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Confluences and Land Cover As Agents of Change: Temporal Habitat Variability Modifies the Movement and Assemblage Change of Headwater Fishes

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Abstract

Interspersed inputs of wood and sediment brings about morphological change at confluences and the extent to which these processes are modified by anthropogenic disturbance has ramifications for stream fish assemblages. In this study, we use three functional groups of headwater fishes to assess the influences of confluence size and land cover on habitat stability, distance moved, movement rate, and assemblage change in a Gulf Coastal Plain drainage in the southeastern United States using a 2X2 design. Our results suggest that differences in habitat stability were described by a hydrogeomorphic gradient, and urban reaches characterized by a confluence size > 0.6 displayed the greatest habitat instability. Water-column specialists in urban reaches were more likely to move when habitat change was limited, whereas movement by this functional group in forested reaches was more likely in response to greater habitat instability. Therefore, the distance moved by water-column specialists was related to land cover. Assemblage change also occurred at a more constant rate in urban reaches in response to habitat instability. There was little evidence that confluence size influenced movement or assemblage stability in these headwater assemblages. Our understanding of the extent to which land cover alters the geomorphic and ecological gradients associated with headwater confluences will be critical to ensure the conservation of sensitive species whose fitness is dependent on the integrity of these habitats.

Introduction

Movement is integral to species survival because it influences colonization, gene flow, and resource use. The movement of a species is a function of its probability of transition between habitat patches (Levins 1966; Wiens 2002). Habitat fragmentation limits the movement of species by disrupting the connectivity and structure of habitat patches (Brown et al. 2001; Fagan 2002). Because organisms move to complete their life histories, even a small degree of fragmentation across an ecosystem can be detrimental to their survival, reproduction and growth. In dendritic river systems (Campbell-Grant et al. 2007), random habitat fragmentation increases the number of patch fragments, variance in patch size (Fagan 2002) and distance between patches, thus diminishing movement of species (Roberts and Angermeier 2007).

Confluences are areas of active geomorphic activity (Rice et al. 2001; Benda et al. 2004). Tributary junctions result in increases in the supply of water, sediment, and wood to the mainstem, thus mainstem channel responses should be greater in magnitude close to or directly downstream of confluences (Benda et al. 2004). Channel widening and declines in stream gradient often occur upstream of confluences as a consequence of greater wood and sediment storage, thus facilitating an increase in the magnitude of flow-related disturbances (Benda and Dune 1997). The magnitude of geomorphic change at confluences in headwater drainages is characterized by high flow events, which transport sediment and wood (Johnson and Rodine, 1984; Hogan et al. 1998). High flow events scour sediment and transport wood downstream, forming depositional areas such as gravel bars and alluvial fans (Benda and Cundy 1990; Benda et al. 2003). Sediment deposition at confluences induces predictable, localized, geomorphic responses in mainstem channels (Benda et al. 2004). For example, decreasing sediment transport at confluences should facilitate reductions in upstream channel gradient and substrate size, while increasing channel meandering and floodplain width in the mainstem. Such changes are counterbalanced in the downstream reach of the mainstem with increases to channel gradient, channel width, substrate size, pool depth, and bar occurrence. Because the supply of sediment is spatially interspersed, depositional areas at confluences will expand and contract in response to temporal variation in the hydrology (Benda et al. 2003). Thus, the upstream and downstream spatial extent of these habitats' influence on confluences should fluctuate with time.

Confluence size (i.e., the ratio between tributary size and mainstem size) and network geometry contribute substantially to the extent of geomorphology at confluences. Discharge-related morphological changes (i.e., channel width, depth), which scale to the size of the tributary in relation to the mainstem, occur at confluences where the ratio between tributary size and main stem size approaches 0.6 to 0.7 (Rhoads 1987). Local network geometry describes the angle at which

tributaries intersect the mainstem. Kilometer-scale variation of tributary effects in the mainstem can be described by local network geometry (Benda et al. 2004). In headwaters, Benda and Cundy (1990) demonstrated how confluence angles may regulate variability of depositional events, where confluence angles greater than 70º should engender high flow deposition, whereas deposition would be less likely at confluences with more acute angles.

Heightened habitat heterogeneity may encourage landscape complementation or supplementation by stream fishes at confluences because patches contain non-substitutable resources (food, spawning habitat) which are in close proximity to one another (Dunning et al. 1992). Thus, temporal assemblage turnover at confluences is often reduced (Dala-Corte et al. 2017), and the combined effects of colonization (Grenouillet et al. 2004; Hitt and Angermeier 2011) and spatial habitat heterogeneity engenders configuration-specific differences in fish abundance and evenness in disturbed stream reaches (Boddy et al. 2019). Therefore, differences in population sizes, species richness, and persistence may all be heightened at these tributary junctions (Thornbrugh and Gido 2010; Boddy et al. 2019). A partial explanation for this, is that patterns of dispersal differ at confluences as a consequence of species traits, thus influencing differences in tributary versus mainstem assemblage structure (Hitt and Angermeier 2008, Cathcart et al. 2015, Cathcart et al. 2018). For example, Cathcart et al. (2015) noted that fish movement patterns at a desert confluence on a large river varied substantially by species as a consequence of sensitivity to seasonal variation, and variability in the hydrologic regime.

Urban and agricultural land cover fragments streams, and habitat fragmentation at small spatiotemporal scales within these systems is intimately tied to land cover at coarser spatiotemporal scales (Wang et al. 2001; Allan 2004; Leal et al. 2016). Thus, broad anthropogenic impacts reduce the connectivity, stability, and diversity of habitat patches at smaller scales (Padgham and Webb 2010). Anthropogenic disturbance disrupts gene flow (Stow et al. 2001) while also degrading regional emergent properties such as species richness (Perkins and Gido 2012) by the elimination of movement pathways. However, the extent to which land cover modifies the role of confluences as agents of habitat change, and therefore, altering stream fish movement and assemblage change, is poorly understood.

Much work has been done to better understand the factors which influence variability in stream fish movement at the reach scale (Albanese et al. 2004, Walker and Adams 2016). Movement preference by an individual is informed by choices in relation to temporal (e.g., seasonality, Albanese et al. 2004, Koed et al. 2006), abiotic (e.g., hydrologic regime, habitat complexity, Albanese et al. 2004) and biotic (e.g., intra and interspecific differences, sex differences, presence of predators, Clark and Schaefer 2016; Pennock et al. 2018) factors made at multiple spatial extents (Belica and Rahel 2008; Clark and Schaefer 2016; Pennock et al. 2018). Regarding abiotic factors, habitat complexity (Baras 1992, Ronni and Quinn 2001; Albanese et al. 2004; Clark and Schaefer 2016), macrohabitat variability (e.g., riffle-pool sequences, Johnston 2000; Lonzarich et al. 2000; Roberts and Angermeier 2007) and alterations in stream discharge (Schaefer 2001; Koster and Cook 2008; Cooke and Taylor 2012) are frequently cited as important factors driving non-migratory patterns of movement in stream fishes. However, it is unclear whether alterations to these abiotic factors as a consequence of land cover and confluence size would yield similar effects on stream fish movement.

In this study, we examine habitat structure, movement, and stream fish assemblages at four headwater confluences that differed in size and surrounding land cover. We used mark-recapture methods to assess movement rate and assemblage change at the reach scale. We applied an information-criterion approach to test which habitat characteristics best described movement and assemblage change across confluence size or land cover factors. We predicted that 1) urban reaches characterized by a confluence size > 0.6 would exhibit the greatest habitat instability, 2) the distance moved by movers would vary as a consequence of land cover and confluence size, 3) movement rate and assemblage change would be associated with distinct reach scale components of habitat stability mediated by land cover and confluence size, and 4) stream fishes in urban reaches will exhibit a more rapid response (e.g., movement, assemblage change) to habitat instability.

