Evaluation of macrofaunal effects on leaf litter breakdown rates in aquatic and terrestrial habitats

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Abstract Decomposition of the organic matter is a key process in the functioning of aquatic and terrestrial ecosystems, although different factors influence processing rates between and within these habitats. Most patterns were described for temperate regions, with fewer studies in tropical, warmer sites. In this study, we carried out a factorial experiment to compare processing rates of mixed species of leaf litter between terrestrial and aquatic habitats at a tropical site, using fine and coarse mesh cages to allow or prevent colonization by macroinvertebrates. The experiment was followed for 10 weeks, and loss of leaf litter mass through time was evaluated using exponential models. We found no interaction between habitat and mesh size and leaf litter breakdown rates did not differ between fine and coarse mesh cages, suggesting that macroinvertebrates do not influence leaf litter decomposition in either habitat at our studied site. Leaf breakdown rates were faster in aquatic than in terrestrial habitats and the magnitude of these differences were comparable to studies in temperate regions, suggesting that equivalent factors can influence between-habitat differences detected in our study.

Key words: decomposition, leaf litter, litter bags, macroinvertebrates, tropical ecosystems.

INTRODUCTION

Decomposition of organic matter is a key process in the functioning of both aquatic and terrestrial eco-systems, enabling the recycling of nutrients and chemical elements, and sustaining important food chains formed by organisms that use this resource (Vannote *et al.* 1980; Takeda & Abe 2001; Cebrian & Lartigue 2004). Physical, chemical and biological processes contribute to the decomposition of dead organic matter, reducing it to elements that can be released to the system and, thus, be available for uptake by the organisms (Swift *et al.* 1979; Gessner *et al.* 1999).

Several factors influence decomposition processes in natural ecosystems such as differences in temperature, composition of the organic matter, and structure of decomposer assemblages (Swift *et al.* 1979; Aerts 1997; Royer & Minshall 2003; Hättenschwiler & Gasser 2005). However, there are important differences in decomposition rates along river floodplains, such as those found between terrestrial and aquatic habitats (Thomas 1970; Webster & Benfield 1986; Wagener *et al.* 1998; Hutchens & Wallace 2002; Cebrian 2004). For example, leaf litter decomposition

rates are faster in aquatic habitats due to constant leaching, physical abrasion, and smaller temperature ranges to which decomposing organisms are exposed, facilitating their action (Thomas 1970; Janssen & Walker 1999; Hutchens & Wallace 2002). However, most previous studies have been carried out in temperate regions, although decomposition processes can be very different in tropical regions, with a stronger effect of microorganisms (Heneghan *et al.* 1999; Irons *et al.* 1994; Takeda & Abe 2001).

Large variation in decomposition rates can also be found within habitats. Differences in decomposition rates among terrestrial sites are attributed to several factors such as climatic differences (Aerts 1997; Kätterer *et al.* 1998; Schuur 2001; Salamanca *et al.* 2003), differences in habitat structure and forest types (Didham 1998; Neher *et al.* 2003; Xuloc-Tolosa *et al.* 2003; Sjörgesten & Wookey 2004), litter quality (Swift *et al.* 1979; Aerts & de Caluwe 1997; Loranger *et al.* 2002; Kraus *et al.* 2003; Osono & Takeda 2005) and soil decomposer assemblages (Heneghan *et al.* 1999; Takeda & Abe 2001; Schädler & Brandl 2005; Vasconcelos & Laurance 2005). On the other hand, variation in aquatic habitats such as streams has been reviewed by Webster and Benfield (1986) and Royer and Minshall (2003), and includes differences due to physical and chemical factors (Chergui & Pattée 1988; Irons *et al.* 1994; Suberkropp & Chauvet 1995; Dangles *et al.* 2004), type of riparian forest and land use patterns (Whiles & Wallace 1997; Sponseller & Benfield 2001; Danger & Robson 2004), and the effects of litter

quality (Petersen & Cummins 1974; Webster & Benfield 1986; Royer & Minshall 2001) and macroinvertebrates (Wallace & Webster 1996; Rosemond *et al.* 1998; Graça 2001; Graça *et al.* 2001; Wright & Covich 2005).

