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Breakdown and Invertebrate Colonization of Dead Wood in Wetland, Upland, and River Habitats

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Breakdown and invertebrate colonization of dead wood in wetland, upland, and river habitats

A. Braccia and D.P. Batzer

Abstract: Breakdown of woody debris in river and upland habitats as well as the interactions between wood and invertebrates have been well described. Studies of wood in wetlands are rare, and far less is known about breakdown and invertebrate use of wood in these transitional habitats. This study experimentally assessed breakdown and invertebrate colonization of wood in a floodplain wetland and directly related patterns in the wetland to adjacent river and upland habitats. Over a 2.7 year period, we monitored breakdown and invertebrate presence in 10 cm diameter × 150 cm long sweetgum (*Liquidambar styraciflua* L.) logs in a floodplain wetland (*n* = 8), river (*n* = 5), and upland (*n* = 4) habitat. Mass loss, decay condition change, and C/N ratios of wetland wood more closely resembled upland than river wood. The overall invertebrate assemblage associated with wetland wood was also more similar to that associated with upland than river wood. Breakdown and invertebrate colonization of wood in the floodplain wetland shared more characteristics with upland than river wood, perhaps because of the seasonal nature of flooding in the wetland. However, the ecology of wood in wetlands also had unique characteristics compared with either the uplands or the river.

Résumé : La décomposition des débris ligneux dans les habitats riverains et secs a été bien décrite ainsi que les interactions entre les débris ligneux et les invertébrés. Les études portant sur les débris ligneux dans les zones humides sont rares et leur décomposition ainsi que leur utilisation par les invertébrés dans ces habitats de transition sont beaucoup moins connues. La décomposition des débris ligneux et leur colonisation par les invertébrés dans les zones humides sur une plaine inondable ont été étudiées de façon expérimentale et reliées directement à la situation dans les habitats riverains et secs adjacents. Sur une période de 2,7 ans, nous avons suivi la décomposition et la présence des invertébrés dans des billes de liquidambar d'Amérique (*Liquidambar styraciflua* L.) de 10 cm de diamètre × 150 cm de longueur dans des habitats de zones humides sur une plaine inondable (*n* = 8), des habitats riverains (*n* = 5) et des habitats secs (*n* = 4). La perte de masse, les changements dans l'état de décomposition et le rapport C/N des débris ligneux dans les zones humides se rapprochaient davantage de ce qui a été observé dans les zones sèches que dans les zones riveraines. L'assemblage global des invertébrés associés aux débris ligneux dans les zones humides était également plus semblable à celui qui a été observé dans les zones sèches que dans les zones riveraines. La décomposition des débris ligneux et leur colonisation par les invertébrés dans les zones humides sur une plaine inondable partageaient plus de caractéristiques avec la situation des zones sèches qu'avec celle des zones riveraines, peut-être à cause de la nature saisonnière des inondations dans les zones humides. Cependant, l'écologie des débris ligneux dans les zones humides avait également des caractéristiques propres comparativement à celles des zones riveraines ou sèches.

[Traduit par la Rédaction]

Introduction

Wood debris is an important ecological resource in many habitats. Breakdown rates of wood have been well described in forests (see review by Mackensen et al. 2003) and streams (Diez et al. 2002; Spanhoff and Meyer 2004), and wood breakdown in upland forests can be more rapid than in streams or rivers (Dahlström and Nilsson 2006). Recently, researchers have begun to address wood breakdown in wetlands. In a Canadian peatland, Moore et al. (2005) found that wood breakdown rates could be very slow, whereas in a Florida mangrove swamp, Romero et al. (2005) found that wood breakdown rates could be relatively rapid, at least when the wood was on the sediment surface.

Wood is an especially important resource for invertebrates (food, habitat), and in turn invertebrates may play important roles in the breakdown process of wood. Again the relationships between invertebrates and wood are well established for uplands and streams but are just beginning to be explored for wetlands (Braccia and Batzer 2001; Lockaby et al. 2002). In uplands, wood can benefit invertebrates by serving as food (Schuurman 2005), habitat (Evans et al. 2003), or both (Vanderwel et al. 2006). In streams, wood primarily benefits invertebrates by serving as habitat or as a substrate for biofilms consumed by invertebrates (Hax and Golladay 1993; Drury and Kelso 2000; Johnson et al. 2003; Spanhoff et al. 2006). A subset of aquatic invertebrates are xylophages (Anderson et al. 1978; Hoffmann and Hering 2000). However, in wetlands, the nature of the relationship between invertebrates and wood is largely unknown (Braccia and Batzer 2001; Lockaby et al. 2002).

