URBAN WETLAND STRUCTURE AND ITS RELATIONSHIP TO
EXOTIC PLANTS, BIODIVERSITY, AND WEST NILE VIRUS RISK

by

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Lena Struwe, Ph.D.

And approved by

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ABSTRACT OF THE DISSERTATION

Urban wetland structure and its relationship to
exotic plants, biodiversity, and West Nile virus risk

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Dissertation Director:
Lena Struwe, Ph.D.

Wetlands provide crucial ecosystem functions that aid water security, stormwater management, and biodiversity conservation. However, the underlying mechanisms that influence headwater wetlands in urban landscapes are poorly understood. Further, biodiversity loss may reduce ecosystem function and increase the transmission risk for some enzootic diseases, such as West Nile virus (WNV). My research aimed to: 1) assess wetland vegetation structure and the importance of fragment size and landscape position on biodiversity; 2) test the importance of flooding conditions for mitigating invasive plant dominance in forested wetlands using Japanese stiltgrass (*Microstegium vimineum*) as my study system; and 3) identify relationships between vegetation structure, fragment size, and the relative abundance of competent avian WNV hosts and mosquito vectors. I used a combination of measurative and experimental research methods to address these objectives, the third of which was part of a collaborative interdisciplinary research grant. Vegetation structure was measured in 36 plots located in six forested wetlands and data loggers were used to monitor aboveground flooding. Avian and mosquito research teams coordinated
with my sampling points. My results illustrate the capacity for urban headwater wetlands to support a diverse flora, as well as the complex interactions between human activities and wetland structure and function. Red maple, oak, sweetgum, and green ash were the dominant tree species. Half of the 287 plant species identified only occurred at 1-2 sample points. Groundcover composition reflected the confluence of hydrogeomorphology, and past and present human actions. Connectivity via nearby streams or ditches had a greater impact on exotic plant richness than did wetland patch size. Aboveground flooding prior to seedling emergence significantly reduced the distribution of Japanese stiltgrass. Avian species richness was positively correlated with plant richness. In contrast, mosquito richness was negatively correlated to plant richness. WNV hosts and vector abundance both increased with maple (Acer spp.) tree canopy dominance. Cumulative host abundance averaged 24% and was composed primarily of American Robin, which showed large interannual shifts in fragments <15 ha. The relative abundance of competent vectors ranged from 5 to 26% and their populations demonstrated less interannual variation than were observed in the host populations.
Dedication

This dissertation is dedicated to Dr. Joan G. Ehrenfeld, an inspiring scientist and mentor.

I hope that this dissertation would have made you proud.
Acknowledgements

Words cannot express the gratitude I feel for all of those who have helped, encouraged and guided me in the completion of my degree. This dissertation is not only the culmination of my efforts, but also all those that have contributed along the way, whether great or small. First and foremost, I wish to thank my advisors Drs. Joan Ehrenfeld and Lena Struwe. I am honored to have worked with Joan and her lab. She was an eminent ecologist who equally championed the value of urban and pristine wetlands. Lena was a superb mentor and advocate for me when I truly needed it most. Additional thanks to my committee members, Drs. Steven Handel, Jean Marie Hartman, and Laura Schneider, each of whom added a perspective to my research that was greatly appreciated. Special thanks to Jean Marie, who treated me like one of her own students, and provided invaluable guidance and encouragement.

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CHAPTER 1

A review of mechanisms that influence urban wetland systems and the importance of identifying and conserving their biodiversity

Urban wetland fragments do not fit the traditional definition of an “isolated” wetland because they are surrounded by residential and industrial development rather than upland vegetation and soils (Sharitz and Gresham, 1998; Mitsch and Gosselink, 2000; Leibowitz, 2003). Urban development, however, has been identified as a form of anthropogenically mediated isolation for wetland systems (Tiner, 2003). Urban-rural comparisons support the hypothesis that urban ecological systems are unique. Woodland structure and function is also different between urban and rural wetlands due to site-specific urban stressors and contaminants (McDonnell et al., 2008).

Wetlands are often typified as heterogeneous landscapes dominated by vegetation that regularly experiences disturbance and other abiotic stressors. Within an urban landscape, anthropogenic actions alter the natural processes that regulate wetland plant assemblages, making them more susceptible to invasion by nonnative plant species. Further, upland or invasive plant species may have a competitive advantage in the absence of specific abiotic stressors (Grime, 1977). Previous research suggested that anthropogenically disturbed wetlands with altered hydroperiods have greater invasive and facultative wetland species, while areas with undisturbed flooding conditions have more obligate wetland plants (Ehrenfeld and Schneider, 1993; Owen, 1999). In the wake of these abiotic alterations, wetlands in urban environments possess reduced resistance and resilience to biological invasions, and loss of local biodiversity (Breden et al., 2006).
Altered disturbance patterns and low levels of environmental stress are hypothesized to increase invasibility of a given habitat (Alpert et al., 2000). For example, high levels of white-tailed deer herbivory change ecosystem processes and have been shown to accelerate the spread and dominance of invasive species (Côté et al., 2004; Dávalos et al., 2015b). This has been demonstrated in local New Jersey forests where Japanese stiltgrass (*Microstegium vimineum* (Trim.) A. Camus), garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande), and Japanese barberry (*Berberis thunbergii* DC.) were found to have reduced distribution in deer enclosures (Eschtruth and Battles, 2009). These three species have also been found to alter soil and nutrient processes (Ehrenfeld et al., 2001; Kourtev et al., 2003; Rodgers et al., 2008; Schramm and Ehrenfeld, 2010).

Unlike most weedy plants, invasives such as Norway maple (*Acer platanoides* L.) (Galbraith-Kent and Handel, 2008), Japanese barberry (Silander and Klepeis, 1999), and Japanese stiltgrass (Flory et al., 2007) tolerate low light levels. Although these species may thrive in reduced light environments, few may additionally tolerate the stressors of anoxic wetland soils.

Flood frequency, duration, and depth determine wetland plant assemblage composition. Wetlands within developed landscapes experience shorter, shallower, and more frequent, “flashy” flooding; that is, a high intensity, short duration hydrologic disturbance (Ehrenfeld and Schneider, 1993; Ehrenfeld et al., 2003; Groffman et al., 2003). Wetland draining, and subsequent lowering of the water table, affects soil properties and plant species composition (Groffman et al., 2003). Many facultative plant species (see Table 1: Terms and definitions) may tolerate reduced soil oxygen characteristic of short term flooding, but become increasingly unable to tolerate areas with prolonged flooding.
and anoxic soils (Grime, 1977; Kozlowski, 1984). The low flood tolerance characteristic of exotic species may buffer forested wetlands against invasion (Barden, 1987; Price et al., 2011). Altered wetland hydroperiods therefore make forested wetlands more susceptible to pervasive, shade-tolerant invasive species (Bowman Cutway and Ehrenfeld, 2009; Martin et al., 2009).

Ecosystem invasibility can be determined by landscape and local environmental conditions. Historical and surrounding land-use affect urban woodland plant assemblage structure (Thibault and Zipperer, 1994; DeGasperis and Motzkin, 2007; Bowman Cutway and Ehrenfeld, 2009; Kuhman et al., 2010), fragment and edge dynamics (Luken et al., 1991; Harper et al., 2005), the ability of riparian areas to serve as conduits (Stohlgren et al., 1998; Tabacchi et al., 2005), and fragment connectivity (Noss, 1999; Esbah et al., 2009; Mortensen et al., 2009). Local scale environmental variables (Alpert et al., 2000; Ehrenfeld, 2008; Farrer and Goldberg, 2009), biodiversity (Robinson et al., 1995; Tilman, 1997; Levine, 2000), and disturbance (Owen, 1999; Levine and Stromberg, 2001; Eschtruth and Battles, 2009) can be mechanisms for nonnative species establishment. Watershed scale nutrient loading, sediment movement, land use/land cover (LULC), and hydroperiod perturbations reduce urban wetland ecosystem health, making them more susceptible to biological contaminants such as invasive species.

The deleterious effects of invasive plant species on ecosystem function are pronounced. Previous research indicates that nonnative plants alter nutrient cycling and litter inputs (Ehrenfeld, 2003; Farrer and Goldberg, 2009; Weidenhamer and Callaway, 2010). However, the structural shifts in vegetation composition following exotic plant invasion are more noticeable to wildlife as well as community stakeholders. Reduced
vegetation heterogeneity and biodiversity is common in the wake of an invasion (Oswalt et al., 2007; Davies, 2011). This trend has been documented for invasive species common in the northeastern US, such as Japanese stiltgrass (Adams and Engelhardt, 2009; Flory and Clay, 2010), reed canarygrass (*Phalaris arundinacea* L.) (Magee and Kentula, 2005), and Norway maple (Galbraith-Kent and Handel, 2008), and oriental bittersweet (*Celastrus orbiculatus* Thunb.) (Fike and Niering, 1999).

