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RESEARCH PAPER — OPEN ACCESS

Habitat associations of fish and aquatic turtles in an East Texas Stream

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Abstract – The community structure of stream communities are treated as bioassays of stream ecosystems and changes to species patterns within those communities reflect response to multiple stressors including natural fluctuations in environmental variables. Research has focused on the structure of fish assemblages and there is increasing interest in environmental factors structuring turtle communities. Both fishes and turtles can be sampled using common methods, but are rarely studied together. Our objective was to compare distribution of fish and turtle species based on measured environmental variables in East Texas, USA. Species distributions were influenced by flow, substrate, and emergent vegetation. Results from Monte Carlo permutation tests suggest that downed woody debris and water temperature also had a strong influence on species distributions. Co-correspondence analysis showed considerable overlap of species scores in the absence of environmental variables. The five macrohabitats sampled exhibited varying degrees of connectivity and thus species mixing, which is driven by annual fluctuations in precipitation. Results from this study suggest that turtles and fishes can be considered simultaneously and exhibit similar patterns of species distribution across the landscape, at least at local scales.

Key-words: Aquatic vertebrate communities / ordination / fish / turtles

Résumé – Les associations d'habitat de poissons et tortues aquatiques dans les rivières de l'est du Texas. Les structures des communautés dans les rivières sont considérées comme des essais biologiques d'écosystèmes et les changements des compositions d'espèces au sein de ces communautés reflètent une réponse à des stress multiples, y compris les fluctuations naturelles des variables environnementales. La recherche s'est d'abord focalisée sur la structure des assemblages de poissons et il y a aujourd'hui un intérêt croissant pour les facteurs environnementaux qui structurent les communautés de tortues. Les tortues et les poissons peuvent être échantillonnées en utilisant des méthodes communes, mais ils sont rarement étudiés ensemble. Notre objectif était de comparer la distribution des espèces de poissons et de tortues sur la base de variables environnementales mesurées dans l'Est du Texas, USA. Les répartitions des espèces ont été influencées par le débit, le substrat et la végétation émergée. Les résultats de tests de permutation de Monte Carlo suggèrent que les débris ligneux sédimentés et la température de l'eau ont également une forte influence sur la répartition des espèces. L'analyse de co-correspondance a montré un chevauchement considérable des scores d'espèces en l'absence de variables environnementales. Les cinq macrohabitats échantillonnés présentaient des degrés divers de connectivité et donc des mélanges d'espèces, causés par les fluctuations annuelles des précipitations. Les résultats de cette étude suggèrent que les tortues et les poissons peuvent être considérés simultanément et présentent des profils similaires de distribution d'espèces à travers le paysage, au moins à l'échelle locale.

Mots-clés : Communautés aquatiques de vertébrés / ordination / poisson / tortues

1 Introduction

Streams have long been the subject of ecological research that tests hypotheses explaining species assemblage structure, and this is, in part, because standardized sampling methods allow collection of reliable samples of fishes and aquatic macroinvertebrates (Grossman *et al.*, 1982). Knowledge of fish and aquatic macroinvertebrate community ecology has been used to develop biotic indices for determining condition of streams and watersheds (Natural Resources Conservation Service, 2003). Essentially, the structure of communities

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is treated as a bioassay of stream ecosystems under the assumption that fish and/or macroinvertebrate community patterns should reflect the relative status of an ecosystem in response to multiple stressors (Prentice and Cramer, 1990).

A large body of work has been published on the role of abiotic factors in structuring fish assemblages (Matthews and Hill, 1980; Matthews and Styron, 1981; Jackson *et al*., 2001). Abiotic processes (*e.g*., flow, temperature, nutrient and chemical fluxes) in stream systems are unpredictable, thus, virtually all ecological processes are influenced by spatially and temporally variable biological and physical characteristics of streams (Pringle *et al*., 1988; Townsend, 1989). Variability in the availability of biotic and abiotic resources requires fish to move between habitats in order to obtain those resources (Dunning *et al*., 1992). This variation is governed by alternating periods of inundation and separation related to annual or semi-annual flooding. These flood pulses are considered one of the most important hydrological features of stream systems (Flood Pulse Concept; Junk *et al.*, 1989). Flood pulses allow for biotic interchange between streams and their associated floodplain habitats (backwaters, oxbows, marshes) altering both species composition, influx of nutrients, and chemical processes in both lentic and lotic habitats (Junk *et al*., 1989; Bayley, 1995).

Although fish have been used extensively for bioassessment of aquatic ecosystems, it would be useful to explore the utility of sampling additional vertebrate groups, particularly those that can be sampled effectively with a standard methodology. Many other species of aquatic vertebrates, including turtles (Bodie *et al*., 2000; Ernst and Lovich, 2009), and crocodilians (Subalusky *et al*., 2009), also exhibit differential habitat use based on sex, seasonal behavior, life history stage, and seasonal fluctuations in and availability of habitat. But, multiple vertebrate taxa are rarely studied simultaneously when addressing the ecology of riparian habitats. Because community structure may be strongly influenced by dispersal (Conner and Simberloff, 1979), or biotic interactions (Diamond, 1975) or both (Ernest *et al*., 2008, Velland, 2010), it would be beneficial to study assemblage patterns of different taxa utilizing similar habitats.

