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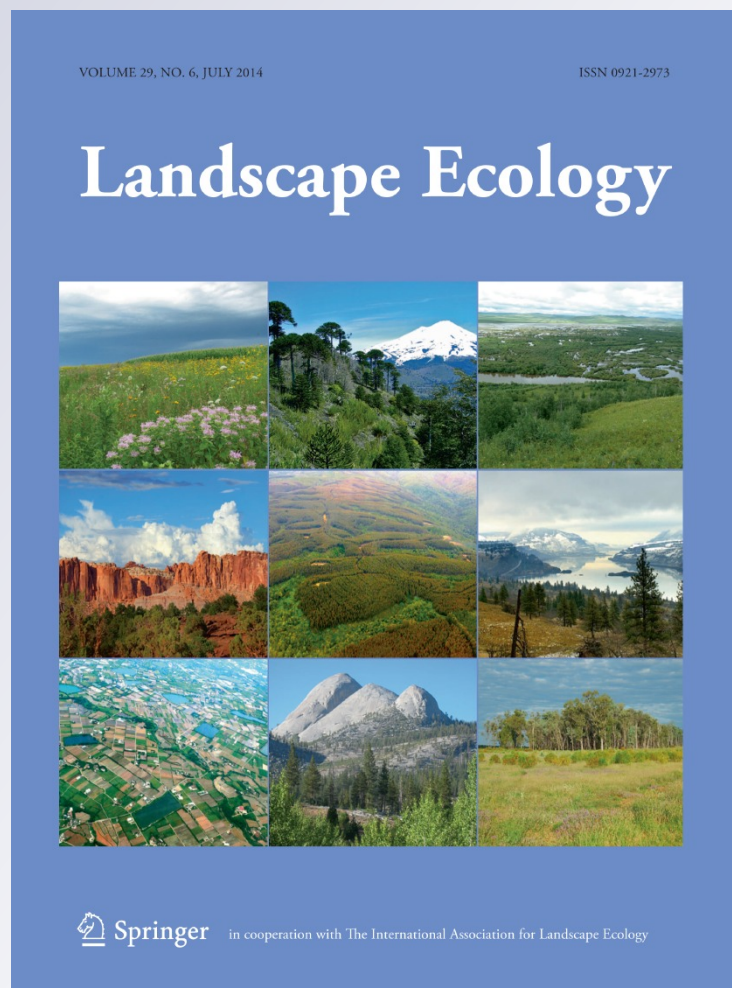
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Spatial and temporal organization of macroinvertebrate assemblages in a lowland floodplain ecosystem

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Abstract An important goal in ecology is to understand controls on community structure in spatially and temporally heterogeneous landscapes, a challenge for which riverine floodplains provide ideal laboratories. We evaluated how spatial position, local habitat features, and seasonal flooding interact to shape aquatic invertebrate community composition in an unregulated riverine floodplain in western Alabama (USA). We quantified sediment invertebrate assemblages and habitat variables at 23 sites over a 15-month period. Dissolved oxygen (DO) varied seasonally and among habitats, with sites less connected to the river channel experiencing frequent hypoxia ($<2 \text{ mg O}_2 \text{ L}^{-1}$) at the sediment–water interface. Differences in water temperature among sites were lowest ($<1 \text{ }^\circ\text{C}$) during winter floodplain

inundation, but increased to $>14 \text{ }^\circ\text{C}$ during spring and summer as sites became isolated. Overall, local habitat conditions were more important in explaining patterns in assemblage structure than was spatial position in the floodplain (e.g., distance to the main river channel). DO was an important predictor of taxonomic richness among sites, which was highest where hydrologic connections to the main river channel were strongest. Compositional heterogeneity across the floodplain was lowest immediately following inundation and increased as individual sites became hydrologically isolated. Our results illustrate how geomorphic structure and seasonal flooding interact to shape floodplain aquatic assemblages. The flood pulse of lowland rivers influences biodiversity through effects of connectivity on hydrologic flushing in different floodplain habitats, which may prevent the development of harsh environmental conditions that exclude certain taxa. Such interactions highlight the ongoing consequences of river regulation for taxonomically diverse floodplain ecosystems.

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Introduction

Ecological patterns in riverine landscapes are shaped by the hydrologic regime, including the nature and

strength of connectivity among main channel, sub-surface, and lateral subsystems (Fisher et al. 1998; Ward et al. 2002). For larger, lowland rivers, lateral connectivity can include significant hydrologic exchange with adjacent floodplains, which comprise a shifting mosaic of lotic, lentic, and terrestrial habitats. In the absence of hydrologic regulation, floodplain ecosystems are notoriously dynamic in space and time (Benke et al. 2000; Malard et al. 2006), and heterogeneity in habitat structure and connectivity is thought to promote high levels of biodiversity (Tockner et al. 1999; Lake et al. 2006). Despite this recognition, understanding how communities are organized and maintained across floodplain habitats remains a challenge with implications for the management and conservation of river ecosystems (Sheldon et al. 2002).

Floodplain community dynamics are overwhelmingly influenced by the flood pulses that deliver water, resources, and biota to laterally distributed habitats (Junk et al. 1989; Tockner et al. 2000). Over long time scales, the flood regime interacts with the geomorphic surface of river valleys to create a diversity of water bodies, which include 'lotic' environments associated with side channels (e.g., sloughs or anabranches), as well as 'lentic' habitats represented by a variety of floodplain lakes and wetlands (Boulton and Lloyd 1991; Ward et al. 1999). At shorter time scales, seasonal flood pulses can induce rapid temporal change to the structure of these aquatic habitats (Tockner et al. 2000; Malard et al. 2006), many of which show marked fluctuations in size over the course of an event (Benke et al. 2000). These dynamics include shifts in the overall extent and turnover of different habitat types (Van der Nat et al. 2003), changes in the nature and strength of hydrological connection (Malard et al. 2006), and spatially and temporally intermittent drying of water bodies (Lake et al. 2006). As a result, the expansion and contraction of the flood pulse is thought to govern the overall spatial heterogeneity of key habitat variables across the floodplain of large river systems (e.g., Malard et al. 2000; Thomaz et al. 2007).

