

INVERTEBRATE ASSEMBLAGES ASSOCIATED WITH LEAF LITTER IN THREE FLOODPLAIN WETLANDS OF THE PARANÁ RIVER

Alicia Poi de Neiff, María Eugenia Galassi, and María Celeste Franceschini

Centro de Ecología Aplicada del Litoral, CECOAL, (CONICET)

Ruta 5, Km 2,5, 3400 Corrientes, Argentina, C. C. 291

E-mail: guadalupepoi@gmail.com

Abstract: We analyzed invertebrate abundance and richness associated with decomposing litter across three riverine wetlands with different inundation regimes located in the alluvial floodplain of the Paraná River. Three replicate bags were incubated for different types of leaf litter that were dominant in each wetland for five sampling dates, yielding a total of 165 litterbags. The number of invertebrates per g of remaining leaf litter differed among wetlands and was affected by leaf litter type and incubation date within each wetland. In contrast to abundance, differences in invertebrate composition were more pronounced across wetlands than across leaf litter types within a wetland. Different species dominated in each of the three wetlands. When we compared the number of invertebrates per g remaining of a single litter type (*Eichhornia crassipes*) across the three wetlands, variability in density was explained by the NH_4^+ content of the water and dissolved oxygen concentration. Many invertebrates associated with litter may not be directly involved in shredding the material, and collectors dominated invertebrate assemblages at study sites. Although both litter quality and wetland condition affect the invertebrates colonizing leaf litter, our results suggest that spatial heterogeneity, linked to connectivity, plays an important role in determining invertebrate assemblages.

Key Words: hydrologic connectivity, leaf decomposition, riparian wetlands

INTRODUCTION

Most of the available literature examining leaf litter decomposition in aquatic habitats has occurred in low order streams (Chauvet et al. 1993), as inputs of whole leaf litter are considered crucial to small stream ecology (Vannote et al. 1980, Webster and Benfield 1986). Floodplain wetlands are also characterized by large inputs of leaf detritus, which is temporarily stored and processed before its transport into the rivers (Merritt and Lawson 1992). The position of wetlands in the drainage network, source of water, and the chemical composition of the water all affect the decomposition process (Brinson 1993, Neiff 1996).

Invertebrates are among the most abundant and diverse organisms in freshwater wetlands (Sharitz and Batzer 1999) and are affected by ecological conditions. In small forested streams, variation in leaf litter quality and seasonal changes in decomposition affects the composition of the invertebrate assemblage (Cummins et al. 1989, Merritt and Lawson 1992, Richardson et al. 2004). Other studies have indicated that differences in the invertebrate assemblage were more pronounced across streams than across leaf litter species within a stream (LeRoy and Marks 2006). Very little information is available

about invertebrates that feed on detritus in riparian wetlands (Mitsch and Gosselink 1993), even though these invertebrates are a trophic resource for many animals (Magee 1993). In addition, the role of invertebrates in litter processing in tropical waters is unclear because the assemblages often contain a lower proportion of shredders, which feed on large particulate organic matter, than collectors, which feed on fine particulate organic matter (Dudgeon and Wu 1999, Gonçalves et al. 2006, Rueda-Delgado et al. 2006).

The floodplain of the Paraná River, a seventh order channel, encompasses an array of different types of wetlands (Neiff 2001) with many leaf litter types that vary in palatability. Decomposition rates have been shown to be affected by both litter quality and wetland characteristics, including the degree of connectivity of floodplain wetlands within the larger fluvial system (Poi de Neiff et al. 2006). In this paper, we analyzed the abundance and species richness of invertebrates colonizing nine types of leaf litter across three riparian wetlands within the Paraná River floodplain. At each wetland, we analyzed the relationship between litter types and invertebrate assemblages. To test the effect of wetland characteristics on the litter colonization, we compare the invertebrate assemblages of one species across three

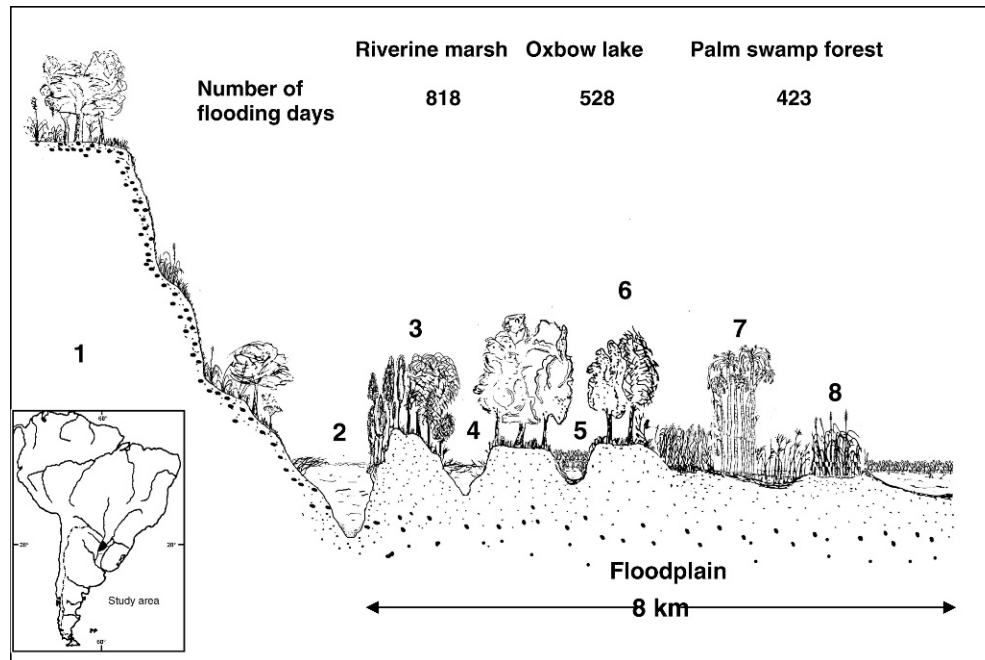


Figure 1. Cross-section of the Paraná River floodplain, 30 km downstream from the confluence with the Paraguay River. 1) Left bank, 2) main channel, 3) riverine forest, 4) riverine marsh with several aquatic plants, 5) oxbow lake with free floating macrophytes, 6) mixed gallery forest, 7) palm forest, and 8) swamp dominated by cattail and floating meadows.

sites with different physical, chemical, and hydrologic conditions. Our hypothesis was twofold: first, leaf litter of different types, which decompose at different rates, will support different invertebrate assemblages both in terms of composition and abundance, and second, leaf litter from the same plant species will support similar invertebrate assemblages, regardless of wetland type.