Direct comparisons among upland, aquatic, and wetland

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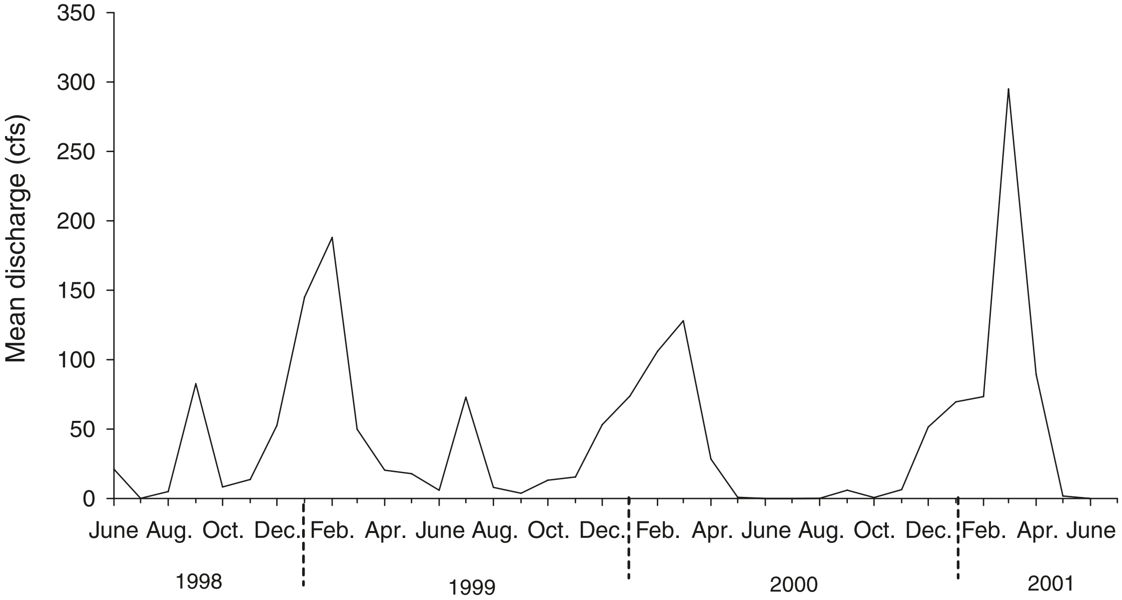
Fig. 1. Hydrograph of the lower Coosawhatchie River over the study period from September 1998 to April 2001. Data are from a United States Geological Survey gauge (02176500) near the study area.



habitats are rare. In a Swedish forest, Dahlström and Nilsson (2006) compared characteristics and volumes of wood in forests and embedded streams. They found that the same kinds of wood dominated both habitat types (i.e., inputs were the same), but because of slower breakdown rates in streams, density of wood was greater in streams than in uplands. Moore et al. (2005) contrasted wood breakdown in an upland and peatland site, and found that decay of wood embedded in peat was much slower than in the upland. Thorp et al. (1985) contrasted invertebrate colonization of submerged wood in a cypress–tupelo swamp and an inflow stream and found that wood in the stream supported a more diverse and productive invertebrate community.

In this study, we introduced similar logs to adjacent floodplain wetland, upland, and river habitats and then monitored wood breakdown and invertebrate colonization for 32 months. This experiment directly assessed similarities and differences in the ecological dynamics of wood among different habitat types and permitted us to frame processes in poorly studied wetlands to those in better known upland and riverine ecosystems. We hypothesized that wood breakdown in the wetland would exceed that in the river but might be either faster or slower than in the upland, depending on whether periodic wetting of the wetland wood accelerated or slowed breakdown by microbes, fungi, and invertebrates. In terms of invertebrates, we anticipated that very different communities would colonize wood in the wetland, upland, and river habitats, but overall invertebrate biomass might be similar among habitats. In addition, we suspected xylophagous invertebrates would be most abundant in upland wood and least abundant in river wood but had no basis for predicting their relative abundance in wetland wood.

Methods

Study site

Study sites were located along the Coosawhatchie River, a fourth order blackwater river that drains an approximately 1000 km^2 watershed on the Atlantic Coastal Plain of South Carolina, USA. We worked along the lower reaches of this river in Jasper County (32°33′N, 80°54′W), where because of the very flat topography an extensive floodplain exists that floods seasonally (winter and spring of most years, see Fig. 1). At this location, the Coosawhatchie floodplain is a bottomland hardwood forest (Sharitz and Mitsch 1993), and common trees included sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), swamp tupelo (*Nyssa sylvatica* Marsh. var. *biflora* (Walter) Sarg.), water tupelo (*Nyssa aquatica* L.), bald cypress (*Taxodium distichum* (L.) Rich.), and various oaks (*Quercus* spp.). Adjacent uplands included mixed hardwood (sweetgum, oaks) and pine (*Pinus* spp.) forest and managed pine plantations. In this area, we chose habitats representative of (*i*) forested floodplain wetland, (*ii*) hardwood forest upland, and (*iii*) river channel to conduct our experiment. Because habitat types were not replicated, caution should be exercised in extrapolating our results generally to floodplain, upland, or river habitats.