Freshwater turtles exhibit relatively high species richness in the southeastern United States (Iverson, 1992; Buhlmann *et al*., 2009) and often make up a considerable fraction of the total biomass in the habitats in which they occur (Iverson, 1982; Congdon *et al.*, 1986). Many freshwater turtle species tend to show preferences for either lentic or lotic habitats, but not both (Anderson *et al*., 2002; Dreslik and Phillips, 2005; Riedle *et al*., 2015). Species living in sympatry may demonstrate selection for specific microhabitats based on basking structure, canopy cover associated with basking structure, flow, depth, or substrate (Lindeman, 2000; Barko and Briggler, 2006; Riedle *et al.*, 2015). There is variation in these habitat associations, because flood pulses drive species exchanges between backwater scours, wetlands, and the river channel (Bodie and Semlitsch, 2000; Bodie *et al*., 2000).

Previous work has demonstrated that turtles can be sampled simultaneously with fishes using common methods (Barko *et al*., 2004: Barko and Briggler, 2006), and with this in mind, we sampled both fishes and turtles over three summers at one site managed by the Texas Department of Wildlife Parks in eastern Texas. Our objective was to describe habitat associations by fishes and turtles sampled using common methods to describe habitat associations of aquatic vertebrates at this site.

2 Methods

2.1 Study Area

Our study area was located in Anderson County, Texas, on the Texas Parks and Wildlife Department (TPWD) managed Gus Engeling Wildlife Management Area (WMA). Gus Engeling WMA is a 4,434-ha property encompassing a large portion of the Catfish Creek ecosystem. Catfish Creek is a tributary in the Middle Trinity River Basin, encompassing 730 ha and 32 km of Anderson and Henderson counties and considered a Natural National Landmark (Telfair, 1988). Twenty-four small creeks feed Catfish Creek, most of which are spring fed. Habitats associated with the Catfish Creek ecosystem include post-oak (*Quercus stellata*) savanna, bottomland hardwoods, marshes, swamps, bogs, and springs. Aquatic habitat at Gus Engeling WMA is represented by Catfish Creek and its tributaries, adjacent scours and backwater habitat, open canopy marshes, several small ponds and larger lakes (Figure 1). Aquatic habitat is augmented by a series of levees and flood-control gates, built in cooperation with Ducks Unlimited, to provide wetlands for waterfowl. In addition, there are several ponds or "borrow" pits associated with the levees.

2.2 Sampling

We sampled aquatic habitats at Gus Engeling WMA using a variety of trap gear between late May and late July, 2007−2008 and between April and late July 2009. Our net gear consisted of large and small fyke nets, two sizes of hoop nets, two sizes of collapsible box traps, and one size of sea bass/dome traps. The large fyke net (Christensen Nets; www.christensennetworks.com) was 4.5 m in length (front frame to cod end) with a single 14.5 m × 88 cm lead. The two anterior rectangular frames were 120 cm × 88 cm followed by five, 88-cm diameter round hoops, with three 3-cm diameter stretchable funnels leading to the cod end. Square mesh size was 1 cm. The smaller fyke net (Christensen Nets; www.christensennetworks.com) was 3.3 m in length from the front frame to cod end, and had a single 7.4 m × 67 cm lead. The two rectangular front frames were 95 cm × 67 cm, followed by four 67 cm diameter hoops. Both fyke nets had a single vertical slit funnel within the rectangular frames. There were two 31-cm diameter stretchable funnels leading to the cod end. Square mesh size was 1 cm. The larger hoop (turtle net; Memphis Net and Twine; www.memphisnet.net) consisted of three 88-cm diameter metal rings and one 31-cm diameter stretchable funnel. Overall trap length was 245 cm, and square mesh size was 2.5 cm.

The collapsible box traps and sea bass traps were purchased from Memphis Net and Twine (www.memphisnet.net). The mini catfish hoop net had four 47-cm diameter fiberglass hoops, two 27-cm diameter stretchable funnels, and an overall length of 155 cm. Square mesh size was 2.5 cm. Small box

