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ARTICLE

Variation in Invertebrate and Fish Communities Across Floodplain Ecotones of the Altamaha and Savannah Rivers

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Abstract In floodplains of large rivers, different ecotones—zones of transition between adjacent ecological systems—develop where the river and uplands interact with the floodplain. Unique communities of invertebrates and fish may develop in each of these ecotones and in the floodplain interior. In our study, we sampled the river-floodplain ecotone, the upland-floodplain ecotone, and the interior of floodplains of the Altamaha and Savannah Rivers, Georgia, USA to assess how water quality, invertebrate community structure, total invertebrate abundance and biomass, and fish abundance and species richness varied across floodplains. In terms of water quality, electrical conductivity was greatest in the river-floodplain ecotone, while pH and temperature did not vary among sites. Nonmetric multidimensional scaling ordination indicated that overall invertebrate community composition across the floodplain was similar, and was dominated by wetland organisms that likely reside permanently on the floodplain. Total abundance and biomass of invertebrates was greater in the river-floodplain ecotone than the upland-floodplain ecotone, with levels in the floodplain interior being intermediary. Fish abundance and species richness was greater in the river-floodplain ecotone than other sites. Managers should consider lateral variation in invertebrate and fish assemblages across floodplains when planning management of river-floodplain ecosystems.

Keywords Community structure · Connectivity · Ecotonal interaction · Hydrology · Macroinvertebrates

Introduction

The flood-pulse concept as proposed by Junk et al. (1989) states that linkages between floodplains and river channels maintain both habitats as productive and diverse ecosystems. Flood pulses can affect suspended sediments and nutrients that flow from the river to the floodplain and organic detritus and algal biomass that flow from the floodplain to the river (Amoros and Roux 1988; Ward and Stanford 1995; Ward 1999). Many abiotic factors can change across the floodplain including nitrate, suspended solids, and small particulate organic matter (Tockner et al. 1999). In a study along the Lower Rhine and Meuse Rivers, higher concentrations of salts, nutrients, and metals were found in floodplain lakes that had more frequent and prolonged periods of floodplain inundation (Van den Brink et al. 1993). Other studies indicate that hydrologic connectivity can also influence biotic life within the floodplain (Ward et al. 1999) with greater fish abundance and species richness (Sullivan and Watzin 2009) or more diverse and productive plant communities (Bornette et al. 1998; Leyer 2006; Bayley and Guimond 2009) existing in areas with a greater connection to the river.

Anthropogenic modifications of river systems (e.g., dams, levees) can alter river-floodplain interactions. Dams

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affect over half of all large river systems of the world (Nilsson et al. 2005) with many of these dams used for hydroelectric power, flood control and water storage (Walker 1985; Dynesius and Nilsson 1994; Power et al. 1995). Dams, levees, dikes, floodwalls, and embankments limit the lateral exchange of nutrients and organic matter between the river and floodplain (Sparks 1995). Understanding how biota distributes across floodplains will permit a more complete assessment of how floodplain ecosystems will be ecologically altered by human modification.

While floodplains are often called ecotones, Wissinger (1999) maintains that for large floodplains (and for invertebrates) this label may be misleading. Rather he suggests that floodplains are unique wetland habitats onto themselves and the ecotones present are between the river and floodplain and between the upland and floodplain. As indicated above, the river-floodplain ecotone has been reasonably well studied for fish and plants, but less so for invertebrates (but see Gladden and Smock 1990; Smock 1994; Gallardo et al. 2008). Interactions across the upland-floodplain ecotone have to our knowledge never been addressed, at least for invertebrates. Our study tests the validity of Wissinger's (1999) hypothesis in the large floodplains of two major Southeastern US rivers. We examined invertebrate and fish communities in river-floodplain ecotones, upland-floodplain ecotones, and the interior of the floodplains. We predicted that organisms of riverine origin would dominate the river-floodplain ecotones, organisms of terrestrial origin would dominate the upland-floodplain ecotones, and a unique wetland fauna would dominate the interior of the floodplain.

Methods

Study Rivers

Study sites were located on the floodplains of the Altamaha and Savannah Rivers. The headwaters of the Altamaha River start in north-central Georgia and flow through the Piedmont and Atlantic Coastal Plain physiogeographic regions before emptying into the Atlantic Ocean. The major tributaries of the Altamaha River are the Oconee and Ocmulgee Rivers (Fig. 1). Currently, while some dams exist on these tributaries, they are not managed for flood control and flood pulses downstream in the Altamaha are natural (Fig. 2). The Savannah River also flows through the Piedmont and Atlantic Coastal Plain and some of the headwaters originate in the Blue Ridge Mountains (Fig. 1). Flows in the Savannah River are heavily regulated by three large dams and reservoirs, built primarily for flood control to prevent downstream flooding, and flood pulses are muted (Fig. 2). Recently, the US Army Corps of Engineers has initiated releases of water from the lowest dam on the Savannah River (J. Strom Thurmond Dam) to better mimic natural flood pulses, but no pulses were released during the two study years.

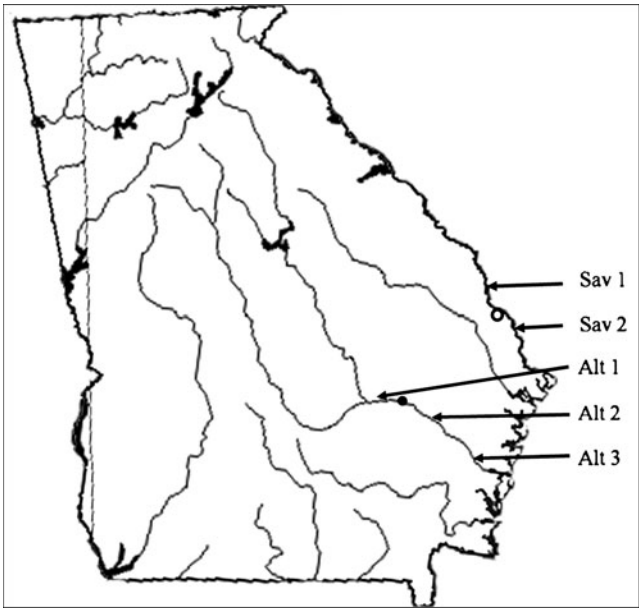

Fig. 1 Map indicating the five study locations along the floodplains of the Altamaha (Alt) and Savannah (Sav) Rivers. The circles are USGS Gauge Stations where hydrological data was collected, USGS gauge 02225000, near Baxley, Georgia (*closed*) and Savannah River, USGS gauge 02198500, near Cylo, Georgia (*open*)

