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**Temporary Woodland Pools of the Pennyroyal
Plain: Investigating the Effects of Disturbance on
Aquatic Macroinvertebrate Communities**

Brandy N. Schnettler

Temporary Woodland Pools of the Pennyroyal Plain:
Investigating the Effects of Disturbance on Aquatic Macroinvertebrate Communities

By
Brandy N. Schnettler

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A Thesis

Presented to

The College of Graduate Studies

Austin Peay State University

In Partial Fulfillment

Of the Requirements for the Degree of

M. S. Biology

Brandy N. Schnettler

August, 2016

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Brandy Nichole Schnettler

July 25, 2016

DEDICATION

I dedicate this work to my daughters, Olivia and Phoebe Schnettler, whose love of the natural world has been inspirational. Tough days in the field, long nights in the lab, and endless days writing were always bearable when they ended with little hugs and "I love you, mommy." Livvy and Pheebies, I couldn't have done this without you. Yes, "mommy loves bugs," but you two far more.

Thank you to the many friends that enthusiastically helped with my field and lab work. I would like to extend special thanks to, "my other," Mattie Underwood. As my closest friend in graduate school, you have been an incredible supporter. My fieldwork and making it through graduate school (sane) would not have been possible without you. Food, fieldwork, cat talk, birding, Fun-day Field-day Fridays... I'm so happy I got to share this time with you. Thank you to my mom, dad, sister, and grandmother for your encouragement and support throughout graduate school and life. Next, I would like to thank, my high school biology teacher and mentor, Pam Perry. You have always been an inspiration to me and are, without question, the reason I first chose to teach. Finally, thank you to my husband, John. You dug through dumpsters for my research, watched kids when I worked, kept me laughing, and encouraged me when I was in a funk. I cannot thank you enough for having confidence in me.

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ABSTRACT

Brandy N. Schnettler. Temporary Woodland Pools of the Pennyroyal Plain: Investigating the Effects of Disturbance on Aquatic Macroinvertebrate Communities.

(under the direction of Dr. Steven W. Hamilton)

Temporary woodland pools are common throughout the Pennyroyal Plain north of Clarksville, Tennessee. We studied the effects of disturbance on aquatic macroinvertebrate community structure in these wetlands. The karst geology and poorly drained, silt loam soils create abundant temporary woodland pools within a landscape surrounded by row crop agriculture, grazing, and timber cutting. Our objective was to test for correlations, if any, between community structure and land use. We used canopy density, canopy height, and vegetative buffer as disturbance metrics. Mean maximum water level was also measured as an estimate of hydroperiod. Macroinvertebrates were collected from ten sites using activity traps and substrate sampling. Specimens were classified as active or passive dispersers once identified. Significant associations were indicated between disperser ability and site ($X^2=2927.626$, $p=0.0001$), which is best explained by variation in maximum water level and vegetative buffer. Mean maximum water level was negatively correlated with the proportion of active dispersers ($p=0.0064$, $R^2=0.6256$) and positively correlated with passive dispersers ($p=0.0078$, $R^2=0.6079$). Mean vegetative buffer and mean maximum water level were negatively correlated ($p=0.0075$, $R^2=0.6116$). These findings suggest that well-buffered sites are more ephemeral, likely a result of decreased runoff. The most ephemeral study sites were also determined to have the most unique communities compared to each other and all other

sites. Disturbance may impact temporary woodland pools by increasing their permanence and decreasing their biodiversity.

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CHAPTER I

INTRODUCTION

Temporary Woodland Pools

The ephemeral nature of temporary woodland pools are highly dependent upon and extremely sensitive to seasonality and climate (Wiggins et al. 1980). Semi-permanent pools are affected by seasonal changes in water levels, however, true temporary pools have periods of drying that can last for months (Wiggins et al. 1980, Colburn 2004, Carl & Blumenshine 2005, Malchik et al. 2009, Semlitsch & Bodie 1998, Tiner 2003, Zedler 2003). The small size of temporary woodland pools and their isolation result in most being easily subject to disturbance or destruction and it has been argued that even the smallest pools are essential habitat. Isolation of temporary woodland pools resulting in unique distribution patterns and community structure contributes to genetic variability (Semlitsch & Bodie 1998). Many of the species present in temporary

- 1) Semi-permanent pool: water levels fluctuate seasonally, but rarely dry
- 2) Autumnal pool: fill in Fall, flooded for 8-9 months, dry for 3-4 months
- 3) Vernal pool: fill in Spring, flooded for 3-4 months, dry for 8-9 months.

Wissinger (1999) compiled a more extensive classification of hydroperiods and has suggested that more categories of hydroperiod are needed in order to account for regional variations that occur as a result of differences in climate, geology, and geography.

In addition to their ephemeral nature, temporary pools are also defined as being fishless, small (when compared to other permanent lentic water bodies), shallow (<1m), and hydrologically independent (Wiggins et al. 1980, Tiner 2003, Zedler 2003, Calhoun et al. 2003, Colburn 2004). This common set of characteristics may encompass a diverse set of temporary pools that are functionally unique and distinct.

Loss of Temporary Woodland Pools

Nearly 50% of the world's estimated wetlands have already been destroyed and continued anthropogenic activity negatively impacting temporary woodland pools will undoubtedly result in irreversible loss of biodiversity (Semlitsch & Bodie 1998). Deforestation, filling, draining, land-use changes, ground-water depletion, mosquito control, and invasive species contribute to the demise or alteration of isolated wetlands (Colburn 2004, Carl & Blumenshine 2005, Maltchik et al. 2009, Semlitsch & Bodie 1998, Tiner 2003, Zedler 2003). The small size of temporary woodland pools and their isolation result in most being easily subject to disturbance or destruction and it has been argued that even the smallest pools are essential habitat. Isolation of temporary woodland pools resulting in unique distribution patterns and community structure contributes to genetic variability (Semlitsch & Bodie 1998). Many of the species present in temporary woodland pools are unable to migrate, thus, the species composition at each pool is unique and may include endemic or endangered species (Semlitsch & Bodie 1998, Zedler 2003, Maltchik et al. 2009). The less mobile nature of many temporary pool species also reduces the chance of re-colonization after a disturbance (Semlitsch & Bodie 1998). Calling temporary pools "isolated" is also misleading in that they usually have intimate relationships with upland forests, nearby streams, rivers, lakes, or other temporary pools (Colburn 2004). Altering or destroying temporary woodland pools likely affects surrounding areas and vice versa (Colburn 2004).

Currently, there is little legislation protecting temporary woodland pools, although the Environmental Protection Agency (EPA) and the U.S. Army Corps of Engineers have sought to increase jurisdiction to include all wetlands (Mannina 2011). Until jurisdiction is expanded, wetlands not covered under Section 404 of the Clean Water Act are at considerable risk unless they are under state regulation. Approximately 15 states have programs that provide "considerable protection" for isolated wetlands (Kusler 2001). Many other states have programs for protecting and restoring isolated wetlands, however costs and staffing limit their abilities (Kusler 2001). In order to preserve and restore wetland biodiversity, stronger legislation must be put in place for all states (Semlitsch and Bodie 1998)

A Critical Habitat

Temporary woodland pools are essential habitat to many species and provide ecosystem services such as reduction run-off and flooding, nutrient cycling, and water purification (Tiner 2003). The habitat provided by temporary woodland pools supports many endemics, a diverse group of organisms that would otherwise not persist in the absence of these habitats (Semlitsch & Bodie 1998, Zedler 2003). The absence of fish, a significant predator of invertebrates and small vertebrates, decreases rates of predation on larval amphibians (Colburn 2004). Fishless pools provide an ideal breeding ground for many amphibians, such as the Mole Salamander (*Ambystoma talpoideum*) and Bird-voiced Treefrog (*Hyla avivoca*), both currently listed as threatened in Kentucky (Carl &

Blumenshine 2005, Kentucky Dept. of Fish and Wildlife Services 2016). Additionally, a fishless habitat supports increased invertebrate diversity and abundance, which serve as food sources to other species (Carl & Blumenshine 2005).

Migrating waterfowl in particular rely on temporary woodland pools for refuge and invertebrates as food sources (Van Der Hoek & Cuppen 1989, Batzer & Wissinger 1996, Maltchik et al. 2009). Waterfowl and other bird species, such as Common Grackles (*Quiscalus quiscula*) and Killdeer (*Caradrius vociferus*) take advantage of the drawdown phase in temporary pools when water levels become low and invertebrate densities are high (Magee et al. 1999).

Role of Macroinvertebrates in Temporary Woodland Pools

In addition to larvae and wholly aquatic macroinvertebrates serving as prey to amphibians and waterfowl, emerging insects, particularly chironomid midges, are important food sources for many waterfowl, wetland birds, and others such as Tree Swallows (*Tachycineta bicolor*), Purple Martins (*Progne subis*), Red-winged Blackbirds (*Agelaius phoeniceus*) (Batzer & Wissinger 1996; Wrubleski 1999; Ward 2005), and bats (Colburn 2004). Groves (1979) identified nine bat species feeding on emerging insects, including the federally endangered Indiana Bat (*Myotis sodalists*) in temporary wetlands of Kentucky.

Many macroinvertebrates are also predatory and of considerable importance in determining food web structure (Batzer & Wissinger 1996, Calhoun et al. 2003).

Predators are significantly larger in temporary wetlands when compared to congeneric species in permanent water bodies due to selective pressure from predation from fish (Batzer & Wissinger 1996). Cannibalism is also common in temporary wetlands, particularly as drawdown increases densities, and may play a role in increasing development rates as well as decreasing competition (Batzer & Wissinger 1996). The contribution of nutrients to the system from leeching and bacterial colonization of detritus is notably greater than that of shredder-detritivores, species feeding on decaying leaves and other coarse organic matter (Batzer & Wissinger 1996). However, shredder-detritivores contribute to the breakdown of allochthonous material by feeding on detritus, a significant source of nutrients in forested systems such as temporary woodland pools (Batzer & Wissinger 1996, Alexander 1997, Brooks 2000). Grazers, feeding on attached primary producers like algae, are present in temporary pools and are primarily represented by gastropods (Colburn 2004, Sasamoto 2010). Chironomids and oligochaetes are also significant consumers of algae, but nutrient acquisition is through collector-gathering (consumption of fine organic matter) or detritus (Sasamoto 2010, Batzer & Ruhí 2013).

Macroinvertebrates found in Temporary Woodland Pools

Adaptation for extreme environmental conditions, primarily low dissolved oxygen and desiccation, is essential for all associated species in temporary woodland pools. Macroinvertebrates must be adapted to persist through drying periods or migrate to avoid

desiccation (Wiggins et al. 1980). Macroinvertebrates in temporary woodland pools can be divided into two groups based on dispersal ability and adaptations for persistence through dry periods (Williams 1987).

