Effects of Introduced Small Wood in a Degraded Stream on Fish Community and Functional Diversity

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Abstract - Though the effects of introduced wood on fishes is widely studied for salmonids in upland coldwater streams, there are few studies on this topic conducted in the Coastal Plain of the southeastern US. This research gap is problematic because the introduction of wood is a critical component of efforts aimed at conserving the threatened fish diversity of the Coastal Plain, but managers lack data on the effects of installed wood on fish communities. Over a nearly 4-year study period, we contrasted the effects of introduced, small, wood bundles on the fish community in a channelized and deeply incised sand-bed Coastal Plain stream with an unmanipulated reference treatment. The central question was whether or not stream reaches with introduced wood had greater taxonomic and functional diversity than unmanipulated reference reaches within the same stream. The introduction of modest amounts of small wood had measurable and biologically significant positive impacts on fish community composition and perhaps functional diversity relative to stream reaches lacking wood. However, species-specific responses varied among treatments, suggesting the design of wood installations has an impact on whether or not management goals are achieved.

Introduction

The effects of introduced wood on stream fishes is seemingly well studied, but most publications have focused on salmonids in cold water, upland habitats. Few published studies that explicitly examined the effects of introduced wood on fishes are available from the Coastal Plain of the southeastern US (Schneider and Winemiller 2008; Shields et al. 2003, 2006; Warren et al. 2009). This research gap is problematic for several reasons. Many Coastal Plain streams lack fallen wood due to habitat alteration and subsequent degradation, making the introduction of wood a critical component of preserving fish diversity (Warren 2012). Studies from sites elsewhere in North America fundamentally differ from the Coastal Plain region in factors like geology, hydrology, land-use history, and available habitat (Meffe and Sheldon 1988; Montgomery et al. 2003; Shields et al. 1998, 2000); thus, results from these studies cannot be assumed to apply to Coastal Plain streams. In addition, the effects of wood on fish abundance and diversity are inconsistent (Roni et al. 2014, Stewart et al. 2009). Finally, efforts to mitigate the negative effects of human development on fishes are hampered by a lack of data to inform effective strategies to restore, enhance, and maintain fish diversity and stream habitat.

The lack of information on fish–wood interactions in the region seems odd because a high proportion of southeastern fishes are imperiled (Jelks et al. 2008), and fishes in lowland Coastal Plain streams are likely more dependent on wood than

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fishes in upland streams with rocky cover. Southeastern Coastal Plain streams generally lack coarse rock substrate, and fishes are reliant on wood to provide habitat complexity and stability as well as spawning substrate, and as a source of diverse invertebrate prey, cover, and current and drought refugia (Crook and Robertson 1999, Monzyk et al. 1997, Montgomery et al. 2003, Pilotto et al. 2014, Shields et al. 1994, Smock and Gilinsky 1992, Warren 2012, Warren et al. 2002).

Results from the few studies examining the effects of introduced wood on fishes in warmwater streams in North America, including those outside the Coastal Plain, show a gradient in responses among species from negative to positive as well as changes in stream morphology due to altered hydrology (Angermeier and Karr 1984, Gatz 2008, Hrodey and Sutton 2008, Warren et al. 2009). Experimental reaches with introduced wood generally have more diverse sediments, lower flow, and greater depths than reaches without wood (Angermeier and Karr 1984, Webb and Erskine 2005). Overall results from manipulative studies are generally consistent with observational studies from the Coastal Plain showing fish and wood relationships (Meffe and Sheldon 1988, Scott and Angermeier 1998, Warren et al. 2002).

Studies of stream invertebrate communities provide direct and indirect evidence for the effects of wood on fishes in lowland streams. The presence or introduction of wood in streams influences invertebrate density, richness, and biomass (Benke and Wallace 2015, Benke et al. 1985, Pilotto et al. 2014) and likely has invertebrate-mediated effects on fishes (Benke et al. 1985, Gary and Hargrave 2017). However, as for fish, the introduction of wood has variable effects on benthic communities (Leps et al. 2016, Palmer et al. 2010), which renders invertebrate-mediated effects on fishes uncertain.

The study of introduced wood as fish habitat has almost exclusively focused on large wood (LW; here defined as ≥10 cm diameter, ≥100 cm long). Only 2 publications have reported the effects of introduced small wood (SW, <10 cm diameter, 100 cm long) on fishes in lowland warmwater streams (Schneider and Winemiller 2008, Warren et al. 2009). The study of SW deserves more attention because: (1) LW is often removed from streams by humans (Benke et al. 1985, Hrodey and Sutton 2008, Shields et al. 2000), (2) deforestation of riparian zones and poor land management lower rates of recruitment of LW into streams (Hrodey and Sutton 2008, Keeton et al. 2007, Warren 2012, Williams 1989), and (3) LW is often rapidly transported out of streams by flashy flows resulting from stream channelization and incisement (Shields et al. 1994, Warren 2012), a process that apparently occurs in confined streams worldwide (Kramer and Wohl 2017, Wyżga et al. 2017). Under these conditions (i.e., heavily modified, channelized, and incised, sand-bottomed Coastal Plain streams), LW is often relatively rare and SW, when present, provides most of the available structure and habitat for aquatic organisms (Hrodey and Sutton 2008; Shields et al. 1994, 2006; Warren et al. 2002; Wohl 2004). Degraded, channelized, and incised streams are common in the southeastern Coastal Plain (Schoof 1980, Wohl 2004), especially for streams running through agricultural lands (Pierce et al. 2012). These streams generally also have depauperate fish communities relative to less-disturbed streams (Etnier 1972, Lau et al. 2006, Roth et al. 1996, Sullivan et al. 2004). The study presented here used installed SW bundles in a degraded Coastal Plain stream to investigate whether or not the fish community would show greater taxonomic and functional diversity in reaches with installed wood than in unmanipulated reaches that largely lacked wood.

