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

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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.

1. 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 et al., 1979; Coûteaux et al., 1995; Cadisch 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. 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 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 under such circumstances (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

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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 colonise 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 vs. macro- and meso-invertebrates and their interactions 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 (Myers 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 et al., 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.

2. Materials and methods

2.1. 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 and 38% of sand), acidic ($pH_{CaCl_2} = 3.9$) 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 differed considerably in tree species richness and composition. Species richness of trees increased with increasing successional stage (mean number of tree species per $1000\ m^2 \pm SD$; three replicate sites per successional stage: stage A, 23 ± 5; stage M, 38 ± 6; stage F, 42 ± 3; $p < 0.01$, ANOVA, Gießelmann et al., in press), and species composition differed between the successional stages (Fig. S1). Additionally, the litter quality in terms of N content increased and C/N ratio decreased along the chronosequence (Fig. 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 $0.75\ m \times 0.75\ m$ on each of the nine replicated sites. Litter was sampled for 8 months (September 2007 until April 2008). Litter traps were emptied for every 2 weeks. Collected leaf litter was oven dried and stored under dry conditions. Thirty-six nylon litter bags with a coarse mesh size ($5\ mm \times 5\ mm$) and 36 with a fine mesh size ($20\ \mu m \times 20\ \mu m$; size of bags $25\ cm \times 25\ cm$) were filled with $3 \pm 0.1\ g$ 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 and put into separate envelopes to avoid loss of particulate leaf material through the mesh during transit from the field back to the laboratory. 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.

2.2. 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 macro- and meso-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):

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

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:

$$\mathrm{HDD}_{a1\_1} = (D_{a1\_1A1} - D_{a2A1}) + (D_{a1\_1A1} - D_{a3A1}) + \cdots + (D_{a1-1A1} - D_{f3A1}) \quad (2)$$

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:

$$\mathrm{ADD}_{a1} = (D_{a1A2} - D_{a2A2}) + (D_{a1A3} - D_{a3A3}) + \cdots + (D_{a1F3} - D_{f3F3}) \quad (3)$$

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

$$H = \frac{\mathrm{HDD}_{a1\_1} + \mathrm{HDD}_{a1\_2} + \mathrm{HDD}_{a1\_3} + \cdots + \mathrm{HDD}_{f3\_3}}{N - 1} \quad (4)$$

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.

3. 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 generally weak effects (below 5% in most cases; Figs. 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 (Fig. 1).

Table 1
The effects of mesh size (coarse and fine) and home vs. 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 × Home vs. away	2	0.01	1.92	0.28
Residual	642	0.01		

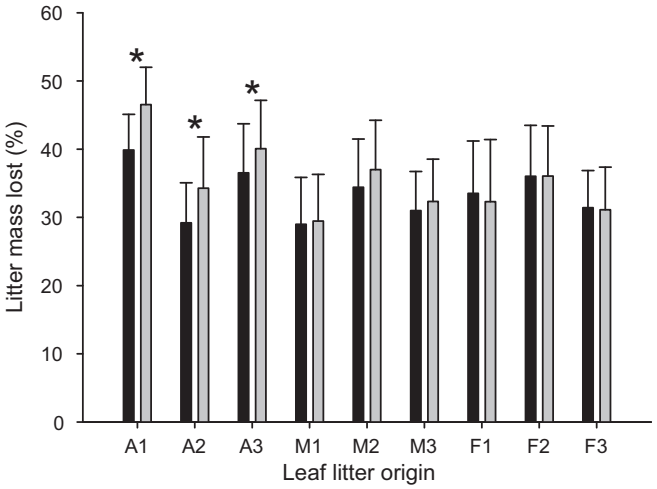

Fig. 1. Difference between leaf litter decomposition with and without macro- and meso-invertebrates for all mixtures averaged over sites. Mixtures A1–A3 originate from sites of successional stage A, mixtures M1–M3 originate from sites of successional stage M, and mixtures F1–F3 originate from sites of successional stage F. Black bars: without macro- and meso-invertebrates; grey bars: with macro- and meso-invertebrates; errors are standard deviation; asterisks indicate pair wise ANOVA 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 (Fig. 2). The overall decomposition rate of mixtures did not differ significantly between successional stages (Fig. 1; ANOVA: with macro- and meso-invertebrates: $p = 0.51$; without macro- and meso-invertebrates: $p = 0.15$). 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 (Fig. 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 (Fig. 4).

