Short Research Note

## Macroinvertebrate succession during leaf litter breakdown in a perennial karstic river in Western Brazil

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## Abstract

Leaf litter is a major basal resource to stream ecosystems, but few studies addressed their role in karst systems, mainly in intermittent springs and lakes. Patterns of resource use in perennial rivers are poorly known, although the input of leaf litter strongly influences macroinvertebrate assemblage structure. In this study, we evaluated the structure of macroinvertebrate assemblages along the decomposition of leaf litter in a tropical karst river, using leaf litter cages made of coarse nylon mesh (25 mm) to allow colonization by macroinvertebrates. The experiment was followed weekly for 10 weeks. The assemblages were dominated by snails (90.5% of total fauna), hyalellid amphipods, and larval chironomid midges, with highest abundances in the intermediate stages of the experiment, resulting in a gradient in assemblage structure. The large abundance of snails, which are common in other karst systems, suggest that this group may have an important role in decomposer food webs, facilitating or directly contributing to leaf breakdown.

Energy flows in lotic ecosystems are mainly influenced by the sources of basal resources for consumers, which in turn may depend on the size and longitudinal position of the watercourse (Vannote et al., 1980). For example, streams and narrow rivers generally receive less radiation due to the presence of gallery forests, resulting in lower primary production values; thus, their main source of energetic resources is the input of dead organic matter from the adjacent forests (Wallace et al., 1997). In this way, the decomposition of the organic matter, mainly from vascular plants, is a key process in these ecosystems (Vannote et al., 1980).

Leaf litter decomposition in aquatic ecosystems involves a sequence of leaf mass loss, resulting from the dissolution of organic compounds, microbial conditioning and mechanical fragmentation by macroinvertebrates (Webster & Benfield, 1986). These processes contribute to reduce the organic matter to its elements, releasing nutrients that become available for uptake by the organisms present. However, interactions among these processes can influence the flows of material and energy through the decomposer food chains (Gessner et al., 1999). Also, decomposition rates can be influenced by abiotic factors such as temperature, water flow and chemistry (Webster & Benfield, 1986), and the composition of gallery forests, including the nutritional value of leaves and the presence of defensive mechanisms against herbivores (Whiles & Wallace, 1997).

Karst systems are distinct freshwater ecosystems, which provide an interface between subterranean and surface waters (Smith et al., 2003). Several factors influence the composition of macroinvertebrate assemblages in these systems, such as migration patterns, flow permanence and input of leaf litter (Smith et al., 2003; Barquin & Death, 2004). Although leaf litter is an important resource for the fauna, few studies evaluated decomposition processes in these habitats (Casas & Gessner, 1999), focusing mainly in temporary lentic habitats (Kelley & Jack, 2002). In forested, perennial karst streams, the input of leaf litter could be a critical resource for the animal communities, as suggested for headwaters (Casas & Gessner, 1999). However, studies were carried out mainly in temperate regions (Vivas & Casas, 2002). In this study, we evaluated patterns of macroinvertebrate colonization during leaf litter decom-

position in a tropical river. This study was carried out in the Rio Sucuri spring, Bonito district, western Brazil (56° 28'W, 21° 07'S). This region 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 carbonate rocks, and has characteristics of initial phases of karstic development such as areas of water penetration and sub-surface outflow (Dias, 2000). The climate is tropical, with marked wet (October-May) and dry (June-September) seasons. Mean daily air temperatures vary between 16.6 and 37.5 °C along the year, whereas mean annual rainfall varies between 1200 and 1500 mm (Dias, 2000). The riparian vegetation of Rio Sucuri is semi-deciduous forest and, although large parts in the region have been converted to pasture, in the spring region the forest extends about 50 m from the river. The spring has a mean width of 30 m, mean depth of 0.5 m and trees cover about 60% of the water surface; the substrate is composed mainly by silt, and is covered by macrophytes, leaf litter and coarse woody debris. Water temperatures vary between 20.9 and 22.8 °C along the year, and the water is very transparent, with highest values of alkalinity (116 mg  $l^{-1}$ ), pH (7.2), hardness (109 mg  $CaCO_3 l^{-1}$ ) and conductivity  $(311 \ \mu S \ cm^{-1})$  in the dry season (M. Costacurta, unpublished data).