Field-Site Description

The study site was located at West Cypress Creek, a 3rd-order Coastal Plain stream typical of the Little Tallahatchie River system in north-central Mississippi (Fig. 1). The area near West Cypress Creek consists of low rolling hills (maximum relief about 130 m), and land use is a mix of *Pinus* (pine) plantations, pine–hardwood forest, row crops, and scattered housing. Streams within the area have sand as their primary substrate and substrate particles >16 mm diameter are exceedingly rare (Warren et al. 2002). Natural stream-bed controls are uncommon (Shields et al. 1997, Warren et al. 2002) and are not apparent in West Cypress Creek. In-stream wood is also uncommon (Warren et al. 2002). Extensive channelization throughout the Little Tallahatchie River watershed has caused West Cypress Creek to be deeply incised (5–6 m) and channelized with unstable banks and a highly unstable stream bed; the stream is wide and uniformly shallow and experiences flashy flows. We selected West Cypress Creek as our study site because we hypothesized that a

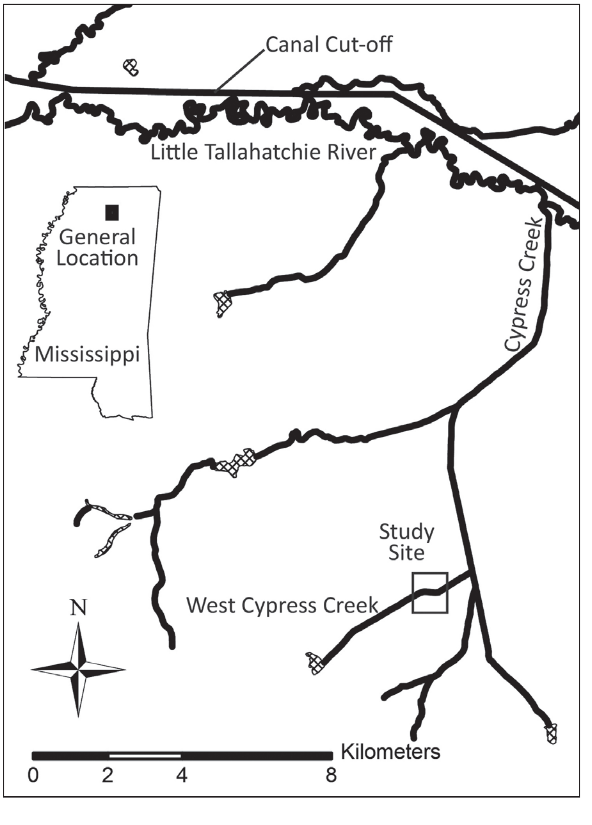

Figure 1. Map of the general location of the study in north-central Mississippi and the location of the study site in West Cypress Creek showing channelized stream reaches from the headwaters of West Cypress Creek downstream to the old channel of the Little Tallahatchie River and the channelized Tallahatchie Canal cut-off.

highly degraded stream would be more likely to show a response to our treatments than less-degraded streams that contained more wood.

Deforestation, channelization, and construction of headwater impoundments are all common on streams in the Coastal Plain of the southeastern US. Managers employ these tools to mitigate flooding, improve drainage, and to efficiently use all available land for agricultural purposes. However, all 3 practices cause streams to become incised and disconnected from floodplains (Wohl 2004). Channelized and incised streams result in wide, shallow, homogenous stream habitat with unstable banks and often highly mobile stream beds with limited stable structures, including woody debris (Shields et al. 1994, Sullivan et al. 2004, Wohl 2004). West Cypress Creek is apparently representative of many other highly degraded small- to medium-sized streams throughout the southeastern Coastal Plain, especially in agricultural areas.

The study reach was typical of the rest of West Cypress Creek and other similar-sized streams in the area. Variation in the types and amounts of available habitat was minimal. The study reach consisted almost entirely of a sand-bed run with scattered undercut banks and a few small, shallow, ephemeral pools along the bank. SW and organic debris were the primary available cover types. LW was rare, and SW and detritus were ephemeral. Two headwater impoundments were upstream of our study reach (~3.1 km and 3.3 km). A bridge located downstream (~150 m) had a short segment of rip-rap crossing the stream bed that had a slightly steeper gradient than the rest of the stream and partially isolated the study reach. Watershed area upstream of the study reach was ~21 km^2.

The fish fauna within degraded channelized streams in the region is generally dominated by small cyprinids tolerant of harsh and variable environments (Adams et al. 2004; Shields et al. 1994, 1998, 2003). Compared with other less-disturbed streams in the area, fish assemblages tend to be less diverse (Shields et al. 1994, Warren et al. 2002).

Methods

Study design and measurement of response variables

The study reach was about 455 m in length. We divided the reach among 3 treatments with 2 replicates in each: reference, patchy, and dense. We installed SW brush bundles in the patchy and dense treatments. The patchy treatment consisted of 3 patches of bundles that occupied the wetted width of the stream. Each was ~12 m long (Fig. S1 in Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s17-1-S2388-Sterling-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2388.s1). There was ~12 m of unmanipulated stream between patches (~60 m length total/treatment). The dense treatment was identical to the patchy treatment, but we filled the two 12-m gaps between patches with more bundles leaving no gaps. The wetted-width changed over time; thus, the number of bundles in the stream varied and we replaced bundles as needed, but at least 2 weeks prior to sampling.

The third treatment consisted of 2 unmanipulated reference reaches. Reference reaches were also about 60 m long and had small amounts of ephemeral cover, small side-pools, and scattered undercut banks that changed rapidly through time. We made no attempt to remove habitat from the reference reaches. We categorized 3 segments of the stream within the study reach as open and collected no data in those reaches. From downstream to upstream, the order of the stream segments within the study reach was: patchy 1 (60 m), open 1 (60 m), dense 1 (60 m), reference 1 (60 m), open 2 (10 m), reference 2 (60 m), patchy 2 (60 m), open 3 (25 m), and dense 2 (60 m).

We constructed brush bundles from freshly cut ~1.5–2-m–tall deciduous shrubs. Stem diameters were ~1.5–3.5 cm diameter. We used zip ties to bind together 3–4 shrubs and fastened them to steel rebar driven into the stream bed.

We sampled the study reach 9 times from July 2009 to May 2013 at ~4–7-month intervals. We employed single-pass backpack electroshocking with 3 people dipnetting in an upstream direction to collect fishes from the entire reach in 1 day. We allocated sufficient effort to thoroughly sample the entire area of each treatment. We identified fishes in the field and released them near the center of the capture reach. We preserved in 5% buffered formalin and brought back to the laboratory for identification all fish for which field identifications were impossible.

Taxonomic and functional diversity indices

To quantify fish community diversity, we calculated 3 indices for each treatment for each of the 9 samples: rarefied species richness (Colwell et al. 2012); Hurlbert's probability of an interspecific encounter (PIE; Hurlbert 1971), which is a measure of evenness (i.e., probability that 2 individuals drawn randomly from the sample represent different species); and the Berger–Parker dominance index, which is the proportion of the most common species for a given sample (Berger and Parker 1970). To estimate rarefied species richness, we used the program EstimateS (Colwell 2013) and the individual-based option (Colwell et al. 2012) to produce estimates for each sample through time. Hurlbert's PIE has the advantage of not confounding richness and evenness in 1 number (e.g., Shannon index), which renders estimates easy to interpret (Hurlbert 1971). Likewise, using the proportion of the most abundant species in a sample is a straightforward and easily interpretable estimate of dominance. We employed the formula function in a spreadsheet to calculate evenness and dominance.

