favour the activity and efficiency of subsequent microbial processes.

Overall macro- and meso-invertebrates seems to play only a minor role in our study and the major part of decomposition is due to the activity of microbial decomposers. Microbial decomposers, such as saprophytic fungi, have been suggested to be specialised on the decomposition of a

certain substrate (Lodge et al., 1995; Hansgate et al., 2005; Kubartová et al., 2009). We found considerable differences between the communities of fungi between successional stages of our study site (Gießelmann, Martins et al. in preparation). Furthermore, a high degree of functional diversity of saprophytic fungi has been shown in numerous studies (Goddard and Bradford, 2003; Paulus et al., 2006; Hanson et al., 2008; McGuire, 2010). Specificity and diversity within and between sites should all favour HFA. However our study did not support this expectation. Our results do not necessarily point to a functional redundancy of individual species. It is more likely that the lack of HFA is due to the ability of bacteria and fungi to shift their community composition on short temporal scales and thereby to adjust community composition to the quality of a certain substrate. Therefore, despite the supposed specificity of single species, the flexibility and dynamics of the microbial community translates into a functional redundancy of the total community. This implies that microbial species either reach the site from outside or many species occur within a site at low abundances and increase in abundance according to the local conditions. This ability of the microbial decomposer community to adjust its community composition could also be responsible for the similarity in decomposition rates of the specific mixtures from the different successional stages (Figure 1), although litter quality improved along the chronosequence (Feeny, 1976; Coley et al., 1985).

Overall, our study provides a glimpse into the highly complex decomposer subsystem of a diverse tropical forest ecosystem. We did not found a strong specialisation of the decomposer community on the decomposition of its home litter along a chronosequence of forest succession. Thus, the general ecosystem functionality regarding litter decomposition appears to be able to recover quickly during forest regeneration. Similar patterns have been found in other forests (Ostertag et al., 2008). We suppose that this functional flexibility of the decomposer community is due to the ability of the microorganisms to adjust to the decomposition of different substrates by shifting their community structure on short time scales due to rapid population growth or growth of hyphae. Nevertheless, further studies are needed to examine this idea in more

detail. Furthermore, HFA may occur on a smaller spatial scale that is within sites of the same successional age. Here litter of single species may occur in part as a kind of “monoculture” immediately beneath a tree individual leading to a small scale mosaic of different litter types and associated communities of microbial decomposers specialised to the particular litter type. Within such a small scale perspective, conditions are comparable to forests with few tree species where HFA effects are supposed to be common (Ayres et al, 2009a,b).