METHODS

Site Descriptions

Downstream from the confluence with the Paraguay River, the alluvial floodplain of the Paraná River spreads over 8 km from the main channel. Our study area was located on the west bank of Paraná River within the RAMSAR Site Wetlands Chaco (Argentina). On this margin, we selected three riverine wetlands with different inundation regimes (Figure 1).

Nearest the main channel, the riverine marsh (27°28'09"S; 58°52'39"W, Site A) was colonized by floating *Eichhornia crassipes* Mart. (Solms) (waterhyacinth) and rooted *Polygonum acuminatum* Kenth. (smartweed) and *Panicum elephantipes* Nees ex Trin (switchgrass). Associated riverine forest on sand bars had monospecific tree stands of *Tessaria integrifolia* Ruiz et Pav. (aliso de río) or *Salix humboldtiana* Willd. (willow). The second site was an

oxbow lake (27°27'S; 58°51'W, Site B) located 2 km away from the river. It supports a high biomass of the floating macrophyte *E. crassipes*, and on its levees has mixed gallery forest dominated by *Nectandra angustifolia* (Schrad) Nees et Mart. (laurel), *Peltophorum dubium* (Spreng) Tanb. (ibirá-pitá), and *Banara arguta* Briq. (granadillo). The third site, a palm swamp forest (27°26'S; 58°54'W, Site C) was dominated by *Copernicia alba* Morong. (palm) and various macrophytes (*E. crassipes*, *Typha latifolia* L. {cattail} and *Paspalum repens* Bergius {water paspalum}).

The flow regime of the Paraná River is irregular compared to other large South American Rivers, with floods of different intensity, recurrence, and amplitude (Neiff 1996). Thus, in the alluvial floodplain wetlands, large morphological and biotic spatial gradients are observed in relation to topographic positions relative to overflow levels that determine frequency and timing of connection to the river course and exchange of nutrients (Neiff 2001). Between January 1996 and January 1999, the Paraná River experienced an extreme flood event with record discharges and duration (Neiff *et al.* 2000). This event provided an opportunity to investigate invertebrate colonization because a high proportion of the floodplain was flooded. The riverine marsh was more connected with the main channel than the two other sites (Figure 1).

Table 1. Composition of leaf litter types in the studied sites and its decomposition rates. L: Lignin; N: Nitrogen; *k*: decay coefficient (after Poi de Neiff et al. 2006).

| Wetland type | L% | N% | <i>k</i> day ⁻¹ |
|---|-------|------|----------------------------|
| Riverine marsh | | | |
| <i>Tessaria integrifolia</i> | 11.65 | 2.13 | 0.0720 |
| <i>Salix humboldtiana</i> | 13.76 | 1.81 | 0.0190 |
| <i>Polygonum acuminatum</i> | 3.90 | 1.60 | 0.0220 |
| <i>Panicum elephantipes</i> | 5.60 | 1.47 | 0.0108 |
| <i>Eichhornia crassipes</i> | 1.04 | 2.13 | 0.0670 |
| Oxbow lake with mixed gallery forest | | | |
| Mixture of <i>Nectandra angustifolia</i> , <i>Peltophorum dubium</i> and <i>Banara arguta</i> | 21.72 | 1.71 | 0.0063 |
| <i>Eichhornia crassipes</i> | 2.35 | 2.05 | 0.0220 |
| Palm swamp forest | | | |
| <i>Copernicia alba</i> | 25.71 | 1.21 | 0.0032 |
| <i>Typha latifolia</i> | 18.2 | 1.28 | 0.0041 |
| <i>Paspalum repens</i> | 3.38 | 1.39 | 0.0081 |
| <i>Eichhornia crassipes</i> | 2.35 | 2.05 | 0.0199 |

Experimental Design and Analysis

This study was designed to analyze the relative importance of litter quality and wetland condition to invertebrates. To test the effect of litter types on invertebrate assemblages we compared nine types of litter dominant in each of the three sites described above (*T. integrifolia*, *S. humboldtiana*, *P. acuminatum*, *P. elephantipes*, mixed gallery forest, *C. alba*, *T. latifolia*, *P. repens*, and *E. crassipes*). The litter types selected provided a wide range of litter quality and decomposition rates (Table 1, Poi de Neiff et al. 2006). We used a second comparison with only *E. crassipes* in each of the wetlands, to focus on site effects.

Leaves of *T. integrifolia* and *S. humboldtiana*, and the mixed gallery forest (*N. angustifolia*, *P. dubium*, and *B. arguta*) were collected after abscission into litter traps at the marsh's riverine forest and oxbow's mixed gallery forest, respectively. Recently senesced leaves of *C. alba* were obtained from the palm forest floor. At the end of the annual macrophyte growing season, we collected standing dead and wilted *E. crassipes* leaves from all three wetlands, *P. acuminatum* and *P. elephantipes* leaves from the riverine marsh, and *T. latifolia* and *P. repens* leaves from the palm swamp forest.

Air-dried leaves (10 g) were placed into 20 × 20 cm nylon litterbags. The large leaf size of palm led us to use 20 g of this litter type in 20 × 30 cm litter bags to prevent leaf fragmentation. We used 2 mm mesh to prevent the loss of leaf fragments through the larger mesh of coarser bags. Most of the litter types selected in our study were structurally very weak and fragment quickly.