To quantify functional fish-community diversity, we calculated 2 indices for each treatment for each of the 9 samples (Fig. S2 inSupplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s17-1-S2388-Sterling-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2388.s1): functional richness and functional evenness (Cornwell et al. 2006; Mason et al. 2005; Villéger et al. 2008, 2010). Each of the indices accommodates multiple functional traits and is measured in a multidimensional hypervolume. Functional richness is the volume of functional-trait space occupied by a given assemblage of species and was estimated using convex hulls. We calculated functional evenness using a minimum spanning tree that connected all species and measured the uniformity of species' distribution and abundance along the tree (Fig. S2 in Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s17-1-S2388-Sterling-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2388.s1).

We employed a principal coordinates analysis based on Gower's distance to create the functional space from which functional diversity estimates were calculated (Maire et al. 2015; Villéger et al. 2008, 2010). All calculations were carried out in R ver. 3.3.1 (R Core Team 2016) using R scripts and functions available online at http://villeger.sebastien.free.fr/homepage.html (Villéger 2016). We estimated 13 functional traits for each species to consider various aspects of ecological function including life history, physiology, habitat, and trophic variables (Table S1 in Supplemental File 1, available online at http://www.eaglehill.us/SENAonline/suppl-files/s17-1-S2388-Sterling-s1, and, for BioOne subscribers, at http://dx.doi.org/10.1656/S2388.s1). We obtained functional traits for each species from the online FishTraits database (Frimpong and Angermeier 2009, 2013) and from Ross (2001).

Statistical analyses

To test for differences among treatments for each of the 5 diversity indices, we used a repeated measures MANOVA as implemented in JMP ver. 13.0 (SAS Institute, Cary, NC). For studies using repeated measures over time with multivariate data, 2 of the most common methods of analysis are mixed-model approaches and longitudinal MANOVA. We chose to use MANOVA because the approach and output are familiar to a wide audience, results are easily interpretable, and, for simple balanced designs such as ours with no missing data, MANOVA performs as well as the mixed-model approach. As a parametric method, data is assumed to be distributed normally, though the method is robust to moderate violations of this assumption (O'Brien and Kaiser 1985, Sall et al. 2005). The method is limited to balanced data with no missing values and with qualitative differences among repeated samples (e.g., different seasons), and does not accommodate categorical variables. We $\log_{10}$-transformed the rarefied richness data (McDonald 2014) and Logit-transformed all other diversity indices (Warton and Hui 2011). Our visual inspections of data histograms for each index confirmed that they were distributed normally. Alpha was adjusted ($\alpha = 0.027$) for pairwise comparisons among treatments using a false-discovery–rate method (Narum 2006).

In some studies, functional richness is correlated with species richness (Villéger et al. 2008); thus, we performed correlation analysis between the 2 indices for each treatment. We square-root–transformed and relativized the data to the standard deviate (McCune and Grace 2002).

Characterizing differences in fish communities

We employed several methods to examine differences in community composition among treatments. We summarized rank abundance (catch/unit of effort [CPUE], fish/s) of species by treatment. Two nonmetric multidimensional-scaling (NMDS) ordinations were created using species and family abundance data in PC-ORD ver. 6.21 (McCune and Mefford 2011) to array species and families in sample (i.e., treatment) space (transpose analysis), which indicates the ecological preferences of each species and family (McCune and Grace 2002). We quantified relative proportional abundance of families with >1 representative species among treatments (±95% confidence intervals) to produce a visual representation (bar graphs) of fish-family responses. We estimated confidence intervals using 10,000 iterations in the Resampling Stats add-in for Excel (Statistics.com LLC 2009). We combined the data into a single "wood" treatment for ordinations to render them more easily interpretable and present results for the rank-abundance data for each woody treatment and the 2 woody treatments combined.

Results

Taxonomic and functional diversity indices: MANOVA and correlation

We detected differences among treatments for rarefied richness (MANOVA: F = 34.16, df = 2, $P < 0.024$). Pairwise comparisons showed that rarefied richness was higher in dense than in reference reaches (F = 34.16, df = 1, $P < 0.01$), but patchy and reference reaches were not significantly different (F = 12.98, df = 1, $P < 0.037$). No differences occurred between patchy and dense reaches (F = 5.03, df = 1, P = 0.11) (Fig. 2). Likewise, there were no interactions between time and treatment (F = 0.7, df = 16, P = 0.76).

For evenness, differences existed among treatments (MANOVA: F = 12.52, df = 2, $P < 0.035$). Pairwise comparisons showed the dense treatment had higher evenness than the reference treatment (F = 23.02, df = 1, $P < 0.017$), but the patchy and the reference treatments were not significantly different (F = 13.19, df = 1, $P <$ 0.036) No differences occurred between the patchy and the dense treatments (F = 1.36, df = 1, P = 0.33; Fig. 2). There were no interactions between time and treatment (F = 1.15, df = 16, P = 0.37).

We detected differences in species dominance among treatments (MANOVA: F = 15.67, df = 2, $P < 0.026$). Pairwise comparisons showed dominance was lower in the dense than in the reference treatments (F = 24.42, df = 1, $P < 0.013$) and in the patchy than in the reference treatments (F = 17.16, df = 1, $P < 0.026$). No differences were detected between the patchy and the dense treatments (F = 1.41, df = 1, P = 0.32) (Fig. 2). There were no interactions between time and treatment (F = 0.97, df = 16, P = 0.51).

For functional richness, we detected no significant differences in the overall test (MANOVA: F = 5.02, df = 2, P = 0.11. Pairwise comparisons showed no significant difference in functional richness between the dense and the reference treatments (F = 9.37, df = 1, $P < 0.053$), between the patchy and the reference treatments (F = 4.15, df = 1, P = 0.13) or between the patchy and the dense treatments (F = 0.1.41, df = 1, P = 0.36) (Fig. 3). There were no interactions between time and treatment (F = 0.83, df = 16, P = 0.64).

Mean functional evenness was highly similar among treatments and not significantly different (F = 0.89, df = 2, P = 0.49; Fig. 3). Correlations between functional richness and species richness showed mixed responses, but all were non-significant ($P > 0.31$): reference, r = 0.13; patchy, r = -0.25; and dense, r = -0.07.

