AQUATIC INVERTEBRATE BIOMASS AND COMMUNITY COMPOSITION IN GREENTREE RESERVOIRS AND NATURALLY FLOODED FORESTS IN THE MISSISSIPPI ALLUVIAL VALLEY AND INTERIOR FLATWOODS

By

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The Mississippi Alluvial Valley (MAV) contained vast bottomland hardwood forests into the 20th century. Humans cleared forests, and altered hydrology, yet the MAV remains important for North American waterfowl and other wildlife. To estimate standing crops of aquatic invertebrates as food in hardwood bottomlands for wintering waterfowl, I quantified dry mass of invertebrates in naturally flooded forests (NFFs) and greentree reservoirs (GTRs) during winters 2008–2010. The MAV had greater invertebrate mass in NFFs ($\bar{x}$ = 18.39 kg/ha; SE = 2.815 [CV = 15.3%]) than GTRs ($\bar{x}$ = 5.16; SE = 0.492 [CV = 9.5%]), compared with lesser masses in Mississippi Interior Flatwoods' GTR ($\bar{x}$ = 2.26; SE = 0.320) and NFF ($\bar{x}$ = 1.45; SE = 1.305). Invertebrate diversity was greatest in NFFs and in depths from 10–40 cm. Flooding GTRs ≤ 40 cm and managing naturally dynamic hydrology may benefit invertebrates, ducks, and associated bottomland hardwood communities.

Keywords: aquatic invertebrate, forested wetland, waterfowl, Mississippi Alluvial Valley

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CHAPTER I

AQUATIC INVERTEBRATE BIOMASS IN GREENTREE RESERVOIRS AND NATURALLY FLOODED BOTTOMLAND HARDWOOD FORESTS

Introduction

Until the 20th century, bottomland hardwood (BLHW) forests, other wetlands, and uplands, including forested ridges and prairies, covered most of the 10 million hectares of the Mississippi Alluvial Valley (MAV) from southern Illinois near the confluence of the Mississippi and Ohio Rivers southward into Louisiana (Cowardin et al. 1979, Reinecke et al. 1989, Fredrickson 2005*a*). During the 1950s–1970s, extensive removal of hardwoods for wood products and agriculture caused significant deforestation in the MAV (Sternitzke 1976, Schoenholtz et al. 2005). Additionally, channelization, wetland drainage, construction of flood control levees, and landscape modification for human use significantly altered natural hydrology and land coverage in the MAV (Reinecke et al. 1989, King et al. 2006). Today < 25 % of BLHW forested area remains (Twedt and Loesch 1999), but conservation initiatives are increasing the area of BLHWs (Fredrickson 2005*a*).

Before anthropogenic impacts in the MAV, forested wetlands had dynamic seasonal and annual hydroperiods, which typically vary in duration, frequency, and depth of flooding and influence productivity and biodiversity of these systems (White 1985,

Fredrickson 2005*a*). Bottomland hardwood forests are important for many wildlife species, because they are among the most productive plant communities on earth (Heitmeyer et al. 2005). Over 70 species of trees occur in BLHWs and more taxa of angiosperms, birds, mammals, reptiles, and amphibians thrive in BLHW in the MAV than elsewhere in the United States (Heitmeyer et al. 2005). Bottomland hardwood forests are especially important as wintering habitat for ducks (e.g., mallard, *Anas platyrhynchos;* wood duck *Aix sponsa*) because they provide energy- and protein-rich foods. Red oak (Genus: *Quercus*, Subgenus: *Erythrobalanus*) acorns are the primary source of energy for waterfowl in BLHW forests, and aquatic invertebrates (categorized as invertebrates identifiable without the aid of magnification Wehrle et al. 1995) supply protein and other nutrients for ducks and other wildlife in these forests when flooded (Dabbert and Martin 2000, Batema et al. 2005, Heitmeyer et al. 2005).

Leaf litter is an important component of BLHW's influence on the distribution and abundance of invertebrates, because it provides structural habitat and surface area for colonization of algae and microbes which provide food for invertebrates (Batema et al. 1985). Energy from leaf litter and associated microbes in BLHW systems is transferred first to a diverse group of invertebrates before being consumed by waterfowl (Fredrickson and Reid 1988, Batema et al. 2005). Protein-rich invertebrates nutritionally diversify diets of wintering ducks otherwise high in carbohydrates from native and agricultural seeds (Fredrickson and Taylor 1982, Delnicki and Reinecke 1986). Nutrients in invertebrates are important for building body mass for migration and for female ducks undergoing egg follicle development and winter-spring prebasic molt (Heitmeyer and Fredrickson 1990, Richardson and Kaminski 1992, Barras et al. 1996). Therefore,

estimating available waterfowl foods in habitat types (i.e., BLHW forests, agricultural fields, moist-soil impoundments) of the MAV is an objective of the Lower Mississippi Valley Joint Venture.

The mission of the Lower Mississippi Valley Joint Venture, of the North American Waterfowl Management Plan, is to implement goals and objectives of national and international bird conservation plans within the Lower Mississippi Valley region. One such goal is estimating foods available to wintering waterfowl. The Joint Venture has current estimates of food resources (i.e., agricultural grains, moist-soil seeds and tubers) available for wintering waterfowl at the scale of the MAV. Current estimates of winter foods available to waterfowl in BLHW forests in the MAV are based on information from a few sites (Batema et al. 2005, Reinecke and Uihlein 2006, Reinecke and Kaminski 2007, Murray et al. 2009). Another goal of the Joint Venture is to reduce uncertainty in estimates of foods for ducks in BLHW forests. Precise estimates (i.e., CV < 15%) of food available (i.e., invertebrate biomass) to wintering waterfowl in BLHW forests comparable to Stafford et al. (2006) and Kross et al. (2008) in rice and moist-soil respectively, will improve estimates of duck carrying capacity in the MAV. The evaluation of invertebrate biomass in flooded BLHW forests under different hydrological influences (i.e., natural vs. artificial flooding) could identify variables possibly influencing this food resource.

Ecologists have assessed use of green-tree reservoirs (GTR) and naturally flooded forests (NFF) by wintering waterfowl in the MAV (Sherman et al. 1995, Heitmeyer et al. 2005). A GTR is an area of BLHW forest surrounded partly or completely by a levee and artificially or naturally flooded in autumn-winter to provide forested wetland for

waterfowl (Reinecke et al. 1989). Whereas, NFFs are oak bottomlands that are not impounded and flood from natural hydrological events and exhibit less impact on the forest community, structure, and function (Wehrle et al. 1995, Fredrickson 2005*a*). Typically, GTRs were created in mature stands of red oaks which provide wintering ducks with flooded forested wetlands and hunters with duck hunting opportunities. Continuous flooding of GTRs leads to rapid turnover in the forest community from red oak to flood tolerant tree species due to extended hydroperiods.

Studies of invertebrate biomass and community composition in paired GTRs and NFF have been conducted at local (i.e., within state) but not regional scales (i.e., MAV wide; Batema 1987, Wehrle et al. 1995, Batema et al. 2005). Batema (1987) estimated invertebrate biomass at Mingo National Wildlife Refuge (NWR) and Duck Creek Conservation Area in Missouri in the early 1980's, Wehrle et al. (1995) estimated invertebrate biomass in two physiographic regions of Mississippi in the late 1980s, and Batema et al. (2005) summarized previous studies of invertebrates in forested wetlands. I investigated invertebrate biomass and community structure at the same study areas as Batema et al. (1987) and Wehrle et al. (1995) and expanded the scale of investigation to include other sites in the MAV. Specifically, my objectives were to (1) estimate dry mass (CV $\leq$ 15%) of invertebrates in NFFs and GTRs, (2) explain variation in winter biomass of invertebrates in relation to environmental and temporal factors, and (3) relate results to previous studies and make appropriate management recommendations.

Study Areas

Mingo National Wildlife Refuge and Duck Creek Conservation Area, Missouri

Mingo NWR and Duck Creek Conservation Area are adjoining properties managed by the U.S. Fish and Wildlife Service and Missouri Department of Conservation, respectively (hereafter Mingo/Duck Creek). Mingo/Duck Creek is located at the northern end of the MAV near Puxico, Missouri (36°N, 90°W; Fig. 1.1) in the Mingo Basin which is a former channel of the Mississippi River, 18,000–25,000 years ago, prior to the river cutting through Crowley's Ridge and flowing southward in its current course (Saucier 1970). The abandoned river channel became a fertile swamp underlain by Sharkey-Gideon clay alluvium (Soil Survey Staff 2008). The Mingo Basin receives an average 123 cm of precipitation annually, with November receiving the most rain on average (Batema 1987). Mingo/Duck Creek is presently segmented and drained by a ditching district, and water flow is managed and diverted into the St. Francis River. Mingo/Duck Creek is located within Stoddard, Bollinger, and Wayne counties in southeastern Missouri (Batema 1987). Mingo/Duck Creek is approximately 10,400 ha and contains the only remaining large tract of BLHW in the MAV in Missouri (Heitmeyer et al. 1989). Mingo/Duck Creek is composed of approximately 7,000 ha of BLHW, 2,100 ha of interspersed marsh and open water, 400 ha of croplands and 260 ha of seasonally flooded moist soil impoundments. The surrounding landscape is a mosaic of agricultural lands, bluffs, tall-grass prairie, and bottomland and upland forests. The GTRs present at Mingo/Duck Creek were developed during the 1940s; they contain approximately 60 % red oaks (*Quercus palustris, Q. phellos,* and *Q. pagoda*) of similar

age (70–80 years). Year round flooding of the GTRs in the 1940s and 1950s reduced the original BLHW coverage of 1,058 ha to about half its size in ~ 10 years (Fredrickson 2005*a*). Currently, flooding of the GTRs occurs in late October to early November and full pool is reached by mid- to late November. The pools remain at stable depths until drawdown in early February.

White River National Wildlife Refuge, Arkansas

White River NWR is managed by the U.S. Fish and Wildlife Service and is located near St. Charles, Arkansas (34°N, 91°W; Fig. 1.1). It encompasses a 145 km stretch of the lower 160 km of the White River near its confluence with the Mississippi River. The refuge is located within portions of Arkansas, Desha, Monroe, and Phillips counties, Arkansas. A large portion of the refuge is situated between levees and the White River, enabling the natural hydrology to remain intact through short duration and frequent flooding. Soils at White River NWR are mostly Kobel and Sharkey silty clays, which are productive alluvial soils (Soil Survey Staff 2008). White River NWR receives an average 130 cm of precipitation per year, with December being the wettest month. It is presently the largest public land BLHW tract in the MAV, covering approximately 64,750 ha (Oli et al. 1997). Its composition is approximately 62,300 ha of BLHW, 1,600 ha of marsh and open water, 770 ha of crop and grasslands. Average stand age for trees within my study plots was 70–80 years old and 30–40 % red oak (e.g., mostly *Q. texana*).

Delta National Forest, Mississippi

Delta National Forest (DNF) is managed by the U. S. Department of Agriculture Forest Service and is the only national forest which is exclusively BLHW in the United States. The DNF is composed of over 24,000 ha of BLHW interspersed with palustrine wetlands (Lowney and Hill 1989). It is located 23 km southeast of Rolling Fork, Mississippi (32°N, 90°W; Fig. 1.1) in Sharkey County in west-central Mississippi (Reinecke et al. 1989, Wehrle et al. 1995). The Sunflower and Little Sunflower Rivers and their adjacent floodplains are the major hydrological features in DNF. Both rivers are tributaries of the Yazoo River, and periodically cause overbank flooding of parts of DNF during winter and early spring. The floodplain is poorly drained and retains local ponding for extended periods because of extant Sharkey clay alluvium soil (Soil Survey Staff 2008). The DNF receives an average 145 cm of precipitation annually, with April being the wettest month. There are approximately 2,000 ha of GTRs in DNF. Impoundments are flooded between mid- to late November and remain at full pool until drained in February. The BLHW trees in the Sunflower GTR are approximately 75–80 years old and are comprised of approximately 40 % red oaks (*Q. texana* and *Q. phellos*).