Three replicate bags were incubated for each treatment (eight treatments with non *E. crassipes*

litter types and three treatments with *E. crassipes* litter) for five sampling dates, for a total of 165 litterbags. In September after the wetlands were flooded, five 3-bag sets were placed between two layers of wire mesh (Hill and Webster 1982) and anchored to the bed of each of the three sites. The time intervals assigned to the incubation date were based on reported differences in decomposition rates of different litter types at sites located near or farther from the river (Neiff and Poi de Neiff 1990, Poi de Neiff and Casco 2001). Thus, bags were removed at: 7, 17, 24, 30, and 40 days in the riverine marsh; 7, 17, 30, 68; and 97 days at the oxbow lake; and 7, 30, 40, 68, 97, and 125 days from the palm swamp forest. Note that day 7 and 30 day incubations were used at each site.

After each incubation period, one set of three bags for each litter type was removed, and bags were transported separately in plastic bags out of the field. In the laboratory, leaves were washed through a sieve (125 μm mesh), and all animals were sorted under a microscope and stored in 70% ethyl alcohol. Invertebrates were identified to the lowest possible taxonomic level using keys in Brinkhurst and Marchese (1989), Angrisano (1992), Dominguez et al. (1994), Lopretto and Tell (1995), and Trivinho-Strixino and Strixino (1995). Functional feeding groups were assigned following Trivinho-Strixino and Strixino (1993) and Merritt and Cummins (1996). The results were tabulated as invertebrates per litter bag and invertebrates per remaining litter dry weight.

Physical and chemical data were taken at each site at the end of each incubation period. Specific conductivity, dissolved oxygen, and pH were recorded using a Checkmate 90 (Corning) conducti-

meter, an Oxi-330 portable oximeter (WTW), and a digital pH meter-330 (WTW), respectively. Water samples were filtered within 1–2 h of collection through pre-washed Gelman DM-450 (0.45 μ m-pore) membranes. Using spectrophotometric analyses, NH_4^+ was assessed using the indophenol blue method, $\text{NO}_3^- + \text{NO}_2^-$ by cadmium reduction, and total phosphorus by the molybdenum blue method with persulfate oxidation (APHA 1998).

Statistical Analyses

Comparison among Litter Types. At each site, comparisons among leaf litter types of invertebrate per g remaining litter and per litter bag were made with Wilcoxon tests. A dendrogram of dissimilarity (Jaccard distance) among invertebrates from different types of litter was obtained by the complete linkage method (Legendre and Legendre 1998). To examine spatial patterns in invertebrate assemblages, the abundance of 29 dominant species were ordinated using non-metric multidimensional scaling (NMDS) of Bray-Curtis similarities in PC-ORD (Version 4.17, 1999, MJM Software, Gleneden Beach, OR, USA). For that analysis we used the number of invertebrates per g dry weight at 7 and 30 days (incubation dates in common for all leaf litter types and wetlands), plus the final incubation date. To test for differences among sites we used a multi-response permutation procedure (MRPP) in the same program.

Comparison among Wetland Conditions. To test the relationship between environmental factors and invertebrates abundance across sites, we used forward, stepwise-multiple regression. The dependent variable was the number of invertebrates per g remaining of *E. crassipes* litter and the independent variables were dissolved oxygen content, pH, electrical conductivity, $\text{NO}_3^- + \text{NO}_2^-$, NH_4^+ , total phosphorus, and water temperature of each site during the incubation time. The dissolved oxygen, conductivity, pH and nutrient concentrations were log-transformed when necessary. Single-factor analysis of variance (ANOVA) with post hoc Tukey tests was used to test for significant differences among the three wetland conditions. All analyses were performed with STATISTICA 6.0 (StatSoft 2001).

RESULTS

Environmental Features

Among the three sites, water was most acidic at the palm swamp forest and contained the most dissolved oxygen at the riverine marsh (ANOVA, P

< 0.05 ; Table 2). Water temperatures did not differ among sites. During the incubation, $\text{NO}_3^- + \text{NO}_2^-$ concentrations significantly differed among sites ($P < 0.05$), decreasing with distance from the river (Table 2). $\text{NH}_4\text{-N}$ concentration was higher at the riverine marsh than either the oxbow lake or palm swamp forest. There were no significant differences in phosphorus concentration among sites.

Invertebrate Assemblages in Relation to Litter Types

Nine major classes or orders of invertebrates were associated with leaf litter in the three study wetlands, comprising 44 families and 82 morphospecies (Table 3). A total of 44, 42, and 24 taxa occurred in the palm swamp forest, the riverine marsh and the oxbow lake, respectively. Twenty-three taxa were shared by two of the wetlands, and seven genera occurred in all three sites. Dissimilarity of invertebrates among wetlands was high, and cluster analysis based on presence-absence separated the riverine marsh from the other two sites (Figure 2). Invertebrate compositions within individual wetlands were fairly uniform (Figure 2), even though litter types in samples varied. Only a few taxa dominated the invertebrate assemblages. Chironomidae, oligochaetes, conchostracans, caddisflies, ostracods and snails were the most abundant invertebrates, but different species and functional feeding groups dominated in the three wetlands.

A NMDS community ordination had an acceptably low final stress (12.08%) and instability (< 0.0001), and a three-dimensional solution explained 70% of the total variation in the data set (43% of the variation loaded on Axis 3 and 31% loaded on axis 1; Figure 3). The riverine marsh samples were grouped mainly on the lower left quadrant of the plot, while samples from the palm swamp forest clustered on the opposite quadrant (Figure 3). A MRPP procedure confirmed that invertebrate assemblages differed significantly among the three wetland types ($A = 0.14$, $p < 0.00001$). Axis 3 was driven primarily by the abundance of *Ablabesmyia* sp. ($r = -0.641$), *Trieminentia corderoi* Harman ($r = -0.518$), *Dero (Aulophorus) furcatus* Müller ($r = -0.471$), *Cyclestheria hislopii* Bair ($r = -0.462$), and *Neotrichia* ($r = -0.436$). Axis 1 was driven primarily by the abundance of *Pristina macrochaeta* Stephen ($r = 0.714$) and *Dero (Dero) multibranchiata* Stieren ($r = 0.570$).