Ranked abundance

Ranked abundance (CPUE) for each treatment showed that most species had 1 of 3 responses (Table 1): a positive response to the woody treatments and a negative one to the reference; a positive response to the reference and a negative one to the woody treatments; or a mixed response showing higher abundance in the reference and dense treatments and lower abundance in the patchy treatment. The most abundant species for all treatments was *Notropis rafinesquei* (Yazoo Shiner), which showed a negative response to the woody treatments. Two commonly sampled sunfishes *Lepomis megalotis* (Longear Sunfish) and *Lepomis macrochirus* (Bluegill) were more abundant in the reference and the dense treatments than in the patchy

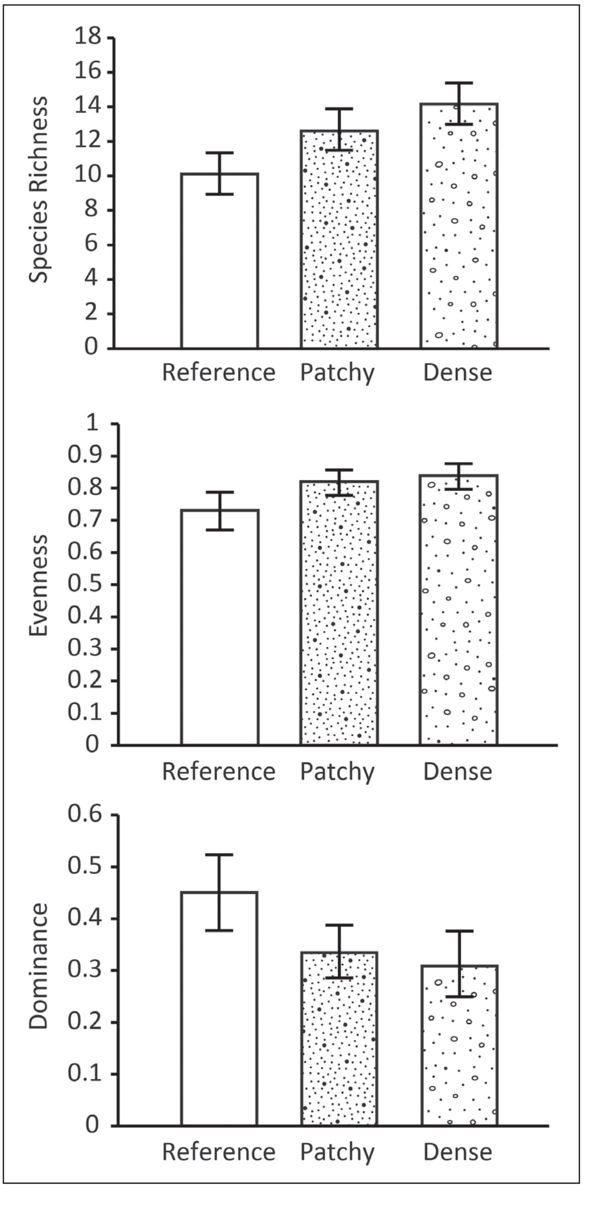

Figure 2. Mean values for each taxonomic diversity index is shown (± 95% CIs) for each treatment.

treatment; however, *Lepomis cyanellus* (Green Sunfish) showed little response to any of the treatments. Cyprinids varied in their responses with some showing a pattern similar to Bluegills, e.g., *Pimephales notatus* (Bluntnose Minnow), others showed a positive response to the woody treatments, e.g., *Notemigonus crysoleucas* (Golden Shiner) and *Cyprinella venusta* (Blacktail Shiner), others showed a negative response to the woody treatments, e.g., Yazoo Shiner, and still others showed little response at all, e.g., *Cyprinella camura* (Bluntface Shiner).

Percina sciera (Dusky Darter) and *Noturus miurus* (Brindled Madtom) showed among the strongest positive responses to the woody treatments. Two other darter species, *Etheostoma lynceum* (Brighteye Darter) and *Etheostoma artesiae* (Redspot Darter), also showed positive responses to the woody treatments. However, the frequently sampled *Noturus phaeus* (Brown Madtom) only showed a weak positive response to the woody treatments similar to another catfish, *Ameiurus natalis* (Yellow Bullhead).

NMDS ordinations

Ordinations of species in treatment space described gradients in wood density. The final NMDS ordination of fish species in treatment space recommended a 3-dimensional solution and had moderate stress (10.2) and low instability (<0.0001) (Fig. 4). Separate runs with random starting points returned very similar results; however, only the third axis was meaningful. On axis 3, samples described a gradient from woody treatments to the reference treatment. Yazoo Shiners were

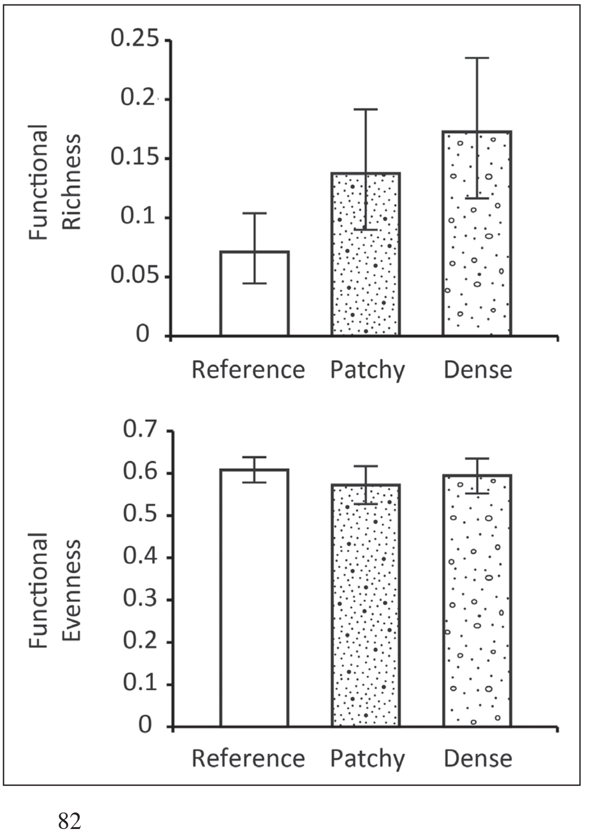

Figure 3. Mean values for each functional diversity index is shown (± 95% CIs) for each treatment.

most strongly associated with the reference treatment. *Etheostoma gracile* (Slough Darter), *Luxilus chrysocephalus* (Striped Shiner), and *Semotilus atromaculatus* (Creek Chub) were also associated with reference reaches. Species showing the strongest associations with wood were Redspot and Brighteye Darters, *Ameiurus melas* (Black Bullhead), *Micropterus salmoides* (Largemouth Bass), and several minnows: *Hybognathus nuchalis* (Mississippi Silvery Minnow), *Lythrurus fumeus* (Ribbon Shiner), and Golden Shiner (Table 2).

