

SHORT COMMUNICATION

Leaf-litter decomposition in Amazonian forest fragments

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Most of the forests of the Amazon basin grow on nutrient-poor soils (Jordan 1982). Despite this, these forests remain productive through a variety of nutrient conservation mechanisms and a very effective system of organic matter decomposition and nutrient cycling (Jordan 1982). When an area of forest is fragmented however, the remaining patches experience modified microclimatic conditions (Camargo & Kapos 1995, Didham & Lawton 1999), and changes in floristic composition (Laurance *et al.* 1998), which can affect the decomposer community (Didham *et al.* 1996, Souza & Brown 1994) and consequently the decomposition process.

Relatively little is known about the effects of forest fragmentation on leaf-litter decomposition, and in a study at the Biological Dynamics of Forest Fragments Project near Manaus unexpected results were found (Didham 1998). Decomposition was not affected by distance to edge in the continuous forest, but was faster near than far from the edges of large (100 ha) fragments (Didham 1998). Based on this, one might well have expected a negative effect of fragment area on the decomposition rate, as small fragments have proportionately more edge-affected area than large fragments. However, the opposite trend was found, with leaf-litter decomposing more slowly in smaller than in larger fragments and continuous forest (Didham 1998). Consequently, generalizations about the effects of Amazonian forest fragmentation on leaf-litter decomposition remain difficult to draw. Furthermore, fragmented landscapes are highly dynamic. For instance, the fragments used by Didham initially abutted cattle pastures, but when we started this study 6y later the pastures had been replaced by regenerating forest (see Mesquita *et al.* 2001). This shift in the habitat

structure surrounding fragments may have helped to ameliorate microclimatic conditions (Camargo & Kapos 1995, Didham & Lawton 1999) or speed the recovery of the decomposer fauna (Quintero & Roslin in press). Both of these could affect rates of leaf-litter decomposition, suggesting that the effects detected earlier by Didham (1998) may be transient in nature.

Here, differences in rates of decomposition according to edge distance and fragment size were assessed through direct measurement of weight loss from litterbags, and the indirect calculation of decomposition from the ratio of litterfall and litter standing crop (Anderson & Swift 1983). Because we used the same litter composition in all sites (cf. Didham 1998), the first of these methods allows us to conclude that potential differences in decomposition rates are due to differences in microclimate or in the activity of decomposer organisms. The second method allows us to further explore the potential for local differences in the composition of the leaf material to influence decomposition rates.

The study was carried out at the Biological Dynamics of Forest Fragments Project (BDFFP). The study site spans an area of *c.* 20 × 50 km located 70 km north of Manaus, Brazil (2°30'S, 60°W). This area was partially fragmented during the late 1970s and early 1980s when large tracts of forest were cleared to create pastures for cattle grazing. In total, 25 study plots (40 × 100 m each) were established in 14 out of the 23 BDFFP forest reserves (Gascon & Bierregaard 2001). Four plots were located in 1-ha fragments, six in 10-ha fragments, seven in 100-ha fragments, and the remaining plots were located in continuous forest areas. Plots within the same forest reserve were located at least 100 m apart. With a few exceptions, plots were parallel to the forest edge. Edge distance was measured as the distance from the centre of the plot to the nearest edge.

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For estimation of decay rates using litterbags, 500 mesh litterbags were filled with 6 g (dry-weight) of leaves of four tree species (1.5 g of each species). The species used in the litterbags were *Scleronema micranthum* (Bombacaceae), *Protium hebetatum* (Burseraceae), *Eschweilera coriacea* and *Eschweilera wachenheimii* (Lecythidaceae). These species were among the 10 most common species in our study area and were present in all reserves studied (BDFFP Records). Live, mature leaves were collected directly from the canopy of each tree (4 to 5 randomly selected trees per species) using a telescopic pruner. The leaves were then air-dried for 2 wk prior to the beginning of the experiment in August 2000. The litterbags (20 × 24 cm) were made of nylon, with 1-mm mesh in order to minimize the loss of small leaf fragments while handling. Three 1-cm² perforations were made on each side of the litterbags to allow macro-fauna to enter. Twenty litterbags were placed on the soil surface on each plot. The plots were divided into 10 quadrats of 20 × 20 m each and two litterbags were placed in a random location within each quadrat. Four bags were removed from each plot 50, 105, 190, 290 and 360 d after the beginning of the experiment. The leaves in these bags were then cleaned of debris, dried at 70 °C for 48 h, and weighed to the nearest 0.01 g.