Noxubee National Wildlife Refuge, Mississippi

Noxubee NWR is managed by the U.S. Fish and Wildlife Service and is located in the Interior Flatwoods (IF) Region in east-central Mississippi (Pettry 1977, Wehrle et al. 1995). The refuge is located 25 km south of Starkville, Mississippi (33°N, 88°W; Fig. 1.1). Major hydrological features of Noxubee NWR include the Noxubee River, its tributaries, and Bluff and Loakfoma Lakes. The Noxubee River meanders through the

refuge and retains a natural and dynamic hydrology, and soils generally are fine sandy loams (Soil Survey Staff 2008). Noxubee NWR receives on average 142 cm of precipitation per year, with April being the wettest month. The refuge is approximately 19,400 ha and is composed of approximately 18,000 ha of BLHW and upland forest and 950 ha of seasonally flooded impoundments. There are 4 GTRs at Noxubee NWR, I sampled in GTR1 which was constructed in the 1960s and is flooded generally each year from late November-February. The forest stand in GTR1 is approximately 65–75 years old and is comprised of approximately 35 % red oaks (*Q. pagoda, Q. phellos,* and *Q. nigra*).

Methods

Invertebrate sampling

I collected samples within spatially balanced research plots from study sites in the MAV and IF during winters 2008–2010. At Mingo/Duck creek, I sampled invertebrates in winter 2009–2010 in GTR Pool 2 in Duck Creek Conservation Area and in NFFs within Mingo NWR wherein Batema (1987) also sampled in the 1980s. At White River NWR, I sampled invertebrates in winter 2009–2010 within spatially balanced research plots throughout the NFF. I did not sample from a GTR because one did not exist at this location. At DNF, I collected invertebrate samples in the East and West compartments of the Sunflower GTR in winters 2008–2009 and 2009–2010, respectively, wherein Wehrle et al. (1995) also sampled in the late 1980s. My NFF samples were collected where seasonal flooding occurred outside of GTRs near the 740 road in 2008–2009, wherein

Wehrle et al. (1995) also sampled in the late 1980s. I collected samples from flooded spatially balanced research plots in 2009–2010 within the NFF. At Noxubee NWR, I collected samples in winters 2008–2010 from GTR 1. The Noxubee River overflowed its banks only in winter 2008–2009; thus, I collected samples in the NFF that winter.

I selected 10, 0.2–ha, circular sampling plots within each paired GTR and NFF. I chose 10 plots per flooding regime to expedite sample collection and processing because I collected multiple sweep net samples per plot. I used a generalized random tessellation stratified spatial design to spatially balance plot centers within GTRs and NFFs (Stevens and Olsen 2004). I implemented this sampling strategy to minimized possible effects caused by the variation within the forest floral community. I used ArcGIS 9 ArcMap version 9.2 to generate sampling areas 0.05–0.32 km from roads or right of ways to expedite access to flooded forest land representative of the study area, using guidance from biologists or managers at each area. I used a commercially available rectangular sweep net (23 x 45 cm, 500 µm mesh) to collect invertebrates from the substrate upward through the water column (Murkin et al. 1994, Wehrle et al. 1995, Gray et al. 1999). I used a sweep net to enable comparison of my data with those of Wehrle et al. (1995), who sampled invertebrates in some of the same GTRs and NFFs in the 1980s. Moreover, sweep nets more accurately sample invertebrate communities than do core or plankton-net samplers in BLHW forests (Cheal et al. 1993, Gray et al. 1999). Additionally, I collected data at each sampling location on environmental factors possibly influencing invertebrate biomass (i.e., water depth, water temperature, dissolved oxygen, pH). I used a meter stick to record water depth and other factors were recorded with an YSI 550A

handheld dissolved oxygen instrument. I only analyzed water depth because of equipment failure during data collection of other factors.

I attempted to take 4 samples in each of the 10 circular plots within GTRs and NFFs (n = 40), but all plots were not inundated during my sampling episodes so I sampled ≥ 5 flooded plots to ensure at least 20 sweep net samples per GTR or NFF. A randomly generated number from 1 to 360 provided a compass azimuth for initial sample site selection within each plot. I obtained each subsequent sample location within plots 90 degrees right of the previous location. If plots were partially flooded, I collected samples only on random bearings within the flooded portion of the plot. I collected samples during winters 2008–2009 (n = 235) and 2009–2010 (n = 556) except when sites were not flooded or flooded too deeply to enable access (Table 1.1). I froze samples on site soon after collection and stored them in a freezer until transport to a laboratory at Mississippi State University because other common forms of preservation (i.e., 10% formalin solution) were not feasible.

Sample preservation and processing

I stored all samples in a freezer at -10˚ C to preserve invertebrate biomass and other organic matter from decomposition (Murkin et al. 1994, Stenroth and Nyström 2003). I used an initial set of 88 samples in an experiment to test if sucrose and water, salt and water, and tap water alone (control) differentially floated invertebrates for ease of detection and enumeration (Flannagan 1973, Kaminski and Prince 1981). I did not detect a difference in recovery rates of invertebrates among floatation media ($F_{2,68}$ = 0.186, P = 0.831) and hence used tap water to process all remaining samples (J. Foth, Mississippi

State University, unpublished data). I placed thawed samples in a bucket containing approximately 2 L of warm tap water and agitated contents by hand for 30 sec to disassociate invertebrates from leaf litter. I laid horizontally a plastic half-cylinder, with 1.5 cm diameter apertures (large sieve) into a 500 µm sieving bucket and poured the sample into the bucket to separate leaf litter, invertebrates attached to litter, and other organic matter from floating invertebrates. I poured invertebrates and other material passing through the large sieve into the sieve bucket in a plastic bag and I also placed plant matter remaining on the large sieve into another bag. I removed invertebrates by hand from both portions of the sweep net sample, and counted and sorted invertebrates to Family (Pennak 1989, Merritt and Cummins 2008). I dried invertebrates in an oven at 60º C for 18–24 hours to a constant mass (Murkin et al. 1994) and then weighed each Family to the nearest 0.0001g.

I separated leaf litter and other organic matter from invertebrates remaining in the large sieve. Initially, I removed 20–30 leaves randomly from each sample and rinsed each leaf in water to remove attached invertebrates, identified each leaf to species, and determined species-specific abundance of leaves per sample. I next calculated percentage of red oak leaves in each sample because red oaks are economically important, provide important waterfowl forage (i.e., acorns), and forest type influences nutrient exchange in BLHW forests (Batema et al. 2005). I dried all leaf and organic matter at 60° C for 12 hours. Having a weight of dry mass litter may be influential in explaining invertebrate biomass because invertebrates glean algal and microbial biomass from their surfaces.

Statistical analyses

Invertebrate biomass in paired greentree reservoirs and naturally flooded forests

I only used data from spatially and temporally paired samples from GTRs and NFFs at the same site (Table 1.1) because I was interested in possible differences in invertebrate biomass between flooding regimes. I used factorial analysis of variance (ANOVA) in Program R version 2.11.0 to test if invertebrate biomass (dry mass; kg/ha and mg/m^3) varied with study area, flooding regime, sampling period, or the interaction of study area and flooding regime. Specifically, independent variables included study area (i.e., Mingo/Duck Creek, DNF, and Noxubee NWR), flooding regime (GTR and NFF), and sampling period (early winter [November – December] and late winter [January – February]). I grouped samples into early and late winter, because monthly numbers of samples were unbalanced (n = 116, November; n = 273, December; n = 210, January; n = 192, February). Invertebrate mass data to was natural log transformed to normalize distributions and correct heterogeneous variances (Quinn and Keough 2002). However, separate analyses of transformed and raw data yielded similar outcomes, so I present results herein from analyses of raw data. To account for unequal variances between sites and flooding regimes, I used a WEIGHT statement in the *lme* package. I compared Akaike's information criterion corrected (AIC_C) values between models with equal and unequal variances and determined that models with unequal variances had superior fit to the data (Akaike 1974, Zurr et al. 2009). Because I typically collected multiple sweep net samples within a plot, I suspected possible violation of independence among sampling units. Therefore, I calculated degree of independence among samples

within plots (e.g., intra-class correlation coefficient), and compared a mixed model that included Plot ID as a random effect and a model without Plot ID as a random effect using hypothesis testing ($\alpha = 0.05$). Although, I found small intra-class correlation (0.008), indicating sweep-net samples of invertebrate biomass within plots were correlated weakly (Zurr et al. 2009), hypothesis testing revealed the model with Plot ID as a random effect improved model fit ($P < 0.001$, $n = 431$). Therefore, I treated individual sweep samples as primary sampling units and accounted for any lack of independence within plots by using a random effect of Plot ID (Zurr et al. 2009).

I also used a mixed model ANOVA to test if invertebrate biomass (kg[dry]/ha) was related to covariates measured at sample sites, including red oak leaf mass, water depth, and leaf species richness. I performed this test without including study site and flooding regime as explanatory variables, because I was interested in these possible relationships across study sites. I encountered unequal variances in invertebrate biomass among regions and sampling period and accounted for heterogeneity using a WEIGHT statement in the *lme* package. I again treated Plot ID as a random effect and tested if invertebrate biomass varied with the aforementioned covariates. After all models were run, I compared AIC_C scores (Burnham and Anderson 2002) with the *MuMIn* package in Program R. I considered models with $\Delta AIC_C \leq 2$ as competitive and $\Delta AIC_C = 0$ as the model explaining most variance in invertebrate biomass (Burnham and Anderson 2002).

Site-specific and Mississippi Alluvial Valley-wide invertebrate biomass

I pooled invertebrate biomass data across GTRs and NFFs at each paired site to generate site-specific estimates of invertebrate biomass. Additionally, I report only NFF

data across sites to generate a MAV-wide estimate because GTRs contribute only 1-2% of total BLHW forests. I generated means, standard errors, and coefficients of variation for invertebrate biomass (kg/ha and mg/m^3). I used sweep net samples as my sampling unit because previous analysis revealed improved model fit when Plot ID was random.

Results

Invertebrate biomass in paired greentree reservoirs and naturally flooded forests

Invertebrate biomass data (kg/ha and mg/m^3) were right skewed and exhibited heterogeneous variances (kg/ha [F = 15.975, P < 0.001, GTR n = 273, NFF n = 158] and mg/m^3 [F = 48.940, P < 0.001, GTR n = 273, NFF n = 158]). Therefore, I natural log transformed invertebrate biomass data but analyzed transformed and raw data. Both analyses resulted in same statistical outcomes, so I presented analyses of raw data only. I did not include year as a fixed effect in my analysis, because I was not able to explain unequivocally any detected yearly variation in invertebrate biomass. Additionally, GTRs and NFFs were not always flooded concurrently during winters 2008–2010. Thus, my results are from sampling events when GTRs and NFFs were flooded.

I detected a flooding regime by site interaction for invertebrate biomass when analyzed on an areal scale (i.e., kg/ha; $F_{2, 66}$ = 6.356, P = 0.003). Specifically, I detected invertebrate biomasses to be greatest 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 = 1.1527, n = 155]; Mingo/Duck Creek [$\bar{x}$ = 5.23 kg/ha, SE = 1.820, n = 40]). Invertebrate biomass did not

differ between northern and southern MAV sites (Fig. 1.2). At Noxubee NWR, however, invertebrate biomass was slightly greater (17%) in the GTR ($\bar{x}$ = 1.32 kg/ha, SE = 0.226, n = 78) than the NFF ($\bar{x}$ = 1.12 kg/ha, SE = 0.951, n = 41; Fig. 1.2).

I also found a flooding regime by site interaction for volumetrically scaled invertebrate biomass (mg/m^3; $F_{2, 66}$ = 10.166, P < 0.001). Invertebrate biomass was greatest in NFFs at DNF ($\bar{x}$ =127.44 mg/m^3, SE =37.5684, n = 101) and Mingo/Duck Creek ($\bar{x}$ = 195.27 mg/m^3, SE = 102.725, n = 16) compared to their paired GTRs (DNF [$\bar{x}$ =21.19 mg/m^3, SE = 4.611, n = 155]; Mingo/Duck Creek [$\bar{x}$ = 23.25 mg/m^3, SE = 7.29, n = 40]). Similar to area-based estimates, invertebrate biomass at Noxubee NWR was 1.35 times greater in the GTR ($\bar{x}$ = 6.41 mg/m^3, SE = 1.268, n = 78) than the NFF ($\bar{x}$ = 4.72 mg/m^3, SE = 3.792, n = 41; Fig. 1.3).

I modeled variation in invertebrate biomass (kg/ha) relative to measured covariates and region (i.e., MAV or IF). The additive model of red oak leaf mass, region, and sampling period explained most variation in invertebrate biomass (ω_i = 0.373; Table 1.2). Additionally, I considered the additive model containing red oak leaf mass, region, water depth, and time period competitive with the previous model (ω_i = 0.251), because it was ≤ 2 ΔAIC_C units of the best model.

