ECOSYSTEM SERVICES MITIGATED BY ECOTONAL WETLANDS IN A RIPARIAN AND AN AGRICULTURAL LANDSCAPE IN THE SOUTHEASTERN US

by

GABRIELA A. CARDONA RIVERA

(Under the Direction of Darold Batzer)

ABSTRACT

Many wetlands exist between completely aquatic and terrestrial environments, often acting as ecotonal zones harboring water, flora and fauna from both terrestrial and aquatic origins. These ecotones are renowned for providing ecosystem services such as water retention, nutrient processing, and for acting as extended landscapes for colonization. However, climate change and anthropogenic changes to the wetland landscape threaten ecotonal wetlands and their capability and efficiency to carry out those ecosystem services. Hence, it is important to study the dynamics of ecosystem services in these wetlands and to identify and describe the environmental factors that influence them.

Here, I assessed ecosystem services mitigated by ecotonal wetlands in an agricultural landscape, and in a river-floodplain system in Georgia, USA. In the Iron Horse Farm, I described how an ecotonal wetland adjacent to an agricultural landscape acted as refugium for arthropods known to prey on agricultural pests. This ecosystem service is not as well-known as those related to hydrology. During flood pulses In the Lower Ogeechee River, I observed how macroinvertebrate assemblages were present in both the river and the floodplain, and both were strongly influenced by their location along the river. Each habitat had specific indicator taxa across the locations, though rivers were also influenced by seasonality, and floodplains by pulse size. In the same flood pulses, I also assessed how different water quality measures varied in the riverine-floodplain system. Most metrics were influenced by pulse size such that most evidence of nutrient processing between the river and the floodplain habitats was detectable during smaller pulses. On the other hand, large pulses displayed a level of homogenization where water quality measures were comparable between the two habitats. This shows that established paradigms describing riverine floodplain interaction (e.g. the River Continuum Concept, Vannote et al. 1980, and the Flood pulse concept, Junk et al. 1989) require further development.

INDEX WORDS: agriculture, aquatic macroinvertebrates, ecotones, flood pulses, pest control, river-floodplain dynamics, wetland ecology.

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DEDICATION

First, I dedicate this dissertation to the ones who did everything in their power to get me to where I am. To mom Milagros Rivera Muñiz for raising me to believe in myself and in my dreams. Wherever I needed to go, she made it happen. To my little brother Diego for being an inspiration to see the world under the best light, and to my sister Aolanis for inspiring me to approach life with passion. To my grandparents Eli Rivera Vargas, and Magdalena Rivera Muñiz for being key to my upbringing, for the many care packages, and for praying for me whenever I sounded stressed over the phone. They are the best field work partners, cheer leaders, and confidants a granddaughter could ask for.

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CHAPTER 1

INTRODUCTION

Wetlands often act as ecotonal zones between fully aquatic and terrestrial landscapes. They are renowned for carrying out ecosystem services such as retaining sediments, water and nutrients as well as for harboring a diverse fauna and flora (Heimlich et al.1998; Brinson and Malvárez 2002; Constanza et al. 2014; Matteson et al. 2020; Ballut-Dajud et al. 2022). However, worldwide, wetland landscapes are threatened, and natural wetland loss is estimated between 54-57% (Davidson 2014). These losses have been largely attributed to urbanization, agriculture, and industry (Ballut-Dajud et al. 2022). Fluet-Chouinard et al. (2022) estimate that most of the wetland loss is driven by losses in the United States, followed by China, India, Russia, and Indonesia. As these ecosystems become less available, so does their ability to carry out ecosystem services efficiently (Constanza et al. 2014). Hence, it is important to identify and understand wetland ecosystem services across different landscapes.

With our studies, I aimed to describe ecotonal wetlands in an agricultural landscape, and in a riparian landscape. A vast number of wetlands in the US have been drained for agricultural purposes. Consequently, these landscapes lose the ability to perform ecosystem services that would otherwise benefit many aspects of agriculture (Brinson and Malvárez 2002). On the other hand, riverine floodplains are threatened by changes in the flow regime by the constructions of dams, urban runoff, as well as climate change related effects (Brinson and Malvárez 2002; Mishra et al. 2022). At the present time, wetland restoration projects continue to develop, and most of the success for these is measured by their efficiency at carrying out certain ecosystem services (Gordon et al. 2020). Moreover, as climate change induces extreme drought and flood events (Lake 2003; Hirabayashi et al. 2007; Li et al. 2022), wetlands and their benefits, as well as the resiliency of wetland organisms become even more endangered. With our studies, I shed light on different ecosystem services provided by ecotonal wetlands: 1) the use of agricultureadjacent wetlands as refugia for beneficial insects (predators, pollinators), 2) the fluctuations of nutrients across river-floodplain interactions during flood pulses, and 3) the distributions of invertebrate assemblages in riverine-floodplain systems during inundation events.

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CHAPTER 2

WETLANDS PROVIDE A SOURCE OF ARTHROPODS BENEFICIAL TO AGRICULTURE: A CASE STUDY FROM CENTRAL GEORGIA¹

¹ Cardona-Rivera, G.A et al. *Journal of Entomological Science*, *56*(3), 424-440. Reprinted here with permission from the publisher.

ABSTRACT

We described the overlap of arthropod communities between agricultural lands and adjacent wetlands using transect sampling, to determine if these juxtapositions might be influencing abundances of beneficial arthropods in agricultural lands. We further assessed experimentally whether these beneficial arthropods migrating from wetlands may potentially enhance crop productivity. Large numbers of predaceous carabid beetles and spiders moved from the wetlands into the agricultural lands; both of these groups can be important to biological control of crop pests. However, our exclusion experiments did not detect significant impacts of these predators on herbivorous insects or on crop productivity. Numerous studies have established that natural habitats adjacent to crop lands serve as refuge to beneficial arthropod communities and enhance overall biodiversity. Wetlands adjacent to agricultural lands appear to serve the same function. Our study suggests that wetlands may provide the ecosystem service of enhancing numbers of arthropods beneficial to agriculture, a service not established previously, and a factor that may motivate farmers to conserve wetlands that they own.

INTRODUCTION

Wetlands often occur in juxtaposition with agricultural lands, and their proximities suggest wetlands and agricultural lands likely interact in many ways. Ecologically, wetlands are key habitats for sediment retention, nutrient cycling, and high biodiversity (Brinson and Malvárez 2002, Heimlich et al. 1998, Matteson et al. 2020). Wetland bacteria can metabolize components of fertilizers, especially nitrate, improving soil and water quality (Heimlich et al. 1998). By retaining water and sediment, wetlands prevent crop runoff from reaching downstream habitats (Brinson and Malvárez 2002, Matteson et al. 2020, Steinman et al. 2003). Wetlands abate floods and maintain soil moisture by retaining water in dense plant stands and clay soils. Besides plants, wetlands provide habitat for a range of animal species (e.g., arthropods, amphibians, birds).

Historically, vast amounts of wetland in the United States have been drained for agriculture (Brinson and Malvárez 2002, Steven and Lowrance 2011), and farmers often consider wetlands as wastelands (Rijsberman and de Silva 2006). Yet, many of the remaining wetlands still occur on farms and ranches, which makes their conservation and preservation a challenge (Brinson and Malva' rez 2002, Heimlich et al. 1998). Although draining a wetland to convert it to agricultural land may seem more profitable to a farmer than keeping it in its natural state, once drained, wetlands lose their ability to provide various ecosystem services to agriculture (Brinson and Malvárez 2002, Lemly 1994). These "free" services from wetlands would otherwise be very costly to obtain (Denny 1994, Heimlich et al. 1998). If the negative perception of wetlands to farmers can be changed and the benefits of wetlands to agriculture made better known, perhaps farmers would be induced to voluntarily preserve wetlands on their lands.

Natural habitats adjacent to crop lands allow the preservation of arthropod biodiversity and, consequently, improve ecosystem resilience in an otherwise homogeneous environment (Duelli et al. 1999, Duelli and Obrist 2003, Wood and van Halsema 2008). Wetlands adjacent to agricultural lands likely serve as refuge for arthropod communities beneficial to crops (Brinson and Malvárez 2002, Denny 1994). We hypothesize that significant overlap exists in the invertebrate communities between agricultural lands and adjacent wetlands and that beneficial arthropods (i.e., predators, parasitoids, pollinators) and possibly pests (herbivores) will move from the wetlands into the agricultural lands. We further suspect that natural enemies from the wetlands will enhance productivity of crops by controlling pests.

METHODS

We tested our hypotheses by monitoring distributions of invertebrates (predators, parasitoids, pollinators, herbivores) in adjacent wetland-cropland systems and by experimentally excluding large natural enemies of pests from crops adjacent to wetlands to assess if the natural enemies are affecting crop yields.

Study sites

All studies were conducted at the Iron Horse Farm (33843037.100N 83818003.300W); an agricultural research facility of the University of Georgia located in Greene Co., GA. Associated with the farm are extensive wetlands, including wet meadows, alluvial swamps, and floodplains (see Matteson et al. 2020 for maps and a geological description of the farm). We worked with a wet meadow site (0.2 ha) that was bordered by row crop agriculture and an alluvial swamp (10 ha) that was bordered by managed grasslands initially (2016, 2017) and then subsequently by soybean, *Glycine max* (L.) Merrill, row crop (2018). The alluvial swamp was a bottomland hardwood forest with an embedded beaver wetland, and the wet meadow comprised assorted emergent moist-soil herbaceous and grassy vegetation.

Distributional sampling

At both the wet-meadow/row-crop setting and the alluvial swamp/grassland setting, we selected 4 parallel 50-m transects as our treatment units: (1) in the wetland interior (~20 m from the agricultural lands); (2) along the wetland edge (~2 m from the agricultural lands); (3) along the agricultural land edge (~5 m from the wetlands); and (4) in the interior of the agricultural lands (~20 m from the wetlands). To monitor a range of invertebrate types, we employed 3

sampling approaches: (1) pitfall traps sampled ground-dwelling invertebrates; (2) sweep netting sampled plant-dwelling invertebrates; and (3) "bee bowls" sampled pollinators and parasitoids.

Pitfall traps consisted of open wide-mouth glass jars (volume 237 ml, diameter 100 mm) sunk to their rims into the soil at random locations (6–8) along each transect. We filled them approximately half-way with 95% ethanol as a preservative. We used ethanol to ensure the croplands would not become contaminated by spilled preservative for possible future research efforts at the farm. We acknowledge that some aerially colonizing insects (e.g., vinegar and fruit flies, bark beetles) might be attracted to the ethanol, so we only quantified ground-dwelling organisms. Further attractivity of traps would then be similar in all transects. Pitfall traps were left in place for 24 h. If needed, additional ethanol was added to jars to preserve captured invertebrates, the samples were returned to the laboratory, and invertebrates were removed via hand-sorting, identified, and quantified.

Sampling was initiated ~2 wk after the crop plants had sprouted and then every 6 wk thereafter, until crops had matured (in late summer). Sampling was conducted in both agriculture-wetland settings over the 2016 and 2017 seasons. In conjunction with pitfall sampling, we used sweep netting (40 cm diameter) of vegetation to collect invertebrates living on plants (crops, grasses, wetland plants), at randomly selected locations (6–10) along each transect (described above). Each 1-m long sweep was transferred to a labeled plastic bag, samples were transported to the lab and frozen to kill invertebrates, and specimens were hand-picked under a dissecting scope, identified, and quantified.

In 2017, we additionally sampled pollinators and parasitoids using yellow, white, and blue colored "bee bowls." The small plastic bowls were placed at random locations (8) along the

same transects used for pitfall and sweep net sampling, partially filled with soapy water, and left in place for 24 h. Upon retrieval, specimens captured were preserved in ethanol and transported to the lab for identification and quantification.

Exclusion experiments

Distributional sampling suggested that ground beetles (Carabidae) and ground-dwelling spiders (Araneae) were readily moving from the wetlands into the croplands. Moreover, it is known that these beneficial organisms can be efficiently sampled with pitfall traps (Duelli et al. 1999), as verified by our distributional sampling. Thus, we targeted those organisms to examine if the wetland fauna was enhancing productivity of adjacent crops. In a transect inside the croplands, and ~10 m from the wetland edges, we erected circular cages (60 cm diameter) of 3 designs as our treatment units: (1) exclusion cages had walls of 12- mm wire mesh, from the soil surface to a height of 40 cm to limit entry of large, ground-dwelling carabid beetles and spiders; (2) "faux" exclusion cages were of the same design but with a 5-cm gap along the bottom edge to permit entry of large ground-dwelling beetles and spiders, and (3) open habit with no cage (6 replicates of each cage design/experiment). Studies were initiated ~2 wk after the crop plants had sprouted and continued for the subsequent 4 wk in summer 2018. We conducted studies in 1 corn, *Zea mays* L., field, adjacent to the wet meadow, and 1 soybean field, adjacent to the alluvial swamp.

After exclusion cages were erected, 2 pitfall traps were set in each cage for 24 h to assess population levels of ground-dwelling arthropods and to facilitate removal of residual beetles and spiders from full exclusion cages. After 4 wk, pitfall traps were re-set and retrieved after 24 h. Then, plants inside the cages were swept with a sweep net to collect plant-dwelling arthropods. Finally, the central plant in each cage was harvested, including the roots, to obtain above-ground and below-ground material. In the lab, invertebrates collected in pitfalls and sweeps were sorted, identified, and quantified. Plant material both above ground (leaves, stems, and fruits) and below it (roots) was oven dried (105°C) for 48 h and weighed to assess dry mass. Roots were gently rinsed to remove soil prior to drying.

Analyses

For distributional sampling, organisms in pitfall, sweep net, and bee bowl samples were identified to family (or order; depending on their life stage or if they were not insects) using standard keys (Triplehorn and Johnson 2005). We relied on the family level as a finer level taxonomic determination was not practical for many groups and specimens (immatures); Mueller et al. (2013) report that for community analyses, results at the family-level are typically congruent with analyses at the genus level, but we interpret analyses with caution. We then determined which groups were likely to be ecologically influential by identifying those taxa that occurred in at least 25% of the samples and restricted our analyses to them. We assessed samples in the wet-meadow/row-crop and alluvial-swamp/grassland systems, and samples from the 2016 and 2017 study years, independently. We assessed spatial and temporal distributions of ecologically important invertebrates using 2-way ANOVA in R (version 3.4.0) that accounted for transects (wetland interior, wetland edge, agricultural edge, and agricultural interior) as treatments and the sample date, and their interaction; with individual samples (pitfalls, sweeps, bee bowls) as statistical replicates. If the edge and interior transects within a habitat (wetland, agricultural land) displayed similar levels for a metric, displayed by similar behaviors in their graphed statistical interactions, they were pooled and evaluated simply as either wetland or

agricultural land. Data were $\log (x+1)$ transformed prior to analyses to meet assumptions of normality and equal variance. Because a case study approach was used (2 wetland-agricultural associations), we cannot infer broader application of specific results, but simply use the analyses to demonstrate potential links between wetlands and croplands.