Several mathematical models are used to describe litter decay. We used the exponential model (Jenny *et al.* 1949, Olson 1963), because it is considered the most biologically reasonable (i.e. litter decomposition is initially rapid due to leaching of water-soluble compounds, but decreases over time). For each plot the decay rate, k , was calculated using the function:

$$X = e^{(-kt)}, \text{ where } X \text{ is the remaining leaf mass at time } t.$$

We quantified fine litter production and standing crop for 1 y (beginning in September 1999) in 20 of the 25 plots used for the litterbag experiment. Ten litter traps, whose contents were removed at 2-wk intervals, were installed in each plot. Each trap covered an area of 0.25 m² (0.5 × 0.5 m) and was placed 1 m above soil level, in the centre of each quadrat. In addition, every 2 or 3 mo, we randomly took two samples (25 × 25 cm each) of litter from the forest floor around each trap (providing a total of 120 samples per plot in 1 y), with samples being taken from a different location during subsequent collections. The litter collected from the soil surface and from litter traps was dried (at 60 °C for 2–3 d), sorted into the following categories: leaves, twigs < 2 cm in diameter, flowers, fruits, trash (i.e. fine plant and animal residues), and weighed. We calculated litterfall/standing crop ratios by dividing the total annual leaf litter production (t ha⁻¹), by the average leaf litter standing crop on the soil surface (t ha⁻¹) over the same 1-y period.

The effect of forest area and edge distance on litter decomposition was analysed using simple regression

analyses, and for these analyses all reserves within continuous forest were assumed to be 10,000 ha in size. For reserves in which we established more than one plot, an average value of the observed decomposition rates was calculated using data from all plots, and the resulting mean values were used in the statistical analyses. We also re-analyse the data taking a less conservative approach, and considering different plots within the same reserve as true replicates, which is a reasonable assumption given the large distance (> 100 m) that separated these plots.

Data from the litterbag experiment showed that after 1 y, 90.8% (range 80–100%) of the original leaf material contained in the litterbags had decomposed. The single exponential model used to explain the temporal dynamics of litter decay fitted the data well, explaining 59–96% of the data variation. We did not detect a significant difference in decomposition rate according to forest area, regardless of whether we treated multiple plots within the same forest reserve as true replicates ($r^2 = 0.022$, $F_{1,23} = 0.048$, $P = 0.829$; Figure 1a) or not ($r^2 = 0.003$, $F_{1,12} = 0.040$, $P = 0.844$). Furthermore, there was no significant effect of distance from forest edge on rates of leaf-litter decomposition ($r^2 = 0.002$, $F_{1,23} = 0.047$, $P = 0.830$; Figure 1b).

Similar results were obtained when decomposition rates were determined by calculation of litterfall/litter standing crop ratios. We did not detect a significant difference in decomposition rates according to forest area regardless of whether we treated multiple plots within the same forest reserve as true replicates ($r^2 = 0.022$, $F_{1,18} = 0.404$, $P = 0.533$) or not ($r^2 = 0.069$, $F_{1,10} = 0.741$, $P = 0.409$; Figure 1c). Also, there was no effect of distance from forest edge ($r^2 = 0.027$, $F_{1,18} = 0.504$, $P = 0.487$; Figure 1d).

This study is one of the first to comprehensively assess the effects of tropical forest fragmentation on a key ecosystem process. In contrast to an earlier experiment performed in the same study area (Didham 1998), our litterbag experiment revealed no differences in decomposition rates according to fragment area or edge distance. It is difficult to determine what caused the disparity in results between the two studies, as multiple causes may be involved. These include inter-annual differences in rainfall, differences in sampling methodologies, different species used in the litterbags, and the duration of the experiments. However, although Didham (1998) measured decomposition in litterbags for a shorter time interval (100 d in his study versus 360 d in ours), our results are the same regardless of whether we calculate decomposition rates using only data from the first 100 d of the experiment. Furthermore, the differences in types of leaves used in the litterbags (here leaves of the four most common forest species, while in his study leaves of the pioneer