Table 1. Ranked abundance (CPUE, fish/s) for each fish species and each treatment; Woody = patchy and dense combined. Key: ANAT: *Ameiurus natalis,* AMEL: *Ameiurus melas,* NMIU: *Noturus miurus,* NPHA: *Noturus phaeus*, PSCI: *Percina sciera*, EART: *Etheostoma artesiae*, EGRA: *E. gracile*, ELYN: *E. lynceum*, LCYA: *Lepomis cyanellus*, LGUL: *L. gulosus*, LMAC: *L. macrochirus*, LMAR: *L. marginatus*, LMEG: *L. megalotis*, MSAL: *Micropterus salmoides*, CCAM: *Cyprinella camura*, CVEN: *C. venusta*, LCHR: *Luxilus chrysocephalus*, NCRY: *Notemigonus crysoleucas*, NRAF: *Notropis rafinesquei*, NATH: *Notropis atherinoides*, LUMB: *Lythrurus umbratilis*, LFUM: *Lythrurus fumeus*, PNOT: *Pimephales notatus*, SATR: *Semotilus atromaculatus*, HNUC: *Hybognathus nuchalis*, ASAY: *Aphredoderus sayanus*, FOLI: *Fundulus olivaceus*, ECLA: *Erimyzon claviformis*, GAFF: *Gambusia affinis*

Reference		Patchy		Dense		Woody	
Species	CPUE	Species	CPUE	Species	CPUE	Species	CPUE
NRAF	0.1252	NRAF	0.0701	NRAF	0.0959	NRAF	0.0824
FOLI	0.0402	FOLI	0.0467	FOLI	0.0434	FOLI	0.0451
LMEG	0.0257	LMAC	0.0206	LMAC	0.0327	LMAC	0.0264
LMAC	0.0241	LMEG	0.0152	LMEG	0.0259	LMEG	0.0203
PNOT	0.0216	CCAM	0.0141	PNOT	0.0200	CCAM	0.0150
CCAM	0.0137	NPHA	0.0125	CCAM	0.016	PNOT	0.0146
SATR	0.0107	SATR	0.0122	NPHA	0.0115	NPHA	0.0120
NPHA	0.0096	PNOT	0.0096	LCYA	0.0100	SATR	0.0105
LCYA	0.0074	LCYA	0.0077	SATR	0.0086	LCYA	0.0088
GAFF	0.0059	NMIU	0.0037	NMIU	0.0053	NMIU	0.0045
ANAT	0.0028	GAFF	0.0032	GAFF	0.0051	GAFF	0.0041
LUMB	0.0022	PSCI	0.0032	ANAT	0.0041	ANAT	0.0034
CVEN	0.0019	ANAT	0.0028	PSCI	0.0036	PSCI	0.0034
NMIU	0.0019	CVEN	0.0028	CVEN	0.0032	CVEN	0.0030
ASAY	0.0016	ASAY	0.0023	LUMB	0.0029	LUMB	0.0021
ECLA	0.0010	ELYN	0.0016	NCRY	0.0023	ASAY	0.0021
LGUL	0.0010	ECLA	0.0015	ASAY	0.0018	NCRY	0.0018
MSAL	0.0008	NCRY	0.0015	ECLA	0.0018	ECLA	0.0017
ELYN	0.0006	LUMB	0.0014	MSAL	0.0016	ELYN	0.0014
LCHR	0.0006	EART	0.0009	LGUL	0.0012	MSAL	0.0010
NCRY	0.0006	LGUL	0.0007	ELYN	0.0011	LGUL	0.0009
PSCI	0.0006	MSAL	0.0005	NATH	0.0007	EART	0.0006
AMEL	0.0006	LFUM	0.0002	LCHR	0.0005	NATH	0.0003
EGRA	0.0002	AMEL	0.0002	EART	0.0004	LCHR	0.0002
EART	0.0000	LMAR	0.0001	LMAR	0.0002	AMEL	0.0002
LMAR	0.0000	EGRA	0.0000	AMEL	0.0002	LMAR	0.0002
HNUC	0.0000	LCHR	0.0000	HNUC	0.0001	LFUM	0.0001
LFUM	0;0000	HNUC	0.0000	EGRA	0.0000	HNUC	0.0001
NATH	0;0000	NATH	0.0000	LFUM	0.0000	EGRA	0.0000

Similarly, the ordination of families in treatment space revealed a wood-density gradient. The final NMDS ordination of fish families in treatment space

