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The Impact of Leaf Litter Diversity on the Colonization of Aquatic Insects

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**THE IMPACT OF LEAF LITTER DIVERSITY ON THE
COLONIZATION OF AQUATIC INSECTS**

by

Daniel Edwards

A Thesis Presented in Partial Fulfillment
of the Requirements of the Degree
Master of Science

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ABSTRACT

Ephemeral pools provide habitat to a wide diversity of aquatic insects which colonize pools to establish new populations in higher quality habitats. These pools rely on nutrient inputs from the surrounding terrestrial landscape, predominantly through leaf litter. Using mesocosms, we tested for the effect of leaf litter diversity (richness and functional diversity) on the colonization of aquatic insects. Leaf litter influences characteristics of a pool (tannins, water color, and nutrients) which may make them more or less desirable to potential colonizers. I added unique mixtures of leaf litter with different numbers of species (0, 3, 5, 7, and 9) and calculated functional diversity for each. I also examined which characteristics make different mesocosms more attractive to potential colonizers. Colonizers preferred mesocosms with leaves rather than ones without. Leaf litter functional diversity was a better predictor of colonizer abundance than leaf species richness. I found that colonizer communities were largely influenced by N:P ratios, conductivity, water color, and tannins. By understanding the relationship between leaf litter diversity and colonizing aquatic insects, we can understand the community dynamics of ephemeral pools.

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DEDICATION

to my many friends and family,

and the insects, without which who would I be?

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CHAPTER 1

INTRODUCTION

1.1 Background

With declines in global biodiversity, it is paramount to understand the ramifications of this loss on ecosystems (Thomas, 2013). Changes in species diversity can be accompanied with changes in functional diversity (Hector, 2011). Species diversity is quantified by the number of species (i.e., species richness) and their relative abundance, whereas functional diversity is the variation and dispersion of functional traits in a community (Mason et al., 2005). Both species richness and functional diversity can correlate with ecosystem function (Cadotte, 2017; Xu et al., 2020). However, the relationship between species richness and functional diversity can be variable and largely depends on how these metrics are quantified, such as the number of traits used to measure functional diversity (Daam et al., 2019; Petchey & Gaston, 2002; Suárez-Castro et al., 2022).

Species richness is relatively straightforward to measure: count the number of species in a given community. However, functional diversity is more complex and requires the use of indices. Functional diversity is defined in Petchey and Gaston (2006) as the variation and dispersion of functional traits represented in the species within a community that impact ecosystem function. There are three main components to functional diversity indices: (1) functional richness, the amount of functional trait space

occupied by species in a community, (2) functional evenness, how evenly species are distributed through functional trait space, and (3) functional divergence, how extreme species traits are within the functional trait space (Figure 1-1) (Mason et al., 2005; Mason & de Bello, 2013). Different indices emphasize different elements of these components to assess functional diversity. These metrics for both functional diversity and species richness can be used to assess change in community organization.

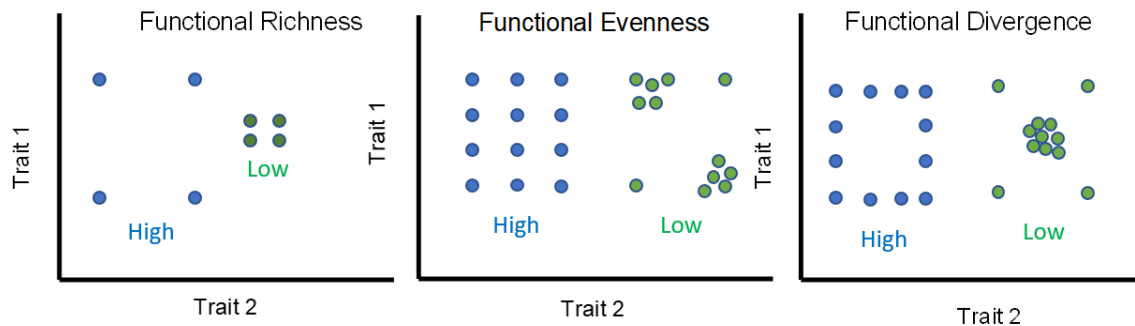


Figure 1-1: Components of functional diversity. Each point represents a single species in a community. Blue is a functionally diverse community, and green is a less diverse community.

Forest ecosystems are undergoing significant changes in community organization from climate change, altered disturbance patterns, and anthropogenic activity, and these changes can have direct effects on aquatic systems (Häder & Barnes, 2019; Karr et al., 2004). In particular, North American forests have experienced dramatic shifts in species composition through the loss of dominant species (e.g., American Chestnut, Ash, Eastern Hemlock) due to invasive species and disease, and dramatic changes in forest succession and composition due to anthropogenic activities such as fire suppression and logging (Abella et al., 2019; Abrams, 2003; Elliott & Swank, 2008; Jenkins et al., 1999). These changes in forest structure and succession impact tree species diversity. This can occur

as invasive species extirpate other species or as the practice of fire suppression reduces the presence of fire tolerant species (Liebhold et al., 2017; Nowacki & Abrams, 2008). These changes in species diversity and composition of forests can impact the terrestrial ecosystem as well as the aquatic ecosystem.

Aquatic systems are an integral part of forest ecosystems and are important for denitrification, processing of organic matter, and the movements of nutrients (Capps et al., 2014; Lewis-Phillips et al., 2020). The terrestrial landscape can directly influence aquatic ecosystems through the input of senesced leaves and organic material (Wetzel, 1995). Aquatic ecosystems derive a significant proportion of their energy from allochthonous inputs like litterfall (Marcarelli et al., 2011). Litterfall into an aquatic ecosystem is rarely derived from a singular plant species and is instead typically a mixture of different plant species (Cornwell & Grubb, 2003). Increased terrestrial plant species surrounding aquatic systems results in increased resource diversity in the form of litterfall that can support both aquatic community biodiversity and ecosystem stability (Handa et al., 2014; Leroy & Marks, 2006). Increased leaf litter diversity can promote increased microbial and macroinvertebrate community biomass and leaf litter decomposition rates (Kominoski et al., 2007; Santschi et al., 2018). Given many forest ecosystems have lost plant species diversity, this is likely to impact forest aquatic systems.

Leaf litter inputs are especially critical to aquatic communities in ephemeral pools. Ephemeral pools are discrete units on a landscape and are isolated from other aquatic systems and associated nutrient flows (Zedler, 2003). Consequently, ephemeral pools derive most of their energy inputs from terrestrial leaf litter and are particularly

sensitive to nutrient and resource limitation (Leroy & Marks, 2006; Marks, 2019; Wallace et al., 1997; Webster & Benfield, 1986). Leaf litter supports microbial communities and detritivorous insects, which are prey for higher trophic levels (Ferreira et al., 2020; Marks, 2019; Webster & Benfield, 1986). The composition and quality of leaf litter regulates colonizers through site selection in mesocosm pools and is prioritized by colonists over landscape characteristics except for the presence or absence of fish, which exhibits the strongest colonization pressure (Dodd & Buchholz, 2018; Pintar et al., 2018; Pintar & Resetarits, 2017a; Stoler & Relyea, 2021). Thus, terrestrial leaf litter is critical to the formation and maintenance of colonizing communities.

Leaf litter alters aquatic habitat characteristics in addition to providing potential nutritional resources. These changes to habitat characteristics by leaf litter can include water chemistry as well as, zooplankton and algae biomass (Stoler & Relyea, 2011). Zooplankton are important prey items for predators and algae is important for herbivores (Chessman, 1986; Pintar & Resetarits, 2017b). Beetles have been shown to colonize pools in response to the presence of zooplankton prey items (Pintar & Resetarits, 2017b). Beetles in the genus *Laccophilus*, although very similar morphologically, have preferences for difference physical attributes of ponds such as temperature, vegetation, and shading (Zimmerman, 1960). Understanding the role of specific characteristics play in colonization may help to understand how leaf litter diversity may influence colonization.

Functional diversity and species richness could be important for the colonization of aquatic insects. Species of leaf litter have distinct traits that can alter water differently (Stoler & Relyea, 2011, 2016). Some species' traits can disproportionately influence

aquatic environments (Cameron & LaPoint, 1978; Montez et al., 2021). In mixes of leaf litter there are interaction between species which can increase the overall quality by diluting negative traits and compensating for nutrient deficiencies (Handa et al., 2014). Leaf mixtures with higher diversity (functional and richness) have been shown to have faster decomposition rates (Kominoski et al., 2007; Rabelo et al., 2022). This could suggest positive relationships between colonization and leaf litter diversity. Functional diversity and richness may both correlate positively with colonization but functional diversity can capture the variation in traits and so may be a better measure of colonization

1.2 Colonization

Ephemeral pools are composed of discrete patches of suitable aquatic habitat, which are separated by an inhospitable terrestrial landscape (Zedler, 2003). Aquatic invertebrates must navigate between these suitable patches to establish new populations (MacArthur & Wilson, 1963). Colonizing invertebrates include predators that regulate lower trophic levels, and detritivores that facilitate nutrient cycling by processing leaf litter (Ngai & Srivastava, 2006; Stepanian et al., 2020). Movement between patches provides many advantages to colonist species, such as an increase in population gene flow, prospective lack of competitors, and to escape unfavorable conditions (Pintar & Resetarits, 2017a). However, gaining these benefits comes at a risk; there is the possible inability to locate a mate or suitable habitat and a risk of predation (Bilton, 2014; Stenseth & Lidicker, 1992). Colonization by aquatic invertebrates is a balance of risks and rewards which must be navigated for successful colonization (Pintar et al., 2018). Unlike other aquatic ecosystems, discrete ephemeral pools are almost entirely reliant on

colonization for their community to gain new members (Batzer & Wissinger, 1996).