Invertebrate biomass in BLHW forests in the MAV and IF varied temporally during winters 2008–2010. In early winter (November – December), mean invertebrate biomass was 2.89 kg/ha in the IF and 9.89 kg/ha in the MAV. In late winter (January – February), invertebrate biomass decreased slightly in the IF (1.55kg/ha) and MAV (7.56kg/ha; Fig. 1.4). Invertebrate biomass at sample sites varied positively with dry mass of red oak leaves (Fig. 1.5). The next best model contained the same explanatory

variables plus water depth. I detected a slightly negative relationship between invertebrate biomass and water depth.

Site-specific and Mississippi Alluvial Valley-wide invertebrate biomass

Delta National Forest contained the greatest overall invertebrate biomass across both winters ($\bar{x}$ = 9.02 kg/ha, SE = 1.183, *n* = 368). White River NWR had the greatest invertebrate biomass in winter 2009–2010 ($\bar{x}$ = 18.0 kg/ha, SE = 3.740) but number of samples obtained there were small (*n* = 28) because of inaccessibility due to flooding. Noxubee NWR had the least invertebrate biomass over both winters ($\bar{x}$ = 2.13 kg/ha, SE = 0.338, *n* = 259). The MAV-wide estimate of invertebrate biomass for NFFs and years combined was $\bar{x}$ = 18.39 kg/ha (SE =2.814, CV = 15.30%, *n* = 145; Table 1.3). When I combined data across regions, flooding regime, and years, the estimate of invertebrate biomass was increasingly precise (CV = 9%; Table 1.3).

Similarly, I tested invertebrate biomass volumetrically (Table 1.2). Delta National Forest had the greatest invertebrate biomass across both winters ($\bar{x}$ = 1056.08 mg/m^3, SE = 261.983, *n* = 368). The second sampling year differed in greatest biomass between the kg/ha estimate and the mg/m^3 estimate. Noxubee NWR contained the least invertebrate biomass when both winters were combined ($\bar{x}$ = 281.78 mg/m^3, SE = 87.713, *n* = 259). To generate a MAV-wide estimate, I combined NFF data across years and calculated an estimate of mean invertebrate biomass which I deemed precise ($\bar{x}$ = 18389.93 mg/m^3, SE = 2814.65, CV = 15.31%, *n* = 145; Table 1.3). For MAV and IF data across sites years, the estimate of invertebrate biomass was increasingly precise (CV = 10%; Table 1.3).

Discussion

Bottomland hardwood forests remained expansive wetlands into the early 20th century in the MAV and currently exist in remnant patches with varied hydrology and management (Fredrickson 2005*b*). Forests in the MAV are managed as artificially flooded GTRs (Fredrickson 2005*b*) or as NFFs along major waterways. I found that invertebrate biomass differed between GTR and NFF flooding regimes and between MAV and IF regions (Fig. 1.4). The NFFs had greater invertebrate biomass in the MAV at Mingo/Duck Creek and DNF but invertebrate biomass did not differ between northern and southern MAV sites. I found NFFs to have greater invertebrate biomass than their paired GTRs at all but one site. Unlike Mingo/Duck Creek and DNF, Noxubee NWR had slightly greater invertebrate biomass in the GTR.

Wehrle et al. (1995) reported a similar trend for invertebrate biomass in Mississippi GTRs and NFFs. My invertebrate biomass mean values (kg/ha) are less than half of Wehrle et al. (1995) reported range of mean values. Differences in biomass between studies may be due to possible differences in methodologies (e.g., person taking the sweep sample, distance sampled with dip net, frequency of sampling round) and not due to potentially missed taxa because we both collected similar taxa. My biomass estimates are conservative because the actual recovery rate of invertebrates with a sweep net is unknown, invertebrates are mobile and potentially avoid the net, and benthic invertebrates were not collected from the substrate. Thus, mean values I report are negatively biased compared to actual available food to wintering waterfowl in BLHW forests and could potentially explain differences with previously published work.

In the northern extent of the MAV, Mingo/Duck Creek's NFF had greater invertebrate biomass than its comparable GTR. This relationship in lesser biomass in the GTR may be due to Mingo/Duck Creek's seasonal transition into autumn sooner, which allows area managers to flood impoundments longer possibly creating anoxic conditions earlier in winter. I hypothesize that NFFs had greater biomass because of temporally dynamic hydrology from precipitation events and overbank flooding, which released nutrients and minimized anoxic conditions because NFF areas did not remain flooded most of fall-winter as did GTRs (Batema et al. 1985, Wehrle et al. 1995). Natural processes like decaying plant matter, leached metal (e.g., iron), and stagnant water may have affected biomass in a GTR. At Mingo/Duck Creek during winter 2009–2010, NFF plots dried by mid-winter and were inaccessible to wintering waterfowl in the region. The GTR was filled and maintained at a constant depth throughout late fall-winter which provided consistent habitat for wintering ducks which may have foraged and reduced invertebrate resources.

Similarly in southern MAV, the NFF at DNF contained greater biomass than its paired GTR. The GTR was flooded early in winter and remained at constant depth until drawdown in February (Fig. 1.6). Invertebrates likely colonized newly available forested wetlands in the GTR and invertebrate abundance and biomass plateaued through January. Conversely, hydrology in the NFFs at DNF also was dynamic temporally and spatially. Flood pulses were brief (e.g., 1–10 days) and frequent (n = 3–4 per winter) and resulted in locally ponded areas after floodwaters receded. In the GTR, localized ponding and drawdown likely created aerobic conditions for decomposition of litter and release of nutrients conducive to increase invertebrate populations (Fig. 1.2).

Compared to the MAV sites, the GTR at Noxubee NWR had greater invertebrate biomass than its adjacent NFF. The reversal in pattern of greater biomass in the GTR than the NFF may be related to the hydrology in the Noxubee River watershed. I collected invertebrates in the upper reaches of the Noxubee River and its associated bottomlands. The surrounding hardwood bottomlands contribute large amounts of allochthonous leaf and other detritus (Vannote et al. 1980). 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. The GTR at Noxubee NWR functions as an impoundment with less dynamic hydrology compared to the associated NFF. During flood events, however, the GTR was flushed of stagnant water and received fresh water, leaf litter, and nutrients from the watershed. Thus, I hypothesize that the impounded GTR may capture increased loads of allochthonous organic matter and fresh, well oxygenated water that may stimulate invertebrate populations to increase in abundance and mass.

Differences in flood regimes and agricultural practices of the two regions probably played a role in determining invertebrate foraging structure, population and community dynamics, and biomass. Soil and water fertility is greater in the MAV compared to the IF (Wehrle et al. 1995) because the MAV is primarily fertile alluvial Sharkey clays whereas Noxubee NWR's flood plain consists of fine sandy loams (Soil Survey Staff 2008). Also, study sites in the MAV may have greater inputs of nitrogen and phosphorus, sediments, and pollutants than the IF site, because the MAV is a highly modified agricultural landscape. Inputs of nitrogen and phosphorus may influence algal and microbial growth and boost primary production. The IF around Noxubee NWR has

had little row crop agriculture since the late 1980s and consists of primarily livestock grazing and silvicultural lands (U.S.D.A. 2007). Therefore, added nutrients and increased site fertility may be a factor influencing the MAV's substantially greater invertebrate biomass compared to the IF site.

Invertebrate biomass at all study sites increased as winter progressed until peaking in January. If I continued sampling into spring, another pulse of invertebrate biomass may have been observed. Similar to BLHW forest systems, Manley et al. (2004) found invertebrate densities to increase through winter in MAV rice fields. Other studies throughout the MAV have documented fluctuations in invertebrate biomass from autumn to spring (White 1985, Duffy and LaBar 1994, Hagy 2010). Seasonally dynamic invertebrate populations provide wildlife with abundant renewing food resources during important annual cycle events.

Management and Research Implications

Few food studies at specific locations in the MAV (Batema et al. 1985, Wehrle et al. 1995, Heitmeyer 2006) are driving the North American Waterfowl Management Plan Lower Mississippi Joint Venture's decisions on the value of BLHW forests for wintering waterfowl. Food values for all habitat types of the Lower Mississippi Alluvial Valley are presented in Table 5 of the Joint Venture's current management recommendation (Reinecke and Uihlein 2006, Reinecke and Kaminski 2007). They recommend using a value of 11.4 kg/ha for invertebrate biomass in BLHW forests for conservation planning which is less than my mean and standard errors of invertebrate biomass estimate for winter in NFFs ($\bar{x}$ = 18.39 kg[dry]/ha, SE = 2.815). Concurrent studies on acorn

production and availability along with my invertebrate biomass estimate will strengthen estimates for BLHW food resources for wintering waterfowl especially mallards and wood ducks.

Two fundamentally different flooding regimes of forested wetlands occur in the MAV. A GTR is a manmade impoundment that is artificially or naturally flooded, whereas NFFs are forest lands that lack artificial impoundment and flood naturally. In the MAV, GTRs contribute little (1-2%) to the overall area of BLHWs but are reliable sources of water and food resources for wintering waterfowl especially in drought years. Current management of GTRs benefit ducks and duck hunters (Fredrickson 2005*b*). Flooding a GTR in fall before tree dormancy occurs and to a depth where maneuvering boats is feasible is probably not beneficial to foraging waterfowl, because ducks may not be able to access seeds and invertebrates at depths > 40cm (Fredrickson 2005*a*). Flooding a GTR more shallowly (i.e., 10–40 cm vs. ≥ 1 m) may benefit invertebrate populations and foraging waterfowl. For example, Hagy (2010) reported that most (>90%) mallards and other dabbling ducks foraged in moist-soil wetlands in the MAV amid water depths ≤ 16 cm. A GTR flooded to a depth of 10–40 cm with periodic fluctuation of water depth to mimic natural hydrology may reduce the possibility of food resources becoming inaccessible to wintering waterfowl. I also found the invertebrate community to be most diverse at those depths (Chapter 2).

Management focused on waterfowl and forest health and regeneration in GTRs may increase waterfowl use and hunter satisfaction (Reinecke et al. 1989). Mimicking natural hydrological events in actively managed GTRs provides habitats and wet-dry cycles beneficial for invertebrate survival and reproduction (Batema et al. 2005).

Fluctuating water depth and duration of flooding in a GTR would be beneficial to waterfowl because I found invertebrate biomass to be greater in NFFs compared to GTRs at my MAV sites. However, an intensive management strategy in GTRs may not be feasible with the rising cost of diesel fuel ($\bar{x}$ = \$3.12/gal 2010; $\bar{x}$ = \$3.52/gal 2011). A complex of GTRs with successive gravity fed flooding from one pool to the next would reduce pumping costs and mimic historical flood pulses. Also, if a single GTR was present on site, removal of boards in water control structures during natural flood events and replacement of boards before cessation of the flood event would fluctuate water levels and mimic a dynamic hydroperiod. This may benefit invertebrate populations and communities in GTRs, because it mimics historic hydrological regimes, releases new food and nutrient resources, and reduces anoxic conditions. However, to my knowledge, none of these intensive management strategies have been evaluated experimentally.

Depending on ability of managers to move water in the landscape, having a cluster of GTRs or the periodic fluctuation of water levels in a single GTR to emulate a NFF system would minimize BLHW food resources becoming unavailable to wintering waterfowl. In forested wetlands, invertebrate biomass is difficult to predict at any one point in time but is low cost resource to provide. Invertebrates have minimal basic requirements (i.e., detritus, water) and often produce quick yields of food resources. Additionally, invertebrate biomass cycles through dynamic increases and decreases throughout winter, making them a renewable food resource for waterfowl.

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Table 1.1 Numbers of plots and sweep net samples for aquatic invertebrates collected in greentree reservoirs (GTR) and naturally flooded bottomland hardwood forests (NFF) in study areas during winters 2008–2010.

			GTR		NFF	
Study area	Year	Month	*n* plots	*n* sweep	*n* plots	*n* sweep
Mingo/Duck Creek, Missouri	2009	November	10	40	5	16
		December	10	40	*a*	
	2010	February	10	40		
White River National Wildlife Refuge, Arkansas	2009	December			7	28
Delta National Forest, Mississippi	2008	December	10	40		
	2009	January	10	35	4	9
		February	8	32		
		November	10	40		
		December	10	40	8	32
	2010	January	10	40	5	20
		February	10	40	10	40
Noxubee National Wildlife Refuge, Mississippi	2008	December	10	38	6	15
	2009	January	10	40	8	26
		November	5	20		
		December	10	40		
	2010	January	10	40		
		February	10	40		

[a] No samples collected due to lack of flooding, frozen wetlands, or deep flooding.