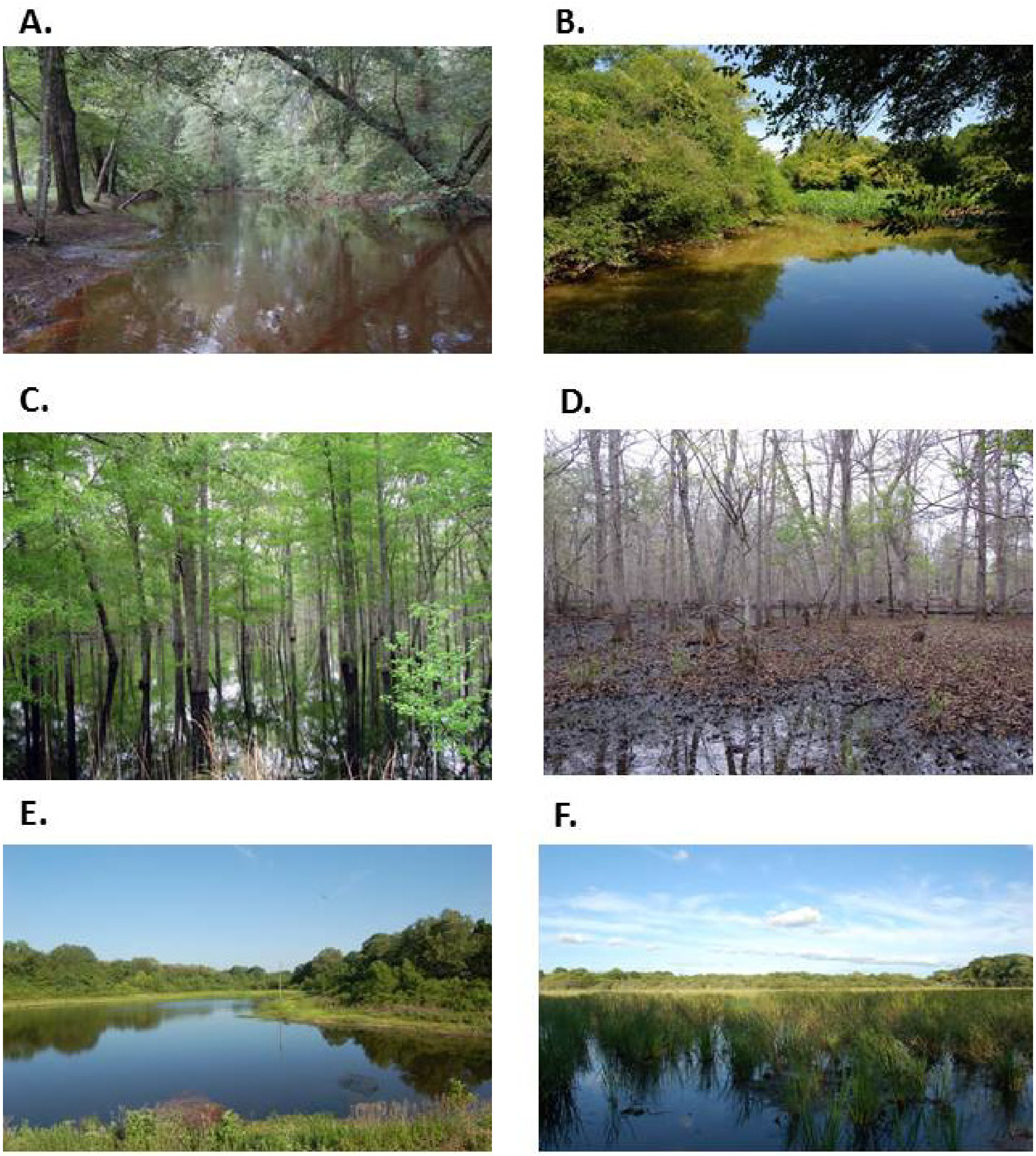

Fig. 1. Representative aquatic habitats at Gus Engeling Wildlife Management Area. A. Catfish Creek, B. a large pool on Catfish Creek, C. flooded backwater, D. the same site as 1C during a period of low water, E. man-made lake, and F. a shallow, heavily vegetated marsh.

traps were 59 cm × 43 cm × 22 cm with a square mesh size of 1 cm. There was a 43-cm, horizontal slit funnel opening on opposite ends of the long axis of the trap. Large box traps were 79 cm × 60 cm × 25 cm with a square mesh size of 1 cm, and had a 60-cm horizontal slit funnel on opposite ends of the long axis of the trap. Dome traps were 96 cm × 64 cm × 61 cm. Square mesh size was 2.5 cm and there were two 15-cm rigid funnels (funnel held open with a plastic ring), located on each end of the trap.

All traps were baited with sardines and/or fresh fish. Traps were checked at least once every 24 h, with trap sets usually completed by early-late afternoon and checked by late morning of the next day. Sampling gear was set so that some portion was exposed above the water surface, providing air space for turtles and other air-breathing organisms. The number of traps set during each trapping season was dependent on availability [which was driven by cost as traps ranged from US $30-1100 depending on trap type]. All trap types were set in all accessible habitat, although the number of each trap type used during each trapping session was dependent upon variables such as depth and flow (Riedle, 2014).