**Acknowledgements**

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## Supplementary Material

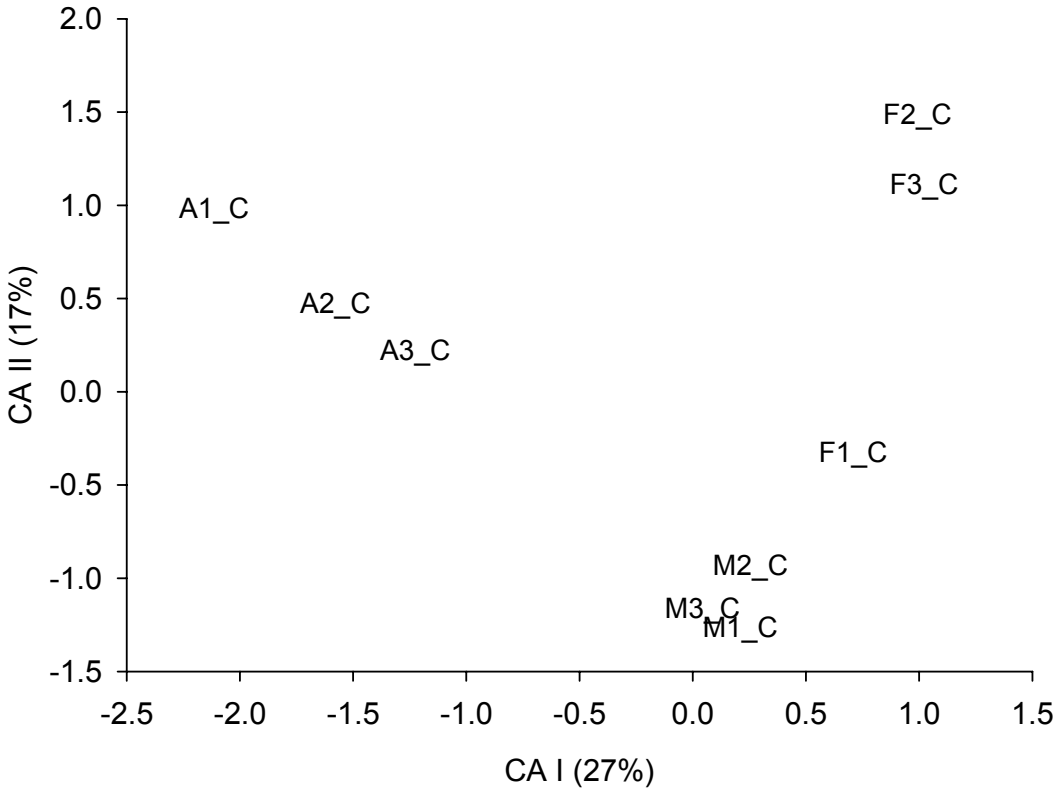


**Figure S1:** Ordination plot of correspondence analysis of tree communities for all study sites in the Cachoeira nature reserve. First or x-axis explained 27 % of total variance second or y-axis 17 % of total variance; compositional differences between stages is significant: $p < 0.01$, adonis, vegan package, R vers. 2.12.1; adopted from Gießelmann, Martins et al. in preparation. Successional stages: A, 10–15 years; M, 30–40 years; F, >100 years.

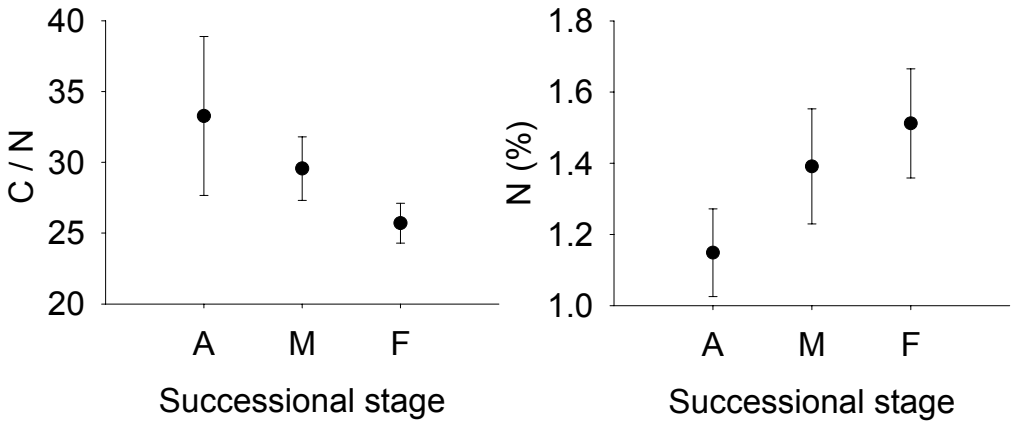


**Figure S2:** C/N ratio and N content for litter of the three successional stages; each point represents the overall mean with standard deviation of 15 litter samples, 5 litter samples per successional stage within three replicate sites; adapted from Balbinot (2009). Successional stages: A, 10–15 years; M, 30–40 years; F, >100 years.