A central hypothesis in floodplain ecology is that the hydrologic template also governs overall patterns of aquatic biodiversity (e.g., Sheldon et al. 2002; Amoros and Bornette 2002; Ward et al. 2002). This hypothesis acknowledges that different taxonomic and functional groups show distinct distributions along

lateral gradients (Winemiller and Jepsen 1998; Tockner et al. 1999), reflecting the constraints imposed by a variety of co-varying habitat variables, including the strength of hydrologic connection, the frequency and magnitude of physical disturbance, substrate composition and stability, resource availability, and drying (e.g., Arscott et al. 2005; Reckendorfer et al. 2006; Leigh and Sheldon 2009). The aggregate effects of these drivers dictate patterns of local richness and species turnover, the details of which may differ with regional and geomorphic setting and be dependent upon which set of proximate factors are most responsible for the distribution of biota. By exploring these general interactions, several studies have shown that invertebrate taxon richness among floodplain habitats may decline with increasing hydrologic connection (Burgherr et al. 2002; Reckendorfer et al. 2006) or be greatest at intermediate levels of connectivity (Tockner et al. 1998; Paillex et al. 2007). Such patterns reflect, in part, the role of physical disturbance (e.g., resulting from high flow velocity) as a constraint to taxonomic richness in the most hydrologically connected floodplain locations (Ward et al. 2002).

Severe physical disturbance across the floodplain is not always a defining feature of the flood pulse (Benke et al. 2000), and for lowland, unconstrained rivers such flood events may exert more ecological influence by replenishing lateral floodplain habitats (e.g., Lake et al. 2006). Indeed, low river gradient, in combination with extensive lateral drainage systems, natural levees, and often dense floodplain forests, can result in comparatively low flow velocities as floodwaters inundate aquatic habitats (Hupp 2000). Where valley floors are unconstrained, overbank floods in these systems typically do not have sufficient energy to displace woody structures on the floodplain (Golladay et al. 2007), and may not flush large numbers of aquatic invertebrates from associated aquatic habitats (Benke 2001). Instead, flood pulses may have positive implications for local floodplain communities through the delivery of water and associated particulate and dissolved resources to different habitats, re-filling temporary water bodies, re-initiating hydrological connections, and preventing the establishment of stressful physical and chemical conditions [e.g., high temperature and low dissolved oxygen (DO)] that correspond to stagnant water and localized drying (e.g., Sheldon and Fellows 2010).

We evaluated how seasonal flood pulses shape spatial and temporal patterns of aquatic invertebrate assemblage structure among floodplain water bodies of a lowland, sub-tropical river (Sipsey River, Alabama, USA). The Sipsey is one of a small number of free-flowing rivers remaining in North America (Benke 1990) and is characterized by a wide, hydrologically active floodplain that becomes inundated at least annually. We surveyed sediment communities from different floodplain habitats to evaluate the local (e.g., temperature) versus landscape (e.g., distance to the main channel) correlates of assemblage structure, and to compare patterns and drivers of invertebrate biodiversity in this lowland river with observations made in other regional settings. We expected that different lotic and lentic environments would be distinguished by a variety of physical and chemical habitat variables that would also influence patterns of assemblage composition. In addition, we hypothesized that the persistence of wetland-like properties (e.g., Batzer and Wissinger 1996) and potential for habitat drying act as major constraints to the distribution of invertebrate taxa. Accordingly, we predicted that the total number of taxa observed over the course of the study would be greatest for locations characterized by less stressful environmental conditions. Finally, we expected that the turnover of species among water bodies (i.e., the compositional heterogeneity, or beta diversity) would be linked to the seasonal flood pulse, and would increase as floodwaters recede and patches become disconnected and assume unique local characteristics (reviewed by Thomaz et al. 2007).

Methods

Study site

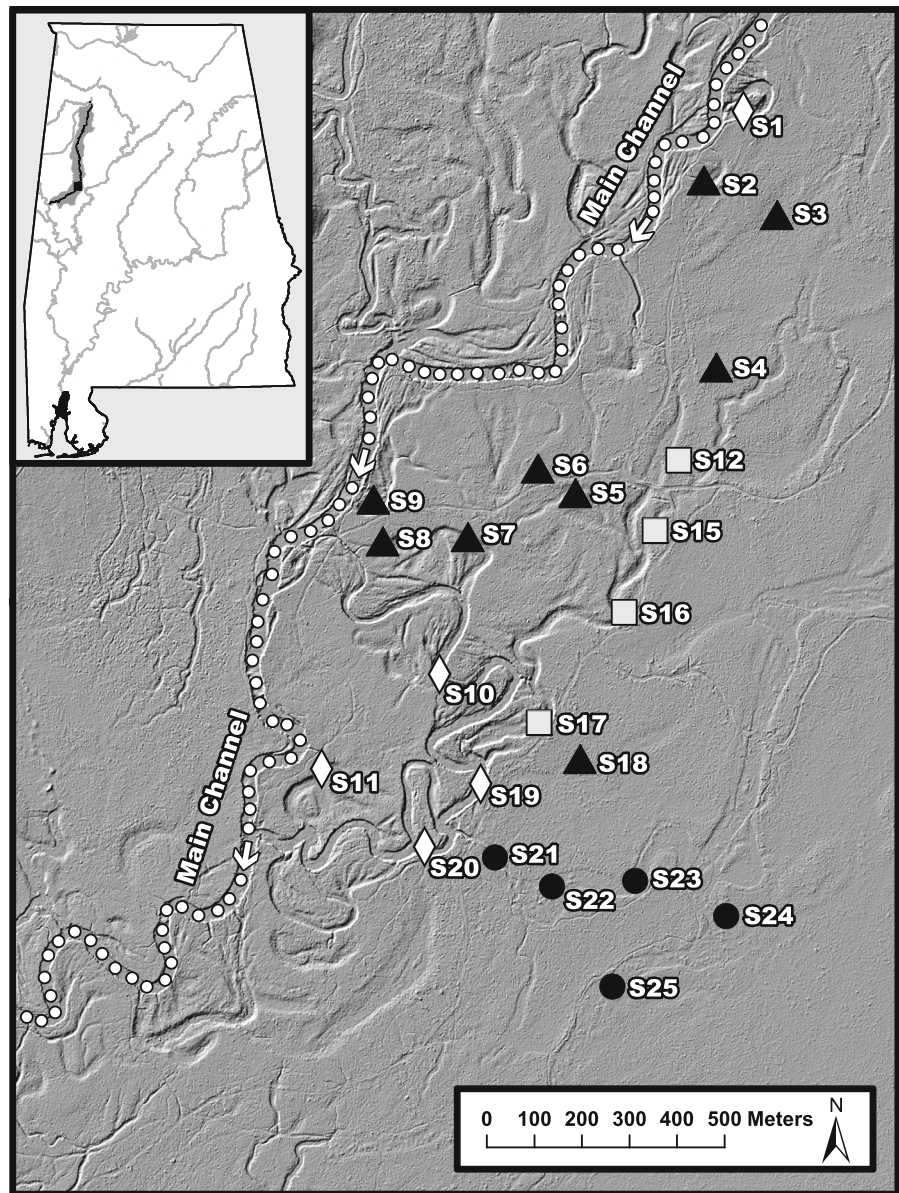
The fifth-order Sipsey River is a tributary of the Tombigbee River, located in west-central Alabama, USA (Fig. 1). The river is approximately 146 km in length and drains a catchment of 2,044 km² that lies predominantly within the East Gulf Coastal Plain province. Mean annual temperature near the research site is 16.0 °C, varying monthly from 5.1 °C in Jan to 26.3 °C in July (NCDC 2011, weather stations: Fayette 012883 and Winfield 2 SW 018998). Mean annual precipitation is 143.0 cm and varies seasonally, with highest rainfall during winter and spring