Thus, factors that alter colonization patterns like changes in resource quality (e.g., leaf litter diversity) can strongly shape ephemeral pool community structure and function.

Colonist species are diverse and differ in the factors that shape their colonization patterns. Adult colonists that reproduce in pools consist primarily of two coleopteran families: dytiscidae and hydrophilidae, and four hemipteran families: corixidae, notonectidae, gerridae, and veliidae. Both coleopteran families are aquatic as both larvae and adults; however, following molting into an adult they will fly and colonize new pools. Aquatic Hemiptera are hemimetabolous and their wings are not fully developed until they reach adult stage, but they can move between pools throughout their ontogeny (Ditrich & Papáček, 2009). Decreased ephemeral pool habitat quality, such as decreasing water depth, increased population density, or lower food availability typically initiates emigration from one ephemeral pool and colonization of a new ephemeral pool (Yee et al., 2009). Detection and assessment of pools by aquatic adults, such as the coleopteran and hemipterans, are driven by their own adult habitat preferences as well as their offsprings' performance (Pintar et al., 2018). Selection for pools can also be a permanent choice, as shortly after colonization, the flight muscles of some colonists, like dytiscids, atrophy to reallocate resources to swimming muscles or reproductive organs (Bilton, 2014). Thus, the selection of ephemeral pool is an important decision colonizers must make.

The specific mechanisms and cues for attraction to pools are largely unknown; however recent work has begun to demonstrate different cues operate at different spatial scales (Binckley & Resetarits, 2009; Pintar et al., 2018; Resetarits & Binckley, 2009).

Long range detection begins after leaving the original pool and is driven by polarotactic cues from horizontally polarized light reflecting off the surface of water and allows detection of bodies of water within non-aquatic matrices (Bilton, 2014; Kriska et al., 2006). Additional research has demonstrated a preference for pools with lower canopy cover, which is consistent with the need for light to locate pools (Binckley & Resetarits, 2009). Assessment of habitat quality on a smaller scale is believed to be primarily driven by olfactory systems through the assessment of chemical cues, although this is largely understudied (Bilton, 2014; Bilton et al., 2001; Resetarits & Binckley, 2014). Subsequently, increasing tree diversity may both decrease colonization if canopy cover is also increased and increase colonization through provision of increased resources as diverse litterfall.

Colonists assess ephemeral pool quality in part from preferences in leaf litter species present in pools, but the mechanisms of this quality assessment are not fully understood. Selection of increased nutritional quality of leaf litter in pools is one potential mechanism (Pintar et al., 2018; Resetarits & Binckley, 2013, 2014). Differences in colonist selection of pools can change over time as resource quantity and quality change. For example, hydrophilids prefer hardwood over coniferous leaf litter early in the season after pools initially fill with water, but in the late summer hydrophilids preferred to colonize pine leaf litter pools as available nutrients in pine became more available and nutrients in hardwood diminished (Pintar & Resetarits, 2017a). Ephemeral pool ecosystems are significantly regulated by their terrestrial leaf litter inputs, however, there is currently no examination of the role of leaf litter diversity plays in shaping the diversity of colonizers.

Selection of colonization site is likely influenced by the trophic position of the colonizer. Herbivorous species may have a strong positive relationship with leaf traits such as nitrogen and phosphorus which promote primary productivity (Dodds & Whiles, 2020). Whereas predatory species may not respond to primary productivity but to prey (herbivorous insects or zooplankton) (Pintar & Resetarits, 2017b). Curry (2022) suggested that functional groups of insects are important when examining the response to added nutrients in aquatic systems, showing that some herbivorous taxa like chironomids increased with added nutrients but predators had negative relationships to increasing primary productivity. Therefore we may see differences in response between trophic levels of colonizers.

1.3 Objectives

My project used mesocosms and leaf litter to (1) examine the effect of species richness and functional diversity of leaf litter on the diversity and abundance of colonizing insects and (2) examine species-specific habitat preferences. Increased leaf litter diversity offers colonizers the opportunity to obtain increasingly diversified resources. I predicted that pools with higher diversity of leaf litter (functional and species richness) would have more diverse colonizer assemblages. I also predicted that there would be a stronger preference for more functionally diverse leaf litter than more species rich leaf litter. Species richness focuses on the number of species whereas functional diversity is directly looking at the variability of traits between species. Therefore, I expect functional diversity to be the primary driver of colonizer diversity.

If functional diversity was preferred by colonizers, I would expect colonizers to prefer specific leaf traits. Therefore, my project also aims to determine the relative

importance of habitat characteristics to different colonizing taxa. This includes both leaf chemistry traits, as well as the physical and chemical parameters of the water. I considered both leaf traits and water parameters because many components of leaf litter are water soluble and influence water variables such as water color and turbidity. Different colonizing insects have different habitat requirements depending upon their life histories and trophic level (Binckley & Resetarits, 2005; Pintar et al., 2018; Pintar & Resetarits, 2020; Yee et al., 2020). Due to different requirements for habitat characteristics, I expect there will be a colonization preference for leaf traits which fulfill their requirements.

1.4 Predictions

1. Colonizer diversity and abundance will have a positive relationship with leaf litter diversity. Functional diversity is more representative of the diversity of leaf litter traits so will have a stronger relationship with the diversity of colonizers and will explain more variability than leaf litter species richness.
2. Colonizers will have species-specific responses to habitat characteristics such as water color, tannins, and leaf litter chemistry. Species will respond to food sources and resources. Herbivores may have a positive relationship with leaf elements that stimulate primary production such as nitrogen and phosphorus. Whereas, predators may respond not to primary productivity but rather prey.

CHAPTER 2

METHODS

2.1 Experimental Design

To explore the relationship between leaf litter diversity and insect colonization, I used pool mesocosms with leaf mixtures that vary in leaf species richness and functional diversity. Functional diversity was estimated using Rao's quadratic entropy, an index of functional divergence (Villéger et al., 2008; Figure 1-1). Rao's Quadratic Entropy is a multivariate approach to functional divergence and uses Euclidian distances to calculate distances between species (Mason et al., 2005; Schleuter et al., 2010). Rao's is a widely used metric to summarize a community's diversity and has been shown to be effective at analyzing patterns of traits among communities (Ricotta & Moretti, 2011).

To mimic natural conditions and create a spectrum of leaf species richness levels, mesocosms had five levels of leaf species richness (0, 3, 5, 7, and 9 species) with leaf species drawn from a set of 20 total species (Table 2-1). Mixtures were drawn from 20 species to ensure variability in species composition in the 9 species mixtures and to minimize overrepresentation of any one species of leaves. There were 10 replicates of each species richness level, except for the control pools with no leaf litter, which have 5 replicates, totaling 45 pools. The control pools allow us to assess whether leaf litter affects colonization and act as comparison with higher levels of leaf species richness.

Table 2-1: Species of trees used for leaf litter mixtures with average tannins and C:N, C:P, and N:P ratios from leaves collected in 2017 used to calculate functional diversity.

Scientific Name	Family	Tannins (mg/g)	C:N Ratio	C:P Ratio	N:P Ratio
<i>Liquidambar styraciflua</i>	Altingiaceae	65.6	73.9	450.5	8.9
<i>Pistacia chinensis</i>	Anacardiaceae	30.2	53.2	130.9	2.5
<i>Ostrya virginiana</i>	Betulaceae	8.6	47.0	715.4	15.9
<i>Taxodium distichum</i>	Cupressaceae	20.0	48.8	192.4	3.9
<i>Triadica sebifera</i>	Euphorbiaceae	107.8	62.7	376.8	9.0
<i>Fagus grandifolia</i>	Fagaceae	19.1	33.1	549.0	9.8
<i>Quercus velutina</i>	Fagaceae	20.0	38.3	360.9	10.4
<i>Quercus stellata</i>	Fagaceae	76.5	56.4	563.4	10.4
<i>Quercus alba</i>	Fagaceae	60.9	34.8	396.8	12.3
<i>Quercus phellos</i>	Fagaceae	28.3	39.1	654.9	13.2
<i>Carya tomentosa</i>	Juglandaceae	6.3	41.7	1000.5	19.3
<i>Morus rubra</i>	Moraceae	20.1	38.3	158.5	5.2
<i>Nyssa sylvatica</i>	Nyssaceae	60.5	61.5	343.1	6.8
<i>Pinus taeda</i>	Pinaceae	25.5	121.2	813.1	10.9
<i>Platanus occidentalis</i>	Platanaceae	13.7	43.6	519.7	16.6
<i>Prunus serotina</i>	Rosaceae	46.8	65.6	154.7	2.5
<i>Pyrus calleryana</i>	Rosaceae	52.8	67.1	543.0	7.8
<i>Acer rubrum</i>	Sapindaceae	51.8	86.0	294.9	4.8
<i>Ulmus parvifolia</i>	Ulmaceae	23.7	35.8	108.6	2.1
<i>Ulmus alata</i>	Ulmaceae	26.9	51.3	278.2	6.3

Each replicate with leaf litter is a unique mixture to avoid confounding species richness with species composition and provide natural variability in species composition for each species richness treatment. I was not interested in the effects of each unique mixture, which would focus on community composition instead of diversity. The use of unique mixtures for each replicate is commonly used in other experiments examining effects of species and functional diversity, such as in Galland et al. (2019) and Martin, Rainford, and Blossey (2015). The use of unique mixtures also creates a wide range of

values for functional diversity in a gradient design (Kreyling et al., 2018), allowing functional diversity to be treated as a continuous variable in analyses. This allows me to test for different mathematical relationships between functional diversity and colonizer diversity. A gradient design maximizes the number of experimental units without replication. I can increase the number of functional diversity experimental units, which allows for a more complete characterization of the relationship between functional diversity and colonizer diversity (Kreyling et al., 2018). This means the specific relationship between functional diversity and colonizers are the focus rather than the relationship of leaf litter mixtures to colonizers. Using a gradient design can be particularly important if these relationships are non-linear, but even in linear relationships gradient designs can outperform replicated designs (Kreyling et al., 2018).