Experimental design

We cut logs (10 cm diameter) of live sweetgum, a tree species common to both the uplands and floodplains, into 150 cm lengths in August 1998. Logs were transported to study sites in early September when the floodplain was dry. An eye-bolt was inserted into one end of each log, and lengths of steel cable were attached to these bolts. In the floodplain wetland habitat, we randomly selected eight of the logs, and secured them to steel posts anchored into the wetland soil using cables. Cinder blocks were attached with nylon ties to four of the logs to ensure submersion during floods, whereas the other four could float. Although we had anticipated that submersion or flotation might be important (Braccia and Batzer 2001), we did not detect any difference in this study, and thus consider all eight logs as replicates. In the upland forest habitat, we tethered another four logs

Table 1. Wood decay classification scheme used for this study (adapted from Maser and Trappe 1984; Robison and Beschta 1990).

Decay class	Bark	Core wood colour	Log shape and texture
Class 1	Attached tightly	Original	Round, no abrasion
Class 2	Attached loosely	Original	Round, no abrasion
Class 3	Absent	Some darkening	Round, smooth, no abrasions
Class 4	Absent	Dark	Round to oval, with abrasions
Class 5	Absent	Dark	Irregular, with many abrasions

(randomly selected) to metal posts. In both the wetland and upland habitats, we ensured that the bottom surfaces of all logs were in full contact with the litter layer. In the river habitat, we attached another five logs to cinder blocks and sunk them to the river bottom, securing each to a tree trunk on the river's bank using cables. This area of the river had low flows because of very flat terrain and proximity to the bank. Because of murky water, we could not assess precise positions of submerged river logs relative to the bottom substrate.

To get an initial sample for each of the 17 logs, we revisited the site 60 days later in November 1998, after the logs had sufficient time to naturally dry (in the upland and wetland habitats) or leach (in the river habitat) and take on the characteristics of typical newly introduced woody debris. A plastic bag (3.8 L) was placed over the free end of each log and then the outer 10 cm of the log was removed with a hand saw, with the cut section being retained in the bag. Wood samples were preserved in alcohol and transported to the laboratory for processing. In the laboratory, each wood sample was categorized into one of five standard decay classes (Table 1) and then gently washed and scrubbed over a 250 μm mesh sieve to collect any invertebrates from the surface bark or wood. Washed wood samples were then measured for volume using water displacement. A representative pie-wedge of each log section, approximately 5 cm high × 3–4 cm base × 1 cm thick (including both core wood and bark), was then collected and both the dry mass (oven-dried at 60 °C for >72 h) and ash-free dry-mass (AFDM; ashed at 500 °C) of the wedge were determined. The remainder of the 10 cm wood section was split with a hammer and wedge and inspected for invertebrates residing in the interior of the wood. Finally, the dry mass of these residual wood pieces (3–7 days of oven-rying) and AFDM of the entire 10 cm section of wood extrapolated from the assessment of the small wedge subsample were determined. Wood bulk density was expressed as grams of AFDM per cubic centimetre of wood.

Invertebrates collected from the wood were preserved in alcohol, identified mostly to the genus level (Peterson 1960; Arnett 1968; Borror et al. 1989; Pennak 1989; Stehr 1991; Thorp and Covich 1991; Merritt and Cummins 1996), enumerated, and measured to the nearest millimetre. Published length–mass regressions were used to calculate invertebrate biomass (Hodar 1996; Benke et al. 1999). Invertebrate biomass and density were reported as AFDM mass or individuals per cubic metre of wood.

The whole procedure was repeated in April 1999 (210 days after wood introduction), November 1999 (390 days), April 2000 (600 days), and April 2001 (960 days). April was selected for sampling because that was the time when the wetland area was most likely to be flooded, and November was near the end of the typical floodplain dry period (Fig. 1). Although sampling over time permitted us to describe temporal trajectories of wood breakdown, we acknowledge that removing the ends of logs periodically could have influenced results (newly exposed wood was typically less decayed than the pieces being removed). For the last April 2001 sample, we powdered small subsamples of core wood and bark separately from each of the 17 wood sections and sent those samples to an analytical laboratory at the USDA Forest Service, Center for Forested Wetland Research in Charleston, South Carolina, where C/N ratios were determined. This metric was used as a measure of relative nutritional quality of core wood and bark among logs.