Novel exotic insects and pathogens that target woodland canopies have a similarly deleterious effect. The 2014 introduction of Emerald Ash Borer (*Agrilus planipennis* Fairmaire) to New Jersey and reintroduction threat of Asian Longhorn Beetle (*Anoplophora glabripennis* Motschulsky) have significant implications for watershed management and water quality. By biomass, ash (*Fraxinus* spp.) is the fifth most abundant tree in NJ (Crocker et al., 2011), with green (*F. pennsylvanica*) and black ash (*F. nigra*) common in northern headwater and riparian ecosystems. Developing EAB larvae feed on transport tissue underlying the bark, effectively girdling the tree, causing tree mortality within 2-6 years. Research by Knight et al. (2013) suggests that the density of ash trees influences the rate of dieback following infestation. The researchers concluded that trees at intermediate densities die more rapidly than trees in forest stands where ash was the dominant or co-dominant canopy species. In comparison, ALB prefers maple (*Acer* spp.) whose biomass is more than twice that of ash (Crocker et al., 2011; USFS, 2013). The loss of ecosystem services should one or both of these genera be lost to invasive pests would be immense (Chapin et al., 2002; Diaz et al., 2007; Flower et al., 2013).

Describing patterns of biodiversity within a landscape and identifying mechanisms potentially responsible for those patterns, such as wetland hydrology, have pertinent
conservation and management implications. Animal biodiversity reflects the structural complexity of a given habitat. These interactions are important to understand for the management of vector-borne diseases that animals pass to humans, such as West Nile Virus (WNV), whose life cycle depends on specific competent host (birds) and water-breeding vector species (mosquitoes). Urban areas may be more prone to vector-borne outbreaks if the proportion of competent hosts and vectors is relatively high (Johnson et al., 2012). Conversely, areas with high animal biodiversity may experience a "dilution effect" (Keesing et al., 2006), resulting in reduced disease risk.

**Dissertation Overview**

This dissertation, composed of four main chapters, combines traditional mensurative and manipulative experiments with collaborative interdisciplinary research in an effort to produce science-driven policy and management practices. Questions driving my research include: To what extent is floristic biodiversity and exotic plant richness indicative of landscape position, wetland size, and hydroperiod? To what degree is invasive plant dominance reflective of hydrology in forested headwater wetlands? What environmental conditions (e.g., hydrology, landscape position, connectivity) limit the distribution of invasive plants in urban wetlands? What wetland traits (e.g., biodiversity, flooding, vegetation structure, fragment size) correlate with competent WNV vectors (mosquito) and host (bird) abundance?

Six urban wetland patches within the headwaters of central New Jersey were selected based on wetland size and adjacent urban (medium/high density residential) land use (Figure 1). Plant communities at these sites are predominately deciduous swamps
dominated by sweetgum, red maple, oak, green ash. Flooding conditions ranged from root zone saturation to semi-permanent aboveground flooding (sensu Cowardin et al., 1979). Plant species biodiversity and vegetation structure (e.g., tree density, herbaceous species cover) were assessed within each field survey macroplot, in coordination with an interdisciplinary research team (2008-2011). I surveyed 36 707-m² macroplots in six wetlands and an additional 108 50-m transects describing the coarse vegetation structure surrounding each macroplot.

The first data chapter of this dissertation describes vegetation structure within each wetland, as well as patterns among the different wetland patch size classes (large>125 ha; medium 35-25 ha; small<15 ha). This foundational chapter was used to inform and structure research questions examined throughout this dissertation, including exotic plant dominance in relation to flooding (Chapter 2) and habitat correlates with competent WNV avian host and mosquito vector relative abundance (Chapter 3). I found that plant species richness was not merely reflective of wetland fragment size, but rather the extent to which humans have altered natural processes such as flooding, as well as browsing by white-tailed deer. Landscape setting was correlated with exotic plant species richness. However, local hydrology and other local community interactions strongly influenced whether invasive plants dominated the local flora.

By manipulating mesocosm flooding duration or depth over a three-week period and monitoring Japanese stiltgrass (Microstegium vimineum) seedling production in flooded vs. control treatments, I was able to conclude that seedling production is inhibited by flooding (n = 63). The control treatment was the only treatment to produce seedlings, even two months following drawdown of the flooded treatments. That is, four days of
shallow flooding during the natural germination period of Japanese stiltgrass may significantly reduce germination of this invasive grass that is changing the structure and function of New Jersey woodlands.

My final chapter is the culmination of an interdisciplinary collaboration that has demonstrated that the presence of wetland patches reduces WNV risk in the surrounding residential areas (Johnson et al., 2012). The research presented here assesses the importance of vegetation structure and plant biodiversity in shaping avian and mosquito species richness, as well as WNV host/vector abundance. As floristic richness increased, avian and mosquito richness increased and decreased, respectively. Competent WNV hosts and vectors responded positively to maple tree dominance, a habitat trait that was correlated with exotic plant richness. American robins were the most abundant WNV host. In small wetlands <15 ha, significant interannual shifts were observed in host relative abundance (19%), however this trend was not seen in larger wetlands >125 ha (11% change). In contrast, the magnitude of interannual variation for WNV vectors was <9%, with the lowest abundances observed in the largest wetland (>225 ha), and the two small wetlands.
References


Table 1: Federal wetland classification terms and definitions (Cowardin et al., 1979).

<table>
<thead>
<tr>
<th>Term</th>
<th>Abbreviation</th>
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<tr>
<td>National wetland plant indicator status</td>
<td></td>
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<tr>
<td>Obligate wetland</td>
<td>OBL</td>
<td>Almost always is a hydrophyte, rarely in uplands.</td>
</tr>
<tr>
<td>Facultative wetland</td>
<td>FACW</td>
<td>Usually is a hydrophyte but occasionally found in uplands.</td>
</tr>
<tr>
<td>Facultative</td>
<td>FAC</td>
<td>Commonly occurs as either a hydrophyte or non-hydrophyte.</td>
</tr>
<tr>
<td>Facultative upland</td>
<td>FACU</td>
<td>Occasionally a hydrophyte but usually occurs in uplands</td>
</tr>
<tr>
<td>Obligate upland</td>
<td>UPL</td>
<td>Rarely is a hydrophyte, almost always in uplands</td>
</tr>
<tr>
<td>Nontidal flooding regimes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temporary</td>
<td>A</td>
<td>Water table often below soil surface, brief phases of surface water present.</td>
</tr>
<tr>
<td>Saturated</td>
<td>B</td>
<td>Substrate saturated for extended periods; surface water rarely present.</td>
</tr>
<tr>
<td>Seasonal</td>
<td>C</td>
<td>Surface water is present for extended periods, especially early spring.</td>
</tr>
<tr>
<td>Seasonal/Saturated</td>
<td>E</td>
<td>Surface water present early spring, saturated for remainder of season.</td>
</tr>
<tr>
<td>Semipermanent</td>
<td>F</td>
<td>Surface water persistent most years; or water table is at/near surface.</td>
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Figure 1: Field research for this dissertation was conducted in six palustrine wetland fragments located in central New Jersey (Middlesex and Union counties). Three wetland size classes were used to categorize the patches by size: large (DS and NL >125 ha); medium (EV and NB 25-35 ha); and small (PP and TE <15 ha). Wetlands DS and NB are headwaters of the Raritan River, while the other four wetlands are part of the Rahway River watershed.
CHAPTER 2
Natural and anthropogenic factors limit plant biodiversity in urbanized wetlands

Abstract

In urban landscapes, forested wetland systems provide critical ecological services and serve as refuge for local flora and fauna. However, the structure and function of these systems are altered by human-mediated disturbances and the introduction of exotic plants and pests. Hydrologic perturbations are particularly important for wetland systems because hydrology strongly influences the expressed plant assemblage. Wetland flooding conditions in urban catchments therefore reflect the surrounding land use, the result of which is often increased flood frequency, and decreased flood duration and extent – these local disturbances alter ecosystem structure and function. Recent establishment of Emerald Ash Borer in northeastern USA underscores the importance of understanding mechanisms that shape forested wetland assemblages. Vegetation structure and plant species richness were sampled in 36 regularly spaced macroplots, spread across six headwater wetlands ranging in size from 9 to 225 ha. Red maple, oak, sweetgum, and green ash trees were the dominant canopy species. In forested macroplots, average tree basal area per ha was highest in the smallest wetland and lowest in the largest wetland (36.3 vs. 22.4 m²/ha). Green ash dominance was negatively correlated with local microrelief, as was the relative cover of herbaceous hydrophytes. Of the 287 species identified, 61% were classified as wetland plants (FAC, FACW, OBL). Total macroplot plant richness was highest in large wetlands, ranging from 23-88, followed by medium (20-60), and small (19-34) wetland fragments. Connectivity via nearby streams or human
disturbance had a greater impact on exotic plant richness than did wetland patch size. Groundcover composition observed in this study reflected the confluence of hydrogeomorphic setting, and past and present human actions. Ordination analysis identified four distinct ground cover assemblages; half were associated with sweetgum while the other half with green ash. Results illustrate the capacity for urban headwater wetlands to support a diverse flora, as well as the complex interactions between human activities and wetland structure and function. Failures to address the intrinsic and economic values of these systems within urbanizing landscapes will result in continued degradation of ecosystem processes and biodiversity loss.