The number of invertebrates per g of remaining leaf litter differed among wetlands and was affected by leaf litter types and incubation date within each wetland (Table 4). Within each wetland, inverte-

Table 2. Mean values and standard errors (S.E.) of physical and chemical variables for the three wetlands during the decomposition experiments. The last three columns show ANOVA comparisons of the variables among sites, with different letters indicating statistically different means (Tukey's test, $p < 0.05$).

| Water quality parameter | Riverine marsh | | Oxbow lake | | Palm swamp forest | | ANOVA | | |
|--|-------------------|-------|-------------------|-------|-------------------|-------|-------|------|---------|
| | Mean | S. E. | Mean | S. E. | Mean | S. E. | F | d.f. | p value |
| Water temperature (°C) | 25.3 ^a | 0.01 | 24.5 ^a | 0.02 | 22.7 ^a | 0.02 | 2.17 | 2.13 | 0.1506 |
| Dissolved Oxygen (mg.l ⁻¹) | 6.2 ^b | 0.05 | 1.3 ^a | 0.15 | 1.6 ^a | 0.05 | 20.18 | 2.13 | 0.0001 |
| Conductivity (µS.cm ⁻¹) | 164 ^b | 0.03 | 202 ^b | 0.04 | 72.6 ^a | 0.03 | 46.69 | 2.13 | 0.0001 |
| pH | 7.1 ^b | 0.002 | 6.5 ^b | 0.01 | 5.9 ^a | 0.01 | 16.74 | 2.13 | 0.0004 |
| N-(NO ₃ ⁻ + NO ₂ ⁻) (µg.l ⁻¹) | 106 ^c | 0.02 | 2.9 ^b | 0.11 | 1.5 ^a | 0.48 | 23.77 | 2.13 | 0.0001 |
| N- NH ₄ ⁺ (µg.l ⁻¹) | 54 ^b | 0.08 | 5.0 ^a | 0.20 | 24.5 ^a | 0.23 | 11.05 | 2.11 | 0.0023 |
| P- PO ₄ ⁻ (µg.l ⁻¹) | 28 ^a | 0.08 | 49 ^a | 0.17 | 86.0 ^a | 1.81 | 0.3 | 2.11 | 0.7462 |

brate abundance differed significantly among leaf litter types (Wilcoxon test, $p < 0.01$), with the exception of three pairs: *T. integrifolia*-*E. crassipes* ($p = 0.636$), *S. humboldtiana*-*P. acuminatus* ($p = 0.086$), and *S. humboldtiana*-*E. crassipes* ($p = 0.112$) at the riverine marsh and *P. repens*-*E. crassipes* ($p > 0.99$) and *T. latifolia*-*C. alba* ($p = 0.102$) at the palm swamp forest. Invertebrate per g of remaining leaf litter increased over time in the riverine marsh and the oxbow lake, peaking after 30 and 68 days of incubation, respectively. At the palm swamp forest, maximum colonization occurred after 30 days for each litter type, and then declined, except for the palm litter (Table 4).

In general, the number of invertebrates per litter bag (Table 4) did not differ among litter types with four exceptions: *P. acuminatum*-*P. elephantipes*, *C. alba*-*P. repens*, *C. alba*-*E. crassipes* and *C. alba*-*T. latifolia* (Wilcoxon test, $p < 0.002$). Note that the initial mass of *C. alba* leaf litter placed into litter bags was greater than for other litter types, and the great quantity and the slow decomposition of the palm litter (Table 1) resulted in low densities of invertebrates per g remaining. Depending on litter type, the maximum number of invertebrates per litter bag was recorded between 17 and 30 days in the riverine marsh and after 30 or 97 days in the palm swamp forest (Table 4). At the oxbow lake (Table 4), *E. crassipes* leaf litter bags supported high invertebrate abundances on days 7 and 17, whereas the mixed gallery forest litter did not provide a good substrate for colonization during this incubation time.

Invertebrate Assemblages in Relation to Wetland Conditions

When we compared the number of invertebrates per g remaining of a single litter type, *E. crassipes*, across the three sites, the abundance of invertebrates

was higher at the riverine marsh than the oxbow lake and the palm swamp forest (Wilcoxon test, $p < 0.0001$). Stepwise multiple regression indicated that dissolved oxygen content measured at the end of the incubation period explained 72% of the variability in invertebrate density (adjusted $r^2 = 0.72$, $p = 0.002$). After 30 days, only the relationship between invertebrate density and ammonium concentration was significant (adjusted $r^2 = 0.81$, $p = 0.001$).

The *E. crassipes* litter incubated in different wetlands supported different taxa. *Trieminentia corderoy* and *Ablabesmyia* sp. were the most abundant taxa at the riverine marsh, *Littoridina guaranítica* (Doering), *Dero (D.) evelinae* Marcus, and *Bothrioneurum* sp. at the oxbow lake, and *Dero (D.) multibranchiata*, *P. macrochaeta*, and *Cytheridella ilosvayi* Daday at the palm swamp forest.

Functional Feeding Groups

Likely shredders included the beetle larva, *Scirtes* sp. (Scirtidae), found in the oxbow lake and palm swamp forest, and *Cricotopus* sp. and *Polypedilum* sp. (Chironomidae) found at all three sites (although the midge abundances were low).