- 1) Active dispersers: These are taxa with strong flight muscles and can easily migrate. Typically, individuals enter temporary pools to breed and migrate to permanent bodies before drawdown. This pattern of migration is commonly referred to as “cyclic colonization” (Batzer & Wissinger 1996; Wissinger 1997). Examples of typical taxa include Coleoptera, Odonata, Hemiptera, and Diptera (Williams 1987, Batzer & Wissinger 1996, Wissinger 1997).
- 2) Passive dispersers: Taxa lack flight abilities and primarily rely on attachment to active dispersers for recolonization, however, studies demonstrating the importance of this mode of recolonization are limited (Wissinger 1999). Examples taxa include Hydracarina, Oligochaeta, Isopoda, Amphipoda, and Bivalvia (Williams 1987, Wissinger et al. 2004). Passive dispersers utilize various strategies for persisting during dry periods. Desiccation resistant eggs are found in many crustaceans. A protective mucus layer is excreted by oligochaetes, leeches, and snails. Other groups without these abilities, such as amphipods and isopods, seek refuge deep in the sediment where sufficient moisture is still present (Wiggins et al. 1980, Wissinger 1999).

An earlier classification of temporary wetland taxa was developed by Wiggins et al. (1980) and divided taxa into 4 groups based on life histories.

- 1) Overwintering residents survive drying by having drought resistant eggs, cysts, or burrowing into moist sediment. Examples include Mollusca, Branchiopoda, Decapoda, and Oligochaeta.
- 2) Overwintering spring recruits develop rapidly, emerge as adults, and oviposit before pools dry. During drought, these group 2 macroinvertebrates aestivate in the dry substrate in various life stages. Examples include Coleoptera (Haliplidae), Trichoptera (Polycentropodidae), Ephemeroptera (Siphonuridae, Leptophlebiidae), and Diptera (Chironomidae, Tabanidae, Stratiomyidae, Ceratopogonidae).
- 3) Overwintering summer recruits oviposit into the dry substrate or vegetation once the pool has dried. They may aestivate as eggs or larvae. Examples include Trichoptera (Limnephilidae, Phyganeidae), Odonata (Lestidae, Libellulidae), and Diptera (Culicidae, Chaoboridae, Sciomyzidae, Chironomidae).
- 4) Non-wintering spring migrants breed in pools and return to permanent overwintering sites before drying occurs. Examples include Coleoptera (Dytiscidae), Odonata (Aeshnidae), Ephemeroptera (Baetidae), and Hemiptera (Belostomatidae).

This classification can be simplified and more universally applied to studies by condensing Groups 2-4 into active dispersers and Group 1 into passive dispersers. Not all studies on temporary wetlands sample multiple times and, thus, may have an underrepresentation of certain groups (e.g., overwintering summer recruits when

sampling in the winter). Additionally, this grouping system was based on research completed in the northeastern U.S. The distributions of many taxa may make this system less applicable to other geographic regions (Williams 1987, Wissinger 1999).

It is noteworthy that in previous studies, uncommon or rare species have been found in temporary pools yet the life histories and adaptations that would allow them to avoid desiccation are not well understood (Colburn 2004). Examples include species of Megaloptera (*Chaulioides* sp.) and various mayfly (Batzer & Sion 1999; Colburn 2004). Consequently, grouping them by dispersal ability has not been completed for most studies.

One explanation of this relationship is that hydroperiod may affect the pool area, thus increasing or decreasing the different "biotic zones" within the pool (Brooks 2000).

Factors affecting Macroinvertebrate Assemblages

Temporary wetland studies have addressed multiple factors to determine the influences on macroinvertebrate community assemblages. Studies have investigated the role of leaf litter (Batzer et al. 2004), water chemistry (Batzer et al. 2004, 2005), hydroperiod (Wiggins et al. 1980, Wissinger 1997, Batzer et al. 2004, 2005, Colburn 2004, Maltchik et al. 2009, Silver et al. 2012), pool morphology (Semlitsch & Bodie 1998, Batzer et al. 2004, Carl & Blumenshine 2005), vertebrate predation (Wissinger & Gallagher 1999), and canopy structure (Batzer et al. 2004, Colburn 2004). Hydroperiod and pool morphology are most often identified as the primary influences of macroinvertebrate assemblages.

Hydroperiod

Temporary pools naturally fluctuate in the length of time they are flooded. Variation in precipitation, evapotranspiration, and evaporation determine the length of hydroperiod (Wiggins et al. 1980, Colburn 2004, Sasamoto 2010). There is little disagreement that hydroperiod has an effect on macroinvertebrate assemblages, specifically abundance (Williams 1997; Batzer et al. 2004, 2005; Maltchik et al. 2009; Silver et al. 2012); however, its influence on species richness is less clear and has produced fewer significant results (Brooks 2000; Batzer et al. 2004, 2005; Maltchik et al. 2009; Silver et al. 2012).

One explanation of this relationship is that hydroperiod may affect the pool area, thus increasing or decreasing the different "biotic zones" within the pool (Brooks 2000). Changes in these life zones may be more influential on macroinvertebrates than hydroperiod alone. Brooks (2000) found a positive association between pond area, the number of habitats within the pond, and changes in macroinvertebrate richness.

Time required for development could limit species distributions (Schneider & Frost 1996, Schneider 1999, Maltchik et al. 2009), although it has been argued that most species in temporary pools are habitat generalists (Wissinger 1997). Based on this hypothesis, macroinvertebrates in pools with shorter hydroperiods would be restricted to taxa with rapid development and short life cycles, such as Culicidae, Chaoboridae, and oligochaetes (Schneider 1999). Pools with longer hydroperiods would support those taxa

found in shorter cycle pools as well as taxa that require longer development, such as Coleoptera, Hemiptera, and Odonata (Schneider 1999).

It is also worth considering that inconsistencies in the degree of taxonomic resolution among studies can produce results that are misleading. It is not uncommon for macroinvertebrates to be identified to family in community studies. Improved taxonomic resolution may reveal significant differences not evident when only identifying to family (Batzer et al. 2004).

Pool Morphology

Pool morphology refers to the depth, surface area, and inter-pool distances of temporary pools. Pool area and macroinvertebrate richness have been shown to be positively correlated (Kiflawi et al. 2003, Colburn 2004, Carl & Blumenshine 2005, Park et al. 2016). Increased “biotic zones,” as discussed previously, can help to explain increased diversity in larger pools (Brooks 2000). Inter-pool distance also influences diversity and has been shown to be primarily important to migration between pools (Semlitsch & Bodie 1998). Temporary woodland pools far from other pools will have a decreased likelihood of individuals migrating to or from that temporary woodland pool. Migration can be important to the restoration of disturbed wetlands via colonization (Semlitsch & Bodie 1998) as well as serving as a mechanism for maintaining species diversity (Wissinger & Gallagher 1999). For active dispersers that seek out permanent bodies of water to overwinter, inter-pool distances may be significant in maintaining the

diversity of temporary habitats, as well as permanent water bodies where species overwinter (Wissinger & Gallagher 1999). In this respect, diversity in temporary wetlands has been explained by some using Island Biogeography Theory described by MacArthur and Wilson in 1967 (Williams 1987, Kiflawi et al. 2003, Carl & Blumenshine 2005). This theory may be appropriate for describing temporary wetlands using inter-pool distances to predict diversity similarly to that of distance of islands to the mainland. Additionally, hydroperiod has been related to colonization rates just as island sizes has, where shorter hydroperiod pools fill more often, colonize more rapidly, and have higher extinction rates compared to longer hydroperiod pools (Williams 1987). Other studies have concluded that inter-pool distance and pool area are less important in maintaining diversity and may only be evident when comparing drastically different habitats (Brose 2003, Batzer et al. 2004).

Surrounding Landscape

It is important to recognize the interconnectedness of habitats with the surrounding landscape. Temporary woodland pools may be viewed as transitional areas, however, most temporary wetlands remain an important component of the landscape and ecosystem for many years (Batzer & Sharitz 1999). Diversity and abundance can vary greatly between temporary woodland pools; however, the factors determining diversity and abundance are not fully understood. The most influential factors seem to be hydroperiod and inter-pool distances (Semlitsch & Bodie 1998, Batzer et al. 2004, Carl &

Blumenshine 2005, Wiggins et al. 1980, Wissinger 1997, Batzer et al. 2004, 2005, Colburn 2004, Maltchik et al. 2009, Silver et al. 2012). The importance of vegetative buffer, canopy structure, and other factors regarding the surrounding landscape remain unclear and poorly studied. For instance, many species living in temporary woodland pools are heavily dependent on upland areas adjacent to pools (Semlitsch 1998). Semlitsch (1998) emphasized the importance of “terrestrial buffer zones” to salamander species as well as other amphibians found in temporary woodland pools. It is suggested that temporary woodland pools and adjacent terrestrial zones be protected to maintain the species diversity found in these habitats (Semlitsch 1998, Brooks 2000).

Macroinvertebrates are recognized as being vital to the trophic structure in temporary woodland pools, yet little is known about the influences of the surrounding landscape on pool richness. To better understand the mechanisms driving changes in temporary woodland pools, studies should seek to address those poorly studied factors. Combined research of all possible influences on diversity can provide a better understanding of temporary woodland pool ecology. In addition, knowledge of the factors affecting diversity can be used to protect temporary woodland pools from potential disturbance or destruction. To date, there have been no studies that have addressed the relationship between macroinvertebrate assemblages, vegetative buffer and run-off, specifically in agricultural areas in the southeastern United States.

Objectives

CHAPTER II

The goal of this study was to determine the association between macroinvertebrate assemblages in temporary woodland pools and varying levels of disturbance, specifically those resulting from agriculture and logging. I hypothesized that macroinvertebrate communities are influenced by disturbance. I predicted, based on previous studies focused on pool morphology and hydroperiod that:

- 1) Temporary woodland pools with more vegetative buffer, higher average diameter at breast height (DBH) of trees, and low disturbance will have increased taxa richness.
- 2) Alternatively, temporary woodland pools with less vegetative buffer, decreased DBH, and high disturbance will have decreased taxa richness.

CHAPTER II

STUDY AREA AND METHODS

Study Area

The Western Pennyroyal Karst Plain is a level IV ecoregion within the Interior Low Plateau physiographic province (Baskin et al. 1994, Drummond 2000). The region, commonly referred to as the "Pennyroyal Plain," is underlain with Mississippian age limestone of the St. Louis and St. Genevieve formations (Klemic 1966, Baskin et al. 1994). Lacking a resistant capstone, the limestone has been easily eroded overtime resulting in a rolling landscape with numerous caves, sinkholes, sinking streams, depressions, and natural wetlands (Baskin et al. 1994, Drummond 2000). Soils in the region vary by landform, but are generally silt-loam and clayey. Specifically in depressions, typical soils are "Robertsville (fine-silty, mixed, mesic type fragiaqualfs, alfisols) in Kentucky and Guthrie (fine-silty, siliceous, thermic typic fragiaqualfs, ultisols) in Tennessee" (Baskin et al. 1994). As a result of the underlying geology and unique soils, the region is dynamic, with continuous erosion creating new depressions, enlarging existing ones, and filling others with sediment (Chester & Ellis 1989, Currans 2002).

