

Aquatic Invertebrate Community Composition, Diversity, and Biomass in Non-impounded Bottomland Hardwood Forests and Greentree Reservoirs

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Abstract: The Mississippi Alluvial Valley (MAV) had extensive bottomland hardwood forests but less than 25% of this area remains forested today. Impounded greentree reservoirs (GTRs), have been managed for wintering waterfowl since the 1930s, and provide a source of aquatic invertebrates and acorns for foraging ducks and other wildlife. However, few studies of invertebrate community-composition, diversity, and biomass have been conducted at regional scales. We collected samples of aquatic invertebrates from three hardwood bottomlands in the MAV and one in the Mississippi Interior Flatwoods region during winters 2008–09 and 2009–10. We compared community composition metrics of aquatic invertebrates between naturally flooded forests (NFF) and GTRs. Five families occurred more frequently in GTRs than NFFs ($P < 0.01$); these were Asellidae, Chironomidae, Cragon-yctidae, Daphniidae, and Sphaeriidae. However, the NFFs had greater invertebrate familial diversity than their paired GTRs for most winter months. Across winters, we found most invertebrate families (65% [early winter] and 82% [late winter]) associated with sites in NFFs and GTRs with depths from 10–40 cm. Because GTRs are typically flooded to depths greater than this range, and flooding of most GTRs results in relatively stable hydroperiods, we re-emphasize need for managing hydrology of GTRs similarly to local NFFs, which may promote increased invertebrate diversity and biomass.

Key words: forested wetland, greentree reservoir, invertebrate, Mississippi Alluvial Valley, waterfowl, winter.

Journal of the Southeastern Association of Fish and Wildlife Agencies 5:125–135

Bottomland hardwood forests in southeastern United States are among the most ecologically diverse wetland systems in North America (Fredrickson 2005a). Until the 20th century, these forests covered most of the 10 million ha of the Lower Mississippi Alluvial Valley (MAV) from southern Illinois near the confluence of the Mississippi and Ohio Rivers southward into Louisiana (Reinecke et al. 1989, Fredrickson 2005a). Anthropogenic changes to regional hydrology for agriculture and urbanization have significantly altered historical dynamic riverine and floodplain dynamics and reduced areal distributions of plant and wildlife communities in the MAV (Reinecke et al. 1989, King et al. 2006). Nonetheless, remnant lowland forests remain important seasonal and year-round habitats for diverse communities of vertebrates and invertebrates (Batema et al. 2005, Heitmeyer et al. 2005, Foth et al. 2014).

Although greatly reduced in area and often highly fragmented, bottomland hardwood forests that are not impounded by a levee(s) and thus naturally flood (NFF) from overbank inundation, rainfall, and runoff persist in the MAV and elsewhere in other major river systems, but primarily only within national and state forests and wildlife refuges or managed private lands (Wehrle et al. 1995, Foth et al. 2014). Artificially flooded greentree reservoirs (GTRs)

also exist throughout the whole of the eastern United States (Wigley and Filer 1989, Deller and Baldassarre 1998). A GTR is an impounded tract of forested wetland that typically is flooded during fall through winter periods of tree dormancy to provide stable wetland habitat for ducks and waterfowl hunting (Reinecke et al. 1989, Fredrickson 2005b). Flooding during fall-winter dormancy enables trees to survive and remain “green,” hence the term GTR. Artificial flooding of GTRs from aquifers or other water sources deviates from natural historic dynamic flood regimes and can alter community composition and abundance of aquatic invertebrates (Wehrle et al. 1995, Batema et al. 2005, Foth et al. 2014). Whereas, purposeful inundation of GTRs provides predictable and continuous flooding during winter, hydroperiods in naturally-flooded forests are dynamic due to variable monthly rainfall and subsequent flooding, ultimately resulting in periodic or pulsed forest inundation (Fredrickson 2005a, b). Evidence suggests mimicking naturally dynamic flood regimes in GTRs may sustain invertebrate communities better than artificially imposed hydroperiods (Fredrickson and Reid 1988, Wehrle et al. 1995, Batema et al. 2005, Foth et al. 2014).

Aquatic invertebrates occupy different trophic niches in bot-

tomland hardwood forests, including shredders, grazers, and predators (Wehrle et al. 1995, Batema et al. 2005). Shredders process coarse particulate matter (e.g., leaf litter) and acquire nutrients from periphyton, whereas grazers glean algae and phytoplankton from substrates, and predators depredate other invertebrates (Vannote et al. 1980, Batema et al. 2005). The food web of these bottomland forests is driven by allogenic and autochthonous inputs of nutrients and detritus from hydrologically connected lotic and lentic wetlands and watersheds (Vannote et al. 1980). Aquatic invertebrates also function in the transfer and cycling of nutrients between producers and consumers (Malmqvist 2002, Mitsch and Gosselink 2007).

Aquatic invertebrates are essential food for many wildlife species (Batzer and Wissinger 1996). For example, birds consume invertebrates year round for protein and calcium needed for growth, reproduction, and other physiological functions (Heitmeyer et al. 2005, 2006; Baldassare and Bolen 2006). Female ducks of several species consume aquatic invertebrates from forested and other wetlands during winter, because females undergo prebasic molt and need proteinaceous foods for producing feathers and other tissues at that time (Heitmeyer 1987, 1988; Richardson and Kaminski 1992; Barras et al. 2001). Wood ducks (*Aix sponsa*) use forested wetlands year round, and invertebrates provide an important source of protein and calcium for females and ducklings (Drobney and Fredrickson 1979, Davis et al. 2007).