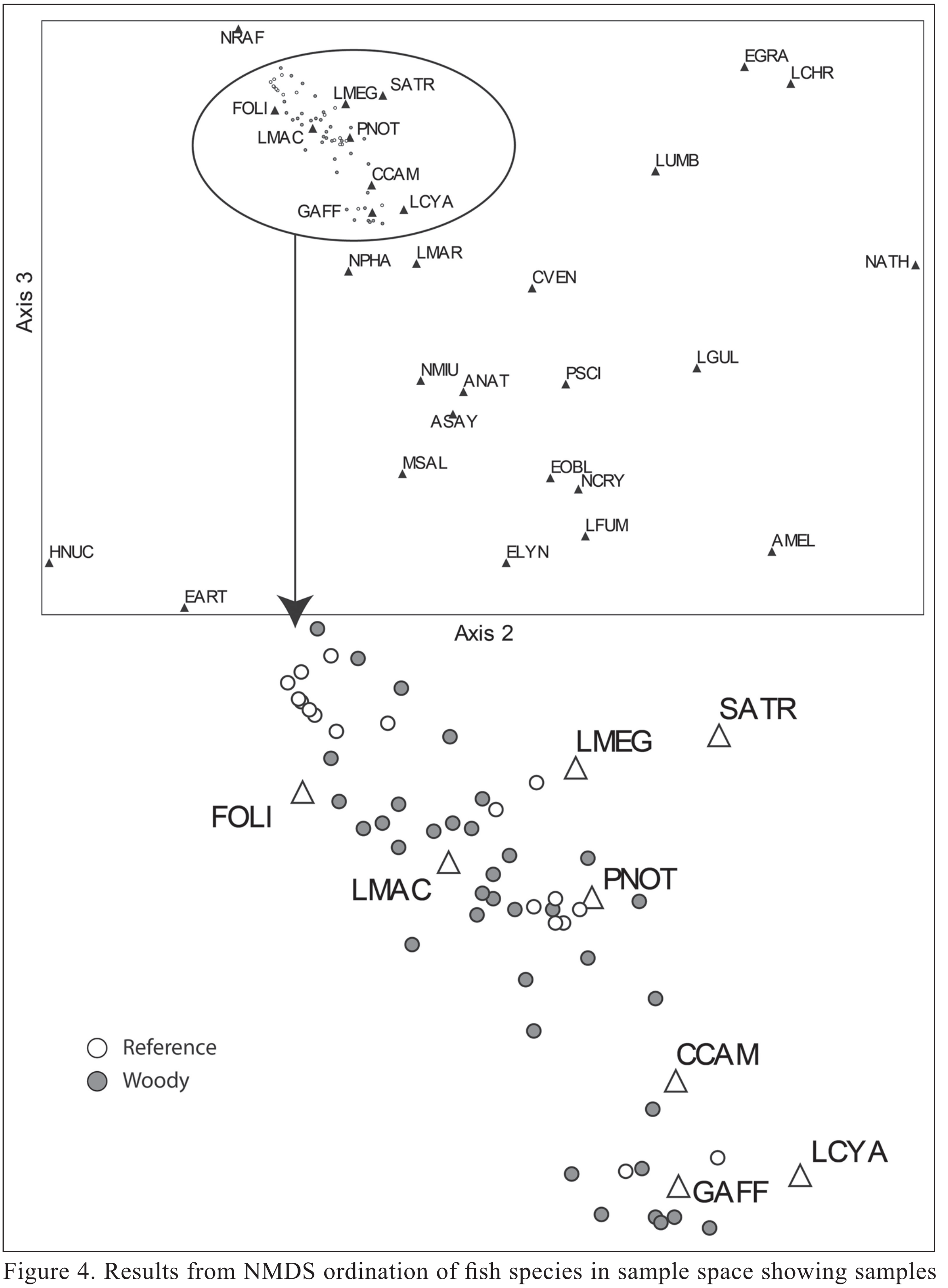

Figure 4. Results from NMDS ordination of fish species in sample space showing samples from woody treatments and reference reaches; key for species abbreviations are in Table 1; the portion of the graph containing sample points is enlarged for clarity.

recommended a 2-dimensional solution and had low stress (0.0003) and instability (<0.00001) (Fig. 5). Separate runs with random starting points returned very similar results; however, only the first axis was biologically interpretable. Samples showed a gradient from woody treatments to the reference treatment that is similar to that from the ordination of species data. Cyprinidae were associated with the reference treatment. Centrachidae and Fundulidae showed little association with either woody or reference treatments. Ictaluridae, Poeciliidae, Percidae, Aphredoderidae, and Catostomidae were all associated with the woody treatments (Table 3).

Proportional data

Relative proportional abundances within families were generally consistent with ordinations and ranked-abundance results. Darters (Percidae) and catfishes (Ictaluridae) showed the strongest positive response to the woody treatments, but differences were not apparent in response between those treatments (Fig. 6). Proportional abundance of Cyprinidae and Centrarchidae showed a gradient in response with apparent differences between all treatments. For all families, abundance was lowest in the reference treatment (Fig. 6).

Table 2. NMDS ordination scores for each fish species on 3 axes.

Species	Axis 1	Axis 2	Axis 3
Ameiurus natalis (Lesueur) (Yellow Bullhead)	-0.1529	-0.0260	-0.2636
Ameiurus melas (Rafinesque) (Black Bullhead)	-0.2803	0.8999	-0.7431
Noturus miurus Jordan (Brindled Madtom)	-0.1697	-0.1529	-0.2282
Noturus phaeus Taylor (Brown Madtom)	-0.0307	-0.3709	0.0979
Percina sciera (Swain) (Dusky Darter)	0.3398	0.2817	-0.2401
Etheostoma artesiae (Hay) (Redspot Darter)	-0.5716	-0.8626	-0.9106
Etheostoma gracile (Girard) (Slough Darter)	1.4525	0.8174	0.7136
Etheostoma lynceum Hay (Brighteye Darter)	0.4855	0.1032	-0.7750
Lepomis cyanellus Rafinesque (Green Sunfish)	-0.0840	-0.2030	0.2831
Lepomis gulosus (Cuvier) (Warmouth)	-0.0489	0.6754	-0.1922
Lepomis macrochirus Rafinesque (Bluegill)	0.0735	-0.4776	0.5269
Lepomis marginatus (Holbrook) (Dollar Sunfish)	-1.7251	-0.1657	0.1227
Lepomis megalotis (Rafinesque) (Longear Sunfish)	0.1446	-0.3790	0.6007
Micropterus salmoides (Lacepède) (Largemouth Bass)	-0.8582	-0.2077	-0.5084
Cyprinella camura (Jordan and Meek) (Bluntface Shiner)	0.0745	-0.3013	0.3569
Cyprinella venusta Girard (Blacktail Shiner)	-0.0672	0.1806	0.0482
Luxilus chrysocephalus Rafinesque (Striped Shiner)	-0.7273	0.9575	0.6617
Notemigonus crysoleucas (Mitchell) (Golden Shiner)	-0.4237	0.3195	-0.5558
Notropis rafinesquei Suttkus (Yazoo Shiner)	0.3561	-0.6992	0.8260
Notropis atherinoides Rafinesque (Emerald Shiner)	0.0552	1.3306	0.1178
Lythrurus umbratilis (Girard) (Redfin Shiner)	-0.0509	0.5515	0.3992
Lythrurus fumeus (Evermann) (Ribbon Shiner)	1.3728	0.3397	-0.6950
Pimephales notatus (Rafinesque) (Bluntnose Minnow)	0.1787	-0.3662	0.4994
Semotilus atromaculatus (Mitchill) (Creek Chub)	0.0044	-0.2673	0.6275
Hybognathus nuchalis Agassiz (Mississippi Silvery Minnow)	1.148	-1.2687	-0.7757
Aphredoderus sayanus (Gilliams) (Pirate Perch)	-0.5887	-0.0557	-0.3304
Fundulus olivaceus (Storer) (Blackspotted Topminnow)	0.1802	-0.5908	0.5824
Erimyzon claviformis (Girard) (Western Creek Chubsucker)	0.3771	0.2357	-0.5210
Gambusia affinis (Baird and Girard) (Western Mosquitofish)	-0.4636	-0.2982	0.2752

Discussion

Examination of P-values from the MANOVA tests show that the results contrasting the patchy with the reference treatment were either marginally significant or insignificant after adjustment for multiple pairwise tests. In contrast, the dense treatment was consistently significantly different from the reference treatment, but the dense treatment was no different than the patchy treatment. To interpret biological differences between treatments at P-values of <0.027 (i.e., dense versus