Historically, the Pennyroyal Plain is believed to have been dominated by fire dependent grasslands and open woodlands (Campbell 2012, Noss 2013). As a result of settlement and fire suppression, the landscape is now approximately 96% forested and agriculture with the latter making up nearly 51% of the total (Drummond 2000). Most

wetlands in the area are surrounded by agricultural fields. Those not directly impacted by row crop agriculture are often forested.

Site Selection and Description

The National Wetlands Inventory (U.S. Fish & Wildlife Service 2015) was used to locate potential sites for sampling. Sites were selected in order to represent a wide range of disturbance levels. Vegetative buffer was chosen as a measure of the impact of adjacent land use. Canopy cover, canopy height, and DBH were chosen as measures of prior disturbance from logging or other major disturbance. Ground-truthing was conducted in April of 2015 at 16 sites selected from the wetland inventory, information from landowners, as well as existing knowledge of wetlands in the area. Study sites were selected based on having adequate water levels for sampling and being generally

In Montgomery County, TN and Logan County, KY, 10 temporary woodland pools were sampled (Figure 1). All sites were forested and either in proximity to, adjacent to, or completely surrounded by agricultural fields. Dominant canopy vegetation varied by site, but generally included Swamp Cottonwood (*Populus heterophylla*), Pin Oak (*Quercus palustris*), Sweetgum (*Liquidambar styraciflua*), Black Willow (*Salix nigra*), Red Maple (*Acer rubrum*), and Willow Oak (*Quercus phellos*). Pools ranged widely in maximum size, from 300-33,500m² (0.03 - 3.35ha). Water in all sites appeared to be high in tannic acid as indicated by the brown, tea-like appearance. Tannins result from the breakdown of leaves (and other herbaceous growth) in water

bodies and can significantly decrease the pH of a water body (Colburn 2004). It is important to note, however, that the geology and use of fertilizer and lime on surrounding land can increase the pH of water in sites that would otherwise be much more acidic (Colburn 2004).

Hydroperiod for study sites was determined to be a result of evaporation and evapotranspiration as no surface water connections were observed. Years of data regarding the flooding and drying patterns would be required to accurately determine the hydroperiod of a temporary wetland (Colburn 2004), however based on observations of water levels throughout our study we believed that the majority of these sites fall into the category of “autumnal pools” as described by Wiggins et al. (1973). Autumnal pools typically fill in the fall, remain filled through the winter, and dry in late spring or early summer (Wiggins et al. 1973, Colburn 2004). The classification of autumnal pools by Wiggins et al. (1973) is based on research of temporary pools in the Northeast that are much wetter compared to pools of the Southeast (Wissinger 1999). For this reason, “Summer Dry” has been suggested as an alternative description of hydroperiod for temporary pools in the Southeast (Wissinger 1999).

Approximate pool area (m^2) at maximum capacity was determined using Google

Earth Engine. Satellite images were used when water was visible through vegetation in

the images. Images were taken at or near a maximum for each site. Images from

the same date were used for each site. Images from the same date were used for each site.

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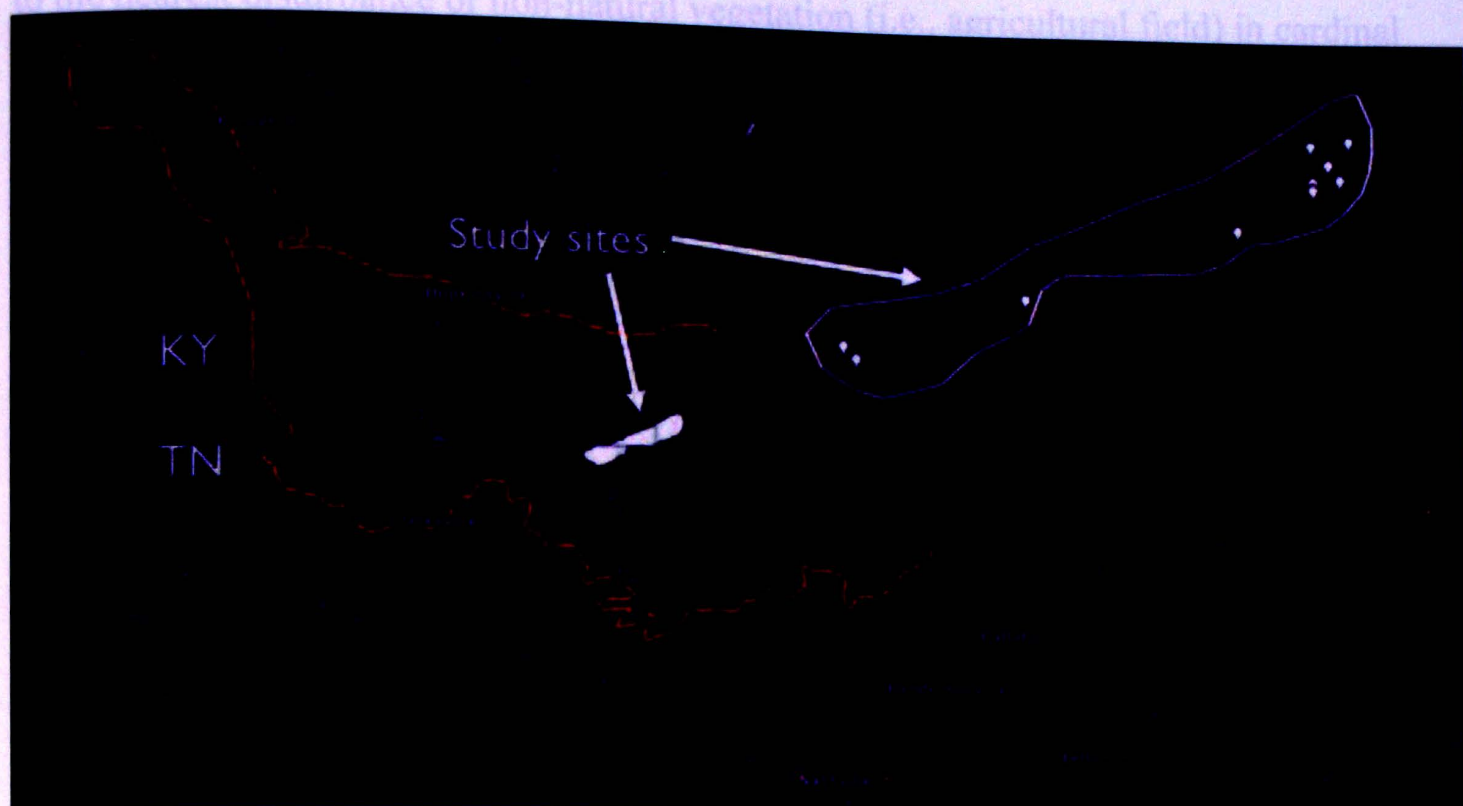


Figure 1. Location of study sites within the Western Pennyroyal Plain Karst Plain ecoregion, Montgomery County, Tennessee and Logan County, Kentucky.

Habitat characteristics and measures of disturbance

Temperature ($^{\circ}\text{C}$), pH, specific conductivity ($\mu\text{S}/\text{cm}$), total dissolved solids (TDS, mg/L), and dissolved oxygen (DO, % saturation and mg/L) were measured using a YSI 600QS multi-parameter meter.

Approximate pool area (m^2) at maximum capacity was determined using Google Earth Pro[®]. Fall satellite images were used when water was visible through vegetation in satellite images and water levels were at or near a maximum for each site. Images from the same year were used for consistent comparisons along with the polygon and area functions of Google Earth Pro[®] to determine approximate pool area.

Mean vegetative buffer (m) for each site was measured from the edge of the water to the nearest disturbance or non-natural vegetation (i.e., agricultural field) in cardinal directions. Distances $\leq 50\text{m}$ were measured physically with meter tape and $> 50\text{m}$ measured using Google Earth Pro®.

Canopy height, canopy cover, diameter breast height (DBH) were determined using methodology from the CVS-EEP Protocol for Recording Vegetation (Lee et al. 2008). Canopy height was approximated to the nearest meter. Canopy cover was measured in percent cover and estimated as a range of ± 10 to 20% depending on variation within the site. For DBH, 10m by 10m plots were established, living trees with a DBH $\geq 10\text{cm}$ were measured using standard DBH tape and notes were taken on the general characteristics of the understory within the plot.

Dominant canopy species were determined by survey of most abundant canopy species. Notes on understory characteristics, such as sapling density, emergent vegetation coverage in pools, presence of conservative species, and dominant species were taken as well.

An accurate measure of hydroperiod would require multiple years of data regarding the duration and frequency of flooding, including the year prior to sampling. Mean maximum water level was chosen as a surrogate and measured using high water marks on trees (Fig. 2c). For each site, 5 trees in the deepest areas of the pool were selected for measurement to calculate a mean maximum water level (cm) using discoloration on the trees.

Macroinvertebrate sampling

All macroinvertebrate sampling took place May 19 - 22, 2015. Eight funnel traps were deployed at each site collected over a period of 48hrs. Four benthic samples were taken from each site.

Funnel traps capture actively swimming fauna in the water column. Traps were constructed from 2L plastic bottles by removing the top 1/3 of the bottle. The removed top portion was inverted into the remaining larger 2/3 of the bottle and secured using zip ties (Fig. 2a-b). Traps were submerged at cardinal points in littoral regions of the pool where water was at least 30cm deep to ensure traps were fully covered. Traps were left in place for approximately 24hrs, after which they were removed and the contents were poured through a 600µm sieve to collect contents. Specimens were placed into 1L containers and preserved in 70% isopropanol. The traps were redeployed to obtain a second set of four samples for the subsequent 24-hour period.

Benthic sampling was performed with samplers constructed from a plastic 5g bucket (18.9L) with the bottom removed. A 20cm by 15cm fine mesh net was used to disturb the substrate in the bucket and collect the contents. All material was placed into 1L container and preserved in 70% isopropanol. On the same day that funnel traps were initially deployed, benthic sampling were collected in the shallow margins at cardinal points in each site.



Figure 2(a). Example of high water marks on trees used for measuring mean maximum water level., (b) funnel trap for macroinvertebrate sampling, and (c) example of positioning for traps in study sites in littoral region

Macroinvertebrate processing

In the laboratory, samples were first poured through a 600 μ m sieve. Debris such as large leaves, rocks, nuts, etc. were thoroughly rinsed over the sieve separated into a debris jar. The remaining material (including that rinsed into sieve) was placed into a 300ml glass culture dish and filled with 70% isopropanol. The sample was examined under a dissecting microscope until all macroinvertebrates were removed. In most cases, macroinvertebrates were identified to genus using standard keys (Thorpe & Covich 1991; Larson et al. 2000; Epler 2001, 2006, 2010; Merritt et al. 2008). Some taxa were left at less resolved taxonomic levels for various reasons including being too immature, poor or damaged specimens, or the common level of identification in most literature for particular taxonomically difficult groups (i.e., Oligochaeta, Acarina, and Nematoda).

Chironomid specimens were mounted on glass microscope slides using CMC-10 and identified to genus using a compound microscope (Epler 2001). Subsampling was completed for sites where specimen numbers exceeded 100.