Based on these analyses, we divided the taxa into 3 categories. (1) Generalist taxa occurred in similar abundances in both habitat types. For these taxa, the existence of a juxtaposition of wetlands and agricultural lands was of minimal consequence. (2) Specialist taxa were significantly more abundant in a single habitat type (wetland or agricultural land), and they exhibited minimal movements between the habitats. For these taxa, as for generalists, the existence of a juxtaposition of wetlands and agricultural lands was of minimal consequence. (3) Transient taxa had population levels that changed over the season between habitats; they were initially more abundant in 1 habitat type but then migrated to the other. For these taxa, the existence of a juxtaposition of wetlands and agricultural lands was consequential.

To identify transient taxa, we used the following winnowing process, based on our ANOVA results: (1) when habitat type (i.e., transect type) was not significant in the ANOVA and no significant interaction existed between habitat and sample date, taxa were considered generalists; (2) when habitat type was significant but no significant interaction existed between habitat and sample date, taxa were considered specialists; (3) when a significant interaction existed between habitat and sample date, taxa were considered potential transients; and (4) if the statistical interaction between habitat and sample date developed because the organism was largely absent from 1 habitat and only abundant in the other habitat on certain dates, the taxon was reassigned as a specialist. In summary, transient taxa were at least occasionally abundant in both wetland and agricultural habitats, but at different times. We then assessed whether transient taxa potentially were beneficial (predators, parasitoids, pollinators), pestiferous (herbivorous), or agriculturally neutral (detritivorous). For taxonomic groups that include taxa falling in more than 1 classification, we assigned them based on their most common designation (Triplehorn and Johnson 2005). Further, it is likely that some predators and parasitoids preyed on other beneficials. Thus, our broad classification should be viewed with caution.

In the exclusion studies, we assessed the experiments in corn and soybean independently. Using 1-way ANOVA, we first assessed possible cage artifacts by contrasting faux cages (with open gaps at their bases) with completely open habitats, for invertebrate abundances and crop plant biomass. If there were no differences between faux-cage and open habitats, these treatments were pooled as "open" habitat. Invertebrate abundances and crop plant biomass between open and exclusion habitats were then contrasted using 1-way ANOVA (with cages as replicates). Data were log (x+1) transformed prior to analyses to meet assumptions of normality and equal variance.

RESULTS

We collected a range of invertebrate taxa (Table 2.1) across the wetland-agricultural land complexes. However, <20% of them were common (occurred in at least 25% of samples). The most abundant taxa collected were Cicadellidae, Araneae, Formicidae, Gryllidae, and Carabidae.

Distributional studies

Most invertebrate taxa that were common across the wetland-agricultural land complex were either generalists or specialists (Table 2.2), and their distributions did not appear to be affected by the juxtaposition of habitats. However, distributions of several taxa were affected by the juxtaposition, where populations in 1 habitat appeared to affect populations in the other (i.e., transients). The most responsive transient taxa were 2 large, mobile predatory groups, carabid ground beetles and ground-dwelling spiders. In the 2016 sampling effort, pitfall sampling indicated that large numbers of ground beetles initially occurred in the wetlands, both the alluvial swamp and the wet meadow, whereas few occurred in the agricultural lands, either the soybean field or the pasture grassland (Fig. 2.1A, B). However, as the season progressed, numbers declined in the wetlands while they simultaneously increased in the agricultural habitats (i.e., highly significant habitat by date interaction terms existed, both p<0.001). In the 2017 season, the same pattern developed in the wet-meadow/row crop complex, albeit somewhat weaker (interaction p=0.007; Fig. 2.1C). That year in the alluvial-swamp/pasture system, the opposite pattern developed where the ground beetles appeared to migrate from the grassland to the swamp as the season progressed (interaction p=0.0002; Fig. 2.1D).

Similarly, in 2016, pitfall sampling indicated that large numbers of ground-dwelling spiders initially occurred in the wetlands, both the alluvial swamp and the wet meadow, whereas few occurred in the agricultural lands, either the pasture grassland or the soybean field. As the season progressed, spider numbers in the wetlands declined while numbers in the paired agricultural lands increased (both interaction terms, p=0.02; Fig. 2.1E, F). In 2017, however, ground-dwelling spiders exhibited either generalist or specialist behaviors, depending on the complex (Table 2.2). A final predaceous insect group affected by habitat juxtaposition were the ants in the wet-meadow and row-crop complex; here the ants were most abundant in the soybean field throughout the season (habitat effect, p<0.0001; Fig. 2.1G), but numbers in the wetland

edge tended to increase over the season, suggesting some movement of ants toward the wetland (interaction, p=0.006).

Some herbivorous insects also were affected by the juxtaposition of wetland and agricultural habitats, although in inconsistent ways. In 2016 sweep net samples, cicadellid leafhoppers initially had low population levels overall and then increased over the season (sample date, p<0.0001), with levels being higher in the wetland (habitat, p=0.0005). However, leafhopper numbers surged in the interior of the soybean field into late summer, perhaps resulting from migration from the wetlands (interaction, p=0.03; Fig. 2.1H). In 2017, leafhopper patterns reversed, with more occurring in the grassland pasture than the adjacent alluvial swamp, but as the season progressed numbers increased in the wetland edge habitat (interaction, p<0.0001; Fig. 2.1I). Gryllidae crickets appeared to move from the alluvial swamp into the adjacent pasture (interaction, p=0.0001; Fig. 2.1J). Drosophilidae vinegar flies appeared to move from the pasture into the alluvial swamp (interaction, p=0.0002; Fig. 2.1K). For other habitat/year combinations, the leafhoppers, crickets, and vinegar flies exhibited either specialist or generalist tendencies (Table 2.2).

Exclusion studies

There were no significant differences in arthropod abundances or plant biomass between the partial and open treatments in either the corn or soybean studies, suggesting that cage effects were not significant; thus, these 2 treatments were combined as "open habitat" to contrast with the full exclusion cages. Fewer carabid beetles were collected in the exclusion cages than the open habitat (p<0.01), indicating that the exclusion cages met the goal of reducing the numbers of those predators in both the corn and soybean studies. However, the cages did not effectively exclude spiders (p>0.05). We did not detect any cascading trophic effects of carabid beetle predation because herbivorous arthropod numbers and plant biomass (above or below ground) did not differ between treatments, in either the corn or soybean fields.

DISCUSSION

We found strong ecological interactions between the wetlands and the agricultural land in our study, with pronounced movements of several common arthropods between the 2 kinds of habitat. Movements of carabid beetles and spiders were especially dramatic and consistent. These organisms constitute 2 of the largest and most abundant predatory taxa in the ecosystems and, thus, are likely among the most ecologically important arthropods that occurred. Carabid beetles and spiders have been identified as playing important roles in the biological control of crop pests elsewhere (Bomford and Vernon 2005, Duelli and Obrist 2003, Holland and Luff 2000, Madeira et al. 2016), although in our system, we could not verify significant effects of these predators on herbivorous insects or any indirect effects on plant growth (it should be noted that pests overall did not seem to be a major problem during our studies). We found weaker and less consistent movements of potential plant pests (i.e., herbivorous arthropods) between the wetlands and the agricultural land and, thus, the presence of the wetlands did not appear to have any major deleterious effects on crop production.

Our use of family-level classification requires that results be viewed cautiously; some responses at the genus level may have remained undetected, and all genera within a family may have occurred and gone undetected. Furthermore, our process of winnowing taxa may underestimate some landscape-level impacts of the juxtaposition of wetlands with agricultural lands. As discussed by Duelli et al. (1999), ground-dwelling arthropods will have different levels

of mobility in habitats of variable vegetation. Although generalist taxa occurring with equal frequency in both wetland and agricultural lands may suggest that the juxtaposition is irrelevant, it is alternatively possible that the juxtaposition of habitats boosted population levels in both habitats (i.e., if the wetlands had not been present, populations in the agricultural lands might have been lower, and vice versa). As previous studies have shown, these abundances may be due more to the range of adaptability of the organisms rather than the actual habitats present specifically (Duelli et al. 1999). Additionally, although specialist taxa may strongly prefer 1 habitat over the other, most were still present in the nonpreferred habitat, meaning that some wetland specialist individuals may "bleed" into adjacent agricultural lands and perhaps have ecological impacts there. Finally, the occurrence of edge-habitat specialists (Table 2.2) may represent an impact of wetland-agricultural land juxtaposition, although it is not clear that the involvement of a wetland in creating the edge habitat was crucial (i.e., any kind of edge habitat may suffice). As described with different habitat types by Duelli and Obrist (2003), Holland and Luff (2000), and Madeira et al. (2016), wetlands, as natural habitats adjacent to crop lands, may serve as compensatory habitat for common species in the area, allowing for higher abundances to develop. In some years and some types of crop lands, transient groups acted as either generalists and/or specialists, suggesting that habitat ecotones function in complex ways. For example, Altieri and Nicholls (2003) found that soil compositions influenced plant-pest interactions. Despite these caveats, our study suggests that broad ecological connections likely exist between wetlands and croplands in terms of the arthropod fauna.

Our case study provides insight into a previously undocumented ecosystem service offered by wetlands, providing a source of beneficial arthropods to agriculture that should be more fully explored across a variety of agricultural settings. By acting as a refuge habitat to arthropods, wetlands may allow more resilient ecosystems to develop with possible benefits to biocontrol for agriculture (Brinson and Malvárez 2002, Duelli and Obrist 2003). Globally, wetlands are valued, for serving as ecotones between land and water, and for contributing to mosaic-like, diverse landscapes (Denny 1994). Many studies have already highlighted the positive impact wetlands have on nearby ecosystems, by contributing to higher biodiversity, nutrient and sediment retention and cycling, and for improving water quality (Brinson and Malvárez 2002, Denny 1994, Heimlich et al. 1998, Steven and Gramling 2011). The possibility that wetlands may provide benefits in terms of pest control adds to this list. However, more study will be required to determine if it is the mere presence of natural habitat, regardless of type (e.g., forest, grassland, wetland), that contributes to higher arthropod abundances (Duelli et al. 1999, Duelli and Obrist 2003) or if wetlands instead provide unique conditions that favor certain key taxa, as described by Madeira et al. (2016).

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Table 2.1 Invertebrate taxa collected in wetland and agricultural land ecosystems in 2016-2017 according to sampling method. Taxa highlighted in **bold** were present in at least 25% of the samples in the respective sampling method and year.

201	16	2017			
Pitfalls	Sweeps	Pitfalls	Sweeps	Bee Bowls	
ARACHNIDA	ARACHNIDA	MOLLUSCA	MOLLUSCA	ARACHNIDA	
Acari	Aranana	Gestropoda	Gestronode	Aranese	
Aranese	Oniliones	MVRIAPODA	ARACHNIDA	COLLEMBOLA	
DIPLURA	ORTHOPTERA	Diplopoda	Araneae	Entomohrvidae	
COLLEMBOLA	Acrididae	Chilopoda	ODONATA	Hypogastruridae	
Entomobryidae	Gryllidae	ARACHNIDA	Coensgrionidae	Sminthuridae	
Hypogastruridae	Tetrigidae	Araneae	Lestidae	ODONATA	
Isotomidae	Tettigoniidae	COLLEMBOLA	ORTHOPTERA	Lestidae	
Sminthuridae	HEMIPTERA	Entomobrvidae	Acrididae	ORTHOPTERA	
MICROCORYPHIA	Anthocoridae	Isotomidae	Grvllidae	Acrididae	
Machilidae	Aphididae	Hypogastruridae	Tetrigidae	Grvllidae	
ORTHOPTERA	Bervtidae	Poduridae	Tettigoniidae	Tetrigidae	
Acrididae	Blissidae	Sminthuridae	HEMIPTERA	Tettigoniidae	
Grvllidae	Cercopidae	ORTHOPTERA	Alvdidae	HEMIPTERA	
Tetrigidae	Cicadellidae	Acrididae	Anthocoridae	Alevrodidae	
Tettigoniidae	Cixiidae	Grvllidae	Aphididae	Aphididae	
DERMAPTERA	Coreidae	Tetrigidae	Blissidae	Blissidae	
Anisolabididae	Delphacidae	Tettigoniidae	Cercopidae	Cercopidae	
HEMIPTERA	Derbidae	DERMAPTERA	Cicadellidae	Cicadellidae	
Alydidae	Geocoridae	Anisolabididae	Coreidae	Delphacidae	
Aphididae	Membracidae	HEMIPTERA	Delphacidae	Geocoridae	
Blissidae	Miridae	Alydidae	Geocoridae	Membracidae	
Cicadellidae	Nabidae	Anthocoridae	Membracidae	Miridae	
Gelastocoridae	Pentatomidae	Aphididae	Miridae	Nabidae	
Geocoridae	Plataspidae	Blissidae	Nabidae	Pachygronthidae	
Membracidae	Reduviidae	Cercopidae	Pachygronthidae	Pentatomidae	
Miridae	Tingidae	Cicadellidae	Pentatomidae	Psyllidae	
Pachygronthidae	COLEOPTERA	Cydnidae	Reduviidae	Reduviidae	
Pentatomidae	Anthicidae	Geocoridae	Tingidae	Tingidae	
Psyllidae	Chrysomelidae	Membracidae	PSOCOPTERA COL DODTED A	THYSANOPTERA	
THING A MODIFIED A	Coccinellidae	Dashumunthidaa	Conchidee	COLEOPTERA	
Dhlaaathrinidaa	Mordellidee	Pachygroninidae	Chravomalidae	Chravomalidae	
COL FORTER V	Dtinidao	Derrilidae	Constinuitidae	Constinuitidae	
Anthicidae	Scarahaeidae	Reduviidae	Curculionidae	Curculionidae	
Carabidae	Stanhylinidaa	Tingidae	Lamonhloaidae	Lamonkloaidae	
Chrysomelidae	HYMENOPTER A	THYSANOPTERA	Meloidae	Ptiliidae	
Coccinellidae	Anidae	Phlaeothrinidae	Mordellidae	Stanhylinidae	
Curculionidae	Braconidae	COLEOPTERA	Nitidulidae	HYMENOPTERA	
Elateridae	Eulophidae	Anthicidae	Ptiliidae	Andrenidae	
Endomychidae	Formicidae	Carabidae	Ptinidae	Apidae	
Meloidae	Ichneumonidae	Chrysomelidae	Staphylinidae	Chrysididae	
Monotomidae	Vespidae	Coccinellidae	Tenebrionidae	Cynipidae	
Nitidulidae	LEPIDOPTERA	Curculionidae	NEUROPTERA	Diapriidae	
Ptiliidae	Geometridae	Elateridae	Chrysopidae	Dryinidae	
Ptinidae	Noctuidae	Laemophloeidae	HYMENOPTERA	Encyrtidae	
Scarabaeidae	Sesiidae	Meloidae	Braconidae	Eulophidae	
Staphylinidae	Attevidae	Monotomidae	Cynipidae	Formicidae	
1 encorionidae	Callinharidaa	Tymoundae	Diapriloae	Hancudae	
Crainidae	Campnoridae	Ptimidae	Encyrtidae	Magachilidae	
Diamiidae	Chironomidae	Scarabasidas	Formicidae	Mamaridee	
Encortidae	Culicidae	Stankulinidaa	Halictidae	Distrosstridae	
Eulophidae	Dolichonodidee	Tenebrionidae	Ichnonmonidae	Scalionidae	
Formicidae	Drosonhilidae	HYMENOPTERA	Mymaridae	Scoliidae	
Ichneumonidae	Empididae	Cyninidae	Platygastridae	Sphecidae	
Mymaridae	Mycetophilidae	Diapriidae	Torymidae	Torvmidae	
Platygastridae	Psychodidae	Encyrtidae	Trichogrammatidae	Trichogrammatidae	
Pompilidae	Simuliidae	Formicidae	Vespidae	Vespidae	
Table 2.1 Continued.