months (March, 15.8 cm) and lowest during the late summer and early autumn (October, 7.8 cm; NCDC 2011, weather stations: Elrod 012632, Fayette 012883, and Winfield 2 SW 018998). Mean annual discharge near the study reach is 24 m³ s⁻¹ with minimum and maximum historical discharge of 0.4 and 665 m³ s⁻¹, respectively [United States Geological Survey, station ID 02446500, Sipsey River, Elrod, AL; Fig. 2]. Low discharge is generally observed during periods of high evapotranspiration and low rainfall in the summer and autumn (from June to November), when stream flow is restricted to the main channel. Discharge increases following litter fall in mid-November and remains high throughout the winter and spring, reaching bankfull stage at ~33 m³ s⁻¹ (S. Starr, personal observation); however, flooding for the most strongly connected floodplain habitats (e.g., large sloughs adjacent to the channel) very likely occurs at a much lower threshold (e.g., Hupp 2000).

As with other free-flowing rivers in this region (Benke et al. 2000; Hupp 2000), floodplain inundation occurs at least once annually, often for extended periods of time (weeks to months) during the winter-spring period. Long-term flow records (1928–2010) indicate that the probability of exceeding bankfull discharge is highest during February and March (when 50 and 54 % of days exceeded this threshold, respectively) and lowest from August to October (0.8–2.5 %). During this study there were roughly ten over-bank flood events, some comprised of multiple peaks in flow, including an event of nearly 500 m³ s⁻¹ observed during winter 2009.

Sampling was conducted within a 2.5-km² area of floodplain along the Sipsey River, located within the Alabama State Forever Wild Land Trust's Sipsey River Swamp Recreation Area and Nature Preserve. We collected invertebrates from 23 sampling stations on the floodplain that encompassed four common aquatic habitat types present at this location: large sloughs (5 stations), medium sloughs (4 stations), tupelo/cypress sloughs (5 stations) and depressional wetlands (9 stations; Fig. 1, Appendix S1). Habitat designations were based on local morphometric features, the nature of hydrological connection to the main channel, and dominant riparian vegetation (Table 1). Large sloughs had relatively deep channels (averaging 0.75 m at sampling stations), and were 15–20 m wide, with direct connection to the main channel in all but the driest periods. Medium sloughs

Fig. 1 Sampling locations within the Sipsey River floodplain study site, Buhl, Alabama, USA. The four habitat types sampled were: large slough (*diamond*), tupelo/cypress slough (*filled circle*), medium slough (*square*), and depressional wetlands (*filled triangle*). *Inset* map of Alabama shows the location of the Sipsey River watershed and our study site (*filled square*). Map topography is based on a 1-m resolution digital elevation model (DEM) derived from LiDAR imaging



were comparatively smaller (10–15 m wide and 0.2–0.7 m deep) with connections to larger sloughs, but no direct link to the main stem during base flow. Tupelo/cypress sloughs had wide, shallow, and complex channels with indistinct boundaries and were characterized by tupelo (*Nyssa aquatica*) and cypress (*Taxodium distichum*) growing within and along the channel. These stations were on average the farthest from the main channel, and both LiDAR imagery and water chemistry patterns indicate that they likely receive water from internal, floodplain sources (i.e.,

springs) as well as from the adjacent hillslope. Finally, depressional wetlands were isolated areas located at slightly higher elevation on the floodplain without channelization or noticeable directional flow, such that surface water connections to the main channel occurred only during periods of high river discharge; two of the depressional wetland stations were associated with a large beaver pond.

This distribution of habitats represents a continuum from 'lotic' (large sloughs) to 'lentic' (depressional wetlands) conditions, which equates to a gradient in

Fig. 2 River discharge and mean daily water temperature (\pm minimum and maximum daily average values) across the 23 sampling sites on the Sipsey River floodplain. Symbols on the hydrograph show sampling dates (open = seasonal, filled = monthly). River bankfull stage and floodplain inundation occurs at a discharge of approximately $33 \text{ m}^3 \text{ s}^{-1}$ (dashed line)

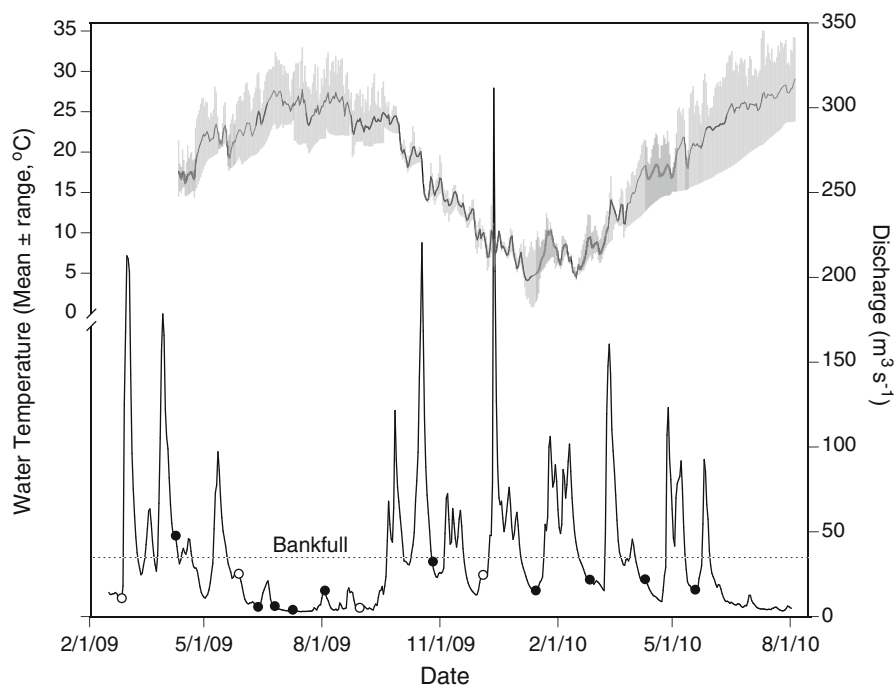


Table 1 Summary of physical and chemical characteristics of sampling stations organized by habitat type