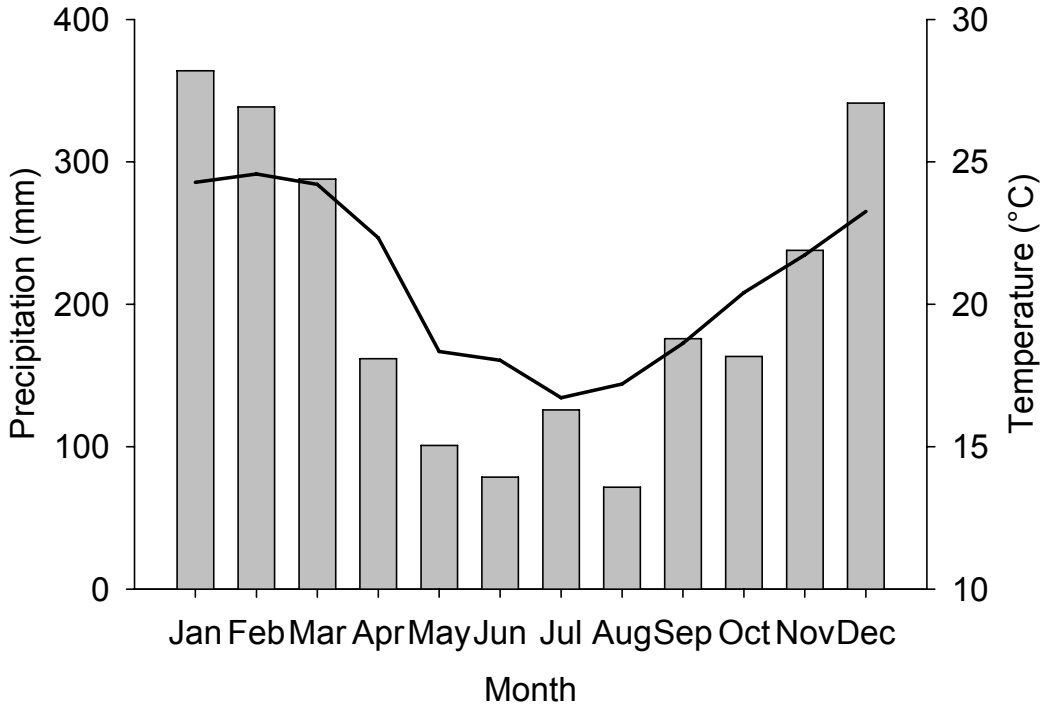


**Figure S3:** Mean monthly precipitation (bars) and temperature (line) averaged over the years 2004-2007. Climate data provided by: "Instituto Tecnológico SIMEPAR", Centro Politécnico da UFPR - CEP 81531-980, Curitiba, Paraná, Brazil.

# Summary

Primary tropical rainforests are increasingly replaced by secondary forests. Whether these secondary habitats are able to maintain the biodiversity and ecosystem functionality of the original forests is still a matter of debate. My dissertation aims to provide insights into the important ecosystem process of litter decomposition and its dynamics during secondary forest succession in the highly endangered Atlantic Rainforest of Brazil. I am intended to draw conclusions on the resilience of the decomposition process after disturbance.

In the first part (Chapter 2) of my thesis I investigated the influence of plant litter species richness, litter mixture composition and macro- and meso-invertebrate activity on litter decomposition. Using a litter-mixing experiment I aimed to draw conclusions on the relationship between the decomposition subsystem and plant species diversity in the Atlantic Rainforest. The results of my experiment indicated that plant species identity and litter mixture composition, but not species richness per se, significantly influenced litter decomposition rates. However, litter decomposition rates were less variable between mixtures of high species richness suggesting a stabilising effect of species richness. Maybe this effect is due to interacting effects between component species as, in many cases, litter decomposition dynamics were non-additive, i.e. observed decomposition rates of litter mixtures differed from what would be expected from the decomposition rates of their component species. The exclusion of invertebrates also influenced litter decomposition, although this effect varied between species and mixtures. In summary, the relationship between the decomposition subsystem and species diversity in the Atlantic Rainforest appeared to be largely idiosyncratic.

In the second part (Chapter 3) I analysed and compared species richness and community composition of litter dwelling fungi and of trees on forest sites of different successional age. I was intended to get insights into the successional dynamics of litter dwelling fungi communities and its relationship to tree succession, because litter dwelling fungi are known to have a substantial impact on litter decomposition. While tree species

richness increased with increasing successional age, species richness of fungi showed no differences among successional stages. Fungi species composition, however, significantly differed between successional stages and was correlated with tree community composition. Beside a fast re-colonisation of fungi following plant succession the occurrence of so called latent species which act as a seed bank for fungal succession seems to be likely. Hence, litter dwelling fungal communities seem to adopt quickly to the respective tree communities. Thus, they appear to be highly resilient or resistant to disturbance.