Floodplain Locations

We selected three locations along the floodplain of the Altamaha River and two along the floodplain of the Savannah River (Fig. 1; Table 1). The Altamaha 1 location was just downstream of the convergence of the Ocmulgee and Oconee Rivers in Bullard Creek Wildlife Management Area (WMA). The Altamaha 2 location was further downstream in the Big Hammock WMA. The Altamaha 3 location was on private lands just above the upper extent of tidal influence. The Savannah 1 location was in Georgia's Tuckahoe WMA, and the Savannah 2 location was in South Carolina's Webb WMA, again just above the upper extent of tidal influence. Tree communities on both floodplain forests were similar, with the dominant trees being *Nyssa aquatic* (water tupelo), *Quercus laurifolia* (laurel oak), *Liquidambar styraciflua* (American sweetgum), and *Quercus lyrata* (overcup oak) (Lee 2008).

At each of the five locations, we chose sites in three different kinds of seasonally flooded habitat: 1) the river-floodplain ecotone, 2) the upland-floodplain ecotone, and 3) the floodplain interior. At each site, we identified low lying areas that would likely flood in winter and spring and retain water throughout the spring, even between flood

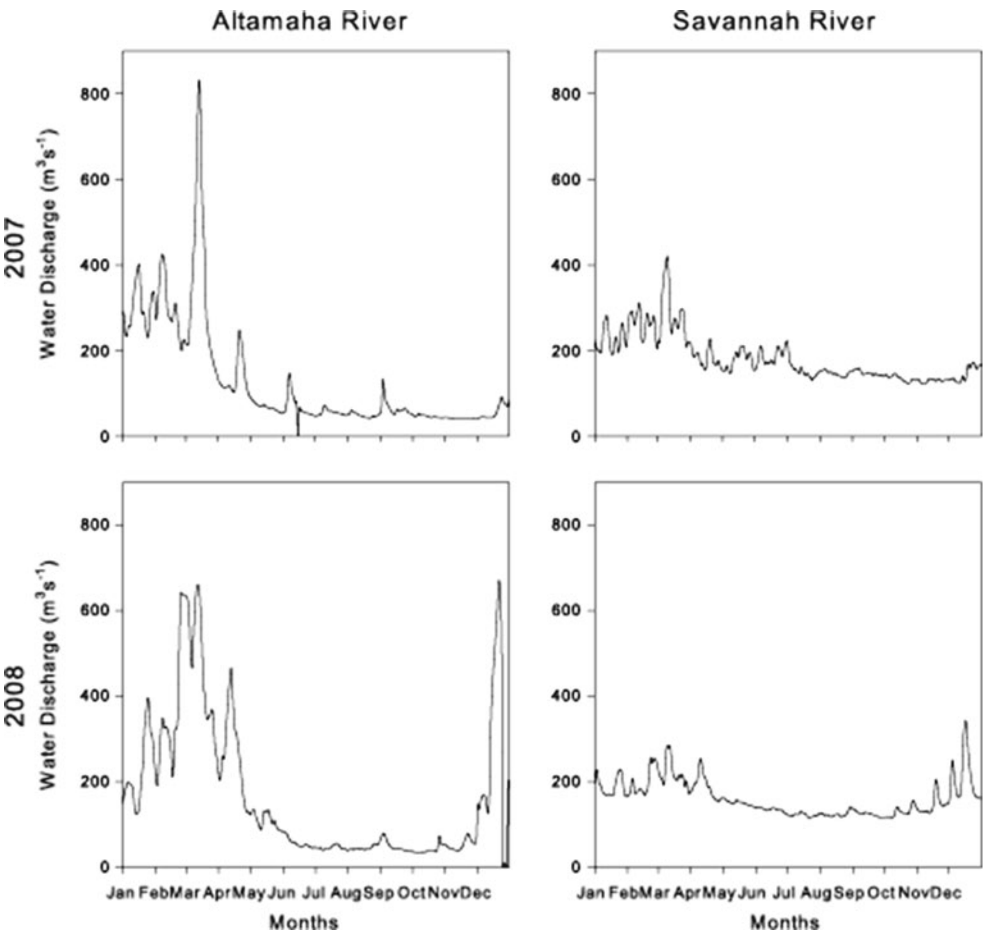

Fig. 2 Hydrographs of the Altamaha River (USGS gauge 02225000 near Baxley, Georgia) and Savannah River (USGS gauge 02198500 near Cylo, Georgia) for 2007 and 2008

events. Previous work in the system (Reese and Batzer 2007) had indicated that aquatic invertebrates (and fish) accumulated in such habitat. Among the three sites at each location, the site in the river-floodplain ecotone was always in the closest proximity to the river channel, and besides proximity was associated with a levee breach that could funnel water (and organisms) directly towards the site. (Only rarely were floods great enough to overtop the levees, and thus most flooding occurred through these breaches.) Sites in the upland-floodplain ecotone were

Table 1 Locations of 15 study sites at five locations along the Savannah and Altamaha River floodplains. Sites were partitioned into three habitats: 1) river-floodplain ecotone ("river"), 2) floodplain interior ("interior"), and 3) upland-floodplain ecotone ("upland"), with relative distances from the river channels estimated using GPS. All "upland" sites were located in floodplain wetlands immediately abutting upland habitat