Habitat	<i>n</i>	Distance (m)	Elevation (m)	Depth (cm)	DO (mg l ⁻¹)	AFDM (g m ⁻²)	Conductivity (μs)	Temperature (°C)
Wetland	9	275 (64–675)	60.4 (59.2–61.3)	42 (0–100)	1.1 (0.1–4.0)	3182 (1057–8587)	72.6 (45.9–104.2)	15.9 (7.0–28.1)
Tupelo/cypress slough	5	797 (541–1141)	60.6 (60.4–60.7)	48 (18–87)	2.2 (0.1–4.6)	2505 (926–5261)	83.5 (38.9–147.4)	16.4 (8.9–22.6)
Medium slough	4	556 (315–683)	60.1 (59.3–61.0)	51 (20–80)	1.7 (0.1–3.5)	2284 (665–4236)	73.3 (54.0–105.7)	18.0 (8.1–27.2)
Large slough	5	276 (47–478)	59.6 (59.1–60.9)	75 (27–110)	4.3 (0.3–8.3)	1790 (784–4491)	81.0 (52.7–111.8)	17.6 (9.4–25.0)

Values are the average and limits (max/min) for each variable measured across all sampling dates for each habitat type. Average depth estimated for wetland habitats includes zero values associated with dry conditions. Temperature data are the average values (and limits) integrated over the two-week period preceding each seasonal sampling date

local hydrologic turnover and connectivity with the river channel and surrounding floodplain. While we did not measure hydrological connectivity directly, this assumed gradient is supported by: (1) presence/absence of flowing water observed during sampling; (2) topographic patterns, with large sloughs typically found at the lowest elevation, and wetlands at the highest; (3) the relative isolation of sampling stations resulting from the physical structure of the floodplain drainage system (e.g., presence/absence of connecting channels); and (4) observed drying of several

depressional wetland sites during extended flood-free periods.

Floodplain sampling

We used two sampling regimes to evaluate spatial and temporal patterns in macroinvertebrate community structure across the floodplain (Fig. 2). First, seasonal samples were collected at all 23 sites on four occasions between February 2009 and December 2009. We complemented this spatially extensive assessment

with monthly to bimonthly sampling at three of the sites [S3 (depressional wetland), S20 (large slough) and S25 (tupelo-cypress slough)] across 14 dates (including seasonal sampling dates) from February 2009 to May 2010 (Fig. 1). Physical and chemical variables were measured concurrent to macroinvertebrate collection and included spot-measurements of DO (mg L^{-1} ; DO), electrical conductivity ($\mu\text{S cm}^{-1}$) and temperature ($^{\circ}\text{C}$) using a YSI ProODO dissolved oxygen meter and YSI 30 conductivity, salinity, and temperature meter, respectively (YSI, Yellow Springs, OH, USA). DO was measured at the sediment–water interface with the goal of capturing conditions most relevant to benthic fauna. Such spot measurements of DO may fail to capture diel variation linked to metabolic processes, and comparisons among sites sampled throughout the day could thus be biased by these temporal changes. To help minimize this bias, sites and habitats were sampled in a different, haphazard order on each date. In addition, we found no significant correlations between either time of day or sampling order and measurements of DO. Water depth was measured at the location of invertebrate sampling. Each station was also instrumented with an Onset HOBO temperature/light data logger (UA-002-64, Onset, Pocasset, MA, USA) placed near the sediment–water interface to collect hourly temperature data, which were condensed to daily mean values. To explore temperature effects on biota, mean daily values were averaged across a 14-day window prior to each sampling date. For the initial sampling, however, no prior temperature data were available, so for that date alone we used spot measurements taken during invertebrate collection in subsequent analyses.

Macroinvertebrates were collected with a Petite Ponar grab sampler (Wildlife Supply Co., Yulee, FL, USA) with an area of 0.023 m^2 and volume of 2.4 L. Three Ponar grabs were collected from each site, homogenized in the field and preserved in 4 % formaldehyde. Samples were sorted in the laboratory and were sub-sampled when animal density was high (96 out of 119 samples). Subsampling was done before organisms were removed from detritus, and ranged from 12.5 to 80 % of the original sample, with a minimum of 200 organisms collected. Specimens were identified to genus, or the lowest taxonomic level possible. Most non-insect taxa were identified at a coarser taxonomic level. Chironomids were slide-mounted prior to identification: where $n \leq 25$

individuals per sample, then all individuals were mounted; when $n \geq 25$, then a representative subsample (25–75 % of total) was mounted. Identifications were made following keys by Burch and Tottenham (1980), Epler (1995, 2001), Merritt et al. (2008) and Thorp and Covich (2010). Once invertebrates were sorted, the remaining organic material was rinsed through a 1 mm sieve, dried at 60°C for a minimum of 48 h, weighed, ashed at 500°C for 6 h, and re-weighed for determination of dry mass (DM) and ash-free dry mass (AFDM). Finally, six of the depressional wetland stations were dry during the summer sampling campaign and were not included in the analysis of community structure or richness on that date.

Analysis of macroinvertebrate assemblage structure

Non-metric multidimensional scaling (NMDS) of Bray–Curtis similarity matrices based on $\log(x + 1)$ abundance data was used to describe spatial and temporal patterns of macroinvertebrate assemblage structure. The first level of analysis used NMDS to assess composition for all 23 sites, across all four major sampling dates, and thus addressed the strength of spatial and seasonal variation considering all locations. We repeated this analysis separately for each of the four seasonal sampling periods (Jan, Mar, Aug, Oct) to more closely address spatial variation in assemblage structure among habitats. For a more finely resolved evaluation of temporal change, we applied NMDS to a community matrix derived from the three sites (S3, S20, and S25) sampled more frequently throughout the year (i.e., 14 dates). For each analysis, we followed NMDS with analysis of similarity and similarity percentages (SIMPER) routines, which were used to test for statistically significant differences in assemblage structure among pre-determined groups (i.e., season and habitat) and to identify those taxa most responsible for observed dissimilarity in composition, respectively.

Spatial and temporal patterns in assemblage structure were further assessed using multivariate dispersion (MD), which describes compositional heterogeneity among samples (Warwick and Clarke 1993) and is used as one measure of beta diversity (Anderson et al. 2006, 2011). We first calculated MD for each sampling station across the 4 seasonal dates to characterize the relative

persistence of composition over time (MD within stations, MD_{ws}). Next, to evaluate how spatial variation in assemblage structure changed over the seasonal flooding cycle, we also quantified MD across all stations (MD across stations, MD_{as}) on each sampling date. We also quantified the spatial heterogeneity in overall abundance as the coefficient of variation (% CV) on each sampling date. If stations were dry, we assumed zero abundance of aquatic taxa when estimating % CV.