Mixtures of species were randomly selected to minimize bias. Functional diversity (using the traits C:N, C:P, N:P, and tannin concentrations) was calculated for each mixture using chemistry data collected in 2017 (Earl, unpubl. data). This chemistry data was obtained using dried leaves analyzed by Louisiana State University's Plant Science Lab. Ratios of carbon, nitrogen, and phosphorus were chosen because they are the primary limiting nutrients of aquatic systems. Tannins can color the water and absorb light which could otherwise be used in photosynthesis (Dodds & Whiles, 2020). Tannins in water have also been shown to be preferred by colonizing amphibians but at the detriment to their offspring (Dodd & Buchholz, 2018; Earl et al., 2012). Leaf species were restricted to being assigned to no more than 5 out of 10 mixtures in each species richness treatment to avoid overrepresentation that might confound species richness treatments with the presence of particular species. Species mixtures were also checked to

ensure species richness, functional diversity, and leaf traits (i.e., C:N, C:P, N:P, and tannin concentrations) are not significantly correlated to each other to avoid having these as confounding variables. Leaves of each species were collected in the fall of 2021, and washed and dried at 40°C in drying ovens and then stored at room temperature until ready for use.

The experiment was conducted at Wafer Creek Ranch, Lincoln Parish, Louisiana starting on May 6th and run until June 29th. The pools were 105 cm wide at the top and 20 cm tall, holding a maximum of 155 liters. They are a good representation of natural pools in size but do not allow for interface with soil like natural pools. They were placed in an open area near a forest edge (Binckley & Resetarits, 2005) and then filled with water. Dechlorinated tap water was added every week as necessary to maintain a consistent minimum depth of 10cm throughout the experiment. The water's maximum depth was 21.5cm, mean was 12.4, and standard deviation was 1.8. Randomly assigned leaf litter mixtures were added to each pool. Mesh screen (1-2mm openings) was placed over the top of each pool and pressed into the water so that colonizers could easily be collected from the pools but could not interact with leaf litter. Debris which fell into the pool was removed several times each week to prevent leaching of foreign material. Additionally, we removed eggs of treefrogs (*Hyla chrysoscelis*) and toads (*Anaxyrus fowleri*) that oviposited in pools to help isolate the effects of leaf litter rather than the presence of frog or toad larvae on insect colonization. Colonizers were collected twice per week for a total of 16 times (Table 3-1). Adult insects were preserved in 70% ethanol for identification to lowest possible taxonomic unit. All species were identified to the species level except for *Hydrocolus*, *Hydrochus*, *Paracymus*, *Sigara*, and *Microvelia*.

These individuals were left at the genus level due to a variety of factors, such as small size and the difficulty in identifying female specimens. Species identifications were confirmed or corrected by Dr. Matthew R. Pintar, after species representatives were determined.

Physical properties and water chemistry were assessed periodically throughout the experiment. Weekly sampled water quality measurements included pH, dissolved oxygen, temperature, and conductivity. Biweekly measurements were taken for turbidity, tannins, and water color. 50 ml water samples were taken, filtered using a glass fiber filter (pore size 0.7 μ m), and dissolved tannin concentrations and water color were measured in the lab using a portable spectrophotometer (Hach, DR3900). The Tyrosine method using tannic acid as the standard was used to measure dissolved tannin concentrations (Clesceri & American Public Health Association, 1989). To measure water color, I measured light absorption at three specific wavelengths (λ 436nm, 525nm, and 620nm) with a spectrophotometer (International Organization of standards 2011). To account for particles filtered out of the water, turbidity was also measured using a turbidity meter prior to filtration (Sper Scientific 860040).

2.2 Statistics

I first tested whether insect colonizers exhibited preference for presence of leaf litter in pools. Specifically, I used Poisson regression to compare colonization between pools with leaf litter to ones without for all colonizers (total abundance), and separate analyses for the abundance of the most common taxa (>80 individuals) hemiptera, hydrophilidae, dytiscidae, *C. glyphicus*, and *L. fasciatus*. Control pools without leaves were left out of further analysis because functional diversity is calculated using leaf traits

and require 3 or more species to provide reliable functional diversity measures (Botta-Dukát, 2005).

Poisson regressions and linear models were used to test for the role of leaf litter richness and functional diversity influencing colonization. Insect colonizer metrics were the dependent variables, including species richness, the Shannon-Weiner index (formula 1), abundances of the most common taxa, and total abundance of colonizers. To determine which model type to use for variables with count data (all except the Shannon-Weiner index), variance and means were compared. Poisson regressions were run when the variance and mean were similar. Linear models were used when variance and means were different, and *L. fasciatus* abundance was transformed to be normal using a square root transformation. To run the models, leaf species richness and functional diversity were independent variables with leaf species richness analyzed as a categorical variable and functional diversity as a continuous variable estimated as Rao's quadratic entropy. Macroinvertebrates have previously been shown to have a parabolic relationship with different environmental variables such as dissolved oxygen and water temperature (Dinsmore et al., 1999; Reisen, 1977). Other studies have shown non-linear negative relationships in response to increased leaf quality in anurans (Stephens et al., 2015). Because of this, models were first run as linear, logarithmic, and quadratic functions to determine the shape of the relationship between colonizers and functional diversity. To compare these functions, Mcfadden's R^2 or the adjusted R^2 was used. Mcfadden's R^2 is a pseudo R^2 that is used to compare Poisson regression models (Long, 1997). Adjusted R^2 was used to determine the best function among linear models. Poisson regression and linear models were then performed using the function (linear, logarithmic, or quadratic)

with the best R^2 to determine the relationship of leaf litter diversity and colonizers. The relationship was assumed linear unless one of the other functions had an R^2 of 0.05 better than linear. A R^2 of 0.05 was used because I believed that it would suggest an improvement rather than just random variability. This was run in R version 4.2.2. (R Core Team, 2022). The package ‘rstatix’ was used in determining significance of variables in each model (Kassambara, 2023)

Formula 1: Shannon-Weiner Index: H' is the diversity index, s is the number of species, P_i is the proportion of individuals of each species (Shannon, 1948).

$$H' = - \sum_{i=1}^s P_i \ln (P_i)$$

I used repeated measures analyses (Run in SPSS version 28.0.1.0 (IBM, 2021)) to assess effects of leaf species richness (categorical variable), functional diversity (continuous variables), and date on water quality variables (conductivity, depth, dissolved oxygen, pH, water color, tannins, temperature, and turbidity). The goal of these analyses was to describe the conditions of pools while insects were making colonization decisions. For all models, the sphericity assumption was violated, so I reported degrees of freedom and P-values using Huynh-Feldt correction (Haverkamp & Beauducel, 2017). This corrects for the violation of the sphericity assumption and has more power than the Greenhouse-Geiser correction (Abdi, 2010). In addition to the repeated measures I ran a Pearson’s correlation to test for correlations between the various variables measured.

To test for community level responses to habitat characteristics, I used nonmetric multidimensional scaling (nMDS) to determine which leaf traits and water physical and chemical characteristics (e.g., water color, tannins, or nutrients) are associated with different colonizer communities. The Bray-Curtis Dissimilarity Index was used to

calculate distances between communities, this was then used to rank those communities based on how similar or dissimilar they are. I used Envfit from the Vegan package in R, to overlay environmental variables with the original ordination axes, this was used to determine dominant taxa and predominant trait-based drivers of communities (Jari Oksanen et al., 2022; Oksanen, 2015). Environmental variables included water chemistry data, which was averaged for each pool. The environmental variables also include initial leaf chemistry used to calculate functional diversity from before leaves were added to the water. Each trait was independently modeled and can account for non-linear relationships. Envfit also generates a significance value through permutation tests (n=999) to determine best fit, which I used to determine which traits were likely driving community structure. This method has been used previously to categorize how environmental data may influence communities (Bando et al., 2015; Debinski et al., 2006).

CHAPTER 3

RESULTS

3.1 Collected Insects

Over the course of the experiment, I collected a total of 1,143 colonizing insects, from 40 species in 8 different families (Table 3-1). Most colonizations occurred mid-May to mid-June (Figure 3-1). Each pool was colonized on average by 28.3 individuals, (range: 5-66). The most dominant taxa were dytiscids with 955 individuals, two of which, *Copelatus glyphicus* and *Laccophilus fasciatus*, also had enough individuals to be analyzed separately. Additionally, hemipterans and hydrophilids were abundant enough to analyze as groups (Table 3-1).

