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## Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape

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**Abstract** Amazonian forest fragments and second-growth forests often differ substantially from undisturbed forests in their microclimate, plant-species composition, and soil fauna. To determine if these changes could affect litter decomposition, we quantified the mass loss of two contrasting leaf-litter mixtures, in the presence or absence of soil macroinvertebrates, and in three forest habitats. Leaf-litter decomposition rates in second-growth forests (> 10 years old) and in fragment edges (< 100 m from the edge) did not differ from that in the forest interior (> 250 m from the edges of primary forests). In all three habitats, experimental exclusion of soil invertebrates resulted in slower decomposition rates. Faunal-exclosure effects were stronger for litter of the primary forest, composed mostly of leaves of old-growth trees, than for litter of second-growth forests, which was dominated by leaves of successional species. The latter had a significantly lower initial concentration of N, higher C:N and lignin:N ratios, and decomposed at a slower rate than did litter from forest interiors. Our results indicate that land-cover changes in Amazonia affect decomposition mainly through changes in plant species composition, which in turn affect litter quality. Similar effects may occur on fragment edges, particularly on very disturbed edges, where successional trees become dominant. The

drier microclimatic conditions in fragment edges and second-growth forests (> 10 years old) did not appear to inhibit decomposition. Finally, although soil invertebrates play a key role in leaf-litter decomposition, we found no evidence that differences in the abundance, species richness, or species composition of invertebrates between disturbed and undisturbed forests significantly altered decomposition rates.

**Keywords** Amazon · Edge effects · Habitat fragmentation · Secondary-forest succession · Nutrient cycling

### Introduction

Litter decomposition is a fundamental process in forest ecosystems, influencing rates of nutrient cycling and carbon flux (Aber and Melillo 1991), and thus any disturbance that affects this process can have pervasive effects on ecosystem functioning. Deforestation and forest fragmentation are currently the most widespread forms of disturbance to tropical forests (Whitmore 1997), yet the resulting effects of such disturbances on litter decomposition are still poorly understood.

The rate at which litter is decomposed is in large part influenced by its chemical composition, by the activity and composition of soil organisms, and by the physical micro-environment (Meentemeyer 1978; Seastedt et al. 1983; Finzi et al. 2001; González and Seastedt 2001; Bradford et al. 2002). All of these three factors are known or presumed to be altered in fragmented forests and in areas of secondary growth. Changes in the physical environment of fragmented forests often include an increase in understory air temperatures, and a decline in air and soil moisture with decreasing distances to forest edge (Williams-Linera 1990; Kapos et al. 1997). Similarly, second-growth forests experience dramatic changes in microclimate, especially during the initial phases of succession (Mesquita et al. 1998). The drier

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microclimatic conditions along forest edges and in early successional forests can, potentially, inhibit the activity of soil macroinvertebrates. These organisms play a vital role in leaf-litter decomposition, by consuming litter and, by physically breaking up organic material, facilitating the activity of microbes (Petersen and Luxton 1982; Bradford et al. 2002). Variations in the abundance, species richness, and composition of many groups of soil invertebrates are known to occur in response to edge effects or changes in vegetation cover (Lasebikan 1976; Belshaw and Bolton 1993; Eggleton et al. 1995; Didham 1997; Carvalho and Vasconcelos 1999; Vasconcelos 1999). Similarly, deforestation and forest fragmentation may affect litter quality by favoring the recruitment of successional-tree species at the expense of old-growth species (Laurance et al. 1998), as these two groups can differ strongly in nutrient, carbon, lignin, and phenolic contents (Coley 1983; Newberry and de Foresta 1985; Mesquita et al. 1998; Xuluc-Tolosa et al. 2003).