2.3 Data collection

All turtles and fishes captured were identified to species and enumerated. To address abiotic factors driving community composition of aquatic turtles and fishes, we attempted to identify variables important to both fishes and turtles based on previous studies. Structural and chemical variables were recorded using methodology similar to those methods utilized for fishes (Edds, 1993) and turtles (Fuselier and Edds, 1994) in separate studies, but using similar analytical methods. All environmental data was collected at each trap set. Structural data included canopy cover, depth, flow, basking availability, substrate composition, and emergent vegetation. Canopy cover was recorded at the trap using a concave forestry densiometer (Lemmon, 1957). Depth was recorded at the opening of the trap gear using a weighted forestry tape measure. Flow was also recorded at the opening of the trap gear using a hand-held flow meter (Global Water Flow Probe, Global Water, Gold River, California, USA) averaging current speed at 5 points between the stream bottom and the surface within the water column. Basking site availability was recorded as the percentage of exposed surface (bank, emergent woody debris) present within an approximately 25-m diameter area surrounding the trap. Emergent vegetation was recorded as the percentage of aquatic vegetation present, estimated visually, within a 25-m diameter area surrounding each trap. Substrate composition was estimated visually and divided into percent sand, mud, clay and detritus and was recorded within a 25-m diameter area surrounding each trap. Clay was defined as a sticky-fined grained soil type that was either yellow or bluish gray in color at this site. Sand was a looser, large granular substrate. Mud was defined as soft, sticky earthy matter that did not fit into the clay or sand substrate types. Detritus was defined as dead and decaying vegetative matter (leaves, woody debris).

Physico-chemical data included water temperature, dissolved oxygen (DO), and pH. Water temperature was recorded by placing a thermometer on the substrate roughly 0.5 m from the shore. Dissolved oxygen was determined using a Winkler Titration Kit (LaMotte, Chestertown, MA, USA). We determined pH using a Colorimetric Octet Comparator kit (LaMotte, Chestertown, MA, USA).

We classified habitat according to five types: Creek (flowing waters associated with Catfish Creek and its tributaries); Backwater (scours and flooded timber associated with the Catfish Creek floodplain); Marsh (shallow, open canopy, heavily vegetated water bodies associated with smaller feeder creeks, springs and bogs); Pond (small manmade water bodies and borrow pits ⩽100 m diameter and consisting of more open water than marshes); and Lake (larger, several ha manmade water bodies).

2.4 Data analysis

We used the PROC GLM procedure for mean comparisons in SAS (SAS Institute, Inc., Cary, NC, 1989) to compare microhabitat variables measured at each site (net) amongst five habitat types identified at Gus Engeling WMA. The PROC GLM procedure relates continuous dependent variables to independent variables. The independent variables act as classification variables, which divide observation into distinct groups, in this case, macrohabitats. We calculated number of captures per net night (1 net set for 1 night = 1 net night) by habitat type for fish and turtles to identify species associations amongst different habitats.

To address relationships between fishes, turtles, and measured environmental variables collected at common sites (traps), we compared species distributions for turtles using ordination analyses. We first used an indirect ordination method that patterns communities based on weighted averages of species scores for individual sites without the inclusion of environmental variables. Since we were sampling two types of communities, fish and turtles, we wanted to compare species distributions between communities. Using co-correspondence analysis covariance is maximized between weighted averages of species scores for one community with those of another community (ter Braak and Schaffers, 2004). Co-Correspondence Analysis was accordingly run in *R* (*R* Development Core Team, 2008), and only for samples where both fish and turtles were captured simultaneously.

We then used a direct ordination method, canonical correspondence analysis (CCA, Palmer, 1993; ter Braak and Verdonschot, 1995), to fit species patterns to environmental variables. CCA is a multiple linear least-squares regression where the site scores, determined from weighted averages of species, are the dependent variables and the environmental variables the independent variables (Palmer, 1993). Essentially, CCA allows one to examine the effect of environmental variables on community patterns (Palmer, 1993; ter Braak and Verdonschot, 1995). One can then compare the variance of the turtle data that is explained by the ordination axes derived by fish in co-correspondence analysis with those derived by environmental variables in canonical correspondence analysis (ter Braak and Schaffers, 2004).

Table 1. Total number of trap nights by trap type and macrohabitat at Gus Engeling Wildlife Management Area, Anderson County, Texas (2006−2009).

	Habitat Type				
Trap Type	Creek	Backwater	Marsh	Pond	Lake
Large Fyke	12	32	5	13	5
Small Fyke	9	22	10	8	3
Mini-hoop	11	21	5	15	7
Large Hoop	166	95	6	26	22
Large Box	42	271	97	84	24
Small Box	12	110	34	27	8
Dome	16	6	6	9	0

3 Results

Total sampling effort at Gus Engeling WMA between 2007−2009 was 1088 net-nights (2007 = 222 net nights; 2008 = 372 net nights; 2009 = 494 net nights; Table 1). The amount of water in each habitat, and thus the amount of habitat available in which to set nets, was highly variable depending on recent precipitation events (Figure 1c, d). We captured 366 turtles of seven species and 2935 fishes of 31 species, only fish species with ⩾5 captures were used in the analyses (Table 2).

Species distributions for both taxa resulting from the co-correspondence analysis were very similar with all but four species of fish and turtles falling out close to the origin of both axes 1 and 2 (Figure 2). Since co-correspondence analysis is based in part on a measure of β-diversity between sampling units (traps), the similarity in the distribution of species scores suggests that most species were captured together at common

Table 2. Catch per unit effort (net night) by habitat type for species captured at Gus Engeling Wildlife Management Area, Anderson County, Texas, 2007–2009.