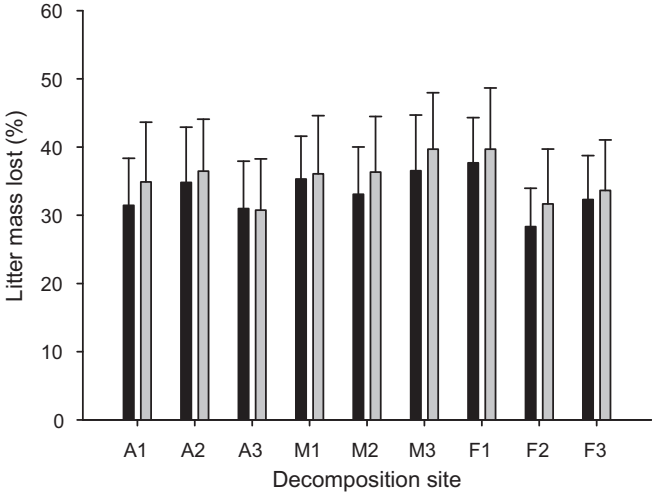

Fig. 2. Difference between decomposition with and without macro- and meso-invertebrates for all sites averaged over mixtures. Sites A1–A3 are in successional stage A, Sites M1–M3 are successional stage M, and sites F1–F3 are successional stage F. Black bars: without macro- and meso-invertebrates; grey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

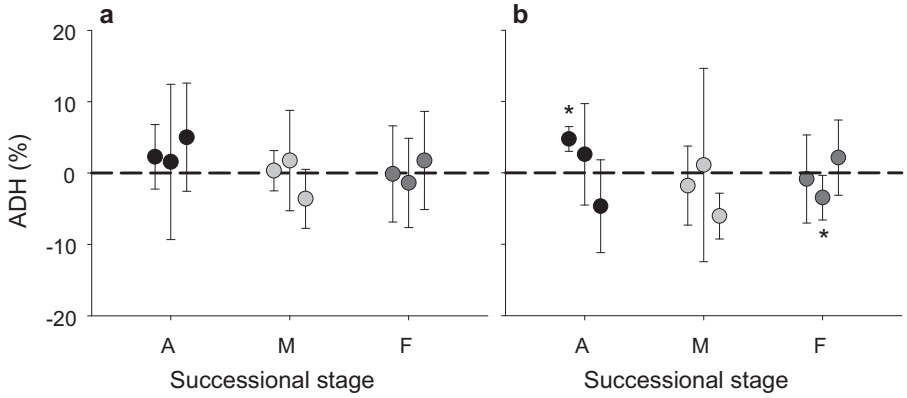

Fig. 3. Mean additional decomposition at home (ADH) as a percentage of the initial litter mass for each site (3 sites per successional stage; 4 replicates per site); (a) with macro- and meso-invertebrates and (b) without macro- and meso-invertebrates; errors are standard deviation; asterisks indicate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

4. 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 (Fig. 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 (Fig. 1). This effect was consistent over sites (Fig. 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.

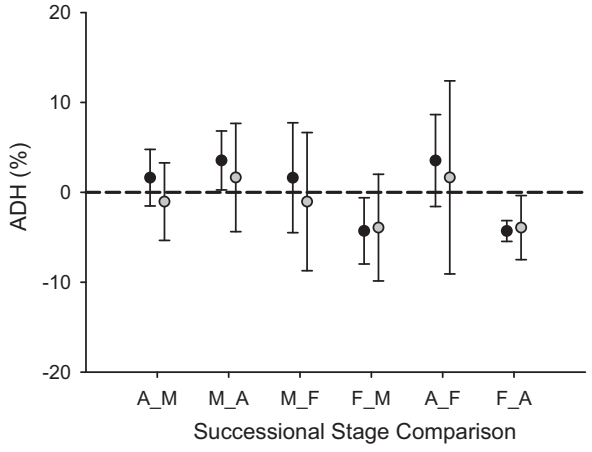

Fig. 4. Additional decomposition at home (ADH) as a percentage of the initial litter mass between different successional stages, averaged over 3 sites with 4 replicates each, and with (black circles) and without (grey circles) macro- and meso-invertebrates. The first letter refers to the successional 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.

Overall macro- and meso-invertebrates seems to play only a minor role in our study. The same is true for possible interactions between microbial decomposers and macro- and meso-decomposers which are likely to happen in coarse bags but are prevented in fine bags. 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, 1995; Hansgate et al., 2005; Kubatová et al., 2009). We found considerable differences between the communities of fungi between successional stages of our study site (Fig. S4; Gießelmann et al., in press). Furthermore, a high degree of functional diversity of saprophytic fungi has been shown in numerous studies (Goddard and Bradford, 2003; Paulus and Gadek, 2006; Hanson et al., 2008; McGuire et al., 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 (Fig. 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" 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).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.apsoil.2011.07.010.

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