Site	Habitat	GPS coordinates		Distance to river (km)
Savannah 1	River	N 32°48.116	W 81°26.042	0.06
	Interior	N 32°48.406	W 81°26.414	0.78
	Upland	N 32°48.444	W 81°26.918	1.54
Savannah 2	River	N 32°33.970	W 81°18.211	0.22
	Interior	N 32°34.093	W 81°18.145	0.57
	Upland	N 32°34.270	W 81°18.145	0.90
Altamaha 1	River	N 31°57.437	W 82°31.603	0.02
	Wetland	N 31°57.380	W 82°31.479	0.16
	Upland	N 31°57.163	W 82°31.479	0.56
Altamaha 2	River	N 31°50.718	W 82°04.328	0.10
	Interior	N 31°51.013	W 82°04.236	1.06
	Upland	N 31°52.426	W 82°05.717	1.31
Altamaha 3	River	N 31°30.597	W 81°39.422	0.06
	Interior	N 31°30.641	W 81°39.271	0.34
	Upland	N 31°41.406	W 81°47.727	5.00

located in low lying wetland habitat that was in close proximity (tens of meters) to the uplands. Sites in the floodplain interior had no obvious direct flow of water from the channel, and instead the water (and riverine organisms) that flowed through those sites undoubtedly entered the floodplain well upstream from our designated sample sites and arrived via a convoluted pathway through a large expanse of floodplain habitat. Direct distances from the river channel to each site were calculated using GPS and are listed in Table 1, but we emphasize that perpendicular distance may not always be a useful metric to quantify the relationship of any one site with either the river channel or adjacent uplands. However, among the three sites at each location, the site in the river-floodplain ecotone should be most influenced by the river and least influenced by the uplands, the site in the upland-floodplain ecotone should be most influenced by the uplands and least influenced by the river, and the site in the floodplain interior should be intermediary in terms of interaction with the river or uplands, and perhaps in terms of biota support a unique wetland fauna.

The 2007 and 2008 sampling years differed in water flow regimes. Rainfall in 2007 was only 60% of the 30-year average rainfall of approximately 150 cm (NOAA website). While rainfall in 2008 was higher, it was still 20% below average. The average monthly discharge on the Altamaha River (USGS gauge near Baxley, Georgia) ranged from 41.1 m^3/s to 367.2 m^3/s over the 2-year study (Fig. 2). The 2007 and 2008 annual river discharge of the Altamaha River was around 44% and 47%, respectively, of the 38-year average annual discharge. The average monthly discharge in the Savannah River (USGS river gauge at Cylo, Georgia) was less variable and ranged from 122.8 m^3/s to 266.7 m^3/s (USGS website) (Fig. 2). The 2007 and 2008 annual river discharge of the Savannah River was around 57% and 47%, respectively, of the 74-year average. The flood season occurred primarily from February through April (Fig. 2), and the low-lying backswamp areas where sampling was conducted first began to flood (from precipitation) in February, and remained flooded at least into April or May. Flood regimes were affected by both annual differences in river flow and local precipitation, with flooding being more extensive and longer in duration in 2008 than 2007. Despite dramatic differences in flow between the Altamaha and the Savannah Rivers (Fig. 2), all of the backswamp habitats used for this study tended to hold some water over most of the winter-spring season, with a few exceptions (see following paragraph).

Invertebrate Sampling

We sampled for invertebrates five times over the course of the study. In 2007, we sampled in late-February/early-March and then again in April. Most sites dried soon after. In 2008, water persisted longer, and we sampled three times: late-February/early-March, April, and May. On these five dates most sites were flooded, except the upland-floodplain ecotone site at Savannah 2, which was dry all of 2007, and the floodplain interior site at Altamaha 3 and upland-floodplain ecotone site at Savannah 1, which were dry in May 2008.

A Hess sampler (860 cm^2, 500 μm mesh, Wildlife Supply Co., Buffalo, NY, U.S.A.) was used to quantitatively sample invertebrates in the water column and on the benthic substrate. This device is essentially a large core, with a collection net off to one side. Four samples were collected at randomly selected locations along a representative transect through each flooded backwater swamp. However, areas that were too deep (>75 cm) to permit use of the Hess sampler could not be sampled, and during very high water periods sampling was restricted to shallower zones. The water column and substrate enclosed by the sampler were vigorously agitated manually to create a slurry and a current was created through the collection net where forced debris, sediments, and invertebrates were trapped. Previous calibration studies indicated that this method efficiently collects invertebrates from floodplains, and data can be expressed quantitatively (Henke 2005).

In the laboratory, samples were sieved into two different size classes; 1) >1 mm, and 2) <1 mm. Because sample volumes were larger due to the size of the Hess sampler and the presence of copious organic matter, samples were sub-sampled. Only a relatively small portion of an individual sample could be sieved at any one time. After sieving was complete, we then subdivided the residual homogenized material into halves or quadrats and then randomly selected one half or quadrat for examination using a stereomicroscope. This process was repeated until all of the material in a sample was processed, and then all of the sub-samples were combined into a single invertebrate sample (and the extrapolation factor was noted, e.g., 50%, 25%, to convert to m^{-2}). Invertebrates were identified to the lowest practical taxonomic level, typically to family or genus (Pennak 1989; Peckarsky et al. 1990; Stehr 1991; Thorp and Covich 1991; Epler 1996; Merritt et al. 2008), and numbers were quantified. Each invertebrate was measured to the nearest millimeter and published mass-length regressions were used to estimate biomass (Rogers et al. 1977; Pearre 1980; Sage 1982; Hodar 1996; Benke et al. 1999; Mercer et al. 2001; Sabo et al. 2002; Baumgartner and Rothhaupt 2003; Stead et al. 2003). When a published mass-length relationship could not be found for a particular invertebrate, we substituted a regression from a similarly shaped organism.

Fish

In concert with invertebrate sampling, fish communities at each site were sampled with a backpack electroshocker (Smith-Root Inc., Model 12-B POW, Vancouver, WA) on a catch-per-unit-effort basis (numbers per 750 s of actual shocking time). Fish were identified to species using keys in Page and Burr (1991), Etnier and Starnes (1993), and Mettee et al. (1996). Each sample was quantified in terms of catch per unit effort by numbers of individuals and numbers of species (i.e., species richness).

Environmental Variables

During each of the five sampling events in every flooded site, we measured pH (Oakton Model pH Testr 2, Vernon Hills, IL, USA) and conductivity and temperature (Oakton Model WD-35607-10) using portable meters. In the initial (February/March) sample of 2008, we collected water samples from each site in plastic bottles, returned the samples to the University of Georgia where total nitrogen (TN) and total phosphorus (TP) were assessed using EPA 353.2, 4500-Norg C and EPA 365.3 methods (EPA 1984; APHA 1999). Previous work in regional floodplains (Reese and Batzer 2007) indicated that TN and TP levels only tended to be high early in the flood season, and subsequently became lower and more homogenized as flooding persisted. Hence, we anticipated maximum variation among sites in the February/March sample.