Table 1.2 *A priori* candidate models examined to explain variation in aquatic invertebrate biomass (kg/ha [dry]) in bottomland hardwood systems in the Mississippi Alluvial Valley and Interior Flatwoods, Mississippi during winters 2008–2010. Models were ranked by Akaike's Information Criterion corrected (AIC_C) and includes number of estimable parameters (K) and model weight (ω_i).

Model	K	AIC_C	ΔAIC_C	ω_i
RO Leaf Mass + Region + Time Period	9	6309.3	0.0	0.373
RO Leaf Mass + Region + Water Depth + Time Period	10	6310.1	0.8	0.251
Region + Time Period	8	6311.2	1.9	0.142
RO Leaf Mass + Region + Leaf Species Richness + Water Depth + Time Period	11	6311.5	2.2	0.124
Region * Time Period	9	6313.1	3.9	0.054
Region	7	6315.1	5.8	0.021
Region * Leaf Species Richness	9	6315.2	5.9	0.019
Region + Leaf Species Richness	8	6316.0	6.8	0.013
RO Leaf Mass	7	6320.3	11.0	0.001
Water Depth * Time Period	9	6321.6	12.4	0.001
RO Leaf + Water Depth	8	6322.1	12.8	0.001
Time Period	7	6322.1	12.8	0.001
RO Leaf * Water Depth	9	6323.0	13.7	0.000
Water Depth + Time Period	8	6323.2	13.9	0.000
null	6	6325.8	16.5	0.000
Leaf Species Richness	7	6327.1	17.8	0.000
Water Depth	7	6327.9	18.6	0.000

Table 1.3 Mean ($\bar{x}$) biomass (kg[dry]/ha and mg[dry]/m^3) of aquatic invertebrates, standard errors (SE), and coefficient of variations (CV) estimated from sweep net samples (*n*) taken in bottomland hardwood forests (greentree reservoirs and naturally flooded forests combined) in the Mississippi Alluvial Valley (MAV) and Interior Flatwoods Region in Mississippi during winters 2008–2010 (November – February).

			kg/ha			mg/m^3		
Winter	Study area	*n*	$\bar{x}$	SE	CV (%)[a]	$\bar{x}$	SE	CV (%)[a]
2008–2009	Delta National Forest, Mississippi	116	6.41	1.41	22.03	3221.34	796.76	24.73
	Noxubee National Wildlife Refuge (NWR), Mississippi	119	1.34	0.46	34.22	599.68	187.14	31.21
2009–2010	Mingo/Duck Creek, Missouri	136	6.20	0.97	15.58	46.67	10.09	21.62
	White River NWR, Arkansas	28	18.00	3.74	20.78	120.88	23.62	19.54
	Delta National Forest, Mississippi	252	10.22	1.60	15.63	793.78	256.27	32.29
	Noxubee NWR, Mississippi	140	2.81	0.48	17.23	11.57	1.94	16.77
2008–2010	Delta National Forest, Mississippi	368	9.02	1.18	13.12	1056.08	261.98	24.81
	Noxubee NWR, Mississippi	259	2.13	0.34	15.85	281.78	87.71	31.13
	MAV	145	18.39	2.81	15.30	18389.93	2814.65	15.31
2008–2010	Winters and areas combined	791	6.60	0.61	9.30	38.89	4.12	10.59

[a] CV = (SE/ $\bar{x}$)*100.

Figure 1.1 Study areas (red) within the Mississippi Alluvial Valley (shaded region) and Interior Flatwoods where aquatic invertebrates were collected in bottomland hardwood forests during winters 2008–2010.

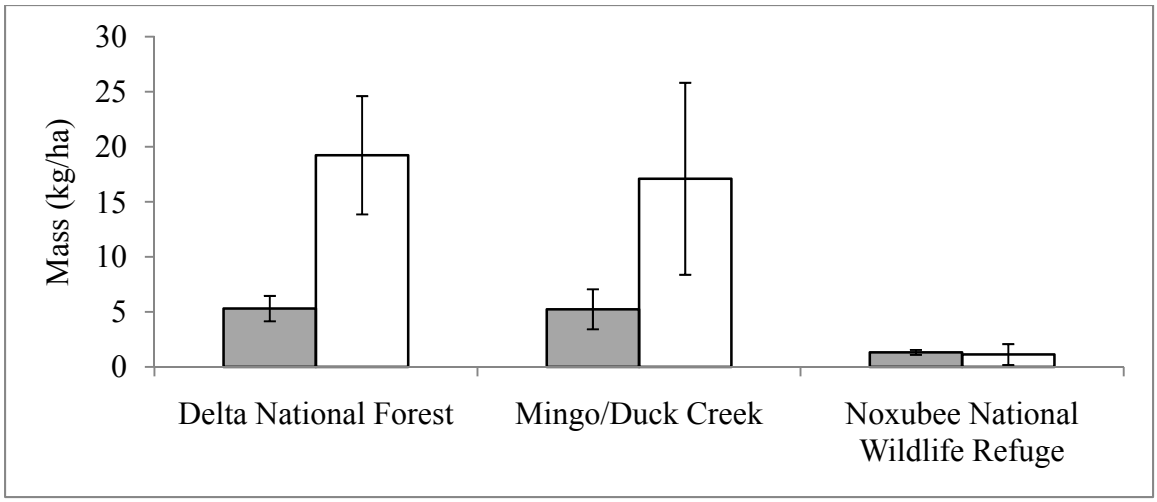

Figure 1.2 Aquatic invertebrate biomass (kg[dry]/ha; ± SE) in greentree reservoir (GTR; ■) and naturally flooded forests (NFF; □) at Delta National Forest ([GTR $\bar{x}$ = 5.297], [NFF $\bar{x}$ = 19.231], *n* = 368; Mississippi), Mingo/Duck Creek ([GTR $\bar{x}$ = 5.2342], [NFF $\bar{x}$ = 17.091], *n* = 136; Missouri), and Noxubee National Wildlife Refuge ([GTR $\bar{x}$ = 1.317], [NFF $\bar{x}$ = 1.122], *n* = 259; Mississippi) during winters 2008–2010.

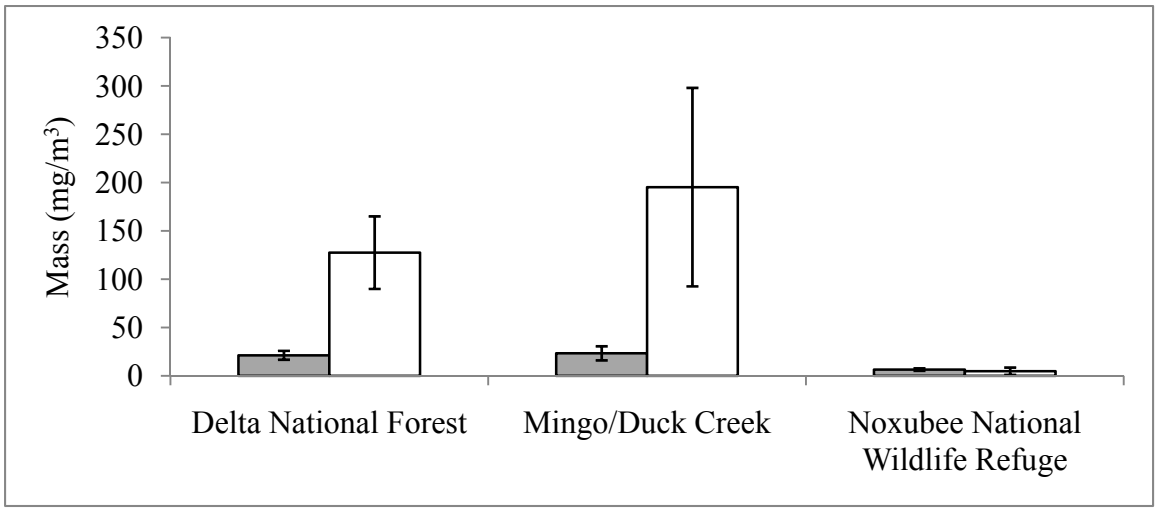

Figure 1.3 Aquatic invertebrate biomass (mg[dry]/m^3; ± SE) in greentree reservoir (GTR; ■) and naturally flooded forests (NFF; □) at Delta National Forest ([GTR $\bar{x}$ = 21.193], [NFF = $\bar{x}$ = 127.441], *n* = 368; Mississippi), Mingo/Duck Creek ([GTR $\bar{x}$ = 23.284], [NFF = $\bar{x}$ = 195.273], *n* = 136; Missouri), and Noxubee National Wildlife Refuge ([GTR $\bar{x}$ = 6.406], [NFF = $\bar{x}$ = 4.721], *n* = 259; Mississippi) winters 2008–2010

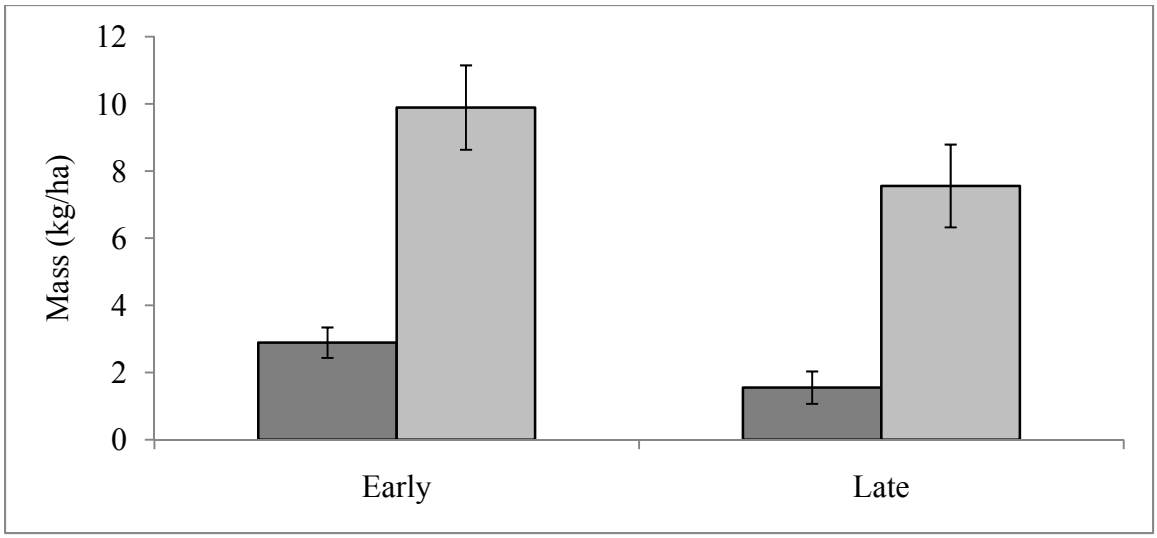

Figure 1.4 Aquatic invertebrate biomass (kg[dry]/ha) in bottomland hardwood forests (i.e., greentree reservoirs and naturally flooded forests combined) in early (November – December) and late (January – February) winters 2008–2010 in the Mississippi Alluvial Valley (early [$\bar{x}$ = 9.89, n = 276]; late [$\bar{x}$ = 7.56, n = 256]; ■) and Interior Flatwoods, Mississippi (early [$\bar{x}$ = 2.89, n = 113]; late [$\bar{x}$ = 1.55, n = 146]; ■).