Materials And Methods

Study System and Design

We conducted our study in the Pascagoula River drainage, which is positioned within the Southern Pine Plains and Hills ecoregion in the Gulf Coastal Plain province, and is the largest unimpounded river system in the contiguous United States (Dynesius & Nilsson, 1994; Hupp, 2000). Streams that drain this region tend to be either alluvial or blackwater systems and are characterized by low gradients and gravel, sand and clay substrates (Hupp, 2000).

Each of our four sites was located at the confluence of two headwater streams. Of the two upstream reaches at each site, we identified the reach with the larger upstream drainage area as the mainstem (Fig. 1A). We then delineated three contiguous 100 m reaches containing alternating riffle and pool patches. We established two factor levels for land cover (urban, forested) and confluence size (> 0.60, < 0.60) for each of the four sites. Confluence size ratios (CSR) are calculated by dividing the drainage area of the smaller stream by the drainage area of the mainstem; a threshold of > 0.6 represents the lowest value at which consistent geomorphic change may be observed because of confluence size (Benda et al. 2004). Two sites (Garraway and Mixon's Creeks) had large (> 0.6) CSR and two (Priest and Sweetwater Creeks) had small CSR. We measured CSR for each site using the National Hydrography Data Plus (NHDPlus) (USEPA and USGS 2016) set in ArcGIS (version 10.0, ESRI). Sites were only chosen if their confluence angle was < 60º to diminish local geomorphic effects that were a symptom of network geometry. The 2016 national land cover dataset (NLCD, https://www.mrlc.gov/data) was used to estimate the proportions of urban and forested land cover within each site's upstream catchment. Our urban sites (Priest and Mixon's Creeks, > 50% urban land cover) were located within the city limits of Hattiesburg, MS, and our forested sites (Garraway and Sweetwater Creeks, 100% forested land cover) were located within De Soto National Forest (Fig. 1B).

Data Collection and Organization

Functional Groups

We established three functional groups from fishes encountered at our sites. The benthic specialists included the bright eye darter (*Etheostoma lynceum*), the gulf darter (*E. swaini*), *and* the blackbanded darter (*Percina nigrofasciata*), water-column specialists included the blacktail shiner (*Cyprinella venusta*), the cherryfin shiner (*Lythrurus. roseipinnis*), the rough shiner (*Notropis baileyi*), and the flagfin shiner (*Pteronotropis signippinis*), and structure specialists included the bluegill (*Lepomis macrochirus*) the longear sunfish (*L.megalotis*), the green sunfish (*L. cyanellus*) and the shadow bass (*Ambloplites arriomus*).

Study Period

Initially, we marked fish in August of 2017 and May of 2018; subsequent mark-recapture events occurred at 4 to 6 week intervals (7 marking events total) and repeated visits to reaches within a site were treated as replicates. We attempted to conduct six recapture events at all four sites across two field seasons; two in the fall of 2017 and four in the spring-summer of 2018. However, flooding in the fall of 2017, resulted in a bridge failure that restricted access to one site. We replaced this site (small CSR, forested land cover) with a new site prior to beginning sampling in the summer of 2018. Thus, we conducted six recapture events at three sites, but only four recapture events were performed at the fourth site. Preliminary analysis suggested that there was not a significant effect of site, despite the unbalanced design (Table S1).

Mark-Recapture Methods

At each patch we made three passes using a 4.8 mm mesh seine and a ETS (Electrofishing Systems) Badger 1 backpack electrofishing unit using pulsed DC (range: 100 to 250 V). All darters > 40 mm standard length (SL), all sunfish

> 80 mm in SL, and all shiners > 40 mm in SL were marked. We gave all fish patch, batch-specific marks using visual implant elastomer (VIE; Northwest Marine Technology, Inc., Shaw Island, WA, USA). Small bodied minnows (Bangs et al. 2013; Neufeld et al. 2015), darters (Roberts and Angermeier 2004), and centrarchids (Laux et al. 2007) exhibit high retention of VIE tags over extended periods. We used three colors and six body locations to produce patch + visit marks. Prior to marking, we anesthetized fish with tricaine methanesulfonate (range = 60–100 mg/L). We marked fish to identify their initial patch of capture. During consecutive mark-recapture events, any fish that had moved received an additional mark specific to the new patch occupied, and all fish were released back to where they were captured. After marking, we held fish for 30 minutes to allow for recovery from anesthesia. Following recovery, we released fish in low velocity microhabitats near the midpoint of the patch from which they were sampled. We used the midpoint distance of the original patch of capture and patch of recapture to establish the beginning and end points of the total distance moved by a fish for all pairs of patches. Because recapture rates of benthic specialists and structure specialists were variable among sites (Table 1), we only analyzed differences in distance moved and movement rate of water-column specialists. Our first recapture event of the 2018 field season allowed us to estimate the percentage of fishes recaptured between our two field seasons. At the end of the 2018 field season, we performed broader sampling (1–2 river km) for each site to identify any individuals that may have moved outside of the study-reaches.

Table 1

Percent recapture rates for trips, years, and between years for three functional groups of fishes (WCS = Water Column Specialists;BS= Benthic Specialists; SS = Structure Specialists) at each mark-recapture site. (Btw=Between). Absolute number of recaptures are in ()

Site	Land cover	Confluence Ratio Size	Trip	Year	Days Btw Trips	Total Recapture %	WCS %	BS %	SS%
Garraway	Forested	>0.6	1	2017	60	15.3% (18)	15.3% (18)	0% (0)	0% (0)
Creek			2	2017	30	14.8% (9)	18.4% (9)	0% (0)	0% (0)
			Mean	2017	45	15.0% (14)	16.9% (14)	0% (0)	0% (0)
			Btw Yrs.		192	1.6% (4)	1.4% (4)	4.5% (1)	0% (0)
			4	2018	21	10.6% (11)	12.0% (10)	10.0% (1)	0% (0)
			5	2018	21	17.5% (21)	19.0% (20)	11.1% (1)	0% (0)
			6	2018	30	14.2% (27)	21.8% (27)	0% (0)	0% (0)
			Mean	2018	24	14.1% (20)	15.9% (19)	7.0% (0.7)	0% (0)
Priest	Urban	<0.6	1	2017	92	9.8% (19)	6.8% (10)	22.2% (5)	27.8% (4)
Creek			2	2017	42	16.5% (18)	17.2% (14)	20.0% (3)	7.7% (1)
			Mean	2017	67	13.2% (19)	12.0% (12)	21.2% (4)	17.8% (3)
			Btw Yrs.		174	3.0% (12)	7.5% (6)	11.7% (4)	15.4% (2)
			4	2018	30	15.4% (23)	10.0% (8)	22.2% (10)	23.3% (5)
			5	2018	30	39.4% (40)	26.8% (11)	45.7% (21)	63.4% (8)
			6	2018	30	38.0% (41)	56.2% (28)	11.5% (7)	35.7% (6)
			Mean	2018	30	30.9% (35)	31.0% (16)	26.5% (13)	40.8% (6)
Mixon's	Urban	>0.6	1	2017	57	7.2% (35)	8.0 % (4)	4.3% (1)	16.6 % (30)
Creek			2	2017	56	23.3% (38)	22.2% (4)	5.3% (19)	29.7% (19)
			Mean	2017	56.5	15.3% (37)	11.1% (4)	2.2% (10)	19.8% (25)