Foth et al. (2014) used sweep-nets to sample aquatic invertebrates from four geographically separate bottomland hardwoods in the MAV and Mississippi's Interior Flatwoods region during winters 2008–09 and 2009–10. They estimated dry mass of aquatic invertebrates from NFFs or NFFs and GTRs combined when both wetland types existed within study areas. The primary goal of Foth et al. (2014) was to generate estimates of invertebrate biomass that partners of the Lower Mississippi Valley Joint Venture of the North American Waterfowl Management Plan (Loesch et al. 1994) could use in planning and implementation of foraging habitat conservation for wintering waterfowl, but they did not report comparative data in aquatic invertebrate biomass and ecological community metrics between NFFs and GTRs. Accordingly, we address community composition, familial richness and diversity, and total biomass of aquatic invertebrates in NFFs and GTRs, based on sweep-net samples. Sweep-nets generally are used to yield data on relative abundance or other indices of aquatic invertebrate communities (Murkin et al. 1994). Kaminski and Murkin (1981) reported no statistical differences in the ability of a sweep-net or a modified Gerking device (i.e., whereby samples enclosed volumes of water for nekton; Murkin et al. 1994) to quantify percent occurrences of invertebrate taxa and abundance. Moreover, sweep-net sam-

ples from this study contained most of the same taxa that Duffy and Labar (1994) collected with core samplers from surface water and underlying substrates in GTRs at Sam D. Hamilton Noxubee National Wildlife Refuge outside of the MAV in east-central Mississippi, which was one of the areas sampled in this study. Thus, we believe our sweep-net sampling adequately characterized invertebrate communities in NFFs and GTRs in our study. Lastly, we also modeled relationships between invertebrate communities and forested wetland metrics (i.e., water depth and litter mass) and provide management implications consistent with our results. Our overarching hypothesis was that invertebrate communities would differ by flooding regimes regardless of study sites, but invertebrate communities would be more influenced by site conditions than flooding regime.

Study Areas

Foth et al. (2014) described their study areas, which are the same as those sampled in this study. Therefore, we refer readers to Foth et al. (2014) and report herein only information we deemed important for this study focused on comparison of aquatic invertebrate communities and biomass between GTRs and NFFs in the MAV and a relatively close area of the Mississippi Interior Flatwoods.

Mingo National Wildlife Refuge (NWR) and Duck Creek Conservation Area (hereafter Mingo/Duck Creek) in southeastern Missouri are contiguous and managed by the U.S. Fish and Wildlife Service and Missouri Department of Conservation, respectively. The site contains 7,000 ha of bottomland hardwood forest, the only remaining large tract of bottomland hardwood forests in the Missouri MAV (Heitmeyer et al. 1989). The sampled GTR, Pool 2, was at Duck Creek and developed during the 1950s. It and other GTRs at Duck Creek were annually flooded by water being purposefully drained from the adjacent Pool 1 (Fredrickson 2005a, Foth et al. 2014). Mingo NWR has a GTR but only NFF were sampled on the refuge, because the GTR was not actively flooded during our study and only flooded passively during heavy precipitation events.

White River NWR is located in west-central MAV in eastern Arkansas. The refuge encompasses a 145-km stretch of the lower White River near its confluence with the Mississippi River. White River NWR contains about 62,300 ha of bottomland hardwood forests and other wetlands (Oli et al. 1997, Foth et al. 2014). Although no GTRs existed in White River NWR, we sampled NFF there to acquire aquatic invertebrate data representative of this large lowland forested wetland in the Arkansas MAV.

Delta National Forest (DNF) is managed by the U.S. Department of Agriculture's Forest Service in east-central MAV in west-central Mississippi. The DNF contains over 24,000 ha of bot-

tomland hardwood forest interspersed with palustrine wetlands and is one of the only two national forests comprised exclusively of bottomland hardwoods in the United States (Lowney and Hill 1989). There are approximately 2,000 ha of bottomland hardwood forests managed as GTRs (Wehrle et al. 1995, Foth et al. 2014). We sampled exclusively in the Sunflower GTR, managed by the Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP). The GTR is flooded by pumping water from the adjacent Little Sunflower River via a pipe underlying Mississippi Highway 16. Sunflower GTR was entirely flooded every year from approximately 1960 until 1990, when MDWFP began flooding each of the GTR's three compartments once every three years. We also sampled the nearest NFF tract in DNF located approximately 17 km south of Sunflower GTR.

Finally, we also sampled a GTR and NFF at the Sam D. Hamilton Noxubee NWR (hereafter, Noxubee NWR), located outside the MAV in the Mississippi Interior Flatwoods region in east-central Mississippi (Pettry 1977). We sampled this site because of previous aquatic invertebrate research there and desire for comparative results beyond the MAV (Duffy and LaBar 1994, Wehrle et al. 1995). The refuge has four GTRs; we sampled GTR 1, to compare results with those of Wehrle et al. (1995) and Duffy and LaBar (1994). The GTRs were constructed in the 1960s and generally flooded annually from late November to mid-February. (Straub 2012, Foth et al. 2014).

Methods

Invertebrate Sampling and Experimental Design

We used the *grts* design option of the SPSURVEY package (Kincaid and Olsen 2011) in Program R 2.11.1 (R Development Core Team 2008) to select random plot centers within each GTR and NFF. We sampled three GTRs (i.e., Duck Creek, DNF, and Noxubee NWR) and four NFF tracts (i.e., DNF, Mingo, White River, and Noxubee NWRs). We established 10 0.2-ha circular sampling plots within each GTR (when one existed) and within an associated NFF at each study area (Foth et al. 2014). Our *a priori* goal was to obtain four random samples within all plots per GTR and NFF per month ($n = 40/\text{GTR and NFF/month}$). Occasionally, some plots in NFFs were not inundated or incompletely inundated; consequently, we took one to three samples from flooded plots within NFFs to obtain greater than 20 NFF samples per month. We attempted to collect samples monthly at all study areas during November–February 2008–09 and 2009–10. However, lack of inundation, ice, or deep flooding precluded sampling some areas and months ($n = 19$; Foth 2011).

We used a 25 × 50-cm rectangular sweep-net to collect invertebrates from the substrate upward through the water column (Wehrle et al. 1995, Foth et al. 2014).