Collector gatherers and filterers dominated invertebrate assemblages at all study sites (Figure 4). In the palm forest, collector-gatherers were the dominant group found on *P. repens* and *C. alba* litter (Figure 4), averaging almost 50% of total invertebrate abundance, and after 30 days, *Dero (D.) multibranchiata* and *Pristina macrochaeta* were the dominant taxa in all types of litter. At the riverine marsh, *Trieminentia corderoi*, *Dero (A.) furcatus*, *Chironomus* sp., and *Campsurus* sp. were the most abundant collector-gatherers. The main collector-filterer at the riverine marsh was a conchostracan, *Cyclestheria hislopiae*. Ostracods (*C. ilosvayi* and *Chlamydotheca* sp.) were the main filterers at the oxbow lake and palm swamp forest. After 30 days,

Table 3. Invertebrates collected from leaf bags in the Paraná River floodplain organized by functional feeding group. In the last columns we list the taxa in common at two or three wetlands, and asterisks (*) indicating invertebrates common to all three sites. Functional Feeding groups (Fg): Cf: collectors-filterers, Cg: collectors-gatherers, P: predators, Sc: scrapers and Sh: shredders. L: list of taxa codes used in the NMDS ordination diagram.

| Taxa occurring in only one wetland | | | | | | Taxa common to at least two wetlands | | |
|------------------------------------|----|----|------------------------------------|----|----|--------------------------------------|-------|----|
| Marsh | Fg | L | Palm | Fg | L | | Fg | L |
| <i>Cyclestheria hislopii</i> | Cf | Cy | <i>Chlamydotheca mckenziei</i> | Cf | | <i>Cytheridella ilosvayi*</i> | Cf | Ci |
| <i>Simocephalus serrulatus</i> | Cf | | <i>Chlamydotheca</i> sp. | Cf | | <i>Grimaldina brazzai</i> | Cf | |
| <i>Diaphanosoma birgei</i> | Cf | | Cyprididae no det. | Cf | | <i>Notodiptomus coniferoides</i> | Cf | No |
| <i>Pseudopsida bidentata</i> | Cf | | Cladocera no det. | Cf | | <i>Littoridina guaranitica</i> | Sc | Lg |
| <i>Ilyocryptus spinifer</i> | Cf | | <i>Ceriodaphnia dubia</i> | Cf | Cd | <i>Drepanotrema lucidum*</i> | Sc | |
| <i>Ceriodaphnia</i> sp. | Cf | | <i>Kurzia latissima</i> | Cf | Kl | <i>Dero (Aulophorus) furcatus</i> | Cg | Df |
| <i>Notodiptomus carteri</i> | Cf | Nc | <i>Euryalona fasciculata</i> | Cf | Ef | <i>Dero (Aulophorus) pectinatus</i> | Cg | |
| <i>Eupera</i> sp. | Cf | | <i>Diaphanosoma</i> sp. | Cf | | <i>Dero (Dero) pectinata*</i> | Cg | Dp |
| <i>Trieminentia corderoi</i> | Cg | Tc | <i>Metacyclops laticornis</i> | Cf | | <i>Dero (Dero) evelinae</i> | Cg | De |
| <i>Hyalella curvispina</i> | Cg | | <i>Pristina macrochaeta</i> | Cg | Pm | Enchytraeidae | Cg | |
| <i>Dicrotendipes</i> sp. | Cg | | <i>Pristina leidyi</i> | Cg | | <i>Caenis</i> sp. | Cg | |
| <i>Micropsectra</i> sp. | Cg | Mi | <i>Dero botrytis</i> | Cg | Db | <i>Campsurus</i> sp. | Cg | Ca |
| <i>Macrocyclus albidus</i> | P | | <i>Dero (Dero) multibranchiata</i> | Cg | Dm | <i>Callibaetis</i> sp. | Cg | |
| Gomphidae no det. | P | | <i>Opistocysta funiculus</i> | Cg | | <i>Cyrnellus</i> sp. | Cg | |
| Coenagrionidae | P | | Tubificidae no det. | Cg | | <i>Chironomus</i> sp.* | Cg | Ch |
| <i>Perithemis</i> sp. | P | | <i>Proisotoma</i> sp. | Cg | | <i>Helobdella</i> sp.* | P | He |
| <i>Oecetis</i> sp. | P | | Ephydridae | Cg | | <i>Ablabesmyia</i> sp.* | P | Ab |
| <i>Laccophyllus</i> | P | | Psychodidae | Cg | | Oribatidae* | P | Or |
| Acarina sp ₁ | P | | <i>Mansonina</i> sp. | Cg | | <i>Berosus</i> sp. | Sc | Be |
| <i>Neotrichia</i> sp. | Sc | Ne | <i>Chaetogaster</i> sp. | P | | <i>Cricotopus</i> sp. | Sh | |
| <i>Biomphalaria</i> sp. | Sc | | <i>Celina</i> sp. | P | | <i>Polypedilum</i> sp. | Sh | Po |
| <i>Uncancylus concentricus</i> | Sc | Uc | <i>Hydrocanthus debilis</i> | P | | <i>Goeldichironomus</i> sp. | Sh | Go |
| <i>Hydrellia</i> sp. | Sh | | <i>Desmopachria</i> sp. | P | | <i>Scirtes</i> sp. | Sh-Cg | |
| Lepidoptera no det. | Sh | | Acarina sp ₂ | P | | | | |
| Oxbow | | | Acarina sp ₃ | P | | | | |
| <i>Latonopsis fasciculata</i> | Cf | | <i>Forcipomyia</i> sp. | Sc | | | | |
| <i>Eupera platensis</i> | Cf | | <i>Drepanotrema cimex</i> | Sc | | | | |
| <i>Bothrioneurum</i> sp. | Cg | Bo | <i>Drepanotrema anatinum</i> | Sc | | | | |
| <i>Oxyethira</i> sp. | Cg | Ox | | | | | | |
| <i>Eristalis</i> sp. | Cg | | | | | | | |
| <i>Monopelopia</i> sp. | P | | | | | | | |
| <i>Gundlachia moricandi</i> | Sc | Gm | | | | | | |

leaf litter of *Paspalum* and *Typha* supported abundant densities of cladocerans (*Euryalona fasciculata* Sars and *Kurzia latissima* Kurtz) at the palm swamp forest.