We also followed each of the four seasonal NMDS analyses with the BIO-ENV routine, a test that compares environmental and community matrices and identifies physical or chemical variables that are most related to variation in assemblage structure (Clarke and Ainsworth 1993). In addition to evaluating the importance of local habitat variables measured during sampling, we used a separate BIO-ENV analysis to assess relationships between composition and both the straight-line distance to the main river channel and the elevation of each sampling station. Distance from each site to the main channel was measured using ArcMap (ArcGIS v9.3, ESRI, Redlands, CA, USA). Station elevation was determined from 1-m resolution digital elevation models derived from light detection and ranging (LiDAR) data associated with the study area. Finally, RELATE analysis (a non-parametric MANTEL test) was used to determine, for each season, the correlation between community similarity and spatial distance between each pairwise combination of sites. All multivariate statistics were carried out in the PRIMER software package (Version 6, Plymouth Marine Labs, Plymouth, UK; Clarke and Warwick 2001, Clarke and Gorley 2006).

Results

Environmental conditions

Physical and chemical habitat variables varied among habitats and seasons (Table 1). Mean DO was generally lowest at depressional wetland and medium slough sites, both of which averaged less than 2 mg L^{-1} across all dates. Only at the large slough and tupelo/cypress slough stations did average DO exceed 2 mg L^{-1} , with individual observations as high as 8.6 mg L^{-1} in the large sloughs during winter 2010. Considering all sampling dates, average DO across

floodplain sampling stations increased with river discharge (Pearson $r = 0.56$, $P = 0.04$, $n = 14$ dates). Mean conductivity varied from $72.6 \pm 2.8 \mu\text{S cm}^{-1}$ for depressional wetlands to $83.5 \pm 7.2 \mu\text{S cm}^{-1}$ in the tupelo/cypress sloughs, which also had the largest range in values across sampling stations and dates (38.9 – $147.4 \mu\text{S cm}^{-1}$). Average standing stocks of organic matter were greatest for depressional wetland ($3182 \pm 246 \text{ g AFDM m}^{-2}$) and lowest in the large slough ($1790 \pm 171 \text{ gm}^{-2}$). Finally, water temperature was similar among habitat types; however, the coldest and warmest average values (7.0 and $28.1 \text{ }^\circ\text{C}$) were observed in depressional wetland sites. The spatial variation in mean daily temperature across the floodplain showed a distinct seasonal pattern: during the late autumn and winter, the difference between the warmest and coldest sampling stations was as little as $0.5 \text{ }^\circ\text{C}$; in the late spring and summer, this difference was as high as $14.2 \text{ }^\circ\text{C}$ (Fig. 2).

Spatial patterns of taxonomic richness

Invertebrate sampling produced a total of 24,853 individuals, representing 143 taxa. The most abundant aquatic taxa found across the floodplain were micro-invertebrates, including Ostracoda (average: 28.4 % of total abundance), Copepoda (16.0 %), Oligochaeta (14.6 %), Acari (5.9 %), and Nematoda (7.9 %). Of the aquatic insects, only the family Chironomidae was notably abundant (14.3 % of total abundance), and it was by far the most diverse group (43 separate taxa). Adults and larvae of aquatic Coleoptera were the next most cosmopolitan insect group across the floodplain, being collected from each habitat type at least once. Odonate larvae were also observed in both lotic and lentic habitats, but were most abundant in the large sloughs. Ephemeroptera and Trichoptera were rare across habitat types, and were for the most part restricted to the large and tupelo-cypress sloughs.

The total number of taxa collected across the floodplain ranged from 59 in the autumn to 72 in the winter (average of 65 taxa per season). Across seasons, both the mean and total number of taxa also varied among sampling stations and habitat types (Table 2). For example, between 16 and 28 taxa were collected from individual depressional wetland stations over the course of the study (average of 21.3). In contrast, approximately twice as many taxa were observed among the large slough stations (range 36–53; average

Table 2 Summary of invertebrate community metrics from the seasonal survey of four habitat types (23 sites) in the Sipsey River floodplain, AL, USA

Habitat	<i>n</i>	Abundance (m ⁻²)	Richness (m ⁻²)	Taxa per station	MD _{ws}
Wetland	9	7131 (±803)	12.2 (±0.8)	21.3 (16–28)	0.75 (±0.11)
Tupelo/cypress slough	5	7883 (±1549)	15.8 (±2.1)	31.4 (21–39)	1.00 (±0.10)
Medium slough	4	11850 (±1178)	14.7 (±0.5)	30.0 (28–32)	1.26 (±0.10)
Large slough	5	6252 (±1069)	21.5 (±1.7)	44.0 (36–53)	1.05 (±0.15)

Habitat types are ordered along a lentic-to-lotic continuum. Abundance and richness are the average (±SE) based on the season-integrated values for each site. Taxa per station shows the average and range of the total number of taxa observed for each site over the course of seasonal sampling. MVD_{ws} (MD_{ws}) is the average multivariate dispersion calculated for each site across seasonal dates

of 44.0). Differences in taxa number among samples were not correlated with total abundance (Pearson $r = -0.08$, $p = 0.46$, $n = 86$). In addition, rarefaction curves indicated that major distinctions among the habitat types did not reflect variation in sampling intensity (Appendix S2). Specifically, higher richness for the large slough habitat was observed despite a comparatively smaller number of samples; in contrast, low richness was found for depressional wetlands, which were sampled with the greatest intensity.

Both the mean and the overall number of taxa collected at each site increased logarithmically with the average DO measured across seasonal sampling dates ($r^2 = 0.55$, $P < 0.001$ and $r^2 = 0.65$, $P < 0.001$, respectively, $n = 23$, Fig. 3a). This general relationship held when considering the overall richness of dominant taxonomic groups, including chironomids ($r^2 = 0.54$, $P < 0.001$, $n = 23$) and micro-invertebrates ($r^2 = 0.54$, $P < 0.001$, $n = 23$); however, the slopes (±SE) of these lines (5.2 ± 1.1 and 2.6 ± 0.5 for chironomids and micro-invertebrates, respectively) suggested that richness of the former group was more sensitive to low DO conditions (Fig. 3b). Across seasons, average richness for the different habitats varied from 12.2 (±0.8, $n = 9$) for depressional wetlands to 21.5 (±1.7, $n = 5$) for large slough sites, with a minimum and maximum of 4 (depressional wetland, summer) and 30 taxa (large slough, autumn), respectively (Table 2). Within individual seasons, richness also increased with DO among sampling stations during the winter (Pearson $r = 0.61$, $P = 0.002$, $n = 23$), spring ($r = 0.53$, $P = 0.008$, $n = 23$) and autumn ($r = 0.80$, $P < 0.001$, $n = 23$) seasons, but was instead positively correlated with sampling depth during the summer ($r = 0.57$, $P = 0.02$, $n = 17$).