At each sample site, we measured water depth (cm) when surface water existed. If surface water was absent, we recorded a zero for depth but included each zero in the within-plot average water depth. We placed samples on ice after collection, transported them to Mississippi State University, and stored them in a freezer until processing (Murkin et al. 1994, Foth et al. 2014). We used tap water and no additives for processing samples, because invertebrate abundance and biomass did not differ between tap water with and without sugar or salt amendment (Foth et al. 2012). We removed invertebrates by hand and identified them to family (Pennak 1989, Merritt and Cummins 2008). We dried sorted samples to a constant mass and weighed invertebrates to estimate total biomass (Foth et al. 2014). Additionally, from the litter in each sweep-net sample, we randomly selected the first 25 whole leaves to provide an index of forest tree species present within our sample plots (Foth 2011). We then dried and weighed all leaf litter and calculated the percentage of red oak leaf mass in each sample. We calculated red oak (*Quercus* spp.) leaf mass because forest composition influences nutrient exchange in bottomland hardwood forests (Batema et al. 2005). The leaf biomass represented an estimate of potential coarse particulate organic matter available per plot for colonization of periphyton and forage for invertebrates.

We assumed *a priori* that sweep-net samples of invertebrates would not be independent within the 0.2-ha sampling plots. Within-plot sample variation in biomass was weakly related but significant ($r = 0.10$; $P = < 0.001$; $n = 431$). Therefore, we accounted for within-plot sample correlation for invertebrate biomass and community metrics by averaging data among individual sweep-net samples within plots and designated plot as the analytic unit (Foth et al. 2014). At sites of previous research (Batema 1987, Duffy and LaBar 1994, Wehrle et al. 1995), we established plots within the same GTRs and NFFs, so our data could be compared with those previous studies.

Statistical analyses and summary

Invertebrate diversity metrics.—We calculated percent occurrence of invertebrate families from our sweep-net samples and used a two-tailed *t*-test, designed for comparing percentages (Sokal and Rohlf 1969), to compare familial percentages between GTRs and NFFs across years and by study area having both wetland types. We designated the number of detected invertebrate families within each study site and month (November–February) as familial richness. We calculated invertebrate familial diversity at each study site and during each month using a Shannon-Wiener index (Krebs 1999, González et al. 2009). We used two separate general linear models in Program R version 2.11.0 to test if invertebrate familial

richness and diversity (response variables) differed ($\alpha=0.05$) between flooding regimes within study areas (NFF and GTR), study areas (Mingo/Duck Creek, DNF, and Noxubee NWR), and month. We only analyzed data when spatially and temporally paired samples from GTRs and NFFs at a site were available within a sample month. We pooled data across years to make overall temporal generalizations from our results, because we likely would be unable to interpret any detected between-year differences. As previously stated, we averaged data among individual sweep-net samples within plots and specified plot as the sampling and analytic unit because of weak correlation among individual sweep-net samples (Foth et al. 2014).

Non-metric multidimensional scaling.—We used a non-metric multidimensional scaling ordination (NMDS; *vegan* package, Program R version 2.11.0) to characterize invertebrate familial composition relative to study sites and NFF or GTR flooding regimes (Wilson and Sheaves 2001). We pooled invertebrate samples across both years but partitioned samples into two time periods (early winter [November–December 2008 and 2009; $n=389$] and late winter [January–February 2009 and 2010; $n=402$]) for analyses, because this temporal partitioning improved balance of sample sizes across months (Foth et al. 2014). For this analysis, we included 17 families that comprised $\geq 1\%$ of the numerical occurrence of invertebrates by flooding regime (Desmond et al. 2002). We used ordinations based on Sorenson/Bray-Curtis distance measurements to represent invertebrate assemblages graphically (Vinson and Dinger 2008). In the *vegan* package, invertebrate relative abundances of remaining families were square root transformed using the Wisconsin double standardization (Oksanen et al. 2010). We used the NMDS analysis in two-dimensional ordination space with 1,000 iterations. We calculated stress values, which indicated deviation between the ordination and the original similarity matrix to evaluate precision of the ordination (Clarke 1993, Desmond et al. 2002). Stress values >0.05 provide an excellent representation in reduced dimensions, >0.1 is good, >0.2 is equivocal, and stress >0.3 provides a poor representation (Clarke 1993). We also fit environmental vectors (i.e., water depth or red oak leaf mass; Foth et al. 2014) with ENVFIT in *vegan* package to the ordination plot to identify their effects on composition of invertebrate communities (Oksanen et al. 2010). We only analyzed the biomass of red oak litter because mast produced by red oak trees is consumed by waterfowl (Barras et al. 2001). If any portion of the invertebrate community was clustered at the terminus of an environmental vector, we interpreted it to be positively correlated with that environmental variable (Dinger and Marks 2007). We plotted values derived from the NMDS ordination and color illustrated plot locations by site to interpret invertebrate communities. The proximity and overlap

between colored plots depicted relative similarities or differences between invertebrate species assemblages at the four study sites.

Invertebrate biomass.—Similar to analysis of diversity metrics, we only analyzed invertebrate biomass data from spatially and temporally paired and sampled GTRs and NFFs within study sites. We used a general linear model in Program R version 2.11.0 to test if invertebrate biomass (response variable) varied between flooding regimes at study areas, month, or the interaction of study area and flooding regime within winter sampling period (Foth et al. 2014).

Results

Invertebrate diversity metrics

We tested for differences in mean percent occurrence of 17 invertebrate families, because other taxa ($n=4$) occurred in $<1\%$ of the samples (Table 1). Five families occurred more frequently in GTRs than NFFs ($P<0.01$; Table 1); these were Asellidae (isopods), Chironomidae (midge larvae), Crangonyctidae (amphipods), Daphniidae (water fleas), and Sphaeriidae (i.e., fingernail clams; Table 1).

During winters 2008–09 and 2009–10, GTRs and NFFs were not always flooded concurrently. Thus, we report results from sampling events when GTRs and NFFs both were flooded ($n=7$ sampling events; GTR [$n=70$ plots] and NFF [$n=46$ plots]). We detected a

Table 1. Percentage (%) occurrence of aquatic macroinvertebrate families in green tree reservoirs (GTRs) and naturally flooded forests (NFFs) in the Mississippi Alluvial Valley and Interior Flatwoods during winters 2008–09 and 2009–10.