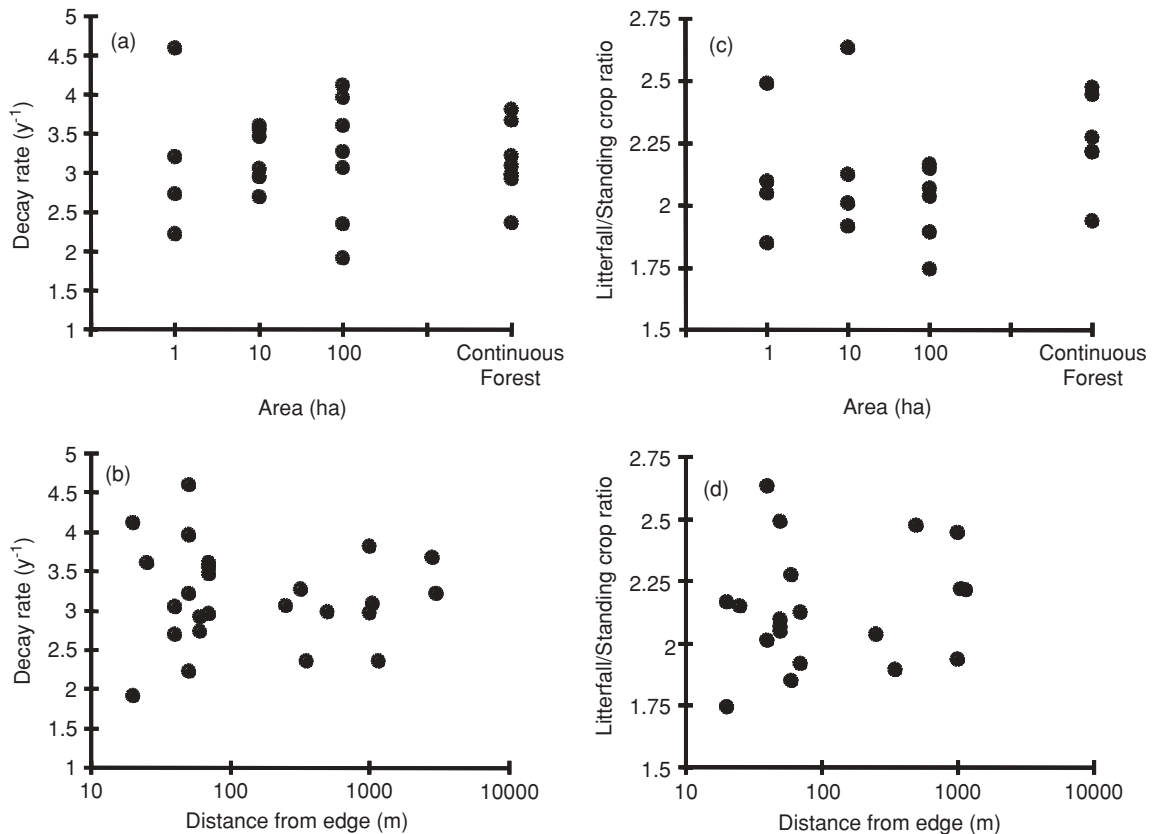


Figure 1. Effects of forest area and distance to forest edge on leaf-litter decomposition rates, as determined through direct measurements of weight losses from litterbags (a and b), and indirectly by calculating the ratio between litterfall and litter standing (c and d). Each point represents a different study plot.

tree *Vismia juruensis*; and in both cases green leaves, which decompose faster than senescent leaves (Fonte & Schowalter 2004)) are probably of little importance, since the same species was used in all habitats being compared.

However, one important difference between the two studies is that Didham (1998) measured decomposition over a large number of distance classes from the forest edge, including the edge itself (0 m). In our study, the centre of the nearest plot was located 20 m from the edge. It is therefore probable that the edge effect detected by Didham (1998) in the 100-ha fragments was in large part driven by the comparatively high rates of decomposition on the edge itself (0 m), as decomposition rates were relatively uniform at greater distances from the edge (Figure 4-b of Didham 1998). This suggests that edge effects on litter decomposition penetrate only a short distance into the fragments. In our study plots, which were located as little as 20 m from the edges of fragments, the rates of decomposition were comparable to those far from forest edges.

Another important difference is that Didham (1998) sampled only two 1-ha fragments, while we sampled

four. Given the large variation in litter decomposition rates observed even in plots located far from the forest edge, it is possible that the area effect detected previously may be due to chance alone. However, if this were the case one would expect that the additional fragments sampled in our study would have elevated rates of litter decomposition when compared to the two previously studied. However, the opposite was true. Didham (pers. comm.) measured decomposition in the 1-ha reserves 2107 and 2108, which in our study were the ones with the highest rates of decomposition for their respective size class. This strongly suggests that the differences in results between our studies are not simply due to differences in experimental design. Rather, they appear to be true differences mediated by changing conditions within the same fragment, which may have resulted from shifts in the matrix habitat surrounding fragments. In his study, Didham (1998) was unable to find a significant correlation between decomposition rates and various microclimatic variables, and suggested that part of the large variance in decomposition rates is due to the action of litter-feeding termites (especially *Syntermes*). Indeed, our measurements indicate that after a period