Spatial and temporal patterns in assemblage structure

NMDS of invertebrate communities across the four seasonal surveys resolved differences in composition with a stress of 0.23 (Fig. 4a). Assemblage patterns (similarity among sites) derived from the entire list of taxa were similar to those observed when evaluating only the micro-invertebrate (following RELATE, $\rho = 0.80$, $P < 0.001$), or chironomid assemblages ($\rho = 0.50$, $P < 0.001$); however, similarity matrices derived from these two dominant groups were only weakly correlated with each other ($\rho = 0.21$, $P = 0.001$). Overall assemblage structure varied among seasons (Global $R = 0.25$, $P < 0.01$), with significant contrasts between all season pairs, except spring and autumn. Based on estimates of MD within each sampling station, community composition tended to be least variable among seasons for depressional wetland sites (MD_{ws} = 0.75 ± 0.11 , $n = 9$) and most dynamic for large (MD_{ws} = 1.05 ± 0.15 , $n = 5$) and medium (MD_{ws} = 1.26 ± 0.10 , $n = 4$) slough stations (Table 2).

NMDS of invertebrate communities within each season resolved differences in assemblage composition with comparatively lower stress (0.18–0.19; Fig. 4b–e). Composition differed among individual habitat types during the winter (Global $R = 0.54$, $P < 0.01$), summer (Global $R = 0.51$, $P < 0.01$) and autumn (Global $R = 0.54$, $P < 0.01$) seasons, but not the spring (Global $R = 0.12$, $P = 0.09$). NMDS of assemblages sampled monthly further illustrated variation in composition among habitat types (stress = 0.22), which were significantly different when assessed over the entire sampling period (Global $R = 0.58$, $P < 0.01$, Fig. 5a).

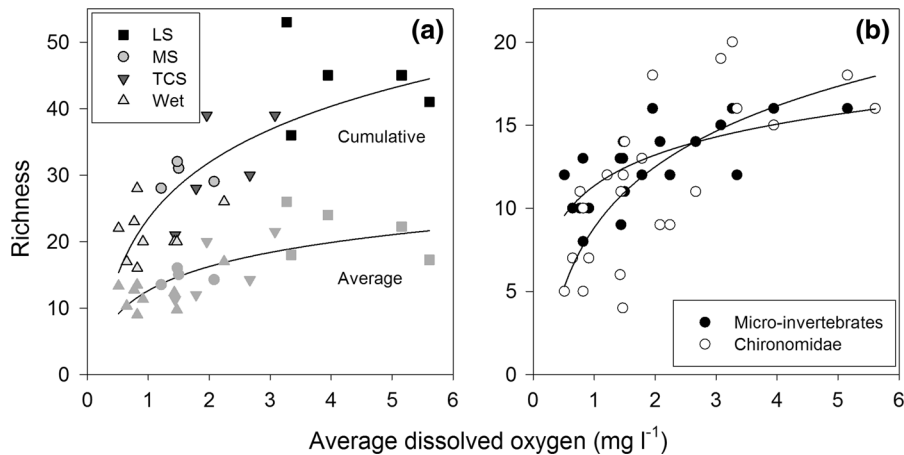


Fig. 3 Relationship between the average and total number of invertebrate taxa **(a)** and the total number of micro-invertebrate and chironomid taxa **(b)** and average dissolved oxygen (mg l^{-1}) concentration measured at each site over the study period.

Average taxa richness is based on the four seasonal sampling dates for each site and is shown as gray, unenclosed symbols. *Wet* depositional wetland, *LS* large slough, *MS* medium slough, *TCS* tupelo/cypress slough

Results from the SIMPER routine on monthly data indicated that these habitat differences were influenced by the distribution of mayflies in the genus *Caenis*, and midges in the genera *Krenopelopia* and *Tanytarsus*, which were abundant at the large slough station, but either absent (in the case of *Caenis*) or rare at the other two sites. The two other habitats were distinguished by (1) differences in the relative abundance of oribatid mites, which were more common in the tupelo/cypress slough, and (2) the variable distribution of several midge taxa in the sub-family Chironominae, including *Omisus*, *Polypedilum*, *Einfeldia*, *Kiefferulus*, *Glyptotendipes*, and *Tribelos* (Appendix S3).

Predictors of assemblage composition

Within seasons, patterns of community composition among stations were correlated with local habitat conditions and, to a lesser degree, variables that related to spatial position in the floodplain. Significant correlations between assemblage structure and habitat variables were observed during the winter ($R = 0.45$, $P < 0.01$), spring ($R = 0.43$, $P < 0.01$), and autumn ($R = 0.53$, $P < 0.01$) seasons. During the winter, community patterns were best correlated with variation in DO and conductivity. In the spring, these patterns were related to variation in DO, water temperature, and depth. In autumn, patterns were linked once again to DO, but also to differences in

conductivity, water temperature, and organic matter standing stock. In addition to habitat variables, during the winter and spring observed patterns in assemblage structure were weakly related to distance from the main channel and floodplain elevation ($R = 0.20$, $P = 0.02$ and $R = 0.21$, $P = 0.05$, for winter and spring, respectively). Similarly, spatial autocorrelation in assemblage structure among stations was also statistically modest, and varied seasonally. During the winter and spring, pair-wise differences in community composition increased with distance between any two stations ($R = 0.29$, $P < 0.01$ and $R = 0.23$, $P < 0.01$, respectively); this spatial organization was weaker during the autumn ($R = 0.15$, $P < 0.04$) and was not observed during the summer ($R = 0.14$, $P < 0.13$).

Temporal patterns of floodplain heterogeneity

Temporal changes in beta diversity (compositional heterogeneity) and the overall heterogeneity of invertebrate abundance across the floodplain were linked to the flood regime (Fig. 5b–c). MD_{as} was generally low immediately following over-bank floods, and increased over time as flood waters contracted (Fig. 5b). Similarly, spatial variation in overall invertebrate abundance also increased over time during flood-free periods (Fig. 5c). Each of these relationships was non-linear, with the largest changes in MD_{as} and heterogeneity in abundance occurring within the first 40 days of post-