Statistical Analysis

Variation among sites in the river-floodplain ecotone, the upland-floodplain ecotone, and the floodplain interior was assessed using factorial ANOVAs with the five locations, the 2 years of study, and/or individual sample dates also used as factors. Response variables included total abundance and biomass of invertebrates, abundance and biomass of individual invertebrate taxa, abundance and species richness of fish, and water pH, conductivity, and temperature (SAS 9.0, SAS Institute Inc., Cary, NC, USA). Biomass and abundance data were $\log_{10}(x + 1)$ transformed prior to analyses to homogenize variance. For TN and TP levels, which were only sampled once, only the five locations and the three habitat categories were used as factors in the ANOVAs. When a significant result was obtained, a Tukey HSD *post hoc* test was conducted to determine differences among levels of a factor.

Variation in overall community composition among the river-floodplain ecotone, the upland-floodplain ecotone, and the floodplain interior was assessed using invertebrate taxon biomass and abundance. Non-metric multidimensional scaling ordinations (NMS) (PC-ORD 5, MJM Software Design, Glenden Beach, OR) were conducted using connection regime, floodplain, and temporal change (year, season) as factors, with Bray-Curtis Similarity as the distance measure for the scaling. When a resemblance matrix suggested groupings, analysis of similarity (ANOSIM) tests (Primer 6, Primer-E Ltd., Plymouth, UK) were conducted to determine significance of the ordination scales. Indicator species analysis (PC-ORD 5) was conducted to identify representative taxa for the river-floodplain ecotone, the upland-floodplain ecotone, or the floodplain interior (Dufrene and Legendre 1997); 5000 random permutations were used for the Monte Carlo analysis to test for significance, with only significant species being reported. Because fish were not present in many collections from upland-floodplain ecotone and floodplain interior sites, among habitat-condition community composition ordination analyses were not conducted.

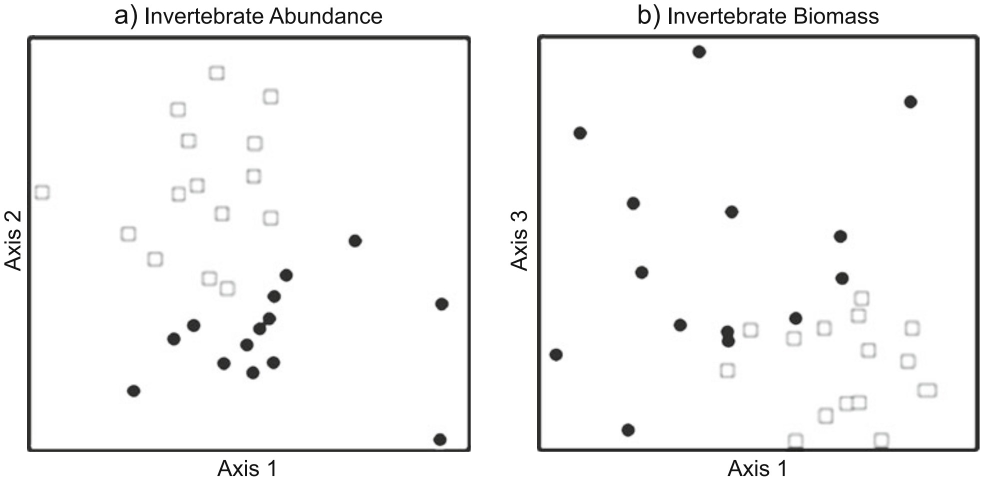

Fig. 3 NMS ordinations in terms of **a** abundance and **b** biomass for five study sites in 2007 and 2008. In each case, samples from 2007 (*solid circles*) and 2008 (*open squares*) separated into distinct groups (ANOSIM, $p<0.001$). NMS stress value for abundance analysis=15.9, and for biomass analysis=11.6

Results

Invertebrate Responses

Temporal Variation Invertebrate total abundance ($F_{1,29}$=2.3, p=0.1460) and total biomass ($F_{1,29}$=0.01, p=0.9350) did not differ between 2007 and 2008. However, in terms of community composition, NMS ordinations for community abundance (Fig. 3a) and biomass (Fig. 3b) both suggested differences between years, which was confirmed by ANOSIM (abundance Global R=0.552, p=0.0001; biomass Global R=0.405, p=0.0010). Many of the invertebrate taxa that contributed the most to overall abundance and biomass differed between 2007 and 2008. *Caecidotea* ($F_{1,29}$=8.8, p=0.0075), Scairidae ($F_{1,29}$=6.1, p=0.0222), Nematoda ($F_{1,29}$=14.7, p=0.0010), Oligochaeta ($F_{1,29}$=8.1, p=0.0095), Chironominae ($F_{1,29}$=18.0, p=0.0004), Collembola ($F_{1,29}$=19.9, p=0.0002), and Planorbidae ($F_{1,29}$=12.5, p=0.0019) had a greater abundance in 2008 than 2007. Cyclopoida ($F_{1,29}$=6.5, p=0.0191) was more abundant in 2007 than 2008. Biomass of cladocerans ($F_{1,29}$=4.4, p=0.0475), Chironominae ($F_{1,29}$=68.0, p<0.0001), Tanypodinae ($F_{2,29}$=1.4, p=0.0058), Dolichopodidae ($F_{2,29}$=6.3, p=0.0020), Cecidomyiidae ($F_{1,29}$=4.5, p=0.0468), and Oligochaeta ($F_{1,29}$=47.3, p<0.0001) was greater in 2008 than 2007.

In terms of seasonality, total abundance ($F_{4,75}$=0.5, p=0.6829) and biomass ($F_{4,75}$=2.1, p=0.0977) of invertebrates did not differ among sampling dates. However, community composition in terms of abundance varied among dates (Global R=0.254, p=0.0001), with February–March 2007 differing from April 2007, April 2008, and May 2008; February–March 2008 also differed from April 2007.

Spatial Variation Total invertebrate abundance and biomass did not differ between the Altamaha and Savannah floodplains. Total invertebrate abundance varied in the different sub-habitats within the floodplain, with sites in the river-floodplain ecotone (11,546 organisms m^{-2}) differing from sites in the upland-floodplain ecotone (2,050 organisms m^{-2}), with sites in the floodplain interior (4,857 organisms m^{-2}) being intermediate ($F_{2,75}$=3.2, p=0.0494, log(x +1) transformed data) (Fig. 4a). Total invertebrate biomass also varied among the different categories of site ($F_{2,75}$=3.4, p=0.0388) (Fig. 4b) with river-floodplain ecotone sites (3,489 mg DM m^{-2}) having greater biomass than upland-floodplain ecotone sites (586 mg DM m^{-2}); floodplain interior sites had an intermediate biomass (1,681 mg DM m^{-2}). A list of all invertebrates at each sampling site can be found in the "Electronic Appendix".