**Introduction**

Wetland vegetation composition is reflective of landscape setting (e.g., headwater or lowland), flooding conditions, and disturbance cycles (e.g., frequency or intensity). Historical and modern land usage alters natural flood conditions, often reducing the duration, depth and extent of flooding, making altered wetlands susceptible to invasion by competitively dominant non-native species (Ehrenfeld et al., 2003). This shift in water levels is particularly important in wetlands because vegetation composition strongly influences the rate of evapotranspiration and the quantity of surface flow (Chapin et al., 2002). Characterizing headwater wetland vegetation is therefore crucial for understanding and mitigating potential impacts of human-mediated alterations (e.g., urbanization, invasive insects) to ecosystem structure and function. For example, interception by trees immediately reduces precipitation throughfall by more than 15% (Chapin et al., 2002). Further, research by Krämer and Hölscher (2009) suggests that higher tree canopy
biodiversity can mitigate stream flows more effectively than similar forests with fewer tree species.

Although the dynamic equilibrium hypothesis generally holds for wetland communities (MacArthur and Wilson, 1963), underlying environmental conditions are also crucial because hydrology is the primary underlying mechanism that shapes the expressed floristic assemblage (van der Valk, A. G., 1981; Blom and Voesenek, 1996; Magee and Kentula, 2005; Toogood and Joyce, 2009; Grabas and Rokitnicki-Wojcik, 2015). Only select plant species possess traits that permit persistence during periods of inundation and soil anoxia (Grime, 1977; Blom and Voesenek, 1996; Kozlowski, 2002; Magee and Kentula, 2005; Toogood and Joyce, 2009). Plants can therefore be one proxy for wetland condition (Euliss et al., 2004) particularly in developed landscapes where water tables have been lowered (e.g., ditching, undercut rivers) and urbanized catchments generate “flashy” wetland hydroperiods (Findlay and Houlahan, 1997; Ehrenfeld et al., 2003; Groffman et al., 2003; Grabas and Rokitnicki-Wojcik, 2015).

Propagule availability and seed bank longevity are particularly important for ecosystem resilience in the wake of natural disturbances such as droughts (De Steven et al., 2006; Touchette et al., 2008), and direct or indirect human-mediated disturbance (Sousa, 1984; Findlay and Houlahan, 1997; Pickett et al., 2001; Grimm et al., 2008; Bried et al., 2013). Air photos from the 1930s (NJDEP, 2012) suggest that more than half of the present day macroplot locations were actively used for cropland, pasture, or silviculture. These types of land uses significantly decrease the native seed bank and alter edaphic processes (Middleton, 2003; Bruland and Richardson, 2005). Despite these past and present impacts, anthropogenically altered wetlands can maintain a diverse flora with
relatively low exotic species abundance (Ehrenfeld, 2005). The physiological stressors of flooding is an establishment barrier that mitigates the high propagule pressure of hydrologically connected wetlands (van der Valk, A. G., 1981; Keddy, 1992; Lockwood et al., 2007). Shading in woodland environments may be an additional barrier to the colonization or dominance of understory invasives (Martin et al., 2009; Schramm and Ehrenfeld, 2010; Stinson and Seidler, 2014), whose superior competitive traits make them poorly suited for less than optimal growing conditions (Grime, 1977; Davis et al., 2000. e.g., low light levels, anoxic soils).

Novel exotic insects and pathogens that target woodland canopies have a similarly deleterious effect. The 2014 emergence of Emerald Ash Borer (EAB) in New Jersey and reintroduction threat of Asian Longhorn Beetle (ALB) have significant implications for watershed management and water quality. By biomass, ash (*Fraxinus* spp.) is the fifth most abundant tree in NJ (Crocker et al., 2011), with green (*F. pennsylvanica* Marshall) and black ash (*F. nigra* Marshall) common in northern headwater and riparian ecosystems. Developing EAB larvae feed on transport tissue underlying the bark, effectively girdling the tree, causing tree mortality in <2 years. In comparison, ALB prefers maple (*Acer* spp.) whose biomass is more than twice that of ash (Crocker et al., 2011; USFS, 2013). Should one or both of these genera be lost to invasive pests, reduced evapotranspiration rates would increase precipitation reaching the forest floor by >25% in some headwater wetland complexes (Chapin et al., 2002; Diaz et al., 2007). Compared to saturated wetlands, the loss of ash trees is expected to be stronger in wetter systems that experience aboveground flooding (Telander et al., 2015), particularly where regeneration has been retarded due to high herbivory pressure (Cadenasso and Pickett, 2000; Liang
and Seagle, 2002; Goetsch et al., 2011; White, 2012). This loss of ecosystem services would increase runoff and local water table depth, the latter causing shifts in assemblage composition, potentially converting forested swamps to emergent marshes (Tilton, 1995; Kozlowski, 2002).

These studies suggest that wetlands in urbanized watersheds serve as biodiversity hotspots and perform critical ecosystem services, both of which may be compromised by direct and indirect human activities. Using a sample of headwater wetlands from urban central New Jersey, I tested the applicability of common ecological theories related to plant species richness including 1) the positive correlation between patch size and biodiversity; 2) exotic plant richness is greater in smaller fragments and those connected via waterways; and 3) compared to pristine wetlands, hydrophyte richness may not be a suitable wetland indicator because edge effects and hydrologic perturbations increase the dominance of upland species. Baseline vegetation structure and tree demographics were also measured to assess plant assemblage structure prior to exotic pest establishment.

**Materials and methods**

**Study sites**

This study was conducted in urban northeastern New Jersey (NJ) within the Arthur Kill (409.7 km²) and Lower Raritan (910.7 km²) Water Management Areas (Figure 1). Urban lands cover 83% of the Arthur Kill and 58% of the Lower Raritan WMAs; wetland area cover also differed between these WMA, at approximately 4.5% and 18%, respectively (NJDEP, 2010). As an urban growth hotspot, this metropolitan region represents how dense populations use, influence, and are affected by the wetland systems in which they live. Six urban wetland fragments within Middlesex and Union
20 counties (NJDEP Raritan water region; Figure 1) were selected as study areas based on fragment size and the occurrence of adjacent medium/high density residential land use (NJDEP, 2007). Residential land use descriptions followed NJDEP (2007), which classified high/medium residential land use based on the number of Dwelling Units Per Acre (high-density: single or multiple dwelling units on 1/8-1/5 acre lots; medium: single units on 1/8-1/2 acre lots). Impervious surface was estimated to cover approximately 65% and 33% of the land surface for high and medium-density residential areas, respectively (NJDEP, 2007).

Wetland fragments ranged in size from 9 ha to 225 ha. Large wetlands (>125 ha) included Dismal (DS, n = 15) and Nomahegan/Lenape (NL, n = 11), Evergreen (EV, n = 3) and North Brunswick (NB, n = 3) were of medium size (35-25 ha), and the smallest wetland patches (<15 ha) were Polansky (PP, n = 2) and Terrill (TE, n = 2). Vegetation sample points were laid along a regular 400 m grid, with the exception of the smallest site, where sample points were 200 m apart. Within the six wetlands, 36 vegetation macroplots totaling 2.54 ha were sampled 2008-2010.

Agricultural land use legacies are prominent in nearly all of the study wetlands, though much of the area became fallow by the mid-20th century. Deciduous forested swamps are the dominant wetland plant assemblage (e.g., Acer rubrum L., Fraxinus spp. L., Liquidambar styraciflua L., Quercus spp. L.), with some scrub-shrub (e.g., Cornus spp. L., Lindera benzoin (L.) Blume, Rosa spp. L.), and emergent communities present.