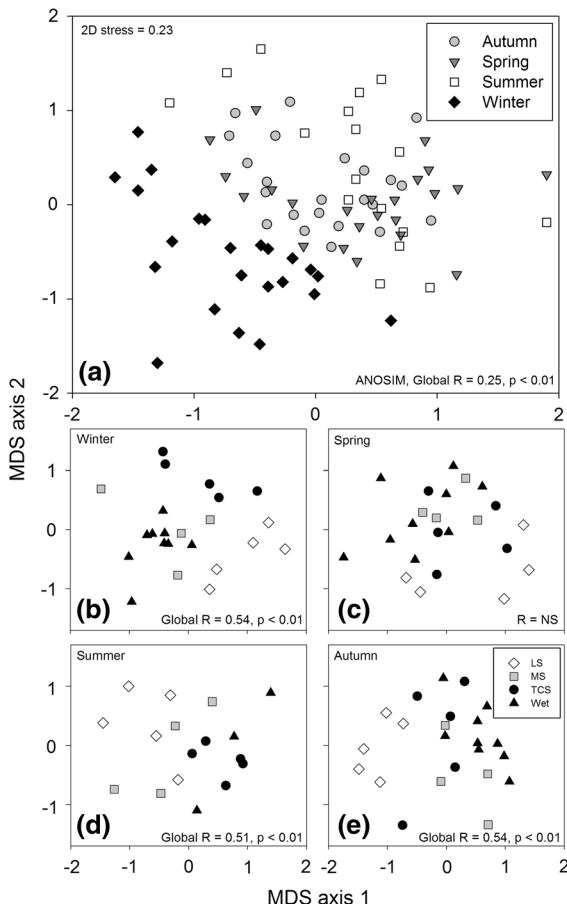


Fig. 4 Non-metric multidimensional scaling ordinations based on Bray–Curtis dissimilarities of log-transformed invertebrate abundance data collected from 23 sites during four seasons (a), and across the four habitat types during winter (b), spring (c), summer (d) and autumn (e) seasons. Only 17 sites were sampled in summer because some sites were dry. *Wet* depositional wetland, *LS* large slough, *MS* medium slough, *TCS* tupelo/cypress slough

flood time. In addition, these temporal patterns in compositional heterogeneity based on all taxa across seasonal and monthly sampling dates were correlated with those based on analysis of only the micro-invertebrate (e.g., from the monthly assessment: $r = 0.85$, $P < 0.01$, $n = 14$) and chironomid assemblages ($r = 0.81$, $P < 0.01$, $n = 14$).

Discussion

The interactions between seasonal inundation and floodplain community patterns observed in the Sipsey

River floodplain are representative of dynamics that, prior to widespread river regulation, would have characterized lowland rivers across the Coastal Plain of the southeastern USA. (Benke 1990). Variation in the composition of sediment communities over space and time in the Sipsey floodplain was best explained by differences in local habitat variables, and much less so by measures of landscape position, such as distance from the river channel or proximity to adjacent sampling stations. The strength of these habitat constraints on the distribution of floodplain biota was responsible for consistent differences in assemblage structure between the more lotic versus lentic water bodies, a pattern that has been observed elsewhere (e.g., Boulton and Lloyd 1991; Leigh and Sheldon 2009). Our results extend these observations to suggest that assemblages of different floodplain habitats are not only distinguishable in space, but also vary in terms of their potential to change over time (as described by MD_{ws}). In addition, results illustrate how overall patterns of alpha and beta diversity across the floodplain are linked to the seasonal expansion and contraction of floodplain aquatic habitats.

Connectivity and spatial patterns of taxonomic richness

In contrast to studies of temperate (e.g., Paillex et al. 2007) and alpine (e.g., Burgherr et al. 2002) floodplains, where flood-associated physical disturbances can constrain local invertebrate biodiversity, we found the highest levels of taxonomic richness at sites that were most closely connected to the main channel (i.e., large sloughs) and most readily flooded (Hupp 2000). Instead of shaping biotic patterns through the effects of physical disturbance, flood pulses in the Sipsey River appeared to exert the most influence on invertebrate biodiversity through their effects on habitat properties, with DO emerging at the strongest statistical predictor of local richness. These observations potentially reflect the direct influence of DO, which is of obvious importance to the distribution of aquatic biota (Verberk et al. 2011), and in our study was highest in the most strongly connected (lotic) floodplain sites, during periods of higher river discharge. Similarly strong effects of DO on the spatial distribution of fishes have been observed in tropical floodplain systems (e.g., Junk et al. 1983; Winemiller and Jepsen 1998). Floodplain forests in the US Coastal Plain can

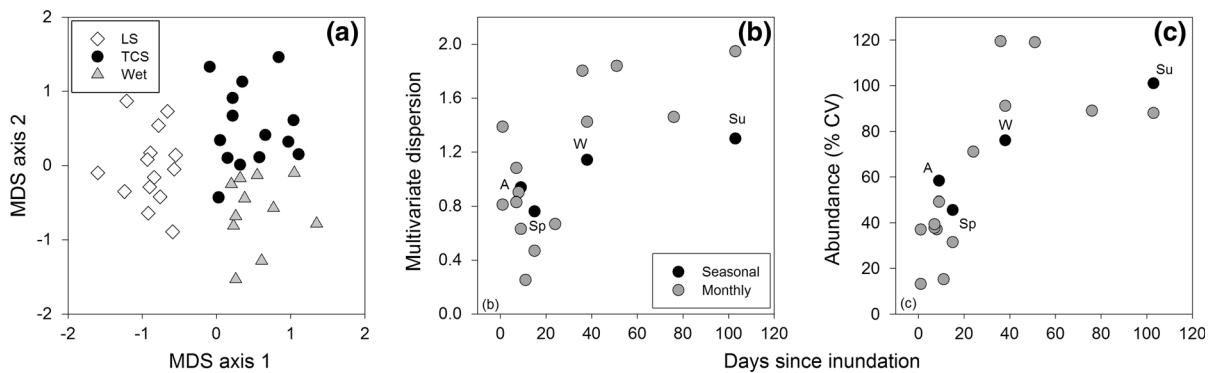


Fig. 5 Non-metric multidimensional scaling ordination based on Bray–Curtis dissimilarities of log-transformed invertebrate abundance data collected at three focal sites on a monthly basis (a). Changes in multivariate dispersion of invertebrate community structure among sites (b) and coefficient of variation in

invertebrate abundance (c) are plotted against time since floodplain inundation at the three sites sampled monthly (grey symbols) and the seasonally sampled sites (black symbols). Winter (W), spring (Sp), summer (Su), and autumn (A) seasons are identified for the seasonal sampling campaign

be highly productive systems (e.g., Wharton et al. 1982; Cuffney 1988) and the combination of detrital inputs, high temperatures, and low gradient combine to promote local organic matter decomposition and so induce periods of widespread anoxia, particularly in permanently inundated areas with low rates of hydrologic flushing (Wharton et al. 1982; Pulliam 1993; Batzer and Wissinger 1996).