Most of the taxa that comprised >1% of the total abundance or biomass did not differ among the river-floodplain ecotone, the upland-floodplain ecotone, and the floodplain interior sites (Fig. 5). *Caecidotea* and Tanypodinae were the only individual taxa that varied among sites. *Caecidotea* abundance was greater in river-floodplain than upland-floodplain ecotones ($F_{2,29}$=3.5, p=0.0481 Tukey's HSD, p<0.05), although *Caecidotea* biomass did not differ across sites ($F_{2,29}$=2.1, p=0.1509). Tanypodinae abundance did not differ among sites ($F_{2,29}$=1.8, p=0.1942), but their biomass was greater in the upland-floodplain ecotone than either the river-floodplain ecotone or the floodplain interior ($F_{2,29}$=9.2, p=0.0014) (Fig. 5).

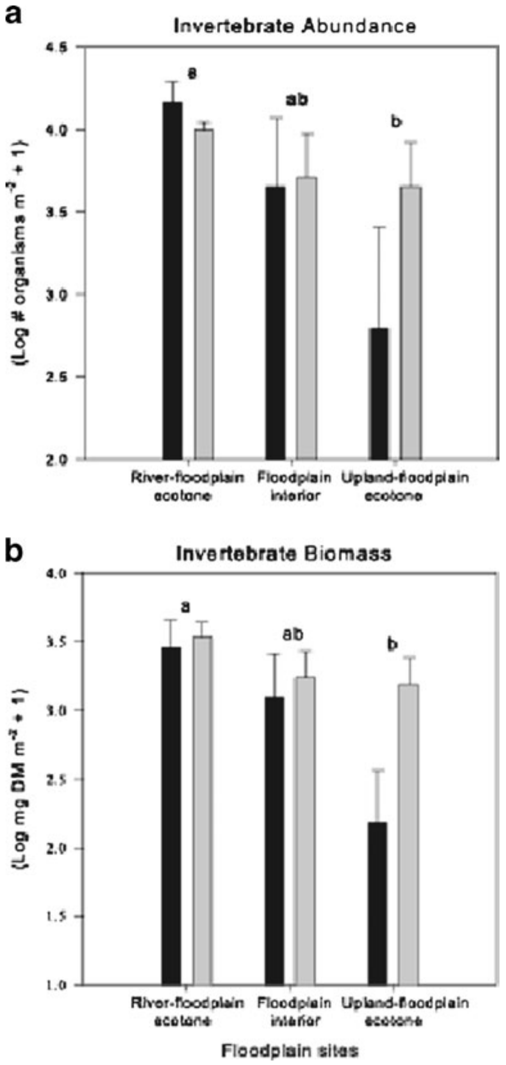

Fig. 4 The total **a** invertebrate abundance and **b** invertebrate biomass among the river-floodplain ecotones, the floodplain interiors, and upland-floodplain ecotones of the Altamaha and Savannah Rivers. The river-floodplain ecotones had the highest abundance and biomass, upland-floodplain ecotones had the lowest abundance and biomass, and the floodplain interior sites had intermediate levels. *Black bars* represent 2007 and grey bars represent 2008, with analyses including both years. *Different letters* denote significant differences among habitat types (Tukey HSD tests, p<0.05). Error bars represent±1 SE

Since community structure varied between years, we assessed differences in community composition among the site categories separately for 2007 and 2008. Whether in terms of abundance or biomass, community compositions in both 2007 and 2008 were similar among sites (2007 abundance, Global R=0.082 p=0.1840; 2008 abundance, Global R=−0.012, p=0.5580; 2007 biomass, Global R=0.025, p=0.3160; 2008 biomass Global R=0.010, p=0.3930) (Fig. 6). However, indicator species analysis showed that *Caecidotea* abundance (Monte Carlo Test, p=0.0452) and biomass (Monte Carlo Test, p=0.0488) was marginally linked to river-floodplain ecotone sites.

Fish

Fish species richness and total abundance did not vary between 2007 and 2008, or among sampling dates. However, fish species richness differed among the different sites ($F_{2,68}$=10.5, p=0.0001), with more species being found in the river-floodplain ecotone (2.88 species/sample) than either the upland-floodplain ecotone (0.57 species/sample) or floodplain interior (0.68 species/sample) (Tukey's HSD, p<0.05) (Fig. 7a). Of the 413 individual fish collected, 78% were collected in the river-floodplain ecotone, 15% at upland-floodplain ecotone sites, and 7% at floodplain interior sites ($F_{2,68}$=9.2, p=0.0003) (Fig. 7b). Modest differences in fish abundance, but not richness, existed among the five different locations (data not presented). A list of fish species caught at the river-floodplain ecotone, the upland-floodplain ecotone, and the floodplain interior is provided in Table 2.

Water Quality

Annual variation was not detected for any water quality parameter measured (Table 3). Water temperatures warmed seasonally ($F_{2,61}$=21.1, p<0.0001), and as the flood season