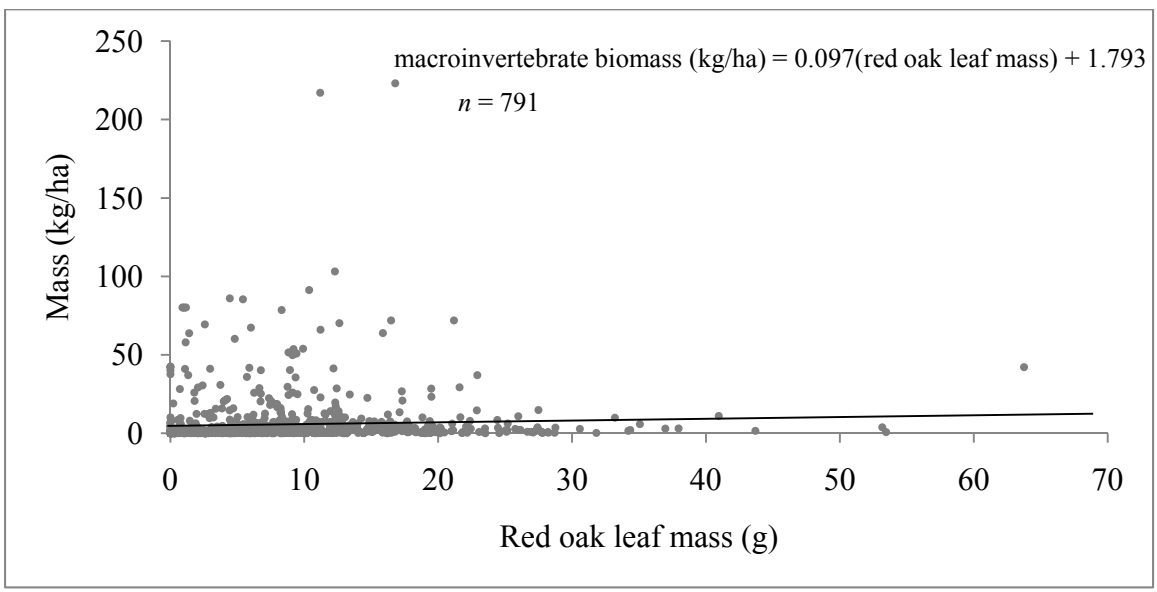

Figure 1.5 Relationship between aquatic invertebrate biomass (kg[dry]/ha) and red oak leaf mass in bottomland hardwood forests (greentree reservoirs and naturally flooded forests) in the Mississippi Alluvial Valley and Interior Flatwoods, Mississippi, winters 2008–2010.

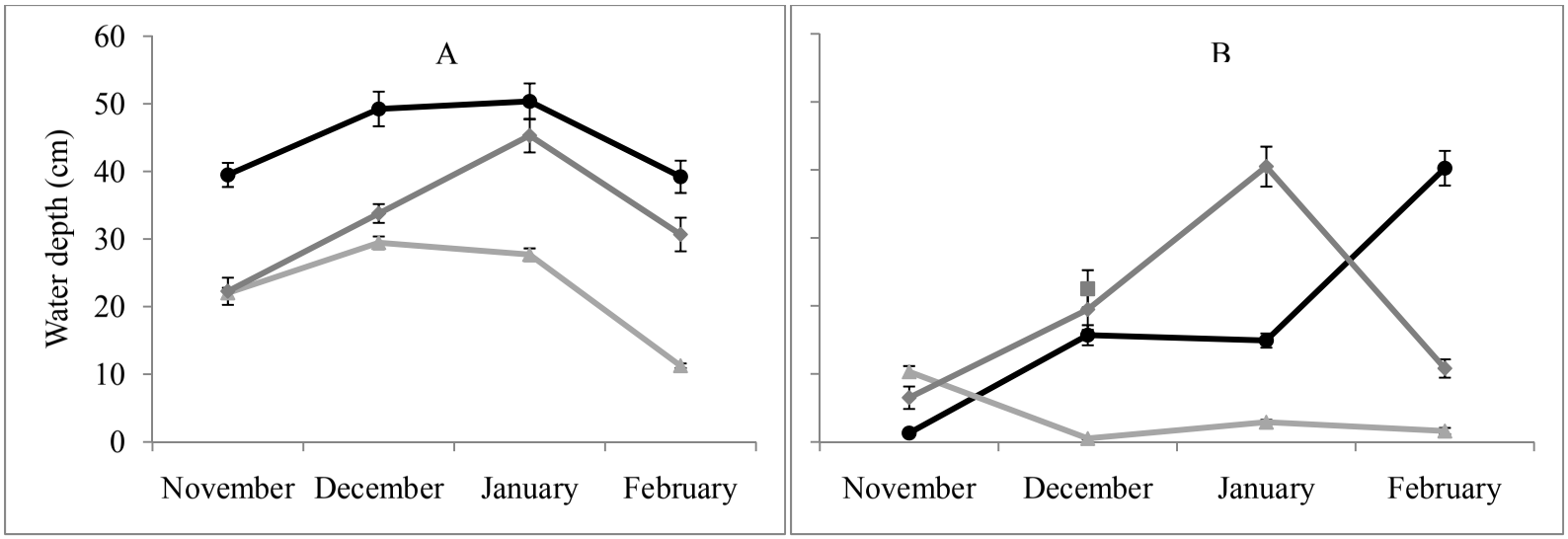

Figure 1.6 Mean water depth (cm; ± standard errors [n = 791]) in greentree reservoirs (A) and naturally flooded forests (B) at Mingo/Duck Creek (▲), White River National Wildlife Refuge (■), Delta National Forest (●), and Noxubee National Wildlife Refuge (♦) during winters 2008–2010.

CHAPTER II

AQUATIC INVERTEBRATE-COMMUNITY COMPOSITION AND DIVERSITY IN GREENTREE RESERVOIRS AND NATURALLY FLOODED BOTTOMLAND HARDWOOD FORESTS

Introduction

Until the 20th century, BLHW forests, other wetlands and deepwater habitats, and uplands, including forested ridges and prairies, covered most of the 10 million hectares of the Mississippi Alluvial Valley (MAV) from southern Illinois near the confluence of the Mississippi and Ohio Rivers southward into Louisiana (Cowardin et al. 1979, Reinecke et al. 1989, Fredrickson 2005*a*). Channelization, wetland drainage, construction of flood control levees, and landscape modification for human use significantly altered natural hydrology and land coverage in the MAV (Reinecke et al. 1988, Reinecke et al. 1989, King et al. 2006).

Before anthropogenic management in the MAV, forested wetlands experienced greatly dynamic seasonal and annual hydroperiods. Despite governmental and local attempts to manage riverine and landscape over-flow hydrology, duration, frequency, and depth of flooding influence seasonal hydrology, plant and animal productivity, and biodiversity of these systems (White 1985, Reinecke et al. 1988, Fredrickson 2005*a*).

For example, long-term hydrologic evolutionary changes within BLHWs have shaped invertebrate life-history strategies such as mobility among pools, high reproductive output, aestivating larvae or eggs, rapid maturity, and short generation time (Batema et al. 2005). Varied life history strategies (i.e., mobility among pools, high reproductive output, aestivating larvae or eggs, rapid maturity, and short generation time) enable invertebrates to respond rapidly to natural and human-influenced seasonal, spatio-temporal flooding such as, consistent, fall-winter seasonal flooding of greentree reservoirs (GTR) by wildlife managers and remaining naturally flooded forests (NFF) now replace basin- and watershed-wide flooding.

A GTR is an impounded portion of BLHW forest that is typically flooded artificially with water from underground or reservoirs to provide seasonal wetlands for migrating and wintering waterfowl and waterfowl hunting (Reinecke et al. 1989, Wigley and Filer 1989). Contemporary flooding regimes in GTRs may alter composition and abundance of aquatic macroinvertebrates (hereafter, invertebrates) compared to NFFs (Wehrle et al. 1995, Fredrickson 2005*a*). Mimicking NFFs short (i.e. 10-30 days) and frequent (i.e., 2-4 times a year) flood duration may be more important to invertebrate ecology and populations than typical stable hydroperiods in GTRs (Fredrickson and Reid 1988, Fredrickson 2005*a*).

Bottomland hardwood forests are the most biologically diverse habitats in North America (Fredrickson 2005*a*). Invertebrates contribute significantly to this diversity and have morphological and behavioral adaptations for their niche (e.g., functional groups [shredders, grazers, collectors, predators]) within lowland forested wetlands (Batema et al. 2005). Shredders process coarse particulate organic matter (e.g., leaf litter) to acquire

nutrients from the associated attached microbial community (Vannote et al. 1980). Grazers glean algae and phytoplankton from surfaces. Collectors process fine particulate organic matter, and predators prey on other invertebrates (Vannote et al. 1980). The food web of BLHW forest is primarily driven by allochthonous and autochthonous inputs of detritus from riverine sources during overflows and the forest itself (Vannote et al. 1980). Invertebrates affect cycling of nutrients by being an intermediate link between primary producers, primary consumers, and predators (Malmqvist 2002, Mitsch and Gosselink 2007).

Aquatic invertebrates are an essential food source for different life stages of many wildlife species. For example, they provide waterfowl with protein and calcium throughout the birds' annual cycle. Invertebrates are important to female ducks during winter because some species undergo winter-spring prebasic molt, and proteinaceous foods are essential for production of new feathers (Richardson and Kaminski 1992, Heitmeyer 2006). Southern populations of wood ducks (*Aix sponsa*) use flooded BLHW forests during fall-spring, and invertebrates are an important protein source for females and ducklings (Drobney and Fredrickson 1979, Cox et al. 1998, Davis et al. 2007).

Little information exists concerning invertebrate diversity and community composition in southeastern forested wetlands (Duffy and LaBar 1994). Therefore, my objectives were to (1) quantify and compare invertebrate community composition in NFFs and GTRs, (2) quantify and compare familial richness, diversity, evenness of invertebrates in NFFs and GTRs, and (3) model invertebrate communities with associated forested wetland metrics (i.e., water depth and litter mass).

Study Areas

For an in-depth description of my study areas refer to Study Areas (Chapter 1).

Methods

Invertebrate sampling

For an in-depth description of my invertebrate sampling methods refer to Invertebrate sampling (Chapter 1).

Sample preservation and processing

For an in-depth description of my sample preservation and processing refer to Sample preservation and prcessing (Chapter 1).

Statistical analysis

Invertebrate composition

My assessment of invertebrate communities in GTRs and NFFs was coarse-grained (i.e., Class, Order, or Family), and I was not able to identify invertebrates to species and thus determine species richness. I identified invertebrates to family level whenever possible (Wehrle et al. 1995) and calculated invertebrate familial percentage occurrence from sweep nets taken in GTRs and NFFs. I used a two-tailed *t*-test to test if familial percentage occurrences differed between GTRs and NFF in winter 2008–2010 (Sokal and Rohlf 1969).

$$t_s = \frac{\arcsin\sqrt{p_1} - \arcsin\sqrt{p_2}}{\sqrt{820.8\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}} \tag{2.1}$$

Where:

p_1 & p_2 = proportions of a family in the two samples

n_1 & n_2 = respective sample sizes

820.8 = constant of arcsine transformations of percentages

Familial richness

I deemed number of detected invertebrate families within each study site and month as familial richness. I used a factorial analysis of variance (ANOVA) in Program R version 2.11.0 to test if invertebrate familial richness differed by study site, flooding regime, and month. Specifically, my 3 fixed independent variables included study sites (Mingo/Duck Creek, DNF, and Noxubee NWR wherein paired GTRs and NFFs existed and were sampled), flooding regime (GTR and NFF), and month (November – February). I suspected a possible interaction of flooding regime and month. I averaged data among individual sweep net samples within plots and specified plot as my sampling and analytic unit. I only analyzed data when spatially and temporally paired samples from GTRs and NFFs at a site where available within a sample month.

Familial diversity

I calculated invertebrate familial diversity at each study site and during each month using a Shannon-Wiener index (Krebs 1999, González et al. 2009).

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \tag{2.2}$$

Where:

H' = diversity

p_i = relative abundance of families

ln = natural log

I used a factorial analysis of variance (ANOVA) in Program R version 2.11.0 to test if invertebrate familial diversity differed by study site, flooding regime, and month, as already described.

Familial evenness

I calculated invertebrate familial evenness for each study site and month (Krebs 1999, González et al. 2009). Evenness is a component of diversity that quantifies how equal the community is numerically among analyzed data (i.e., invertebrate families in this study).

$$J' = \frac{H'}{H'_{max}} \tag{2.3}$$

$$H'_{max} = \ln S \tag{2.4}$$

Where:

J' = evenness

H' = number derived from the Shannon-Wiener diversity index

S = total number of families

I used a factorial analysis of variance (ANOVA) in Program R version 2.11.0 to test if invertebrate familial evenness differed by study site, flooding regime, and month, as already described.