We evaluated the colonization of macroinvertebrates through an experimental study with leaf litter bags carried out in the dry season. The bags were constructed with wire frame in the form of a cage  $(30 \times 30 \times 10 \text{ cm})$ , to avoid leaf compression and simulate the natural deposition of leaf litter on the substrate. The wire frames were covered with nylon net (mesh size = 25 mm), with a finer mesh on the top and bottom of the cages (mesh = 1 mm) to avoid loss of macroinvertebrates when retrieving the cages. Thus, macroinvertebrates could access the leaf litter through the laterals of the cages. Each cage was filled with 300 g (wet mass) of green leaves collected from the adjacent gallery forest. Leaves were randomly collected from trees and shrubs and taken to the laboratory to separate the stems and dry leaves. The remaining material (green leaves) was thoroughly mixed in a container in such a way that the resulting mixture was homogeneous and avoided any trend in species composition.

On 02 June 2004, we established five sites in the Rio Sucuri spring at a minimum distance of 5 m from each other (n = 5). At each site, 10 cages were distributed on the substrate, at a depth of about 1 m. The cages were tied to stakes to avoid losses. During 10 weeks, one cage from each site was carefully collected by inserting each cage into a plastic bag underwater. The samples were later fixed with 4% formaldehyde and taken to the lab. Each sample was opened on a tray, and the remaining material (animals and leaves) was washed and separated. The contents of each tray was filtered through a sieve with 0.5 mm mesh size, preserved in alcohol 70%, and later identified under a stereomicroscope. Variation in assemblage structure during leaf litter decomposition was analyzed with multidimensional scaling (MDS). The similarity matrix was calculated using the Bray-Curtis index on log-transformed abundances to reduce the influence of dominant taxa (Clarke, 1993).

A total of 18,303 macroinvertebrates was collected along the 10 weeks of leaf litter decomposition in the Rio Sucuri, with 14 faunal groups recorded (Supplementary material).<sup>1</sup> There was a gradual increase in the total abundance (Fig. 1), with highest values around the fifth week and later decreases. The assemblages found in leaf litter cages were completely dominated by the hydrobiid snail *Idiopyrgus* sp., with 83% of the total fauna

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*Figure 1.* Variation in total macroinvertebrate abundance found in leaf litter cages in the Rio Sucuri spring, Western Brazil. Values are means  $\pm$  SE.

(Supplementary material). The other three snail species found were less abundant, although occurring in large numbers when compared with other taxa: the thiarid *Melanoides tuberculata* (4.9%), the ampullariid *Pomacea* sp. (1.6%) and the planorbid *Biomphalaria* sp. (0.7%). Other abundant faunal groups were hyalellid amphipods (4.6%) and larval midges (3.3%), whereas the remaining faunal groups represented only 1.5% of the total fauna.

The six dominant faunal groups showed distinct patterns of temporal variation during leaf litter decomposition (Fig. 2). The snail Idiopyrgus sp., hyalellid amphipods and larval chironomid midges showed gradual increases and decreases in abundance during the experiment, and highest values in the intermediate phase. In contrast, Pomacea sp. rapidly colonized the leaf litter and gradually decreased in abundance, whereas the other two snail species, M. tuberculata and Biomphalaria sp., showed no patterns of temporal variation. The results of the MDS reflected the changes in abundance of most faunal groups, with gradual changes in assemblage composition (Fig. 3), and more variation at the end of the experiment, due to the higher numbers of least abundant groups.

In the present study, we recorded dominance of the colonizing fauna by a single snail species, *Idiopyrgus* sp., so that patterns of total abundance largely reflected variation in the abundance of this species. Other common groups included the exotic snail *M. tuberculata* and hyalellid amphipods, although each represented less than 5% of the total fauna. Other studies that analyzed faunal succession during leaf litter decomposition also found dominance by a single or few species or faunal groups. For example, Rosemond et al. (1998) carried out an experiment in Costa Rica and found dominance by Chironomidae, which represented 83% of the fauna in their samples, whereas in a temperate region Hutchens & Wallace (2002) observed that 75% of the total fauna was represented by a single species, the stonefly *Tallaperla* sp. These results suggest that the species abundance distribution of these assemblages can follow a geometric series, where few factors influence assemblage structure as in early stages of succession, resulting in high dominance by few species in the community (Magurran, 1988).