Species	Total	Catch/Unit Effort by Habitat Type				
	Captures	Creek	Backwater	Marsh	Pond	Lake
Redear Slider	264	0.05	0.34	0.18	0.60	1.07
Razorback Musk Turtle	25	0.12	0.03	0	0	0
Common Musk Turtle	18	0.03	0.02	<0.01	<0.01	0
Common Snapping Turtle	17	<0.01	0.04	0.01	0.05	0
Eastern Mud Turtle	24	0	<0.01	0.10	0	0
Alligator Snapping Turtle	12	0.04	<0.01	0	0	0.01
Spiny Softshell Turtle	7	0.03	<0.01	<0.01	<0.01	0
Bluegill	895	0.55	0.52	0.28	0.77	6.96
Flier	481	0.02	0.80	0.18	0.24	0
Yellow Bullhead	316	0.66	0.16	0.47	0.02	0.30
Black Bullhead	280	0.23	0.14	0.15	0.24	0.31
Warmouth	245	0.10	0.35	0.07	0.08	0.22
Black Crappie	233	0.20	0.27	0.20	0.11	0
Redear Sunfish	133	<0.01	0.02	0.01	0.03	1.88
Longear Sunfish	44	0.19	<0.01	<0.01	0	0
Dollar Sunfish	33	0	0.06	0.01	<0.01	0
Spotted Gar	27	0.10	0.01	0	0	0
Bowfin	26	<0.01	0.03	0.03	0.03	0
Green Sunfish	26	0.06	<0.01	0.07	0	0
Spotted Sunfish	26	0.07	0.01	<0.01	0	0
Alligator Gar	25	0.08	0.01	0	0	0
Gizzard Shad	20	<0.01	0.03	0	0	0
Grass Pickerel	20	0.02	0.02	0.03	0	0
Lake Chubsucker	16	0.02	0	0.08	0	0.05
Pirate Perch	16	0	0.03	<0.01	0	0
Golden Shiner	15	<0.01	0.02	<0.01	0	0
White Crappie	9	0.02	0.01	0	0	0
Smallmouth Buffalo	8	0.04	<0.01	0	0	0
Orangespotted Sunfish	8	0.03	<0.01	0.01	0	0
Bantam Sunfish	8	<0.01	<0.01	0.02	0	0
Spotted Sucker	6	0.01	<0.01	0	0	0
Black Bass	5	0	0.20	0.40	0.20	0.20
Channel Catfish	4	1.00	0	0	0	0
Freckled Madtom	4	0.25	0.75	0	0	0
Threadfin Shad	2	0	0	1.00	0	0
Blacktail Shiner	2	1.00	0	0	0	0
Tadpole Madtom	1	1.00	0	0	0	0
Western Starhead Topminnow	1	0	0	0	1.00	0

sites at least once. All turtle species and 74% of the fish species we captured at Gus Engeling WMA were captured within the adjacent backwaters of Catfish Creek at least once (Table 2). The clustering of species scores within the co-correspondence analysis (Figure 2) is representative of this mixing within habitats. There were a few exceptions as eastern mud turtles and bowfin (*Amia calva*) fell out high on axis 2, while spiny softshell turtles (*Apalone spinifera*), and spotted gar (*Lepisosteus oculatus*), fell out low on axis 2 (Figure 2). The first two axes explained 47% of the variance. The next two axes only explained an additional 5% of the variance.

While fish and turtle distributions were very similar among all species minus the influence of measured environmental variables in the co-correspondence analysis, canonical correspondence analysis revealed that species distributions for fish and turtles were governed by flow and substrate along axis 1, and emergent vegetation and depth along axis 2 (Figure 3). Substrate composition itself was correlated with flow (higher percentages of sand and clay at sites with higher flow), and emergent vegetation (increasing percentages of detritus at sites with low flow and increasing emergent vegetation). Based on Monte Carlo permutation tests, the presence of basking