Predators (mainly *Ablabesmyia* sp.) were particularly numerous at the beginning of the experiment in the riverine marsh (Figure 4). At the end of the experiment, Acari (Oribatidae) were abundant predators at the palm swamp forest. Scrapers, primarily *L. guaranitica*, were abundant only after seven days at the oxbow lake (Figure 4).

DISCUSSION

The mean number of invertebrates in our study was in the range (2–176 individuals per g remaining

leaf litter) observed in other studies on decomposition carried out in subtropical wetlands (Poi de Neiff and Neiff 1989, Neiff and Poi de Neiff 1990, Bruquetas de Zozaya and Neiff 1991, Poi de Neiff and Casco 2001, Stripari and Henry 2002). Differences in the number of invertebrates per g among different leaf litter types within each wetland, suggested that invertebrate densities were highest for leaf litter with rapid decomposition rates. Other studies, conducted primarily in streams, have found similar patterns (Webster and Benfield 1986).

In contrast to abundance, variations in invertebrate composition were more pronounced across different wetlands than across different leaf litter types within a wetland. Although invertebrates prefer particular kinds of leaf litter in many

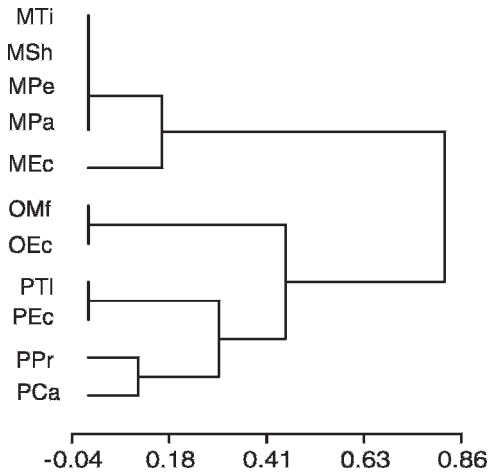


Figure 2. Cluster analysis (complete linkage method) based on dissimilarity of invertebrates by litter type in the studied sites. M: riverine marsh, O: oxbow lake and P: palm swamp forest; Ti: *Tessaria integrifolia*, Sh: *Salix humboldtiana*, Pe: *Panicum elephantipes*, Pa: *Polygonum acuminatum*, Ec: *Eichhornia crassipes*, Mf: mixed forest, Tl: *Typha latifolia*, Pr: *Paspalum repens*, and Ca: *Copernicia alba*.

temperate streams (Cummins et al. 1989), in others, the main source of variation in invertebrate assemblages is among streams (LeRoy and Marks 2006). In our study, the riverine marsh site that was most connected with the main channel was distinct from the other sites with weaker hydrologic connection.

As in forested streams (Chauvet et al. 1993, Gonçalves et al. 2006, Rueda-Delgado et al. 2006), oligochaetes and Chironomidae were the most abundant groups living on leaf litter in the study wetlands. Other authors have observed in other wetlands that Cladocera, Copepoda, and Oligochaeta were the most abundant taxa on decomposing macrophytes (Nessimian and Lima 1997, Stripari and Henry 2002), and we also found this for some sites and some incubation dates.

Among *E. crassipes* litters at the three sites, the major environmental variables influencing invertebrates were NH_4^+ content of the water at 30 days and dissolved oxygen concentration late in the incubation period. Because the riverine forest was more connected to the river and received higher

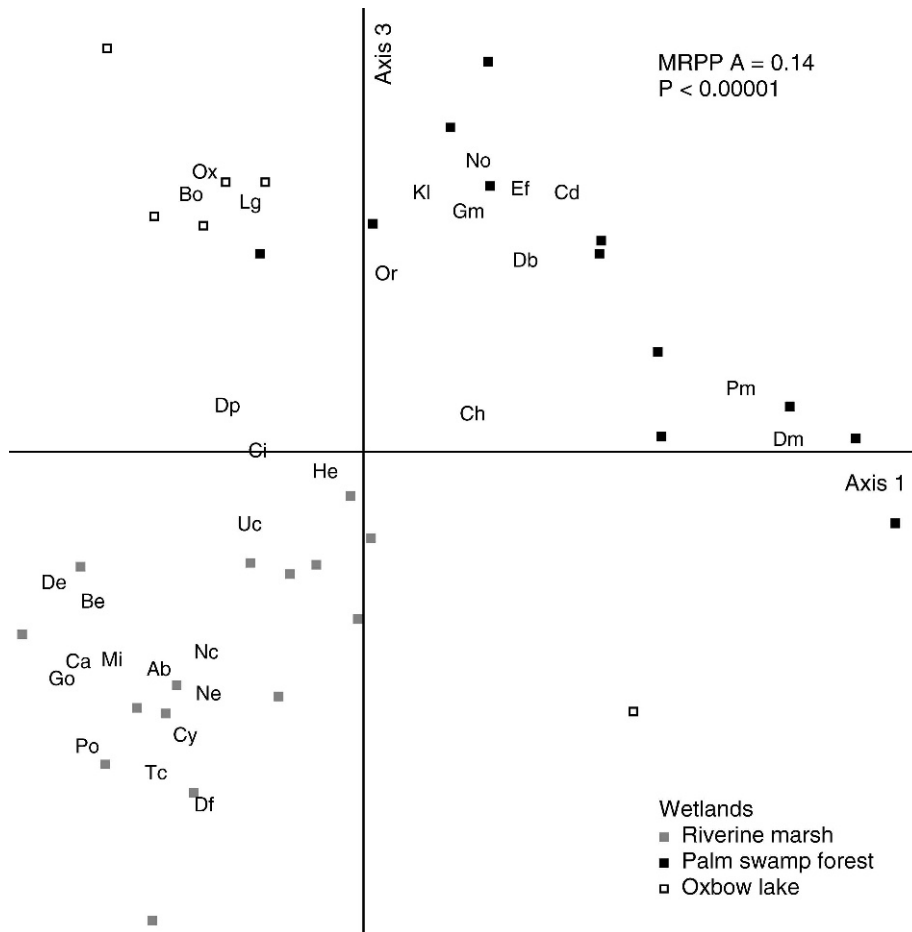


Figure 3. NMDS ordination of invertebrate compositions by litter type for three wetlands. The taxa codes are listed in Table 3.