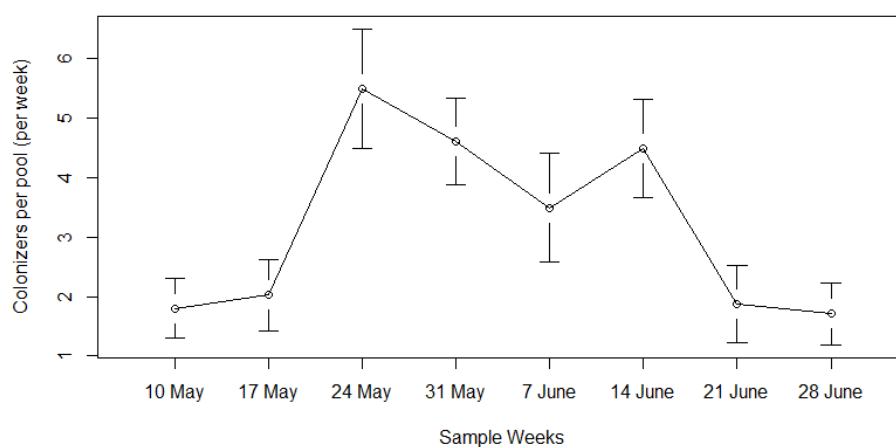


Figure 3-1: Mean insect colonizers per pool per week during the experiment.

Table 3-1: List of species collected throughout the experiment over 16 sampling dates with the total number of individuals collected and the total number of pools that species was found in.

Family/Species	# Specimens	# Pools
Coleoptera	1062	45
Dytiscidae	955	45
<i>Acilius fraternus</i>	1	1
<i>Acilius mediatius</i>	10	6
<i>Bidessonotus inconspicuus</i>	12	10
<i>Celina slossoni</i>	1	1
<i>Copelatus caelatipennis</i>	15	14
<i>Copelatus chevrolati</i>	7	6
<i>Copelatus glyphicus</i>	404	45
<i>Hydaticus bimarginatus</i>	11	9
<i>Hydrocolus spp.</i>	3	3
<i>Hydroporus rufilabris</i>	2	2
<i>Laccophilus fasciatus</i>	402	40
<i>Laccophilus proximus</i>	52	23
<i>Meridiorhantus calidus</i>	2	2
<i>Neobidessus pullus pullus</i>	5	4
<i>Neoporus blanchardi</i>	1	1
<i>Neoporus undulatus</i>	12	10
<i>Thermonectus basillaris basillaris</i>	8	8
<i>Uvarus lacustris</i>	6	5
Hydrochidae	10	8
<i>Hydrochus spp.</i>	10	8
<i>H. jaechi</i>		
<i>H. Rugosus</i>		
Hydrophilidae	99	37
<i>Berosus exiguous</i>	1	1
<i>Berosus infuscatus</i>	6	6
<i>Cymbiodyta chamberlaini</i>	9	9
<i>Enochrus cinctus</i>	2	2
<i>Enochrus consors</i>	1	1
<i>Enochrus fimbriatus</i>	8	6
<i>Enochrus ochraceus</i>	17	15
<i>Helochares maculicollis</i>	1	1
<i>Paracymus spp.</i>	38	19
<i>Tropisternus blatchleyi blatchleyi</i>	3	3

<i>Tropisternus collaris striolatus</i>	11	9
<i>Tropisternus lateralis nimbatus</i>	2	2
Ptilodactylidae	2	2
<i>Ptilodactyla serricollis</i>	2	2
<hr/>		
Hemiptera	81	31
Corixidae	41	24
<i>Hesperocorixa nitida</i>	12	11
<i>Sigara spp.</i>	6	6
<i>Trichocorixa calva</i>	23	16
Gerridae	5	4
<i>Gerris isperatus</i>	3	2
<i>Limnopus canaliculatus</i>	1	1
Notonectidae	25	11
<i>Notonecta irrorata</i>	23	9
<i>Notonecta indica</i>	2	2
Veliidae	12	10
<i>Microvelia spp.</i>	12	10

3.2 Effects of Leaf Litter Diversity on Insect Colonizers

Most colonizers displayed a significant preference for pools with leaves over ones without leaves. This occurred for total colonizer abundance ($F_{1,43} = 4.62$, $p = 0.04$), hemiptera ($F_{1,43} = 14.97$, $p = 0.02$), and hydrophilidae ($F_{1,43} = 6.82$, $p = 0.01$; Figure 3-2). However, this was not true for all colonizers. There was no significant difference between pools with leaves and without for dytiscidae ($F_{1,43} = 2.13$, $p = 0.15$) or the two most abundant species of dytiscids: *Copelatus glyphicus* ($F_{1,43} = 1.05$, $p = 0.31$), and *Laccophilus fasciatus* ($F_{1,43} = 2.43$, $p = 0.13$; Figure 3-2).

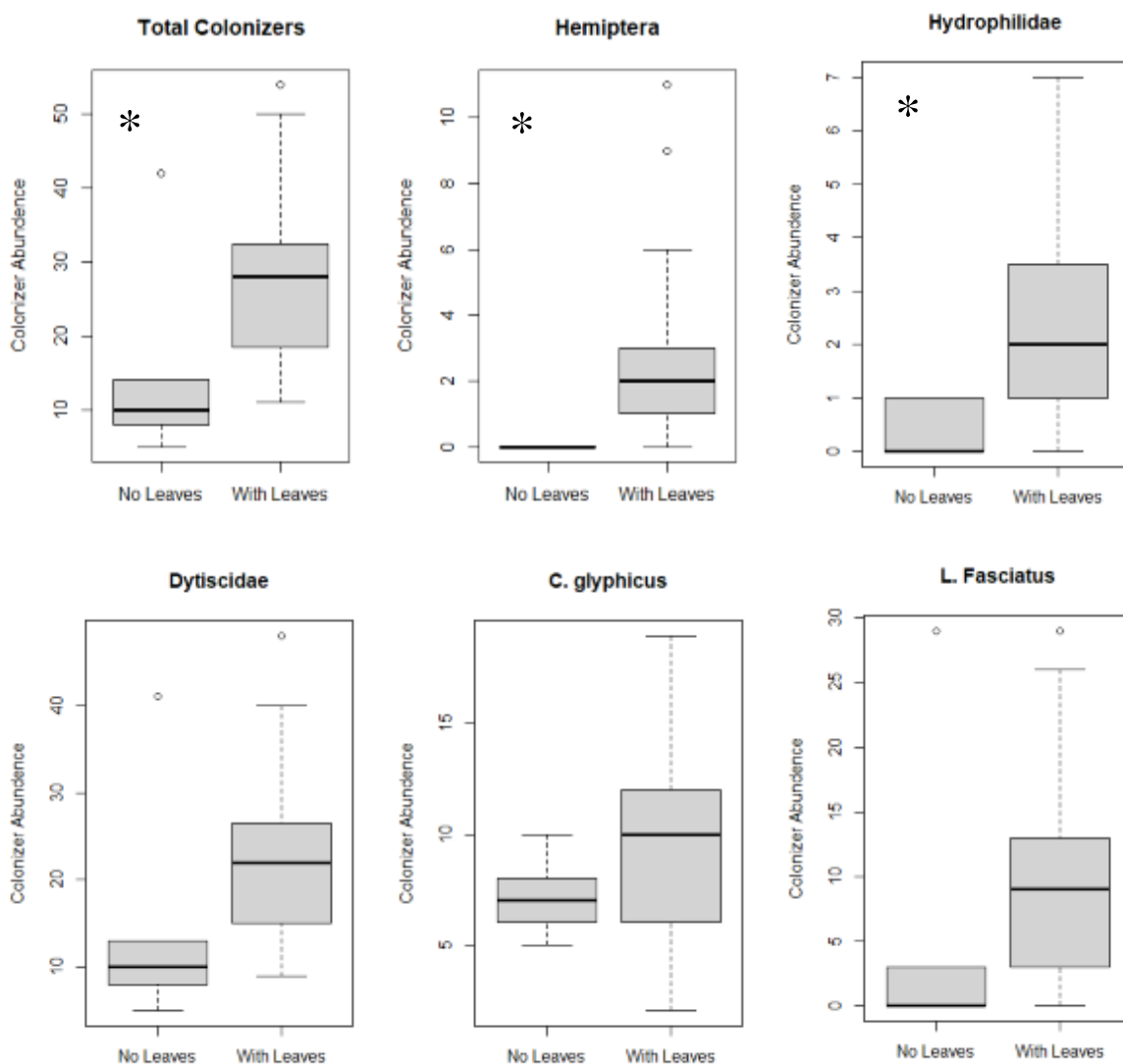


Figure 3-2: Boxplot of total colonizers, Hemiptera, Hydrophilidae, Dytiscidae, *Copelatus glyphicus*, and *Laccophilus fasciatus* for pools with and without leaves. * Indicates statistically significant colonization preference for pools with leaf litter than without.