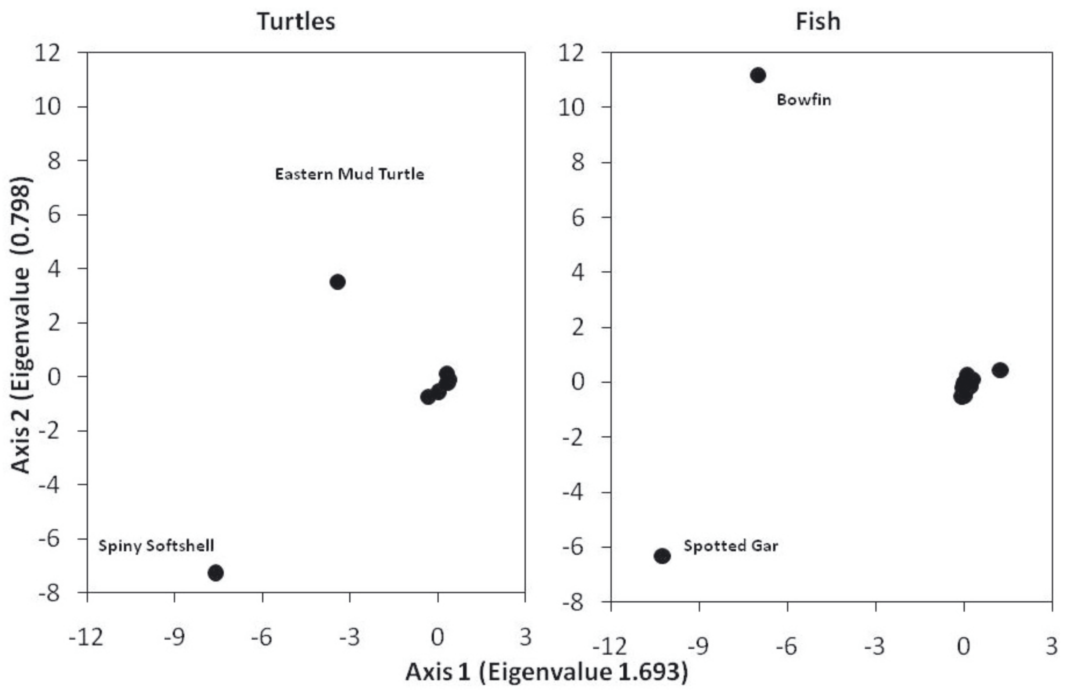

Fig. 2. Distribution of species scores based on first and second axes from Co-corrospondence Analysis for turtles and fishes at Gus Engeling WMA.

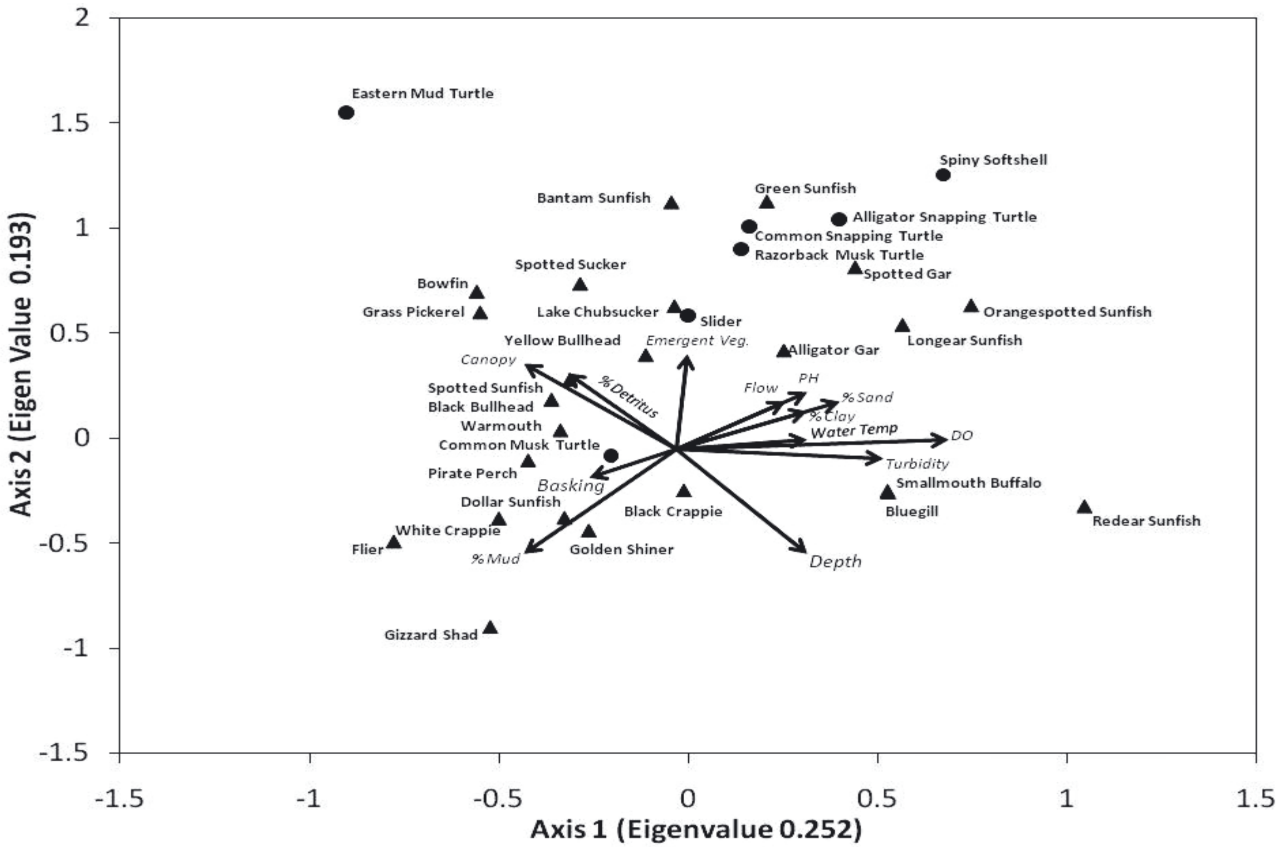

Fig. 3. Distribution of species scores of turtles, fishes, and environmental variables based on the first and second axes in Canonical correspondence analysis at Gus Engeling Wildlife Management Area. Turtle species scores are represented by circles and fish species scores by triangles. Continuous environmental variables are represented by vectors. Vector representation of turbidity is inverse, with decreasing turbidity with increasing distance from the origin. Total inertia for all axes was 12.22.