Hydroperiod, the seasonal pattern of flooding, ranges from saturated to seasonally flooded (sensu Cowardin et al., 1979). Per federal flood condition classification by Cowardin et al. (1979), an area of a wetland may be classified as having two flood classes
(e.g., aboveground flooding in the spring and belowground root zone saturation in summer).

**Field methods**

Plant species biodiversity (richness) and vegetation structure were assessed in 15-m radius macroplots (Figure 2). Macroplot-scale (707 m²) metrics included total plant species richness and tree species Diameter at Breast Height (DBH at 1.3 m height). Dead trees (snags) >10 cm DBH were measured and identified to species when possible. Because thickets provide avian habitat, plot thicket area was estimated (m²), sketched on a plot map, and identified to species. All subplot placements followed a stratified random sampling design. The density of woody stems >1 m in height and <2.5 cm DBH were counted in two-88 m² subplots (Figure 2). Woody seedling density (<1 m height) and herbaceous species percent cover were quantified in eight-1 m² subplots, as measured by individual plant counts and modified Braun-Blanquet cover classes, respectively.

Environmental variables were assessed at several scales throughout the macroplot. Within groundcover subplots, leaf litter depth (cm) and percent cover of soil/leaf litter were assessed. Canopy cover was measured at 5 m intervals along cardinal and inter-cardinal transects (plot n = 24) using a GRS densitometer (Geographic Resource Solutions, Arcata, CA). Percent canopy cover was calculated by dividing the number of obstructed observations by the total. Microtopographic change was measured with a stadia rod at 5-m intervals along the cardinal transects, with measurements relative to the observer at plot center (plot n = 12). These topography data were used to calculate the absolute range of topographic variation (max-min) within each macroplot.
In addition to total plant species richness, some of the vegetation composition and plant biodiversity analyses were conducted relative to a species’ status as native/exotic or as indicative of wetland systems. Characterization of a plant species as native or introduced/exotic followed the USDA PLANTS status (2015); exotic varieties or subspecies were assumed to be exotic for the purpose of this study (e.g., *Phragmites australis* L.; seven species in total). The likelihood that a given plant species is hydrophilic is described by a species’ indicator status as designated in the National Wetland Plant List (NWPL) by Lichvar et al. (2014). Hydrophyte designation from the NWPL include obligate (OBL) plant species, those that almost always occur in wetlands, facultative wetland (FACW) species usually found in wetlands, and facultative (FAC) plants that may occur in wetland and non-wetland systems. Species that may occur in wetlands, but are usually found in non-wetlands are designated as facultative upland (FACU) plants, while those that are almost never found in wetlands are classified as upland (UPL) species (Lichvar et al., 2014).

**Statistical Analyses**

Individual wetland and macroplot data were used to examine trends among floristic attributes and landscape variables, or quantified physical and biotic structure. Linear regression and nonparametric correlation analysis were used to examine these trends, using SPSS statistical package (2008) and SigmaPlot graphing software (Systat Software Inc., 2008). Nonparametric correlation analysis employed Spearman rank, the correlation coefficient ($r_s$) values from which range from +1 to -1, with zero indicating no correlation. Because multiple comparisons were examined with Spearman’s, a significance level of $p < 0.01$ was used and correlation coefficients of $r_s >0.427$ or $r_s <-$
0.427 (Zar, 1999) were deemed significant (n = 36, unless otherwise noted). Scatter plot graphs were used to ensure the majority of the data points fell within the 95% confidence interval, and that a few outliers were not driving the significant correlation trend. First-order Pearson’s partial correlation analysis was used to assess a pair of variables that may also be mediated by a third variable, which is not of interest; this type of analysis helps to mitigate the potential importance of that third variable (M = 3; df = 33). A significance level of p < 0.05 was used for linear regression and one-way ANOVA analyses (n = 36, unless otherwise noted). Data that violated ANOVA assumptions were analyzed with Kruskal-Wallace one-way analysis of variance on ranks using a significance level of p < 0.05.

Unknown plant species as well as two pervasive vines (poison ivy, Virginia creeper) were removed prior to multivariate analysis of the groundcover data. As in Brooks et al. (2011), I found that these two ubiquitous plant species obviated the utility of ordination analyses. Agglomerative Hierarchical Cluster Analysis (HCA) was used to identify assemblage groups, the accuracy of which were then examined through Non-metric Multidimensional Scaling (NMDS), Multiple Permutation Response Procedure (MRPP), and Indicator Species Analysis (ISA). These analyses were performed using PCORD (McCune and Mefford, 1999).

Sorensen’s dissimilarity measure was used for HCA, NMDS, and MRPP. This method emphasizes the presence of species when calculating dissimilarity rather than the absence (Quinn and Keough, 2002). Flexible beta linkages (β = -0.50) were used for the cluster analysis with percent chaining <20% deemed desirable (McCune and Grace, 2002). Ordination analysis with NMDS was started using an automated, random
configuration. Monte Carlo statistical significance was tested by comparing ≤250 iterations of real data to ≤250 iterations of randomized data, using an instability criterion of <0.0005. Variables in the second matrix included green ash tree basal area (FRPE BA), sweetgum basal area (LIST2 BA), and stream order of the largest adjacent watercourse within <75 m of macroplot center. All second matrix variables were log transformed. NMDS scree plots were assessed to determine the optimal number of ordinal dimensions, with stress levels <20 considered significant given the sample size of 36 macroplots (McCune and Grace, 2002). Correlations between individual variables and the ordination scores were assessed via Kendall’s rank correlation coefficient (p < 0.01, τ > 0.302). The null hypothesis of no difference between groups was tested using MRPP, which produces an effect size measure, A. Vales of A < 0 indicate within-group heterogeneity is greater than would be expected by chance (i.e., groups are not supported). Therefore, A > 0.1 is considered significant, when coupled with a significant p-value <0.05 (McCune and Grace, 2002).

The detection of plant species that were unique to a given HCA group was assessed using ISA, which calculates indicator values based on the relative abundance and relative frequency of occurrence for a particular species within a predefined group (Dufrêne and Legendre, 1997). Monte Carlo analyses then tested the significance of species’ placement within a proposed group compared to >5,000 iterations with a randomized data set; species presented here have a significance level of p < 0.05.

Results

Richness surveys of this study identified 286 plant species, with an additional 34 unknown specimens that were only observed in vegetative form. In total, 123 forbs were
identified, 52 graminoids, 9 ferns, 64 species of vines and shrubs, and 47 tree species. Total plant richness ranged from 19 to 88 species per macroplot (707 m²). The greatest difference in biodiversity occurred between two wetlands that were nearly equivalent in size: North Brunswick (NB) and Evergreen (EV) (Figure 4). Large wetland Dismal (DS) contained the most plant species, at 264, while the wetland with the fewest was NB (35). Interestingly, NB was the only wetland to lack invasive plant species in any of the surveyed plots. Because all wetlands except NB steadily continued to add species with increased sampling effort, it is fair to conclude that the floristic diversity of each site underrepresents the actual diversity within a wetland (Figure 5). With the exclusion of the largest wetland, Dismal, the accumulation of species during the first few sampling points appears independent of patch size (Figure 5 inset).

Wetland plants, including those classified as OBL, FACW, or FAC (Lichvar et al., 2014), comprised 39-89% of the local flora (68 ± 2%, Figure 3). The proportion of non-wetland plant species ranged from 11% to 50% (28 ± 2%). Species lacking a wetland classification accounted for an average of 4% (± 0.4%) of local macroplot richness, or 28 species in total.

Half of all of the plant species occurred only in one or two macroplots. Comparing species composition within the three wetland size classes, 41% of plant species were found in both large wetlands (DS, NL), while small wetlands shared 22% of their total floristic diversity (PP, TE). In comparison, medium-sized wetlands EV and NB were most different from one another, only sharing 12% of their combined flora. All wetlands, with the exception of EV, contained at least one plant species that is protected for its rarity within the tri-state region of NJ, NY, and PA (USDA, 2015). The 14 listed
species identified in this study were all classified as hydrophytes (Lichvar et al., 2014), and included two horsetail species (*Equisetum* spp. L.), six monocots (Liliopsida), and six dicots (Magnoliopsida).