Hence, although mounting evidence suggests that litter-decomposition rates in Amazonian forests can be affected by recent anthropogenic disturbances (Didham 1998), critical experiments are still missing. We compared rates of litter decomposition among three forest habitats representing a gradient of increasing disturbance and drier microclimatic conditions. These habitats were the interior and edges of primary forests, and the interior of second-growth forests. Rates of litter decomposition, in the presence or absence of soil invertebrates, were determined for two different litter mixtures, one from second-growth forests (composed almost entirely of leaves of successional species) and one from the interior of primary forests (dominated by leaves of old-growth forest species). This experimental design allowed us to rigorously assess the relative influences and possible interactions of habitat type, litter composition, and invertebrate abundance on rates of litter decomposition.

## Materials and methods

### Study site

Our study site spans an area of ca. 20×50 km in central Amazonia, about 70 km north of Manaus, Brazil (2°30'S, 60°W). In 1979, an experimental project, the Biological Dynamics of Forest Fragments Project (BDFFP), was initiated at this site to determine the ecological consequences of Amazonian habitat fragmentation (Bierregaard and Gascon 2001; Laurance et al. 2002).

Annual rainfall in this area ranges from 1,900 mm to 3,500 mm, with a distinct dry season between June and October (Laurance 2001). The dominant soil type is a Yellow Latosol (Xanthic Ferralsol in the FAO/Unesco classification). The predominant vegetation is locally known as *terra-firme* (non-flooded) forest, which is a primary and evergreen wet forest whose canopy is

30–35 m tall and whose understory is dominated by stemless palms, especially *Astrocaryum* spp. In these forests, the maximum longevities of old-growth tree species range from a few centuries to over 1,000 years (Chambers et al. 1998; Laurance et al. 2004).

As part of the BDFFP, forest fragments of 1, 10, and 100 ha were created as ranchers cleared several thousands hectares of pristine forest to establish pastures for cattle grazing. Because of low productivity, almost all of the pasture areas were abandoned after a few years of use and many of these were gradually replaced, via natural succession, by second-growth forests (10–17 years old at the time of our study). To help maintain fragment isolation, 100 m-wide strips of regrowth surrounding each fragment were cleared and burned at 3–5 year intervals.

### Experimental design

We designed a factorial experiment in which the main factors were habitat (three levels), litter type (two levels), and invertebrate abundance (two levels), and the dependent variable was the percentage of the original leaf material remaining in litterbags. The abundance of soil- and litter-dwelling invertebrates in the litterbags was manipulated using chemical and physical barriers. The litterbags (20×24 cm) were made of non-degradable nylon material, with 1 mm mesh. This mesh size prevents the colonization of the litter by macroinvertebrates (ants, beetles, Diplopoda, etc.), although some elements of the soil mesofauna, such as larger-bodied Acari and Collembola, may be excluded as well (Bradford et al. 2002). Three 1-cm<sup>2</sup> perforations were made on each side of the control bags to facilitate the access of these invertebrates. The treatment bags (without invertebrates) did not have those holes. In addition, the latter were treated with naphthalene, an arthropod repellent that is commonly used in invertebrate-removal experiments (González and Seastedt 2001). Two balls of naphthalene were placed inside each bag at the beginning of the experiment and again 30 and 70 days later. No balls were placed in the control bags.

Litterbags were filled with 6–8 g (mean = 6.84 ± 0.51 g dry weight) of naturally senesced leaves collected in litter traps. Litter collection was performed during the 2 months preceding the beginning of this experiment, during the local dry season, when most trees were shedding their leaves (Luizão 1989). In total, 540 litterbags were used in the experiment, of which half were filled with a mixture of leaves from the interior of primary forests, and the other half with leaves from nearby second-growth forests. We intentionally collected leaves only from secondary forests that had established in areas that did not burn or burned poorly after forest clearing, as fire strongly affects tree-species composition (Mesquita et al. 2001). Abundant species in these areas include *Cecropia sciadophylla*, *Bellucia grossularioides*, and *Vismia* spp. These are all successional trees, which

are known to increase in abundance in small fragments and fragment edges, especially those with high rates of tree mortality and damage (Laurance et al. 1998). In contrast, the leaf mixture collected in interior forests was composed almost exclusively of leaves of old-growth trees, which in our study site are dominated by species in the families Sapotaceae, Lecythydaceae, Burseraceae, and Leguminosae (Rankin-de-Merona 1992), but also include representatives of many rarer families.