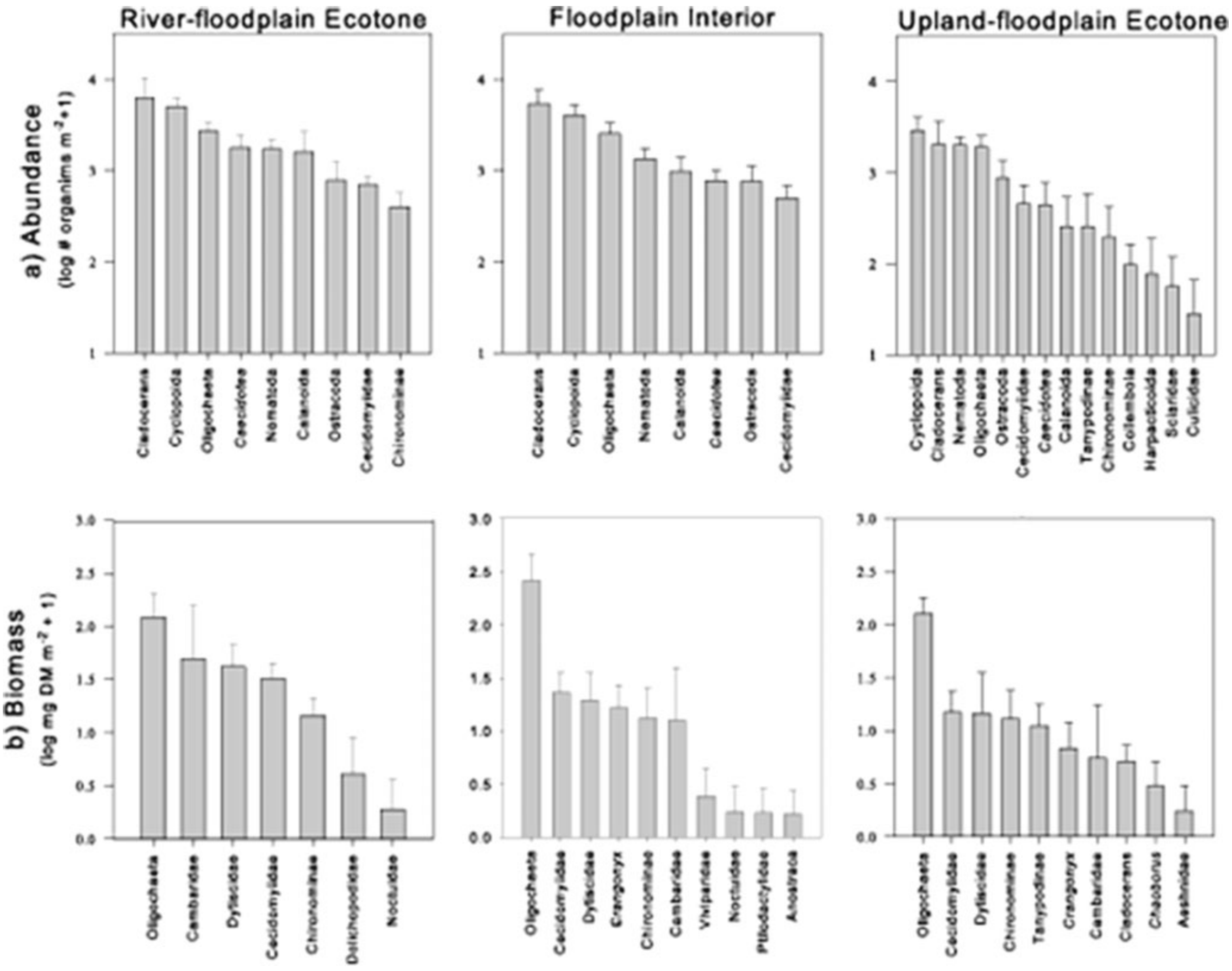

Fig. 5 The organisms that accounted for >1% of the total biomass (**a**) and abundance (**b**) in the river-floodplain ecotone, the floodplain interior, and the upland-floodplain ecotones. With the exception of *Caecidotea* (Asellidae) abundance and Tanypodinae (Chironomidae) biomass (see text) organisms did not vary among habitat types. *Error bars* represent ±1 SE

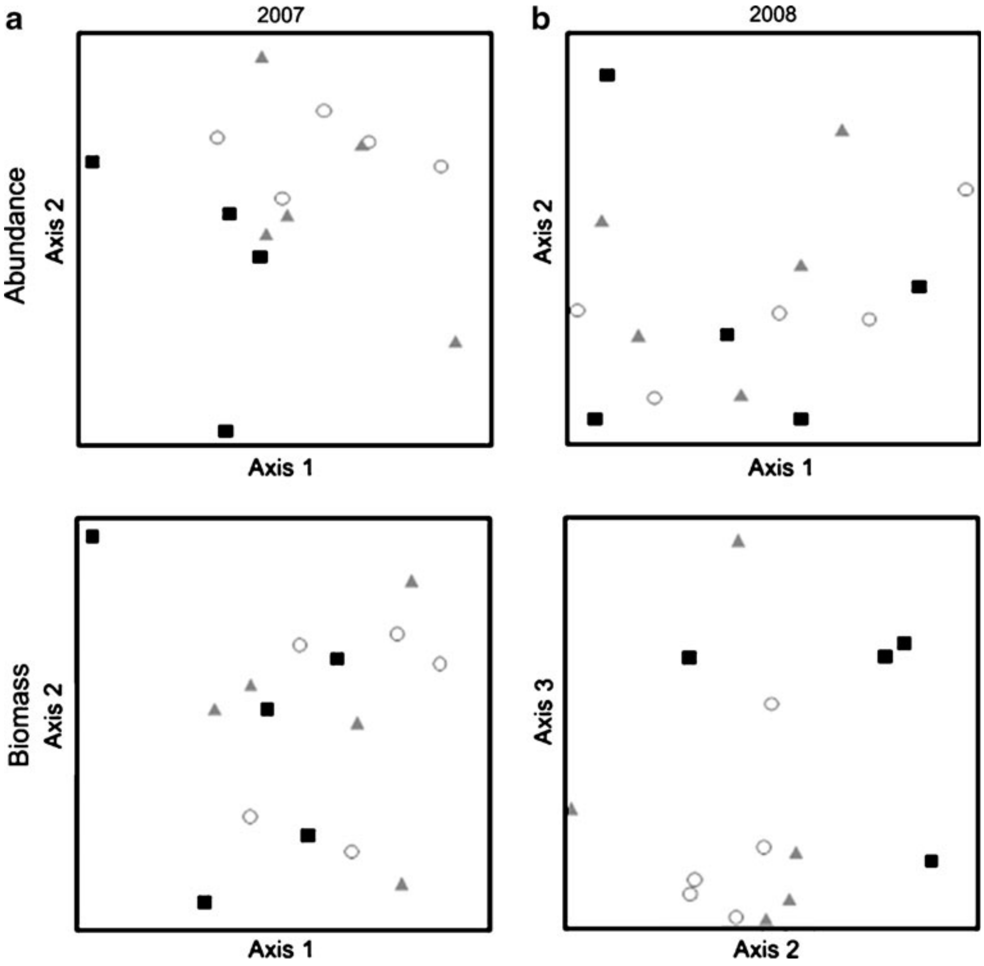

Fig. 6 NMS ordinations of the invertebrate community structure in terms of abundance (*top*) and biomass (*bottom*) in **a** 2007 and **b** 2008 of river-floodplain ecotones (*open circles*), floodplain interiors (*gray triangles*) and upland-floodplain ecotones (*black squares*)

progressed, pH increased from moderately acidic to circumneutral ($F_{2,61}=6.3$, $p=0.0036$; Table 2). Temperature, pH, TN, and TP did not vary significantly among the river-floodplain ecotone, the upland-floodplain ecotone, and the floodplain interior sites (see Table 3). However, electrical conductivity in the river-floodplain ecotone was significantly greater than either the upland-floodplain ecotone or floodplain interior ($F_{2,61}=7.1$, $p=0.0001$; Tukey HSD, $p<0.05$). Variation in water quality parameters among the five different locations was negligible (data not presented).