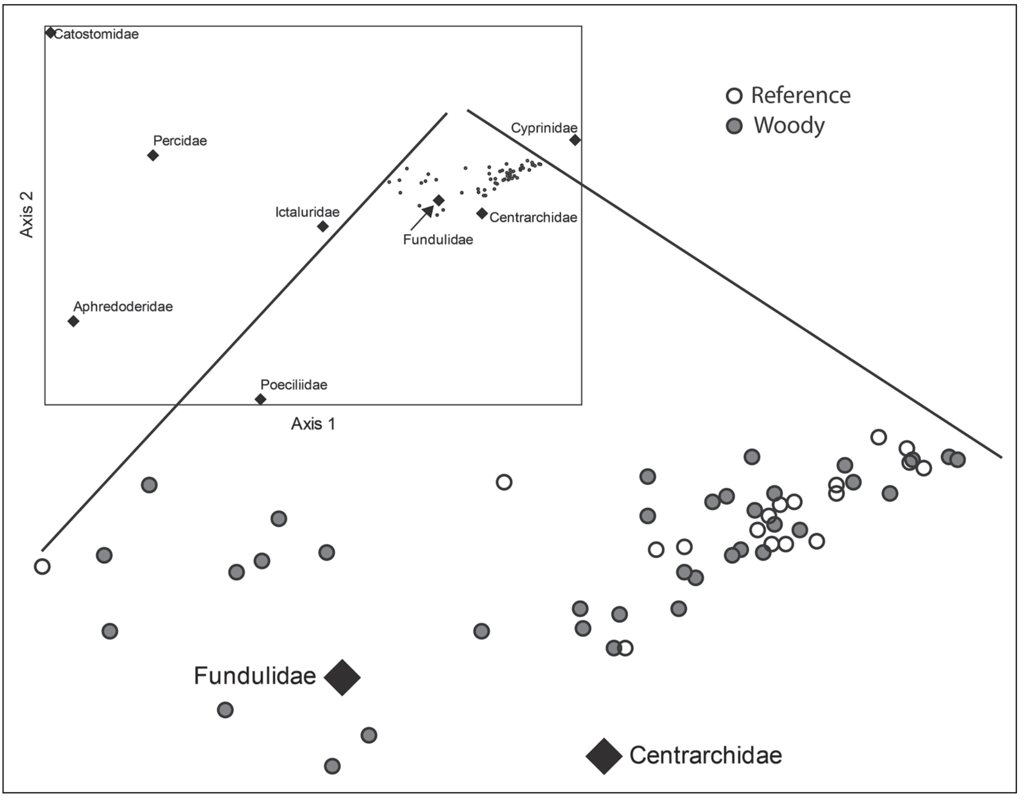

Figure 5. Results from NMDS ordination of fish families in sample space showing samples from woody treatments and reference reaches; the portion of the graph containing sample points is enlarged for clarity.

Table 3. NMDS ordination scores for each fish family on 2 axes.

Family	Axis 1	Axis 2
Percidae	-0.689	0.247
Ictaluridae	0.139	-0.012
Centrarchidae	0.904	0.029
Cyprinidae	1.378	0.238
Fundulidae	0.629	0.199
Catostomidae	-1.294	0.717
Aphredoderidae	-0.998	-0.564
Poeciliidae	-0.069	-0.854

reference) but not when P-values were <0.04 (i.e., patchy versus reference) is unreasonable and lacking in biological rationale (Gelman and Stern 2006). Additional samples would undoubtedly have increased our ability to detect differences, even with adjustments for multiple comparisons, by reducing variance and increasing power. We interpret our results as showing biologically significant differences between woody reaches and reference reaches for each of the 3 taxonomic diversity indices and perhaps a difference between the dense and reference treatments for the functional richness index.

Results showing higher species richness and evenness and lower dominance coupled with suggested higher functional richness in the woody-treatment reaches indicate that within the habitat-starved streams of channelized or incised watersheds (Shields et al. 1994, Warren et al. 2002), even a modest input of wood may have a positive impact on fish community and functional diversity. This conclusion is supported by the proportional-abundance data (Fig. 6). Results were consistent with general expectations (Moulliot et al. 2013, Roni et al. 2014, Warren 2012, but see Stewart et al. 2009), as well as with the few experimental studies from warm-water streams in the US (Angermeier and Karr 1984, Gatz 2008, Hrodey and Sutton 2008, Warren et al. 2009, but see Schneider and Winemiller 2008).

Two factors may have had important impacts on the results of this study. The first is that the downstream road crossing may have been a finer filter to fish passage than we anticipated. Fish species diversity was higher downstream of

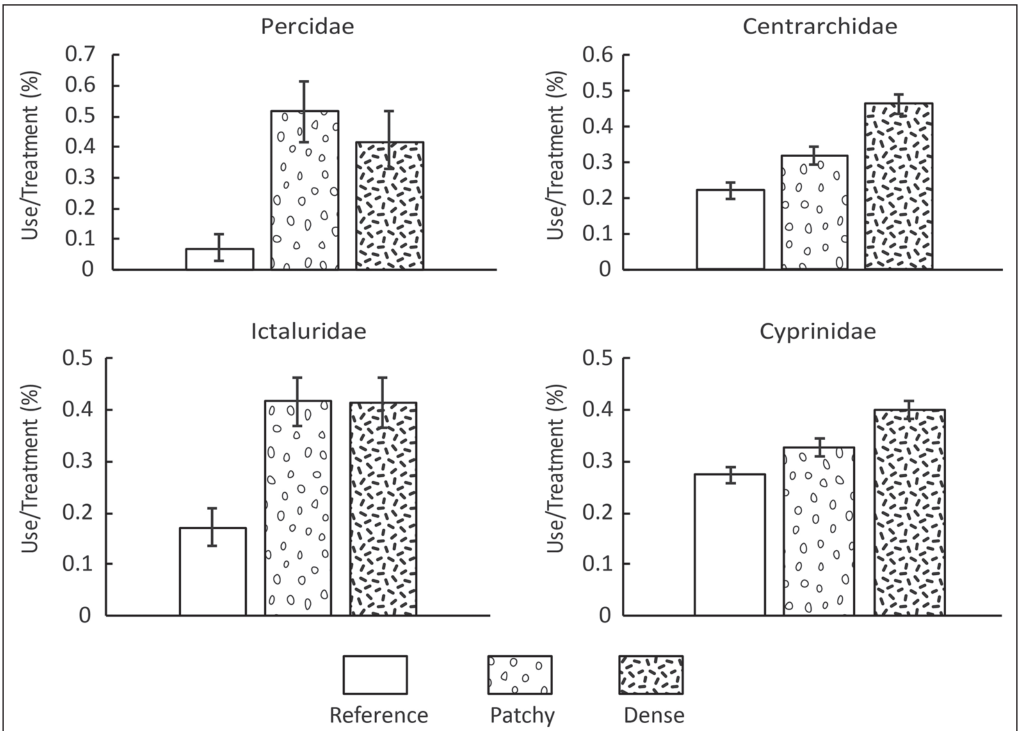

Figure 6. Proportional abundances (± 95% CIs) of fish families with more than 1 species are shown for each treatment.