Table 3. Mean (± SE) environmental variables measured across all nets for each habitat, at Gus Engeling Wildlife Management Area, Anderson County, Texas 2007-2009. Within row means followed by the same letter are not different $\alpha = 0.05$. All within row differences were significant at $P \leq 0.001$.

Variable	Backwater	Creek	Marsh	Lake	Pond
Depth (cm)	36.53 ± 26.07 a	64.06 ± 27.09 b	36.19 ± 26.42 a	49. 09 ± 44.12 e	46.72 ± 27.43 e
Turbidity (cm)	19.45 ± 8.85 a	28.80 ± 10.46 b	24.22 ± 13.76 c	34.09 ± 24.05 d	33.63 ± 26.85 d
Flow (m/s)	0.06 ± 0.97 a	0.96 ± 1.28 b	0.00 ± 0.00 a	0.01 ± 0.13 a	0.00 ± 0.00 a
% Canopy Cover	66.84 ± 39.11 a	90.67 ± 21.92 b	21.05 ± 34.51 c	10.54 ± 22.82 c	29.71 ± 36.57 d
PH	5.95 ± 2.79 a	6.00 ± 1.11 a	5.73 ± 1.54 a	6.39 ± 0.49 ab	6.95 ± 4.56 b
Dissolved Oxygen (ppm)	3.34 ± 3.25 a	5.19 ± 1.77 b	2.61 ± 2.39 c	7.29 ± 0.51 d	5.92 ± 2.52 e
Water Temperature	22.79 ± 7.98 a	24.26 ± 4.89 b	23.93 ± 7.15 abc	25.64 ± 9.4 bcd	27.19 ± 1.85 d
% Sand Substrate	15.25 ± 15.75 a	44.42 ± 23.46 b	14.82 ± 22.78 a	34.00 ± 21.28 c	31.18 ± 27.97 c
% Mud Substrate	35.54 ± 18.91 a	28.22 ± 18.02 b	24.58 ± 16.89 b	23.09 ± 10.99 bc	19.89 ± 22.17 c
% Clay Substrate	12.45 ± 15.50 a	6.17 ± 11.33 b	15.47 ± 18.62 ac	17.09 ± 17.57 ac	30.79 ± 34.75 d
% Detritus Substrate	33.36 ± 15.15 a	21.65 ± 22.43 b	41.65 ± 22.03 c	14.91 ± 7.61 d	13.99 ± 10.36 d
% Basking Availability	14.36 ± 16.58 a	15.99 ± 1.03 ab	1.40 ± 6.17 c	8.72 ± 12.25 d	18.16 ± 17.04 b
% Emergent Vegetation	7.74 ± 18.24 a	5.46 ± 17.67 a	79.49 ± 29.26 b	31.05 ± 30.45 c	26.42 ± 38.96 c

structure and water temperature also had strong influences on species' distributions ($F = 1.73$, $P = 0.034$). Basking structure was generally represented by downed woody debris, and correlated to increased canopy cover and increased detritus. Water temperature was positively associated with sites that had a more open canopy. The percent variance of the species-environmental relationship for the first two axes of the canonical correspondence analysis was 42.7%, while the third and fourth axes explained and additional 27% of the variance.

Characteristics of each macrohabitat type, as described by the environmental variables collected, differed based on substrate, canopy cover, depth, and flow (Table 3). Creek habitats were deep, had high flow rates, dense canopy cover, moderate to high DO, and predominantly sandy substrate. Backwater habitats tended to be shallow, turbid, and had little to no flow, low DO, moderate canopy cover and substrate that was predominantly mud and sand. Marsh habitats were characterized by shallow water, low DO, sparse canopy cover, dense emergent vegetation, and the substrate was predominantly detritus. Pond habitats had low turbidity, low canopy cover, high pH, high water temperature, and sand and clay substrates. Lakes were characterized by deep water, low turbidity, sparse canopy cover, high DO, moderate presence of emergent vegetation, and a mixed substrate of sand, mud, and detritus.

While some species related primarily to characteristics of either lentic or lotic environments, this relationship was not readily obvious when the results of the canonical correspondence analysis was compared to capture rates in Table 2. Bowfin, grass pickerel (*Esox americanus*), and spotted suckers (*Minytrema melanops*) were not clearly associated with specific environmental variables. Within the ordination analyses all three species occurred along gradients associated with marsh habitats. However, captures were evenly distributed in backwater and marsh habitat for bowfin and grass pickerel, but creek and backwater habitat had higher captures of spotted suckers. Bluegill sunfish, redear sunfish, and smallmouth buffalo (*Ictiobus bubalus*) had scores on the first two canonical gradients (Figure 3). All three species were associated with sites characterized by deep water, and decreasing turbidity and dissolved oxygen. Bluegill sunfish were captured most frequently in lake and backwater habitats, redear sunfish in lake habitats, and smallmouth buffalo in creek habitats (Table 2). Whereas each species used different macrochabitats, their CCA axis scores suggest that each species used similar microhabitats within their respective macrohabitat type.