Data analysis

Taxa richness, Peilou's evenness, and Shannon-Weaver Diversity Index were calculated for each site using Microsoft Excel. These are common metrics used in macroinvertebrate community studies and, thus, allow for wider comparisons. Taxa were grouped as passive or active dispersers (Table 1A, 2A) based on previous studies and grouping completed by Williams (1987), Wissinger (1997), and Batzer & Ruhí (2013).

To compare sites based on all taxa found in samples, Percent of Similarity was calculated between sites as:

$$\% \text{ of Similarity} = \sum \text{minimum } (t_{1a}, t_{1b}), (t_{2a}, t_{2b}) \dots$$

where “ t_1, t_2 ” represent the taxa and “a, b” represent the different sites.

All other statistical analyses were conducted using JMP Pro v. 10 (SAS Institute, Cary, NC). To determine if there were any associations between dispersal ability and site, a contingency analysis was used. To identify dependencies among community metrics, dispersal ability, and habitat variables, a pairwise correlations analysis ($\alpha = 0.05$) was used. Following evaluation of the pairwise correlations, single linear regressions were used to further analyze each relationship. In order to quantify the effects of disturbance, mean DBH, mean vegetative buffer, and mean water level data was divided

into "low," "medium," and "high" disturbance based on equal division of the range

values for each variable. To determine the effects of disturbance on community metrics,

a one-way analysis of variance (ANOVA) and post-hoc Tukey HSD to compare all pairs

Habitat

of means was used.

Temperature ranged from 16.48-30.91°C, pH from 5.87-6.42, specific conductivity from 0.07-0.168 $\mu\text{S}/\text{cm}$, TDS from 0.045-0.11 g/L, and DO saturation from 4.2-115.3% (Table 1). Site 2 represented the lowest end of the range for most water chemistry metrics while sites 10 and 12 represented the highest end of these ranges.

Table 1. Water chemistry data obtained from YSI meter

Site	pH	Temperature (°C)	Conductivity ($\mu\text{S}/\text{cm}$)	Total dissolved solids (g/L)	Dissolved oxygen (%)	Dissolved oxygen (g/L)
2	5.87	18.02	0.089	0.058	4.2	0.39
3	6.20	16.48	0.102	0.066	16.3	1.58
7	6.00	19.89	0.096	0.062	7.9	0.78
8	5.97	20.72	0.070	0.045	9.3	0.83
10	6.32	30.91	0.132	0.086	115.3	8.57
12	6.42	22.59	0.168	0.110	17.0	1.46
13	5.87	19.98	0.102	0.066	12.8	1.13
14	6.25	20.93	0.114	0.074	15.6	1.37
15	6.23	20.23	0.109	0.071	17.0	1.53
16	6.00	20.25	0.080	0.052	11.2	1.00

CHAPTER III

RESULTS

Habitat

Temperature ranged from 16.48-30.91°C, pH from 5.87-6.42, specific conductivity from 0.07-0.168 $\mu\text{S}/\text{cm}$, TDS from 0.045-0.11 g/L, and DO saturation from 4.2-115.3% (Table 1). Site 2 represented the lowest end of the range for most water chemistry metrics while sites 10 and 12 represented the highest end of these ranges.

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Canopy height ranged from 15-45m, canopy density from 50-95%, and mean DBH from 13.54-44.75cm (Table 2). Sites 8 and 16 had the highest mean DBH and site 3 the lowest mean DBH. Site 10 had the highest canopy density and sites 2, 3, and 15 had the lowest canopy densities. Pool area ranged from 300-33,500m² (0.03-3.35ha) with the smallest and largest pools being sites 3 and 16, respectively. Mean vegetative buffer ranged from 13.5-188.8m, where site 2 had the highest mean vegetative buffer and site 15 the lowest. Mean maximum water level ranged from 17.1-77.7cm, where site 15 had the highest mean maximum water level and site 10 the lowest.

Table 2: Site characteristics. DBH = tree diameter at breast height (>10 cm)

Site	Max area (m ²)	Mean max water level (cm)	Mean DBH (cm)	Mean vegetative buffer (m)	Canopy height (m)	Canopy density (%)
2	1900	36.2	35.31	188.75	40	50
3	300	50.0	13.54	158.75	15	50
7	7100	39.1	17.33	131.33	35	88
8	3300	59.8	43.37	32.50	40	85
10	5100	17.1	20.62	155.75	35	95
12	1400	55.0	24.89	47.38	30	85
13	2300	57.4	35.75	83.38	30	65
14	7600	61.4	22.46	112.00	35	75
15	6800	77.7	28.85	13.50	45	53
16	33500	46.8	44.75	122.75	40	85

Macroinvertebrates

In total, 11,616 macroinvertebrate specimens of 67 different taxa were collected from all benthic and funnel trap samples (Table 3A). Richness for study sites ranged

from 16-33 taxa (Table 3). Calculations for Peilou's evenness ranged from 0.124-0.658. Shannon-Weavers Indices ranged from 0.343-2.261. Site 3 represented the lowest extreme for all metrics while sites 12 and 13 had the highest richness, evenness, and Shannon-Weaver Indices among all sites.

Table 3. Taxa richness, Peilou's evenness, and Shannon-Weaver index for all study sites

Site	Richness	Evenness	Shannon-Weaver Index
2	28	0.497	1.656
3	16	0.124	0.343
7	25	0.628	2.020
8	29	0.414	1.394
10	33	0.524	1.831
12	31	0.658	2.161
13	31	0.639	2.196
14	28	0.285	0.948
15	29	0.420	1.414
16	27	0.555	1.828

Correlations analysis

Macroinvertebrate associations

A contingency analysis indicated significant associations between dispersal ability and site ($p < 0.0001$; Table 4). For most sites, disperser types were not evenly distributed. For example, in site 2 and 10 the majority were active dispersers. In all other sites, passive dispersers dominated.

Table 4. Total and proportions of active and passive dispersers at each site

Individuals in sample

(% of sample)	Active Disperser	Passive Disperser	Total in sample
Site 2	722 (84.64%)	131 (15.36%)	845
Site 3	90 (21.13%)	336 (78.87%)	426
Site 7	292 (39.35%)	450 (60.65%)	740
Site 8	102 (8.11%)	1155 (91.89%)	1221
Site 10	1493 (65.20%)	797 (34.80%)	2131
Site 12	343 (31.50%)	746 (68.50%)	1037
Site 13	364 (37.68%)	602 (62.32%)	922
Site 14	110 (8.61%)	1167 (91.39%)	1164
Site 15	107 (10.71%)	892 (89.29%)	972
Site 16	479 (30.28%)	1103 (69.72%)	1551

Correlations analysis

The correlation analysis indicated that richness was positively correlated with temperature ($p=0.0344$; Fig. 3, Table 5). Richness and DBH showed no statistically significant association based on the correlations analysis. However, upon further inspection and using the Kernel smoother application that creates a line of best fit, it was determined that a non-linear regression was appropriate and this relationship was significant ($p=0.0273$; Fig. 4).

Table 5. Multivariate pairwise correlations matrix indicating correlation between community metrics and habitat variables.

Variable	by Variable	Correlation	Lower 95%	Upper 95%	Signif Prob
Active Disperser Proportion	DBH (cm)	-0.0174	-0.6400	0.6190	0.9621
Active Disperser Proportion	Canopy opening %	0.0661	-0.5880	0.6679	0.8560
Active Disperser Proportion	Mean Veg Buffer (m)	0.6872	0.1015	0.9191	0.0281*
Active Disperser Proportion	Temperature (C)	0.2168	-0.4781	0.7448	0.5474
Active Disperser Proportion	Area (m)	-0.1404	-0.7075	0.5366	0.6988
Active Disperser Proportion	pH	-0.2590	-0.7640	0.4429	0.4700
Active Disperser Proportion	DO%	0.3525	-0.3562	0.8037	0.3178
Active Disperser Proportion	Elevation (m)	0.5934	-0.0578	0.8904	0.0705
Passive Disperser Proportion	DBH (cm)	-0.0176	-0.6402	0.6189	0.9614
Passive Disperser Proportion	Canopy opening %	-0.0650	-0.6673	0.5887	0.8584
Passive Disperser Proportion	Mean Veg Buffer (m)	-0.6638	-0.9122	-0.0588	0.0363*
Passive Disperser Proportion	Temperature (C)	-0.2254	-0.7487	0.4711	0.5313
Passive Disperser Proportion	Area (m)	0.1504	-0.5293	0.7126	0.6783
Passive Disperser Proportion	pH	0.2711	-0.4270	0.7720	0.4382
Passive Disperser Proportion	DO%	-0.3480	-0.8019	0.3606	0.3244
Passive Disperser Proportion	Elevation (m)	-0.6039	-0.8937	0.0415	0.0645
Passive Disperser Proportion	Active Disperser Proportion	-0.9988	-0.9997	-0.9949	<.0001*
Passive Disperser Proportion	Mean max water level (cm)	0.7797	0.2948	0.9453	0.0078*
Active Disperser Proportion	Mean max water level (cm)	-0.7927	-0.9488	-0.3255	0.0062*
Richness	DBH (cm)	0.4048	-0.3018	0.8243	0.2459
Richness	Canopy opening (%)	-0.4392	-0.8373	0.2633	0.2042
Richness	Mean Veg Buffer (m)	-0.3728	-0.8119	0.3356	0.2886
Richness	Temperature (C)	0.6770	0.0825	0.9161	0.0315*
Richness	Area (m)	-0.0369	-0.6514	0.6068	0.9194
Richness	pH	0.0741	-0.5827	0.6723	0.8388
Richness	DO(%)	0.3821	-0.3260	0.8155	0.2759