In the third part (Chapter 4) I set up a litter-transfer experiment along a successional chronosequence. I tested whether site specific litter decomposes faster on its home site than on other sites within and between successional stages indicating home-field advantage (HFA). I expected this experiment to provide insights into the successional dynamics of decomposers and the resilience of decomposer communities. Overall, my results did not support a home-field advantage of decomposability of site specific litter. Thus, the decomposer community is redundant or highly flexible in its ability to decompose different litter types. However, it should be noted that the effect of macro- and meso-invertebrates seemed to be reduced in my experiment, possibly due to climatic reasons. The high flexibility of the decomposer community could be due to the ability of microbial decomposers to quickly adjust to the decomposition of different substrates by shifting their community structure. Therefore, ecosystem functionality regarding litter decomposition at least partly appears to be highly resistant or able to recover quickly during secondary forest regeneration.

# Conclusions and Outlook

My PhD thesis provided insights into the decomposer subsystem of the Atlantic Rainforest of Brazil. On the one hand the results emphasised the high complexity and idiosyncrasy of the decomposition process due to the varying influence of different litter types and macro- and meso-invertebrate decomposers. On the other hand the micro-decomposer

communities appeared to be highly flexible. This flexibility indicated that at least parts of the decomposer community are able to quickly adjust to the decomposition of varying natural litter mixtures suggesting a high resilience of microbial decomposition after disturbance. Thus, if agricultural areas within the Atlantic Rainforest become abandoned and regenerate to secondary forests, at least the microbial decomposer community is likely to recover quickly following forest succession providing their ecosystem functions for the decomposition process.

Future studies should investigate the presented aspects of decomposition and the successional dynamics of microbial decomposers in more detail. For instance, litter-mixing experiments should consider phylogeny and secondary compounds of component litter types. Microbial decomposers should be studied using high resolution genetic methods such as sequencing to obtain a more comprehensive understanding of the composition and successional dynamics of their communities. Finally, for the effects of the home-field advantage (HFA) on litter decomposition fine-scale studies would be helpful, e.g. whether HFA occurs on much smaller spatial scales for example within sites of the same successional age directly beneath different tree species. I suggest that this scale is probably more relevant for microbial organisms.

# Zusammenfassung

Tropische Primärregenwälder werden in zunehmendem Maße durch Sekundärwälder ersetzt. Es stellt sich daher die Frage, ob diese sekundären Habitate geeignet sind die Biodiversität und Ökosystemfunktionen der ursprünglichen Wälder zu erhalten. Ziel meiner Dissertation ist es, im stark gefährdeten Atlantischen Küstenregenwald Brasiliens, Einblicke in den wichtigen Prozess der Laubstreuzersetzung und seiner Dynamik während der sekundären Waldsukzession zu erhalten. Ich hoffe damit Rückschlüsse auf die Regenerationsfähigkeit des Zersetzungsprozesses ziehen zu können.

Im ersten Teil meiner Arbeit untersuchte ich den Einfluss der Laubartenzahl, der Zusammensetzung der Laubmixturen und der Aktivität der Makro- und Mesoinvertebratenfauna auf die Laubstreuzersetzung. Hierfür nutzte ich ein Mischungsexperiment um Rückschlüsse auf den Zusammenhang zwischen Streuzersetzung und Baumdiversität zu ziehen. Die Ergebnisse zeigen, dass die Zersetzungsrate durch Laubartenidentität und Zusammensetzung der Laubmixturen beeinflusst wurde, nicht aber durch die Laubartenzahl an sich. Allerdings zeigten die Streuzersetzungsraten mit zunehmender Laubartenzahl eine geringere Variabilität, was auf einen stabilisierenden Effekt der Laubartenzahl hindeuten könnte. Dies ist möglicherweise ein Effekt von Interaktionen zwischen den verschiedenen Laubarten innerhalb einer Mischung. In vielen Fällen waren die Streuzersetzungsdynamiken nicht-additiv, die beobachteten Gesamtzersetzungsraten der Mischungen wichen also von denen ab, welche aufgrund der einzelnen Zersetzungsraten der Streuarten zu erwarten gewesen wären. Der Ausschluss von Meso- und Makroinvertebraten beeinflusste ebenfalls die Streuzersetzung. Dieser Effekt variierte jedoch erheblich zwischen den Laubarten und Mischungen. Insgesamt deuten meine Ergebnisse daraufhin, dass der Zusammenhang zwischen Streuzersetzung und Baumdiversität größtenteils unvorhersagbar ist.