Table 4. Mean number (\pm S.E.) of invertebrates per g dry weight of leaf litter and number (\pm S.E.) of invertebrates per leaf bag. The numbers in the first row of each wetland type are the incubation days. See text for differences in the abundance of invertebrates among leaf litter types within each site and the number of invertebrates per g remaining of a single litter type among sites.

| Incubation time | Invertebrates per g dry weight | | | | Invertebrates per leaf litter bag | | | | | |
|-------------------------|--------------------------------|-----------------|----------------|----------------|-----------------------------------|-----------------|------------------|------------------|-----------------|------------------|
| | 7 | 17 | 24 | 30 | 40 | 7 | 17 | 24 | 30 | 40 |
| Riverine marsh | | | | | | | | | | |
| <i>T. integrifolia</i> | 6 \pm 0.8 | 19.9 \pm 39.4 | 99 \pm 39.4 | 117 \pm 47.9 | 172 \pm 98.9 | 20.5 \pm 7.8 | 45.3 \pm 11.7 | 173.5 \pm 7.8 | 135 \pm 8.7 | 66 \pm 23 |
| <i>S. humboldtiana</i> | 4 \pm 1 | 13 \pm 2.7 | 17 \pm 5.6 | 72 \pm 15.1 | 57 \pm 7.02 | 2.5 \pm 6 | 70 \pm 7.1 | 71.7 \pm 26.4 | 296.7 \pm 31 | 237.7 \pm 49 |
| <i>P. acuminatum</i> | 3.5 \pm 1.7 | 13.5 \pm 6.6 | 10.1 \pm 8.9 | 21.9 \pm 1.3 | 21.2 \pm 1.9 | 35.7 \pm 20.1 | 132 \pm 58.2 | 81.6 \pm 10.3 | 152 \pm 11.5 | 107.5 \pm 17.7 |
| <i>P. elephanitipes</i> | 3.6 \pm 0.3 | 9 \pm 1.8 | 4.7 \pm 1.1 | 17.1 \pm 1.3 | 6.46 \pm 2.7 | 30.3 \pm 3.2 | 72.3 \pm 13.2 | 33.7 \pm 5 | 99 \pm 31.2 | 37.7 \pm 13.7 |
| <i>E. crassipes</i> | 10.5 \pm 1.9 | 21.3 \pm 5.1 | 20.0 \pm 2.7 | 31 \pm 4.8 | 176 \pm 89.8 | 75.7 \pm 9.9 | 119.7 \pm 41.8 | 85.7 \pm 8.3 | 80.7 \pm 15.2 | 85 \pm 30.6 |
| Oxbow lake | 7 | 17 | 30 | 68 | 97 | 7 | 17 | 30 | 68 | 97 |
| <i>E. crassipes</i> | 10.3 \pm 1 | 9 \pm 1.97 | 12 \pm 4.5 | 26.4 \pm 3.7 | 12.4 \pm 0.4 | 78.7 \pm 8.5 | 54.3 \pm 13.2 | 52.7 \pm 15.6 | 81.5 \pm 6.4 | 13 \pm 5.3 |
| Mixed gallery forest | 0 | 0 | 2 \pm 1 | 7 \pm 0.9 | 9.7 \pm 3.5 | 0 | 0 | 11.7 \pm 6.5 | 36.7 \pm 6.6 | 47.7 \pm 20 |
| Palm swamp forest | 7 | 30 | 40 | 68 | 97 | 7 | 30 | 40 | 68 | 97 |
| <i>T. latifolia</i> | 3.6 \pm 0.4 | 19.3 \pm 4.2 | 8.8 \pm 0.4 | 9.9 \pm 1.9 | 8.2 \pm 0.7 | 29 \pm 1 | 141.3 \pm 31.8 | 59 \pm 6.9 | 59 \pm 13 | 47.3 \pm 1.5 |
| <i>P. repens</i> | 3.6 \pm 0.2 | 35.8 \pm 7.4 | 28.8 \pm 4.8 | 18.9 \pm 2.3 | 8.35 \pm 0.9 | 22 \pm 2 | 158 \pm 28.6 | 99.3 \pm 15.9 | 63.3 \pm 10 | 25.3 \pm 4.2 |
| <i>E. crassipes</i> | 4.3 \pm 0.8 | 26.1 \pm 1.9 | 12 \pm 1.9 | 21.6 \pm 0.6 | 26.5 \pm 6.7 | 32.7 \pm 4.9 | 169.3 \pm 17.4 | 57 \pm 12.1 | 56 \pm 6.9 | 33 \pm 1 |
| <i>C. alba</i> | 3.5 \pm 0.3 | 9.7 \pm 3.9 | 9.4 \pm 1.4 | 11.8 \pm 0.3 | 6.4 \pm 1.8 | 58.7 \pm 6.5 | 155.7 \pm 67.2 | 136.7 \pm 22.5 | 175.5 \pm 4.9 | 76.7 \pm 28.9 |