Pteromalidae	Syrphidae	Mymaridae	LEPIDOPTERA	LEPIDOPTERA
Scelionidae	Tachinidae	Platygastridae	Erebidae	Geometridae
Scoliidae	Tipulidae	Scelionidae	Geometridae	Hesperiidae
Sphecidae	Ulidiidae	Scoliidae	Noctuidae	Noctuidae
Tenthredinidae		Torymidae	DIPTERA	DIPTERA
Torymidae		Trichogrammatidae	Agromyzidae	Asilidae
Trichogrammatidae		LEPIDOPTERA	Anthomyzidae	Cecidomyiidae
Vespidae		Geometridae	Cecidomyiidae	Chironomidae
LEPIDOPTERA		Noctuidae	Chironomidae	Dolichopodidae
Erebidae		DIPTERA	Chloropidae	Drosophilidae
Noctuidae		Asilidae	Culicidae	Empididae
Pieridae		Cecidomyiidae	Dolichopodidae	Mycetophilidae
DIPTERA		Chloropidae	Drosophilidae	Phoridae
Cecidomyiidae		Dolichopodidae	Empididae	Sciaridae
Chironomidae		Empididae	Mycetophilidae	Syrphidae
Chloropidae		Mycetophilidae	Phoridae	Tabanidae
Dolichopodidae		Phoridae	Sciaridae	Tachinidae
Empididae		Sciaridae	Syrphidae	
Lauxaniidae		Tachinidae	Tachinidae	
Mycetophilidae		Tipulidae	Tephritidae	
Phoridae			Ulidiidae	
Psychodidae				
Sciaridae				
Simuliidae				
Tachinidae				

Table 2.2 Commonly occurring arthropods (collected in >25% of samples, in at least one type of sampler) that did not exhibit obvious movement between wetland and agricultural lands (transient taxa are listed in Figure 2.1), classified by: general function (specialists or generalists); collecting method (pitfalls, sweeping, or bee bowls); agricultural function (potential beneficial {predator, parasitoid, pollinator}, potential pest {herbivorous}, or agriculturallyneutral{detritivorous}); habitat type (wetland, agricultural land, habitat edges); and type of agricultural land (RC=row crop, P=pasture), in the years 2016 (16) and 2017 (17).

Specialists		Generalists			
	Pitfalls	Sweeping	Pitfalls	Sweeping	Bee Bowls
Potential Beneficial	Wetland T Araneae (RC, 17)	axa Tachinidae (RC, 17)	Araneae (P, 17) Formicidae (P/RC, 17) Staphylinidae (P, 16; P/RC, 17)	Araneae (P, 16)	Parasitoids (P/RC, 17) Pollinators (P/RC, 17) Halictidae (P/RC, 17)
Potential Pest	Blissidae (RC, 17)	Cicadellidae (RC, 17) Miridae (RC, 16) Drosophilidae (RC, 17)	Nitidulidae (RC, 17) Curculionidae (P, 17) Acrididae (RC, 17)		
Potential Neutral	Entomobryidae (P/RC, 16; P, 17) Isotomidae (P/RC, 16; RC, 17) Hypogastruridae (P, 16) Sminthuridae (RC, 16)	Gryllidae (RC, 16)	Isotomidae (P, 17) Gryllidae (P/RC, 16; RC, 17)	Gryllidae (P, 16)	
Agricultural Land Taxa			•	•	
Potential Beneficial	Formicidae (P, 16)				
Potential Pest	Cicadellidae (P, 17) Acrididae (P, 17)				
Potential Neutral	Entomobryidae (RC, 17)				
Edge Taxa		7			
Potential Pest	Nitidulidae (P, 17)	Cicadellidae (P, 16) Miridae (P, 16)			
Potential Neutral	Hypogastruridae (RC, 16)				



Figure 2.1 Relative abundances (log (x+1)/sample) of common transient arthropods (A-D, Carabidae; E-F, Araneae; G, Formicidae; H-I, Cicadellidae; J, Gryllidae; K, Drosophilidae) in row crop-wet meadow and/or pasture-alluvial swamp systems, over the summers of 2016 or 2017. In every case, a statistically significant (P<0.05) interaction existed between habitat types and time, suggesting transient movement between habitats. Data from wetland, wetland edge and agricultural land habitats are indicated by black, gray and white bars, respectively. Y-axes sometimes include negative values where error bars (SE) extended into negative ranges. (Non-transient common taxa are listed in Table 2.1).

CHAPTER 3

VARIATION IN MACROINVERTEBRATE ASSEMBLAGES DURING FLOOD PULSES ALONG A RIVER-FLOODPLAIN SYSTEM, GEORGIA, USA²

² Cardona Rivera, G.A., et al. To be submitted to a peer-reviewed journal.

ABSTRACT

Riverine floodplain connections with the main channel are considered key influences on macroinvertebrate assemblages and their distributions. These connections increase habitat and food resource availability, but flooding also imposes stress on macroinvertebrates. We collected macroinvertebrates during the rising and falling limbs of 11 flood pulses in both river and the floodplain habitats along the length of the lower Ogeechee River (Coastal Plain reaches), including both the normal Winter-Spring flood season as well as the tropical storm season. Macroinvertebrate assemblages were mostly influenced by differences between the river and the floodplain, and assemblage turnover was high. In the river channel, assemblages were mostly influenced by the location down the watershed, and by seasonal change (with several indicator taxa unexpectedly being terrestrial invertebrates). In the floodplain, assemblages were also mainly influenced by site location, but also by pulse size. The floodplain indicator taxa for the larger pulses were terrestrial taxa while those for smaller pulses were aquatic. While most taxa, both in the river and on the floodplain, were shared among habitats and sites across the coastal plain, there were some site-specific indicator taxa. As extreme flood and drought events become more frequent in the future, it will be important to better understand macroinvertebrate distributions and their resiliency to hydrologic changes in river channels and their floodplains.

INTRODUCTION

Hydrological conditions are a key factor influencing ecological function and biodiversity in riverine-floodplain systems (Vannote et al. 1980; Junk et al. 1989; Bunn and Arthington 2002). During flood pulses, a lateral connection develops between the river and the floodplain, increasing habitat and food resource availability for aquatic macroinvertebrates (Junk et al. 1989; Benke et al. 2001; Johnson et al. 2023). This increase in resources has been observed to positively influence macroinvertebrate biomass such that macroinvertebrate production can be higher on the floodplain than in the main channel (Benke et al. 2001). The transport of macroinvertebrates between channels and floodplains (and uplands) can develop from both aquatic and terrestrial communities (Junk et al. 1989). Responses of terrestrial organisms to floods have been attributed to displacement during floods (Collier and Quinn 2003), although many terrestrial taxa are obligate floodplain dwellers (Bright et al. 2010, Batzer and Wu 2020).

Regardless of the origin of the taxa, the patterns of movement of macroinvertebrates across riverine floodplain systems has been attributed to many factors including the kinds of habitat in which the organisms normally dwell (Galatowitsch and Batzer 2011), seasonal effects (Johnson et al. 2023), location along the watershed (Vannote et al. 1980, Reese and Batzer 2007, Bright et al. 2010; Batzer et al. 2018), and pulse size or degree of connectivity (Junk et al. 1989; Robinson et al. 2004; Gallardo et al. 2008; Åhlén et al. 2023). Vannote et al. (1980) focused on aquatic invertebrates in river channels and describe changes along the lengths of rivers (i.e., the River Continuum Concept). Junk et al. (1989) focused on interactions between the river channel and adjacent floodplains (i.e., the Flood Pulse Concept). Galatowitsch and Batzer (2001) observed the movement of mayflies from the main river channel to the floodplain and hypothesized it resulted from refugia effects and food resource availability. Johnson et al. (2023) evaluated macroinvertebrate biomass following a pulse after a prolonged drought period and a pulse during a predominantly flooded period; they observed increases in biomass associated with pulses during the flooded period. Reese and Batzer (2007), Bright et al. (2010) and Batzer et al. (2018) expanded on the lateral interaction between the main channel and the adjacent floodplain (i.e., Flood Pulse Concept of Junk et al. 1989), by describing variability in environmental influences on floodplain macroinvertebrate communities from headwater to lower-river

floodplains. Åhlén et al. (2023), Gallardo et al. (2008), and Robinson et al. (2004) observed macroinvertebrate abundances during floods and attributed compositional changes to landscape variability induced by inundation patterns.

The Ogeechee is a useful riverine floodplain system for the observation of river floodplain interactions during flood pulses as it is relatively pristine and is free flowing with no major dams in its watershed (Benke et al. 2000; 2001; Benke and Wallace 2015). This sandy river channel harbors many of its riverine macroinvertebrates on snags (accumulations of plant material on plants or wood). However, the majority of habitat surface area for invertebrates occurs on the flooded floodplain, including most of the system's aquatic invertebrate production (Benke et al. 2001). Undammed rivers such as the Ogeechee are relatively rare but are still susceptible to changes in flow regime through variation in weather and climate (i.e. droughts and floods), as well as other anthropogenic effects (Lake 2003). Since extremes of both drought and floods are becoming more frequent (Hirabayashi et al. 2007; Li et al. 2022), it is important to understand how river-floodplain macroinvertebrate assemblages (both aquatic and terrestrial) are influenced by flood pulses.

Based on this, we set out to ask how floodplain and river macroinvertebrate assemblages are distributed during flood pulses, and which environmental factors influence their distributions and frequencies of occurrence. We hypothesized that A) there would be unique river and floodplain assemblages, with some overlap of more generalist taxa; and B) there would be variation in distributions of assemblages influenced by site location in the watershed, flood season (normal vs. tropical storm seasons), pulse size (small vs. large), and pulse phase (rising vs. falling limbs). We predicted that certain indicator taxa would reflect different environmental conditions. Our study aimed to shed light on macroinvertebrate dynamics during flood pulses and identify the most useful taxa to reflect the influence of these dramatic disturbances.

METHODS

Study Sites

Our study took place in the lower Ogeechee River, a blackwater stream that flows through the Southeastern U.S. Coastal Plain. The river bed is composed of mainly sandy benthic sediment, and the bank has several points of connection with the adjacent floodplain throughout the flood season (Benke et al. 2001). We sampled four sites (Fig 3.1) proximal to USGS gages along the river over the years 2019-2022. The floodplains at these sites were generally natural forest (Dewitz 2021) with trees such as willow (Salix spp.), bald cypress (Taxodium distichum), and bottomland hardwoods (Murray-Stoker et al. 2022). The uppermost site was located 20.1 km downriver from the Grange Gage (USGS 02200120) and is part of a nature reserve (Ogeechee Crossing Park). This site was immediately below the Fall Line, which divides the Piedmont and Coastal Plain ecoregions. The next site was about 1km upriver from the Midville Gage (USGS 02201230) and had a mainly forested landscape with nearby residential properties and agricultural pasture. The lower most sites, Oliver and Ellabell were both located adjacent to their USGS gages (USGS 02202190 and USGS 02202680, respectively) near boat ramps and highway overpasses but mostly surrounded by natural, floodplain forests. The lower-most Ellabell site was just upstream from the upper influence of coastal tides.

To observe flood pulses and determine their size, we evaluated real-time discharge and gage-height data for each site reported by the USGS Current Water Data for Georgia website (https://nwis.waterdata.usgs.gov/ga/nwis/rt). With this data we were able to detect major rain

events and the rising and falling phases of subsequent flood pulses, as well as durations of riverfloodplain connection at each sample site. We sampled both the rising and falling limbs of flood pulses as they reached and exited each site. Most pulses observed occurred during the normal flood season (December-April; Benke et al. 2001), but we also sampled three pulses during the tropical storm season (August-October).

Field sampling and Laboratory processing

We recorded each pulse size based on the peak discharge that reached the uppermost site, Grange, as it represented the volume of water that flowed from the Piedmont portion of the watershed to our coastal plain sites. During each visit we confirmed floodplain-river connection, then sampled both the river and the floodplain. To sample the river, we identified submerged snags and vegetation along the bank, as these are known to be primary habitats for invertebrates in the otherwise sandy Ogeechee channel (Benke 2001; Benke and Wallace 2015; Murray-Stoker et al. 2022). We "jabbed" these sub-habitats with a D-frame net (500 µm mesh net, 30 cm diameter) ten times, a procedure commonly used to sample invertebrates in channels of regional streams (Barbour et al. 1996). For the floodplain, we selected a representative area of inundated habitat and jabbed the D-net ten times in sub habitats as available (benthic mud and leaf litter, woody substrates), across a range of water depths. We transferred each individual river or floodplain sample into sealed, labeled plastic bags. (We returned any vertebrates encountered such as amphibians and fish back to the water.) Lastly, we transported the samples back to the laboratory and stored them frozen until processing.

For processing, we rinsed each sample over a sieve (330 μ m mesh) to separate invertebrates from organic debris and sediment. We collected all larger invertebrate taxa that

were observed in the sieves while rinsing. The remaining fine materials and small invertebrates were subsampled (33%) and hand sorted using a stereo microscope. All invertebrates collected were preserved in 95% Ethyl Alcohol. Taxa were identified to the lowest taxonomic level practical using keys in Rogers and Hill (2008), Thorp and Covich (2009), Merritt et al. (2019), and various other taxon-specific references.