Several studies have evaluated the effect of macroinvertebrates on leaf litter decomposition rates, by restricting their access to decomposing organic matter with fine mesh bags (Boulton & Boon 1991; Bradford *et al.* 2002; Gessner & Chauvet 2002), chemical inhibitors (Heneghan *et al.* 1998, 1999; González & Seastedt 2001), or removal by hand (Lawrence & Wise 2000, 2004). Macroinvertebrate effects can be complex and decomposition processes can be influenced by the relative abundance of different functional groups (Hunter *et al.* 2003; Lawrence & Wise 2004). Large differences were found among experimental treatments where macroinvertebrate abundance was manipulated (Graça 2001), with some studies showing faster decomposition rates when macroinvertebrates were present (Petersen & Cummins 1974; Iversen 1975; Wallace *et al.* 1982; Benstead 1996; Bradford *et al.* 2002), and other studies showing no significant effects (Rosemond *et al.* 1998; Stockley *et al.* 1998), or an interaction with leaf quality (Vasconcelos & Laurance 2005; Wright & Covich 2005).

The effects of macroinvertebrates can change due to differences in assemblage composition, which are commonly found between tropical and temperate regions (Takeda & Abe 2001; Dobson *et al.* 2002). Litter decomposition rates are generally faster in the tropics and, in terrestrial ecosystems, these differences can be related to the presence of decomposer fungi that are more efficient in decomposing lignin and other hard structures, resulting in poorly developed detritus pools (Takeda & Abe 2001). Thus, breakdown of leaf litter by macroinvertebrates can be facilitated by microbial action, and arthropod faunal components can have large effects on decomposition rates in tropical regions when compared with temperate ones (Heneghan *et al.* 1998, 1999; Vasconcelos & Laurance 2005). On the other hand, in streams, the composition of macroinvertebrate assemblages generally differ between tropical and temperate systems, with shredders dominating in decomposing leaf litter in temperate regions (Vannote *et al.* 1980; Graça 2001), but generally having a low prevalence in tropical regions (Rosemond *et al.* 1998; Dudgeon & Wu 1999; Dudgeon 2000; Dobson *et al.* 2002; but see Pearson *et al.* 1989; Cheshire *et al.* 2005; Cummins *et al.* 2005). Fast leaf litter decomposition rates in tropical streams are related to the action of microorganisms due to higher temperatures (Irons *et al.* 1994; Dobson *et al.* 2002), use of litter by macroinvertebrates (Dudgeon & Wu 1999) and consumption of organic matter by shredders (Pearson *et al.* 1989; Cummins *et al.* 2005) or large omnivores such as fish and crustacean

decapods (Wootton & Oemke 1992; March *et al.* 2001).

Thus, leaf litter decomposition processes are strongly influenced by differences in climatic conditions and habitat types, and by the relative effects of different functional groups of decomposer assemblages. In this study, we carried out a factorial experiment to evaluate the effects of macroinvertebrates on leaf litter breakdown in distinct habitats at a tropical site. We hypothesized that (i) leaf litter decomposition rates would be higher at a tropical site than those found in temperate regions, as previously found in other studies; but (ii) the differences between aquatic and terrestrial habitats would be similar. We expected that for a given climatic condition similar factors should influence the differences in leaf litter decomposition in terrestrial and aquatic habitats. For instance, aquatic habitats have more physical abrasion, constant leaching and less temperature variation (see above). Further, we tested the hypothesis that (iii) the presence of macrofauna influence decomposition rates within these habitats. The experiment was carried out in a preserved small river in western Brazil, where there have been few studies on the functioning of ecosystems.

METHODS

Study area

This study was carried out in the spring region of Rio Sucuri (56°28′W, 21°07′S), a small river (extension: 1800 m) in Bonito district, western Brazil. Bonito is located in the southern area of Bodoquena Plateau, with altitudes varying between 400 and 650 m, and is part of the Miranda river watershed, a tributary of the Paraguay River. The plateau is sustained by Precambrian carbonatic rocks, and has characteristics of initial phases of carstic development such as areas of water penetration and subsurface outflow (Dias 2000). The climate is tropical, with marked wet and dry seasons, the latter generally extending from April to September. Mean air temperatures vary between 16.6°C and 37.5°C over the year, whereas mean annual precipitation varies between 1200 and 1500 mm (Dias 2000).