Discussion

Our study supports the contention of Wissinger (1999) that large floodplains support a unique invertebrate fauna, and are not simply ecotones between river channels and uplands. However, we found minimal support for his idea that unique invertebrate communities should exist in floodplain interiors versus river-floodplain and upland-floodplain ecotones (Fig. 8a). Lentic organisms (e.g., dytiscids, *Caecidotea*, cladocerans, ostracods, sphaeriids) that we predicted would be most abundant in the interior of the floodplain were found throughout the entire floodplain, and they dominated the abundance and biomass at every site (Fig. 8b). The river-floodplain ecotone did not have a high abundance or biomass of any lotic organisms (Ephemeroptera, Plecoptera, Trichoptera). In fact, we collected only three mayfly nymphs (Ephemeridae, Ephemerellidae), two caddisfly larvae (Polycentropodidae, Rhyacophilidae), and no stonefly nymphs over the entire duration of the study (Fig. 8b). Other studies in the Southeastern US (Gladden and Smock 1990; Smock 1994; Reese and Batzer 2007) have documented significant migrations of lotic invertebrates into floodplains, but the rivers associated with those events were much smaller than the Altamaha and Savannah Rivers. In contrast to smaller rivers, movements of invertebrates from large rivers into the floodplain may not be pronounced (Reese and Batzer 2007). In terms of the upland-floodplain ecotone, flood tolerant non-aquatic organisms (e.g., springtails, mites, centipedes; see Braccia and Batzer 2001; Adis and Junk 2002) were overall more common than the lotic organisms, but they occurred in similar abundance and biomass across the whole floodplain, and were not more prevalent adjacent to the uplands (Fig. 8b). The lack of unique invertebrate

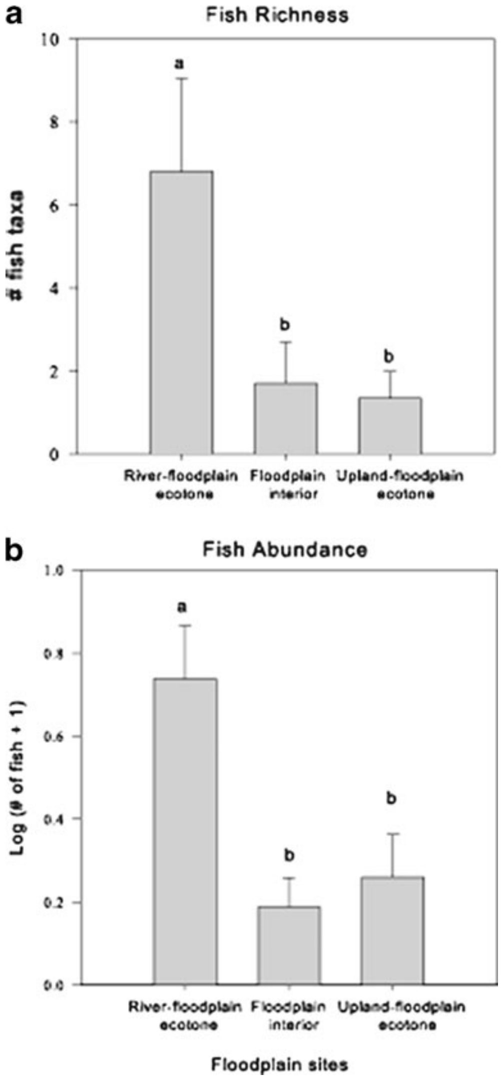

Fig. 7 Variation in **a** fish species richness and **b** fish abundance among the river-floodplain ecotones, the floodplain interiors, and the upland-floodplain ecotones of the Altamaha and Savannah Rivers. Different letters denote significant differences among habitat types (Tukey HSD tests, $p<0.05$). Error bars represent ±1 SE

community assemblages in different portions of the floodplain could perhaps be a response of the temporary nature of backwater swamp hydroperiods. Temporary habitats usually support greater abundance and biomass of habitat generalists than specialists (Scarsbrook and Townsend 1993; Poff et al. 1997; McCauley 2007).

In cases where unique invertebrate community compositions exist across floodplains researchers have focused on permanently rather than seasonally flooded habitat. Gallardo et al. (2008), who studied the floodplain of the Middle Ebro River in Spain, concluded that hydrological connectivity to the river accounted for 28% of invertebrate variability. A study in the Danube River-floodplain (Tockner et al. 1999) concluded that floodplain water undergoes dramatic changes in water chemistry, and biotic communities are directly linked to water levels, which are reflected by hydrological connectivity. In the floodplains of the Altamaha and Savannah Rivers permanently flooded habitat is relatively rare.

Patterns for fish in our study at first glance appear to better support the model of Wissinger (1999). As in other studies (Sullivan and Watzin 2009), the majority of the fish in this study occurred in areas with the highest connection to the river, with fewer occurring in sites more removed. However, the kinds of fish occurring may not be consistent with the concept that the river-floodplain ecotone would be dominated by river channel species. Virtually all of the fishes that were collected (centrarchids, *Esox*, bowfin, mosquitofish; Table 2) are well adapted for wetland habitats. Instead of channel species moving into the floodplain, we may have been observing floodplain species returning to the floodplain. The fact that they concentrated in the river-floodplain ecotone may have developed because the abundance and biomass of their invertebrate foods was greatest there.