Plant species that occurred in more than half of the sampled areas accounted for only 7% of the surveyed flora. Four of these pervasive species were introduced invasives. Forty-nine exotic plant species were identified within all of the biodiversity surveys. Interestingly, wetland patch size had relatively little effect on the abundance of exotic invasives, rather within-class size variations were where the largest difference was observed (Figure 6A). As expected, invasive species richness decreased with increasing leaf litter depth (Figure 6B; ANOVA $F_{1,34}$: 10.492, $p = 0.003$); this trend was not observed for native species richness (Spearman $r_s = -0.260$, $p = 0.126$). Proximity to streams as well as stream size (i.e., stream order) also influences the occurrence of invasive plants. The 25 macroplots that occurred within 75 m of a stream contained twice the number of exotic species ($7.8 \pm 0.8$) when compared to the 11 plots that were not stream-adjacent ($3.7 \pm 3.6$; $F_{1,34} = 7.802$, $p = 0.009$). This effect was even more apparent when comparing plots adjacent to headwater streams (<3 order), which averaged 6 exotics/macroplot ($n = 13$), to larger rivers where exotic richness increased by a third ($9; n = 12$). Hydrophyte richness similarly increased with adjacent stream presence and size ($r_s = 0.457$, $p = 0.005$). With the exception of NB, all macroplots contained 1-15 exotic species. The four most common invasives were Japanese stiltgrass (67% of macroplots; *Microstegium vimineum* (Trin.) A. Camus), multiflora rose (*Rosa multiflora* Thunb.; 61%), marshpepper knotweed (*Persicaria hydropiper* (L.) Opiz; 56%), and garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande; 50%).
Tree canopy structure

Wetlands were predominantly closed canopy systems with a median cover of 88% (>50% canopy closure, n = 30). Remaining macroplots had partially open tree canopies (25-50%, n = 4) or were emergent, open-canopy assemblages (<25% closure, n = 2). Greater canopy closure was positively correlated with canopy species richness ($r_s = 0.462, p = 0.005$). Wet areas with a greater proportion of hydrophytes in the richness surveys had lower tree density ($r_s = -0.403, p = 0.015$). Within all of the six wetlands, trees classified as facultative (FAC) or facultative wetland (FACW) plants accounted for the majority of the relative basal area, which ranged from a low of $50 \pm 16\%$ in NB to a high of $92 \pm 6\%$ in EV.

In closed canopy macroplots, basal area ranged from 15.4 to 45.6 m$^2$/ha (Table 1). Only red maple and sweetgum occurred in all wetlands, accounting for $\geq 25\%$ of the standing basal area. Ash trees (Fraxinus spp.) were present in half of the sample plots, where they contributed $37 \pm 8\%$ of the standing basal area (Figure 7B) and had an average density of $152 \pm 42$ stems/ha ($n = 19$). Green ash (FACW; $n = 12$) was particularly dominant in areas with low variance in microrelief (Figure 7A; $F_{1,11} = 11.834, p = 0.006$). Six oak species (Quercus spp.) presented as dominant or co-dominants in the canopy, the most frequent of which was pin oak ($Q. palustris$ Münchh.; $n = 12$). Some of the largest trees were found in the large wetlands, with maximum DBH reaching 90.2 cm in NL (Liriodendron tulipifera L.) and 78.7 in DS ($Q. palustris$) (Figure 8). In contrast, the two small sites each contained larger trees than either of the medium sites (Table 1). Density of standing dead trees was highest in small wetlands, where snag
density averaged 20 ± 14 stems/ha. Forty to 58% of stems were saplings or subcanopy trees (DBH < 13 cm).

**Understory composition**

Understory woody stem density averaged 2765 stems/ha, and was negatively correlated with adjacent stream size ($r_s = -0.482, p = 0.003$; Table 2). Common shrubs that were present in at least 25% of macroplots included two native species, southern arrowwood (*Viburnum dentatum* L.) and highbush blueberry (*Vaccinium corymbosum* L.), and one exotic: multiflora rose. Native species dominated the woody understory, accounting for 72 ± 7% of small woody stem density (excluding thicket areas). Canopy and subcanopy tree seedlings accounted for 14 ± 5% of the woody understory (≥1 m in height, DBH <2.5 cm). Although this trend was not observed for total stem density, tree seedling density was lower when hydrophytes dominated the local flora ($r_s = -0.525, p = 0.001$).

Thicket area was measured in fewer than 40% of all macroplots (Table 2), half of which contained multiflora rose (50 ± 12%). Further, >60% of macroplot richness surveys included multiflora rose. Patches of solely native species such as swamp rose (*R. palustris* Marsh.), climbing rose (*R. setigera* Michx.), and greenbrier (*Smilax rotundifolia* L.) occurred less frequently, but still accounted for half of the total measured thicket area. The relative cover of the nonnative multiflora rose declined as hydrophyte dominance of the local flora surpassed 70% ($n = 14, r_s = -0.514, p = 0.060$).

**Groundcover plant composition**

Average subplot plant cover was similar between large wetlands, averaging 56% m$^{-2}$; however, this trend was not persistent for small or medium-sized wetlands (Table 2).
When looking at all of the macroplots, herbaceous (Herb) cover was negatively correlated with leaf litter depth (LD). This trend was consistent even when controlling for tree basal area (Pearson partial: $r_{\text{HerbLD-BA}} = -0.433$, $p = 0.009$). Wetter areas with a high abundance of obligate herbaceous species also tended to have lower litter depth ($r_s = -0.589; p < 0.001$), which suggests a relationship between hydrology and leaf litter accumulation.

A negative linear relationship was observed between the relative abundance of herbaceous wetland plants (OBL, FACW, FAC) and within-plot microtopography (Figure 9). Tussock sedge (*Carex stricta* Lam.), which contributes to the development of wetland microrelief, was present in large wetlands DS and NL. Native plant richness was 20% higher when tussock sedge was present ($44 \pm 7; n = 8$) compared to plots where the species was absent ($35 \pm 2; n = 36$). Interestingly, the topographic range of tussock sedge plots was actually 12 cm lower than without the species (41.6 vs. 53.5 cm), and the maximum topographic range was similarly lower (101.1 vs. 121.8 cm). Hydrophytes tended to dominate in relatively level, flat areas where topographic change was <60 cm within the 30-m diameter plot (hereafter “flat”; $F_{1,34} = 5.542$, $p = 0.024$). In fact, hydrophyte relative abundance in flat areas averaged $83 \pm 3\%$ ($n = 24$), while cover in hummock hollow wetlands was 30% lower ($58 \pm 5\%$, $n = 12$; $F_{1,34} = 15.852$, $p < 0.001$). No differences among wetlands were observed between microtopography and the relative cover of herbaceous hydrophytes ($p > 0.05$).

Introduced exotic plant species comprised $14 \pm 3\%$ of the total plant cover and their abundance was positively correlated with the occurrence of bare exposed soil ($r_s = 0.443$, $p = 0.007$; Table 2), and negatively so with leaf litter cover ($r_s = -0.468$, $p =$
As expected, invasive herbaceous cover decreased as leaf litter depth increased ($r_s = -0.435, p = 0.008$). And although macroplots adjacent to streams ($n = 27$) had a greater number of exotic species in the richness surveys ($5 \pm 1$ vs. $7 \pm 1$), this trend did not correspond to significantly greater cover of nonnatives in the herbaceous layer ($5 \pm 5\%$ vs. $9 \pm 3\%/m^2$).

A total of 127 identified plant species were included in multivariate analysis of herbaceous composition using cluster analysis and non-metric multidimensional scaling (NMDS). Group pruning in the cluster dendrogram reflected the importance of physical parameters in shaping the expressed vegetation assemblage, factors such as landscape setting, hydrology, and soil type (Figure 10; chaining = 6.71%). The interactive nature of plant assemblage composition may also be inferred from nonparametric analysis of the herbaceous layer. For example, initial branching of the dendrogram created two clades that differ in the canopy composition: clade A ($n = 22$); and clade S ($n = 14$). Facultative and facultative wetland tree species contributed 30% more to the standing basal area in clade A relative to clade S (89%, 58%, respectively). Tree canopies in the S clade were dominated by sweetgum, a facultative tree typical of alluvial soils (S: 10.2 vs. A: 2.8 $m^2/ha$; $F_{1,34} = 7.323, p = 0.011$). In contrast, green ash, a common floodplain tree, was 9x higher in the A clade (4.4 vs. 0.5 $m^2/ha$; K-S: $H = 5.762, p = 0.016$). Beyond baseline root zone saturation (i.e., “saturated”), these patterns in canopy composition reflected species’ tolerance of vertical and seasonal fluctuations in the water table.

Groups delineated through cluster analysis also shared similar edaphic and vegetations structure characteristics that extended beyond the herbaceous layer. For example, leaf litter depth was 2 cm greater in sweetgum dominant woodlands (S clade:
4.0 ± 1.1 cm) compared to those where ash trees dominated (A clade: 2.1 ± 0.2 cm).