Non-metric multidimensional scaling

I used a non-metric multidimensional scaling (NMDS; *vegan* package) ordination to assess invertebrate communities relative to sites and flooding regimes (GTRs vs. NFFs) in Program R version 2.11.0. I used a NMDS ordination to visually display similarities or dissimilarities in familial composition and structure (Wilson and Sheaves 2001). I identified 25 invertebrate taxa (20 families, 4 orders, and 1 class) but included in NMDS only those taxa (n = 20 families) that comprised, ≥1% of the total occurrence of invertebrates (Desmond et al. 2002). I used ordinations based on Sorenson/Bray-Curtis distance measurements to graphically represent invertebrate assemblages (Vinson and Dinger 2008). In the *vegan* package, invertebrate relative abundances were square root transformed using the Wisconsin double standardization (Oksanen et al. 2010). I performed the NMDS analysis in two-dimensional ordination space with 1,000 iterations. Stress values, which indicate the deviation between the ordination and the original similarity matrix, were calculated to evaluate usefulness of the ordination (Clarke 1993, Desmond et al. 2002). I also fit environmental vectors with ENVFIT in *vegan* package, to the ordination plot to identify their effects on determining invertebrate communities (Oksanen et al. 2010). If any portion of the invertebrate community clustered at the terminus of an environmental vector, I interpreted that it was correlated positively with that environmental variable (Dinger and Marks 2007). I plotted values derived from the

NMDS ordination and connected plot locations to create polygons for each study site. The location of the polygons best represent where study sites fit within the invertebrate community.

Results

Invertebrate familial composition and occurrence

I tested for differences between GTRs and NFFs in mean percentage occurrence of 17 invertebrate families because other taxa (i.e., 3 Families, 4 Orders, and 1 Class) occurred <1% of the time among samples (Table 2.1). Five families occurred more frequently in GTRs than NFFs ($P < 0.01$ Table 2.1); these were *Asellidae* (isopods; GTR = 71.07%, NFF = 63.44%), *Chironomidae* larvae (midges; GTR = 90.74%, NFF = 75.27%), *Cragonyctidae* (amphipods; GTR = 74.55%, NFF = 59.14%), *Daphniidae* (daphnia; GTR = 61.82%, NFF = 43.55%), and *Sphaeriidae* (fingernail clams; GTR = 46.94%, NFF = 35.48%).

Familial richness

During winters 2008–2010, GTRs and NFFs were not flooded concurrently. Thus, I report only results from sampling events when GTRs and NFFs were both flooded. I detected a flooding regime (i.e., GTR or NFF) by month interaction for invertebrate familial richness ($F_{3, 107} = 2.736$, $P = 0.047$). The model explained nearly 39% ($R^2 = 0.387$) of the variation in familial richness. Invertebrate familial richness

differed between flooding regimes in December (GTR [$\bar{x}$ = 8.0, SE = 0.36 families]; NFF [$\bar{x}$ = 6.0, SE = 1.04 families]; Fig. 2.1).

Familial diversity

I also detected a flooding regime by month interaction for invertebrate familial diversity because familial richness is used to calculate diversity and hence would be correlated by mathematical derivation ($F_{3, 107}$ = 5.266, P = 0.002). The model explained 26% (R^2 = 0.264) of the variation in familial diversity. The NFF had greater invertebrate diversity than the GTR in November (NFF [$\bar{x}$ = 1.37, SE = 0.125 natural bels]; GTR [$\bar{x}$ = 0.53, SE = 0.067 natural bels]), December (NFF [$\bar{x}$ = 0.87, SE = 0.166]; GTR [$\bar{x}$ = 0.53, SE = 0.071 natural bels]), and February (NFF [$\bar{x}$ = 1.29, SE = 0.138 natural bels]; GTR [$\bar{x}$ = 0.47, SE = 0.110 natural bels]; Fig. 2.2). Diversity scores did not differ between flooding regimes in January (NFF [$\bar{x}$ = 0.97, SE = 0.110 natural bels]; GTR [$\bar{x}$ = 0.91, SE = 0.073 natural bels]).

Familial evenness

Evenness includes diversity index values because it is a mathematical component of the evenness calculation. Therefore, I detected similar flooding regime by month interaction for invertebrate familial evenness ($F_{3, 107}$ = 5.740, P = 0.001). The model explained about 18% (R^2 = 0.177) of the variation in familial evenness. Consistent with diversity, the NFF had greater familial evenness index values than the GTR in November (NFF [$\bar{x}$ = 0.51, SE = 0.046 natural bels]; GTR [$\bar{x}$ = 0.20, SE = 0.025 natural bels]), December (NFF [$\bar{x}$ = 0.29, SE = 0.056 natural bels]; GTR [$\bar{x}$ = 0.18, SE = 0.024 natural

bels]), and February (NFF [$\bar{x}$ = 0.43, SE = 0.046 natural bels]; GTR [$\bar{x}$ = 0.16, SE = 0.037 natural bels]; Fig. 2.3). Evenness scores did not differ between flooding regimes in January (NFF [$\bar{x}$ = 0.33, SE = 0.037 natural bels]; GTR [$\bar{x}$ = 0.31, SE = 0.025 natural bels]).

Non-metric, multidimensional scaling ordination

I partitioned invertebrate samples into 2 time periods for NMDS analyses (i.e., early winter [November – December] and late winter [January – February]), because monthly numbers of samples were unbalanced (Chapter 1). The NMDS analysis revealed that stress levels were high for model fit (i.e., ≥ 0.2; (Clarke 1993) in both periods (i.e., early = 0.23; late = 0.24), which suggested imprecise ordination of the data. Nonetheless, the ordination reached a solution and displayed sample plots and associated invertebrate families.

During early winter, I found most (65%) invertebrate families associated with sites having mean water depth (i.e., $\bar{x}$ = 30.11 cm, SE = 3.044, n = 18; ranges = 10–40 cm; Fig. 2.4). I plotted water depth and red oak leaf mass over the NMDS output plot. However, neither water depth nor red oak leaf mass were significant (water depth P = 0.086; red oak leaf mass P = 0.545) in influencing the presence of invertebrate families.

During late winter, I found most (82%) invertebrate families associated with sampling sites with mean water depth (i.e., $\bar{x}$ = 30.11 cm, SE = 3.044, n = 18; realized range = 10–40 cm; Fig. 2.5). However, water depth had low overall fit to the ordination (R^2 = 0.06, n = 791), but it was significant likely because of large sample size (P = 0.026). Overlaying water depth on the ordination plot suggests it was more correlated

positively to plots at Noxubee NWR than DNF and Mingo/Duck Creek. Red oak leaf mass was not significant ($P = 0.321$) in influencing presence of invertebrate families in late winter.

Discussion

Invertebrate familial composition and occurrence

Five families (i.e., *Asellidae* [isopods], *Chironomidae* larvae [midges], *Cragonyctidae* [amphipods], *Daphniidae* [daphnia], and *Sphaeriidae* [fingernail clams]) occurred more frequently in a GTR than a NFF because they are generalists (i.e, colonizers and persisters) in wetland habitats (Anderson and Smith 2004, Studinski and Grubbs 2007). In the MAV, GTRs usually are drained in late winter-early spring while trees remain dormant (Fredrickson 2005*b*). Greater occurrence of these 5 families may arise from a source population in late summer, because GTRs have potential to retain water and moisture longer in spring-summer. In mid-late autumn when GTRs typically are flooded before waterfowl hunting seasons, these invertebrate families may be present within the substrate (i.e., aestivating adults, larvae, or eggs) and have the potential to colonize forested wetlands quickly (Batema et al. 2005). Compared to GTRs, NFFs may not hold moisture within their substrate and subsequently invertebrate colonization may be slower and population occurrence and growth less.

Familial richness, diversity, and evenness

Invertebrate familial richness did not differ between flooding regimes except in December. Invertebrate familial richness in GTRs declined from November – February. Although I did not collect data to explain seasonal dynamics of invertebrate populations, decaying leaf litter, metals leached from soil (e.g., iron, aluminum), and stagnant water may have reduced dissolved oxygen and pH and influenced the seasonal decline in invertebrate richness (Jackson and Harvey 1993). Larimore et al. (1959) reported stagnant water in drying stream pools was most detrimental to invertebrate survival in fall and winter. In contrast, mean invertebrate familial richness in NFFs declined from November – December and then increased through February. Dynamic hydrology in NFF may have reduced stagnation because of short frequent flood pulses of water which also may have increased dissolved oxygen levels, nutrient inputs, and pH.

I compared familial richness from sweep net samples to previously published work at my study locations (Table 2.2). I detected more invertebrate families in forested wetlands than Wehrle et al. (1995) and Batema (1987) woring in Mississippi and Missouri, respectively. However, families identified by Wehrle et al. (1995) and Batema (1987) were present in my samples. In forested wetlands in Kentucky, Studinski and Grubbs (2007) reported similar familial richness and composition. Differences in total identified families between my study and previous studies may stem from differences in sampling and processing methods, unknown ecological phenomena, or both.

I also compared invertebrate familial richness in forested wetlands with other wetland habitat types frequently used by waterfowl throughout the annual cycle (Table 2.2). Forested wetlands in my study had greater invertebrate familial richness than moist-

soil wetlands in Delaware (Sherfy and Kirkpatrick 2003). Difference in familial richness may be caused by regional differences in soil and water chemistry, biomass and structure of available plant litter for algal and microbial attachments, sampling and processing differences and other factors. Flooded BLHW forests had lesser invertebrate familial richness (n = 20 families) than other wetlands (Table 2.2). My study was not designed to explain these differences, but future researchers may desire to examine hydrology, light conditions, pH, water chemistry, and plant litter in these wetland for comparative purposes.

I calculated mean familial diversity and evenness of invertebrates in flooded BLHW forests in winter. Diversity and evenness indices differed relative to flooding regime. The NFFs had greater invertebrate diversity than the GTRs in November, December, and February. Familial evenness showed a similar pattern to diversity, primarily because diversity values are used in calculating evenness. The NFFs may have had greater invertebrate diversity and evenness because of underlying hydrology. The NFFs had variable inundation across their landscapes, which created a mosaic of potential habitats for invertebrate families. The observed increase in diversity and evenness in NFFs also may be related to variation in depth and duration and biogeochemical influences (e.g., dissolved oxygen, pH). Thus, NFFs provide a wide range of habitats for invertebrates to colonize, forage, grow, and reproduce compared to the steady hydrology of a GTR.

Relative abundances of invertebrates were more even (i.e., similar) among families in GTRs than NFFs in November, December, and February. The peak in GTR diversity and evenness values in January may be related to flooding events adding leaf

and other organics and fresh nutrient rich water to GTR 1 at Noxubee NWR (Fig. 1.6). I hypothesize that Noxubee NWR was influential in explaining the pulse in diversity in January because DNF and Mingo/Duck Creek did not encounter a flooding event that changed water levels in their GTRs in January.

Non-metric, multidimensional scaling ordination

In early and late winter, the NMDS ordination produced little overlap in invertebrate communities between DNF and Noxubee NWR. Mingo/Duck Creek and White River NWR were intermediate between DNF and Noxubee NWR. I hypothesized *a priori* that invertebrate communities would differ by flooding regimes rather than study sites, but sample plots from GTRs and NFFs were integrated within study sites. Therefore, site specific variables (e.g., soil chemistry, nutrients leached by organic matter, tannin levels and pH, water sources, hydroperiods, etc.) may be more influential in determining the invertebrate community than flooding regime itself, but this hypothesis should be tested in future studies.

I incorporated environmental vectors (i.e., red oak leaf mass and water depth) to explain potential invertebrate community relationships within and among study sites. Red oak leaf mass and water depth did not contribute to the ordination of the invertebrate community in early winter. In late winter, water depth was correlated more positively with plots at Noxubee NWR than other study sites. The relationship between water depth and Noxubee NWR may be a consequence of small sample size of NFF plots (n = 19) in late winter compared to the GTR (n = 120). The GTRs have fairly stable hydrology whereas NFF plots are quite variable in flood duration and depth. The difference in

numbers of NFF and GTR plots in the MAV was not as great (NFF [*n* = 69] and GTR [*n* = 187]) as at Noxubee NWR.