			Btw Yrs.	2018	183	3.9% (14)	2.8 % (2)	0% (0)	5.5 % (12)
			4	2018	30	19.1% (29)	15.0% (10)	0% (0)	25.3% (19)
			5	2018	30	9.3% (39)	7.7% (10)	11.1% (1)	13.0% (28)
			6	2018	30	19.2% (24)	9.1% (1)	0% (0)	22.0% (13)
			Mean	2018	30	15.9% (31)	9.4% (7)	4.2% (0.3)	20.1% (20)
Sweetwater	Forested	<0.6	1	2018	40	9.1% (15)	10.1% (14)	5.3% (1)	0% (0)
Creek			2	2018	21	45.3% (32)	51.0% (26)	37.5% (6)	0% (0)
			3	2018	31	24.6% (33)	24.6% (33)	0% (0)	0% (0)
			Mean	2018	31	26.3% (18)	28.6% (16)	14.3% (2)	0% (0)

Habitat Sampling

Following each sampling event, we collected habitat data along 10 evenly spaced transects perpendicular to flow within each of the three reaches at a site. At one meter intervals along each transect we measured depth (m), current velocity ($m \cdot s^{-1}$), substrate size (modified Wentworth scale, six categories; Cummins, 1962), and the presence (binary variable) of woody structure. We also measured the wetted and bankfull widths (m) for each transect. We calculated mean, absolute reach-scale differences to quantify the degree of change in each habitat variable between sampling events. Reach scale means for each habitat variable were estimated for all sampling trips, and then absolute differences between consecutive trips were calculated for each variable. We then divided the absolute mean differences by the number of days between sampling events to adjust for differences in time. These absolute mean differences were then regarded as reach scale components of habitat stability and incorporated into our models of movement rate and assemblage change.

Data Analyses

Analysis of Habitat Stability

We used principal components analysis (PCA) to reduce the dimensionality of our reach scale components of habitat stability. We retained PCA scores for the first two axes (PC1 and PC2) as descriptors of habitat stability. To test our prediction that urban reaches characterized by a CSR > 0.6 (i.e., Mixon's Creek reaches) would exhibit the greatest habitat instability, we performed one-way ANOVAs on the reach PC1 and PC2 scores with stream as a main effect. We then corrected for multiple comparisons using pairwise t-tests and the Bonferroni method.

Analysis of Distance Moved

We examined differences in movement as a consequence of distance moved, land cover and CSR. We treated distance as a factor with three levels (0 to 30 m = short; 30 to 60 m = intermediate; >60 m = far) and summed the number of movers within each group for each site (n = 11). Movers were pooled into groups regardless of directionality (i.e.,

upstream and downstream moves were pooled). We used Poisson regression to test our hypotheses that the number of movers would vary as a consequence of distance travelled, land cover or confluence size. Because samples within and among groups were uneven, site was included as a random effect. We corrected for multiple comparisons using Tukey's HSD test.

Estimation of Movement Rates and Assemblage Change

We estimated proportional daily movement rates (PDMR) and Bray-Curtis distances of dissimilarity as metrics of movement rate and assemblage change for reaches between sampling events. Sample sizes for estimates of movement (N = 54) and assemblage change (N = 63) differed because we did not recapture any individuals in some reaches during a sampling event. Thus, for a given sampling event, reaches in which we did not recapture any individuals were subsequently dropped from our movement dataset prior to any analyses. We estimated PDMR using the formula $M * R^{-1} D^{-1}$, where M is the number of fish that moved, R is the total number of recaptures within a reach, and D is the number of days since the first marking period of the field season (Warren and Pardew 1998). We estimated PDMR separately for 2017 and 2018 movement data because low recapture rates (1.6–3.9%, see Table 1) suggested that mark loss, emigration, or mortality (electrofishing or natural) were high between years. To estimate assemblage change, we calculated the relative abundance of each functional group within all reaches during each sampling event and then estimated reach scale, Bray-Curtis distances of dissimilarity between sampling events and across all functional groups.

Analysis of Reach Scale, Movement Rates and Assemblage Change

We modeled movement and assemblage change using Beta-regression and Zero-Inflated Beta regression models respectively, because, preliminary analyses suggested that movement rates and Bray-Curtis distances were not normally distributed. As an expansion of generalized linear models, Beta regression models can evaluate the effects of explanatory variables for proportional and probability data falling within the interval (0, 1) by modeling zeros in a dataset as a function of a two-state process (Liu and Eugenio 2018). One of the two states, the zero state, may be defined as the probability of an event being so low that it cannot be readily differentiated from zero. The second state, the normal state, includes both zeros and continuous values falling within the interval (0, 1) (Liu and Eugenio 2018). We assessed whether the addition of "site" as a random intercept term improved model fit. For both response variables, random-intercept, null models were ranked higher than null models (PDMR: $w = 0.76$; Bray-Curtis Distance: $w = 0.74$) justifying the inclusion of a random intercept term. All models converged. Prior to modeling, we tested for the correlation between covariates. Any two covariates that had a Pearson correlation greater than the absolute value of 0.6, were not included in the same model. We standardized all habitat variables by subtracting the mean and dividing by twice the standard deviation.

We constructed both reach and multi-scale models (Table S2). We included six predictors in our reach scale models to identify the abiotic components of habitat stability that best explained variation in movement rates and Bray-Curtis distances. In total, we constructed 23 models to test our hypotheses on movement rate and assemblage change at the reach scale. Multi-scale model sets were configured so that both coarse scale factors, CSR and land cover, could be integrated into our best reach scale models as both additive and interactive effects. Our multi-scale model sets also featured the best reach scale model without land cover or CSR included as additive or interactive effects. Finally, within our multi-scale model sets, both response variables were modeled directly as a consequence of the singular effects of either land cover or CSR or as a consequence of the interaction between these two factors. We included a null model and global model in both model sets. For model sets, we only incorporated two-way interactions. We used Akaike's Information Criterion for small sample sizes (AIC_C) to assess the quality of competing models (Burnham and Anderson 2002). We only used reach scale models with $w > 0.10$ to construct multi-scale models.

Results

Recapture rates

Over the duration of the study period, we marked 2459 fish; the total sum of fish marked varied between sites (Sweetwater Creek: 334; Garraway Creek: 675; Mixon's Creek: 717, Priest Creek: 733). Recapture rates varied by functional group, site, trip, year, and between years (Table 1). The total number of recaptures across all sites were higher in 2018 than in 2017 (Mean + 95% confidence intervals; 2017: 28.67 + 4.19, 51.14; 2018: 75.33 + 0, 163.98), but there was extensive overlap between 95% confidence intervals. The mean percentage of individuals recaptured between years was lower than within years at all sites (Table 1). Our greatest yearly recapture rates for each functional group were all achieved during our 2018 field season at Priest Creek. On average, we recaptured 40.8% of marked structure specialists, 31% of marked water-column specialists, and 26.5% of marked benthic specialists at this site during the 2018 field season (Table 1). Proportionally, across all sites, 61% (152 individuals), of water-column specialists were recaptured in pools, 63% (37 individuals) of benthic specialists were recaptured in riffles, and 93.6% (103 individuals) of structure specialists were recaptured in pools.