The riparian vegetation of Rio Sucuri is semideciduous forest and, although large parts of the region have been converted to pasture, in the spring region the forest extends about 50 m from the river. The dominant tree species are *Inga vera* ssp. *affinis* (DC.) T. D. Penn. (Leguminosae), *Ficus insipida* Willd. (Leguminosae), *Nectandra cissiflora* Nees (Lauraceae), *Chionanthus trichotomus* (Vell.) P. S. Green (Oleaceae), *Spondias lutea* L. (Anacardiaceae), *Peltophorum dubium*

(Spreng.) Taub. (Leguminosae), and *Erythrina speciosa* Andr. (Leguminosae) (V. J. Pott, pers. comm. 2005). The spring has a mean width of 30 m, mean depth of 0.5 m and 60% cover by trees, whereas the substrate is composed mainly of silt, and is covered by macrophytes, leaf litter and coarse woody debris (M. O. Tanaka, unpubl. data 2003). The study was carried out along 150 m of the spring. Water temperatures vary between 20.9°C and 22.8°C over the year. The water moves slowly in the spring region (<0.1 m s^{-1}), and is very transparent, with high values of alkalinity (116 mg l^{-1}), pH (7.2), hardness (109 mg CaCO$_3$ l^{-1}) and conductivity (311 μS cm^{-1}) in the dry season (M. Costacurta, unpubl. data 2002).

Experimental design

We evaluated the effect of macroinvertebrates on leaf litter processing rates in terrestrial and aquatic habitats with a 2-factor experiment (habitat and mesh size), between May and September 2004. We used leaf litter bags with two mesh sizes, 1 mm (fine mesh) and 25 mm (coarse mesh), so that fine mesh bags prevented and coarse mesh bags allowed access of macroinvertebrates to the organic matter. The bags were constructed in the form of a square cage using a wire frame of 30 × 30 × 10 cm, to avoid artificial compression of leaves in the bags and to simulate the natural deposition of leaf litter on the substrate. Each frame was later covered with fine or coarse nylon mesh. In the coarse mesh cages, we covered two walls and the underside of the frame with fine mesh, to reduce loss of fragmented organic matter when collecting the leaf litter bags. Thus, macroinvertebrates could enter the cages through two of the walls. The top of these cages was also covered with fine mesh, so that the organic matter was similarly exposed to solar radiation in both types of cage.

Leaves were previously collected randomly from trees and shrubs along trails and in the forest edge of the riparian forest adjacent to the study site, so that several species were used. Green leaves were separated from dry leaves and stems, and deposited in a container. The leaves were thoroughly mixed in the container in such a way that the resulting mixture was homogeneous and avoided any trend in species composition, to simulate natural litter. Leaves were then blind-picked from the container to fill each cage, until 300 g (wet mass) of mixed green leaves was attained within each cage. We used only green leaves, since previously dried leaf litter in decomposition experiments can influence leaf breakdown rates, accelerating it in aquatic habitats (Boulton & Boon 1991; but see Gessner 1991) and depressing it in terrestrial ones (Taylor 1998). Since we wanted to compare leaf processing rates between habitats, using green leaves

would represent a more natural situation, and the estimates would be less subject to methodological influences. Five bags were separated and taken to the laboratory to determine the initial dry mass of leaves in each bag, which was measured to the nearest 0.01 g after drying at 60°C until mass values stabilized, after five days. Samples had low variance (CV = 0.026), and mean initial dry mass of leaves in each bag was 65.52 ± 0.77 g (mean ± SE).

The experiment was set up in the spring region of the Rio Sucuri. Five locations were randomly chosen in the river, at a depth of about 1 m and located at least 0.5 m from the margin. Five other locations were established in the riparian forest adjacent to the spring, near to trails in the forest. The distance between locations was at least 5 m, so that each location constituted a spatial replicate. At each location, 10 litter bags with fine mesh and 10 litter bags with coarse mesh were randomly distributed at a minimum of 0.3 m from each other. Bags in the water were tied to stakes to avoid losses. The experiment was checked weekly and, during the inspection, one bag of each mesh size was collected from each location, totalling 20 bags collected per week (10 from each habitat) over 10 weeks. Each nylon mesh bag was carefully inserted into a plastic bag, which was closed and taken to the laboratory. The samples from the water were introduced to plastic bags underwater, and later filled with 10% formaldehyde. In the laboratory, each bag was opened and the remaining organic matter was separated and carefully washed. Dry mass of each sample was determined as described above.