Family (common name)	GTR ($n=605$) ^a	NFF ($n=186$)	P^b
<i>Asellidae</i> (isopod)	71.07	63.44	<0.01
<i>Chironomidae</i> (midge larvae)	90.74	75.27	<0.001
<i>Crangonyctidae</i> (amphipod)	74.55	59.14	<0.001
<i>Daphniidae</i> (water fleas)	61.82	43.55	<0.001
<i>Sphaeriidae</i> (fingernail clam)	46.94	35.48	<0.01
<i>Planorbidae</i> (snail)	32.56	55.91	>0.05
<i>Stratiomyidae</i> (soldier beetle)	21.32	19.35	>0.05
<i>Cambaridae</i> (crayfish)	15.21	23.66	>0.05
<i>Physidae</i> (snail)	13.06	26.88	>0.05
<i>Hygrobatidae</i> (water mite)	8.26	5.38	>0.05
<i>Dytiscidae</i> (predaceous diving beetle)	7.60	22.58	>0.05
<i>Culicidae</i> (mosquito larvae)	6.61	9.14	>0.05
<i>Aeshnidae</i> (dragonfly larvae)	3.31	5.38	>0.05
<i>Corixidae</i> (water boatman)	0.33	4.30	>0.05
<i>Tabanidae</i> (horsefly larvae)	3.31	2.15	>0.05
<i>Gerridae</i> (water strider)	1.16	1.61	>0.05
<i>Syrphidae</i> (rat-tail maggot)	0.83	1.08	>0.05
<i>Nepidae</i> (water scorpion)	0.00	0.54	>0.05
<i>Hydrophilidae</i> (water beetle)	0.50	0.00	>0.05
<i>Tipulidae</i> (crane fly larvae)	0.33	0.00	>0.05

a. n = number of sweep-net samples collected and processed within GTRs or NFFs for winters 2008–2010.

b. Two-tailed t -test for percentages (Sokal and Rohlf 1969).

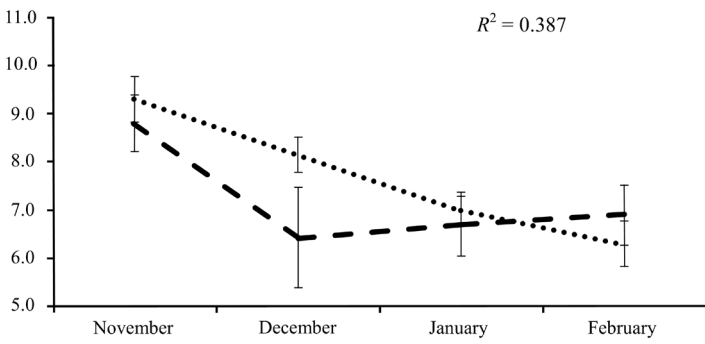


Figure 1. Mean aquatic invertebrate familial richness (i.e., number of families; standard error bars) from greentree reservoirs (•••; $n = 70$) and naturally flooded forests (---; $n = 46$) in the Mississippi Alluvial Valley and Interior Flatwoods, November 2008–February 2010.

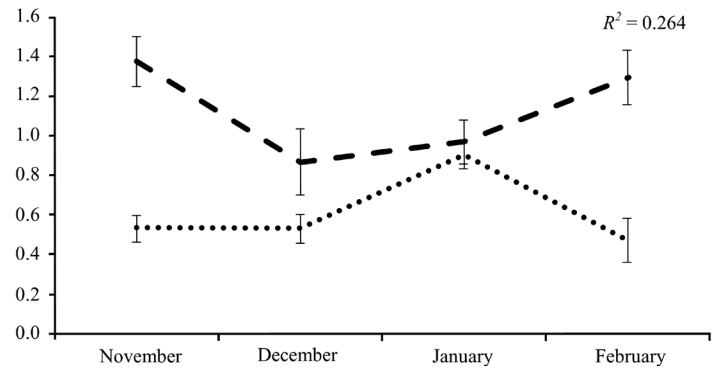


Figure 2. Mean aquatic macroinvertebrate familial diversity and standard error bars from greentree reservoirs (•••; $n = 70$) and naturally flooded forests (---; $n = 46$) in the Mississippi Alluvial Valley and Interior Flatwoods, November 2008–February 2010.

flooding regime (i.e., GTR or NFF) by month interaction for invertebrate familial richness ($F = 2.736$, $df = 3, 107$; $P = 0.047$); richness differed between flooding regimes only in December (GTR [$\bar{x} = 8.0$, $SE = 0.36$ families], NFF [$\bar{x} = 6.0$, $SE = 1.04$ families], Figure 1).

We also detected a flooding regime by month interaction for invertebrate familial diversity, ($F = 5.266$, $df = 3, 107$; $P = 0.002$). The NFF had greater invertebrate diversity than the GTR in November (NFF [$\bar{x} = 1.37$, $SE = 0.125$]; GTR [$\bar{x} = 0.53$, $SE = 0.067$]), December (NFF [$\bar{x} = 0.87$, $SE = 0.166$]; GTR [$\bar{x} = 0.53$, $SE = 0.071$]), and February (NFF [$\bar{x} = 1.29$, $SE = 0.138$]; GTR [$\bar{x} = 0.47$, $SE = 0.110$]; Figure 2), but did not differ between flooding regimes in January (NFF [$\bar{x} = 0.97$, $SE = 0.110$]; GTR [$\bar{x} = 0.91$, $SE = 0.073$]).

Non-metric multidimensional scaling ordination

The NMDS analysis revealed that stress values for model fit of the data were good in both early winter (0.23) and late winter (0.24; Figures 3 and 4, respectively). Plots within Mingo/Duck Creek and White River NWR were intermediate in ordination space between DNF and Noxubee NWR, but little overlap existed between DNF and Noxubee NWR. During early and late winter, we found most invertebrate families (65% and 82%, respectively) were associated with water depths ranging from 10–40 cm ($\bar{x} = 30.11$ cm, $SE = 3.044$, $n = 18$ plots). Axis NMDS1 was correlated with water depth; as plots moved away from the center of ordination space, water depth increased. We plotted water depth and red oak leaf mass over the NMDS output, but neither variable explained presence of invertebrate families in early winter (i.e., water depth $P = 0.086$; red oak leaf mass $P = 0.545$; Figure 3). For late winter, water depth was correlated with the ordination plot ($R = 0.06$; $P = 0.026$; $n = 206$; Figure 4). When overlain on the ordination plot, water depth was more positively correlated in plots at Noxubee NWR than DNF and Mingo/Duck Creek. Lastly, red oak leaf mass did not influence ($P = 0.321$) presence of invertebrate families in late winter.