Using McFadden's R^2 and the adjusted R^2 , the quadratic relationship between colonizers and leaf functional diversity was the best fit for hemiptera, dytiscidae, *C. glyphicus*, and total abundance (Table 3-2). Linear was the best fit for *L. fasciatus*, Hydrophilidae, colonizer richness, and Shannon-Weiner (Table 3-2). Hemiptera

abundance was the only taxa to have a significant relationship with both leaf functional diversity and richness (Figures 3-3a & 3-3b; Table 3-3). Hemiptera colonization was higher in leaf litter richness levels 5 and 9 than 3 and 7. The means of Hemiptera abundance in the 5 and 9 richness levels were 2.7 and 3.1 but in the 3 and 7 richness levels the means were only 1.1 and 1.3. Hemiptera colonization had a quadratic relationship with an intermediate peak when leaf functional diversity was 3.79, and abundance declined for both lower and higher functional diversity values (Figure 3-3a). Dytiscidae, *C. glyphicus*, and total abundance had a significant relationship with leaf functional diversity but not richness (Figures 3-3c, 3-3d, & 3-3e). They had quadratic relationships with intermediate peaks when functional diversity was 3.75 for dytiscidae, 3.61 for *C. glyphicus*, and 3.73 for total abundance. Abundances of both Dytiscidae and *C. glyphicus* were analyzed for a relationship to functional diversity even though they didn't exhibit a significant difference between pools with leaf litter and ones without. This is because in pools without leaves the mean colonizer abundance for dytiscidae was 15.4 and for *C. glyphicus* was 7.2. These means align with the low abundances of the parabolic curve when functional diversity was lowest and highest. Colonizer richness did not have a significant relationship to leaf functional diversity ($\chi^2_1 = 0.34$, $p = 0.56$) or to leaf species richness ($\chi^2_3 = 4.43$, $p = 0.22$) but did have a significant positive relationship to colonizer abundance ($\chi^2_1 = 34.67$, $p < 0.01$). Hydrophilidae, *L. fasciatus*, and Shannon-Weiner Index had no significant relationship with either leaf litter richness or functional diversity (Table 3-3).

Table 3-2: Model fit for Poisson regressions and linear models of colonizer abundance and colonizer diversity to leaf litter functional diversity with different relationships: linear, logarithmic, and quadratic functions. Values are McFadden's R^2 (M) or adjusted R^2 (A), which were used to determine the best fit function, indicated by an * and then used in further analyses

	Functional Diversity & Richness		
	Linear	Logarithmic	Quadratic
Hemiptera ^M	0.16	0.16	0.22*
Hydrophilidae ^M	0.04*	0.03	0.06
Dytiscidae ^M	0.03	0.02	0.16*
<i>C. glyphicus</i> ^M	0.04	0.03	0.17*
<i>L. fasciatus</i> ^A	-0.10*	-0.10	-0.12
Total Abundance ^A	-0.06	-0.06	0.03*
Colonizer Richness ^M	0.47*	0.46	0.47
Shannon-Weiner ^A	-0.02*	-0.01	-0.02

Table 3-3: Model results for the effects of leaf functional diversity (FD) and species richness on insect colonizer total abundance, abundance of most common colonizers, and colonizer diversity. The FD^2 term was only used when the quadratic was a better fit than linear (Table 3-2).

Taxa	Functional Diversity		FD^2		Leaf Litter Richness	
	Test Statistic	P	Test Statistic	P	Test Statistic	P
Poisson Regressions						
Hemiptera	$\chi^2_1 = 4.86$	0.03	$\chi^2_1 = 5.39$	0.02	$\chi^2_3 = 11.25$	0.01
Hydrophilidae	$\chi^2_1 = 0.05$	0.83	NA		$\chi^2_3 = 1.69$	0.64
Dytiscidae	$\chi^2_1 = 14.83$	<0.01	$\chi^2_1 = 17.97$	<0.01	$\chi^2_3 = 4.14$	0.24
<i>C. glyphicus</i>	$\chi^2_1 = 12.11$	<0.01	$\chi^2_1 = 13.80$	<0.01	$\chi^2_3 = 2.64$	0.44
Linear models						
<i>L. fasciatus</i>	$F_{1,35} = 0.12$	0.73	NA		$F_{3,35} = 0.13$	0.94
Total Abundance	$F_{1,34} = 3.47$	0.07	$F_{1,34} = 4.17$	0.05	$F_{3,34} = 0.61$	0.61
Shannon-Weiner	$F_{1,35} = 0.24$	0.62	NA		$F_{3,35} = 0.87$	0.47

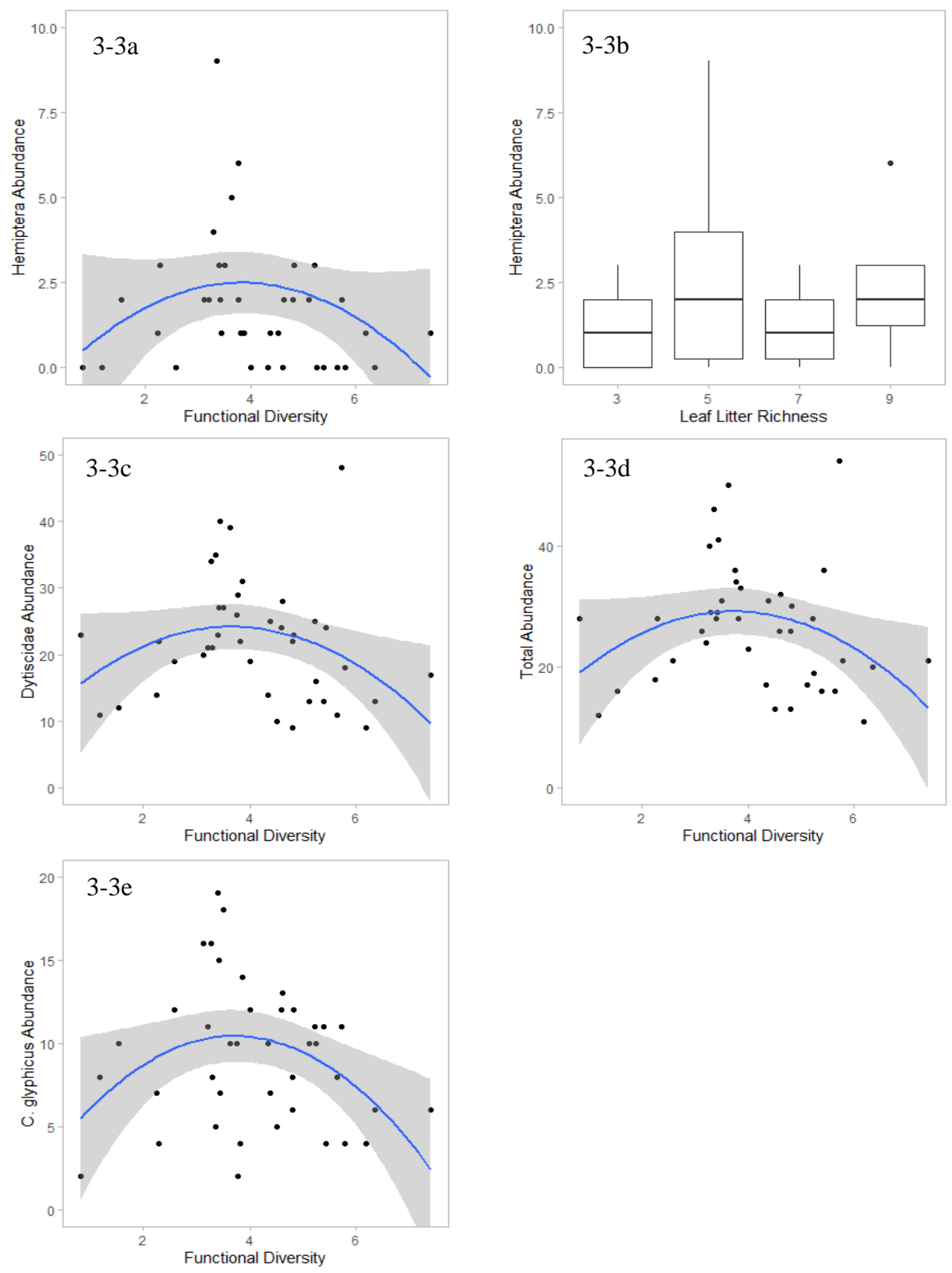


Figure 3-3: Effects of leaf litter functional diversity and species richness on colonizer abundance. The shaded section of the functional diversity plots show the 95% confidence intervals. The lines of the box plot show the first and third quartile.

3.3 Water Quality

There was a significant change for all water quality variables across time, except for turbidity and water color (Table 3-4). There was a gradual increase in conductivity over time, while water depth, temperature, dissolved oxygen, and pH were highly variable over time. Tannins were highest at first sampling but quickly decreased (Figure 3-4). There was no significant change over time for water color or turbidity. There was a significant relationship between leaf litter richness and turbidity. Turbidity was significantly higher in pools with a richness of 9 leaf species than pools with 3, 5, or 7 leaf species. I also ran Pearson's correlation with water quality and leaf traits to determine if they were correlated (Table 3-5). Several strong correlations were present; CP ratios was correlated with NP, water color was correlated with water tannins, and pH was correlated with dissolved oxygen.

Table 3-4: Repeated measures ANOVA results for change of water quality variables over time and their relationship to leaf litter richness and functional diversity.