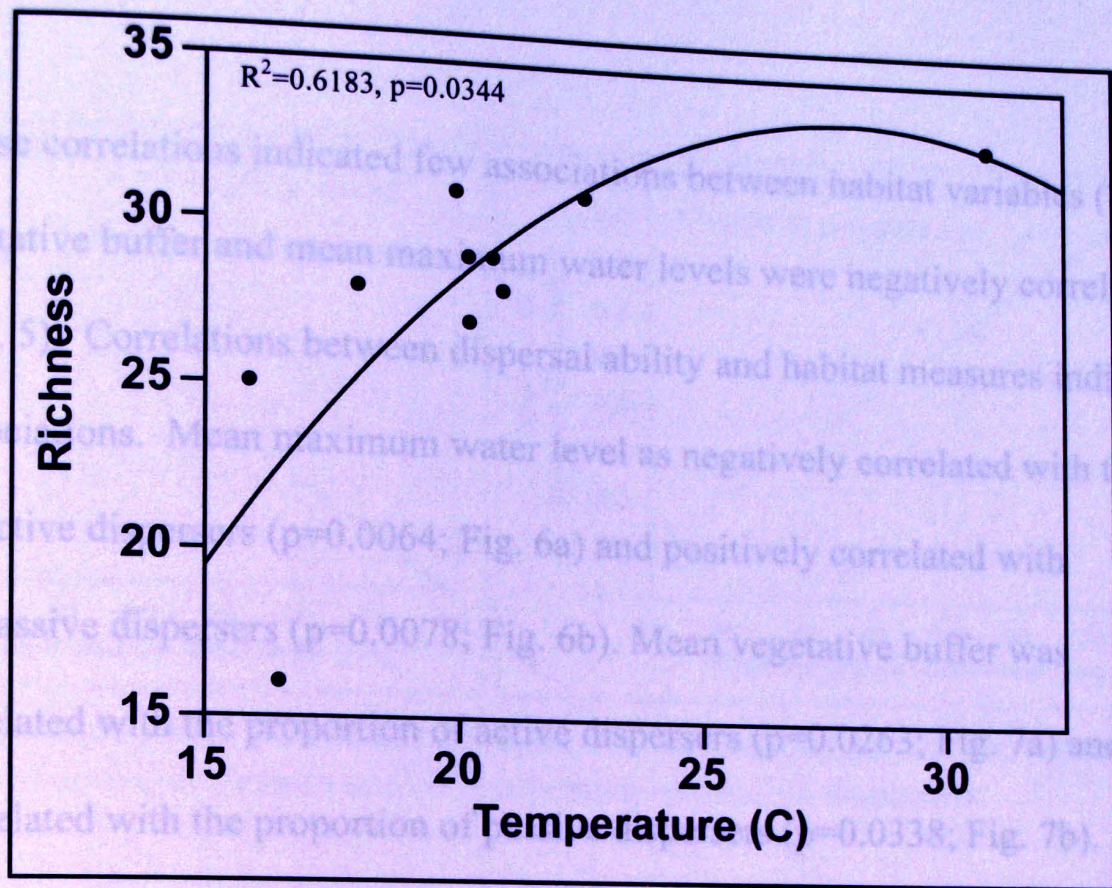


Figure 3. Nonlinear regression of temperature vs. richness.

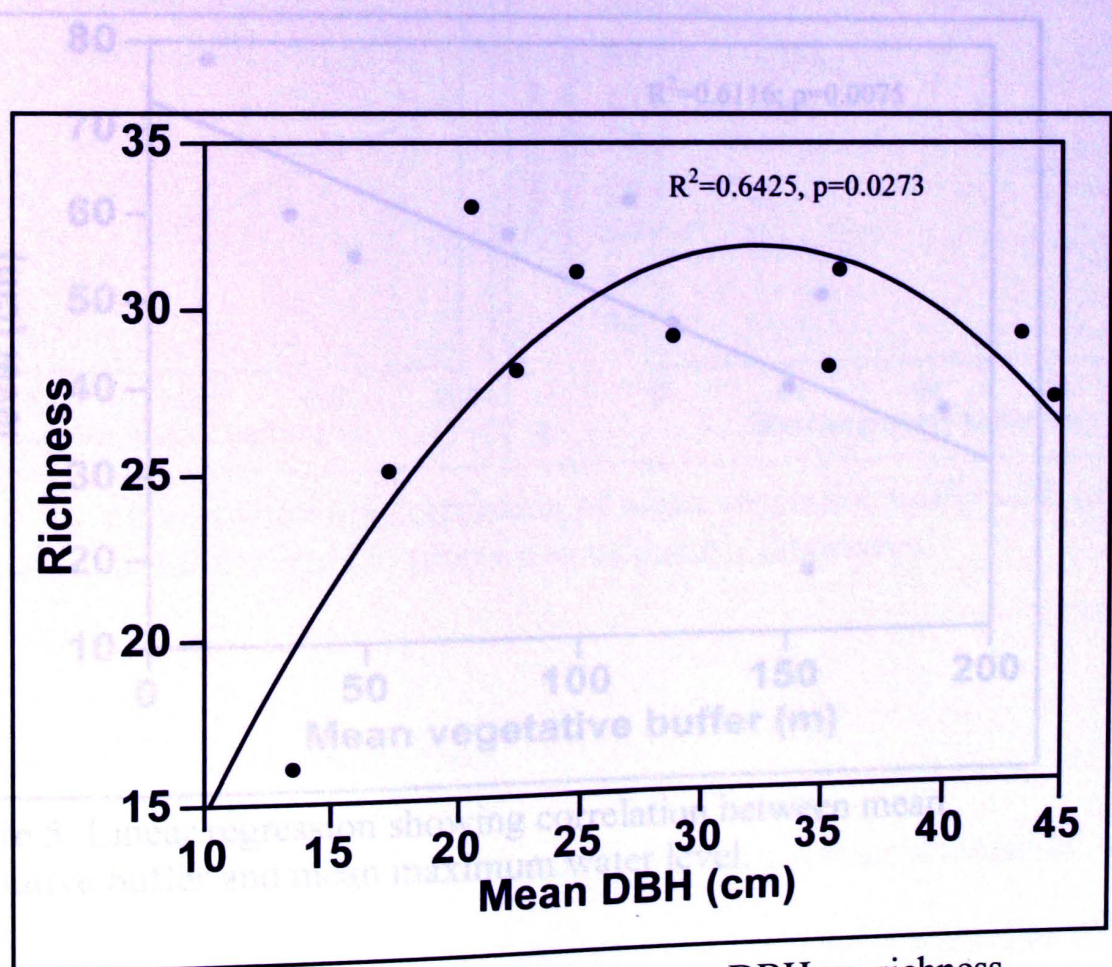


Figure 4. Nonlinear regression of average DBH vs. richness.

Pairwise correlations indicated few associations between habitat variables (Table 5). Mean vegetative buffer and mean maximum water levels were negatively correlated ($p=0.0075$; Fig. 5). Correlations between dispersal ability and habitat measures indicated significant associations. Mean maximum water level was negatively correlated with the proportion of active dispersers ($p=0.0064$; Fig. 6a) and positively correlated with proportion of passive dispersers ($p=0.0078$; Fig. 6b). Mean vegetative buffer was positively correlated with the proportion of active dispersers ($p=0.0263$; Fig. 7a) and negatively correlated with the proportion of passive dispersers ($p=0.0338$; Fig. 7b).

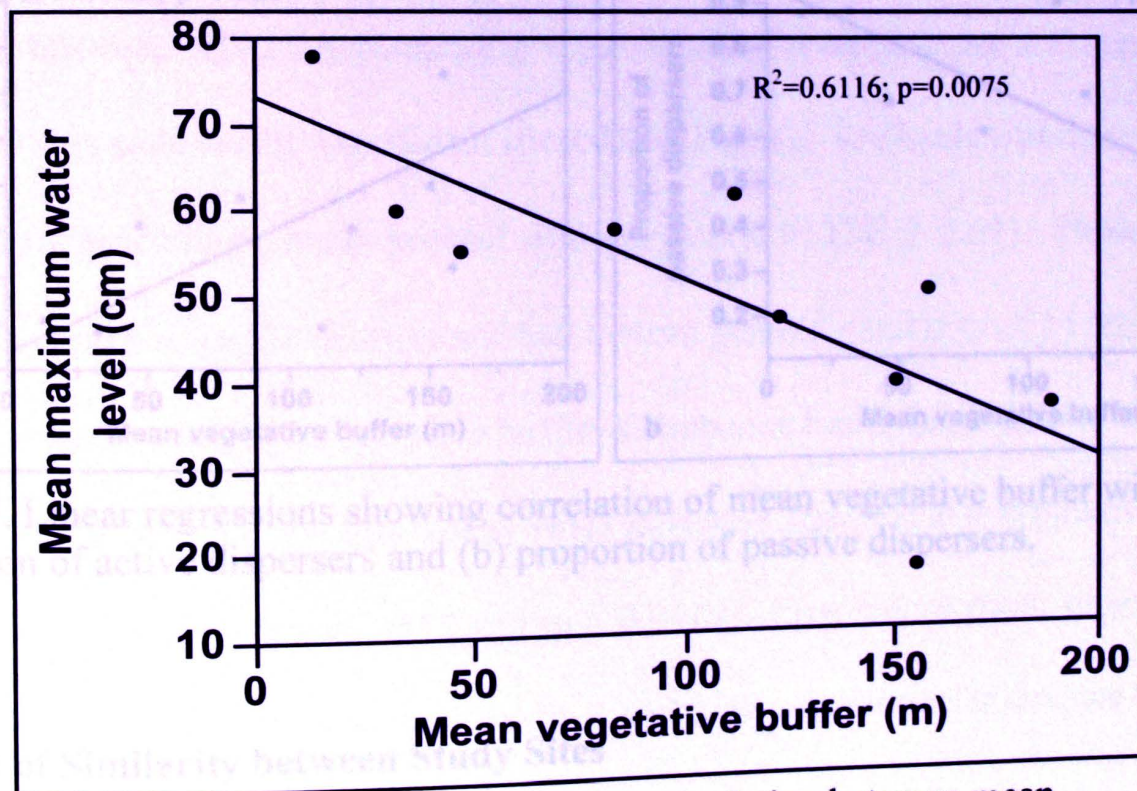


Figure 5. Linear regression showing correlation between mean vegetative buffer and mean maximum water level.

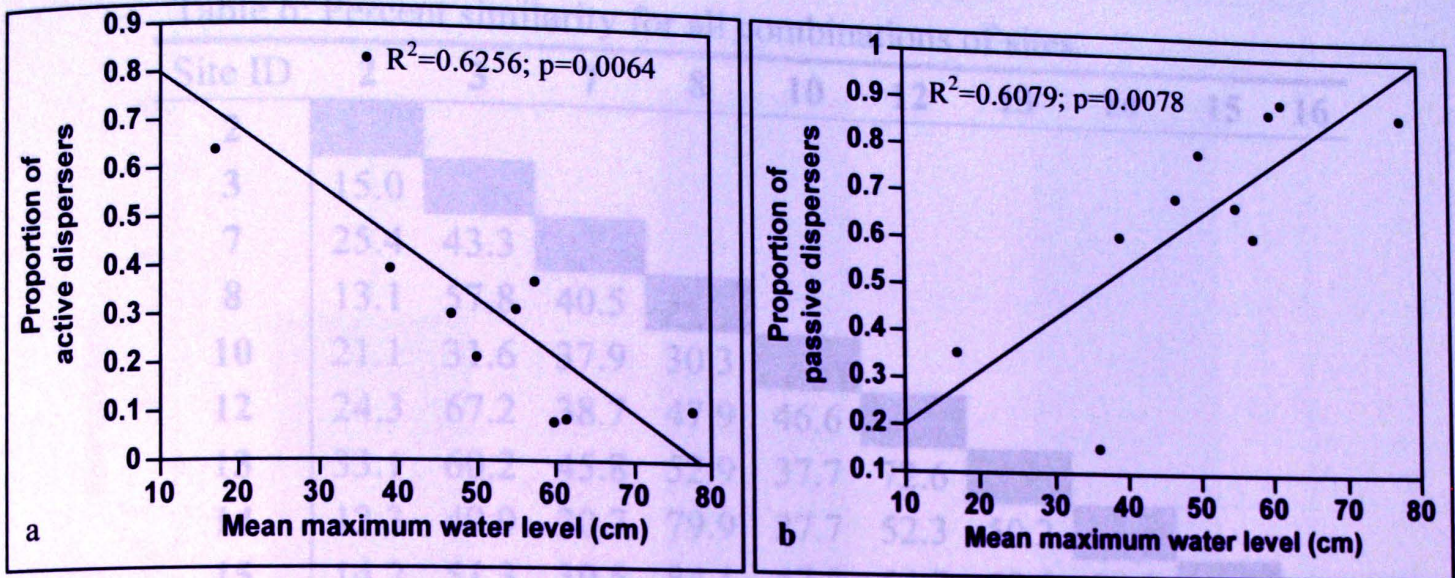


Figure 6. Linear regressions showing correlation of mean maximum water level with (a) proportion of active dispersers and (b) proportion of passive dispersers.