Further, relative abundance of herbaceous hydrophytes was 17% lower in clade S where standing water occurs less frequently than in clade A (57 vs. 74%/m²). Overall, the A clade had a more robust herbaceous layer, with an average cover of 78%/m², compared to 22% in clade S (F₁,₃₄ = 32.436, p < 0.001).

Cluster analysis clearly defined four assemblage groups, highlighting the diversity of vegetation within each wetland, as well as communalities among wetlands. Relative cover of invasive plants in the herbaceous layer varied among the four groups, the highest of which occurred in Group 4 (32 ± 5%), followed by Group 1 (22 ± 8%), Group 3 (11 ± 4%), and Group 2 (4 ± 3%). A similar pattern was observed in the relative abundance of herbaceous hydrophytes, which was highest in Group 4 (77%), particularly in Subgroup 4 (84%), and lowest in Group 2 (43%). MRPP analysis identified these four groups as being significantly distinct in their composition (A = 0.500, p < 0.001). However, further analysis provided support for my delineation of a fifth group, Subgroup 4 (A = 0.542, p < 0.001).

Other components of the ground-layer also differed among the cluster groups even if the data types were not included in the analysis. For example, groups characterized as having poorly drained soils or semi-permanent flooding had the lowest density of tree seedling recruits (e.g., Group 3: 3 plants/10m²). In contrast, groups with saturated/moderately drained soils had the highest density of recruits (e.g., Group 4: 11 plants/10 m²). These patterns in tree recruitment support trends that were discussed earlier between tree stem density, tree seedling density (>1 m ht), and hydrophyte richness.
As with the cluster analysis, wetland site and size had little influence on how macroplot assemblages arranged in the NMDS ordination (Figure 11; stress = 15.99). Instead, groupings reflected local hydrogeomorphic traits that affect vegetation structure even beyond the herbaceous layer. For example, only 9 of the 36 plots lacked adjacent streams (<75 m); five of these plots occurred in Group 2. Adjacent stream order expressed a significant positive correlation with Axis 3 (Kendall $\tau = 0.417$); headwater complexes of Group 4 similarly clustered along this axis. Indicator plant species analysis for this group included sensitive fern, skunk cabbage, and false nettle (Table 3). The riparian subgroup of Group 4 was also strongly associated with whitegrass (Table 3), which typically occurs in partially shaded woodlands that are seasonally flooded.

Because many of the plots in Group 2 lacked riverine influences, this group was negatively positioned along Axis 3, which represented 35.7% of the variation. A ubiquitous facultative plant species typical of saturated forested wetlands, Canada mayflower (*Maianthemum canadense* Desf.), was the indicator species for the second group. As seen in clade S of the cluster dendrogram (Groups 1 & 2), sweetgum BA was negatively correlated with the second ordination axis (Kendell’s $\tau = 0.381$). White edge sedge (*Carex debilis* Michx.), a perennial woodland sedge, was identified as the indicator species for Group 1.

Two graminoid species typical of wetlands with seasonal aboveground flooding were positively associated with the second axis, which represented 13.5% of variation in the ordination. These two species, common rush (*Juncus effusus* L.) and tussock sedge, were identified as indicator species for Group 3, which includes wetlands that are seasonally- to semi-permanently flooded. Similarly, green ash BA was positively
correlated with Axis 2 ($\tau = 0.414$). Groups 3 and 4 are characterized as having more frequent flooding, as influenced by their landscape position (e.g., headwater complex, depression).

*Composition of recent tree seedling recruits*

A total of 764 native canopy and subcanopy tree recruits <1 m in height were counted in groundcover subplots, with higher densities occurring in areas with greater tree basal area ($r = 0.584$, $p < 0.001$). Canopy richness was positively reflected in the diversity of tree recruits ($r = 0.573$, $p < 0.001$). However, interspecific co-occurrence was relatively uncommon as richness averaged <2 species per m$^2$ ($1.5 \pm 0.7$). Further, although 33 native tree species were sampled, only four produced significant seedling recruitment (Figure 12). *Fraxinus* seedling density peaked at 35 plants m$^{-2}$, followed by pin oak (27), sweetgum (21), and red maple (16). Relative recruit density of maple seedlings decreased with increasing herbaceous cover ($r = -0.594$, $p < 0.001$), a pattern not observed in other species. When herbaceous cover exceeded 50%/m$^2$, relative density of maple recruits decreased significantly to 6% ($\pm 3\%$, $n = 16$) from 32% ($\pm 8\%$, $n = 20$; K-W: $H = 10.778$, $p = 0.001$). As with other metrics, no trends were observed between wetland patch size and seedling recruitment. Unlike tree (DBH >2.5 cm) and seedling (>1 m ht) stem density, increased hydrophyte richness did not correspond to a decrease in tree recruit density, suggesting tree recruitment more likely reflects masting cycles and short-term regional climate patterns.

**Discussion**

Patterns presented here highlight the functionality of these wetland systems and their capacity to support biodiversity even in relatively small patches of greenspace.
Three characteristics are apparent when examining this data set. First, plant species richness and invasive plant occurrence were not merely a reflection of wetland patch size. Rather, wetland vegetation structure in the urban landscape of central New Jersey reflected traditional hydrogeomorphic influences, as well as human-mediated affects (e.g., wetland ditching/draining, nonnative species). Second, the preponderance of obligate and facultative wetland plant species indicates that these urban headwater wetlands are saturated with floodwaters long enough that the majority of plants are hydrophilic. Third, the herbaceous layer is indicative of local hydrogeomorphic (HGM) setting and hydrology. Canopy composition also reflects HGM position, with the exception of small wetlands, which reflect the effects of fragmentation.

**Plant species biodiversity and composition**

Floristic richness observed in this study was similar to other values reported for red maple swamps in the northeast. A review of northeastern red maple swamps published by Golet et al. (1993) suggests that tree richness in these systems ranges from 1 to 9 species. Canopy tree richness observed here averaged four species per 707-m² macroplot. Because a broader range of vegetation assemblages were sampled in my study, the cumulative tree species richness observed in my wetlands was much higher (6-31 tree species/wetland) than those reported (Golet et al., 1993). On a regional scale, red maple swamps host 440 plant species. However, a few species generally dominate a given area, even in the herbaceous layer, which averages <20 species site (Golet et al., 1993). Overall, plant richness results presented here were comparable to those reported by Golet et al. (1993) and Ehrenfeld et al. (Ehrenfeld, 2005; Ehrenfeld, 2008).
One of the criteria for delineating a wetland in the U.S. (Environmental Laboratory, 1987) is that at least 50% of the present plant species must be classified as hydrophilic by the National Wetland Plant List (Lichvar et al., 2014). In this study, hydrophytes composed 61% of the total observed flora. The average proportion of obligate wetlands plants observed here, 16%, was within the range observed by Ehrenfeld (2005) for flat-riverine (21%), mineral flat (14%), and riverine (5%) wetlands located in northeastern New Jersey. In that same study, the proportion of exotic plants were highest in riverine settings and lowest in flat-riverine wetlands (17% and 6%, respectively) (Ehrenfeld, 2005). In my research wetlands, nonnative plants accounted for 0-29% (14±1%) of the local flora; I also found that sites near streams contained more nonnative plants.

The interplay between hydrology and microtopography can also be a driver for increased plant biodiversity (Peach and Zedler, 2006), as increased environmental heterogeneity has been shown to increase niche diversity within a system (e.g., Whittaker, 1967; Connell, 1978). Interestingly, invasive species richness was the only diversity metric that responded to changes in microtopography (i.e., <1.25 m elevation change); nonnative plant richness increased with increasing microrelief. This results reflects the subtle differences in root zone saturation and plant assemblages zonation that can be observed in hummock-hollow landscapes (Ehrenfeld and Schneider, 1993; Ehrenfeld, 2000; Peach and Zedler, 2006; Milbau et al., 2009).

Native wetland plants such as tussock sedge naturally develop hummock/hollow microtopography characteristic of sedge meadow wetlands. Research has found that the rate at which hummocks develop is correlated with inundation levels (Lawrence and
Zedler, 2011) and that tussocks increase plant biodiversity by providing more area (space) and a wider range of environmental gradients (Peach and Zedler, 2006). Only 22% of my macroplots contained tussock sedge, all of which occurred only in large wetland patches (>125 ha); and although native plant richness was higher when tussock sedge was present, microrelief was actually lower. These findings support those of Peach and Zedler (2006), but also suggest that my research sites lay along a broader range of hydrologic and potentially community development gradients. Further, my research wetlands have been used as cropland as well as pastureland, which have been respectively shown to decrease (Bruland and Richardson, 2005) and increase (Tesauro and Ehrenfeld, 2007) micrographic variation in wetland systems.