Statistical Analysis

For each individual pulse, we collected up to 16 samples, if it reached all study locations (river and floodplain, rising and falling limbs, and all 4 locations). We evaluated the effects of habitat type (river vs floodplain), location (four sample sites), pulse size (large vs small, see below), season (normal flood vs tropical storm seasons, see below), and pulse phase (rising vs falling limbs) on invertebrate assemblages using a PERMANOVA analysis with the adonis 2 function in the vegan package in R (Oksanen et al. 2022). To visualize the overall distributions of the assemblages of taxa relative to the different factors we plotted their calculated NMDS scores and highlighted spatial patterns for each factor using ellipses. We did not feel that the quantitative efficiencies of the jab sampling in the river and floodplain were directly comparable (e.g., volumes of leaf litter and sediment collected differed dramatically), thus we elected to use presence/absence macroinvertebrate data for habitat contrasts rather than relative abundance. While we could have used relative abundances when analyses addressed only the river or only the floodplain, both PERMANOVA and NMDS analyses for relative abundance data versus a presence-absence matrix were very similar; thus, we opted to use the presence-absence matrix for all analyses. Broader analyses by Mueller et al. (2013) and Pires et al. (2021) report that presence-absence and relative abundance typically generate congruent results. We used the presence/absence matrix evaluated under a Jaccard Similarity Index (JSI) method as our

community distance measure for analyses. Additionally, to assess overall differences between the river and floodplain habitats, we calculated a JSI (Jaccard 1901, 1908).

For both the river and the floodplain, and among the different environmental conditions, we identified indicator taxa using the multipatt function in the *indicspecies* package in R (Cáceres and Legendre 2009). This technique assesses the frequency of occurrence for each taxon and identifies those that most frequently occurred in each of the habitats or environmental conditions.

RESULTS

We sampled 11 pulses. Eight happened during the normal flood season (December-April), and three during the tropical storm season (August-October). We classified 7 as small pulses ranging from peak discharges of 11.7-34.2 m³/s at the uppermost Grange gage, and four as large pulses with peak discharge at Grange ranging from 74.4-331.3 m³/s. Six of the pulses connected the river with the floodplain at all four sites, while others only created connections at a subset of the study sites, typically Grange and Midville (the uppermost sites). There was one exception, where a pulse developed in Oliver and Ellabell after an intense localized rain upstream of the Oliver gage, but this pulse did not include the up-stream sites.

Overall, we collected 39185 invertebrate specimens spread across 119 taxa (see taxa lists in Appendix A). Despite primarily sampling submerged habitat, an unexpectedly large number of terrestrial organisms were collected, several of which were influenced by variation in flood pulses (see following). However, most organisms collected were aquatic (Appendix A).

Environmental effects on taxa distributions in the river and floodplain

PERMANOVA suggested that the major factor that affected invertebrate distributions was the difference between river and floodplain habitats (5.8% of variation explained, Table 3.1, Fig. 3.2A). The NMS plot suggests that the variation in the river exceeded the variation in the floodplain, with the variation in the floodplain being encompassed by the variation in the river (Fig. 3.2A). However, both habitats had unique indicator taxa (Appendix A) and turnover was high (R_{stat}=0.9797), and so the floodplain assemblages were not simply subsets of the river assemblages. The taxa emblematic of the river, as calculated by the indicator taxa analysis, were (in order of priority) Hydroptilidae (p=0.0001), *Peltodytes* (p=0.0003), Lymnaeidae (p=0.0043), Taenopterygidae (p=0.0022), *Gyrinus* (p=0.0103), and *Lepidostoma* (p=0.0242) (Appendix A). For the floodplain, the indicator taxa were Sphaeriidae (p=0.0001), Ostracoda (0.0001), Planorbidae (0.0002), Acari (0.0003), *Neoporus* (p=0.0017), Copepoda (p=0.0058), and Physidae (0.0317) (Appendix A). All the floodplain indicator taxa also occurred in the river, and all the river indicator taxa also occurred in the floodplain (Appendix A).

The Jaccard index of the river versus floodplain samples suggested 47.2% overall assemblage similarity. The uniqueness of the river from the floodplain was mostly driven by numerous different genera or families of Plecoptera, Odonata, and Trichoptera being collected only in the river, and an assortment of terrestrial insect families being collected only in the floodplain (Appendix A).

PERMANOVA indicated that habitat type had interactions with pulse size, location, and season, so we assess those factors in each habitat individually (see following). The overall PERMANOVA and NMS plots both suggest that no differences existed between the rising and falling limbs of pulses (organisms were not being displaced during pulses) (Fig. 3.2B). We do not analyze pulse phase further.

Environmental effects on taxa distributions in the river

Site effects explained 8% of the macroinvertebrate assemblage variation in the river (Table 3.2). Midville (the second uppermost site), Oliver, and Ellabell (the lowermost site) appeared to all overlap and be subsets of the most variable macroinvertebrate community at Grange (the uppermost site) (Fig. 3.3A). Indicator species analyses identified Formicidae (p=0.0304) for Midville, and Valvatidae (p=0.0348) for Ellabell; otherwise, taxa in the river channel were spread across multiple sites. Seasonal change explained about 4% of the macroinvertebrate community distributions in the channel where assemblages in pulses during the normal pulse season appeared to be subsets of the assemblages in the more variable tropical storm season pulses (Table 3.2, Fig. 3.3A). Indicator species analyses identified Amphipoda (p=0.0356) for pulses in the normal flood season, and Cicadellidae (p=0.0002), *Stelnemis* (p=0.0009), and Gerridae (p=0.0058) for the pulses during the tropical storm season. Pulse size effects in the river only explained about 2% of the variation, with assemblages in small pulses appearing to be a subset of those in large pulses (Table 3.2, Fig. 3.3C).

Environmental effects on taxa distributions on the floodplain

In the floodplain, site effects explained 10% of the assemblage distributions where Midville and Oliver were subsets of both the uppermost Grange and lowermost Ellabell sites, with Ellabell displaying the greatest overall variation (Table 3.2, Fig. 3.4A). Indicator species analyses identified Lepidoptera (p=0.0165) for Grange, Scirtidae (p=0.006) for Midville, and *Coptotomus* (p=0.0021) and Valvatidae (p=0.0044) for Oliver. Pulse size effects explained another 5% of the distributions on the floodplain where assemblages in small pulses appear to be a subset of those in large pulses (Table 3.2, Fig. 3.4C). Indicator species analyses identified Ostracoda (p=0.0008), Oligochaeta (p=0.0178), Asellidae (p=0.0210), and Sphaeriidae (p=0.0288) for small pulses, and Chilopoda (p=0.0058), non-Heteroptera hemipterans (p=0.0283) and Formicidae (p=0.0298) for large pulses. Lastly, Seasonal effects explained about 3% of the distributions on the floodplain where, similarly to the river, assemblages in pulses during the normal pulse season appeared to be subsets of the taxa in tropical storm season pulses (Table 3.2, Fig. 3.4B)

DISCUSSION

Environmental drivers of macroinvertebrate assemblages in both river and floodplain habitats

Macroinvertebrate assemblages in riverine floodplains have been known to be influenced, in richness, abundance and production, by flood pulses and the consequential river-floodplain connections (Junk et al. 1989; Benke et al. 2001; Bunn and Arthington 2002; Gallardo et al. 2008; Galatowitsch and Batzer 2011, Turić et al. 2015; Chattopadhyay et al. 2021; Johnson et al. 2023). These connections provide increased habitat, nutrient, and food resource availability to macroinvertebrates and other fauna in the main channel (Junk et al. 1989). We hypothesized that unique taxa assemblages would occur in river and floodplain habitats. In our study, however, we observed that most macroinvertebrate taxa existed in both river and floodplain habitats; habitat type explained <6% of overall assemblage variation, but certain taxa were more frequently found in either the river or the floodplain (Table 3.1, Appendix A). Reese and Batzer (2007), working in coastal plain floodplains of the Altamaha River (adjacent to the Ogeechee), observed high abundances of lentic invertebrates on the floodplain such as dytiscid beetles and isopod crustaceans. Gallardo et al. (2008) found high abundances of aquatic worms and crustaceans on the floodplain of a Spanish River. Benke et al. (2001) observed oligochaetes, chironomids, isopods, amphipods, and microcrustaceans as the main taxa elsewhere in the Ogeechee floodplain. In our sites, we observed a similar pattern in the floodplain where the indicator taxa were mostly gastropods and dytiscids (see Appendix A). In the river, however, the indicator taxa groups were composed of Trichoptera, Coleoptera, and Plecoptera groups (see Appendix A). This, to a certain extent, is expected as the indicator taxa in the floodplain are drought tolerant while the ones in the river are less drought tolerant (Wiggins et al. 1980). Thomaz et al. (2007) describes several studies where river and floodplain environments become homogenized in terms of biota. But they report low community turnover, unlike our study. The fact that most of the variation in our study system was explained by turnover suggests that factors other than habitat type were probably influencing taxa assemblage distributions. Brunke et al. (2003) observed high species turnover, as we did, and attributed it to terrestrial and physicochemical factors creating microhabitats in areas that were not immediately flushed by water. Dong et al. (2021) observed high species replacement (turnover) during high-water periods followed by high nestedness once pulses dissipated, which might explain the high turnover we observed when sampling during actual flood pulses.

Although macroinvertebrate assemblages changed in relative frequencies, all taxa in the floodplain were also collected in the river, with the assemblages on the floodplain largely being a subset of the assemblages in the river (Fig. 3.2A). The two habitats likely depend on each other for maintaining overall assemblage diversity. Galatowitsch and Batzer (2011) observed movements of mayflies from the main channel to the floodplain in a Southeastern Piedmont

River. Since most of the variation in our assemblages was attributed to turnover (Table 3.1), it is possible we were observing dynamic interactions of macroinvertebrates in river-floodplain complexes during flood pulses that maintained taxon presence but altered their frequency, depending on site location and season (for the river) and pulse size (for the floodplain) (Table 3.2).

We also hypothesized that pulse size would affect macroinvertebrate assemblage distributions and frequencies of occurrence, but this was only apparent for assemblages on the floodplain and not in the river (Table 3.2, Fig. 3.4C). Pulse phase (upswing vs downswing had no notable influence anywhere (Table 3.1, Fig. 3.2B). Chattopadhyay et al. (2021) and Dong et al. (2021) observed differences before (rising water periods) and after floods (falling water periods), but their comparisons were spaced months apart. Our sampling of pulses typically spanned only periods of days so it is possible that pulse phase effects may need to be assessed over longer timeframes, or that factors other than pulse phase control assemblages over longer time periods.

Season and site location as drivers for macroinvertebrate assemblages in the river

Site location along the length of the river was the most notable factor influencing macroinvertebrate assemblages in the river (Table 3.2, Fig. 3.3A). Most assemblages in downstream locations appeared to be subsets of assemblages at the uppermost Grange location (Fig. 3.3A). The indicator taxa analyses, however, identified only two taxa that were associated with specific locations, Formicidae, a terrestrial arthropod, in Midville, and Valvatidae, a gastropod with relatively high tolerance for desiccation (Collas et al. 2014) and poor water quality conditions (Wiggins et al. 1980), in Ellabell. Gollizadeh (2021) observed broad dispersal of macroinvertebrate assemblages during floods. It is possible that riverine taxa in our study

became widely dispersed during flood pulses, obscuring spatial patterns along the river. Vannote et al. (1980) describe a river continuum where invertebrate taxa assemblages progressively change from the headwaters to the river mouth. Across our coastal plain reaches, no obvious continuum was evident, however. Instead, specific sites along the river seem to provide conditions conducive for certain taxa (i.e., site-specific variation).

Season was also a notable driver for macroinvertebrate assemblages in the river where pulses in the normal pulse season appeared to be subsets of those observed in the pulses during tropical storm season (Table 3.2, Fig. 3.3C). Chattopadhyay et al. (2021) observed a decline in benthic macroinvertebrate richness and abundance during floods in the summer (March-August). However, they then observed complete recovery of benthic macroinvertebrate communities weeks after the floods. Since most of the taxa observed in the normal pulse season were also present in the tropical pulses, perhaps many of the taxa comprising overall assemblages remain present for long periods and, as observed by Chattopadhyay et al. (2021), recover soon after floods. However, some taxa differed between seasons. Indicator analyses identified Amphipoda for pulses during the normal season, and Cicadellidae, *Stelnemis*, and Gerridae for pulses during the tropical storm season. The terrestrial Cicadellidae are most abundant in the summer, so these organisms were probably dislodged from herbaceous plants growing along the river banks as tropical storm floods swept over them.

Site location and pulse size as drivers for macroinvertebrate assemblages on the floodplain

Similarly to the river, the site location along the watershed was also the main driver for macroinvertebrate assemblages in the floodplain (Table 3.2). Both the macroinvertebrate assemblages in uppermost site, Grange, and the lowermost site, Ellabell, appeared to encompass

those of Midville and Oliver. Grange had some taxa that appeared to be only associated with the floodplain (Fig. 3.4A). It is possible that a continuum of taxa assemblages exists between Grange and Ellabell, with Midville and Oliver acting as transitional locations. Reese and Batzer (2007) observed a continuum of floodplain macroinvertebrate assemblages along the Altamaha River watershed, although most differences in that study were between Piedmont and Coastal Plain reaches. Our results support some of their observations about wetland obligate taxa (Table 3.1) dominating lower river floodplains. For our system, however, each floodplain site appeared to have unique conditions and harbored unique indicator taxa, rather than progressively changing along a continuum. In our study, evidence for continuums in either the river or the floodplain was weak.

Pulse size was also a notable influencing factor on floodplain macroinvertebrate assemblages (Table 3.2, Fig. 3.4C). In smaller pulses, the indicator taxa were identified as Ostracoda, Oligochaeta, Asellidae, Sphaeriidae, all common aquatic wetland taxa (Bright et al. 2010). However, the indicator taxa for large pulses were all terrestrial: Chilopoda, non-Heteroptera hemipterans, and Formicidae. For terrestrial wetland taxa, Batzer and Wu (2019) report that most are adapted to either move to higher ground or tolerate periods of submersion. Large pulses may limit access to high ground, and thus more of these organisms end up submersed than during small pulses. Åhlén et al. (2023), Gallardo et al. (2008), Robinson et al. (2004), and Turić et al. (2010) each detected variation in insect abundance associated with wetland landscape heterogeneity and patterns of inundation. Hence both small and large pulses are likely important to assemblage diversity in the Lower Ogeechee floodplain.