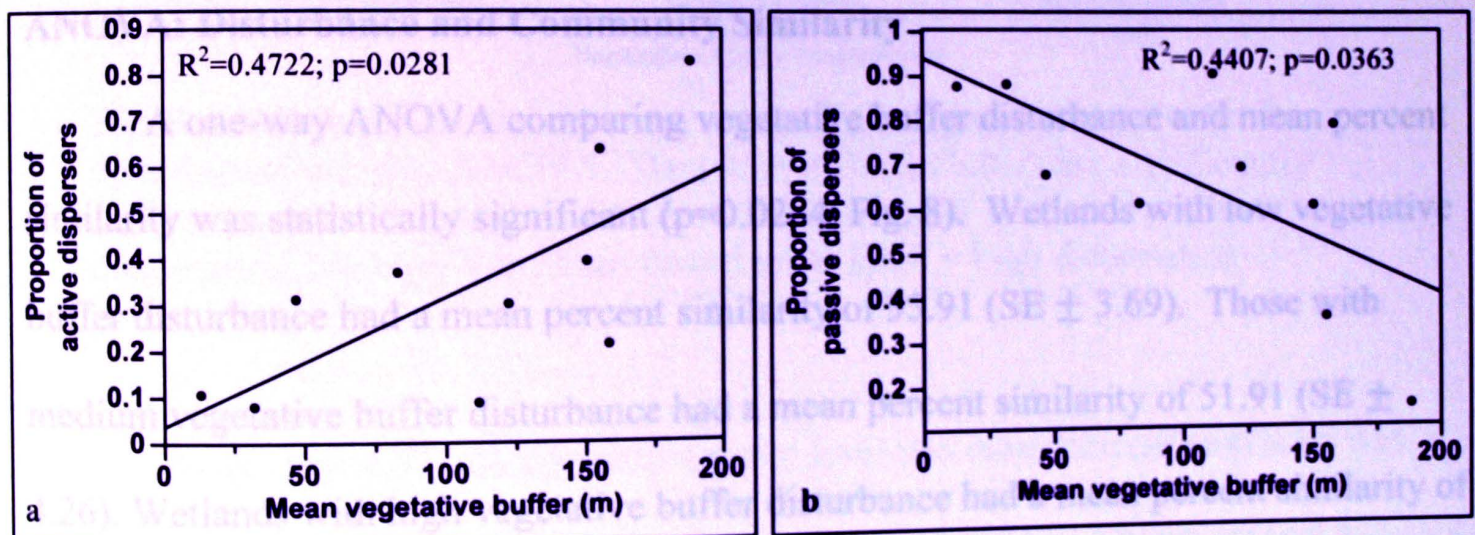


Figure 7. Linear regressions showing correlation of mean vegetative buffer with (a) proportion of active dispersers and (b) proportion of passive dispersers.

Percent of Similarity between Study Sites

Comparison of all sites revealed most study sites were similar (Percent of Similarity > 50%) to at least one other site (Table 6). The exceptions were sites 2, 7, and 10, which were not similar to any other sites (Percent of Similarity \leq 50%).

Table 6: Percent similarity for all combinations of sites.

Site ID	2	3	7	8	10	12	13	14	15	16
2										
3	15.0									
7	25.4	43.3								
8	13.1	57.8	40.5							
10	21.1	31.6	37.9	30.3						
12	24.3	67.2	38.7	47.9	46.6					
13	33.1	60.2	45.8	52.9	37.7	72.6				
14	12.3	49.9	30.7	79.9	27.7	52.3	50.2			
15	14.2	51.3	39.5	84.1	47.8	54.7	58.6	84.0		
16	35.8	55.2	50.0	68.8	34.5	57.8	56.4	59.9	68.7	

ANOVA: Disturbance and Community Similarity

A one-way ANOVA comparing vegetative buffer disturbance and mean percent similarity was statistically significant ($p=0.0284$, Fig. 8). Wetlands with low vegetative buffer disturbance had a mean percent similarity of 35.91 ($SE \pm 3.69$). Those with medium vegetative buffer disturbance had a mean percent similarity of 51.91 ($SE \pm 4.26$). Wetlands with high vegetative buffer disturbance had a mean percent similarity of 53.34 ($SE \pm 4.26$). An all pairs Tukey HSD indicated high and low vegetative buffer disturbance were significantly different ($p = 0.0410$). Low and medium vegetative disturbance ($p = 0.0579$), as well as medium and high vegetative disturbance ($p = 0.9693$) were not significantly different.

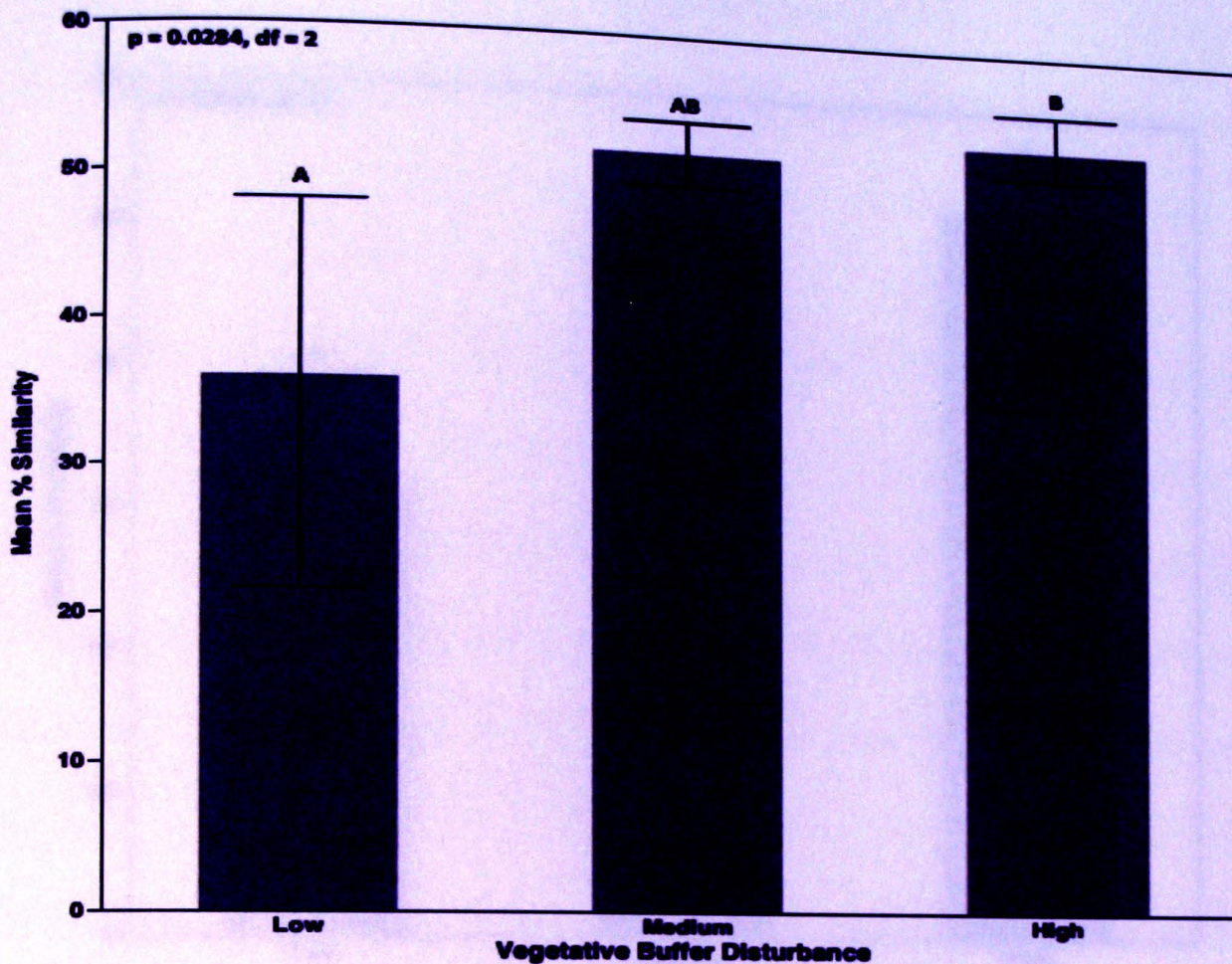


Figure 8. Mean (\pm SE) percent community similarity and vegetative buffer disturbance one-way ANOVA. Bars with different letters are significantly different ($p < 0.05$) based on post-hoc Tukey-Kramer HSD. Low = low disturbance, Medium = medium disturbance, High = high disturbance.

A one-way ANOVA comparing water level and mean percent similarity was statistically significant ($p=0.0034$, Fig. 9). Low water level had a mean percent similarity of 31.90 ($SE \pm 3.15$). Medium water level had a mean percent similarity of 51.63 ($SE \pm 2.44$). High water level had a mean percent similarity of 52.77 ($SE \pm 3.86$). An all pairs Tukey HSD indicated medium and low water levels had significantly different mean percent similarities ($p = 0.0041$). High and low water levels had significantly different mean percent similarities ($p = 0.0041$). High and low water levels had significantly different mean percent similarities ($p = 0.0041$). Medium and high water levels were not significantly different in terms of mean percent similarity ($p = 0.9668$).