Habitat stability

The first two components from the PCA explained 50% of the variance in reach scale components of habitat stability across time (Fig. S1, Table S3). The PC1 axis described a gradient driven primarily by mean absolute difference in depth (1.32) and mean absolute difference in woody structure (1.15). The PC2 axis described a gradient driven primarily by mean absolute difference in current velocity (1.04) and mean absolute difference in wetted width (0.96). Generally, habitat stability in Garraway Creek and Sweetwater Creek reaches appeared to be related to variation along the PC1 axis, whereas habitat stability in Priest Creek and Mixon's Creek reaches appeared to be more closely related to variation along the PC2 axis (Fig. S1). Results for one-way ANOVAs indicated that there was not a significant effect of site on PC1 scores ($p > 0.05$); however, there was a significant effect of site on PC2 scores ($F = 7.28_{3,59}$, $p = 0.0003$). In association with this result, pairwise comparisons indicated that habitat stability in Mixon's Creek reaches was significantly different from habitat stability in Garraway Creek (t= -5.16, df = 30.6, $p = 0.00008$), and Sweetwater Creek reaches (t = 4.0, df = 12.3, $p = 0.01$). Habitat stability in Priest Creek reaches was not significantly different from habitat stability in Garraway Creek or Sweetwater Creek reaches ($p > 0.05$). Also, there was no evidence that habitat stability in Mixon's Creek reaches was significantly different from habitat stability in Priest Creek reaches ($p > 0.05$) or that habitat stability in Garraway Creek reaches was significantly different from habitat stability in Sweetwater Creek reaches ($p > 0.05$).

Distances Travelled

The distribution of distances travelled by water-column specialists varied among sites (Mean ± SD; Garraway Creek: 53.7 m ± 22.3; Mixon's Creek: 84.8 m ± 23.5; Priest Creek: 39.9 m ± 14.9; Sweetwater Creek: 53.5 m ± 17.6). The mean, minimum, and maximum observed distances moved by water-column specialists at Priest Creek and Mixon's Creek were highly dissimilar (e.g., minimum distances moved: Priest Creek = 18.3 m, Mixon's Creek = 56.5 m; Table 2). Conversely, mean, minimum, and maximum observed distances moved by water-column specialists at Sweetwater Creek and Garraway Creek were similar (e.g., minimum distances moved: Garraway Creek = 26.3 m, Sweetwater Creek = 23.7 m; Table 2). No long distance moves outside of our study reaches were detected. Generally, intermediate moves (30 to 60 m) were the most commonly observed (Fig. 2). There was a significant interaction between distance and land cover on the number of movers; multiple comparison results suggested that far moves were significantly (-1.06 ± 0.34, df = 7.37, $p = 0.02$) more common at urban sites as opposed to forested sites, intermediate moves were significantly (0.84 ± 0.23, df = 34.07, $p = 0.003$) more common than far moves at urban sites, and short moves were significantly (0.83 ± 0.25, df = 16.55, $p = 0.01$) more common than far moves at urban sites. There was also a significant interaction between confluence size and distance on the number of movers. However multiple comparison results indicated that only the number of far moves and intermediate moves at small CSR sites differed significantly (-0.91 ± 0.30, df = 3.08, $p = 0.02$).

Table 2
Summary statistics for distances moved b water-column specialists within and among reaches at all four sites

Site	Functional Group	Land cover	Confluence Ratio Size	Mean ± SD Distance (m)	Minimum Distance (m)	Maximum Distance (m)
Garraway Creek	WCS	Forested	> 0.6	53.68 ± 22.30	26.3	88.0
Mixon's Creek	WCS	Urban	> 0.6	84.8 ± 23.54	56.5	113.5
Priest Creek	WCS	Urban	< 0.6	34.94 ± 14.93	18.3	70.5
Sweetwater Creek	WCS	Forested	< 0.6	53.53 ± 17.62	23.7	82.0

Proportional Daily Movement Rates

PDMR was similar among sites (Mean ± SD; Garraway Creek: 0.009 ± 0.012; Mixon's Creek: 0.007 ± 0.009; Priest Creek: 0.006 ± 0.008; Sweetwater Creek: 0.007 ± 0.009). Mean PDMR was similar for forested (0.009 ± 0.011) and urban (0.007 ± 0.008) reaches. Mean PDMR was also similar independent of confluence size (> 0.6: 0.008 ± 0.011; <0.6: 0.007 ± 0.007). Cumulative PDMR was similar for forested reaches (20.2%) and urban reaches (18.8%), and cumulative PDMR for reaches typified by a CSR > 0.6 were similar (20.2%) to the cumulative PDMR of reaches characterized by a CSR < 0.6 (19.4%).

Bray-Curtis Distances

Throughout the study-period, we sampled 776 individuals at Garraway Creek, 458 individuals at Sweetwater Creek, 823 individuals at Priest Creek, and 802 individuals at Mixon's Creek. Mean relative, abundance of water-column specialists was greatest at Garraway Creek (0.77; 0.68, 0.85) and Sweetwater Creek (0.67; 0.59, 0.76) and lowest at Priest Creek (0.49; 0.40, 0.58) and Mixon's Creek (0.27; 0.18, 0.35). Mean relative abundance of benthic specialists was greatest at Priest Creek (0.26; 0.20, 0.32) and Sweetwater Creek (0.25; 0.16, 0.35), and lowest at Mixon's Creek (0.06; 0.02, 0.10) and Garraway Creek (0.13; 0.08, 0.19). Finally, mean relative abundance of structure specialists was greatest at Mixon's Creek (0.69; 0.58, 0.76) and Priest Creek (0.25; 0.19, 0.32), and lowest at Garraway Creek (0.10; 0.03, 0.17) and Sweetwater Creek (0.08; 0.02, 0.13). Pooled reach Means and SDs in Bray-Curtis distances were similar among sites (Mixon's Creek: 0.008 ± 0.004; Garraway Creek: 0.008 ± 0.006; Sweetwater Creek: 0.006 ± 0.003; Priest Creek: 0.006 ± 0.003).

Modeling of PDMR

For our reach scale model set, the best model (w_i = 0.30, pseudo R^2 = 0.18) explained the variation in PDMR of water-column specialists as the outcome of a significant, negative interaction (beta = -1.57 ± 0.50, p = 0.003) between absolute mean difference in current velocity and absolute mean difference in woody structure (Table 3). Our multi-scale modeling results suggested the addition of land cover or CSR did not increase model fit.

Table 3
Top reach and multi scale models of assemblage change (Bray-Curtis Distances) and proportional daily movement rate (PDMR) of water-column specialists sampled at four headwater confluences in the Pascagoula River basin, MS, USA. Values are shown for the number of parameters (*K*), AIC_C, ΔAIC_C and model weights (w_i). Intercept-only (i.e., null) models are designated by periods in place of covariates

Response	Scale	Model	K	AIC_C	ΔAIC_C	*wi*
PDMR	Reach	Woody Structure * Current Velocity + 1| Stream	5	-216.4	0.0	0.42
		(.) + 1| Stream	2	-213.7	2.7	0.11
	Multi	Woody Structure * Current Velocity + 1| Stream	6	-214.1	0.0	0.60
		Woody Structure * Current Velocity + Land Cover + 1| Stream	5	-213.8	0.1	0.19
Bray-Curtis	Reach	Depth * Bankfull Width + 1| Stream	5	-533.9	0.0	0.32
		Depth * Woody Structure + 1| Stream	5	-533.3	0.5	0.23
	Multi	Depth * Bankfull Width + CR + 1| Stream	6	-533.2	0.0	0.28
		Depth * Woody Structure + CR + 1| Stream	5	-532.0	1.2	0.16

The plotting of predicted values suggests that, for reaches in which the absolute change in woody structure availability was small (i.e., approximately 0.001% change), the PDMR of water-column specialists within Mixon's Creek and Priest Creek reaches rapidly increased in relation to changes in current velocity (Fig. 3a). Oppositely, for reaches in which the absolute change in woody structure availability was large (i.e., > 0.001% change), the PDMR of water-column specialists generally appeared to decline within Garraway Creek and Sweetwater Creek reaches, but stayed relatively constant within Priest Creek reaches(Fig. 3b).