Conclusion

Our study shows that, during flood pulses, river and floodplain macroinvertebrate assemblages in the Lower Ogeechee River overlap between habitats, and that their relative frequencies of occurrence mainly depend on the habitat type and the spatial location of those habitats down the watershed. This variability is reflected by both aquatic and terrestrial taxa. Seasonal change was more important for river macroinvertebrate assemblages (Table 3.2), while variation in pulse size was more important for floodplain assemblages. Thus, dynamics exerted by flood pulses do not affect both habitats similarly. With the predicted increases in the severity of drought and increased magnitudes of some individual floods, habitat variability may increase including an overall decrease of floodplain-river connections but more intense connections when they occur (Johnson et al. 2023; Lake 2000). Thus far, most studies show overall recovery of macroinvertebrate richness and abundance in the weeks or months after a flood (Collier and Quinn 2003, Chattopadhyay et al. 2021). However, during the period of intense flooding (i.e., in flood pulses), we see that many taxa are influenced, especially terrestrial taxa. As both extremes (drought and floods) become more frequent because of climate change (Lake 2003; Li et al. 2022; Hirabayashi et al. 2007), it will be important to monitor the resilience of macroinvertebrate assemblages in riverine-floodplain complexes to these events.

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Table 3.1 PERMANOVA Results for the environmental influence of 1) habitat: floodplain vs river habitats, 2) pulse size: peak discharge at the uppermost site, 3) site: 4 study locations, 4) season: normal flood vs tropical storm, and 5) pulse phase: rising vs falling on macroinvertebrate assemblages in river and floodplain samples combined during 11 pulses in the Lower Ogeechee River during the years 2019-2022. Largest effect sizes for factors are highlighted in **bold**.

Factors	\mathbb{R}^2
Habitat	0.05821
Pulse Size	0.02238
Site	0.05157
Season	0.02279
Pulse Phase	0.00693

Table 3.2 PERMANOVA Results from the river only and the floodplain only for the environmental influence of 1) habitat: floodplain vs river habitats, 2) pulse size: peak discharge at the uppermost site, 3) site: 4 study locations, 4) season: normal flood vs tropical storm on macroinvertebrate assemblages during 11 pulses in the Lower Ogeechee River during the years 2019-2022. Largest effect sizes for factors are highlighted in **bold**.

Factors	River (R ²)	Floodplain (R ²)
Pulse Size	0.02120	0.05305
Site	0.08153	0.10500
Season	0.04365	0.03500



Figure 3.1 Sampling locations (blue dots) along the Ogeechee River, Georgia, USA. The orange line above the watershed limit represents the Fall Line. The Latitude and Longitude location in the legend indicate the recorded location where the Ogeechee discharges into the ocean (pink dot). Map edited from StreamStats.



Figure 3.2 River and Floodplain samples. Distribution of macroinvertebrate assemblages during eleven flood pulses observed in the Lower Ogeechee River (river and floodplain samples) during the years of 2019-2022 highlighted by habitat (floodplain vs river; **A**), and by pulse phase (rising vs falling; **B**).



Figure 3.3 Distribution of macroinvertebrate assemblages in the river during eleven flood pulses observed in the Lower Ogeechee River during the years of 2019-2022 highlighted by site location (**A**),season (Normal pulses observed in December-April, and tropical for pulses in August-October; **B**) and by pulse size according to the peak discharge in the uppermost site for each pulse (**C**). Site effects explained 8%, season effects explained 4%, and pulse size explained 2% of the assemblage distributions.

CHAPTER 4

FLOODPULSE SIZE MATTERS: IMPACTS OF RIVER-FLOODPLAIN INTERACTIONS ON WATER QUALITY IN A SOUTHEASTERN USA RIVER³

³ Cardona Rivera, G. A., et al. To be submitted to a peer-reviewed journal.

ABSTRACT

The Flood Pulse Concept (FPC) characterizes the lateral interaction of rivers and their adjacent floodplains as a driver of both water quality and food web dynamics. However, the specifics of how these dynamics work during disturbances such as flood pulses are not well characterized. Given the projected flashy floods among other climate change-related, and anthropogenic alterations on river flows, it is important to understand how flood pulses may impact water quality processes. The Ogeechee River is an undammed, sixth order, blackwater river in Southeast Georgia with near-natural flood pulses, and thus a useful place to test aspects of the FPC. We sampled water from four sites along the length of the Lower Ogeechee River during eleven different flood pulses, in both the river channel and the floodplain, and during the beginning (ascending limbs) and end (descending limbs) of each pulse event. We analyzed NO_x, TN, NH₃, POP-4, DOC, suspended sediment, conductivity, and pH. Flood pulses were categorized by magnitude (discharge volume flowing into the uppermost site during floods) and seasonality (early, late, and tropical flood seasons). Most water quality metrics were affected by a combination of pulse magnitude, location, and seasonality. Unexpectedly, nutrient processing, indicated by differences in concentrations between river and floodplain, was more pronounced in smaller than larger pulses. Our study sheds light on the ability of floodplains to retain and internally process nutrients and other pollutants under future climates with altered precipitation patterns.

INTRODUCTION

Floodplains are located between aquatic river channels and the adjacent terrestrial uplands and can interact with both (Batzer et al. 2018). The geomorphology of these habitats

generates variability in elevation (e.g., natural levees, backswamps) and habitat patch sizes that allows for intermittent wet to dry conditions to develop after local rainfalls, and especially as large flood pulses connect the river channel to the floodplain. It is during these pulses when floodplains most interact with the main river channel, exchanging water, materials, and nutrients between the two habitats (Wohl et al. 2021). During flood pulses and subsequent periods after disconnection, conditions develop for microbial and plant activity to process nutrients on the floodplain (Zhou et al. 2014, Newcomer Johnson et al. 2015; McMillan and Noe 2017; Randle-Boggis et al. 2018; Tomasek et al. 2019; Gordon et al. 2020; Doering et al. 2021; Wohl et al. 2021). Because of this valuable ecosystem service (Costanza et al. 2014, Hopkins et al. 2023), research on floodplain dynamics and floodplain-river interactions has proliferated in recent years (Tockner and Stanford 2002, Beck et al. 2019, Wohl 2021).

Floodplain and river interactions can be complex, influenced by factors such as local and longitudinal landscape variations, lateral interactions, and seasonality (Spink et al. 1998). Lewin and Hughes (1980) characterized floodplain and river interactions during a flood pulse by an ascending limb and initial inundation followed by a descending limb and recession, creating a sequence of reversing flows between the river and floodplain. They suggest that the efficiency of water transfer between the main channel and floodplain will depend on the local landscape characteristics of the floodplain. Subsequently, Junk et al. (1989) proposed the Flood Pulse Concept, characterizing the interactions between tropical rivers and their adjacent floodplains including influences on nutrients and biota. Tockner et al. (2000) expanded the Flood Pulse Concept beyond the tropics to address seasonality and local variation in flooding, and explained the different ways in which floodplain-river interactions can vary in tropical versus temperate systems. Batzer et al. (2018) described how flood pulse interactions, and their effects on nutrient

and biotic dynamics, change from the headwaters to lower reaches of rivers. Finally, Benke et al. (2000) noted that floods can be unpredictable, and sometimes brief, with flooding patterns being mainly influenced by seasonal changes in evapotranspiration. All these studies demonstrate the complexity of factors influencing flooding patterns and nutrient dynamics, and consequently, floodplain function.

There is evidence that hydrologic connectivity and residence time influences nutrient retention (Wolf et al. 2013; Newcomer Johnson et al. 2016; McMillan and Noe 2017; Tomasek et al. 2019) by increasing surface area and opportunity for internal nutrient processing. Noe and Hupp (2009), Beck et al. (2019), and Majora et al. (2020) further expanded on the influences of inundation for nutrient processing by highlighting the importance of connection and residence time by floodplain landscape and size. The location of the floodplain in the watershed was also described as a major influencing factor in nutrient dynamics by altering the microbial assemblages and their rates of biochemical processing and particulate nutrient depositional rates (Boon et al. 2014; Zhou et al. 2014; Randle-Boggis et al. 2018; Gordon et al. 2020; Doering et al. 2021; Wohl et al. 2021). Although these studies identify various factors that influence floodplain function, there are still questions regarding how nutrient dynamics change during flood pulses occurring in different environmental and geographical conditions. As climatic patterns change, with rain events and droughts becoming more extreme and unpredictable (Li et al. 2022; Mishra et al, 2022), it is becoming increasingly important to better understand how these alterations may affect floodplain ecosystem services. Further, many floodplains have already lost considerable ecological functionality due to a range of human activities, such as the construction of dams and levees (Sparks and Spink 1998; Scott et al. 2014; Mishra et al. 2022). It is particularly important to understand nutrient dynamics during flood pulses, since floodplain

restoration projects often include nutrient processing as one metric of a project's success (Gordon et al. 2020).

The Ogeechee River in eastern Georgia, USA is an undammed, blackwater river. Its relatively pristine condition allows observation of natural flood pulses and makes it a useful place to test hypotheses about how flood pulses vary, and how they affect various ecological processes. In this study, we set out to assess the influences of pulses on different water quality metrics (nutrient, ions, and sediments) by assessing 1) the physical character of pulses themselves, including their size (discharge volume), location and timing; 2) the longitudinal patterns of the pulses (river vs. floodplain); and 3) the seasonality of the pulses. We hypothesized that: (A) water quality measures (nutrients, ions, sediment) would differ between river and floodplain habitats, and these differences would become amplified during larger pulses as they moved more materials and created longer floodplain residence time; (B) water quality would differ among locations along the river as flood pulses moved downstream, and (C) variation in water quality would be most evident during pulses that occur in warmer periods in the flood season, when microbial activity was greatest. With this project we aimed to further shed light on the complexity of floodplain water quality dynamics and especially on the efficiency of pulses and floodplains to process and remove potentially harmful nutrients.

METHODS

Ogeechee River and sampling site descriptions

The Ogeechee River is an undammed, blackwater, sixth order stream mainly located in the Coastal Plain of Georgia, USA (Benke et al., 2000; See also Fig 3.1). On Coastal Plain reaches, the floodplain width ranges between 1-3 km (Pulliam 1993). We sampled four sites along the Lower Ogeechee River, from immediately below the Fall Line (transition of Piedmont ecoregion to the Coastal Plain ecoregion) to upstream of tidal influence, over the years 2019-2022. The general land use for all floodplain sites was natural forest (either deciduous, evergreen, or mixed) according to The National Land Cover Database (Dewitz 2021). The uppermost site was 20.1 km downriver from the Grange Gage (USGS 02200120) and is part of a nature reserve (Ogeechee Crossing Park) and has a drainage area of 1293 km². In this site the river and floodplain connect at multiple locations during floods. The next sampling site was about 1 km upriver from the Midville Gage (USGS 02201230) with a drainage area of 3471 km². It was the most developed sampling location, with residential properties and agricultural pasture near the otherwise forested site. The lower river sites, Oliver (6164 km²) and Ellabell (7744 km²) (USGS 02202190 and USGS 02202680, respectively) were both located immediately adjacent to their respective USGS gages, near boat ramps and highway overpasses, but surrounded by otherwise natural forest landscapes. The last site was located approximately 11.4 miles away from USGS gage by the US17, near Richmond Hill, which is the only gage in the lower Ogeechee River that reflects tidal influence (see Fig. 3.1).

To observe pulse size, we monitored real-time discharge and gage height data for each site (https://nwis.waterdata.usgs.gov/ga/nwis/rt). With preliminary observations of hydrographs during flood events following major rains, we were able to determine threshold flood pulse sizes when the river and floodplain connected at each site during the rising limbs of pulses. Whenever logistically possible, we sampled the connecting pulses that developed over the 2019 to 2022 period at the uppermost Grange sampling site, and then followed those pulses as they flowed downstream until they passed through the lowermost Ellabell site (however, some of the smaller pulses dissipated before reaching Ellabell). The pulses typically lasted between three to five days

from the ascending limbs to the descending limbs at the Grange site but were extended for a week or weeks when the pulses reached the lowermost sites. We sampled during two pulse phases for each pulse: the ascending limbs of pulses as soon as practical after the river and floodplain connected, and the descending limbs after pulses crested but there was still visual evidence of river-floodplain connection (Fig. 4.1). Most pulses occurred during the normal flood season (December to April: Benke et al. 2000), but we also sampled three pulses that developed during the tropical storm season (August-October).

Field sampling

For each pulse, we recorded the peak discharge at Grange as a metric for flood pulse magnitude (this reflected the volume of water that flowed into our study area from the upper Piedmont portions of the watershed). During each visit, for each ascending and descending limb of a pulse, we would first verify that the river and floodplain habitats were connected, and then sampled both the river channel and the adjacent inundated floodplain interior. We measured pH and conductivity with a multiprobe near the main channel's bank, and on the floodplain itself in an area away from the levee connections to ensure we were assessing floodplain waters. At these same locations, we collected water samples in acid-washed 1-liter bottles for laboratory assessments of nutrients, dissolved organic carbon (DOC), and in 1-gallon bottles for suspended sediments. We transported all samples on ice to the laboratory. Samples for nutrient and DOC analysis were frozen until we could thaw and filter the water through 0.45 µm pore size membrane filters, then stored frozen again until analysis. For pulses that reached downriver to all four sites, our sampling efforts generated 16 samples for each metric: i.e. samples in the river and floodplain, during the rising and descending limbs of pulses, at each of 4 locations along the river (Fig. 4.1).

To assess water conditions that developed in the river and on the floodplain long after they disconnected following the normal flood season, we also repeated the sampling regime in May, June, and July of 2022, a period when no pulses developed, and the river and floodplain had no surface water connection.

Laboratory processing

Nutrient analyses were performed at the Water and Soil Laboratory in the University of Georgia within a month of collection. Colorimetry analyses methods were used to measure concentrations of ammonia (NH₃), nitrate-nitrite (NO_x), and phosphate (PO₄) (Environmental Protection Agency standard methods 350.1, 353.2, and 365.1 respectively) (USEPA, 1993a; 1993b, 1993c). Dissolved organic carbon (DOC) was measured on a Total Organic Carbon Analyzer with a Shimadzu module according to the Standard method 5310 (American Public Health Association, 2018). Total Nitrogen (TN) was measured according to the American Society for Testing and Materials (ASTM, 2016), ASTM D8083 standard method.

To determine suspended sediment concentrations, we first shook the 1-gallon samples by hand, then vacuum-filtered them (approximately 3.8L each) through pre-weighed 0.45 µm pore size Millipore Sigma Membrane filters. Since volumes varied somewhat among samples, we recorded the exact volume filtered for each. The filters were then dried (40°C) for 24 hours, then transferred to a desiccator for cooling until their weights were measured. After determining the dry weight for a sample, we subtracted the initial filter weight. For samples using multiple filters we summed values. For final concentrations, we divided those weights by the volume of water filtered.
Statistical Analysis

We used Analysis of Variance to analyze the effects of pulse size (large vs. small; as measured and categorized at the Grange upstream gage), habitat (river vs. floodplain), pulse phase (ascending vs. descending limbs), location (4 sample sites along the river), and season of the year, as well as the interactions between factors, for each response variable.