Statistical analyses

The November 1998 sample served as our initial measure of the wood. Although some negligible loss in nonwater mass might have occurred since the logs were cut, we designated logs on this date as now being woody debris and having 100% of their dry masses. We then expressed subsequent AFDM loss for each log as a proportion of its baseline mass. We assumed that any increase in mass from the baseline was due to measurement error and assigned a 100% value to such samples. Decay coefficients (k) were determined by calculating ln(mass final / mass initial) and then converting rates to a daily mass loss. We examined proportional mass loss of wood over the study period (November 1998 – April 2001) for each habitat type (wetland, upland, river) using simple regression and then contrasted relative mass loss among habitats using analysis of covariance (ANCOVA) followed by Scheffe multiple range tests. Time (days) served as the covariate in the ANCOVA. Proportional values were arcsin-transformed prior to analyses, to normalize data. We repeated this analysis with the ln-transformed data used to calculate k values, but we do not present those results because they were very similar to those using the actual proportions.

To assess whether wood decay condition changed temporally in each habitat type and whether rates of change differed among habitats, we simply viewed those data graphically. To supplement interpretations from inspection, we then mirrored the regression and ANCOVA approaches used to assess wood mass loss, acknowledging that the 1–5 scale for decay condition violated the normality assumption. C/N ratios of core wood and bark samples collected in April 2001 were contrasted separately among habitat types using one-way ANOVA followed by Scheffe tests.

Relative abundances of invertebrates in the overall assemblages associated with wetland, upland, and river habi-

Fig. 2. Wood breakdown of wetland, upland, and river logs from November 1998 through to April 2001: (A) mass loss and (B) decay state (see Table 1). All logs were 10 cm in diameter and 150 cm long from sweetgum (*Liquidambar styraciflua*) freshly cut in September 1998 and transferred to the study site. Mass loss (A) declined over the 2.7 year period of study for wetland logs (r^2 = 0.30, p = 0.0003, k = 0.00021% AFDM·day^{-1}) and upland logs (r^2 = 0.254, p = 0.0234, k = 0.00033% ADFM·day^{-1}), but not for river logs (r^2 = 0.070, p = 0.2061). Decay condition (B) also changed markedly in both upland logs (r^2 = 0.778, p < 0.0001) and wetland logs (r^2 = 0.593, p < 0.0001) but only modestly in river logs (r^2 = 0.216, p = 0.0193).

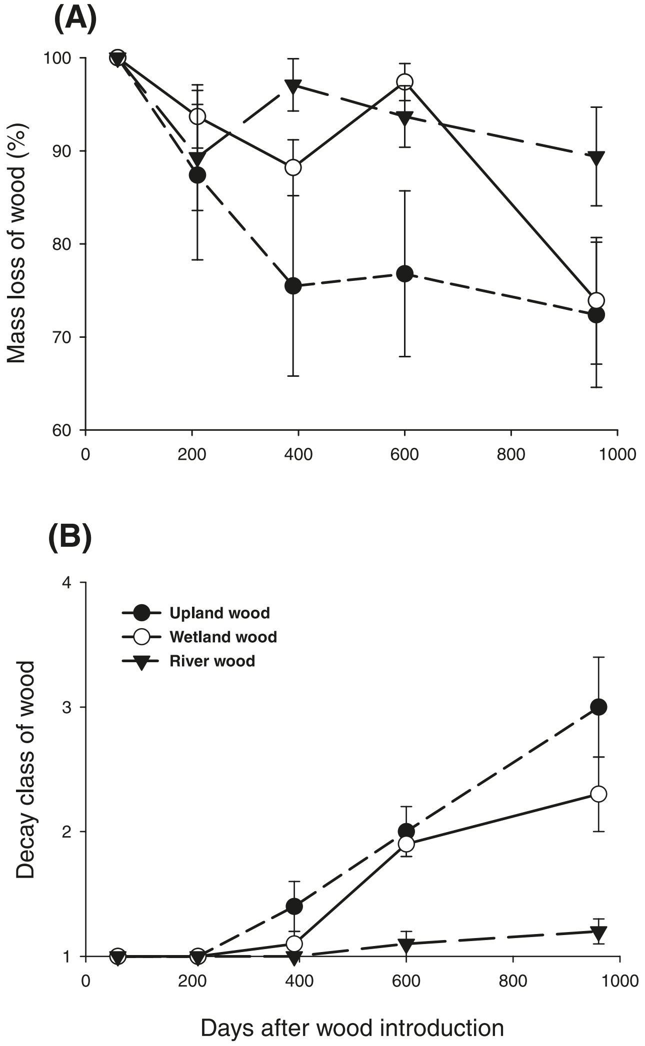
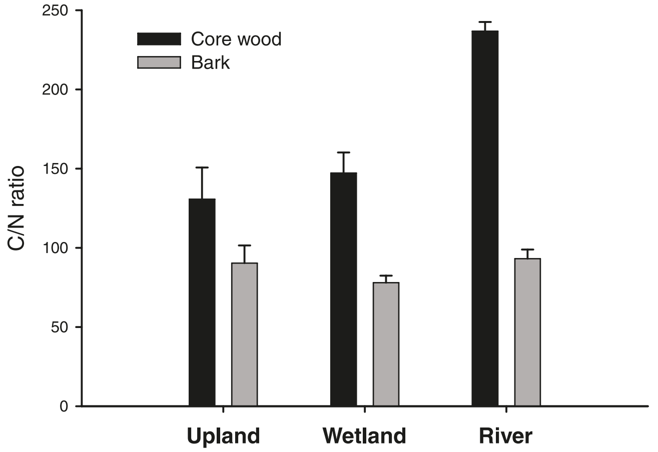