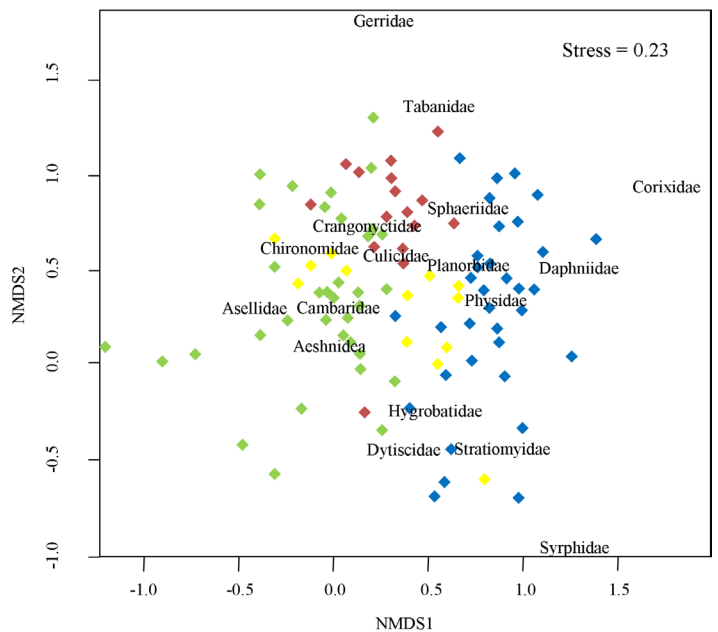


Figure 3. Non-metric multidimensional scaling ordination of invertebrate families ($\geq 1\%$ of total occurrence) in early winter (November and December 2008–2009) at Mingo/Duck Creek (red), White River National Wildlife Refuge (yellow), Delta National Forest (blue), and Noxubee National Wildlife Refuge (green). Points in close proximity represent similar assemblages, whereas points farther apart indicate differing assemblages. Stress evaluates the precision of the ordination.

Invertebrate biomass

We detected a flooding regime by study area interaction for invertebrate biomass (i.e., kg/ha; $F = 6.356$, $df = 2, 66$; $P = 0.003$). Specifically, invertebrate biomasses were greatest and similar in NFFs at DNF in Mississippi ($\bar{x} = 19.23$ kg/ha, $SE = 5.376$, $n = 101$) and Mingo/Duck Creek in Missouri ($\bar{x} = 17.09$ kg/ha, $SE = 8.723$, $n = 16$) compared to their paired GTRs (DNF [$\bar{x} = 5.297$ kg/ha, $SE = 1.153$, $n = 155$]; Mingo/Duck Creek [$\bar{x} = 5.23$ kg/ha, $SE = 1.820$, $n = 40$]). Invertebrate biomass did not differ between northern and south-

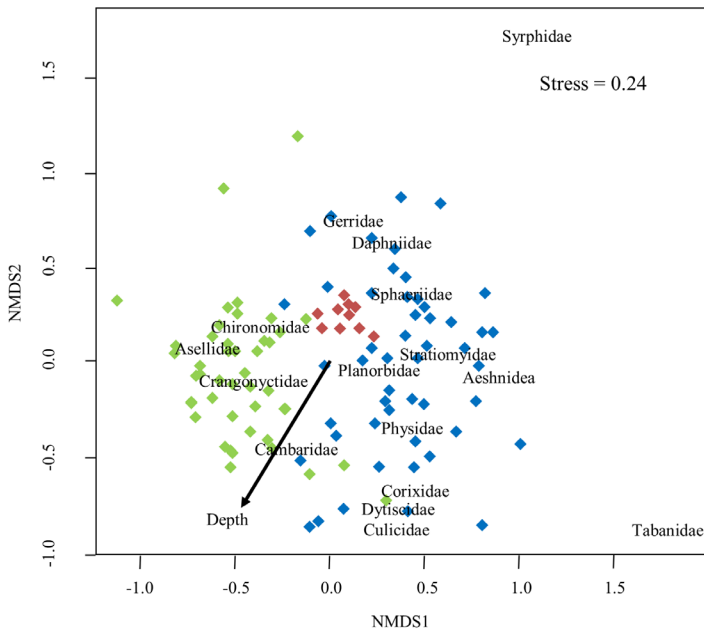


Figure 4. Non-metric multidimensional scaling ordination of invertebrate families ($\geq 1\%$ of total occurrence) and environmental vector (water depth) in late winter (January and February 2009–2010) at Mingo/Duck Creek (red), Delta National Forest (blue), and Noxubee National Wildlife Refuge (green). Points in close proximity represent similar assemblages, whereas points farther apart indicate differing assemblages. Stress evaluates the precision of the ordination.

ern MAV sites (Figure 5). Invertebrate biomass at Noxubee NWR was markedly less than at MAV sites but did not differ at Noxubee NWR between GTR and NFF sites ($\bar{x} = 1.32$ kg/ha, SE = 0.226, $n = 78$; $\bar{x} = 1.12$ kg/ha, SE = 0.951, $n = 41$; Figure 5).

Discussion

Invertebrate diversity metrics

Five invertebrate families, including isopods, midge larvae, amphipods, water fleas, and fingernail clams, occurred more frequently in GTRs than NFFs, possibly because of their colonizing and aestivating adaptations (Anderson and Smith 2004, Studinski and Grubbs 2007). Usually, GTRs are drained in late winter-early spring when trees are dormant (Fredrickson 2005b). Greater occurrence of these families may arise from source populations in summer and autumn, because GTRs have the potential to retain water and soil moisture longer in spring and summer than NFFs (Fredrickson 2005b). In mid- to late autumn, when GTRs typically are flooded for waterfowl hunting seasons, these invertebrate families may have been present within the substrate (i.e., aestivating adults, larvae, or eggs) or were translocated to GTRs from water sources used to flood GTRs (Batema et al. 2005). Compared to GTRs, the duration of seasonal flooding in NFFs is less; thus, invertebrate colonization may be slower and population occurrence and growth less than in GTRs (Hatten et al. 2014).