In der zweiten Studie analysierte und verglich ich die Artenzahl und Artenzusammensetzung von streubewohnenden Pilzen und von Bäumen

auf Waldflächen unterschiedlichen Sukzessionsalters. Anhand der Ergebnisse sollten Erkenntnisse über die Sukzessionsdynamiken streubewohnender Pilzgemeinschaften, welche maßgeblich an der Streuzersetzung beteiligt sind, im Zusammenhang zur Baumsukzession gewonnen werden. Während die Baumartenzahl mit zunehmendem Sukzessionsalter der Flächen anstieg, zeigten die Artenzahlen der Pilze keinen signifikanten Unterschied zwischen den einzelnen Altersstadien. Die Artenzusammensetzung der Pilze hingegen unterschied sich signifikant zwischen den Flächen unterschiedlichen Sukzessionsalters und korrelierte zudem mit der Artenzusammensetzung der Baumgemeinschaften. Eine Erklärung für die gefundenen Mustern ist einerseits eine schnelle Neubesiedlung durch Pilze die der Baumsukzession folgt, andererseits das Vorhandensein von sogenannten „latenten-Arten“, welche als eine Art Samenbank für die Pilzsukzession dienen. Streubewohnende Pilzgemeinschaften scheinen sich also sehr schnell der jeweiligen Baumartenzusammensetzung anzupassen und wären somit in hohem Maße resilient oder resistent gegenüber Störungen.

Im dritten Teil führte ich ein Streu-Transfer-Experiment entlang eines Sukzessionsgradienten durch. Ich untersuchte, ob ortspezifische Laubstreu an ihrem Herkunftsort schneller als an anderen Orten abgebaut wird und zwar innerhalb und zwischen den Sukzessionsstadien. Ein schnellerer Abbau auf dem Herkunftsstandort, würde auf einen Heimvorteil (HFA – home-field advantage) in der Streuzersetzung hindeuten. Das Experiment sollte Einblicke in die Sukzessionsdynamiken und die Regenerationsfähigkeit der Zersetzerorganismen und ihrer Funktionalität liefern. Insgesamt deuteten meine Ergebnisse nicht auf einen Heimvorteil in der Zersetzung von ortspezifischer Laubstreu hin. Die Zersetzergemeinschaft ist also in ihrer Fähigkeit verschiedene Streuarten zu zersetzen in hohem Maße redundant oder hochgradig flexibel. Es muss allerdings erwähnt werden, dass der Effekt der Makro- und Mesoinvertebratenfauna in meinem Experiment, wahrscheinlich aus klimatischen Gründen, stark reduziert war. Die hohe Flexibilität der Zersetzergemeinschaft könnte auf der Fähigkeit der mikrobiellen Zersetzer beruhen, sich schnell auf die Zersetzung unterschiedlicher

Substrate einzustellen, indem sie ihre Gemeinschaftsstruktur ändert. Die Ökosystemfunktionalität in Bezug auf den Streuzersetzungsprozess scheint also, wenigstens teilweise, in hohem Maße resistent oder fähig zu sein, sich schnell im Laufe der Sekundärsukzession zu erholen.