Green ash trees dominated in mineral flat headwater wetlands where changes in microrelief were <0.5 m (Figure 7b). Hydrophyte cover as also negatively correlated with microtopographic range (Figure 9). These findings could be useful for identifying and managing present green ash stands, which are presently threatened by the exotic emerald ash borer. Canopy regeneration was particularly low in ash dominated stands, so the loss or reduction in forest canopy will likely be followed in the short term by increased inundation levels (Toogood and Joyce, 2009; Telander et al., 2015). Given the high occurrence of hydrophytes in these areas, it is likely that this forested ash assemblage will revert to a wet grassland or emergent marsh following this disturbance.

Tree canopy composition

Woodlands reflected a range of community development from early- (BA < 20 m²/ha) to mature, late-successional stands (BA > 30 m²/ha; Rheinhardt et al., 2009). Following this designation, 19 of my macroplots would be classified as mature forest and
their average BA was only slightly lower than the reference values reported by Rheinhardt et al. (2009) for the NJ coastal plain (35.9 vs. 37.1 m²/ha). Tree density in red maple-dominated swamps is reported to range widely (827-1570 stems/ha), with stillwater wetlands exhibiting greater density than floodplain wetlands (Golet et al., 1993). Pickett et al. (2001) suggests that urban systems have higher stem density compared to rural systems due in part to fragmentation, which creates unnatural community edges. The stem density of my wetlands was lower than has been observed in other urban forested wetlands (Burton et al., 2005), which may point to differences in hydrology.

The effects of forest fragmentation on canopy structure were apparent in small wetlands (<15 ha) which had a disproportionally high number of small stems (DBH<10 cm). Increased abundance of sub-canopy species, such as black cherry (*Prunus serotina* Ehrh.) in Polansky (PP <10 ha). A review by Harper et al. (2005) found understory light transmittance and soil temperature were greater along forest edges, leading to lower soil moisture compared to forest interiors. The review also suggests that edges have comparatively higher recruitment rates, plant growth, mortality, and vegetation density; ruderal or edged-adapted species may also be more abundant. Edges of these small wetlands were generally sharp (i.e., no vegetation sidewall), which likely increases the distance of edge influence that is estimated to extend up to 75 m (Harper et al., 2005).

Relative to large urban wetlands, smaller wetland patches are more sensitive to stormwater influxes from the surrounding landscape due to their relatively limited storage capacity (Tilton, 1995; Mitsch and Gosselink, 2000). Stormwater discharge pipes emptied into several of the wetlands, but small wetlands appeared particularly vulnerable
to the resulting drastic changes in hydroperiod. In an extreme instance, adjacent
development built less than a decade prior converted a forested scrub/shrub portion of TE
into a permanently flooded marsh. This juxtaposition of wetland assemblages within TE
(<12 ha) is cause for the variance observed in many of the presented metrics. High woody
stem density of medium-sized wetland site NB likely explains the disparate herbaceous
diversity of that site. Previous research by Keddy (1989) supports this conclusion, finding
that herbaceous species richness and abundance increased following shrub removal (i.e.,
reduced competition and shading) when compared to intact control plots. Other studies
have found that woody understory density increases with wetness (Golet et al., 1993, and
references therein).

**Understory and groundcover**

The designation of scrub-shrub wetland assemblages (NJDEP, 2007) was the least
accurate of those surveyed in this study, which likely reflected the difficulty of
delineating forested wetland assemblages via air photo interpretation (Kudray and Gale,
2000). Each of the four macroplots that held a scrub-shrub classification were dual listed
as forested or emergent. The high variability that I observed in understory woody stem
density suggests that the scrub-shrub classification is underrepresented in the
NJDEP/NWI wetland mapping for this area.

The scrub-shrub assemblage type, and understory development in general, has
been reduced due to regionally high densities of white-tailed deer (*Odocoileus
virginianus* L.). Previous research has shown that chronic over-browsing by deer
decreases forest structural complexity and retards the regeneration of canopy and
subcanopy trees (Cadenasso and Pickett, 2000; Goetsch et al., 2011; White, 2012). Liang
et al. (2002) demonstrated that two resilient understory species common in my sites, spicebush (*Lindera benzoin* (L.) Blume) and ironwood (*Carpinus caroliniana* Walter), respectively experience density-independent (favored) and density-dependent foraging by white-tailed deer. Deer exclosures in that same study also demonstrated that deer browsing caused greater rates of mortality in tree seedling recruits, the strongest effects were seen in ironwood and green ash; marginal effects were observed for red maple and tuliptree (*Liriodendron tulipifera* L.) recruit. Interestingly, mortality of sweetgum recruits expressed no difference between the control and exclosure (Liang and Seagle, 2002). In addition to herbivory patterns, the wide variation in seeding density among my sites also potentially reflects the occurrence of uneven annual seed production (Silvertown, 1980). These results have important implications for canopy regeneration in my research sites, particularly in green ash swamps, due to the recent establishment of the exotic Emerald Ash Borer to New Jersey.

Four groundcover assemblages were identified, reflecting the landscape setting, soil, and hydrology of the local macroplot area. Although the herbaceous layer reflected the importance of hydrogeomorphology in shaping assemblage composition, this adaptive stratum also highlighted the caveats in applying Brooks et al. (2011) HGM classification system in urban landscapes where soils, hydrology, or microtopography have been altered (Ehrenfeld et al., 2003). For example, headwater wetland complexes may become hydrologically isolated, resulting in decreased periods of inundation, soil saturation, and soil/nutrient replenishment (Tilton, 1995; Richardson et al., 2011).

As both a mechanism for disturbance as well as dispersal, stream overbank flow has long been recognized as the primary mode of exotic species establishment in riparian
As would be expected, my surveys found exotic plant richness to be higher in areas near streams. Unexpectedly, stream proximity did not necessarily translate to greater cover of invasive herbs. Relative cover, however, was higher near rivers (>2 order).

Leaf litter disturbance is another mechanism by which exotic species may establish, an effect that has been demonstrated for several invasive species present in my research wetlands (Oswalt and Oswalt, 2007; Schramm and Ehrenfeld, 2010; Warren et al., 2011; Stinson and Seidler, 2014). I did observe a negative correlation between litter depth and exotic plant richness, but leaf litter depth in wetlands is strongly (negatively) linked to inundation. Pervasive nonnative earthworms (Groffman et al., 2004; Nuzzo et al., 2009; Dávalos et al., 2015a), coupled with white-tailed deer over browsing (Côté et al., 2004; Eschtruth and Battles, 2009) can also alter leaf litter composition and forest soil process in a manner that may facilitate exotic plant invasion (Dávalos et al., 2015b). Therefore, leaf litter accumulation may aid community resistance to invasion for saturated/temporarily flooded woodlands; this may be particularly true in soils with a low pH (Dávalos et al., 2015b). However, I would not expect this trend to hold where inundation is seasonal/semi-permanent; in these locations, microtopography will likely play a greater role in providing suitable conditions for establishment (Davis et al., 2000; Milbau et al., 2009).

**Conclusion**

Despite their location within urbanized watersheds, my research wetlands expressed a diverse array of plant species, including several of conservation concern. Compared to medium and large-sized wetlands, small patches appeared more sensitive to
hydrologic perturbations stemming from land development. Tree demographics varied among wetland size classes, edge effects were apparent in the smallest patches, while deer over browsing was apparent in nearly all wetlands. Interestingly, plant species richness was not solely a product of wetland patch size, rather a combination of hydrogeomorphology and land use history. Exotic plant richness more strongly reflected hydrologic connectivity than wetland size. Hydrophytes dominated the flora, and their NWPL indicator status was useful in identifying distinct groundcover assemblages that were associated with green ash and sweetgum stands.
References


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Systat Software Inc. 2008. SigmaPlot. 11.2.0.5. San Jose California USA.


Table 1: Common tree species’ basal area (m²/ha) among the six wetlands, described as mean (Standard Error of the Mean). Species or data not present in a wetland are marked as “—”. Average (SEM) tree species richness and stem density includes all trees and saplings within each macroplot (DBH >2.5).