All variables were evaluated in Q-Q plots for outliers and distribution of their residuals. Identified outliers were removed from the analyses. To improve normality and homoscedasticity, we sqrt(x) transformed the values for NO_x, TN, NH₃, DOC, PO4-P, and suspended sediments. Since the data for pH already derives from a log function, we visually inspected data distributions for deviations from normality, but did not detect any. Conductivity data were assessed similarly, and deviations were not evident.

We used 1-way ANOVA in R (version 4.2.2) to first determine individual environmental effects (pulse size, pulse phase, habitat, location, and season) for each factor (nutrients, DOC, pH, and) conductivity. We further explored variables in significant effects (e.g., variation explained by each individual site) using Tukey HSD tests. We subsequently used 2-way ANOVA to test for interactions between paired effects (See Supplemental Tables S2-9). Since pulse magnitude was a major driver for most measurements in preliminary analyses, we also analyzed the data for large and small pulses independently with 1-way ANOVAs for each of the remaining individual effects. To determine whether floodplain and river conditions were different after the habitats disconnected following the normal flood season, we analyzed those data using paired T-tests.

RESULTS

Pulses

From 2019 to 2022, we evaluated eleven pulses that connected the river and floodplain habitats, at least at the uppermost sites of Grange and Midville (See Appendix B 1). Seven of these pulses connected the floodplain with the river at all four sampling locations (pulses F, B, J, K, I, D, H in Figs. 4.2-4.9, and Appendix B 1); the other four pulses dissipated downstream from the Midville location. Out of all 11 pulses, we classified six as small pulses ranging from peak discharges of 11.7-34.2 m³/s at the uppermost Grange gage, and five were classified as large pulses with peak discharge at Grange ranging from 74.4-331.3 m³/s. Five of the pulses occurred early in the normal flood season (December-February) when temperatures were cool and minimal surface water was present on the floodplains prior to the pulses; three of the pulses occurred late in the flood season (March-May) when temperatures were warm and recent pulses had previously inundated much of the floodplain; and three of the pulses occurred during the tropical storm season (August-October) when temperatures were hot but the floodplains had been largely dry prior to the pulses (See Appendix B 1). Out of these, two of the small pulses happened in the early season, two in the late season, and two in the tropical storm season. For large pulses, three were in the early season, one in the late season, and one in the tropical storm season. Pulse height amplitudes were highest at the Grange gage, with the maximum gage height stage reaching 5.4 m for the largest pulse, while that same pulse was 3.8 m high when it reached the Ellabell gage.

Pulse size (small vs. large) had an evident influence on most water quality response metrics (see following). However, it was common for statistical interactions to exist between pulse size and other factors (especially with season). Thus, after assessing overall influences of the main effects, we conducted subsequent analyses for variation within the sets of small and large pulses individually for those cases where both pulse size was statistically different and interactions with other factors were also evident.

Water quality metrics

Nitrate/Nitrite (NO_x)

The most notable influence on NO_x concentrations was pulse size (p<0.0001), with concentrations being higher in small than large pulses (Fig. 4.2, Table 4.1). Concentrations were marginally higher in the river than the floodplain habitat (p=0.0559; Fig. 4.3). However, concentrations were not detectably different between when the pulses were arriving (ascending limb) or exiting (descending limb) (p=0.4342; Fig. 4.2). Interpreting NO_x levels, however, was complicated by the interaction of pulse size and habitat (p=0.0163), which developed because floodplain samples having lower concentrations than the adjacent river channel samples were only evident during smaller pulse sizes (Fig. 4.2; see also Appendix B 2). Location in the watershed was a notable influence (p=0.0013) on NO_x concentrations, with levels at the Midville site (2nd site) being higher than at the Ellabell site (4th site) (see Appendix B 10). However, NO_x levels did not differ notably among the different flooding seasons (Table 4.1).

Ammonia (NH3)

Unlike most other metrics, pulse size did not notably affect NH₃ levels (Table 4.1, Fig. 4.3). Additionally, unlike most other metrics, levels clearly differed between river and floodplain habitats, being higher in the floodplain (p=0.0077; Table 4.1, Fig. 4.3), especially during smaller flood pulses (See Appendix B Table 3). However, levels did not change as water passed through

a site (ascending and descending limb phases were very similar; Table 4.1, Fig. 4.3). In terms of setting, location had a pronounced influence on NH_3 (p=0.001), with levels increasing as water moved downstream. Season was also important (p=0.023), with NH_3 levels being lowest in the early season pulses (Fig. 4.3).

Total Nitrogen (TN)

TN levels were influenced by pulse size (p<0.0001), with levels being higher in smaller than larger pulses (Fig. 4.4, Table 4.1; see also Appendix B 11). Neither location, habitat, nor pulse phase had any notable impacts on TN levels (Table 4.1). Levels were also affected by season (p=0.0110). A statistically notable interaction existed between pulse size and season (p<0.0001), which appeared to be driven by seasonal inconsistency within each pulse size (Fig. 4.4; see Appendix B 4). There was also a statistically notable interaction between season and location (p=0.0020; Fig. 4.4; see also Appendix B 4, Appendix B 12).

Phosphate (PO₄-P)

PO₄-P levels appeared to be affected by pulse size (p=0.0023) but not notably by habitat or pulse phase (Table 4.1, Fig. 4.5). Levels were higher in the larger pulses compared to small pulses (Fig. 4.5). Location had a detectable influence (p=0.0003), with levels increasing slightly as water moved downstream (see Appendix B 13). In terms of influence by season (p=0.0008), PO₄-P levels were lowest in the early season pulses. Additionally, there was a statistical interaction between pulse size and season (p=0.0001), mainly due to high PO₄-P levels occurring during one late-season, large pulse (Fig. 4.5; see also Appendix B 5).

Dissolved Organic Carbon (DOC)

Pulse size was a major factor affecting DOC concentrations (p<0.0001), but in this case, DOC was higher in the larger pulses than the smaller pulses (Table 4.1, Fig. 4.6; see also Appendix B 14). Levels were marginally different between the river and the floodplain habitat (p=0.0770). However, between the ascending and descending limbs of pulses, DOC concentrations were relatively homogenous (p=0.9696) (Table 4.1, Fig. 4.6). Location was also an influencing factor (p<0.0001), with DOC progressively increasing from upstream to downstream locations (see Appendix B 14). DOC also varied by season (p=0.0006), with DOC levels tending to be lowest in early season pulses (Table 4.1, Fig. 4.6). There were indications of possible interactions between habitat and season (p=0.0764), and habitat and pulse size (p=0.0892) (see Appendix B 6).

Conductivity

Conductivity levels were strongly affected by pulse size, location, and season (all p<0.0001, Table 4.1), but neither habitat (p=0.2558) nor pulse phase (p=0.231) appeared to influence conductivity. Conductivity was lower in large than small pulses (Fig. 4.7, see Appendix B 7). A statistical interaction was indicated between pulse size and season (p=0.0042); the highest levels of conductivity were observed in small, tropical season pulses (Fig. 4.7). Conductivity was highest in the downriver sites (see Appendix B 15).

pН

Levels of pH were influenced strongly by pulse size (p<0.0001), wherein pH was higher in the small than large pulses, and marginally by habitat (p=0.0527) (Table 4.1, Fig. 4.8). There was no clear pattern related to pulse phase. Levels of pH were lower in the floodplain than the river, primarily during small flood pulses (see Appendix B 8, and Appendix B 16). Location (p<0.0001) and season (p<0.0001) were also notable influences on pH levels (Table 4.1). In terms of location effects, for both pulse sizes, the lowest pH overall occurred in the lowermost site, Ellabell (see Appendix B 16). Additionally, a statistical interaction between pulse size and season was indicated (p=0.0009; see also Appendix B 8), primarily because the highest pH levels occurred during late season but only in small pulses, while the lowest levels occurred during tropical pulses (Fig. 4.8).

Suspended Sediments.

The amounts of suspended sediments were influenced by pulse size (p=0.0147), location (p=0.0211), and seasonality (p=0.0010) (Table 4.1). In terms of location, the highest levels were observed at Midville and the lowest at Ellabell (see Appendix B 17). There was also a statistical interaction between pulse size and seasonality (p=0.0001; see Appendix B 9); the most variability in seasonality was apparent in the tropical pulses (Fig. 4.9).

Disconnected Conditions

After the river and floodplain habitats disconnected in summer (2022), water qualities in the river and floodplain diverged, as compared to during flood pulses, with concentrations of NO_x (higher in the river; p=0.0027), NH₃ (higher in the floodplain; p=0.0433), and DOC (higher in the floodplain; p=0.0292), as well as pH (higher in the river; p=0.0036) values, in the river and the floodplain habitats differing. However, TN and PO₄-P concentrations, and conductivity levels were still not detectably different (p=0.7809, p=0.6583, and p=0.1424 respectively) between the river and floodplain (Table 4.2).

DISCUSSION

Ecosystem services that floodplains provide include their ability to retain flood waters and to process nutrients, due to the river-floodplain interconnections that occur during flood pulse events (Tockner et al. 2002; Wolf et al. 2013; Costanza et al. 2014; Hopkins et al. 2023). Our study is among the first to directly assess what occurs as water rises and falls during flood pulses. We had hypothesized that water quality measures (nutrients, ions, sediment) would differ between river and floodplain habitats, and that these differences would become amplified during larger pulses as they move more materials and create longer residence time. This hypothesis was for the most part rejected. Most differences between river and floodplain habitats developed only during smaller pulses (Figs. 4.2-4.9, see Appendix B 2-7). We had also hypothesized that nutrients would differ among locations along the river, created by flood pulses flowing downstream, and that differences would be most evident during pulses that occurred in warmer periods of the flood season, when microbial activity is greatest. Both hypotheses were largely supported.

Pulse sizes affect both habitat homogenization and heterogeneity

Flood pulse size was an important influence on most of the water quality metrics that we measured, with these for the most part being higher in the smaller pulses (Table 4.1, Figs. 4.2, 4.4,4.6-4.9). This is consistent with the results of Noe and Hupp (2009), who also observed differentiation by inundation time and floodplain size; floodplains that received larger loads from the adjacent rivers retained lower amounts of nutrients. Additionally, Majora et al. (2020) observed more habitat heterogeneity in water quality metrics during low water periods than in higher water phases. For our study, however, this was not simply an artifact of dilution; when

assessing pulse magnitudes within the sets of large and small pulses, there was no clear evidence of the smallest pulses in either set of pulse sizes having the highest concentrations of compounds (Figs. 4.2-4.7).

River and floodplain habitats are believed to have different factors influencing their nutrient processing because anoxia develops more frequently in floodplain wetlands, altering the microbial assemblages that occur (Boon et al. 2014; Randle-Boggis et al. 2018; Gordon et al. 2020; Doering et al. 2021). Their interaction during flood pulse events has been reported to be key for the uptake and reduction of harmful nutrient concentrations in watersheds such as nitrate and phosphorus (Zhou et al. 2014, Newcomer Johnson et al. 2015; Gordon et al. 2020, Wohl et al. 2021). Much of the biogeochemical processing in wetlands occurs in anoxic subsurface zones of wetland soils where suitable bacterial conditions (Wohl 2021) for those processes occur (e.g. denitrification; Zhou et al. 2014). In large flood pulses we observed an apparent homogenization of the floodplain and river habitats where differences in concentrations of nutrients (NO_x, TN, PO4-P, and DOC), suspended sediments, and measurements of pH, and conductivity were small between both the river channel and the adjacent floodplain, and during both the ascending and descending phases of all pulses (Table 4.1; Figs. 4.2, 4.4-4.6). Gordon et al. (2020) estimated that maximum denitrification happens in floodplains with a residence time of at least five days, and in slow-flowing water conditions. Scott et al. (2014) also observed an increase in the spatial variability of water chemistry during the falling limb of a large flood pulse and attributed it to increased time for biogeochemical processing. Perhaps the durations of large pulses in our study were simply too short and flows were too rapid for significant biogeochemical differences to develop between the river and the floodplain, or between ascending and descending limbs of

pulses; however, that does not fully explain why clearer indications of nutrient processing appeared to occur during small pulses.

While significant evidence of processing of many materials was not detectable during large flood pulses, we found that unique conditions in the river channel and floodplain redeveloped in the post flood period. After the river and floodplain disconnected (Table 4.2), the floodplains became more acidic, had lower levels of NO_x, and higher levels of DOC and NH₃ than the river. This combination of conditions is expected from a floodplain wetland system as anoxic conditions can decrease pH, promote microfauna involved with denitrification as well as nitrogen mineralization, and DOC increases from leaching of floodplain organic matter (Boon et al. 2014). Noe and Hupp (2007) observed variations in nutrient processing in a floodplain with brief inundation, low residence time, and low nutrient loading. There is also evidence that flood disturbances, as well as habitat and seasonal effects, can affect bacterial networks and their functions in riverine floodplains (Boon et al. 2014; Randle-Boggis et al. 2018; Gordon et al. 2020; Doering et al. 2021). It is possible that our system can more efficiently process nutrient concentrations loaded from smaller pulses, while in large pulses available processing agents (i.e. flora and microbes) decline in abundances or become overwhelmed.

NH₃ concentration was the only metric consistently higher in the floodplain regardless of flood pulse size (Table 4.1; Fig. 4.3, see Appendix B 3). Rates of utilization of NH₃ during nitrification and the volatilization of ammonia in the water are known to differ between rivers and floodplains due to different oxygen levels (oxic vs anoxic) and sediment deposition patterns (Wohl 2021). These differences may persist even when oxygen availability homogenizes during pulses. Wohl (2021) explains that in floodplains where the water budget depends significantly on river inputs, deeper surface waters during inundation can increase inputs of sediment N and ammonium as well as N mineralization and retention. It is possible that in our system NH₃ was an exception to homogenization due to rates of transport from floodplain sediments to surface flood waters during the pulses. During a spring pulse, Noe and Hupp (2007) observed increases in N concentrations at higher rates than their measured conductivity, indicating that biochemical reactions in the floodplain, more than mixing, were the cause of these nutrient concentration increases. These processes could in turn release NH₃ to the water column. It is possible that the typically low oxygen conditions of the floodplain remained low enough that indications of nitrification were not detectable in our measurements compared to indicators of denitrification. In our system, negligible differences in conductivity existed between the river and the floodplain habitats (no clear evidence of distinctions as sink or source). However, smaller pulses had detectably higher conductivity than larger pulses, and there was also a notable interaction between pulse size and season effects (Fig. 4.7; see also Appendix B 7). Moreover, these differentiations between pulse sizes were not as clear for NH₃ as it was for conductivity (Figs. 4.3 and 4.7). Hence, all these possible scenarios should be further explored with soil and more surface water analyses as Noe and Hupp (2007) also observed variations to nutrient processing in a riverine floodplain during floods in different seasons.