Litterbags were placed in three forest habitats. These included the interiors of primary forests (>250 m from the edge of continuous forest or 100-ha forest fragments), the edges of primary forests (<100 m from the edge of 1-, 10-, or 100-ha forest fragments), and the interiors of (>200 m) of nearby second-growth forests. Measurements in the BDFFP landscape demonstrate that there is a difference of up to 10% in understory relative humidity between second-growth forests and the interiors of primary forests, whereas the edges of primary forests are intermediate between the two (E.M. Bruna, unpublished data).

The distance used to distinguish between edge and interior forest was determined from previous studies of forest dynamics, which indicate that most edge effects penetrate up to 100 m from the edge (Laurance et al. 2002). Twenty plots of 20×20 m each were randomly established in each habitat type, with a minimum distance of 50 m between plots located in the same habitat. In each plot, nine bags (all with the same type of leaf mixture and invertebrate treatment) were arranged in a 3×3 array (with 10 m spacing). Three randomly selected bags were removed from each plot on 30, 70, and 120 days after the beginning of the experiment (December 2001). Invertebrates were extracted by placing the contents of the bags in Berlese funnels for 5 days. After that, the dried litter was cleaned of debris (roots, soil, etc.) and weighed to the nearest 0.01 g.

#### Leaf chemical analyses

Initial concentrations of lignin in the leaf-litter from secondary and primary forests were measured using the acid detergent method (Goering and Van Soest 1970), while for determination of carbon and nitrogen contents (percent dry weight), we followed the methodology of Skoog et al. (1998). Leaves from a given forest type were combined to make a composite sample, thoroughly mixed, and finely milled. All analyses were repeated three times to minimize any analytical errors.

#### Statistical analyses

The effects of habitat, litter type, and invertebrate abundance on leaf-litter decomposition were assessed using repeated-measures ANOVA. Decomposition was expressed as the proportion of the initial litter mass remaining after 30, 70, and 120 days. No transformation

of the data was needed as visual inspection of probability plots indicated that the data did not deviate markedly from a normal distribution (Wilkinson 1996).

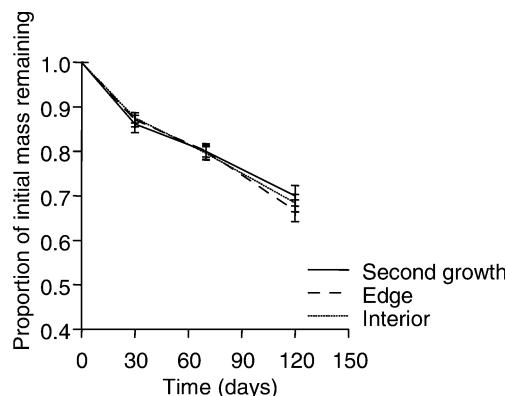
Repeated-measures ANOVA was also used to assess the magnitude of the invertebrate-exclusion treatment. Invertebrate abundance was expressed as the number of individuals per sample. To meet the assumption of normality, data were  $\log(X+1)$ -transformed prior to analysis.