Water Quality Variables	Time	Time*FD	Time*Richness	Richness	FD
Conductivity	F _{2.2,77.3} =6.36 p=0.002	F _{2.2,77.3} =1.30 p=0.28	F _{6.6,77.3} =0.54 p=0.79	F _{3,35} =0.68 p=0.68	F _{1,35} =2.19 p=0.19
Depth (cm)	F _{3.5,120.9} =11.98 P<0.001	F _{3.5,120.9} =0.70 P=0.58	F _{10.4,120.9} =0.95 P=0.49	F _{3,35} =0.34 p=0.8	F _{1,35} <0.01 p=0.97
Dissolved Oxygen	F _{4.9,1956.6} =6.57 P<0.001	F _{4.9,1956.6} =0.33 P=0.89	F _{14.6,1956.6} =0.66 P=0.82	F _{3,35} =0.15 p=0.93	F _{1,35} =0.30 p=0.59
pH	F _{4.4,154.7} =4.40 P=0.001	F _{4.4,154.7} =0.29 P=0.9	F _{13.3,154.7} =0.68 P=0.78	F _{3,35} =0.24 P=0.87	F _{1,35} =0.12 P=0.73
Water Color	F _{2.6,92.5} =1.70 P=0.17	F _{2.6,92.5} =0.48 P=0.68	F _{7.9,92.5} =2.00 P=0.06	F _{3,35} =1.41 P=0.26	F _{1,35} =2.21 P=0.15
Tannins	F _{1.3,45.4} =21.45 P<0.001	F _{1.3,45.4} =2.14 P=0.15	F _{3.9,45.4} =2.03 P=0.11	F _{3,35} =0.77 P=0.52	F _{1,35} =1.65 P=0.21
Temperature	F _{2.8,99} =8.70	F _{2.8,99} =0.36	F _{8.5,99} =0.49	F _{3,35} =0.86	F _{1,35} =1.83

Turbidity	P<0.001	P=0.77	P=0.87	P=0.47	P=0.19
	F _{3,105} =2.18	F _{3,105} =0.98	F _{9,105} =1.61	F _{3,35} =3.60	F _{1,35} =0.47
	P=0.095	P=0.41	P=0.12	P=0.02	P=0.19

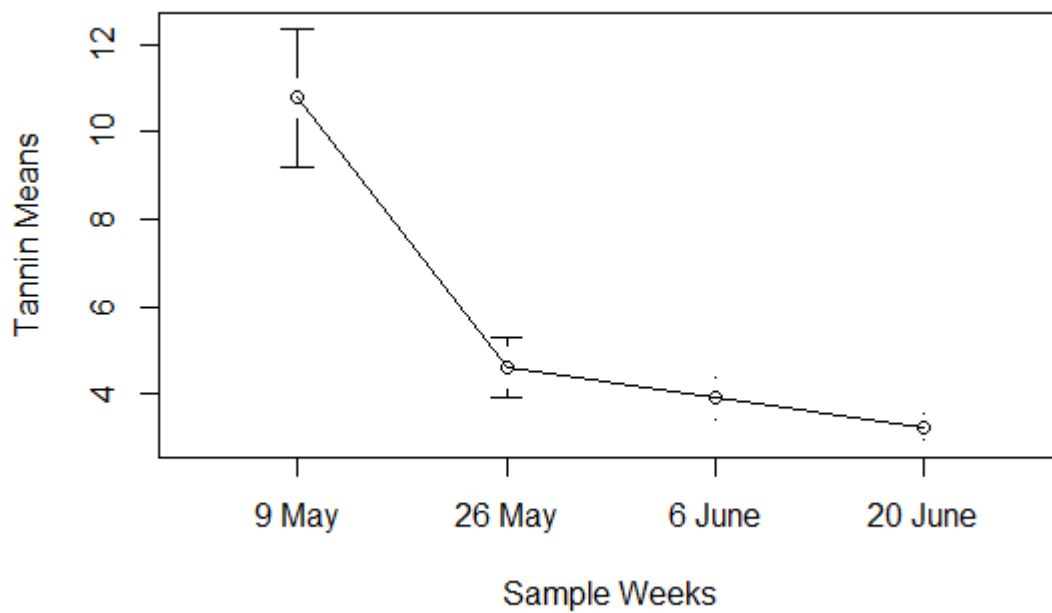


Figure 3-4: Template for inserting figures.

For the nMDS of colonizer communities, data was standardized with Bray-Curtis dissimilarity in 2 dimensions which yielded a stress of 0.13. To explain the ordination, envfit maximized correlations at 999 permutations for both taxa and environmental factors. Taxa describing the most variability in community structure ($p < 0.01$) were *Copelatus glyphicus*, *Laccophilus proximus*, *Laccophilus fasciatus*, *Hesperocorixa nitida*, and *Notonecta irrorata* (Figure 3-5). The environmental factors which were most likely affecting community structure ($p < 0.05$) were the water tannin concentration, conductivity, water color, and the ratio of nitrogen to phosphorus of leaf litter (Figure 3-5). These traits split into two major groups: 1) the water tannin concentration and color and 2) ratio of N:P and conductivity. Higher abundances of *N. irrorata* and *C. glyphicus* were associated with darker water color and higher tannins. Higher abundances of *L. proximus* were associated with conductivity and N:P ratios. *Hesperocorixa nitida* and *L. fasciatus* abundance were not strongly associated with either (Figure 3-5).

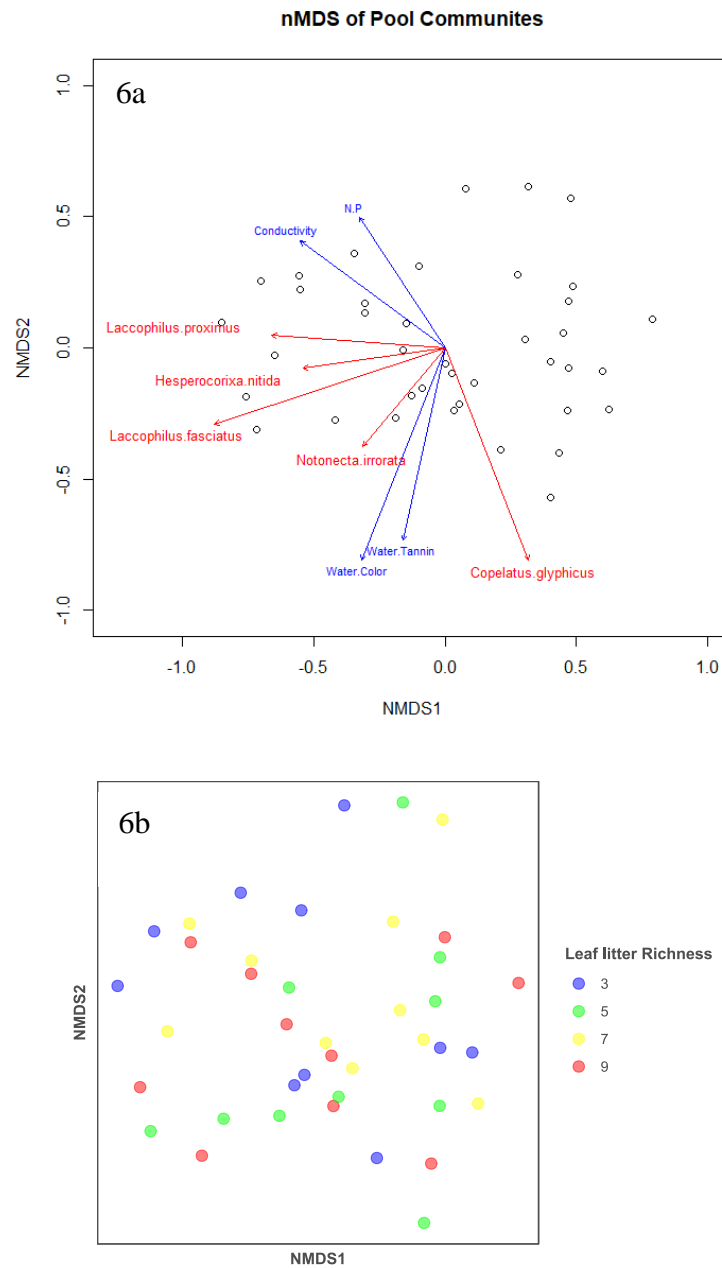


Figure 3-5: (6a) nMDS of colonizing taxa (red) ($p < 0.01$) and environmental variables (blue) ($p < 0.05$) which are responsible for driving colonizer communities in pools (circles) with different mixtures of leaf litter. (6b) nMDS showing communities and their associated leaf litter richness levels with no clear pattern.

CHAPTER 4

DISCUSSION

4.1 Leaf Litter Diversity Influences Colonization

Invasive species, disease, and land use change can alter forest composition through the loss and additions of tree species and impact aquatic systems via leaf litter (Kreutzweiser et al., 2019). Terrestrial leaf litter is an integral part of pond ecosystems (Leroy & Marks, 2006; Marks, 2019; Stoler & Relyea, 2020; Wallace et al., 1997; Webster & Benfield, 1986). Previous studies have shown that leaf traits can impact freshwater community dynamics by altering energy and nutrient flow (Rubbo & Kiesecker, 2004; Stoler et al., 2016; Stoler & Relyea, 2011). Mesocosms with different leaf litter species can be preferred by colonizing insects (Pintar & Resetarits, 2017a; Earl et al., unpubl. data). Here, I have demonstrated that leaf litter functional diversity can predict community assembly of aquatic insects. In general, leaf litter functional diversity had a parabolic (i.e., quadratic) relationship with insect colonizer abundance, with the highest abundance at an intermediate leaf functional diversity and lower insect abundance at low and high leaf functional diversity. Contrary to predictions, colonizer species diversity was not related to either leaf litter functional diversity or species richness. Together, my results suggest that leaf litter functional diversity is an important predictor of colonizer abundance in mesocosms suggesting changing forest composition can influence aquatic insects. However, the degree of importance of an addition or loss of a

specific species depends on the traits of that the species which are being added or removed.