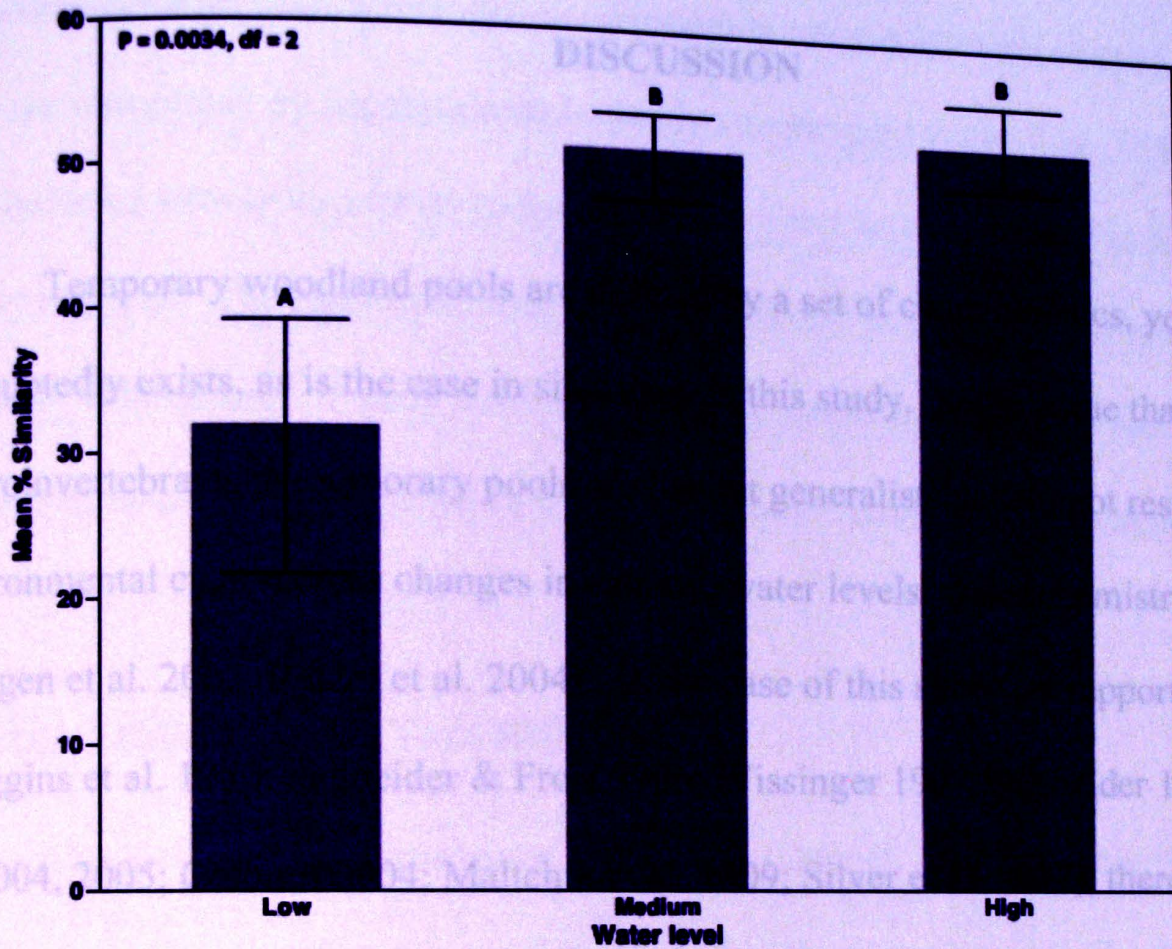


Figure 9. Mean (\pm SE) percent community similarity and water level one-way ANOVA. Bars with different letters are significantly different ($p < 0.05$) based on post-hoc Tukey-Kramer HSD. Low = low water level, Medium = medium water level, High = high water level.

Correlation between Habitat Variables

Correlations between habitat variables may prove vital to restoration and better understanding of these habitats. The negative correlation between mean vegetative buffer and mean water level in sites is attributed here to disturbance. In agricultural regions, runoff is a consequence of vegetation removal and soil compaction (Raghavan et al. 1990). The relationship between mean maximum water level and vegetative buffer is negative as well (e.g., increased vegetative buffer has been shown to significantly reduce water level; Zedler et al. 1998, Dousskey 2001, Zedler 2003). Wetland pools is driven by precipitation, well-

CHAPTER IV

DISCUSSION

Temporary woodland pools are defined by a set of characteristics, yet variation undoubtedly exists, as is the case in sites used in this study. Some argue that macroinvertebrates in temporary pools are habitat generalists and do not respond to environmental cues such as changes in canopy, water levels, water chemistry, etc. (Tangen et al. 2003, Batzer et al. 2004). In the case of this study, as supported by others (Wiggins et al. 1980; Schneider & Frost 1996; Wissinger 1997; Schneider 1999; Batzer et al. 2004, 2005; Colburn 2004; Maltchik et al. 2009; Silver et al. 2012), there is evidence that macroinvertebrate communities respond to environmental cues.

Correlation between Habitat Variables

Correlations between habitat variables may prove vital to restoration and better understanding of these habitats. The negative correlation between mean vegetative buffer and mean water level in sites is attributed here to disturbance. In agricultural regions, runoff is a consequence of vegetation removal and soil compaction (Raghavan et al. 1990). The relationship between mean maximum water level and vegetative buffer is likely a result of runoff. Increased vegetative buffer has been shown to significantly reduce agricultural runoff (Uusi-Kämpä et al. 1998, Dosskey 2001, Zedler 2003). Although the initial filling of temporary woodland pools is driven by precipitation, well-

buffered sites are exposed to decreased runoff compared to sites that are poorly buffered. Evapotranspiration plays a role also in maintaining more ephemeral sites as well-buffered sites are surrounded by vegetation and often have emergent vegetation. In this study, well-buffered sites have a lower mean maximum water level compared to sites that are poorly buffered. The result is shorter hydroperiods and an overall more ephemeral nature for well-buffered sites. Poorly buffered sites have longer hydroperiods and are exposed to more sporadic flooding events as a result of greater runoff from surrounding fields.

Effects of Disturbance on Taxa Richness

The Intermediate Disturbance Hypothesis (Connell 1978) explains the observed relationship between richness and DBH (Fig. 5) in the temporary woodland pool study sites. It is hypothesized that communities with high disturbance will have low richness due to increased competition and fewer resources, while communities with low disturbance will have low richness as a consequence of competitive exclusion. Conversely, a community with intermediate disturbance level would have the highest richness resulting from the overlap of both, low and high disturbance communities (Hutchinson 1953, Connell 1978, Townsend et al. 1997). Mean DBH, one measure of disturbance in these communities, appears to support this trend in richness (Fig. 5). Sites with higher mean DBH, representing less disturbance (e.g., sites 8 & 16), and sites with lower mean DBH, suggesting greater disturbance (e.g., 3 & 10), tend to have lower richness than those with more intermediate mean DBH values. It is worth noting that few

wetlands within this region are undisturbed, however a larger sample size including more “low disturbance” sites may make this relationship clearer.

Richness was also positively correlated with temperature (Fig. 4). Study sites represent an array of canopy openings, vegetative densities, and successional states. Temperature variation is influenced by water depth, canopy cover, and emergent vegetation (Williams 1987, Rose & Crumpton 1996, Williams et al. 2008). For this study, site 10 had the highest recorded temperature (30.91°C; Table 2) as well as the lowest mean maximum water level (17.1cm; Table 3). In contrast, site 7 had the lowest recorded temperature (15.89°C; Table 2) and a much higher mean maximum water level (39.1cm; Table 3). One explanation of the observed relationship is the differing thermal stability of pools. Deeper pools are likely to be more stable, whereas shallow pools are expected to have greater daily fluctuations (Williams 1987) which probably explains the higher temperature observed in site 10. It is likely richness is associated with multiple habitat variables, including temperature, and these in turn are influenced by levels of disturbance and pool morphology, as shown in previous studies (Semlitsch 1998; Brooks 2000; Kiflawi et al. 2003; Colburn 2004; Carl & Blumenshine 2005; Studinski & Grubbs 2016).

Effects of Habitat Variables on Distribution of Taxa with Differing Dispersal Abilities

The combined effects of vegetative buffer and runoff resulting in different hydroperiods explains the varying distribution of dispersal ability across sites. Passive

dispersers contain taxa that have drought resistant adaptations, but most require moist soil or access to the water table (Wiggins et al. 1980, Schneider 1999). Active dispersers, as a group, are not highly adapted for desiccation; however, many have rapid development and would be expected to have a greater presence in pools that have a longer dry phase (Wissinger 1997, Schneider 1999). The ability of active dispersers to migrate allows them to colonize ephemeral sites for breeding and then disperse to permanent overwintering sites. Furthermore, the inability of passive dispersers to thrive in these sites results in less competition for non-predatory developing larvae of active dispersers. Overall, colonization is a significant factor structuring community assemblages in highly ephemeral pools (Wissinger 1999). Conversely, competition and predation are more influential in pools with increased permanence (Wissinger 1999). Schneider and Frost (1996) reported similar results to this study using the life history grouping described by Wiggins et al. (1980), however, their study did not address vegetative buffers.

Community Similarity Among Study Sites

Calculating percent of similarity among study sites provided a more detailed comparison of sites regarding specific taxa and their proportions. Generally, study sites had at least one other site to which they had high similarity (>50%), with the exception of study sites #2, #7, and #10. Post hoc analysis of these sites revealed they are at the extreme ends for mean maximum water level and mean vegetative buffer suggesting these are the most ephemeral. Furthermore, these three sites also contain the highest

proportions of active dispersers compared to other study sites consistent with the hypothesis that active dispersers are favored in more ephemeral pools.

Study sites #2, #7, and #10 had very low percent of similarities to all sites even when compared to one another. It is hypothesized, based on these results, that vegetative buffer in agricultural fields protects temporary woodland pools from runoff and thus maintains their ephemeral nature. Additionally, compared to poorly buffered sites, more ephemeral pools maintain a more unique community. A Tukey-Kramer HSD and one-way ANOVA comparing water level to mean percent similarity supports this hypothesis as sites #2, #7, #10 were grouped as “low water level” and had significantly lower mean percent similarity than other sites. “Medium” and “high” water levels were indistinguishable based on the Tukey-Kramer HSD also providing evidence that less ephemeral sites are more similar. While the Tukey-Kramer HSD only indicated significant differences in mean percent similarity between low and high vegetative disturbance groupings, a trend of increased vegetative for more ephemeral sites was seen. One possible explanation for these more unique communities is that in more isolated temporary wetlands, migration may be limited (Wissinger 1999). Colonization may be primarily by active dispersers that overwinter in the adjacent terrestrial landscape, reiterating the importance of vegetative buffers around wetlands (Wissinger 1999). In contrast, poorly buffered sites have more similar communities. As a consequence of runoff, poorly buffered sites may also be at risk of becoming more permanent. Increased permanence for pools could alter species composition, increase the proportion of

predators, as well as the likelihood of introduction of fish (Semlitsch & Bodie 1998, Wissinger 1999).

It is notable that recent logging disturbance was evident in site #10. The understory was exceptionally dense with saplings and drawdown was rapid compared to other sites. The macroinvertebrate community was dominated by dipteran larvae of the families Culicidae and Chironomidae (>60% of the total sample). While vegetative buffer may prevent excess runoff, logging and other disturbance was evident within some wetlands and contributed to an understory dense with saplings. Disturbance of vegetation creates opportunity for shade intolerant vegetation and saplings to grow. Although water loss must be considered a result of evapotranspiration and surface evaporation, it has been shown that shade provided by larger trees reduces surface evaporation. The larger trees still remove water via evapotranspiration, but these effects are negated by some degree due to decreased surface evaporation (Limpens et al. 2014). In the case of site #10, the understory was dense with saplings and herbaceous growth, however little shading was provided. It is hypothesized that site #10 had its hydroperiod dramatically reduced as a result of increased surface evaporation in combination with high rates of evapotranspiration. As a consequence of disturbance, only rapidly developing dipterans were able to successively reproduce during the more abbreviated wet phase, as seen in other studies (Schneider & Frost 1996, Schneider 1999).