Modeling of Bray-Curtis Distances

Two models of Bray-Curtis distance were associated with $w_i > 0.10$. The best model had moderate support ($w_i = 0.31$) and suggested that reach scale Bray-Curtis distances were best explained by a significant interaction (beta = 0.24 ± 0.07, $p = 0.003$) between absolute mean difference in depth and absolute mean difference in bankfull width (Table 3). Multi-scale modeling results suggested the addition of CSR did increase model fit, though the increase in fit was nonsignificant (beta = -0.16 ± 0.12, $p > 0.05$). The second best model was weakly supported ($w_i = 0.23$), and suggested that reach scale, Bray-Curtis distances were best explained by a significant, interaction (beta = 0.16 ± 0.06, $p = 0.007$) between absolute mean difference in depth and absolute mean difference in woody structure (Table 3). Multi-scale modeling results suggested the addition of CSR in this model did increase model fit (Table 3), though the increase in fit was nonsignificant (beta = -0.13 ± 0.12, $p > 0.05$).

The plotting of predicted values suggests that, for reaches in which the absolute change in bankfull width was small (i.e., approximately < 3% change), reach scale Bray-Curtis distances generally declined within Garraway Creek and Sweetwater Creek reaches (Fig. 4a), while remaining static within Priest Creek reaches. Oppositely, for reaches in which the absolute change in depth was large (i.e., > 3% change), reach scale Bray-Curtis distances generally appeared to increase within Priest Creek and Garraway Creek reaches, remained fairly constant in Mixon's Creek reaches, and declined within Sweetwater Creek reaches (Fig. 4b). Despite the inclusion of confluence size in the best multi-scale model, plots of predicted values do not support any effect of this predictor on assemblage change.

Discussion

In this study, we assessed the influences of confluence size and land cover on habitat stability, the movement ecology of a functional guild, and on temporal assemblage change at four headwater confluences in a Gulf Coastal Plain dendritic river system. Hydrogeormorphic processes altered components of reach scale habitat stability, influencing the rate of movement of water-column specialists, and promoting assemblage change at these four headwater confluences. Our analyses yielded five primary findings: (1) a hydrogeomorphic gradient (PC2) associated with differences in land cover altered habitat stability (2) along this gradient, urban reaches with a confluence size > 0.6 (i.e., Mixon's Creek reaches) exhibited the greatest habitat instability, (3) differences in habitat complexity modified the PDMR of water column-specialists at the reach scale, (4) water column-specialists were more likely to make short or far moves as a consequence of upstream land cover and (5) absolute change in components of channel morphology (e.g., depth, bankfull width) regulated within-reach stream fish assemblage change. Our results highlight the influence of confluence size and land cover on differences in habitat stability and assemblage change, and the movement rate of freshwater fishes in headwaters. Because the movement and assemblage datasets used for this study were small (N = 51, N = 63); replication was low (9–18), reducing the power of analyses.

Effect of land cover on habitat stability

Our results indicated that land cover facilitated habitat change among all reaches more so than confluence size. Differences in habitat change between sites was associated with differences in the magnitude of geomorphic variation (e.g., changes in bankfull width, current velocity, Fig. S1, Table S3). Priest Creek and Mixon's Creek reaches were characterized by greater bankfull widths, greater variation in wetted width, diminished availability of woody structure, shallower depths, and greater variance in current velocity (Table S4). These differences were reduced in Garraway Creek and Sweetwater Creek reaches. Our results also suggested that reach-scale Priest Creek habitat was not more stable than reach-scale Mixon's Creek habitat, or that that reach-scale Sweetwater Creek habitat was not more stable than reach-scale Garraway Creek habitat, reducing the probability that habitat stability was influenced by CSR. In small, coastal plain streams, limited impervious cover (< 11%) may increase flashiness, and limit the influence of base flow on total stream discharge (Schneid et al. 2017). However, the extent to which land cover alters active channel width (Utz and Hilderbrand 2011; Schneid et al. 2017), and sediment transport (Kang and Marston 2006; Riley 2009; Hardison et al. 2009) in Coastal Plain streams remains unclear. For example, low gradient drainages in Oklahoma and Georgia were characterized by low alterations to sediment transport size and channel enlargement despite increases in watershed urbanization (Kang and Marston 2006; Riley 2009). However, increases in active channel width are reported for other small, urban Coastal Plain drainages (Hardison et al. 2009; Schneid et al. 2017). Our results indicate that there was little variation in mean sediment size during the study period across all sites, but urban drainages were typified by greater variability in active channel width (Table S5). Utz and Hildebrand (2011) suggested that the stability of sediment structure in small, urban Coastal Plain streams may be related to bed material. Coarse substrate particles, which are often in great abundance in Piedmont and montane drainages, are rarely present in Coastal Plain streams.

Effect of confluence size on habitat stability

Our prediction that urban reaches characterized by a confluence size > 0.6 would exhibit the greatest amount of habitat instability was supported. In relation to other sites, Mixon's Creek reaches were associated with much greater variability in bankfull width, wetted width, and substrate size (Table S4). Furthermore, mean percent occurrence of woody structure at this site was effectively zero for the duration of the study period for all study reaches (Table S4).

Excluding trends associated with depth, reach scale habitat parameter means for Garraway Creek and Mixon's Creek (i.e., our two sites with confluence sizes > 0.6) are in disagreement with the predictions of Benda et al. (2004). Annual mean depth for mainstem downstream reaches at both sites was consistently greater than the mean depth of mainstem upstream reaches at both sites. However, mean bankfull width was greater in the mainstem downstream reaches at both

sites, and generally, substrate size was greater in the mainstem upstream reach at both sites. Finally, in opposition to the predictions of Benda et al. (2004), the percent occurrence of woody structure was generally greater in mainstem downstream reaches at both sites.

Effect of habitat stability on the movement rate of water-column specialists

Differences in the availability of woody structure altered the size of the effect of hydrologic (e.g., current velocity) variation on movement rates of water-column specialists. Overall, Garraway Creek and Sweetwater Creek reaches were characterized by a much higher percentage of woody structure throughout the study period than Priest Creek and Mixon's Creek reaches (Table S4). Our prediction that stream fishes would exhibit greater movement as a consequence of habitat stability in urban reaches was supported. For reaches in which absolute change in woody structure availability was small (approximately 0.001% absolute change), in relation to growing absolute change in current velocity (Fig. 3a), movement rates of water-column specialists appeared to increase within and among Mixon's Creek and Priest Creek reaches. Conversely, for reaches in which absolute change in woody structure availability was large (> 0.001% absolute change), movement rates seemed to decline in response to cumulative absolute changes in current velocity. Movement rates seemed to decline steeply within and among Garraway Creek and Sweetwater Creek reaches, but decreased moderately within and among Priest Creek reaches (Fig. 3b).

Because large wood accumulation in small streams may last for hundreds of years (Dollof and Warren, 2003), in-stream wood regulates hydrological and sediment transfer processes which facilitates habitat heterogeneity and stabilization (Angermeier and Karr, 1984; Gurnell, et al. 2005; Dolloff and Warren 2003). Consequently, the maintenance of deepwater or pool habitats is greatest in small streams typified by a large volume of in-stream wood. Pool and deepwater habitats provides stream fishes refuge from droughts and stream reaches typified by small, shallow pools (Lisle & Hilton, 1992) are often species depauperate and exhibit greater variation in species abundance (Schlosser, 1987). Thus, stream fish are less prone to move in physically, complex habitats (Roni and Quinn 2001; Belica and Rahel 2008; Clark and Schaefer 2016).