Leaf litter functional diversity demonstrated a parabolic rather than linear relationship with colonizer abundance. Colonization increased with functional diversity until hitting the apex (average functional diversity 3.72) and then decreased beyond the apex (Figure 4-1). This parabolic relationship between colonizers and leaf litter functional diversity suggests that too few or too many extreme traits in leaf litter are unfavorable for colonization. The parabolic shape of our response of colonizers to functional diversity may be explained with two hypotheses. (1) Colonizing insects are responding to increased primary productivity and/or (2) colonizing insects are responding to prey populations.

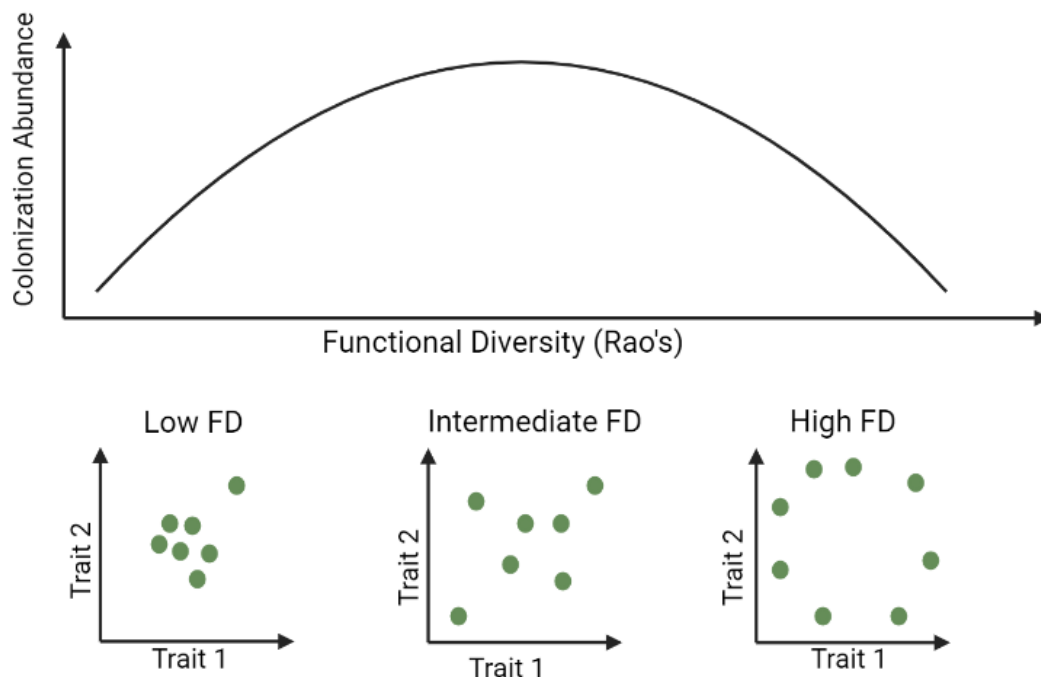


Figure 4-1: Colonization preference for intermediate levels of leaf litter functional diversity (a) and an illustration of different levels of leaf functional diversity (FD) for three example pools where each dot is a species of leaf litter in that pool shown in trait space.

4.1.1 Hypothesis 1: Response to Increased Primary Productivity

Increased functional diversity of leaf mixtures can increase nutrient transfer and decomposition (Handa et al., 2014; Rabelo et al., 2022). Abundant nutrients from species with more extreme nutrients can leach out of leaves and be taken up by the microbial communities growing on nutrient poor species (Rabelo et al., 2022). This supports the role that a species' leaf litter with more extreme traits can contribute disproportionately to an ecosystems' function (Marsh et al., 2000). This could suggest that higher levels of functional diversity are more suitable for producer communities as they are less likely to

be restricted by nutrient limitation, leading to colonizers preferring intermediate levels of functional diversity which are not as highly dominated by primary productivity.

The leaf litter mixtures with higher functional diversity and more extreme traits can lead to increased primary productivity and possibly eutrophication (Rabelo et al., 2022). Increased primary productivity, which can result from eutrophication, often displays parabolic relationships with macroinvertebrates because when primary productivity is reduced the community is nutrient deficient but when primary productivity is in excess there is eutrophication (King & Richardson, 2007). Though we did not measure primary production, increasing levels of eutrophication can negatively affect aquatic beetles and although some aquatic beetle species are specialists of eutrophic environments, they are generally considered to be deleterious to aquatic beetle populations (Cooper et al., 2005; Gioria, 2014; Rosset et al., 2014). This is largely based on the rarity to find aquatic beetles in eutrophic ponds, but the reason is thought to relate to water chemistry or hinderance of movement (Gioria, 2014). Eutrophication can alter water quality, cause more extreme fluctuations in dissolved oxygen, and alter patterns of dominant primary producers thereby impacting herbivore food resources (Liston et al. 2008; Dodds & Whiles, 2020). Eutrophication and increased primary productivity may cause the low abundances of colonizers in the high functional diversity pools but there was also low abundance in the low functional diversity pools

This low abundance in low functional diversity pools may be caused by a lack of nutrients and primary productivity. Colonizing insects are found to be more abundant with added nutrients to mesocosms (Binckley & Resetarits, 2008; Pintar et al., 2018). Macroinvertebrate abundance in ponds is positively correlated to primary productivity

(Mermillod-Blondin et al., 2020) However, these studies did not find an intermediate level of nutrients were preferred by colonizers. This could be because they did not have high enough nutrients levels to become eutrophic and get a parabolic relationship. Ultimately this leads to a higher abundance of colonizers at intermediate levels of functional diversity because both high and low functional diversity are less suitable for colonization.

4.1.2 Hypothesis 2: Response to Prey Populations

Most colonizers in this study were predators, of the analyzed taxa Dytiscidae, *C. glypticus*, and *L. fasciatus* are predatory their entire lives. Hydrophilidae are predatory during their entire larvae phase but are herbivorous as adults. Of the hemipterans that colonized pools 78% of individuals were predatory. Due to so many predators most of our colonizers are not directly feeding on leaf litter, but feeding on prey taxa (zooplankton and larval insects) that feed on leaf litter and periphyton (Pintar & Resetarits, 2017b). In a mesocosm colonization experiment which modified zooplankton abundance found predatory aquatic insects abundance to be driven by zooplankton prey abundance (Pintar & Resetarits, 2017b). Zooplankton often have their highest population densities and species richness when nutrients (specifically nitrogen and phosphorus) are at intermediate levels, this is because zooplankton communities are bound by primary productivity (Duré et al., 2021). With increasing nutrient availability phytoplankton populations increase linearly causing eutrophication. Zooplankton abundance is constrained by phytoplankton which alter oxygen regimes and their population is highest at intermediate levels of nutrient availability (Duré et al., 2021; Ger et al., 2014). It is

therefore possible that leaf litter functional diversity alters primary productivity which then affects predatory insects' prey items, altering their colonization choice.

4.1.3 Effect of Leaf Litter Richness

Species richness can be considered a proxy for the variation in traits between species (Hunter, 2016). Species richness can be important to functional diversity and is correlated with functional diversity in both natural systems and simulations (Petchey & Gaston, 2002). However, leaf litter species richness has been shown to be a poor predictor of aquatic invertebrate abundance (Ferreira et al., 2012). My findings support that leaf litter species richness was unimportant in influencing most colonizers when controlling for leaf functional diversity. The only exception was Hemiptera, the only taxa to have a significant relationship with richness. There was a preference for pools with 5 and 9 species and less colonization occurred in pools 3 and 7 species. This does not show a clear relationship and further research is needed to confirm this pattern. Additionally, Hemiptera is a coarse taxonomic level, and our colonists are split among four families and which are functionally distinct groups. There may have been patterns for specific families but their abundances were too low to analyze. Notonectids likely follow similar colonization patterns as dytiscids with a preference for prey as they are also predatory for their entire lives. However, of the colonizing corixids, 43% are herbivorous and so may respond more to specific leaf traits, the other 57% of individuals belong to *Trichocorixa*, are specialist predators of Chironomidae larvae (Merritt et al., 2008). This likely would cause conflicting colonization motivations among the family. My findings indicate a limited role of leaf litter richness in predicting communities of aquatic insects. This is consistent with other work emphasizing traits and trait diversity

as a better predictor of community function than species richness (Díaz & Cabido, 2001; Wardle et al., 1997).