the crossing (K.A. Sterling and M.L. Warren Jr., unpubl. data), and though we anticipated immigration from this larger species pool, it did not occur or at least was highly limited, and may have decreased the effect of the treatments on the fish community. A second factor was that our woody-bundle installations were ephemeral. Though we maintained the bundles through time, we lost a substantial proportion of the bundles after every flood event, which then had to be replaced. The lack of stable habitat and cover through time likely decreased the effect of the treatments on the fish community. This contention is supported by evidence within the Cypress Creek drainage showing that fish assemblages are highly unstable and reactive to flashy flows, likely because fishes lack stable habitat and cover (Adams et al. 2004). Had our wood-bundle installations been permanent, it is likely we would have observed a more pronounced response.

Mean values for the 3 taxonomic diversity indices and the proportional abundance data suggest there may be a gradient in fish community response to the treatments, with the dense treatment showing the largest response. However, this result was likely due to more than just the wood introduced into the stream. The installation of wood bundles certainly provided complex cover, but also created areas of higher and slower current velocities as well as areas with deeper and shallower water around the bundles relative to the reference treatment, which had more or less homogenous flow and water depths. These observations are consistent with changes observed in another study (Angermeier and Karr 1984). Differences in flow velocity were also apparent between the dense and patchy treatments. The patchy treatments mostly created areas of swifter currents, and the dense treatments created areas of both slow and swift currents. This flow pattern was reflected in the responses of species as shown in the ranked abundance data. For example, Longear Sunfish and Bluegills had lower abundances in the patchy treatment compared with the dense and reference treatments, likely due to the presence of swift water. Unfortunately, we did not measure water depths and velocities across treatments through time to investigate the effects of these variables on fish populations. Even so, it is likely that the overall positive response of the fish community to the input of wood was due at least in part to the creation of more-variable current velocities and water depths (Dolloff and Warren 2003).

As summarized in the Introduction, fishes in lowland, soft-bottom streams rely on wood to provide habitat complexity and stability, cover, spawning substrate, current and drought refugia, and diverse invertebrate prey. We believe most, if not all, of these factors were likely influential in explaining our results, and other fish–wood relationship studies from northern Mississippi support this view. For example, Brown Madtoms and *Aphredoderus sayanus* (Pirate Perch) used woody cover with species-specific structural characteristics, showing that fishes select for certain characteristics and perhaps partition woody resources, allowing for greater species diversity (Monzyk et al. 1997). Sunfishes (*Lepomis* spp.) showed close associations with LW, perhaps because of increased pool volumes, refuge from stronger currents, greater invertebrate food resources, and cover from predation within degraded streams (Shields et al. 1998, Warren et al. 2002). A study that installed 3 types of SW or detritus bundles showed that use by a diverse fish assemblage was higher in streams that were more degraded and lacked woody cover, and also that use increased after a spate in degraded streams, but not in a less degraded stream, which suggests cover was limiting in the streams that were more degraded and fishes used the installed bundles as a high-flow refuge (Warren et al. 2009).

These regional results and our own are consistent with the literature across the Coastal Plain and other warmwater, lowland streams (Angermeier and Karr 1984, Gatz 2008, Hrodey and Sutton 2008, but see Schneider and Winemiller 2008); however, published studies, including ours, are mostly limited to describing patterns, and actual processes are understudied. Study results are consistent and our study stream is typical of many lowland, soft-bottom streams; thus, we believe our results are applicable to other highly degraded lowland streams, especially channelized streams running through agricultural lands. Confirmation of our findings is warranted, and we plan on replicating this study in other streams. Our study was limited in scope, but further research could include measurement of physical stream-habitat variables, flow, changes in the volume of wood through time, biomass and length of fishes, different spatial scales, and other components of the stream community (e.g., presence and/or abundance of invertebrate insects, crayfishes, amphibians, or fungi).

Mean functional richness, but not mean functional evenness, showed an apparent gradient in response to the addition of wood—reference reaches had the lowest mean values, values for the patchy treatment were intermediate, and the dense treatment had the highest values (Fig. 3). However, the lack of a clear positive or negative correlation between functional and rarefied species richness across samples and treatments precludes any definitive conclusion regarding why functional richness was apparently higher in the dense treatment. This result deserves to be explored further. The lack of differences among treatments for functional evenness is likely due to functional redundancy and relatively small changes in abundance among species and treatments.

General agreement emerged among our descriptive results (ranked abundance, ordinations, and proportional abundances) that darters and madtom catfishes showed the strongest response to the introduction of SW. This finding is consistent with results from 2 studies that included streams in the Little Tallahatchie River system and that examined, among other factors, the effects of LW (Warren et al. 2002) and SW (Warren et al. 2009) on fish communities.

Species-specific responses differed within families, and there were apparent positive, negative, mixed, and neutral responses to the woody treatments. This result shows that introducing SW to streams may not benefit all species and that the design of SW installations may greatly affect whether or not management goals are achieved (Angermeier and Karr 1984, Gatz 2008, Langford et al. 2012, Warren et al. 2009).

Overall, though results point to significant differences for 3 of 5 taxonomic and functional-diversity indices, numerical differences among treatments were moderate. However, an apparently small or moderate numerical shift in abundance or number of species present may have a great impact on stream communities (Dangles and Malmqvist 2004, Jackson et al. 2001, Taylor and Warren 2001) and especially on ecosystem functioning (Leitão et al. 2016, Martin et al. 2016, Mouillot et al. 2013). Investigation of the effects of fish community changes in response to the addition of wood on stream ecosystem function in lowland streams is an area ripe for investigation (e.g., Gary and Hargrave 2017).

Our results indicate that the introduction of modest amounts of SW in degraded Coastal Plain streams can increase fish community and perhaps functional diversity within stream reaches with introduced wood relative to reaches without installed wood. Notably, this increase was accomplished using only a few hand tools and limited personnel. A next step in researching the effects of SW on Coastal Plain stream fishes is to estimate whether or not the addition of SW increases species diversity, abundance, and ecosystem function over a larger spatiotemporal scale using stable installations of wood.

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