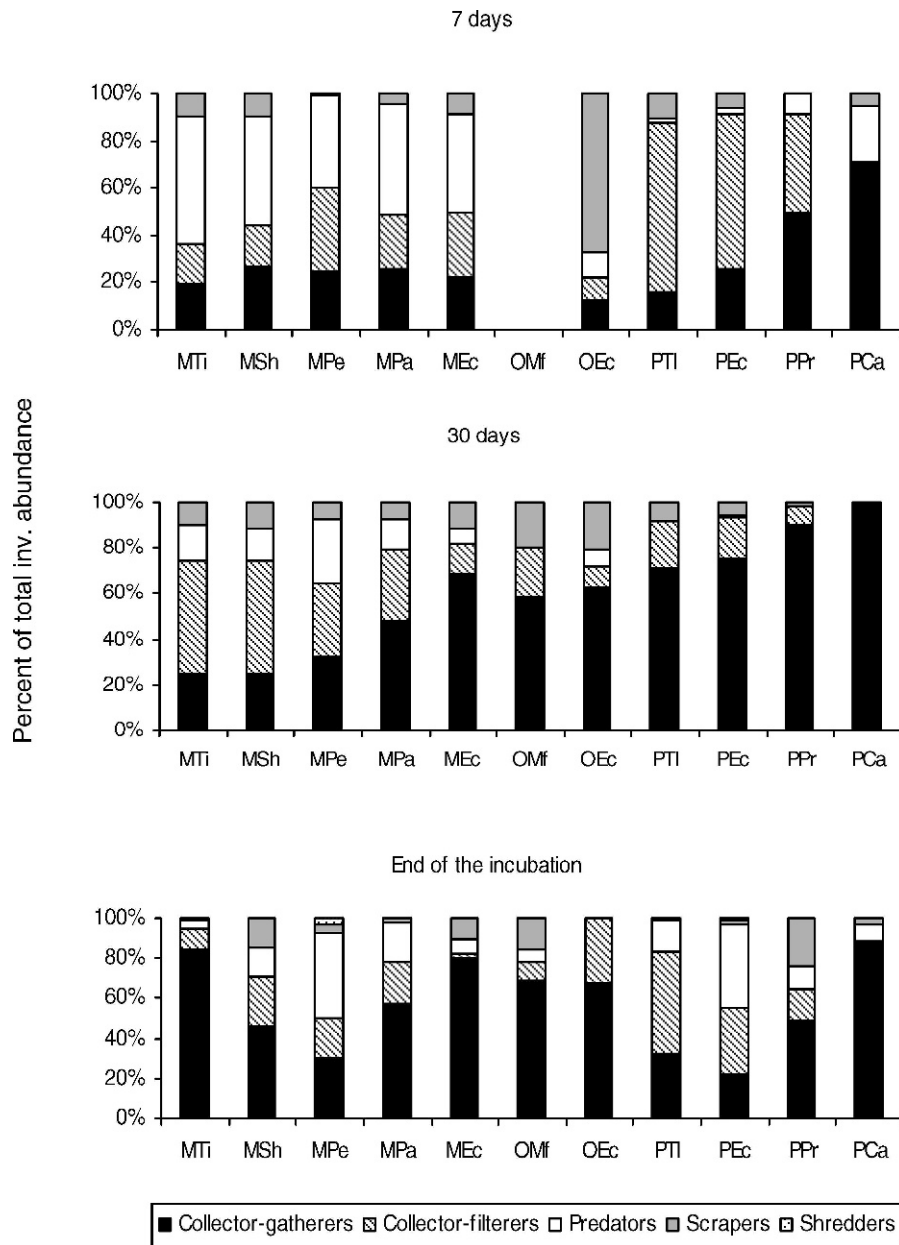


Figure 4. Proportion of the number of invertebrate feeding groups after 7 days, 30 days, and at the end of the incubation. M: riverine marsh, O: oxbow lake, and P: palm swamp forest; Ti: *Tessaria integrifolia*, Sh: *Salix humboldtiana*, Pe: *Panicum elephantipes*, Pa: *Polygonum acuminatum*, Ec: *Eichhornia crassipes*, Mf: mixed forest, TI: *Typha latifolia*, Pr: *Paspalum repens*, and Ca: *Copernicia alba*.

nutrient loads, decomposition of *E. crassipes* was faster there than at the oxbow lake or palm swamp forest. A decrease in $\text{NO}_3^- + \text{NO}_2^-$ concentration in sites located farther from the river may be due to denitrification and reduction to NH_4^+ by microorganisms (Carignan and Neiff 1992), both anaerobic processes. Colonization by invertebrates of *E. crassipes* leaf litter was also directly linked to low oxygen content in the oxbow lake and palm swamp forest. Low invertebrate densities have been fre-

quently associated with low dissolved oxygen concentrations in Amazon floodplain lakes (Junk and Robertson 1997) and other Paraná oxbow lakes (Poi de Neiff and Carignan 1997).

Many of the invertebrates associated with leaf litter in the Paraná floodplain may not be directly involved in shredding the litter. Other studies have suggested that an apparent lack of shredders in tropical systems reflects sampling deficiencies that exclude macroconsumers such as crabs (Wetzen et

al. 2002) or fishes or shrimps (Rosemond *et al.* 1998). Yet others suggest that a low abundance of shredders is an important characteristic of these systems (Neiff and Poi de Neiff 1990, Dudgeon and Wu 1999, Stripari and Henry 2002, Capello *et al.* 2004, Gonçalves *et al.* 2006). Although the mesh size of the litterbags prevented colonization by crabs and shrimp in our experiment, these macroconsumers were scarce at the study sites; shrimp are absent and *Trichodactylus borellianus* Nobili crabs are only sporadically present in floating meadows and benthic communities (unpublished data). Lacking shredders, variable weight loss of litters could result from differential fragmentation rates (as indicated Stewart and Davies 1989 for streams).

Although both litter quality and wetland condition affect the invertebrates colonizing leaf litter, our results suggest that spatial heterogeneity, linked to connectivity, played a particularly important role in determining invertebrate assemblages. Abiotic variables related to hydrologic connectivity such as nutrient content and dissolved oxygen affected invertebrates colonization of the same litter type. Changes in the inundation regime could lead to the loss of the spatial heterogeneity by modifying the composition of the riparian vegetation (Neiff 2001) and the leaf litter quantity (Neiff and Poi de Neiff 1990). Conservation of the RAMSAR Site Wetlands Chaco requires maintenance of connectivity to provide a wide range of litter inputs and diverse habitat conditions.

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