Data analyses

Leaf breakdown rates for each site were calculated using the exponential model $Y_t = Y_0 e^{-kt}$ (Olson 1963), where Y_t is the dry mass after t days, Y_0 is the initial dry mass, and k is the daily decomposition rate. The effects of habitat and mesh size on breakdown rates were evaluated with a 2-way fixed factors ANOVA (Habitat and Mesh size), using k-values as the dependent variable ($n = 5$). The residuals were graphically checked for variance homogeneity, and the significance level used was $P < 0.05$.

RESULTS

The exponential model provided a good fit to the leaf breakdown process in both habitats, with values of R^2 ranging between 0.78 and 0.98 (Table 1). There was no significant interaction between Habitat and Mesh size, and no differences were detected on processing rates between bags with distinct mesh sizes (Table 1). However, processing rates differed between habitats,

Table 1. Results of 2-way ANOVA comparing the effects of habitat and mesh size on leaf litter breakdown rates, and values of adjusted regressions on the estimates of mean *k*-values for each treatment combination

Source of variation	d.f.	MS	F	P
Habitat	1	658.1×10^{-6}	59.64	<0.001
Mesh size	1	5.6×10^{-6}	0.51	0.488
Habitat × mesh size	1	5.5×10^{-6}	0.50	0.489
Error	16	11.0×10^{-6}		
	k	R^2	$F_{1,9}$	P
Terrestrial, coarse mesh	−0.0050	0.78	32.1	<0.001
Terrestrial, fine mesh	−0.0054	0.89	71.9	<0.001
Aquatic, coarse mesh	−0.0183	0.98	406.7	<0.001
Aquatic, fine mesh	−0.0156	0.96	227.2	<0.001
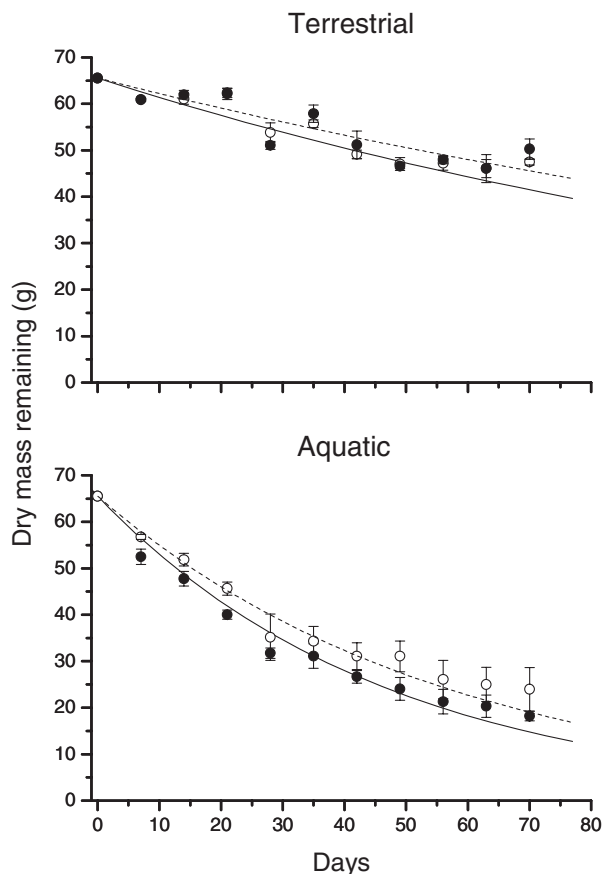
Fig. 1. Mean dry mass (±SE) of decomposing leaves remaining on each collection date in aquatic and terrestrial habitats with (solid circles and lines) and without (open circles, dashed lines) access of macrofauna to leaf packs. Lines represent adjusted exponential models for the mean values of remaining leaf mass.

with faster breakdown of leaf litter from samples in the water (Fig. 1). In the terrestrial habitat, final dry mass in the coarse mesh bags was 52.9 ± 3.1 g (mean ± SE), representing 81% of the initial dry mass, whereas in the fine mesh bags the corresponding value was 47.4 ± 0.6 g, which represented 72% of the initial dry mass. On the other hand, the final dry mass in the aquatic habitat was 11.9 ± 2.1 g in coarse mesh bags, representing 18% of the initial dry mass, and 15.6 ± 4.2 g in fine mesh bags, which represented 24% of leaf litter initial dry mass.