The presence of fish often reduces invertebrate abundance and biomass (Riera et al. 1991; Batzer and Wissinger 1996), and thus fish predation may have dampened differences between the river-floodplain ecotone and other parts of the floodplain, making our estimates of invertebrate variation conservative. Fish can also influence the size

Table 2 Fish species present in the river-floodplain ecotone, the floodplain interior, and the upland-floodplain ecotone. Bolded fish species were only found in one habitat

River-floodplain ecotone	Floodplain interior	Upland-floodplain ecotone
Ameiurus nebulosus	*Cyprinella leedsi*	*Amia calva*
Amia calva	*Esox americanus*	*Centrarchus macropterus*
Aphredoderus sayanus	*Esox niger*	*Esox americanus*
Centrarchus macropterus *Cyprinella leedsi*	*Gambusia* spp. *Labidesthes sicculus*	*Gambusia* spp.
Elassoma zonatum	*Lepomis gulosus*	
Esox americanus *Esox niger*	*Lepomis macrochirus*	
Gambusia spp.		
Heterandria formosa		
Labidesthes sicculus		
Lepomis auritus		
Lepomis gulosus		
Lepomis macrochirus		
Lepomis marginatus		
Notemigonus crysoleucas		
Notropis petersoni		

Table 3 Variation in water quality parameters in floodplains of the Altamaha and Savannah Rivers. Ecotonal effects reflect differences among the river-floodplain ecotone (R), the floodplain interior (I), or upland-floodplain ecotone (U) (see Table 1), and temporal effects reflect annual or seasonal variation. When ANOVA testing indicated significance ($P<0.05$), *post hoc* Tukey HSD tests were conducted and results are indicate in the table. Dash (-) indicates effect not assessed

Parameter	Range	Ecotonal effect	Temporal effect
Conductivity	39–448 μS/cm	R > I = U	NS[a]
Temperature	9.5–23.5°C	NS	Feb < April = May
pH	6.20–7.8	NS	Feb = April < May
Total phosphorus	0.07–0.90 mg/L	NS	–
Total nitrogen	0.85–5.62 mg/L	NS	–

[a] *NS* not significant

structure of invertebrates by preferentially choosing the larger organisms (Flecker and Allan 1984; Luecke 1990; Machiusi and Baker 1991; Wellborn 1994). In our study, *Caecidotea* had a higher abundance in the river-floodplain ecotone but biomass did not differ across the floodplain. This suggests a lower proportion of large *Caecidotea* individuals in the river-floodplain ecotone, which may have resulted from size-selective predation.

Why might lentic invertebrates well adapted for life on the floodplain concentrate in the river-floodplain ecotone? Variation across the floodplain may reflect a productivity gradient. Although we did not test productivity directly, we measured electrical conductivity, which has been positively correlated with productivity elsewhere (Rawson 1961; Russell-Hunter 1970). Conductivity was greatest in the river-floodplain ecotone (although concentrations of total nitrogen and total phosphorous were not). Other studies have found that floodplain areas nearer the river supported higher primary production than areas further removed from the river (Forsberg et al. 1988; Van den Brink et al. 1993; Hein et al. 1999; Bayley and Guimond 2009). In other floodplain systems, floodplain areas nearer the river have also been shown to support greater invertebrate abundance and biomass (Gladden and Smock 1990; Gallardo et al. 2008).

Another possible difference among sites that might influence invertebrate abundance and biomass is the period of inundation. Hydroperiod has been shown to influence species richness in floodplains along an Australian arid-zone river (Sheldon et al. 2002) and abundance in lowland headwater streams (Gladden and Smock 1990). In our study, total period of inundation was not directly measured but some sites dried before others (see "Methods" section for differences). However, all sampling sites in this study were seasonally flooded and each held water long enough for most invertebrates to complete development. Because wetland invertebrates in seasonal habitats routinely deal

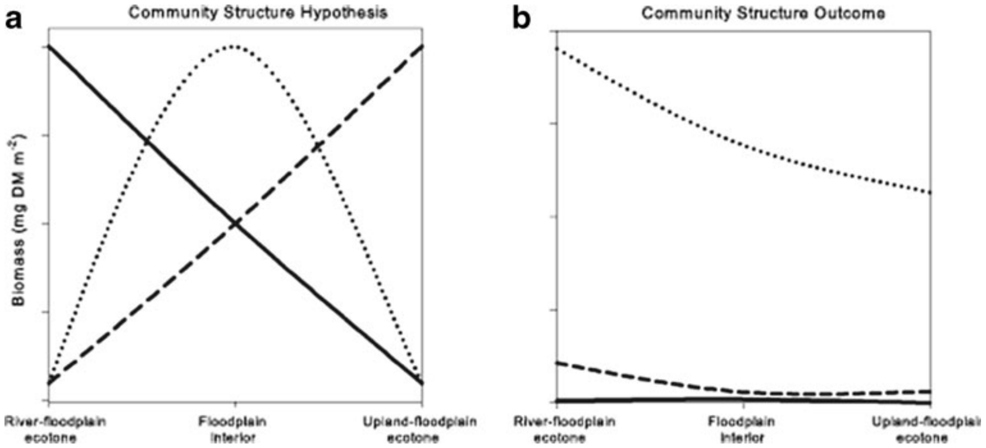

Fig. 8 **a** An idealized depiction of our original hypothesis (adapted from Wissinger 1999) that invertebrate community structure should differ across the floodplain, with lotic riverine organisms (*solid line*) dominating the river-floodplain ecotone, non-aquatic organisms (*dashed line*) dominating the upland-floodplain ecotone, and lentic wetland organisms (*dotted line*) dominating the floodplain interior. **b** A depiction of the outcome of our study based on actual biomass data, which shows that lentic organisms (*dotted line*) dominated all areas (although biomass declined with increasing distance from the channel), non-aquatic organisms (*dashed line*) were prevalent across the entire floodplain (although at low biomass), and lotic organisms (*solid line*) were very rare across the whole floodplain

with large variation in hydroperiod (enduring drought and deluge years), it seems unlikely that the relatively modest variation in hydroperiod among our study sites was a major factor in structuring invertebrate communities (see also Batzer et al. 2004).

Our findings may have implications for river management. In the Altamaha and Savannah Rivers, river-floodplain connectivity appeared to affect distributions of fish and the invertebrates on which they feed, both concentrating in the river-floodplain ecotone. Should river-floodplain connectivity be inhibited, invertebrates that use the floodplain might decrease and become less available to predatory fish. Invertebrates also provide other ecosystem services such as contributing to litter breakdown (Short and Holomuzki 1992), which may also be impaired by reduced connectivity. Although we did not see a dramatic difference between the regulated Savannah River and the unregulated Altamaha River in terms of invertebrates and fish, water resource managers should endeavor to maintain a high degree of river-floodplain connection to allow fish access to the invertebrate resources and preserve other ecological functions on floodplains.

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