The variation in the abundance of faunal groups along our experiment suggests a gradient in assemblage structure, with highest abundance values of some groups in the intermediate stage and lower values both in early and later stages. Although we do not have biomass data, the largest individuals such as Pomacea sp. were also found in the intermediate stages, suggesting a similar trend. Also, there were changes in assemblage composition between the early and final stages as indicated by the MDS analysis, with fewer groups in the early stage, possibly due to differences in colonization abilities. Other studies also found highest abundances in the intermediates stages (Gessner & Dobson, 1993; Rosemond et al., 1998), but different results found in other studies suggest that these patterns are not general (Benstead, 1996; Rowe et al., 1996; Stockley et al., 1998). In general, macroinvertebrates gradually colonize the available resource and, as leaf litter breakdown proceeds, the resource becomes limiting and the animals disperse to new resource patches (Benstead, 1996). However, Stockley et al. (1998) found highest abundance of invertebrate shredders in their first sampling (1 month after setting up the experiment), with a strong decay in the following periods. They suggested that the shredder peak could have matched the period of maximum leaf conditioning by microbial action, after which the resource would have been rapidly degraded, thus reducing shredder abundance. However, they do not have the abundance data from the start of the experiment until their first sampling, after 1 month, and our results indicate that abundances increase during the first 4 weeks of colonization;



*Figure 2.* Variation in the abundance of the main faunal groups found in leaf litter cages in the Rio Sucuri spring, Western Brazil. Values are means  $\pm$  SE.

thus, their pattern could be similar to the described in our study. On the other hand, Rowe et al. (1996) found increasing abundances of invertebrate shredders during leaf litter breakdown, but their study may have not been long enough to result in lower values of leaf biomass. In our study, after 10 weeks of leaf breakdown, only about 18% of the original leaf mass remained in the leaf litter cages (Ribas et al., in press), suggesting that the lower abundances found in this period reflected the lower leaf biomass left.

The most abundant functional feeding group found in our study was composed by scrapers,

since snails are classified into this group (Cummins et al., 2005). Scraper numbers were dominated by the small hydrobiid *Idiopyrgus* sp., although other species such as *M. tuberculata* and *Pomacea* sp. also occurred in relatively high abundances when compared to other faunal groups. These snails may feed on microalgae and macrophytes, and produce celullases that help in the digestion of leaf material (Dillon, 2000). Although they are classified as scrapers, the snails may contribute to leaf litter breakdown, since we commonly found the soft part of the leaves completely eaten in the cages, only remaining the hardest parts composed



*Figure 3.* MDS ordination of macroinvertebrate assemblages found in leaf litter cages in the Rio Sucuri spring, Western Brazil. Values beside the symbols indicate the week evaluated. Stress = 0.10.

by veins. Hydrobiid species such as Potamopyrgus jenkinsi can grow on a diet of leaves from terrestrial plants (Hanlon, 1981); ampullariid species such as Pomacea canaliculata are both microphagous and generalist macrophytophagous, with the ability both to scrape or rip macrophyte leaves (Estebenet, 1995), whereas the diet of M. tuberculata can be composed mainly by detritus (Dudgeon & Yipp, 1985). Leaf conditioning and softening after introduction in the water could facilitate consumption by snails and, depending on their size, density, and ability to consume dead leaves, they could influence leaf litter breakdown by acting as shredders (Heller & Abotbol, 1997; Heard & Buchanan, 2004). Thus, not all snails should be regarded as scrapers, but they could be regarded both as shredders or scrapers in future classification systems of functional groups.

The contribution of allochthonous organic matter is of extreme importance to energy flows in lotic systems. The consumption of leaf litter or attached periphyton by freshwater snails can be significant in different systems (Chergui & Pattee, 1991; Heller & Abotbol, 1997). Non-insect taxa such as snails and amphipods can be very abundant in springs (Barquin & Death, 2004) and perennial rivers (Habdija et al., 1995), and may influence positively the energy flows in these karst ecosystems, through decomposer food chains. Thus, in addition to other well-studied factors such as flow permanence and water chemistry (Smith et al., 2003), the basal resource formed by leaf litter may have a large importance on the assemblage structure of karst systems.

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