Invertebrate familial richness did not differ between flooding

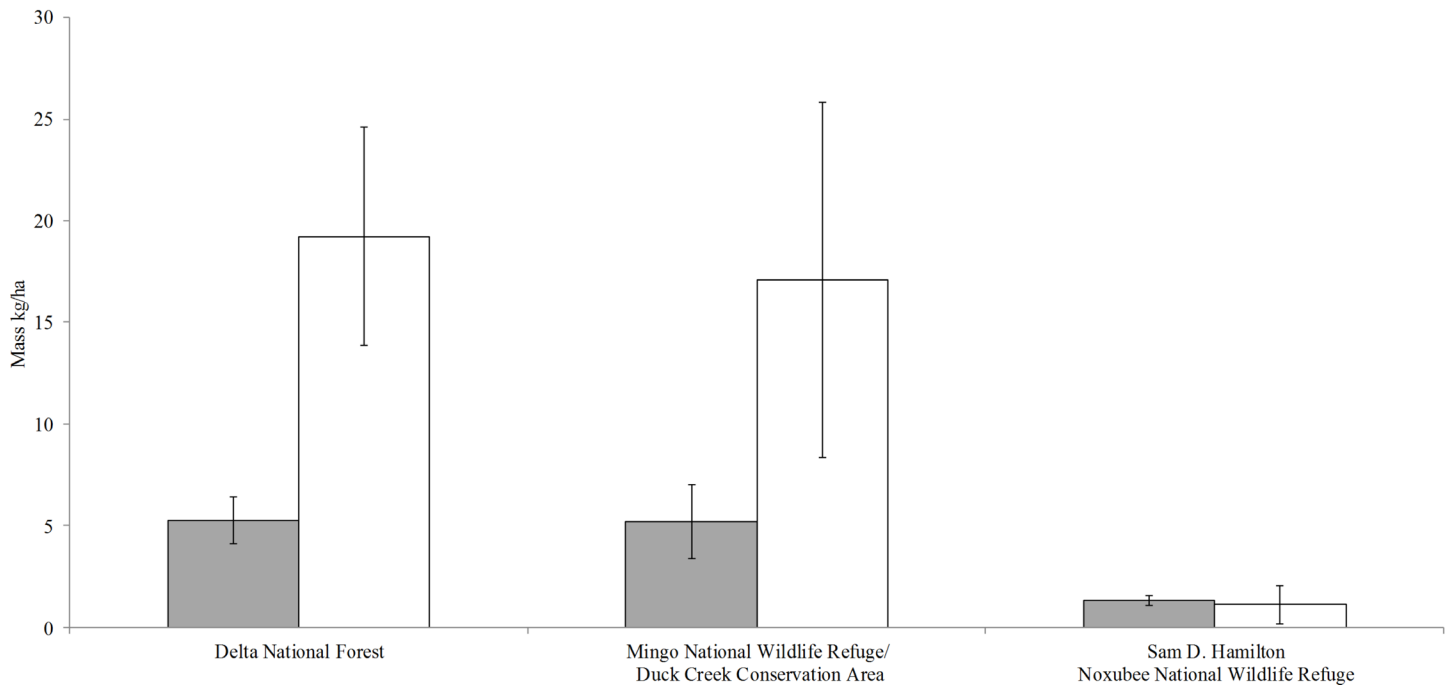


Figure 5. Aquatic invertebrate biomass (kg dry/ha; \pm SE) in greentree reservoir (GTR; \blacksquare) and naturally flooded forests (NFF; \square) at Delta National Forest ($n = 368$; Mississippi), Mingo/Duck Creek ($n = 136$; Missouri), and Noxubee National Wildlife Refuge ($n = 259$; Mississippi) during winters 2008–09 and 2009–10.

regimes except in December, when eight and six families were recorded from GTRs and NFFs, respectively. Richness declined in GTRs through winter during flooded episodes or later when GTRs were being drained. Although we did not collect data to explain seasonal dynamics of invertebrate populations, decaying leaf litter, metals leached from soil (e.g., iron), and stagnant water together may have reduced dissolved oxygen or pH and influenced the seasonal decline in invertebrate richness (Jackson and Harvey 1993). In contrast, mean invertebrate familial richness in NFFs declined from November to December but then increased through February, perhaps in relation to new flood water, increasing day length, warming ambient and water temperatures during late winter, or other factors such as allochthonous inputs of nutrients (e.g., Manley et al. 2004, Foth 2011). Spatio-temporal dynamic hydrology in NFFs compared to more stably flooded GTRs may have reduced stagnation because of short, frequent flood pulses of water which may have increased dissolved oxygen levels, nutrient inputs, and pH. Reese and Batzer (2007) reported that headwater floodplains, with dynamic hydrology, were characterized by rapidly developing aquatic and terrestrial invertebrate communities (e.g., mosquitoes, micro-crustaceans). In our study, numerical abundance was approximately 33% more for mosquito larvae and about twice as many *Physidae* and *Planorbidae* snails in NFFs than GTRs. Decreases in invertebrate familial richness as winter progressed in GTRs and NFFs also may have been related to depredation of invertebrates by foraging ducks, fish, or predaceous invertebrates, but simultaneous surveys of predator feeding ecology and invertebrate occurrence and abundance in bottomland forests are needed to evaluate this possibility (Flotemersch and Jackson 2003, Callcutt et al. 2011, Foth et al. 2014).

We compared published familial richness and composition be-

tween our and other studies (Table 2). We detected more invertebrate families than Wehrle et al. (1995) and Batema (1987) working in Mississippi and Missouri, respectively. However, all families identified by Wehrle et al. (1995) and Batema (1987) were present in our samples. Additionally, winter invertebrate taxonomic composition of Duffy and Labar's (1994) invertebrate samples was similar to ours. We found 12 more families than that study encountered with core sampling alone; however, their core sampling method collected four families we did not encounter. Differences in identified families between our study and others may be related to differences in sampling and processing methods, ecological and environmental phenomena, year effects, or a combination of these.