Fig. 3. C/N ratios of core wood and bark from sweetgum logs after 2.7 years of wood breakdown in upland, wetland, and river habitats (p = 0.2030).



tats were assessed using detrended correspondence analysis (DCA). This multivariate method simultaneously ordinates species abundances and samples along axes based on maximum correlations (ter Braak 1995), so that samples with similar taxa are closer together in ordination space. To explicitly test overall invertebrate community differences among wetland, upland, and river habitats (both abundance and biomass), we used ANOSIM (analysis of similarity, Primer version 6 software, Plymouth, UK) with a Bray–Curtis distance measure. To assess patterns in total invertebrate biomass regardless of taxon, we compared relative invertebrate biomass per volume of wood among habitats on each sample date using one-way ANOVA followed by Scheffe tests and compared patterns over the entire period of study using ANCOVA followed by Scheffe tests. We expressed invertebrate biomass in terms of wood volume because, unlike wood mass, the volume of wood samples in all habitats did not change appreciably from the beginning to the end of the study.

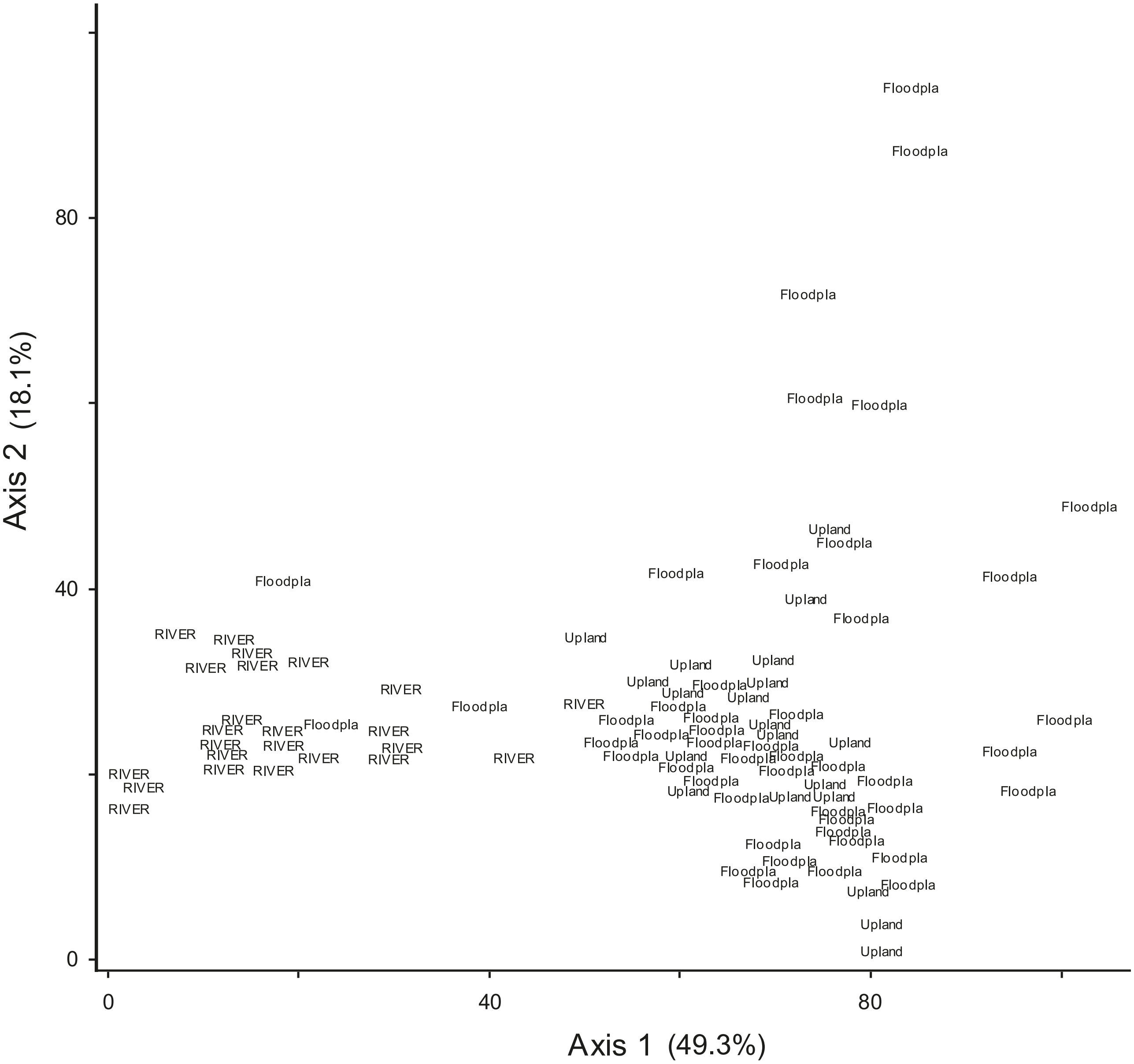
Results

Wood breakdown

The mass of wood remaining as a proportion of each log's original mass declined over the 2.7 period of study for wetland logs and upland logs, but not for river logs (Fig. 2A). Post-hoc tests indicated that breakdown rate was most rapid in upland logs, marginally slower in wetland logs (p = 0.0496), and significantly slower in river logs (p = 0.0084). Breakdown rates in wetland and river logs did not differ. Breakdown rates for wetland and river logs on occasion showed modest, yet implausible, mass increases; these anomalies probably resulted from a combination of natural variation within the logs plus processing and