Effects of landscape variation and seasonality on water quality

In Southeastern USA rivers floodplain widths gradually increase downstream (Batzer et al. 2018). For the Ogeechee River floodplains became larger, and pulses took longer to disconnect as they flowed downriver. It was clear that flood height amplitudes declined as pulses flowed downstream. For some of the smaller pulses, the river and floodplain only connected at the upper portions of our study area (see Appendix B 1), and by the time the pulses reached the lower reaches, amplitudes were insufficient for water to enter the floodplain. Mayora et al.

(2020) observed differentiation along the Parana River and adjacent floodplains, and as we observed, they suggest that large flood events create local homogenization, but that flood pulses can be affected by landscape variation among locations. For the Ogeechee River, we found that NO_x, NH₃, PO₄-P, DOC, suspended sediments, conductivity, and pH (but not TN) varied along the length of the river (Table 4.1, see Appendix B 10-11, 13-16). Environmental factors unrelated to the pulses themselves appeared to be unique for each location along the river. Large floodplains of coastal plain river are characterized by darkly stained waters, high in DOC, and thus it was not unexpected that DOC levels increased downstream in our study, for all pulses. The fact that conductivity was also influenced by location (Table 4.1; see Appendix B 7) may suggest that local inputs of groundwater play a part in differentiation among locations.

Seasonality is a major influence on the water budget in the Ogeechee River, and for flood pulse development (Benke et al. 2000). Although precipitation is fairly constant year-round in Georgia, most flood pulses develop in winter and early spring when evapotranspiration rates are low (Benke et al. 2000). In our study, other than for two tropical storms, the largest pulses tended to occur in the December to February period. Varying pulse sizes as well as seasonal changes in weather likely contributed to seasonal changes for most of the water quality metrics that we measured. The fact that most nutrients (TN, NH₃, PO₄-P, and DOC) as well as pH and conductivity were influenced by seasonality (Table 4.1) means that nutrient loading and processing will vary not only by the volume of water but by the season in which floods happen. Further, when evaluating nutrient levels along with conductivity and pH by pulse size, seasonality was evident within both pulse sizes (see Appendix B 7-8). One notable fact is that much of the variation in the water quality data among different flood pulses sizes occurred for tropical storm pulses (Figs. 4.2-4.7). This highlights the importance of evaluating off-season

pulses to assess floodplain and river interactions, as they may behave differently as compared to pulses during the regular pulse season.

Implications

Our results suggest that ongoing changes in climate that affect flood pulses may affect how river-floodplain complexes function. Wilbanks et al. (2023) monitored nutrient concentrations in a nearby southeastern river (Savannah River) during both droughts and normal water conditions and found differences between the two; nutrient processing evidently changes during droughts, which supports our observations about the importance of flood pulse size. Murray-Stoker et al. (2023) noted a dramatic decline in invertebrate biomass in the Ogeechee River channel over the past 30 years and hypothesized that this decline was related to declining floodplain-river channel interaction due to declining flood pulse magnitudes. By understanding variations in water quality in different conditions in both river channels and floodplains, we can develop a better idea of how floodplains affect river channels, and how river channels affect floodplains (i.e., how the Flood Pulse Concept functions; Junk et al. 1989; Tockner et al. 2000, 2002; Wolf et al. 2013; McMillan and Noe 2017; Beck et al. 2019). Additionally, since we observed variations in water quality related to pulse magnitude, we can also better develop plans for flood regulation for dammed rivers, and shed light on the efficacy of nutrient retention and processing in adjacent floodplains and rivers after varying degrees of connection is induced by different levels of water discharge. Studies like ours can also serve as a foundation to predict how climatic changes in precipitation and temperature may affect rivers and floodplains by altering the flood pulses that connect them. Water budgets are expected to change in the future as floods become flashier with large, but shorter floods occurring at unexpected times, and droughts also becoming more frequent (Li et al. 2022). Long-term trends in discharge in the Ogeechee

River already suggest this is happening (see Appendix B 18), with flow variation becoming amplified during the tropical storm season and diminished in the normal flood season. With these changes, the efficiency of floodplains as sinks for pollutant nutrients may also change (Sparks and Spink 1998; Gordon et al. 2020; Mishra et al. 2022).

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Table 4.1 P values from 1-way ANOVAS for water quality constituents for the eleven flood pulses observed from 2019-2022. Location refers to the four sites sampled downriver, pulse size to the peak discharge recorded at the uppermost site (Grange) for each pulse, season to early, late, and tropical periods, habitat to the differences between the river and floodplain samples, and pulse phase to differences between the ascending limb vs the descending limb of each pulse. The values in **bold** represent those that displayed the most notable differences both statistically and graphically (see Figs. 4.2-4.9).

Metric/Effect	Pulse Size	Habitat	Pulse Phase	Location	Season
NO _x	<0.0001	0.056	0.434	0.0013	0.164
NH ₃	0.207	0.0077	0.926	0.0001	0.0023
TN	<0.0001	0.947	0.803	0.121	0.0110
PO ₄ -P	0.0023	0.625	0.394	0.0003	0.0008
DOC	<0.0001	0.077	0.970	<0.0001	0.0006
Conductivity	<0.0001	0.256	0.231	<0.0001	<0.0001
pН	<0.0001	0.053	0.628	<0.0001	<0.0001
Sediments	0.0147	0.497	0.804	0.0211	0.0010

Table 4.2. Average values for nutrient concentrations (mg/L), conductivity (μ S/sec), and pH for the river and floodplain habitats during disconnected conditions in the summer of 2022. Metrics in **bold** differed the most (p<0.05) between habitats.

	NO _x	NH ₃	TN	PO ₄ -P	DOC	Conductivity	pН
River	516.4	56.1	893.8	18.3	16643.3	71.7	6.58
Floodplain	162.9	147.5	839.1	21.4	25905.8	140.0	5.84



Figure 4.1 Discharge at each sampling site's USGS gage during a large pulse sampled for this study in 2020. Each dot represents a sampling event for the ascending and descending pulse phases at each site.



Figure 4.2 Sqrt-transformed NO_x concentrations (mg/L) by pulse size. Pulse A is the smallest pulse recorded according to the peak discharge at the uppermost sampling site (Grange), and Pulse K is the largest pulse (see Appendix B 1). Values are represented for both habitats (grey for the floodplain or FP, and black for the river channel or R), and by season (yellow for early, green for late, and light blue for tropical). Effects of pulse size (p<0.0001) and location (p=0.0013) were statistically different, as was the interaction of pulse size and habitat (p=0.0163) (See Appendix B 2).



Figure 4.3 Sqrt-transformed NH₃ concentrations (mg/L) by pulse size. Pulse A is the smallest pulse recorded according to the peak discharge at the uppermost sampling site (Grange), and Pulse K is the largest pulse (see Appendix B 1). Values are represented for both habitats, (grey for the floodplain or FP, and black for the river channel or R), and by season (yellow for early, green for late, and light blue for tropical). Effect's location (p=0.0001), habitat (p=0.00077), and season (p=0.0023) were statistically different, as was the interaction between location and season (p=0.0292) (See Appendix B 3).



Figure 4.4 Sqrt-transformed TN concentrations (mg/L) by pulse size. Pulse A is the smallest pulse recorded according to the peak discharge at the uppermost sampling site (Grange), and Pulse K is the largest pulse (see Appendix B 1). Values are represented for both habitats,(grey for the floodplain or FP, and black for the river channel or R), and by season (yellow for early, green for late, and light blue for tropical). Effects of pulse size (p<0.0001), and season (p=0.0110) were statistically different, as was the interaction between pulse size and season (p<0.0001) (See Appendix B 4).



Figure 4.5 Sqrt-transformed PO₄-P concentrations (mg/L) by pulse size. Pulse A is the smallest pulse recorded according to the peak discharge at the uppermost sampling site (Grange), and Pulse K is the largest pulse (see Appendix B 1). Values are represented for both habitats, (grey for the floodplain or FP, and black for the river channel or R), and by season (yellow for early, green for late, and light blue for tropical). Effects of pulse size (p=0.0023), location (p=0.0003), and season (p=0.0008) were statistically different, as was the interaction between pulse size and season (p=0.0001) (See Appendix B 5).



Figure 4.6 Sqrt-transformed DOC concentrations (mg/L) by pulse size. Pulse A is the smallest pulse recorded according to the peak discharge at the uppermost sampling site (Grange), and Pulse K is the largest pulse (see Appendix B 1). Values are represented for both habitats, (grey for the floodplain or FP, and black for the river channel or R), and by season (yellow for early, green for late, and light blue for tropical). Effects of pulse size (p<0.0001), location (p=0.0003), season (p=0.0006) were statistically different. There was also a possible interaction between habitat and pulse size (p=0.0892) (See Appendix B 6).



Figure 4.7 Conductivity (uS/cm) by pulse size. Pulse A is the smallest pulse recorded according to the peak discharge at the uppermost sampling site (Grange), and Pulse K is the largest pulse (see Appendix B 1). Values are represented for both habitats, (grey for the floodplain or FP, and black for the river channel or R), and by season (yellow for early, green for late, and light blue for tropical). Effects of pulse size (p<0.0001), location (p<0.0001), and season (p=0.0042) (See Appendix 7).



Figure 4.8 pH by pulse size. Pulse A is the smallest pulse recorded according to the peak discharge at the uppermost sampling site (Grange), and Pulse K is the largest pulse (see Appendix B 1). Values are represented for both habitats, (grey for the floodplain or FP, and black for the river channel or R), and by season (yellow for early, green for late, and light blue for tropical). Effects of pulse size (p<0.0001), location (p<0.0001), and season (p<0.0001) were statistically different, as was the interaction between pulse size and habitat (p=0.0009) (See Appendix B 8).



Figure 4.9 Sqrt-transformed suspended sediments concentration (g/L) by pulse size. Pulse A is the smallest pulse recorded according to the peak discharge at the uppermost sampling site (Grange), and Pulse K is the largest pulse (see Appendix B 1). Values are represented for both habitats, (grey for the floodplain or FP, and black for the river channel or R), and by season (yellow for early, green for late, and light blue for tropical).Effects of pulse size (p=0.0147), location (p=0.0211), and season (p=0.0010) were statistically different. There were also statistically different interactions between the effects of pulse size and season (p=0.0001) (See Appendix B 9).

CHAPTER 5

CONCLUSIONS

Ecotonal wetlands are well known for their high biodiversity as well as for retaining water and processing potentially harmful nutrients (e.g. from agricultural runoff) that would otherwise persist in the adjacent main channel (Heimlich 1998; Brinson and Malvárez 2002; Constanza et al. 2014; Matteson et al. 2020). Other ecosystem services that are not as well-known include their ability to act as refugia for fauna from the adjacent landscapes during changes in season as well as drastic disturbances like floods (Brinson and Malvárez 2002). As climate change and anthropogenic effects continue to threat the persistency and resiliency of ecotonal wetlands (Brinson and Malvárez 2002; Lake et al. 2003; Hirabayashi et al. 2007; Ballut-Dajud et al. 2022; Li et al. 2022) and their ecosystem services, it is important to understand the dynamics of the latter, and to identify influencing ecological factors.

In our study at the Iron Horse Farm, we observed movements of beneficial arthropods (e.g. spiders and predacious carabid beetles) from a wetland to its adjacent agricultural lands. Additionally, we found no indication that the wetland was also acting as refugia for potential plant pests. Hence, that ecotonal wetland is providing the ecosystem service of serving as refuge and possibly increasing abundances of arthropods that could act as natural pest control in the adjacent crop lands. This study provided a different view of the wetland landscape that would otherwise be considered a wasteland by most farmers.

During flood pulses in the Lower Ogeechee river-floodplain system, we observed how the floodplain, an ecotonal wetland between forested terrestrial uplands, and the main river channel,

harbored many of the same macroinvertebrate taxa. Both assemblages from the river and from the floodplain were influenced by location along the river. However, river assemblages were also influenced by seasonal effects while floodplain assemblages were more affected by pulse size. This shows that although invertebrate assemblages can rely on both habitats to maintain overall community abundances, they can be affected by different environmental factors. The fact that most locations along the channel, both in the river and in the floodplain, had distinct indicator taxa but that continuums of change were not well developed, shows that more work on assemblage controls is required.

Finally, we identified environmental factors influencing changes in water quality (nutrient concentrations, pH, conductivity, and suspended sediments) during the same flood pulses at the Lower Ogeechee river-floodplain system. One of the main environmental factors was pulse size, and it unexpectedly showed the most detectable differentiations of water quality measures between the river and the floodplain habitats during the small pulses. During large pulses, there was an apparent homogenization for most water quality measures between the river and the floodplain. Other factors influencing these water quality were more predictable, including variation by location along the river and seasonal variation. Our study showed that the ecosystem service of nutrient processing for which ecotonal wetlands are renowned is very complex.

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APPENDICES

Appendix A- Chapter 3 Appendix. Taxa in the river and floodplain samples during the observation of 11 pulses in the Lower Ogeechee River during the years 2019-2022. The indicator taxa for the river and the floodplain are identified in bold.