We also compared invertebrate familial richness in forested wetlands with other wetland types (Table 2). Forested wetlands in our study had greater invertebrate familial richness than moist-soil wetlands in Delaware (Sherfy and Kirkpatrick 2003). Hagy and Kaminski (2012) encountered a total of 11 orders of invertebrates in moist-soil wetlands in the MAV and Noxubee NWR, and we encountered 13 orders across our forested wetland sites in the MAV and Noxubee NWR. Difference in richness may be caused by regional differences in soil and water chemistry, biomass and structure of available plant litter for algal and microbial colonization, sampling and processing differences, year effects, or a combination of these and other factors. Nonetheless, forested wetlands may harbor diverse invertebrate communities in winter because of surface area and complexity of litter from woody and herbaceous plants and wetland hydrology (Batema et al. 2005). However, flooded bottomland hardwood forests had lower invertebrate familial richness ($n=20$ families) than emergent wetlands ($n=35-47$ families; Table 2). Our study was not designed to explain these differences, but future researchers may desire to examine invertebrate richness

Table 2. Invertebrate familial richness in different managed and unmanaged wetlands in the United States.

Season	Wetland type	Location	Familial richness			Reference
			Managed	Unmanaged	Total	
Autumn	Pasture wetlands	Florida	— ^a	—	45	Steinman et al. (2003)
	Seasonal wetlands	California	—	—	35	Marchetti et al. (2010)
Winter	Forested wetlands	Mississippi Alluvial Valley	19	18	20	This study
		Missouri	—	—	12	Batema (1987)
		Mississippi	9	8	9	Wehrle et al. (1995)
		Kentucky	20	—	20	Studinski and Grubbs (2007)
	Playa wetlands	Texas	69	42	70	Anderson and Smith (2000)
	Moist-soil impoundment	Delaware	11	—	11	Sherfy and Kirkpatrick (2003)
Spring	Playa wetlands	Texas	—	47	47	Hall et al. (2004)
Summer	Emergent wetlands	West Virginia	38	25	38	Balcombe et al. (2005)
	Everglades	Florida	—	—	53	Rader and Richardson (1994)

a. — denotes a lack of information on management in wetland

in relation to differences in water depth, frequency, and duration of flooding and drawdown events, turbidity, pH, soil and water chemistry and temperature, and plant litter in these wetlands to improve our understanding of invertebrate community dynamics in GTRs and NFFs (e.g., Hatten et al. 2014).

The NFFs had greater invertebrate diversity than the GTRs in November, December, and February. The NFFs may have had greater invertebrate familial diversity because of variable hydrologic regimes and other associated environmental conditions across their basins. Tronstad et al. (2005) found that numerous invertebrates emerged from formerly dry floodplain soils after being inundated, and peak numbers occurred in frequently inundated sites (Batzer 2013). The observed greater diversity in NFFs also may be related to variation in depth, flood duration, and biogeochemical influences (e.g., dissolved oxygen, pH, nutrient inputs, periodic flushing of tannins and metals). Thus, dynamic hydrologic regimes of NFFs may provide more suitable habitats for invertebrates to colonize, forage, grow, and reproduce than within the relatively static hydrologic regime in GTRs.

Non-metric, multidimensional scaling ordination

The NMDS ordination analysis produced little overlap in invertebrate community composition between DNF and Noxubee NWR for early and late winter periods. Mingo/Duck Creek and White River NWR were intermediate between DNF and Noxubee NWR. We hypothesized that invertebrate communities would differ by flooding regimes regardless of study sites, but invertebrate communities were influenced more by geographic site than flooding regime. Therefore, site specific variables (e.g., soil chemistry, nutrients leached by organic matter, tannin levels and pH, water sources, and hydroperiods; Wehrle et al. 1995, Miller et al. 2008) may be more influential on structure of the invertebrate community than flooding regime itself, but this hypothesis also should be tested in future research.

We incorporated environmental covariates (i.e., red oak leaf mass and water depth) into the ordination analysis to explain potential invertebrate community relationships within and among study sites. Most GTRs are flooded to full capacity and have relatively stable depths for several months during fall and winter, often with little or no additional freshwater input besides that from rainfall and runoff simultaneous with organic matter decomposition through invertebrate and microbial activity (Fredrickson 2005b). Red oak leaf mass and water depth were not correlated with invertebrate communities in early winter. In late winter, the water depth vector plotted on the NMDS output was more associated with plots at Noxubee NWR. This relationship also may have been confounded by small sample size at Noxubee NWR for NFF plots

($n = 19$) compared to plots in the Noxubee GTR ($n = 120$). Alternatively, the ordination and positive relationship between invertebrate communities and water depth at Noxubee NWR and not elsewhere may have been linked to the GTR generally being flooded to shallower prescribed depths (<0.5 m) during winter except after periodic deep inundations from overbank flooding of the Noxubee River (Foth 2011).

Invertebrate biomass

We found that invertebrate biomass differed between GTR and NFF flooding regimes and between MAV and Mississippi Interior Flatwoods regions (Foth 2011; Figure 5). The MAV NFFs at Mingo/Duck Creek and DNF harbored 3–4 times greater invertebrate biomass than their respective paired GTR, but invertebrate biomass within GTRs and NFFs did not differ between northern and southern MAV sites. Invertebrate biomass was markedly less at Noxubee NWR in the Mississippi Interior Flatwoods but biomass did not differ between Noxubee NWR NFF and GTR sites (Figure 5).

Wehrle et al. (1995) reported a similar trend for invertebrate biomass in GTRs and NFFs in the MAV and Mississippi Interior Flatwoods, perhaps because of increased soil nutrient richness in the MAV compared to Mississippi Interior Flatwoods (Pettry 1977). Our invertebrate biomass mean values (kg/ha) were less than half of the range of means reported by Wehrle et al. (1995). Possibly, these differences might be due to differences in methodologies and time and environmental periods between these studies separated by 20 years. However, it is unlikely this was driven by taxonomic differences as we both collected similar taxa (Wehrle et al. 1995, Foth 2011). Foth et al. (2014) reported contemporary estimates of invertebrate biomass for NFFs individually and NFFs and GTRs combined and recommended that habitat conservation planners and managers adopt 18.39 kg(dry)/ha as a revised estimate for invertebrate biomass for naturally flooded forests, because this estimate was derived from landscape-scale sampling in the MAV and Mississippi Interior Flatwoods, was reasonably precise (CV = 15%), and less than 2% of remaining hardwood bottomland in the MAV is impounded GTRs.