Ultimately, using an indirect ordination method, co-correspondence analysis, in conjunction with a direct ordination method, our canonical correspondence analysis, revealed differing patterns of habitat use across a landscape. Using β-diversity measurements of weighted species scores of sampling gear, co-correspondence analysis demonstrated considerable species mixing at the backwater interface between lentic and lotic environments. With the inclusion of environmental variables measured at each trap, we were able to infer preferred microhabitats for each species sampled.

4 Discussion

The dynamic nature of streams and resultant habitat heterogeneity supports regional species diversity (Galat *et al.*, 1998; Michener and Haeuber, 1998), and local assemblages are influenced by the periodic connectivity provided by flooding (Galat *et al.*, 1998; Winemiller *et al.*, 2000). The spatial arrangement of floodplain habitats is critical, because many species use different habitats during different life history stages (Welcomme, 1979; Schlosser, 1991; 1995). Species-specific dispersal abilities, and size and position of floodplain habitats are important determinants of the structure of fish (Taylor, 1997; Taylor and Warren, 2001) and turtle assemblages (Anderson *et al.*, 2002; Dreslik and Phillips, 2005; Riedle *et al.*, 2015).

While we observed considerable species mixing at the interface between lentic and lotic habitats, not all fish and turtle species were associated with Catfish Creek or its scours. Exceptions included bluegill and redear sunfish, two common centrarchid fishes that are regularly stocked in ponds and lakes (Robison and Buchanan, 1988; Table 2). Compared to other turtles, the eastern mud turtle generally was captured at relatively ephemeral sites. Juvenile bowfins were generally captured at sites along the edges of backwater scours characterized by shallow water and low DO. Eastern mud turtles are relatively terrestrial compared to other aquatic turtles, and also have the ability to estivate (Ernst and Lovich, 2009), and the bowfin is a primitive air breathing fish (Johansen *et al*., 1970). These physiological adaptations to ephemeral habitats may explain why co-correspondence analysis grouped these two species together.

The addition of environmental variables within the canonical correspondence analysis, showed that the distribution of both aquatic turtles and fishes at Gus Engeling WMA were associated with gradients related to flow and substrate regimes with predictable groupings of both taxa related to specific microhabitat characteristics. Flow, substrate, and emergent vegetation were particularly important in determining species distributions. Results from our Monte Carlo permutation tests suggested that downed woody debris was a major determining factor in species distributions. Riparian areas, the sources of woody debris, act to regulate the thermal profile of aquatic habitats by shading all or parts of a stream or water body (Welty *et al*., 2002). Woody debris within stream channels introduces organic matter and nutrients, maintains physical habitat by decreasing bank incision, decreases sediment flux, and controls pool spacing and bar formation (Abbe and Montgomery, 1996; Brooks *et al*., 2004). Subsequently, the introduction of woody debris into an aquatic environment results in increase of productivity and diversity of fishes and invertebrates (Meffe and Sheldon, 1988; Robertson and Crook, 1999).

Fishes use submerged woody debris as overhead cover from predation, and visual isolation between individuals (Robertson and Crook, 1999). Fishes may also receive a secondary benefit in the form of food from an increase in abundance and richness of aquatic invertebrates associated with woody debris (Angermeier and Karr, 1984; Everett and Ruiz, 1993). Woody debris is important to turtles for aerial basking and refugia (Chaney and Smith, 1950) and as foraging sites (Moll, 1976; Gibbons and Lovich, 1990). Presence of woody debris dictate the distribution of basking emydid turtles (Lovich, 1988; Lindeman, 1999) as well as bottom dwellers such as *Macrochelys* that depend on submerged woody debris for cover (Riedle *et al*., 2006; Shipman and Riedle, 2008).

We observed that both taxa exhibit predictable assemblages based on macro- and microhabitat preferences. Both vertebrate taxa also exhibit use of other aquatic habitats based on water levels and availability. Habitat complexity within stream systems allows both aquatic turtles and fish to meet their energy requirements and provides important spawning and nursery habitats (Schlosser, 1991; Schlosser, 1995; Fausch *et al*., 2002). Bowfin and alligator gar (*Atractosteus spatula*) are medium to large fishes, but most of my captures at GEWMA were represented by small juveniles in shallow, heavily vegetated habitats, similar to findings by Etnier and Starnes (1993) and Echelle and Riggs (1972).

Lawton (1999) described community ecology as a "messy science" as multiple processes can underlie the patterns of interest. Vellend (2010) attempted to simplify the study of community ecology by stating that the composition and diversity of species are influenced by only four classes of process. These classes were described as selection represented by deterministic fitness differences among species, drift or stochastic changes in species abundance, speciation, and dispersal or the movement of organisms across space. Although our study did not address speciation, we observed cases of habitat selection, drift, and dispersal. Selection in the case of habitat partitioning among closely related species, and drift and dispersal dependent upon water levels and connectivity between habitats. Biodiversity is affected by changes in physical and biological characteristics of landscapes, including movement of individual organisms (Pressey *et al.*, 2007), and therefore understanding the life history needs of all aquatic organisms is essential for management of wetland and riparian corridors (Galat *et al.*, 1998; Bodie *et al.*, 2000; Semlitsch and Bodie, 2003).

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