Effect of land cover on distances travelled by water-column specialists

Our finding that land cover appears to have more strongly influenced the distances travelled by water-column specialists adds further credence to our argument that the movement rate of this functional group was more pronounced in urban reaches due to reduced habitat complexity and greater variability in channel morphology. Longer distance moves were more often detected within among Mixon's Creek and Priest Creek reaches as opposed to Sweetwater and Garraway Creek reaches. Thus, it is not surprising that 1) the greatest observed distance moved by a water-column specialist (113 m) and benthic specialist (97 m) were both recorded within Mixon's Creek reaches, and 2) all observed moves > 90 m occurred within Priest Creek (n = 1) or Mixon's Creek (n = 3) reaches. Because we did not recapture any sunfish within Garraway Creek or Sweetwater Creek reaches, we do not report a maximum distance travelled by an individual within this functional group.

Effect of habitat stability on assemblage change

The temporal and spatial scales at which field studies are implemented often makes disentangling the relationship between assemblage change and habitat stability difficult. Despite this, we did detect some patterns that we believe are worth highlighting. Despite the inclusion of CSR in the best multi-scale model of assemblage change, plots of predicted values do not support a strong confluence size effect. For reaches in which changes in bankfull width were minimized (.e.g., Fig. 4a), assemblages in Sweetwater Creek and Garraway Creek reaches were more likely to remain stable through time. In opposition, assemblage change among Priest Creek and Mixon's Creek reaches remained fairly constant

(approximately 0.007–0.0085, Fig. 4a). Therefore, our prediction that stream fish assemblages would exhibit a more rapid response in urban reaches was supported. Greater habitat stability in Garraway Creek and Sweetwater reaches may have facilitated assemblage stability within these reaches. The literature supporting the positive effect of environmental stability on stream fish assemblage stability is vast (Gorman and Karr 1978; Ross et al. 1985; Grossman and Sabo 2010; Matthews et al. 2013). Reduced environmental stability coupled with the greater vagility displayed by individuals within Mixon's Creek and Priest Creek reaches may have reduced the probability of these reaches remaining stable through time. Generally, Priest Creek and Mixon's Creek reaches were characterized by greater variability in wetted width and bankfull width (Table S5). For reaches in which absolute change in bankfull width was large, assemblage differences were more likely to decline in Sweetwater Creek reaches as opposed, to Priest Creek and Mixon's Creek reaches (Fig. 4b). In opposition, assemblage differences were amplified in Garraway Creek reaches which were subject to an increase in absolute change in bankfull width (Fig. 5B). The dichotomy in observed differences between these two sites in relation to greater variation in channel morphology is interesting and deserves further research; confluence size may have contributed to these discrepancies in assemblage change.

Conclusions

We assumed that there would be an interaction between confluence size and land cover, and thus, urban reaches with a larger confluence size would exhibit the greatest variability in habitat and movement. Geomorphic characteristics were most variable at Mixon's Creek, subjecting water-column specialists to greater geomorphic change. Thus individuals in these reaches were more likely to move greater distances. However, there was no statistical evidence that land cover or confluence size contributed to substantial variation in movement rate or assemblage change.

We used a 2 X 2 design to assess the effects of confluence size and land cover on stream fish movement and assemblage change. Most movement studies have sought to understand what proportion of populations are mobile (Skalski and Gilliam 2000; Fraser et al. 2001; Rodriguez 2002), what ecological factors regulate movement at the reach scale (Albanese et al. 2004; Belica and Rahel 2008; Walker and Adams 2016); and how physical barriers may prevent movement (Warren and Pardew, 1998; Knott, Mueller, Pander and Geist, 2020; Williams et al. 2020). Additionally, studies assessing the role of confluences on meta-assemblages have mostly examined their effects at the landscape scale (see Smith and Kraft 2005; Kiffney et al. 2006; Angermeir and Hitt 2008; Hubbell et al. 2020), and few studies have been conducted to investigate their influence on movement (but see Cathcart et al. 2018). No observational studies to our knowledge have attempted to connect local geomorphic change at confluences to variation in reach scale movement in a natural setting. Thus our study provides baseline data for future studies further investigating the relationship between confluences and land cover on movement and assemblage change at the reach scale. A key weakness of our study was our reduced sample sizes; however, to address our stated objectives, a smaller number of sites was deemed necessary to effectively deploy a movement study using mark-recaptures methods. Future studies should consider the use of other tagging methods (e.g., passive integrated transponders; acoustic tags) to increase the number of replicates (e.g., marking of individuals), but also allowing for long-term monitoring to better understand how confluences and land cover may influence movement and assemblage change in headwaters.

Declarations

Competing Interests

The authors declare there are no competing interests.

Conflict of Interest Statement

The authors have no conflict of interest regarding the submission of this manuscript.

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Availability of Data

The data that support the findings of this study are available from FigShare (https://figshare.com/authors/Joshua_Hubbell/10065745)

Availability of Code

The code used in the analyses in this study is available from FigShare (https://figshare.com/authors/Joshua_Hubbell/10065745)

Ethics Approval

All sampling protocols were approved by the University of Southern Mississippi's Animal Care and Use Committee (IACUC 09-007).

Author's Contribution Statement:

Conceived and designed the investigation: JPH, JFS. Performed field and/or laboratory work: JPH. Analyzed the data: JPH. Contributed materials, reagents, and/or analysis tools: JPH. Wrote and edited the paper: JPH, JFS.

Consent to Participate

Not Applicable

Consent for Publication

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Figure

Figure 5 not available with this version.

Supplementary Table

Supplementary Table 5 not available with this version.