In the northern extent of the MAV, Mingo NWR's NFF had greater invertebrate biomass than its paired GTR at Duck Creek. This result may be due to Mingo/Duck Creek's earlier phenological transition into autumn and flooding. Earlier and longer flooding could possibly promote anoxic conditions earlier in winter. We hypothesize that NFFs at both northern and southern latitudes had greater biomass because of temporally dynamic hydrologic regimes from precipitation events and overbank flooding that released nutrients and reduced anoxic conditions as NFF areas did not remain flooded most of fall-winter as did GTRs (Batema et

al. 1985, Wehrle et al. 1995). Natural processes like plant decay, leached metals (e.g., iron), and water potentially with low dissolved oxygen may have reduced invertebrate biomass in the GTR. Additionally, at Mingo/Duck Creek during winter 2009–10, NFF plots dried by mid-winter and were inaccessible to wintering waterfowl in the region. The GTR remained flooded, and waterfowl may have foraged upon and reduced invertebrate resources during winter (Foth 2011).

Similarly, in southern MAV, the NFF at DNF contained greater biomass than its paired GTR. The GTR was flooded in late fall and remained at relatively constant depths until drawdown began in February. Invertebrates likely colonized newly available forested wetlands in the GTR, and invertebrate abundance and biomass plateaued through January (Foth 2011). Conversely, hydrology in the NFFs at DNF also was dynamic temporally and spatially. Flood pulses during the study were short (i.e., 1–10 days) and periodic ($n=3-4$ per winter) and resulted in locally ponded areas after floodwaters receded. Localized ponding and drawdown likely created aerobic conditions for decomposition of litter and release of nutrients conducive to increasing invertebrate biomass.

Though somewhat ecologically different from the MAV sites, the GTR and NFF at Noxubee NWR had similar invertebrate biomasses. The lack of difference between the two flooding regimes may be related to the hydrology in the Noxubee River watershed. We collected invertebrates in the upper reaches of the Noxubee River and its associated bottomlands where it is classified as a third order river system (Vannote et al. 1980). The surrounding hardwood bottomlands contribute large amounts of allochthonous leaf and other detritus. When the Noxubee River overflows its banks, water disperses much leaf litter from the flood plain. The swift flood pulse may disperse litter and food resources of invertebrates and invertebrates themselves into the GTR. The GTR at Noxubee NWR functions as an impoundment with less dynamic hydrology compared to its contiguous NFF. During flood events, however, the GTR was flushed of stagnant water but received fresh water, leaf litter, and nutrients from the watershed. Therefore, we hypothesize that the impounded GTR may capture increased loads of allochthonous organic matter, fresh oxygenated water, and invertebrates that may account for the slight but non-significant increase (17%) in invertebrate biomass.

In conclusion, obviously, neither our study nor others previously could fully replicate historical hydrological dynamics of NFFs or impounded GTRs, nor compare historic with contemporary aquatic invertebrate communities relative to artificial and natural flooding regimes in these forested wetlands. Nevertheless, our contemporary comparison of invertebrate richness, diversity, and biomass during winter between NFFs and GTRs enhances our un-

derstanding of the possible effects of recent natural versus artificial flooding regimes on invertebrate communities and biomass and provides insights for management of these wetlands in the southeastern United States. Additionally, our sweep-net samples may have incompletely characterized aquatic invertebrate communities and biomass on our study areas, so there is need for future research to compare our invertebrate community compositions and biomasses with samples collected with sweep nets and core samplers for perhaps increased accurate collection of nekton and benthos. Despite these possible limitations, no previous study has compared aquatic invertebrate community ecology and biomass between NFFs and GTRs at a landscape scale in two ecoregions in the southeastern United States (i.e., MAV and Mississippi Interior Flatwoods).

Management Implications

Invertebrate community composition may be similar between GTRs and NFFs, but invertebrate diversity and biomass generally were greater in NFFs than GTRs. Although GTRs have less invertebrate biomass than NFFs, most invertebrate families (85%) were found within both flooding regimes. A GTR also provides consistent forested wetland for wintering waterfowl and waterfowl hunting opportunities. Pulses of fresh water along with dispersion of stagnant water in NFFs may allow invertebrate families that are sensitive to low pH, dissolved oxygen, and nutrient inputs to colonize, grow, and reproduce (Leslie et al. 2012). Therefore, mimicking NFF hydrologic regimes in GTRs by capturing rain and flood waters and periodic removal and addition of water-elevation boards from control structures may lead to increased invertebrate biomass and diversity in GTRs (Wehrle et al. 1995, Fredrickson 2005b, Foth et al. 2014). If managers flooded GTRs near the 10–40 cm depths and fluctuated water levels throughout winter, GTRs might function hydrologically more like NFFs. This may facilitate foraging by wintering waterfowl, especially dabbling ducks (Tribe: *Anatini*) using GTRs and NFFs. Hagy and Kaminski (2012) reported >90% of foraging dabbling ducks in moist-soil wetlands were associated with water depths <20 cm. Therefore, managers should provide shallower and dynamic water depths in managed forested wetlands (Fredrickson 2005b).

Acknowledgments

We thank A. Leach, K. Wigen, C. Asa, J. McInnis, K. Brock, and E. Interis for dedicated field assistance, processing samples in the laboratory, and providing continuous input. Additionally for assistance or support, we thank the USDA, Forest Service, Center for Bottomland Hardwoods Research, Stoneville, Mississippi; the U.S. Fish and Wildlife Service's Mingo and Noxubee NWRs, The Delta

National Forest, and the Missouri Department of Conservation's Duck Creek Conservation Area; the Mississippi State University Forest and Wildlife Research Center (MSU-FWRC); the James C. Kennedy Waterfowl and Wetlands Conservation Endowed Chair and Center at MSU; and Clemson University for provisions of Davis' and Kaminski's time, respectively. We also thank the Delaware Division of Fish and Wildlife for providing support for J. Foth's time and travel to present this manuscript. Finally, we thank the Journal reviewers and the subject editor for providing helpful input and improving our manuscript. Our manuscript has been approved for publication as MSU-FWRC Publication No. WFA406.

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