Future Directions

This study and others (Wiggins et al. 1980, Wissinger 1997, Batzer et al. 2004, 2005, Colburn 2004, Maltchik et al. 2009, Silver et al. 2012) have shown that macroinvertebrate community assemblages are dependent on hydroperiod. The role of vegetative buffer in agricultural wetlands is significant in determining hydroperiod and, thus, macroinvertebrate communities. Temporary woodland pools that are well-buffered are generally more ephemeral and more unique in terms of community composition.

The region of the Pennyroyal Plain and temporary wetlands found there are understudied. Continued sampling of the current study sites, particularly site #10, a recently logged site, can provide information on the recovery of wetlands following a major disturbance. Additional studies can focus on temporary woodland pools comparing a wider range of vegetative buffers, specifically exploring “low” and “medium” vegetative disturbance. In this study, the all pairs Tukey HSD produced from the one-way ANOVA exploring vegetative buffer disturbance did not differentiate between “low” and “medium” disturbance levels. A trend however is present as seen in the regressions. This suggests that a larger sample size may help to define a minimum buffer that would distinguish “low” and “medium” disturbance. A study of this magnitude may help to validate the current study as well as determine a minimum vegetative buffer adequate for protection of temporary woodland pools.

CHAPTER VI

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CHAPTER V

APPENDICES

Table 1A: Taxa grouped as passive dispersers for all study sites

Site ID	2	3	7	8	10	12	13	14	15	16
AMPHIPODA										
<i>Crangonyx</i>	2					6				
<i>Gammarus</i>	4	7	6		3	23		1		
Bivalvia										
Sphaeriidae	47	61	166	175	74	77	69	68	52	169
COLLEMBOLA	19		2	29	19	1	2	5		1
DECAPODA										
Cambaridae		1	1	1	4	5	2	1	2	5
<i>Cambarus</i>	1	1		4	2	2	1	2	1	
GASTROPODA										
Physidae	3	4	4	1			14		8	2
Planorbidae	2	4	91	32	4	21	32	4	52	91
HIRUDINIDAE	1	5	5					1	5	
ISOPODA										
<i>Caecidotea</i>	56	90	31	20	187	170	102	27	27	50
OLIGOCHAETA	7	163	144	886	418	390	338	1050	718	755
HYDRACARINA	8		2	36	105	52	44	13	27	31
Total individuals	150	336	452	1184	816	747	604	1172	892	1104
# of taxa	11	9	9	9	11	11	8	10	9	7
Proportion of site	0.17	0.79	0.61	0.90	0.36	0.68	0.61	0.91	0.87	0.69

Table 2A: Taxa grouped as active dispersers for all study sites

Site ID	2	3	7	8	10	12	13	14	15	16
COLEOPTERA										
<i>Acilius</i>	15	1	1	7	1	7	27	1	25	42
<i>Acilius fraternus</i>		32				2	2	4	1	1
<i>Agabates acuductus</i>				3		2		1		1
<i>Agabus</i>	3				6		1	4	2	2
<i>Bidessonotus</i>	6							2		
<i>Cybister</i>							1			
<i>Dibolocelus</i>									1	
Dytiscidae			1	1	12					1
<i>Dytiscus</i>	3		1				8			
<i>Enochrus</i>					2					
<i>Hydaticus</i>							2		2	1
<i>Hydaticus bimarginatus</i>					1					
<i>Hydaticus cinctiperinis</i>										1
<i>Hydrochara</i>	4	3	4	7	26	7	8	1	9	32
<i>Hydroporus falli</i>					1					
<i>Rhantus</i>			2							
<i>Tropisternus</i>							8	13	5	2
<i>Uvarus</i>	4			1	2					
DIPTERA										
Athericidae										
<i>Atherix</i>	2		1					1		1
Ceratopogonidae							2			2
<i>Bezzia</i>										
<i>Ceratopogon</i>										
Chaoboridae					2	2	89	37	29	9
<i>Chaoborus</i>	2						1		2	8
Chironomidae								1		1
<i>Bryophaenocladus</i>					2					2
Chironominae					8	1	1			2
Chironomini genus III						1				2
Chironomini genus IV						2	4			8
<i>Chironomus</i>			50	8	11	2	52	46	36	16
<i>Gymnometriocnemus</i>						2	2		1	3
<i>Kiefferulus</i>							22	197	3	12
<i>Limnophyes</i>										4
<i>Mesosmittia</i>										1
<i>Omisus</i>										1
Orthocladinae										295
	492	1		38		26	4	2		4
				5						

Table 2A cont.: Taxa grouped as active dispersers for all study sites

Site ID	2	3	7	8	10	12	13	14	15	16
<i>Pentaneura</i>						3				
<i>Phaenopsectra</i>				1						
<i>Polypedilum</i>	46		204	22	206	105	2	14	1	56
<i>Psectrotanypus</i>		32				2	2	4	1	
Tanypodinae						2				
<i>Tanypus</i>		1								
Culicidae			3	3						
<i>Aedes</i>	6			1	1059	2	1			
<i>Anopheles</i>	1									
<i>Culex</i>			1	2						
Cyclorrhaphous- Brachycera				8	5		1	2	9	4
Empididae					2		1			
Orthorrhaphous- Brachycera	3	1	1		28	4	9	2		5
Psychodidae					30	2				
<i>Psychoda</i>					10			3		
Tipulidae										
<i>Tipula</i>									1	
HEMIPTERA										
<i>Buenoa</i>	1		1			1			3	4
Corixidae		1	4	4		5	2	3	1	1
<i>Gerris</i>	1									
Notonectidae										
<i>Notonecta</i>				1				1		
Mesoveliidae					1					
Stratiomyidae										
<i>Allognosta</i>									3	
Scirtidae					8					
MEGALOPTERA										
<i>Chauliodes</i>	1			2	1	14				
ODONATA										
Libellulidae				1					1	
<i>Sympetrum</i>				1			1			
Lestidae										
<i>Archililestes grandes</i>			1							
Total=	722	90	292	102	1439	343	364	110	107	479
# of taxa	16	8	15	16	21	18	22	16	19	18
Proportion of site	0.83	0.21	0.39	0.08	0.64	0.31	0.37	0.09	0.10	0.3

Table 3A. Macroinvertebrate abundance data for all activity traps and benthic samples combined for each site. Community metrics (richness, evenness, and Shannon-Weaver Diversity Index) were also calculated for each site.

SITE ID	2	3	7	8	10	12	13	14	15	16
AMPHIPODA										
<i>Crangonyx</i>	2					6				
<i>Gammarus</i>	4	7	6		3	23		1		
BIVALVIA										
Sphaeriidae	47	61	166	175	74	77	69	68	52	169
COLLEMBOLA										
	19		2	29	19	1	2	5		1
COLEOPTERA										
<i>Acilius</i>	15	1	1	7	1	7	27	1	25	42
<i>Acilius fraternus fraternus</i>										1
<i>Agabetes acuductus</i>				3		2		1		1
<i>Agabus</i>	3				6		1	4	2	2
<i>Bidessonotus</i>	6							2		
<i>Cybister</i>							1			
<i>Dibolocelus</i>							1		1	
Dytiscidae			1	1	12					1
<i>Dytiscus</i>	3		1				8			
<i>Enochrus</i>					2					
<i>Hydaticus</i>							2		2	1
<i>Hydaticus bimarginatus</i>					1					
<i>Hydaticus cinctiperinis</i>										1
<i>Hydrochara</i>	4	3	4	7	26	7	8	1	9	32
<i>Hydroporus falli</i>					1					
<i>Rhantus</i>			2		1					
Scirtidae					8					
<i>Tropisternus</i>						8	13		5	2
<i>Uvarus</i>	4			1	2					
DIPTERA										
Athericidae										
<i>Atherix</i>	2		1							1
Ceratopogonidae							1			2
<i>Bezzia</i>						2				
<i>Ceratopogon</i>								2		1
Chironomidae						1				
<i>Bryophaenocladus</i>				2			1			
Chironominae				8	1	1			2	2
Chironomini genus III					1					

Table 3A cont. Macroinvertebrate abundance data for all activity traps and benthic samples combined for each site. Community metrics (richness, evenness, and Shannon-Weaver Diversity Index) were also calculated for each site.

SITE ID	2	3	7	8	10	12	13	14	15	16
Chironomini genus IV					2	4				
<i>Chironomus</i>		50	8	11	2	52	46	36	16	8
<i>Gymnometriocnemus</i>					2	2		1	3	
<i>Kiefferulus</i>	132		16	12		22	197	3	12	4
<i>Limnophyes</i>										1
<i>Mesosmittia</i>				2	1			1		
<i>Omisus</i>	492	1	38		26	4	2		1	295
Orthocladinae			5			2				4
<i>Pentaneura</i>						3				
<i>Phaenopsectra</i>				1						
<i>Polypedilum</i>	46		204	22	206	105	2	14	1	56
<i>Psectrotanypus</i>		32				2	2	4	1	
<i>Chaoborus</i>	2			2	2	89	37	29	9	8
Culicidae			3	3						
<i>Aedes</i>	6			1	1059	2	1			
<i>Anopheles</i>	1									
<i>Culex</i>			1	2						
Empididae					2		1			
Cyclorrhaphous-Brachycera				8	5		1	2	9	4
Orthorrhaphous-Brachycera	3	1	1		28	4	9	2		5
Psychodidae					30	2				
<i>Psychoda</i>					10			3		
<i>Allognosta</i>									3	
Tanypodinae						2				
<i>Tanypus</i>		1								
<i>Tipula</i>									1	
DECAPODA										
Cambaridae		1	1	1	4	5	2	1	2	5
<i>Cambarus</i>	1	1		4	2	2	1	2	1	
GASTROPODA										
Physidae	3	4	4	1			14		8	2
Planorbidae	2	4	91	32	4	21	32	4	52	91
HEMIPTERA										
Corixidae		1	4	4		5	2	3	1	1
Gerris	1									
Mesoveliidae					1					

Table 3A cont. Macroinvertebrate abundance data for all activity traps and benthic samples combined for each site. Community metrics (richness, evenness, and Shannon-Weaver Diversity Index were also calculated for each site.

SITE ID	2	3	7	8	10	12	13	14	15	16
Notonectidae										
<i>Buenoa</i>	1		1			1			3	4
<i>Notonecta</i>										
HIRUDINIDAE	1	5	5					1	5	
HYDRACARINA	8		2	36	105	52	44	13	27	31
ISOPODA										
<i>Caecidotea</i>	56	90	31	20	187	170	102	27	27	50
MEGALOPTERA										
<i>Chauliodes</i>	1			2	1	14				
NEMATODA				11	7	7	19	7	6	9
ODONATA										
Lestidae										
<i>Archililestes grandes</i>			1							
Libellulidae				1					1	
<i>Sympetrum</i>				1			1			
OLIGOCHAETA	7	163	144	886	418	390	338	1050	718	755
Taxa Richness	28	16	25	29	33	31	31	28	29	27
Evenness	0.497	0.124	0.628	0.414	0.524	0.658	0.639	0.285	0.42	0.555
Shannon-Weaver Index	1.656	0.343	2.02	1.394	1.831	2.261	2.196	0.948	1.414	1.828