Figures

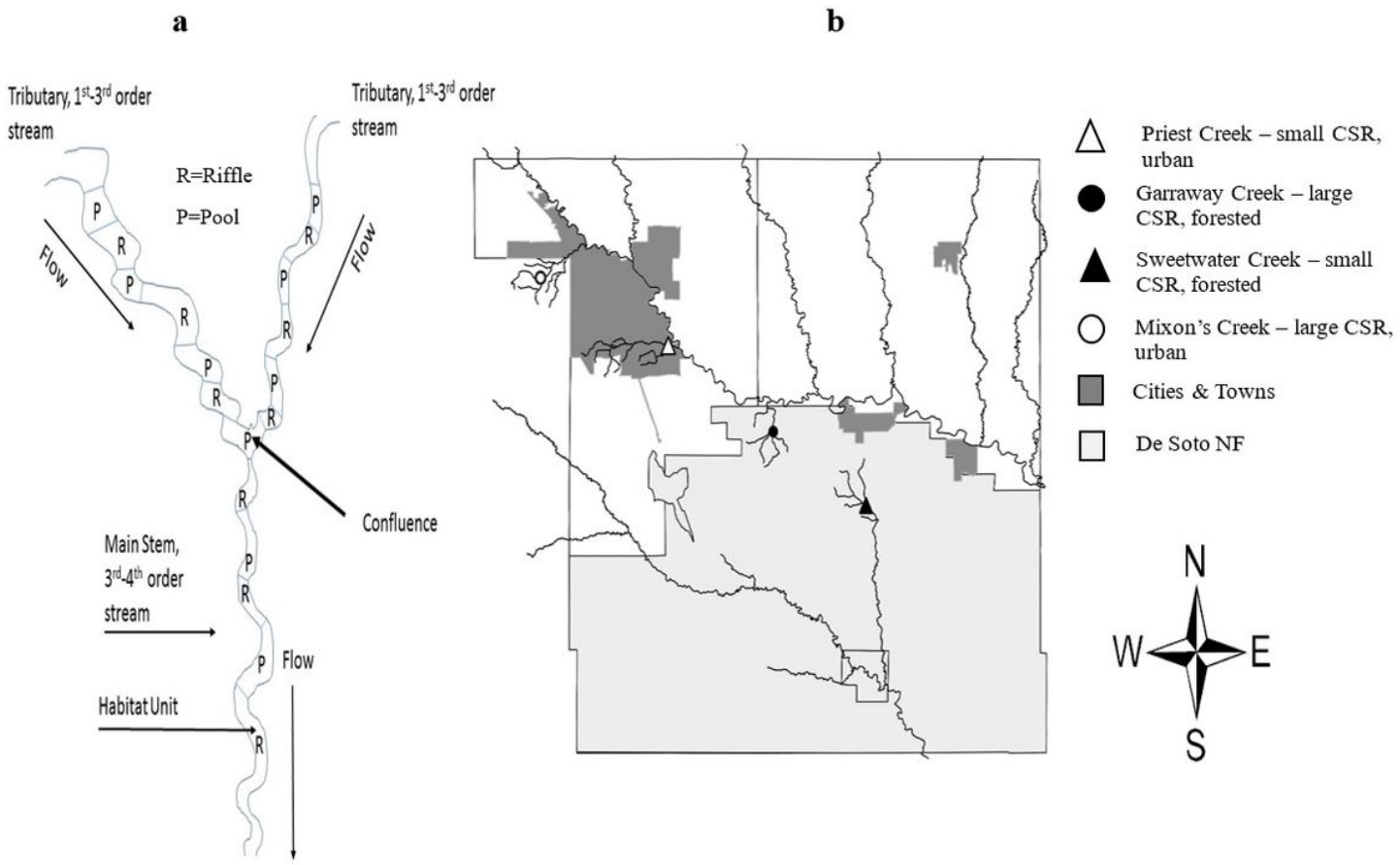

Figure 1

a: Diagram of site layout. Each site was located at a confluence and consisted of three 100 m reaches. Pools and riffles were delineated as patches of habitat. b: Map of our four mark-recapture sites near Hattiesburg, MS in greater Forrest County Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

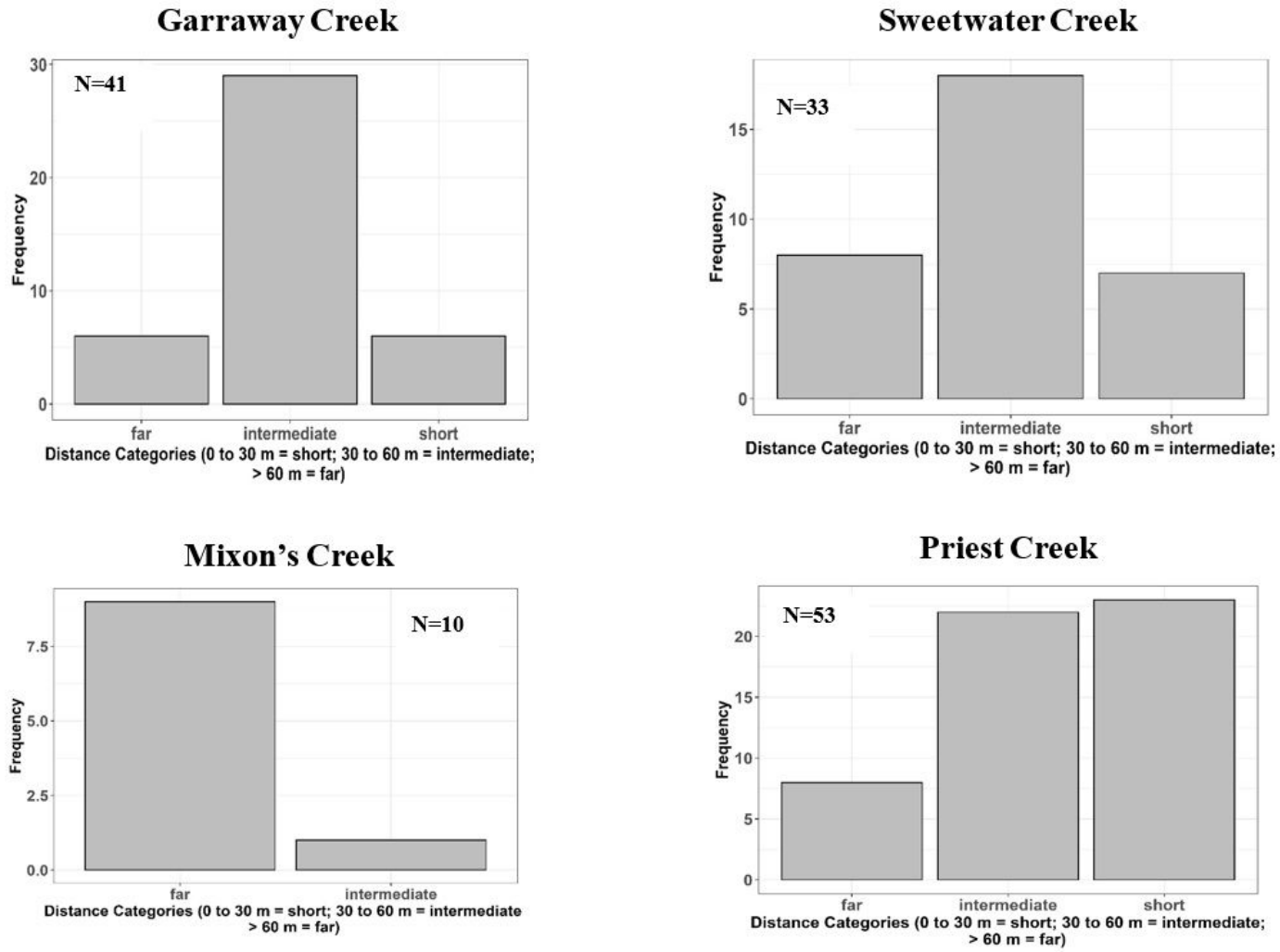

Figure 2

Frequency distributions for three movement categories, regardless of directionality (i.e., upstream or downstream) in relation to distance moved for each mark-recapture site in the Pascagoula River basin, MS.