Higher Taxa	River (n= 92 taxa)	Floodplain (n=86 taxa)
Cnidaria		Hydrozoa
Annelida	Oligochaeta	Oligochaeta
Mollusca	Lymnaeidae	Lymnaeidae
	Physidae	Physidae
	Planorbidae	Planorbidae
	Sphaeriidae	Sphaeriidae
	Valvatidae	Valvatidae
Crustacea	Amphipoda	Amphipoda
	Asellidae	Asellidae
	Cambaridae	Cambaridae
	Cladocera	Cladocera
	Copepoda	Copepoda
	Ostracoda	Ostracoda
Myriapoda		Chilopoda
	Diplopoda	Diplopoda
Acari	Acari	Acari
Araneae	Araneae	Araneae
Collembola	Isotomidae	Isotomidae
	Onychiuridae	Onychiuridae
	Poduridae	Poduridae
	Sminthuridae	Sminthuridae
Ephemeroptera	Baetisca	Baetisca
	Caenidae	
	Ephemerella	Ephemerella
		Leptophlebiidae
	Stenonema	
Odonata	Amphiagrion	
	Argia	
	Boyeria	
	Calopteryx	
		Epiaeshna
	Epitheca	
	Erythrodiplax	
	Hagenius	

	Nasiaeschna	Nasiaeschna
	Macromia	
	Somatochlora	
	Sympetrum	
Orthoptera	Acrididae	
L		Gryllidae
	Mogoplistidae	
Plecoptera	Attenuria	
Ĩ	Cloroperlidae	
	Hansonoperla	
	Perlodidae	
	Taenoptervgidae	Taenoptervgidae
Hemiptera:Heteroptera	Aphididae	Aphididae
F		Aradidae
	Belostoma	
	Blissidae	
	Gerridae	
	Hesperocorixa	Hesperocorixa
		Hydrometridae
	Notonecta	Notonecta
		Tingidae
	Ranatra	
	Trichocorixa	Trichocorixa
	Veliidae	
Hemiptera: "Homoptera"	Cicadellidae	Cicadellidae
fiempiera fiemepiera	Cercopidae	
		Other non-Heteroptera
Thysanoptera		Thripidae
ing sunop to tu	Phlaeothripidae	Phlaeothripidae
Coleoptera	Tindeotinipidae	Ancyronyr
Coleopteru		Anthicidae
	Ridessonotus	Bidessonatus
	Carabidae	Carabidae
	Chrysomelidae	Chrysomelidae
	Contotomus	
	Curculionidae	Curculionidae
	Dinautus	Dingutus
	Dineulus	Dutiscus
	Dryonidae	Dryopidae
	Flateridae	Dryopidae
	Cyrinus	Curinus
	U alimbus	Gyrmus
	паприя	Llistaridas
		nyarobius

	Hydrocanthus	
		Ilybus
	Laccophilus	Laccophilus
		Lampyridae
	Macronychus	
	Neoporus	Neoporus
	Peltodytes	Peltodytes
		Scarabaeidae
	Scirtidae	Scirtidae
	Staphylinidae	Staphylinidae
	Stelnemis	Stelnemis
		Silvanidae
		Tenebrionidae
		Thermonectus
		Tropisternus
Neuroptera		Corvdalidae
Hymenoptera	Braconidae	Braconidae
ing monoprona	Cynipidae	Cynipidae
		Ceraphronidae
		Encyrtidae
	Formicidae	Formicidae
	Scelionidae	Scelionidae
		Mymaridae
Trichoptera	Calamoceratidae	
	Hydropsychidae	
	Hydroptilidae	Hydroptilidae
	Ironoquia	
	Lepidostoma	Lepidostoma
	Leptoceridae	
	Phryganea	
	Pycnonsyche	
Lepidoptera	Lepidoptera	Lepidoptera
Diptera	Chaoboridae	Chaoboridae
Diptoru	Chironomidae	Chironomidae
		Cecidomviidae
	Ceratopogonidae	Ceratopogonidae
	Dolichopodidae	Dolichopodidae
	Empididae	Donenopoulaie
	Muscidae	Muscidae
		Psychodidae
	Simuliidae	Simuliidae
		Strationvidae
		Tabanidae
	Tipulidae	Tipulidae
1	inpunduo	1 ipulluuv

Appendix B1-Chapter 4 Appendix. Summary of pulse sizes (A being the smallest and K the largest) according to the peak discharge at the uppermost site (Grange) sampled in the Lower Ogeechee River. Early pulses were observed in December-February, late pulses in March-May, and tropical season pulses in August to October (2019-2022). Sites reached refers to how many of the four sampling sites resulted in river-floodplain connection for the pulse.

Pulse by size	Discharge (m ³ /s)	Season	Collection Year	Sites Reached
А	12	Tropical	2020	1
В	24	Late	2019	4
С	30	Early	2020	2
D	30	Late	2021	4
Е	33	Tropical	2021	2
F	34	Early	2019	4
G	74	Early	2021	2
Н	156	Late	2022	4
Ι	157	Tropical	2020	4
J	261	Early	2019	4
К	331	Early	2020	4
Appendix B 2-Chapter 4 Appendix. ANOVA analyses significance for sqrt-transformed data for Nitrate-Nitrite (NOx) concentrations for environmental effects sampled in the Lower Ogeechee River during 11 flood pulses in the years 2019-2022. The lowest p-values are indicated in **bold**. Size refers to large versus small pulses, location refers to the 4 sampling sites along the river, habitat refers to river versus floodplain, pulse phase refers to upswings versus downswings of pulses, and season refers to early, late, and tropical season periods.

NOx							
Main Effects		Interaction	Interactions				
		Location	Habitat	Pulse Phase	Season		
Location	0.0013	-	-	-	-		
Habitat	0.0559	0.6613	-	-	-		
Pulse phase	0.4342	0.8182	0.2504	-	-		
Season	0.1638	0.0242	0.2251	0.4620	-		
Size	<0.0001	0.0443	0.0163	0.6248	0.0754		
Small Pulses					·		
Location	0.0350						
Habitat	0.0061						
Pulse Phase	0.3415						
Season	0.0137						
Large Pulses							
Location	0.0068						
Habitat	0.6520						
Pulse Phase	0.6680						
Season	0.0736						

Appendix B 3-Chapter 4 Appendix. ANOVA analyses significance for sqrt-transformed data for Ammonia (NH₃) concentrations for environmental effects sampled in the Lower Ogeechee River during 11 flood pulses in the years 2019-2022. The lowest p-values are indicated in **bold**. Size refers to large versus small pulses, location refers to the 4 sampling sites along the river, habitat refers to river versus floodplain, pulse phase refers to upswings versus downswings of pulses, and season refers to early, late, and tropical season periods.

NH ₃									
Main Effects		Interactions	Interactions						
		Location	Habitat	Pulse Phase	Season				
Location	0.0001	N/A	-	-	-				
Habitat	0.0077	0.6258	-	-	-				
Pulse Phase	0.9258	0.8220	0.8178	-	-				
Season	0.0023	0.0045	0.3394	0.0853	-				
Size	0.2071	0.0292	0.1650	0.4348	0.8414				
Small Pulses									
Location	0.0481								
Habitat	0.0102								
Pulse Phase	0.6620								
Season	0.0256								
Large Pulses	;								
Location	0.0001								
Habitat	0.3361								
Pulse Phase	0.5831								
Season	0.0195								

Appendix B 4-Chapter 4 Appendix. ANOVA analyses significance for sqrt-transformed data for Total Nitrogen (TN) concentrations for environmental effects sampled in the Lower Ogeechee River during 11 flood pulses in the years 2019-2022. The lowest p-values are indicated in **bold**. Size refers to large versus small pulses, location refers to the 4 sampling sites along the river, habitat refers to river versus floodplain, pulse phase refers to upswings versus downswings of pulses, and season refers to early, late, and tropical season periods.

TN									
Main Effects		In	Interactions						
			Lo	ocation	Habitat		Pulse Phase	Season	
Location		0.1212	-		-		-	-	
Habitat		0.9466	0.	3528	-		-	-	
Pulse Phase		0.8031	0.	6525	0.9520		N/A	-	
Season		0.0110	0.	0020	0.8489		0.1876	-	
Size		<0.0001	0.	1795	0.2610		0.2484	<0.0001	
Small Pulses									
Location	0.	0047							
Habitat	0.	1890							
Pulse Phase	0.	2549							
Season	<	0.0001							
Large Pulses									
Location	0.	31107							
Habitat	0.	5478							
Pulse Phase	0.	6126							

Season

0.0006

Appendix B 5-Chapter 4 Appendix. ANOVA analyses significance for sqrt-transformed data for Phosphorus as Phosphate (PO₄-P) concentrations for environmental effects sampled in the Lower Ogeechee River during 11 flood pulses in the years 2019-2022. The lowest p-values are indicated in **bold.** Size refers to large versus small pulses, location refers to the 4 sampling sites along the river, habitat refers to river versus floodplain, pulse phase refers to upswings versus downswings of pulses, and season refers to early, late, and tropical season periods.

PO ₄ -P							
Main Effects		Interactions					
		Location	Habitat	Pulse Phase	Season		
Location	0.0003	-	-	-	-		
Habitat	0.625	0.2602	-	-	-		
Pulse Phase	0.394	0.5480	0.8285	-	-		
Season	0.0008	0.0518	0.6315	0.0176	-		
Size	0.0023	0.0671	0.3747	0.4721	0.0001		
Small Pulses							
Location	0.0443						
Habitat	0.3844						
Pulse Phase	0.4006						
Season	0.0007						
Large Pulses							
Location	0.0023						
Habitat	0.4677]					
Pulse Phase	0.4110]					
Season	< 0.0001						

Appendix B 6-Chapter 4 Appendix. ANOVA analyses significance for sqrt-transformed data for values for Dissolved Organic Carbon (DOC) concentrations for environmental effects sampled in the Lower Ogeechee River during 11 flood pulses in the years 2019-2022. The lowest p-values are indicated in **bold.** Size refers to large versus small pulses, location refers to the 4 sampling sites along the river, habitat refers to river versus floodplain, pulse phase refers to upswings versus downswings of pulses, and season refers to early, late, and tropical season periods.

DOC							
Main Effects		Interactions	Interactions				
		Location	Habitat	Pulse Phase	Season		
Location	<0.0001		-	-	-		
Habitat	0.0770	0.2356	-		-		
Pulse Phase	0.9696	0.1465	0.8449	-	-		
Season	0.0006	0.2133	0.0764	0.2820	-		
Size	<0.0001	0.6694	0.0892	0.9722	0.1621		
Small Pulses				·	-		
Location	0.0128						
Area	0.0220						
Pulse Phase	0.8727						
Season	0.0325						
Large Pulses							
Location	<0.0001						
Area	0.9541						
Pulse Phase	0.9881						
Season	<0.0001						

Appendix B 7-Chapter 4 Appendix. ANOVA analyses significance for measured Conductivity (mS/cm) for environmental effects sampled in the Lower Ogeechee River during 11 flood pulses in the years 2019-2022. The lowest p-values are indicated in **bold.** Size refers to large versus small pulses, location refers to the 4 sampling sites along the river, habitat refers to river versus floodplain, pulse phase refers to upswings versus downswings of pulses, and season refers to early, late, and tropical season periods.

Conductivity								
Main Effects		Interaction	Interactions					
		Location	Habitat	Pulse Phase	Season			
Location	<0.0001	-	-	-	-			
Habitat	0.2558	0.3198	-	-	-			
Pulse phase	0.231	0.5954	0.7859	-	-			
Season	<0.0001	0.0762	0.1522	0.6058	-			
Size	<0.0001	0.3773	0.9921	0.2358	0.0042			
Small Pulses								
Location	0.0004							
Habitat	0.3841							
Pulse Phase	0.1149							
Season	0.0024							
Large Pulses								
Location	<0.0001							
Habitat	0.2685							
Pulse Phase	0.9250							
Season	<0.0001							

Appendix B 8-Chapter 4 Appendix. ANOVA analyses significance for measured pH for environmental effects sampled in the Lower Ogeechee River during 11 flood pulses in the years 2019-2022. The lowest p-values are indicated in **bold.** Size refers to large versus small pulses, location refers to the 4 sampling sites along the river, habitat refers to river versus floodplain, pulse phase refers to upswings versus downswings of pulses, and season refers to early, late, and tropical season periods.

рН								
Main Effects		Interaction	Interactions					
		Location	Habitat	Pulse Phase	Season			
Location	<0.0001	-	-	-	-			
Habitat	0.0527	0.2455	-	-	-			
Pulse Phase	0.6283	0.8092	0.6919	-	-			
Season	<0.0001	0.5791	0.1614	0.2944	-			
Size	<0.0001	0.3253	0.2873	0.4566	0.0009			
Small Pulses								
Location	0.1037							
Habitat	0.0399							
Pulse phase	0.8825							
Season	<0.0001							
Large Pulses								
Location	<0.0001							
Habitat	0.4867							
Pulse Phase	0.3959							
Season	0.3584							

Appendix B 9-Chapter 4 Appendix. ANOVA analyses significance for sqrt transformed data for values for Suspended Sediments (g/L) for environmental effects sampled in the Lower Ogeechee River during 11 flood pulses in the years 2019-2022. The lowest p-values are indicated in **bold**. Size refers to large versus small pulses, location refers to the 4 sampling sites along the river, habitat refers to river versus floodplain, pulse phase refers to upswings versus downswings of pulses, and season refers to early, late, and tropical season periods.

Suspended Sedin	ment levels					
Main Effects	Interaction	Interactions				
		Location	Habitat	Pulse Phase	Season	
Location	0.0211	_	-	-	-	
Habitat	0.4974	0.6625	-	-	-	
Pulse Phase	0.8037	0.9267	0.2763	-	-	
Season	0.0010	0.5110	0.3120	0.1690	-	
Size	0.0147	0.7150	0.7678	0.8187	0.0001	
Small Pulses						
Location	0.0965					
Habitat	0.5613					
Pulse Phase	0.9993					
Season	<0.0001					
Large Pulses						
Location	0.0656					
Habitat	0.7769					
Pulse Phase	0.7049					
Season	0.0091					



Appendix B 10-Chapter 4 Appendix. Sqrt transformed NOx (mg/L) concentrations in small vs large pulses by location downriver. Effects of location (p=0.0013) and pulse size (p<0.0001) were statistically different.



Appendix B 11-Chapter 4 Appendix. Sqrt transformed NH_3 (mg/L) concentrations in small vs large pulses by location downriver. Effects of location (p=0.0001) were statistically different.



Appendix B 12-Chapter 4 Appendix, Sqrt transformed TN (mg/L) concentrations in small vs large pulses by location downriver. Effects of location (p=0.0003) and pulse size (p<0.0001) were statistically different.



Appendix B 13-Chapter 4 Appendix. Sqrt transformed PO_4 -P (mg/L) concentrations in small vs large pulses by location downriver. Effects of location (p=0.0003) and pulse size (p=0.0023) were statistically different.



Appendix B 14-Chapter 4 Appendix. Sqrt transformed DOC (mg/L) concentrations in small vs large pulses by location downriver. Effects of pulse size (p<0.0001) and location (p=0.0003) were statistically different.



Appendix B 15-Chapter 4 Appendix. Conductivity (mS/cm) concentrations in small vs large pulses by location downriver. Effects of pulse size (p<0.0001) and location (p<0.0001) were statistically different.



Appendix B 16-Chapter 4 Appendix. pH in small vs large pulses by location downriver. Effects of pulse size (p<0.0001) and location (p<0.0001) were statistically different.



Appendix B 17-Chapter 4 Appendix. Sqrt transformed suspended sediments (g/L) in small vs large pulses by location downriver. Effects of pulse size (p=0.0147) and location (p=0.0211) were statistically different.



Appendix B 18-Chapter 4 Appendix. Annual discharge in the Ogeechee River from 1970-2020, in the typical winter-spring flood period (Dec-May, upper plot) and the tropical storm season (June-Nov, lower plot). Annual discharge is declining overall (lines), but the range of annual variability in the Dec-May period is declining while the range of annual variability in the tropical storm season is increasing. (Data from Oliver USGS gage).