Leaf litter half-lives predicted by the exponential model in the terrestrial habitat were 20.8 and 18.3 weeks for the coarse and fine mesh bags, respectively. In the aquatic habitat, the predicted values for the coarse and fine mesh bags were 5.5 and 6.3 weeks, respectively, although empirical values for half the dry mass were detected around the fourth week for both treatments (Fig. 1). In this week, leaf litter dry mass in the coarse mesh bag was 31.8 ± 1.1 g and represented 48% of the initial dry mass, whereas in the fine mesh bag the dry mass found was 35.2 ± 5.0 g, representing 54% of the initial leaf litter dry mass.

There was large variation in leaf litter breakdown among spatial replicates, mainly after the fourth week of the experiment (Fig. 1), resulting in variation in the estimates of the coefficient of decay (*k*) among spatial replicates. The coefficient of variation for estimates of *k* along the experiment differed between mesh bags within the habitats. In the aquatic habitat, values were 0.334 and 0.195 for the fine and coarse mesh bags, respectively, whereas in the terrestrial habitat the corresponding values were 0.163 and 0.330.

DISCUSSION

Several studies have found a positive effect of macro-invertebrates on leaf litter breakdown rates (Graça 2001; Schädler & Brandl 2005; Wright & Covich 2005). Although in some cases invertebrates have a clear role in the decomposition process, differences in breakdown rates recorded using fine and coarse mesh bags can be amplified due to methodological problems. For example, leaf litter in coarse mesh bags can be more subject to physical abrasion by abiotic factors such as water motion in aquatic habitats (Boulton & Boon 1991; Janssen & Walker 1999) and heavy rains and soil particle movement in terrestrial habitats.

These factors can also lead to greater losses of leaf fragments from coarse mesh bags in relation to fine mesh ones, reducing the amount of remaining leaf litter. Thus, higher turnover rates of organic matter can occur in coarse mesh bags and a difference in remaining leaf litter when compared with fine mesh bags may or may not be detected depending on the amount of leaf litter that enters or leaves the coarse mesh bags.

In the present study, we found no differences in leaf litter breakdown rates using litter bags with distinct mesh sizes in either habitat, terrestrial or aquatic. Other studies also failed to find differences in leaf litter processing rates between bags with and without access for macroinvertebrates (Rosemond *et al.* 1998; Stockley *et al.* 1998; Janssen & Walker 1999). In these studies, two reasons have been proposed to explain the similar processing rates found between bags. First, the bags used to restrict the access of macroinvertebrates to experimental leaf litter may not completely isolate some species. For example, Janssen and Walker (1999) used leaf litter bags with 1 mm and 10 mm mesh sizes, and found that in both bag types the shrimp *Paratya australiensis* (Atyidae) was commonly found, suggesting that the sampled individuals colonized the fine mesh bags during the larval phase. Similarly, Rosemond *et al.* (1998) found that larvae of Chironomidae could colonize leaf litter despite efforts to restrict macroarthropod access, resulting in similar breakdown rates. Second, coarse mesh bags can accumulate more organic matter from outside the bags

than the fine mesh bags (but see above). The accumulation of organic matter could compensate the decay of leaf litter caused by macroinvertebrate action (Stockley *et al.* 1998), or increase the variability among replicates, obscuring the effect of consumers in leaf litter breakdown rates. In our study, we tried to minimize this effect by restricting macroinvertebrate access to only two walls of the coarse mesh cages. Thus, our results suggest that either leaf litter breakdown rates do not depend on macroinvertebrate access, or there could be colonization of the fine mesh cages by small or juvenile macroinvertebrates, as suggested by Janssen and Walker (1999). Further studies are necessary to evaluate the effects of macroinvertebrates on leaf litter breakdown, since different results have been found at other tropical sites (Vasconcelos & Laurance 2005; Wright & Covich 2005).

This study evaluated leaf litter processing rates simultaneously in aquatic and terrestrial habitats in tropical regions, and we found faster breakdown occurring in the water. These results support other studies carried out in temperate regions (Thomas 1970; Webster & Benfield 1986; Hutchens & Wallace 2002). The differences in processing rates between these habitats, both from the present study and those carried out in temperate regions are of similar magnitude (Table 2), suggesting that equivalent factors could influence leaf litter breakdown in distinct geographical areas. The faster processing of leaf litter in the river is probably related to physical and chemical properties of the water. High leaching

Table 2. Examples of estimated daily leaf litter breakdown rates (k, coefficient of decay) for terrestrial and aquatic habitats in temperate and tropical regions, with and without access of the macrofauna