measurement error. Analyses of wood mass loss were further complicated by the fact that temporal patterns for upland and wetland logs might not be linear (Fig. 2A). Mass loss in upland logs was initially rapid and then slowed, whereas mass loss in wetland logs was initially slow and then accelerated (however, the interaction term for the ANCOVA was not significant; p = 0.1599).

Analyses of wood decay condition supported the results for wood mass loss. A graphical depiction of wood decay condition (Fig. 2B) in the wetland, upland, and river logs over the study period clearly shows that wetland and upland wood conditions changed temporally and that change in these two habitats was very similar. The graph also shows that condition change in the river logs was negligible and much slower than in either the upland or wetland logs. Supplemental regression testing indicated that the patterns observed were not likely due to chance (Fig. 2B), and post-hoc tests indicated that condition change in wetland and up-

Fig. 4. Detrended correspondence analysis of invertebrate taxa composition (abundance) associated with river logs (n = 24), floodplain wetland logs (n = 48), and upland logs (n = 20) in species space. The greatest proportion of variation in the species data set was explained by axis 1 (eigenvalue = 49.3). Eigenvalues for axes 2 and 3 were 18.1 and 16.3, respectively. Individual samples are represented by the labels “river,” “floodpla,” and “upland.” ANOSIM (Bray–Curtis distance measure of relative abundances) indicated that communities in the river were much different than in the upland (R = 0.823, p < 0.001) or floodplain wetland (R = 0.704, p < 0.001), but communities in the floodplain wetland and upland were only marginally different (R = 0.076, p = 0.08).



land logs was similar, but both the wetland and upland logs changed more than did the river logs.