# Schlussfolgerung und Ausblick

Die vorliegende Studie bietet Einblicke in das Zersetzersystem im Atlantischen Küstenregenwald von Brasilien. Die Ergebnisse betonen einerseits die hohe Komplexität und Unvorhersagbarkeit des Zersetzungsprozesses durch den variierenden Einfluss verschiedener Laubarten und Zersetzern der Makro- und Mesoinvertebratenfauna. Auf der anderen Seite lassen die sie auf eine hohe Flexibilität der zersetzenden Mikrofauna schließen. Diese Flexibilität zeigt, dass wenigstens ein Teil der Zersetzergemeinschaft fähig ist, sich schnell an die Zersetzung unterschiedlicher Streumixturen anzupassen. Dies deutet auf eine starke Resilienz der mikrobiellen Zersetzung bei Störungen hin. Es ist also anzunehmen, dass sich wenigstens die mikrobielle Zersetzergemeinschaft im Laufe der sekundären Waldsukzession schnell erholt und ihre Ökosystemfunktion für den Zersetzungsprozess bereitstellt.

Zukünftige Studien sollten die dargestellten Aspekte des Zersetzungsprozesses und die Sukzessionsdynamiken mikrobieller Zersetzer detaillierter untersuchen. Beispielsweise sollten Laubstreu-Mischungsexperimente die Phylogenie der genutzten Pflanzen sowie deren sekundäre Inhaltsstoffe stärker berücksichtigen. Um genauere Erkenntnisse über die Zusammensetzung und Sukzessionsdynamik mikrobieller Zersetzergemeinschaften zu erlangen, sollten diese mittels hoch auflösender genetischer Methoden (Sequenzierung) untersucht werden. Des Weiteren wäre es sinnvoll, das Auftreten eines Heimvorteils in der Streuzersetzung (HFA) auf einer kleineren räumlichen Skala zu untersuchen, zum Beispiel innerhalb der Untersuchungsflächen des gleichen Sukzessionsstadiums, direkt unter verschiedenen Baumarten. Diese Skala ist möglicherweise relevanter für mikrobielle

Zersetzerorganismen. Außerdem sollte der Effekt von Makro- und Mesoinvertebraten in Hinblick auf das Auftreten eines möglichen Heimvorteiles noch einmal genauer untersucht werden.

# Appendix

## Curriculum Vitae

### Persönliche Daten

| | |
|---|---|
| Familienname: | Gießelmann |
| Vorname: | Urs Christian |
| Geburtsdatum: | 20.07.1979 |
| Geburtsort: | Siegen |
| Staatsangehörigkeit: | deutsch |

### Schulausbildung

| | |
|---|---|
| **1987 - 1990** | Gemeinschaftsgrundschule Fellinghausen |
| **1990 - 1999** | Friedrich Flick Gymnasium Kreuztal<br>Abschluss: Allgemeine Hochschulreife |

### Hochschulausbildung

| | |
|---|---|
| **09/2000 - 10/2006** | Biologiestudium an der Philipps-Universität Marburg<br><br>Diplomarbeit in der Arbeitsgruppe Allgemeine Ökologie und Tierökologie bei Prof. Dr. Roland Brandl im Rahmen des BMBF Projektes *BIOTA*<br><br>Titel der Arbeit: „Aspects of coloniality in the sociable weaver (*Philetairus socius*)“ |
| **seit 10/2006** | Promotion an der Philipps-Universität Marburg in der Arbeitsgruppe Allgemeine Ökologie und Tierökologie bei Prof. Dr. Roland Brandl im Rahmen des BMBF Projekt *Mata Atlântica*<br><br>Titel der Arbeit: „Litter decomposition in the Atlantic Rainforest of Brazil“ |
| **05/2010 - 02/2011** | Fortbildung zum akademischen Geo-informatiker über ein Fernstudium an der Universität Salzburg (UNIGIS_eXpress) |

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# Abgrenzung der Eigenleistung

Soweit nicht anders erwähnt, wurden alle präsentierten Studien von mir selbst geplant, durchgeführt und ausgewertet. Das abschließende Verfassen der Manuskripte erfolgte in Zusammenarbeit mit den genannten Koautoren.

Die Daten zur Untersuchung der Baumarten in der zweiten Studie (Kapitel 3) wurden von Kelly Geronazzo Martins und Gustavo Pacheco erhoben. Die statistische Auswertung der Daten führte ich in enger Zusammenarbeit mit Kelly Geronazzo Martins durch.