## Results

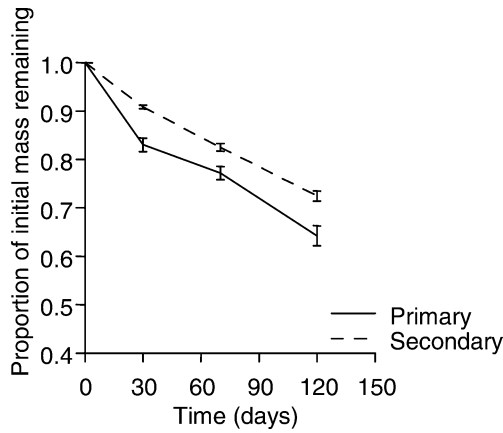
Of the three factors analyzed, invertebrates, litter type, and habitat, only the latter did not significantly influence leaf-litter decomposition. Comparable rates of leaf-litter decomposition were found in the interior and edges of the primary forests and in the nearby secondary forests ( $F_{2,48}=0.25$ ,  $P=0.78$ ; Fig. 1). In contrast, a significant effect of litter type was detected ( $F_{1,48}=57.39$ ,  $P<0.001$ ), and this effect did not interact with the effects of habitat ( $F_{2,48}=1.99$ ,  $P=0.15$ ). Leaves from second-growth trees decomposed much more slowly than did those from the interior of primary forests (Fig. 2). Although leaves from secondary and primary forests had similar initial concentrations of carbon and lignin (Table 1), the former had a significantly smaller concentration of nitrogen, and higher C:N and lignin:N ratios ( $t$ -tests,  $P<0.001$  in all cases; Table 1).

The invertebrate-exclusion treatment negatively affected litter decomposition ( $F_{1,48}=63.87$ ,  $P<0.001$ ), but the magnitude of the effect was dependent upon litter type (faunal-treatment × litter-type interaction;  $F_{2,48}=37.23$ ,  $P<0.001$ ). The presence of invertebrates greatly accelerated the decomposition of leaves from the interior of primary forests, but not that of leaves of successional species from second-growth forests (Fig. 3).

The exclusion treatment we applied did not completely prevent the colonization of leaf litter by invertebrates (Fig. 4). However, invertebrate abundance



**Fig. 1** Changes in leaf-litter mass in three different forest habitats in central Amazonia: second-growth forests, the interior of primary forests, and primary forest-edges. Values shown are the mean ± 1 SE



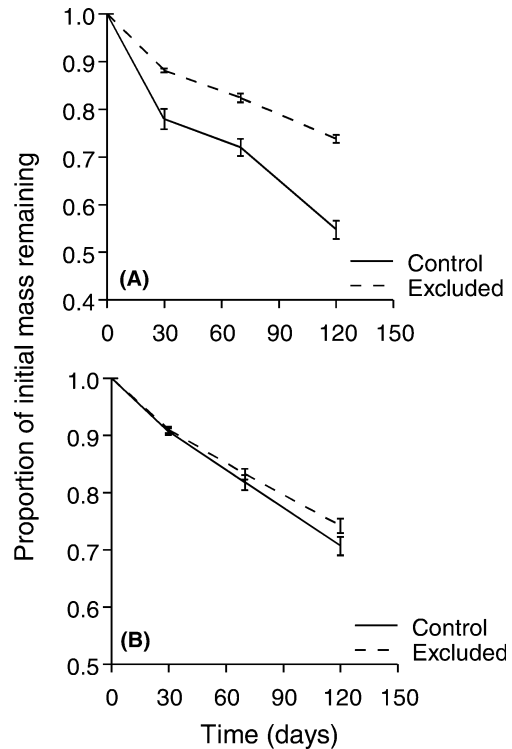
**Fig. 2** Changes in mass of leaf litter from primary and secondary forests. Values shown are the mean  $\pm$  1 SE

was significantly lower in the treatment bags than in the control bags ( $F_{1,58} = 60.9$ ,  $P < 0.001$ ). Furthermore, there were strong differences in faunal composition between treatments. Almost all individuals extracted from the invertebrate-exclusion bags were mites (Acari). Mites were also the dominant group in the control bags; but in addition, these contained many macroinvertebrates, including many ants as well as beetles (larvae and adults), Collembola, cockroaches, Diplopoda, dipteran larvae, Embioptera, Isopoda, pseudoscorpions, and spiders. The difference in invertebrate abundance between control and treatment bags was noticeably lower during the last 50 days of the experiment (time  $\times$  treatment interaction:  $F_{2,116} = 5.14$ ,  $P = 0.009$ ; Fig. 4), probably due to a concomitant decline in the concentration of naphthalene in the treatment bags.