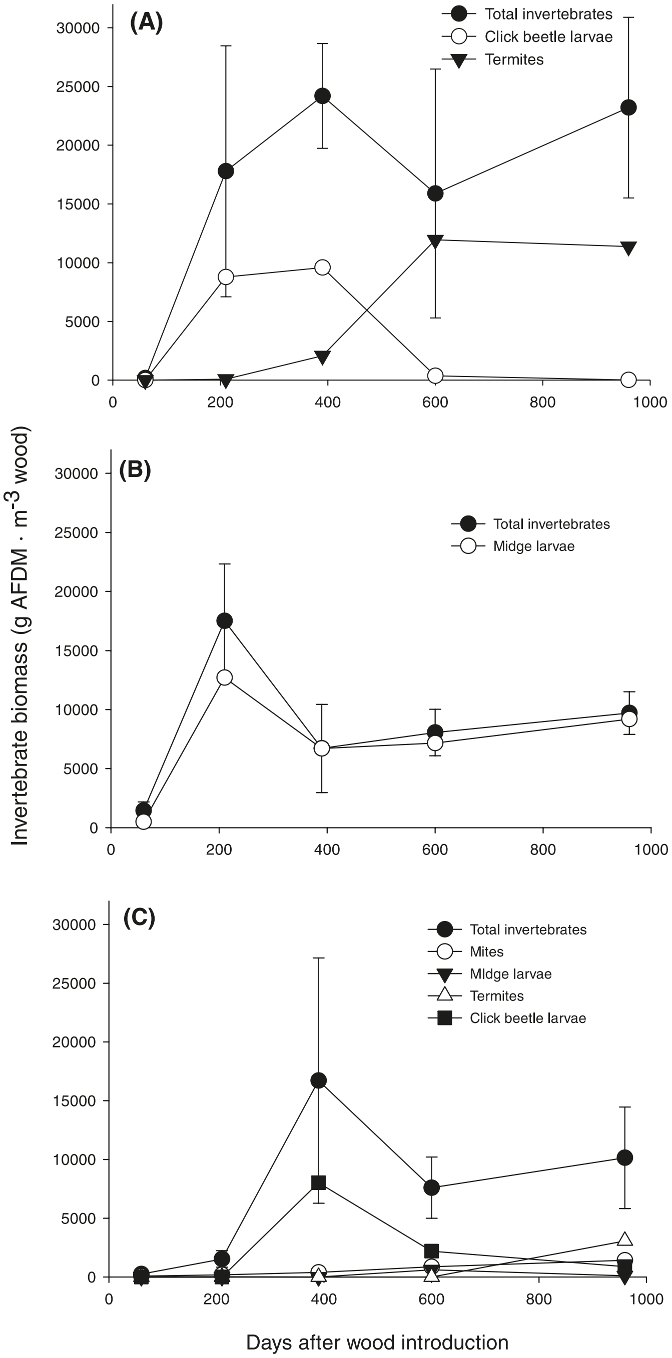
At the study’s end, C/N ratios in core wood from upland and wetland logs were similar, but ratios in both were lower than in core wood from river logs (Fig. 3). C/N ratios of surficial bark were much lower than for core wood, but ratios for bark did not differ among wetland, upland, or river logs (Fig. 3).

Invertebrates associated with wood

Based on the graphical display from DCA, the invertebrate fauna on river logs was distinctly different from that on upland logs; river samples formed a distinct cluster on the bottom left side of the ordination, whereas upland samples grouped on the bottom right side of the ordination (Fig. 4). The invertebrate fauna from wetland logs was more similar to the fauna from upland logs than to the fauna from river logs (i.e., most wetland samples clustered with upland samples on the bottom right of the ordination). However, the fauna from wetland logs was more variable than the fauna from either the river or upland logs. A few wetland samples were associated with river samples, whereas several formed a small, distinct cluster on the top right of the ordination (Fig. 4). Results from ANOSIM supported these patterns (see caption for Fig. 4).

Although many invertebrate families inhabited the 17

Fig. 5. Invertebrate biomass on or in (A) upland logs, (B) river logs, and (C) wetland logs from November 1998 through April 2001.



logs, only click beetle larvae (Coleoptera: Elateridae), termites (Isoptera: Rhinotermidae), midge larvae (Diptera: Chironomidae), and (or) mites (Acarina: Oribatidae) contributed substantially to the total invertebrate biomass. In upland logs, invertebrate biomass was dominated by click beetle larvae in the first year, and thereafter by termites (Fig. 5A). In river logs, invertebrate biomass was overwhelmingly dominated by midge larvae for the duration of study (Fig. 5B). The invertebrate fauna in wetland logs supported a mixture of upland and aquatic organisms, with the bulk of the biomass comprising click beetle larvae, but with termites (up to 30%) and midges (up to 8%) contributing a substantial portion of total biomass for at least one sampling period (Fig. 5C). Wetland logs were unique from logs elsewhere, in that mites were very common (with densities as high as 150 000 mites·m^{-3} of wood). Despite their small body sizes, these density levels resulted in mites contributing a substantial (>10%) portion of the overall biomass in wetland logs on several sampling dates (Fig. 5C).

Total biomass of invertebrates associated with wood differed somewhat between wetland and river logs (p = 0.0278; Fig. 5). Invertebrate biomass from upland logs was similar to biomass from either wetland or river logs. The difference in invertebrate biomass between wetland and river logs developed because river logs were colonized more rapidly. On the initial 60 day sample in November 1998 (p = 0.0329) and the 210 day sample in April 1999 (p = 0.0401), invertebrate biomass on river logs was greater than on wetland logs. However, thereafter, we did not detect any differences in invertebrate biomass among wetland, river, or upland logs.