4.2 Influence of Pool Variables on Colonization

Specific pool characteristics are important to different colonizing insects and together determine aquatic insect community composition (Pintar & Resetarits, 2017a; Yee et al., 2020). Ephemeral pool water characteristics fell into two distinct groups: 1) pools with increasing levels of conductivity and N:P ratios and 2) pools with increasing water color and tannin concentrations. *Laccophilus proximus* is the only dominant taxa which appears to be attracted to pools with higher water conductivity and N:P. *L. proximus* is considered a pioneer species and can readily colonize less favorable ponds, which may suggest unique colonization cues (Zimmerman, 1960). *Copelatus glyphicus* appears to be attracted to pools with lower N:P ratios, as its vector is in the opposite direction of the N:P ratio vector. Both increased conductivity and the N:P ratios can correspond to high primary productivity (Dodds & Whiles, 2020; Stephens et al., 2015). This could be suggestive of *C. glyphicus* avoiding pools with excess primary productivity.

The second primary drivers of insect communities were leached tannins and water color. Tannins degraded over the course of the experiment and were likely a larger influence earlier on. Tannins can prevent light penetration which could otherwise fuel primary productivity (Dodds & Whiles, 2020). Tannins from leaf litter have also been linked to low dissolved oxygen in water (Earl et al., 2014). When tannins are elevated in water, it can have negative effects on macroinvertebrates (Cameron & LaPoint, 1978) and anurans (Dodd & Buchholz, 2018). Water color had no statistically significant change

over time. Water color can provide protection from predators such as fish (Wissel et al., 2003) and can reduce the amount of primary productivity through shading (Lindholm et al., 2018). However, much of the color of water originates from the leachate which in part is tannins (Montez et al., 2021). Colonization can have a strong positive relationship with water color (Bentley & Day, 1989; Li et al., 2009). Both *N. irrorata* and *C. glyphicus* were most associated with communities along increasing levels of water color, preferring darker colors, and increased leached tannins. This could be due to a preference for water that the primary productivity is more limited in and therefore not eutrophic. Water color can be influenced by a wide assortment of factors and more research is needed to understand the role of water color on colonization.

4.3 Differences Between Dytiscidae and Hydrophilidae

I examined Hydrophilidae, Dytiscidae, and Hemiptera abundances. The most abundant family was Dytiscidae. This family of beetles is predacious as adults and larvae and do not feed on leaves (Merritt et al., 2008; Yee, 2014). Hydrophilids preferred to colonize in pools with leaves, but they did not exhibit a significant response to leaf litter diversity. Hydrophilid adults are omnivorous, and their larvae are predatory. The adults can directly utilize leaf litter, and I saw greater hydrophilidae abundance in pools with leaves than without. I expected hydrophilids to have a stronger selection for leaf litter richness and functional diversity, because they could benefit from leaf litter more than the dytiscids. Hydrophilids are more sensitive to leaf litter quality than other taxa (Pintar & Resetarits, 2017a). The difference between our studies may be explained through our low abundance of hydrophilids. Of the colonizing beetles in my study, only 9.3% were hydrophilids compared to 52% in their study.

There are also morphological differences between Dytiscidae and Hydrophilidae which could affect their ability to assess pool quality. Aquatic coleopteran adults are areopneustic, meaning they must surface to collect air. Because of this, they do not have gills and so carry air with them when submerged. Dytiscids carry air with them underwater in their subelytral cavity and breathe through abdominal spiracles (Siegfried Kehl, 2014). Hydrophilids carry air underwater on their ventral surface using hydrofuge pubescence or specialized water retaining hairs. To assist with maintaining this air pocket some hydrophilid antenna are modified to assist with air retention and rely on their maxillary palpi as primary sensory structures with apically concentrated sensillia, a type of hairlike sensory organ (Oliva, 1992). This is different from dytiscids who rely predominantly on their antenna as their primary sensory structures which they can use to navigate terrestrial and aquatic environments (Siegfried Kehl, 2014). These morphological differences may also help to explain the differences between hydrophilid and dytiscid's preferences for leaf litter diversity. The differences in sensory systems may result in the differences in the sensitivity of detection, or they may use different leaf litter cues altogether. Further research into the sensory systems of these beetles could be important to understand how they respond to cues and why different responses may be seen between the two families.

4.4 Preference for Leaf Litter

The preference for leaf litter by colonizing insects has previously been documented and is further supported here (Pintar & Resetarits, 2017a, 2017c). Total abundance, hemiptera, and hydrophilidae all had a colonization preference for pools with leaf litter. However, dytiscidae, *C. glyphicus*, and *L. fasciatus* showed no difference in

abundance between pools with and without leaf litter. This may be due to the limited number of control pools ($n = 5$) compared to total pools with litter in the experiment ($n = 40$). There is also the possibility that pools were influenced by a spatial contagion. Pintar and Restarits (2017c) tested for bottom-up spatial effects of added leaf litter to mesocosms and found that a low-quality pool could be perceived as higher quality if near a high-quality pool. This could also explain the results we saw in our pools with no leaves. However, the specific distance needed to eliminate the influence of a spatial contagion for colonizing insects is unknown. Pintar and Restarits (2017c) placed pools 0.5 m apart and found a spatial effect, while my pools were one meter apart. It is still possible that we had a spatial effect since the maximum distance that a spatial effect can occur is unknown. Future studies should maximize distances between pools to minimize the risk of spatial effects. It is also possible that there may not be a preference for pools with leaves among dytiscids, but rather they were colonizing pools based on characteristics rather than the specific leaf traits. This could fit with hypothesis 2 discussed above where colonizers are responding to prey populations rather than the specific leaf traits.

Understanding trophic interactions between leaf litter, primary productivity, zooplankton, and colonizing insects is an important next step forward. Previous studies have shown complex interactions in response to leaf litter (Stoler & Relyea, 2011), but little work has been done to connect the two trophic levels. Pintar and Resetarits (2017b) showed a preference of colonizers for mesocosms with higher zooplankton abundance. Aquatic beetles also exhibit top-down controls of zooplankton communities (Cobbaert et

al., 2010). Dytiscids can consume zooplankton both as adults and larvae, and some have morphological adaptations to capture them (Friis et al., 2003).

Leaf litter is important for the colonization of aquatic insects. I predict that the colonization of these insects can shape communities of herbivores and alter nutrient flows. When predatory insect colonization is higher, herbivore population will be smaller. This could result in leaf litter resources being able to persist for a longer amount of time in the water, sustaining invertebrate populations for longer. When functional diversity is too high or too little, there may not be a large influx of colonization and communities may be dominated by specialists who are adapted to nutrient limitation or eutrophic environments. Future work understanding trophic interactions between the macroinvertebrate community and microbial community could be important to fully understand how leaf litter influences colonization of aquatic insects.

CHAPTER 5

CONCLUSION

These findings demonstrate that leaf litter diversity influences colonization, but that leaf richness is less important than functional diversity. There was a significant difference between levels of leaf litter richness among Hemiptera, but this will need future research to elucidate. Leaf litter functional diversity had a parabolic relationship with colonizer abundance, Dytiscidae, Hemiptera, and *C. glyphicus*, with an intermediate peak suggesting the importance of extreme leaf traits in influencing aquatic insect colonization. I suggest two hypotheses to explain this parabolic relation: 1) Colonizing insects are responding to primary productivity and 2) Colonizers are responding to prey. I determined that N:P ratios and conductivity are a driver of aquatic insect communities potentially through primary productivity. I also determined that water color and tannins were a driver of community structure.

The pools in this experiment provide a good analog for studying ephemeral pools. Ephemeral pools are an endangered ecosystem, which provide shelter to many aquatic insects and amphibians who use these pools, because they are devoid of their normal predators such as fish (Batzer & Wissinger, 1996). Many of the aquatic insects which colonize pools are largely understudied and their conservation status is unknown. However, there is evidence that their populations are declining. A 28-year study in Germany demonstrated that aquatic beetle populations were declining on average 1-2%

annually (Roth et al., 2020). Aquatic insect populations are also strongly linked to bird populations and insectivorous bird declines (Lewis-Phillips et al., 2020; Manning & Sullivan, 2021). This research could help to inform management to help conserve at risk species found in these ephemeral pools. The emphasis should not be on maximizing tree species but rather to promote tree functional diversity to an intermediate level as that was preferred by all taxa which responded to leaf functional diversity.

By establishing that N:P, conductivity, water color, and tannins drive colonization this could provide information on how to conserve aquatic communities. This could also have implications for management of pest species such as *Culex* mosquitoes, which are vectors for West Nile Virus, encephalitis, and filariasis (Bhattacharya & Basu, 2016). Many dytiscids and larval hydrophilids are predators of mosquitoes. By seeking optimal leaf litter for beetles, predation on mosquitoes could increase (Bofill & Yee, 2019; Pintar & Resetarits, 2020). Certain leaf species can also be considered an ecological trap for mosquitos, when an oviposition site is perceived as higher quality but is deleterious to the offspring (Gardner et al., 2018). Developing further ideas about the role specific leaf traits play in shaping pool communities could help to promote biodiversity and manage disease vectors.

This project has implications for land management, biodiversity maintenance, and ecosystem health. Understanding the role of leaf litter helps to understand linkages between terrestrial and aquatic systems, which can inform property owners of how to manage for heath in both ecosystems. As climate change shifts habitable ranges of plant species, there will be implications for aquatic systems. Aquatic invertebrate biodiversity is largely understudied, unrepresented, and unprotected. By gaining further

understanding of the implications of leaf litter in aquatic systems, we can work to protect these sensitive ecosystems

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