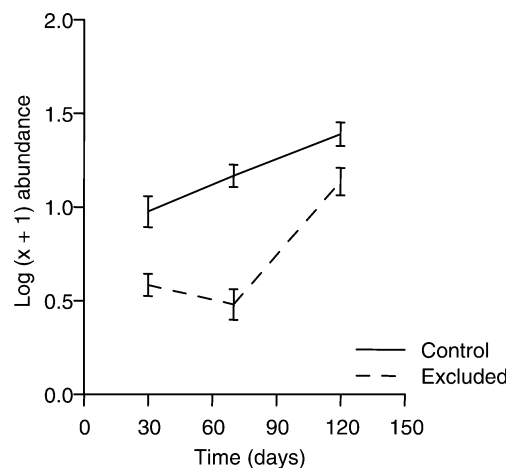
## Discussion

Microclimatic effects associated with changes in vegetation cover

The three habitats we studied were chosen because they represented a gradient of microclimatic conditions resulting from forest disturbance. Because second-growth forests and fragment edges had a drier microclimate, we expected decomposition to be slower there than in the interior of primary forests. However, for similar organic materials, decomposition rates were virtually the same across the different habitats, indicating that among-habitat differences in microclimate were



**Fig. 3** Effects of invertebrate exclusion on mass loss of leaf-litter from primary (a) and secondary forests (b). Values shown are the mean  $\pm$  1 SE



**Fig. 4** Differences in leaf-litter invertebrate abundance (log transformed) in the control and invertebrate-exclusion treatments. Values shown are the mean  $\pm$  1 SE

**Table 1** Initial concentrations of lignin, carbon, and nitrogen in leaf litter from second-growth forests (composed mainly of successional tree leaves) and from the interior of primary forests (composed predominantly of old-growth forest tree leaves)

Leaf-litter mixture	Lignin (%)	C (%)	N (%)	C:N ratio	Lignin:N ratio
Secondary forest	53.5 (0.5)	48.4 (0.3)	0.94 (0.01)	51.7 (0.3)	44.0 (0.6)
Primary forest	52.0 (0.8)	49.4 (0.8)	1.54 (0.07)	32.1 (1.2)	23.8 (1.2)

Values are the means from three replicates (with standard errors in parentheses)

not sufficiently large to affect decomposition. In fact, previous studies indicate that abiotic edge gradients in air temperature, evaporative drying rate, and litter-moisture content in fragmented forests do not correlate with leaf-litter decomposition rates (Didham 1998). Similarly, studies on tropical forest succession have found little or no effects of the forest physical environment on litter decomposition. For instance, Ewel (1976) measured rates of leaf-litter decomposition in clearcuts, young secondary forests, and primary forests in Guatemala, and found that decomposition rates were about the same in all sites, except those that were cleared of all vegetation. Xuluc-Tolosa et al. (2003), studying a successional dry-forest gradient in tropical Mexico, showed that the environmental conditions for litter decomposition in a 50 year-old stand were as favorable as those in a 13 year-old stand, and only slightly better than those of a 3 year-old stand. Collectively, these results suggest that only extreme levels of disturbance, such as occurs in large, anthropogenic clearings, cause changes in microclimate that are strong enough to inhibit the activity of decomposer organisms that in turn affect leaf-litter decomposition rates.

#### Effect of soil invertebrates

Soil- and litter-dwelling invertebrates have major direct and indirect effects on leaf-litter decomposition (Petersen and Luxton 1982) and thus, not surprisingly, our faunal-exclusion treatment resulted in reduced decomposition rates. Comparing the average amount of leaf-litter remaining in litterbags 120 days after the beginning of the experiment, we estimated that the decomposition rates were 5 and 35% lower in the treatment bags (invertebrates excluded) than in the controls, for leaves of successional and old-growth forest species, respectively. Working over a much longer interval (18 months), González and Seastedt (2001) found that the faunal effect on leaf-litter decomposition varied from 1.6% to 66.2%, depending on litter type and climate. The effect they observed was proportionally greater in wet and warmer than in cold and drier climates. In addition, the effect was generally greater for leaf litter with a higher N content (González and Seastedt 2001), a trend also observed in our study.