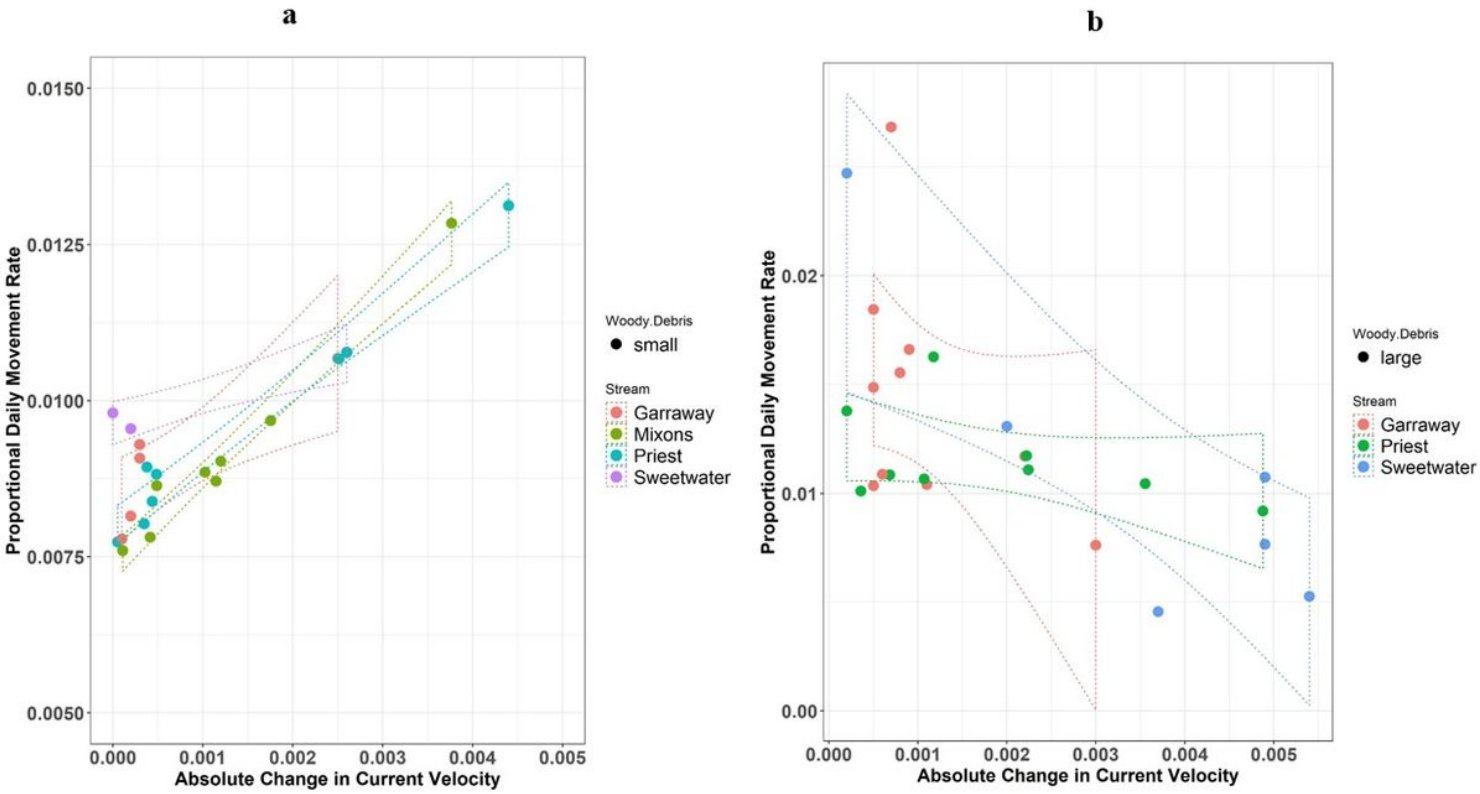

Figure 3

Plot of predicted values from zero-inflated Beta regression as a result of an interaction between absolute mean differences in woody structure and current velocity on the proportional daily movement rate (PDMR) of water-column specialists. To ease interpretation of our results, we split our dataset in half, and converted woody structure into a factor with two levels (a: small change = ≤ 0.001%; b: large change = > 0.001%) to identify differences in PDMR as a consequence of the interaction between the two habitat variables. The number of plotted points along each regression represents the number of reaches associated with that level of change in woody structure for each site. *No predicted estimates of PDMR for Mixon's Creek were associated with a large change in woody structure. Dashed boxes represent 95% confidence limits for each regression

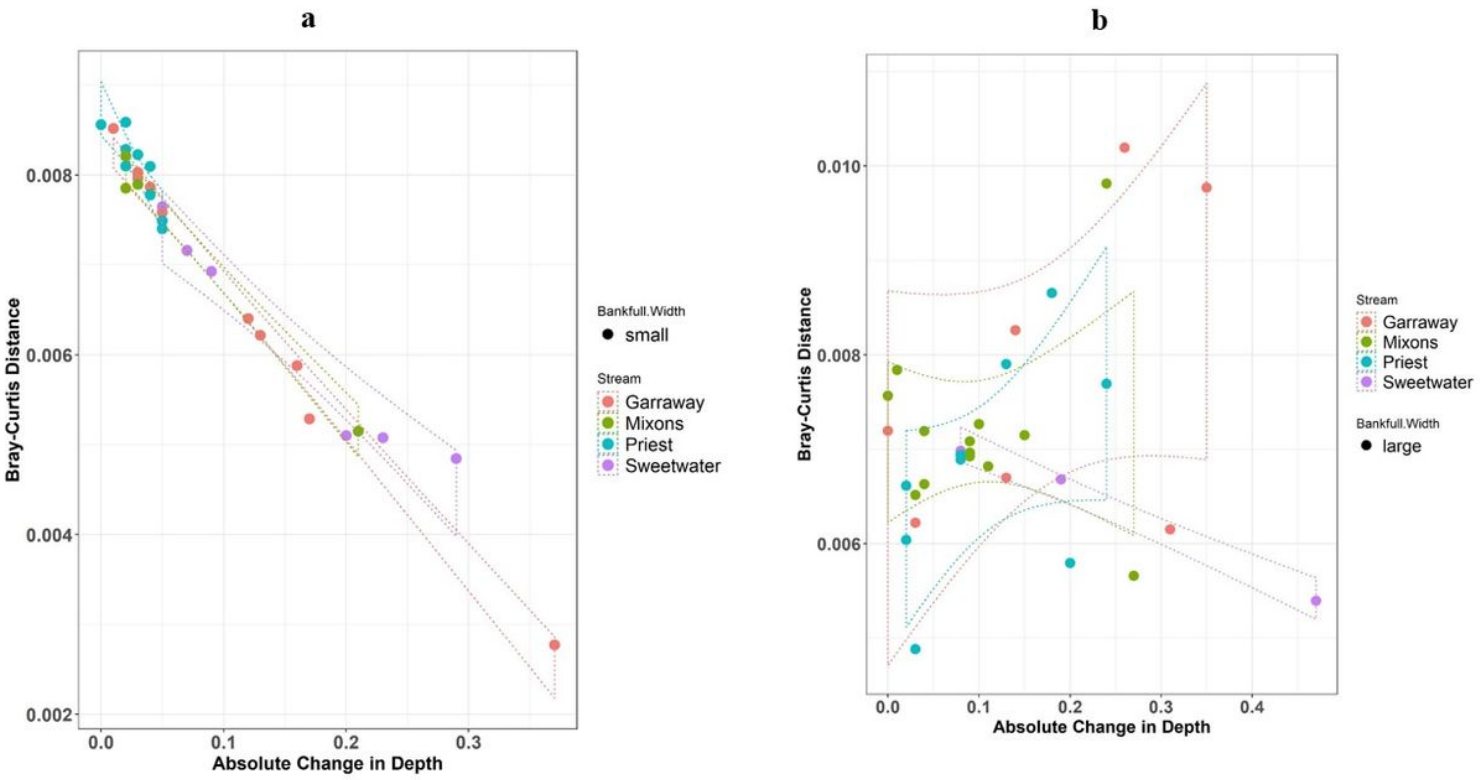

Figure 4

Plot of predicted values from zero-inflated Beta regression as a result of an interaction between absolute mean differences in bankfull width and depth on Bray-Curtis distances. To ease interpretation of our results, we split our dataset in half, and converted bankfull width into a categorical factor with two levels (a: small change = ≤ 3%; b: large change = > 3%). to identify differences in Bray-Curtis distance as a consequence of the interaction between the two habitat variables. The number of plotted points along each regression represents the number of reaches associated with that level of change in bankfull width for each site. Dashed boxes represent 95% confidence limits for each regression

Supplementary Files

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- TableS2.docx
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