Discussion

Breakdown of logs in the Coosawhatchie floodplain shared more characteristics with upland logs than with river logs. The conditions of both upland and wetland logs changed similarly over the study period, and by its end, bark on most logs in these habitats was either loose or had fallen off and the core wood was disintegrating. Fungi were commonly observed on both upland and wetland logs. In contrast, bark on most river logs remained firmly attached to logs even after 3 years, and core wood had not changed appreciably. Fungi were not obvious. Mass loss of wetland logs was intermediate between upland and river logs. In the initial years, mass loss of wetland logs was slow, as it was for river logs, whereas mass loss was rapid in upland logs. During the later period of study, patterns changed. Mass loss of upland logs slowed, whereas it accelerated in wetland logs, and by the end of the study, wetland and upland logs were very similar in bulk density. Mass loss of river logs was slow for the duration of study. C/N ratios of core wood in upland and wetland logs were similar, with ratios for both being lower than for river logs; this suggests that core wood was a more valuable food resource for invertebrates in upland and wetland logs than for invertebrates in river logs. However, nutritional value of bark was similarly high across all habitats. Because we only measured C/N ratios once, we cannot assess whether patterns varied temporally (as they did for other wood characteristics).

In terms of invertebrate use, wetland logs shared similarities with both upland and river logs, but were in some ways unique. The click beetle larvae and termites that dominated upland logs and the midge larvae that dominated river logs each made up a substantial portion of the biomass on wetland logs. However, overall the invertebrate community in the wetland logs tended to more closely resemble an upland than an aquatic fauna (see also Braccia and Batzer 2001). Yet, although termites dominated the biomass in every upland log, we found these invertebrates in only two of the eight wetland logs (and one had only low termite numbers).

In a previous descriptive study of 125 pieces of natural woody debris at the Coosawhatchie floodplain, in various states of decay, we found termites in only two pieces of wood (Braccia and Batzer 2001). Perhaps intermittent flooding deters termite colonization. The use of wetland logs by large numbers of mites was unique compared with either upland or river logs. Lockaby et al. (2002) also found large numbers of mites associated with wetland wood in the Atchafalaya River basin of Louisiana, and thus mites might be a generally important resident of woody debris in wetlands of the southeastern USA. In terms of overall resource use by invertebrates, wetland logs also more closely mimicked upland logs than river logs. River logs were largely two-dimensional surficial resources for invertebrates, whereas wetland and upland logs were a resource that occurred in three dimensions, with both bark and core wood being important. It was noteworthy that, despite invertebrates being restricted to a relatively small portion of river logs, overall invertebrate biomass on this material equaled or exceeded the biomass on upland or wetland logs.

In the upland logs of this study, termites were probably important to wood breakdown. In wetland logs, the influence of invertebrates on wood breakdown was unclear. Mites and those termites that occurred might have contributed to wood breakdown, and biomass of both of these organisms peaked when breakdown rates accelerated during the final year of study. However, whether the oribatid mites in this study could directly consume wood is not known; most of the other invertebrates in wetland wood were not xylophages. In the river logs, we saw little evidence of invertebrate boring into the core wood, and most midges were associated with bark; thus, invertebrates probably contributed minimally to breakdown of river logs. The lack of aquatic xylophages often found on wood in streams and rivers elsewhere (e.g., McKie and Cranston 2001) may reflect the relatively stagnant conditions of the coastal plain river used for this study.

Wetlands are viewed by many as a subset of aquatic habitats, and paradigms developed for rivers, streams, or lakes are frequently adapted for wetlands (Thorp et al. 1985; Batzer et al. 2006). However, in terms of breakdown of woody debris and invertebrate use of the resource, the Coosawhatchie floodplain functioned more like an upland than like an aquatic habitat. In tidal mangrove wetlands, wood on sediment surfaces also breaks down at rates comparable to rates in uplands (Romero et al. 2005). In contrast, in northern peatlands, Moore et al. (2005) found that wood buried in peat decayed much more slowly in the peatland than in wood in adjacent uplands, with decay coefficients for the wetland wood being comparable to those for aquatic systems. However, wood on the peatland surface had highly variable decay rates. In a permanently flooded swamp, invertebrate communities colonizing wood were dominated by aquatic forms (Thorp et al. 1985). In terms of woody debris dynamics, perhaps intermittently flooded wetlands, such as the Coosawhatchie floodplain, function more like uplands, whereas permanently flooded wetlands may function more like aquatic habitats.

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