Another hypothesis regarding water depth as an explanatory variable in invertebrate communities at Noxubee NWR in late winter may be the primary water source (i.e., Bluff Lake instead of the Noxubee River) and resulting possible anoxia that occurs after the GTR is flooded beginning in late fall. At Noxubee NWR, GTR1 is initially filled in late fall with water from Bluff Lake and remains at full capacity (i.e., 25–45 cm; Chapter 1, Fig. 1.6) until drawdown in February. At DNF, the Sunflower GTR is flooded with water from the Sunflower River and also remains at full capacity (i.e., 40–50 cm; Chapter 1, Fig. 1.6) until drawdown in February. Anoxic conditions result through depletion of oxygen by metabolic processes associated with decomposition (Euliss et al. 1999). Many GTRs are flooded to full capacity and stable depths for months with little or no additional freshwater input while organic matter decomposes through invertebrate and microbial activity (Fredrickson 2005*b*). Also, GTR 1 periodically receives water from adjacent Noxubee River when it overflows, whereas the Sunflower GTR is inundated rarely by the Sunflower River. In December 2008 and January 2009, GTR 1 received fresh water and nutrient inputs from the Noxubee River when it overflowed its banks. I hypothesized the ordination displayed water depth as being more correlated with Noxubee NWR than other sites, because GTR 1 was flooded shallower during winter and periodically received inputs from the Noxubee River.

Management and Research Implications

Invertebrate communities may be similar between GTRs and NFFs (Table 2.1), but invertebrate biomass was significantly greater in NFFs (Chapter 1). Although GTRs have less invertebrate biomass than NFFs, they provide consistent forested wetland habitat for wintering waterfowl and most (85%) invertebrate families were found in both flooding regimes. The addition of fresh water and release of stagnant water in GTRs may release more sensitive families from physical constraints of colonization, growth, and reproduction (i.e., low pH and dissolved oxygen). Therefore, mimicking NFF hydrology in GTRs by capturing rain and flood waters and periodic removal and addition of boards from water control structures may lead to an increase in invertebrate biomass in GTRs.

Overall, NFFs had greater familial diversity of invertebrates than GTRs. The NMDS ordination illustrated most invertebrate families in early (65%) and late (82%) winter were associated with depths from 10–40 cm. If managers flooded GTRs near this range of depths and fluctuated water levels during winter, GTRs may function more similar to NFFs. Consistent with results from my study, Wehrle et al. (1995) reported NFFs to have greater invertebrate abundance and biomass than GTRs and recommended managers emulate natural hydrology or decrease flood duration in GTRs. Hagy (2010) reported > 90% of foraging dabbling ducks (Tribe: *Anatini*) in moist-soil wetlands were associated with water depths < 20 cm. Therefore, managers should provide shallower water depths in managed wetlands (Fredrickson 2005*b*). Finally, when rainfall and riverine flood events occur, managers should take advantage of fresh water inputs and periodically remove and replace boards from water control structures to entrap these inputs.

The NMDS analysis revealed that invertebrate communities were ordinated more by location than flooding regime. Assessing environmental factors (i.e., water source, nutrients, contaminants, etc.) possibly influencing forested wetlands on a site-specific basis may help managers provide wintering waterfowl with abundant plant and animal food resources. Because of equipment failures, I was not able to relate invertebrate data to environmental variables including pH, dissolved oxygen, and water temperature. Future research on invertebrate communities in BLHW forested wetlands should focus on consistently collecting information on environmental variables (e.g., soil chemistry, nutrients leached by leaves, decomposition rates of leaf litter, water sources, pH, dissolved oxygen, conductivity, etc.) to help explain spatial and temporal variation in invertebrate abundance and community metrics.

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Table 2.1 Percentage (%) occurrence of aquatic invertebrate families in greentree reservoirs (GTRs) and naturally flooded forests (NFFs) in the Mississippi Alluvial Valley and Interior Flatwoods during winters 2008–2010.

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

Table 2.2 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		70	70	Anderson and Smith (2000)
	Moist-soil impoundment	Delaware	11		11	Sherfy and Kirpatrick (2003)
Spring	Playa wetlands	Texas		47	47	Hall (2004)
Summer	Emergent wetlands	West Virginia	38	25	38	Balcombe et al. (2005)
	Everglades	Florida			53	Rader and Richardson (1994)

[a] Blanks denote a lack of information on management in wetlands

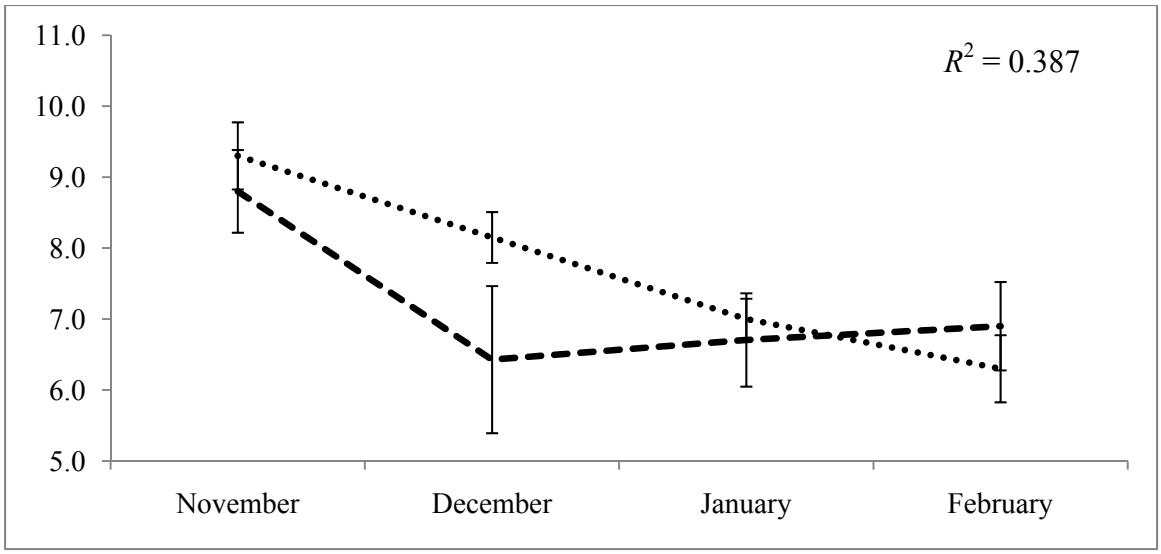

Figure 2.1 Mean aquatic invertebrate familial richness (i.e., number of families; standard error bars) from greentree reservoirs (**...** ; *n* = 70) and naturally flooded forests (**– – –** ; *n* = 46) in the Mississippi Alluvial Valley and Interior Flatwoods, November 2008 – February2010.

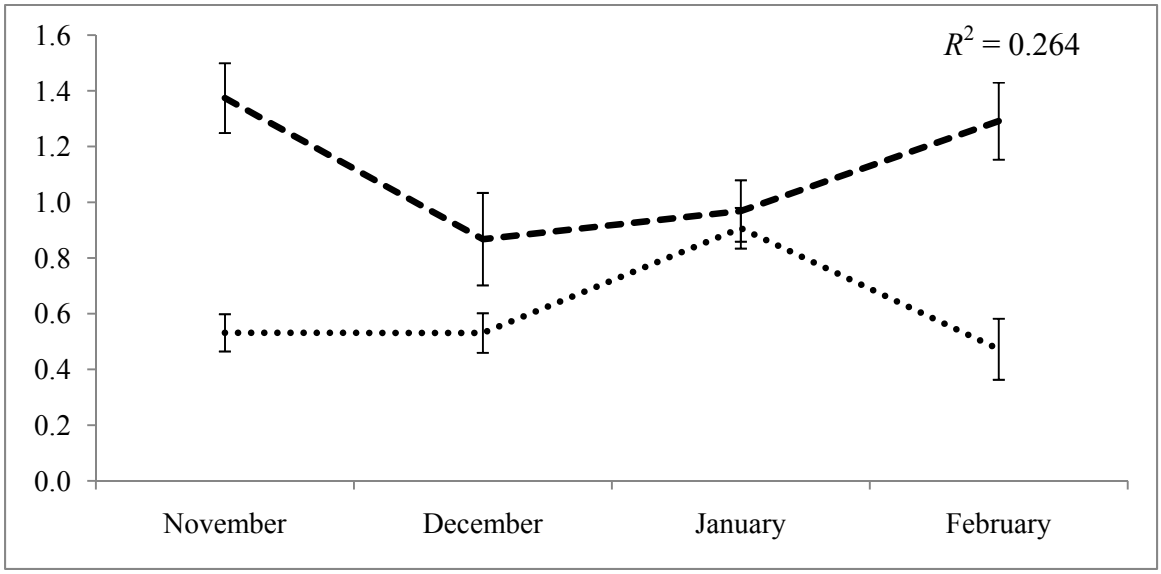

Figure 2.2 Mean aquatic invertebrate familial diversity and standard error bars from greentree reservoirs (**...** ; *n* = 70) and naturally flooded forests (**– – –** ; *n* = 46) in the Mississippi Alluvial Valley and Interior Flatwoods, November 2008 – February2010.

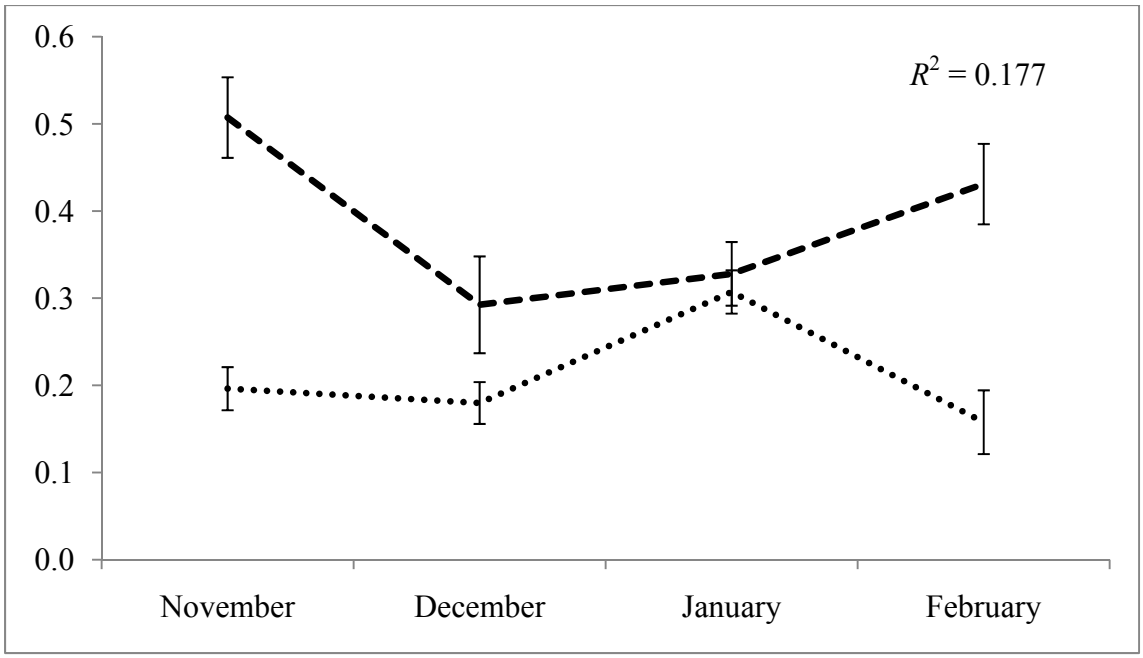

Figure 2.3 Mean aquatic invertebrate familial evenness and standard error bars from greentree reservoirs (**…** ; *n* = 70) and naturally flooded forests (**_ _ _** ; *n* = 46) in the Mississippi Alluvial Valley and Interior Flatwoods, November 2008 – February2010.