Region	Habitat	Macrofaunal access	k	Reference
Tropical	Aquatic	No	0.0158	This study
Tropical	Aquatic	No	0.0159–0.0266	Wright and Covich (2005)
Tropical	Aquatic	Yes	0.025	Benstead (1996)
Tropical	Aquatic	Yes	0.010–0.047	Dobson *et al.* (2003)
Tropical	Aquatic	Yes	0.0180	This study
Tropical	Aquatic	Yes	0.080–0.090	Rosemond *et al.* (1998)
Tropical	Aquatic	Yes	0.020–0.559	Irons *et al.* (1994)
Tropical	Aquatic	Yes	0.0375–0.0395	Wright and Covich (2005)
Tropical	Terrestrial	No	0.0054	This study
Tropical	Terrestrial	No	0.0019–0.0021	McGroddy *et al.* (2004)
Tropical	Terrestrial	No	0.0012	Aidar and Joly (2003)
Tropical	Terrestrial	Yes	0.0050	This study
Tropical	Terrestrial	Yes	0.002–0.003	Ostertag *et al.* (2003)
Tropical	Terrestrial	Yes	0.0011–0.0065	Loranger *et al.* (2002)
Temperate	Aquatic	Yes	0.0186–0.0461	Royer and Minshall (2001)
Temperate	Aquatic	Yes	0.0175–0.0318	Hutchens and Wallace (2002)
Temperate	Aquatic	Yes	0.018–0.064	Graça *et al.* (2001)
Temperate	Terrestrial	No	0.0007–0.0011	Kaneko and Salamanca (1999)
Temperate	Terrestrial	No	0.0010–0.0012	Salamanca *et al.* (2003)
Temperate	Terrestrial	Yes	0.0018–0.0022	Hutchens and Wallace (2002)
Boreal	Aquatic	Yes	0.033–0.072	Jonsson *et al.* (2001)
Boreal	Aquatic	Yes	0.005–0.019	Haapala *et al.* (2001)

rates of soluble compounds in the water favour faster decomposition of plant material, enabling consumption of leaf litter by the decomposers (Thomas 1970), whereas, water movement facilitates physical abrasion and softening of leaves (Webster & Benfield 1986; Boulton & Boon 1991). Further, lower abiotic variation in the water contributes to the occurrence and action of decomposing micro-organisms (Hutchens & Wallace 2002).

Although the general patterns in leaf litter break-down between terrestrial and aquatic habitats are rel-atively clear, the differences in processing rates within habitats can be larger than between habitats (Table 2). For example, Dobson *et al.* (2003) found almost a five-fold difference of *k*-values among plant species in a tropical stream, and Hutchens and Wallace (2002) found an almost two-fold difference in the breakdown rates of red maple leaves between two temperate streams. These differences can sometimes be even larger than those recorded between geographical regions. The largest values for leaf litter breakdown rates were recorded in tropical streams, although low values were also found, sometimes lower than those recorded for temperate and boreal streams (Table 2). The same pattern of faster breakdown of leaf litter in the tropics was recorded in terrestrial habitats, although some studies found similar values of *k* in tropical and temperate regions (Table 2).

The differences within habitats in the same geo-graphical regions can also be due to differences in the type of leaf litter formed by distinct species, since leaves with more lignin or with lower nutritional value tend to decompose more slowly (Petersen & Cummins 1974; Aerts & de Caluwe 1997; Loranger *et al.* 2002; Kraus *et al.* 2003). For example, Webster and Benfield (1986) reviewed 117 studies that evaluated leaf litter processing rates in lakes, streams, and wetlands in temperate regions, and found differences larger than one order of magnitude among species of vascular plants from different families. Thus, differences in leaf structure and chemical composition must strongly influence variation in breakdown rates found in studies carried out at distinct places. Most studies describing leaf litter processing used leaves from a single or few species, so that generalizations of the decomposition process to systems with higher plant species diversity are not possible (Gessner & Chauvet 2002). The rela-tionships between plant species diversity and leaf litter breakdown are complex (Hättenschwiler & Gasser 2005), and more accurate descriptions of decomposi-tion processes in high diversity communities such as those found in tropical regions should include the different plant species that contribute to leaf litter, such as in this and other studies (Benstead 1996; Schädler & Brandl 2005; Vasconcelos & Laurance 2005), so that variation among species is incorporated in the estimates of processing rates.

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