of 100 d, litterbags attacked by litter-feeding termites had a decomposition rate 52% greater than unattacked ones (A. Rubinstein unpubl. data). A survey conducted 6 y after isolation of the BDFFP fragments revealed that small (1 and 10 ha) fragments had a lower diversity and abundance of litter-feeding termites than nearby continuous forest areas (Souza & Brown 1994). However, it is likely that the abundance of litter-feeding termites had returned to pre-isolation levels at the time of our study, since there were no significant differences in the proportion of litterbags attacked by termites with respect to forest area or distance from edge (A. Rubinstein unpubl. data). Such presumed recovery of the litter-feeding termite fauna may help explain why litter decomposition occurred at the same rate in fragments as in continuous forest.

Our indirect calculation of decomposition by means of leaf-litter turnover rates (Figure 1) further supports the conclusion that previously observed differences in litter decomposition (Didham 1998) were transitory. Given that litterfall and litter standing crop were not performed in the same year as the litterbag experiment, this minimizes the chances that differences in results between Didham's study and ours were generated by inter-annual differences in rainfall or other abiotic variables. Our results add to another recent study that suggests that tropical forest communities (and processes) are more resilient to land-use change than previously anticipated (Quintero & Roslin, in press). However, such resilience may be determined in part by how the surrounding matrix is managed. The type of matrix has strong influence on tree mortality rates in the fragments (Mesquita *et al.* 1999), and consequently in the degree of floristic changes in these same fragments. As indicated elsewhere (Vasconcelos & Laurance in press), it is likely that the major effect of forest fragmentation on litter decomposition is an indirect one, mediated through changes in floristic composition.

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LITERATURE CITED

- ANDERSON, J. M. & SWIFT, M. J. 1983. Decomposition in tropical forests. Pp. 287–309 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds). *Tropical rain forest: ecology and management*. Blackwell Scientific Publications, Oxford.
- CAMARGO, J. L. C. & KAPOV, V. 1995. Complex edge effects on soil moisture and microclimate in Central Amazonian forest. *Journal of Tropical Ecology* 11:205–221.
- DIDHAM, R. K. 1998. Altered leaf-litter decomposition rates in tropical forest fragments. *Oecologia* 116:397–406.
- DIDHAM, R. K. & LAWTON, J. H. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31:17–30.
- DIDHAM, R. K., GHAZOU, J., STORK, N. E. & DAVIS, A. J. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* 11:255–260.
- FONTE, S. J. & SCHOWALTER, T. D. 2004. Decomposition of greenfall vs. senescent foliage in a tropical forest ecosystem in Puerto Rico. *Biotropica* 36:474–482.
- GASCON, C. & BIERREGAARD, R. O. 2001. The Biological Dynamics of Forest Fragments Project: the study site, experimental design, and research activity. Pp. 31–42 in Bierregaard, R. O., Gascon, C., Lovejoy, T. E. & Mesquita, R. (eds). *Lessons from Amazonia: the ecology and conservation of a fragmented forest*. Yale University Press, New Haven.
- JENNY, H., GESSEL, S. P. & BINGHAM, F. T. 1949. Comparative study of decomposition of organic matter in temperate and tropical regions. *Soil Science* 68:419–432.
- JORDAN, C. F. 1982. The nutrient balance of an Amazonian rain forest. *Ecology* 63:647–654.
- LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M., LAURANCE, S. G., HUTCHINGS, R. W. & LOVEJOY, T. E. 1998. Effects of forest fragmentation on recruitment patterns in central Amazonia. *Conservation Biology* 12:460–464.
- MESQUITA, R. C. G., DELAMONICA, P., & LAURANCE, W. F. 1999. Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation* 91:129–134.
- MESQUITA, R. C. G., ICKES, K., GANADE, G. & WILLIAMSON, G. B. 2001. Alternative successional pathways in the Amazon basin. *Journal of Ecology* 89:528–537.
- OLSON, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322–331.
- QUINTERO, I. & ROSLIN, T. In press. Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. *Ecology*.
- SOUZA, O. F. F. & BROWN, V. K. 1994. Effects of habitat fragmentation on Amazonian termite communities. *Journal of Tropical Ecology* 10:197–206.
- VASCONCELOS, H. L. & LAURANCE, W. F. In press. Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. *Oecologia*.