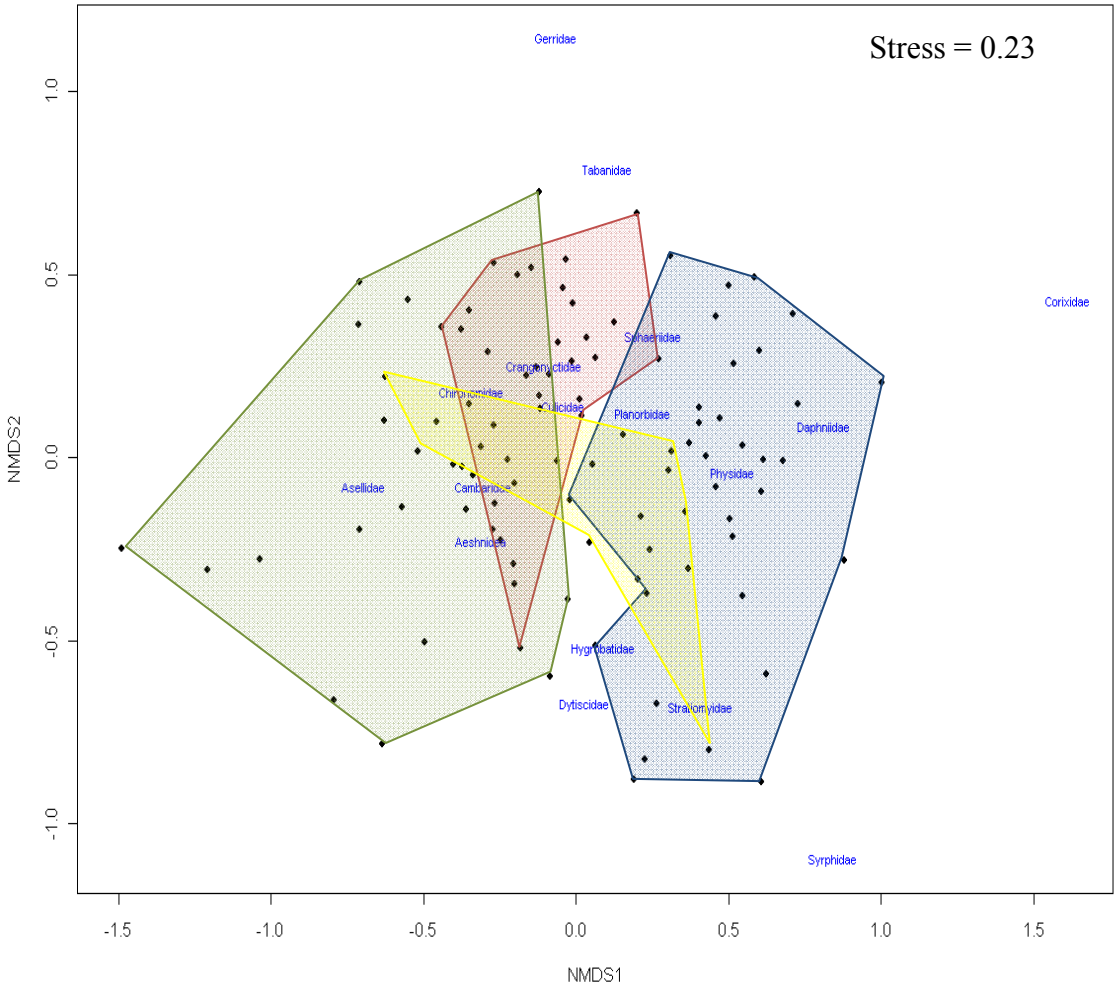

Figure 2.4 Non-metric multidimensional scaling ordination of invertebrate families (≥1% of total occurrence) in early winter (November and December 2008–2009) at Mingo/Duck Creek (red), White River National Wildlife Refuge (yellow), Delta National Forest (blue), and Noxubee National Wildlife Refuge (green). Points in close proximity represent similar assemblages, whereas points farther apart indicate differing assemblages. Stress evaluates usefulness of the ordination, and stress > 0.2 indicates low ordination fit (Clarke 1993).

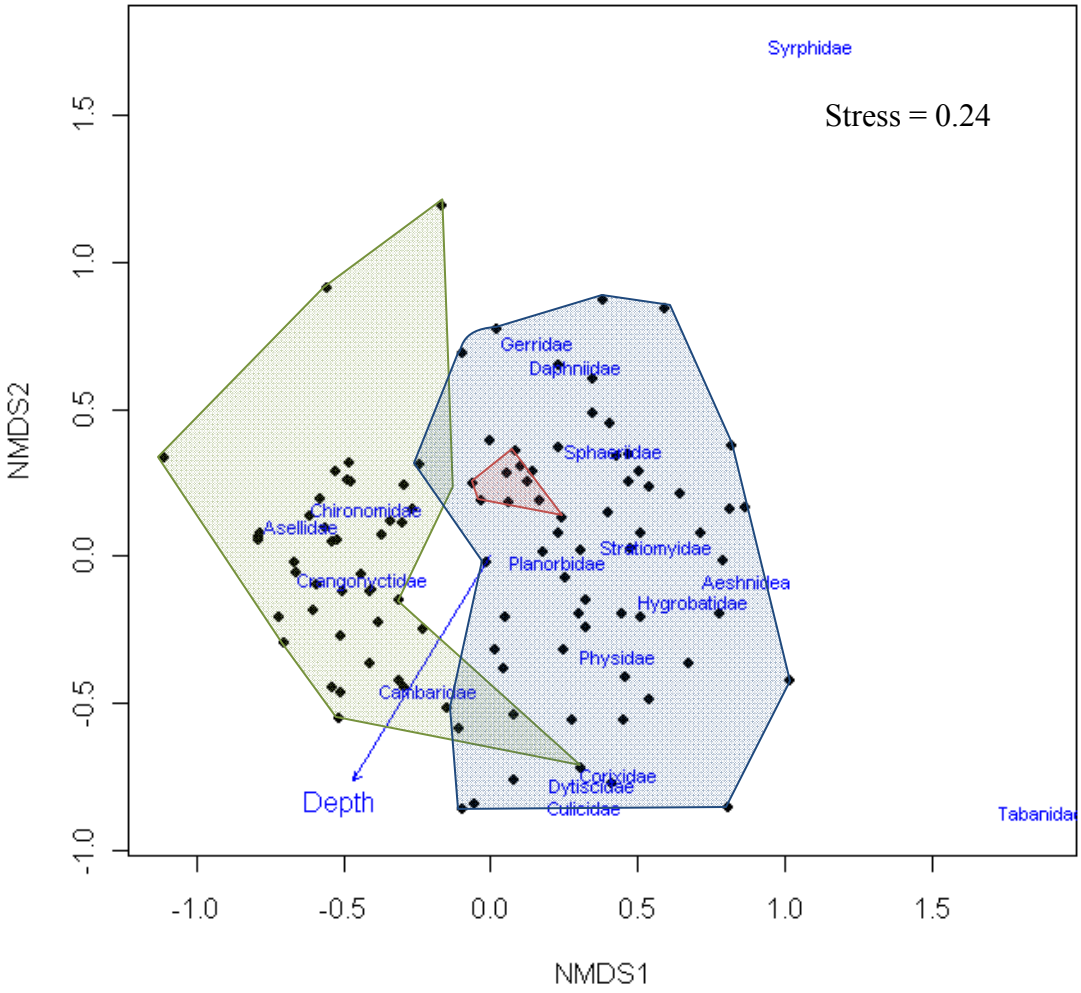

Figure 2.5 Non-metric multidimensional scaling ordination of invertebrate families (≥1% of total occurrence) and environmental vector (water depth) in late winter (January and February 2009–2010) at Mingo/Duck Creek (red), Delta National Forest (blue), and Noxubee National Wildlife Refuge (green). Points in close proximity represent similar assemblages, whereas points farther apart indicate differing assemblages. Stress evaluates usefulness of the ordination, and stress > 0.2 indicates low ordination fit (Clarke 1993).

CHAPTER III

SYNTHESIS

Until the 20th century, bottomland hardwood (BLHW) forests, other wetlands and deepwater habitats, and forested ridges and prairies, covered most of the 10 million hectares of the Mississippi Alluvial Valley (MAV) from southern Illinois through Louisiana. Today, < 25 % of BLHW forested area remains (Twedt and Loesch 1999). Bottomland hardwood forests are especially important as wintering habitat for ducks (e.g., mallard, *Anas platyrhynchos;* wood duck *Aix sponsa*) because they provide energy- and protein-rich foods including acorns, samaras, and other plant seeds and invertebrates.

Protein-rich invertebrates nutritionally diversify diets of wintering ducks which are otherwise high in carbohydrates from native and agricultural seeds (Fredrickson and Taylor 1982, Delnicki and Reinecke 1986). Nutrients in invertebrates are important for building body mass for migration and for female ducks undergoing winter-spring prebasic molt (Heitmeyer and Fredrickson 1990, Richardson and Kaminski 1992, Barras et al. 2001). Therefore, studying invertebrate communities in flooded BLHW forests under different hydrological influences identify variables possibly influencing abundance and structure of invertebrate communities and help estimate carrying capacity of these forests for wintering waterfowl, based on biomass estimates of acorns and invertebrates from concurrent studies.

Studies of invertebrate biomass and community composition in greentree reservoirs (GTR) and naturally flooded forests (NFF) have been conducted at local but not regional scales (i.e., MAV wide; Wehrle et al. 1995, Batema et al. 2005). Thus, my objectives were to (1) estimate dry mass (CV ≤ 15%) of invertebrates in NFFs and GTRs, (2) explain variation in winter biomass of invertebrates in relation to environmental and temporal covariates, (3) quantify and compare invertebrate community composition in NFFs and GTRs, (4) quantify and compare familial richness, diversity, and evenness of invertebrate communities in NFFs and GTRs, (5) model invertebrate communities with associated forested wetland metrics (i.e., water depth, litter mass), and (6) relate results to previous studies and make appropriate management recommendations.

In Chapter I, I estimated dry mass of invertebrates in NFFs and GTRs. The MAV had > 3.5 times invertebrate mass in NFFs ($\bar{x}$ = 18.39 kg/ha; SE = 2.815[CV = 15.3%]) than GTRs ($\bar{x}$ = 5.16; SE = 0.492 [CV = 9.5%]). The GTR ($\bar{x}$ = 1.32 kg/ha, SE = 0.226, n = 78) at Noxubee National Wildlife Refuge in the Mississippi Interior Flatwoods (IF) region had a similar standing crop of invertebrates in an adjacent NFF ($\bar{x}$ = 1.12 kg/ha, SE = 0.951, n = 41). The Lower Mississippi Valley Joint Venture (LMVJV) currently uses 11.4 kg/ha as an estimate for invertebrate biomass in BLHW forests (Reinecke and Uihlein 2006, Reinecke and Kaminski 2007). My estimates from MAV NFFs and GTRs average 11.8 kg/ha and both are precise (CV ≤ 15%). Because GTRs in MAV only encompass 1–2% of the overall area of BLHWs, I recomend the LMVJV should consider using my estimate of invertebrate biomass from NFFs which is 1.6 times greater than LMVJV's current estimate.

In the MAV, GTRs provide a consistent source of forested wetland habitat for wintering waterfowl especially in drought years. A complex of GTRs with gravity fed flooding regimes among GTRs may emulate natural flood pulses. If only a single GTR is present, removal and replacement of boards in water control structures during and after natural flood events would mimic dynamic hydrology. Flooding GTRs more shallowly (i.e., 40 cm) and mimicking a more natural hydrology may benefit invertebrate populations, foraging waterfowl, and other plant and animal communities in BLHW forests.

In Chapter II, I quantified and compared invertebrate community composition and diversity metrics between NFFs and GTRs. Most (85%) invertebrate families occurred in GTRs and NFFs. Additionally, invertebrate familial diversity and evenness indices were greater in NFFs than GTRs during most of winter. However, invertebrate familial richness in GTRs and NFF displayed different trends during winter. Familial richness in GTRs declined, whereas NFF richness declined from November – December then increased January – February. I cannot explain these different trends but speculate they may be related to differences in flood depth and duration. Because most invertebrate families occurred in both GTRs and NFFs and diversity metrics were greater in NFFs, GTR management should emulate natural dynamic hydrology potentially increasing invertebrate biomass to levels in NFF.

The NMDS ordination plot revealed that sites flooded 10–40 cm had more diverse invertebrate communities than those flooded outside this range. If managers flooded GTRs within this range and fluctuated water levels during winter, GTRs may function ecologically more similar to NFFs. Similarly, Hagy (2010) found most (> 90%) dabbling

ducks forage in ≤ 16 cm of water in moist-soil impoundments. Waterfowl may forage at similar depths in BLHW forested wetlands, but feeding ecology of ducks in forested and emergent wetlands has not been investigated in the MAV.

Future research on BLHW forested wetlands should focus on: (1) GTR management relative to waterfowl responses to varied flood depth and duration in conjunction with BLHW restoration and hunter satisfaction surveys by waterfowl hunters using managed areas (Fredrickson 2005, St. James 2011), (2) effects of silvicultural practices on waterfowl use and invertebrate populations, and (3) evaluate invertebrate abundance and communities in relation to environmental variables (e.g., light, soil chemistry, litter mass, decomposition rates of litter, nutrients leached by leaves, water sources (e.g., riverine, lacustrine, aquifers, pH, dissolved oxygen, conductivity, etc.). Such holistic investigations will help sustain the ecology of BLHW forests.

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