Despite these potential causal relationships, spot measurements of DO should be interpreted with caution, and observed statistical correlations may also reflect the importance of other co-varying factors, such as water temperature, depth, and hydrologic permanence (i.e., local drying), which likely interact to influence overall patterns of richness and assemblage structure. Previous research in the Sipsy floodplain has shown that some, but not all, aquatic invertebrate taxa can actively migrate with the ‘wetting front’ as local habitats dry (Tronstad et al. 2005a). Furthermore, several dominant groups (e.g., chironomids, ceratopogonids, ostracods) are able to survive in active or dormant states during dry periods and recover and emerge as adults upon inundation (Tronstad et al. 2005b). Thus, our observed spatial patterns of assemblage structure could reflect the distribution of behavioral or physiological traits that allow particular taxa to colonize and develop in more ephemeral habitats, which in several cases also happened to be characterized by low DO and elevated temperatures. Overall, our results support the general idea that ‘connectivity’ has important effects on the distribution of invertebrate communities across the

Sipsy floodplain. The specific mechanisms underlying these patterns remain unresolved; however, patterns appear to be linked to the effects of flood pulses on hydrologic flushing, local habitat conditions, and flow permanence among diverse water bodies.

Spatial and temporal patterns in assemblage structure

In addition to the observed spatial patterns in richness, different floodplain habitats were themselves differentially variable in terms of overall taxonomic turnover across seasons. Specifically, estimates of MD over seasonal time scales at each sampling station suggested that communities at the depressional wetland stations were less temporally dynamic than those in the more lotic habitats (Table 2). These differences are further demonstrated by comparing average richness and cumulative richness among sites (Fig. 3a), which indicated considerably more turnover in taxa for the more lotic versus lentic habitats. In a quite different floodplain setting, Burgherr et al. (2002) also documented variation in temporal dynamics in assemblage structure, but in that case differences among sites were linked to spatial patterns of physical disturbance and habitat stability in an alpine landscape. In contrast, for the Sipsy floodplain, variation in temporal dynamics among stations appeared to result from strong environmental filters (sensu Poff 1997) at the more lentic sites, which may constrain the potential number of taxa able to maintain populations

in these habitats. The widespread hypoxia described above is one likely candidate for this type of environmental filter, as are temperature extremes, and periodic drying observed for these more isolated habitats. In addition to these local habitat constraints, greater hydrologic connectivity in the more lotic compared to lentic habitats may also allow for dispersal and establishment by a relatively broader array of taxa over time. These hypotheses are not mutually exclusive, and both local habitat features and variation in hydrologic connectivity likely interact to govern temporal change in assemblage composition within different water bodies (Sheldon et al. 2010).

While there were clear overall differences in assemblage structure among habitats, the strength of these distinctions changed over time. In fact, during the spring we were unable to detect any differences in composition among the different lotic and lentic habitats. For this period, the only 'landscape' correlates of community pattern across the floodplain were the distance to the main channel and the proximity of pairwise sampling stations (i.e., a pattern reflecting distance-decay dynamics; Soininen et al. 2007). This spatial pattern is consistent with a greater role for dispersal as a driver of community composition, which may reflect a more well-connected floodplain community subject to relatively homogeneous conditions throughout a winter–spring season characterized by prolonged periods of inundation. For all other seasons, habitat designations served as much stronger organizers of floodplain communities when compared to these purely spatial descriptors, such that even closely collocated sampling stations had distinct assemblages that reflected unique local conditions. Understanding variation in the strength of local habitat controls versus dispersal-driven patterns is a general challenge in community ecology (Urban 2004), and transitions in the relative importance of these classes of drivers have been documented along longitudinal gradients from headwater to mainstem riverine habitats (Brown and Swan 2010). Our results indicate that these shifts in relative control over assemblage structure may also occur over time in ecosystems subject to these seasonal flood pulses.

Compositional heterogeneity and the flood pulse

Understanding how fluvial processes and hydrologic connectivity interact to shape patterns of beta diversity

has been a key focus of floodplain research (Ward et al. 1999, Gray and Harding 2009). In this study, changes in beta diversity, described in terms of compositional heterogeneity, were clearly linked to the expansion and contraction of the flood pulse. Specifically, the seasonal drawdown of floodwaters drove increases in MD across floodplain sampling stations, a pattern observed when evaluating all invertebrate taxa, as well as when focusing on dominant taxonomic groups. These shifting spatial patterns were also mirrored by measures of heterogeneity in total invertebrate abundance, which were also lowest immediately following floods, and then increased over time as the hydrological system contracted. Moreover, the observed increases in compositional heterogeneity during the contraction of the flood pulse are conservative in that they do not include the taxonomic turnover resulting from aquatic habitat loss during the summer and subsequent immigration of semi-aquatic and terrestrial invertebrates, which is common in floodplain environments (Adis and Junk 2002, Steward et al. 2011). Many floodplain patches along the Sipsey River will shift seasonally between aquatic and terrestrial phases and the changes in local composition that occur during these transitions (e.g., Tronstad 2005a, b) would likely increase our estimates of MD during periods of low flow.

Temporal changes in spatial heterogeneity during the flood pulse, as observed in the Sipsey floodplain, have been documented elsewhere for a range of aquatic habitat variables (e.g., temperature, conductivity, nutrients), as well as for several biotic groups (see review by Thomaz et al. 2007). More generally, increased beta diversity with greater environmental patchiness has been observed across terrestrial and aquatic ecosystems (e.g., Cottenie et al. 2003; Tuomisto et al. 2003). In riverine systems, such increases in compositional heterogeneity among water bodies may be associated with internal and/or external drivers that emerge as individual patches contract in size, become hydrologically isolated, and assume unique physical characteristics and community trajectories (Stanley et al. 1997, Thomaz et al. 2007). While we are unable to identify the specific mechanisms driving these changes in the Sipsey floodplain, correlations between assemblage dissimilarity and habitat variables (e.g., DO and temperature) suggest that, as sampling stations become

hydrologically isolated, constraints on the distribution of biota imposed by the divergence in environmental conditions among patches influence the overall compositional heterogeneity in the landscape. In addition, while not considered here, spatial variation in predator abundance may also lead to divergent community changes as water bodies become isolated and drying ensues (e.g., Greig et al. 2013). The Sipsey River and floodplain play host to a diverse assemblage of fish, which includes predators that can be found across multiple habitat types (e.g., sunfishes, *Lepomis* spp; Rypel et al. 2012), and the potential importance of top-down influences on community patterns in this system merits further study.

Conclusion

This study illustrates the importance of a natural flow regime for controlling the interactions between hydrology and geomorphology that are clearly of central importance in driving community structure of aquatic floodplain ecosystems. Most comparable river systems in the region, and increasingly many across the globe, no longer experience the seasonal flood pulses that shape temporal and spatial variability in physical habitat conditions, biotic structure, and ecosystem processes. In particular, our results highlight the ‘replenishing’ effect (sensu Lake et al. 2006) that flood pulses have on the habitats and communities of lowland floodplains; severing this connection through hydrologic regulation has likely led to the establishment of water bodies unable to support their original levels of invertebrate species diversity. As a rare surviving exception, the Sipsey River represents both a model ecosystem for researching spatiotemporal patterns across floodplain landscapes and an example of how many river systems affected by regulation would function under a restored, natural flow regime.

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