Working in our same study site, Didham (1998) detected significantly slower leaf-litter decomposition in small (1-ha) forest fragments than in larger forest tracts, and suggested that this might have resulted from the patchy distributions of invertebrates, particularly litter-feeding termites. Small fragments are virtually entirely saturated by edge effects (Laurance et al. 2002), so if litter invertebrates had altered abundances or activity in these fragments and on forest edges generally, then differences in litter decomposition between edges and interiors should disappear when invertebrates are excluded, but that was not the case in our study.

#### Effect of litter type

In contrast to other studies in both tropical (Ewel 1976; Xuluc-Tolosa et al. 2003) and boreal forests (Wardle et al. 1997), we found that the leaves of successional tree species decomposed much more slowly than did those of old-growth forest species. Our results agree with those of Mesquita et al. (1998), who also worked in central Amazonia and who reported decay rates of successional species that were 2.4–4.7 times lower than those of old-growth forest species. However, from the study of Mesquita et al. (1998), it was unclear whether low decomposition rates resulted from differences in litter quality between successional and old-growth forest species or from other differences between secondary and primary forests. As Mesquita et al. (1998) argued “many important agents of decomposition may be absent from degraded secondary forests, thus affecting decomposition rates irrespective of the kind of leaf material”. Our results show that the decomposition rates of successional species are slower than those of old-growth forest species independently of forest-habitat type, indicating that litter quality, not the local environment, determined the observed differences in decomposition rates. Similar results were obtained by Xuluc-Tolosa et al. (2003) in Mexico, who found that changes in leaf-litter decomposition rates along a successional gradient were mostly caused by changes in litter quality, and not in the physical environment. In contrast, Gholz et al. (2000) observed that the leaf-litter of *Drypetes*, a tropical tree from Puerto Rico, decomposes much faster than pine litter in its native habitat than in “conifer habitats”, indicating that, for at least some species, the effect of litter quality can interact with that of the physical environment.

The slower decomposition rate of successional species detected here is probably related to the lower quality of their leaves for the decomposer fauna. In particular, we found that the leaves of successional species had a significantly lower initial concentration of nitrogen than did the leaves of old-growth forest species, as well as higher C:N and lignin:N ratios. It is well established that species with low N contents decompose more slowly than do those with higher N (Taylor et al. 1989; Sundarapandian and Swamy 1999; Xuluc-Tolosa et al. 2003). Plant litter with a high N content and low C:N ratio has higher microbial activity (Zhang and Zak 1995), as nitrogen is essential for microbial function (Singh and Gupta 1977). Successional tree species in central Amazonia as well as in French Guiana also have a high phenolic content (Newberry and de Foresta 1985; Mesquita et al. 1998), and phenolics are known to negatively affect litter decomposition (Baldwin et al. 1983).

These results indicate that land-use changes in central Amazonia alter litter decomposition only indirectly, by favoring the establishment of successional tree species whose leaves are difficult to decompose. Given that edge effects greatly increase the establishment of successional trees (e.g. Laurance et al. 1998), then it is likely that the

same type of indirect effect we observed will also influence leaf-litter decomposition on forest edges. However, there is no evidence that forest fragments in our study area have yet changed enough in floristic composition, at least with respect to litter-nitrogen concentrations, to alter litter-decomposition rates (Vasconcelos and Luizão 2004). Although successional tree species have significantly increased in abundance near fragment edges, they still account for only a relatively small proportion of all trees (<8% on average; W.F. Laurance, unpublished data), and thus contribute relatively little to overall litter production. However, the results from our study area may be conservative, because our fragments are relatively young (<25 years old) and are protected from other disturbances, such as logging and surface fires, that plague some Amazonian forests (Laurance et al. 2002). Because these additional disturbances can interact synergistically with forest fragmentation (Gascon et al. 2000), the prevalence of pioneer trees in non-protected fragments will likely be greater, with potentially important consequences for leaf-litter decomposition, nutrient cycling, and forest productivity.

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