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common</th>
<th>NWI code</th>
<th>DS*</th>
<th>NL</th>
<th>EV</th>
<th>NB</th>
<th>PP</th>
<th>TE*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acer rubrum</em> L.</td>
<td>red maple</td>
<td>FAC</td>
<td>5.48 (1.4)</td>
<td>5.42 (1.9)</td>
<td>13.89 (2)</td>
<td>3.70 (2.9)</td>
<td>6.67 (0.4)</td>
<td>5.49 (—)</td>
</tr>
<tr>
<td><em>Fraxinus americana</em> L.</td>
<td>white ash</td>
<td>FACU</td>
<td>0</td>
<td>2.18 (1.3)</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>F. pennsylvania</em> Marsh.</td>
<td>green ash</td>
<td>FACW</td>
<td>3.06 (1.3)</td>
<td>3.34 (2.2)</td>
<td>6.64 (3.4)</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Liquidambar styraciflua</em> L.</td>
<td>sweet-gum</td>
<td>FAC</td>
<td>5.96 (2.6)</td>
<td>2.49 (1.0)</td>
<td>1.83 (1.8)</td>
<td>7.62 (2.3)</td>
<td>14.23 (7.8)</td>
<td>28.18 (—)</td>
</tr>
<tr>
<td><em>Liriodendron tulipifera</em> L.</td>
<td>tuliptree</td>
<td>FACU</td>
<td>0</td>
<td>4.16 (2.4)</td>
<td>1.10 (1.1)</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Nyssa sylvatica</em> Marsh.</td>
<td>black tupelo</td>
<td>FAC</td>
<td>1.10 (0.8)</td>
<td>0.02 (0)</td>
<td>0.33 (0.2)</td>
<td>6.10 (1.8)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Quercus alba</em> L.</td>
<td>white oak</td>
<td>FACU</td>
<td>1.21 (0.8)</td>
<td>0</td>
<td>0</td>
<td>6.38 (2.6)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Q. palustris</em> Münchh.</td>
<td>pin oak</td>
<td>FACW</td>
<td>3.41 (1.9)</td>
<td>5.91 (2.3)</td>
<td>5.84 (3.1)</td>
<td>0</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>Q. rubra</em> L.</td>
<td>red oak</td>
<td>FACU</td>
<td>0.97 (0.7)</td>
<td>0.83 (0.8)</td>
<td>0</td>
<td>8.11 (3.7)</td>
<td>15.22 (9.7)</td>
<td>21.16 (—)</td>
</tr>
</tbody>
</table>

- Total average BA (m²/ha) 25.44 (3.4) 30.06 (2.3) 30.78 (1.1) 33.95 (2.0) 36.25 (1.4) 22.18 (22)
- Largest DBH (cm) 78.7 90.2 68.1 56.3 71.7 81.1
- Total density (# stems/ha) 682 (114) 447 (89) 824 (104) 1085 (250) 528 (14) 293 (265)
- Sapling density (DBH <13 cm) 353 (88) 215 (83) 370 (59) 627 (146) 210 (40) 145 (125)
- Tree richness (707 m²) 5.6 (0.6) 6.3 (1.3) 6.0 (1.0) 6.3 (0.3) 4.0 (1.0) 4.0 (—)

Dismal (DS) n = 14; Lenape/Nomahegan (LN) = 11; Evergreen (EV) n = 3; North Brunswick (NB) = 3; Polansky Park (PP) n = 2; Terrill (TE) n = 1. *Non-forested macroplot (basal area <0.01 m²/ha) was excluded from the basal area and density calculations.
Table 2: Data from the understory and groundcover subplots are summarized as sample means with standard error of the mean (SEM) in parenthesis. Understory woody density included shrubs and tree seedling (≥1 m height and <2.5 cm DBH), the latter are presented as relative density within the understory. Growth form (i.e., “tree”) and nonnative exotic classification follows the USDA PLANTS database (2015).

<table>
<thead>
<tr>
<th>Site</th>
<th>Woody stems/ha</th>
<th>Tree seedling % relative density</th>
<th>Thicket area m²/ha</th>
<th>Herbs cover %/m²</th>
<th>Relative % wetland spp</th>
<th>Relative % exotic</th>
<th>Bare soil %/m²</th>
<th>Leaf litter depth cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>DS</td>
<td>4400 (1120)</td>
<td>15 (7)</td>
<td>1435 (591)</td>
<td>62 (11)</td>
<td>64 (6)</td>
<td>14 (3)</td>
<td>8 (4)</td>
<td>3.4 (0.3)</td>
</tr>
<tr>
<td>NL</td>
<td>330 (190)</td>
<td>0</td>
<td>37 (26)</td>
<td>63 (11)</td>
<td>78 (5)</td>
<td>39 (7)</td>
<td>18 (7)</td>
<td>2.1 (0.3)</td>
</tr>
<tr>
<td>EV</td>
<td>1320 (440)</td>
<td>29 (12)</td>
<td>65 (65)</td>
<td>83 (13)</td>
<td>88 (3)</td>
<td>25 (9)</td>
<td>11 (4)</td>
<td>1.7 (0.6)</td>
</tr>
<tr>
<td>NB</td>
<td>5500 (2000)</td>
<td>3 (1)</td>
<td>43 (43)</td>
<td>9 (5)</td>
<td>25 (15)</td>
<td>0</td>
<td>0</td>
<td>4.8 (0.7)</td>
</tr>
<tr>
<td>PP</td>
<td>3300 (340)</td>
<td>2 (2)</td>
<td>0</td>
<td>6 (5)</td>
<td>58 (1)</td>
<td>9 (9)</td>
<td>0</td>
<td>4.2 (1.1)</td>
</tr>
<tr>
<td>TE</td>
<td>1380 (1150)</td>
<td>0</td>
<td>0</td>
<td>55 (22)</td>
<td>72 (28)</td>
<td>33 (33)</td>
<td>8 (8)</td>
<td>1.3 (1.1)</td>
</tr>
</tbody>
</table>

DS, Dismal (n = 15); NL, Nomahegan Lenape (n = 11); EV, Evergreen (n = 3); NB, North Brunswick (n = 3); TE, Terrill (n = 2); PP, Polansky (n = 2).
Table 3: Groundcover plant species that are unique to one of the four groups depicted in the ordination analysis. All plants listed below are native hydrophytes (FAC-OBL).

<table>
<thead>
<tr>
<th>PLANTS code</th>
<th>Scientific name</th>
<th>Common Name</th>
<th>NWI code</th>
<th>Group</th>
<th>Max IV</th>
<th>Monte Carol p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>BOCY</td>
<td><em>Boehmeria cylindrica</em> (L.) Sw.</td>
<td>false nettle</td>
<td>FACW 4</td>
<td>77</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>CADED</td>
<td><em>Carex debilis</em> var. <em>debilis</em> Michx.</td>
<td>white edge sedge</td>
<td>FACW 1</td>
<td>39</td>
<td>0.022</td>
<td></td>
</tr>
<tr>
<td>CAST8</td>
<td><em>Carex stricta</em> Lam.</td>
<td>tussock sedge</td>
<td>OBL 3</td>
<td>75</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>JUEF</td>
<td><em>Juncus effusus</em> L.</td>
<td>common rush</td>
<td>OBL 3</td>
<td>72</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>LEVI2</td>
<td><em>Leersia virginica</em> Willd.</td>
<td>whitegrass</td>
<td>FACW 4</td>
<td>39</td>
<td>0.048</td>
<td></td>
</tr>
<tr>
<td>MACA4</td>
<td><em>Maianthemum canadense</em> Desf.</td>
<td>Canada mayflower</td>
<td>FAC 2</td>
<td>72</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>ONSE</td>
<td><em>Onoclea sensibilis</em> L.</td>
<td>sensitive fern</td>
<td>FACW 4</td>
<td>44</td>
<td>0.035</td>
<td></td>
</tr>
<tr>
<td>SYFO</td>
<td><em>Symlocarpus foetidus</em> (L.) Salisb. ex W.P.C. Barton</td>
<td>skunk cabbage</td>
<td>OBL 4</td>
<td>39</td>
<td>0.040</td>
<td></td>
</tr>
<tr>
<td>VISO</td>
<td><em>Viola sororia</em> Willd.</td>
<td>common blue violet</td>
<td>FAC 4</td>
<td>44</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

National Wetland Inventory (NWI) National Wetland Plant List codes: facultative (FAC); facultative wetland (FACW); and obligate (OBL) wetland plant. Max IV: maximum observed indicator value.
Figure 1: A landscape view of the six wetland sites: Dismal (DS), Lenape/Nomahegan (NL) (>125 ha); Evergreen (EV), North Brunswick (NB) (<35 ha); and Polansky (PP), Terrill (TE) (<12 ha). Two 15-m radius macroplots were sampled in each of the small wetlands (PP, TE). Three macroplots were sampled in the medium-sized wetlands (EV, NB), while large 11 and 15 macroplots were sampled in the large wetlands, NL and DS, respectively.
Figure 2: Schematic of the macroplot sampling methods. Tree species DBH, total plant species richness, and thicket area (m²) were measured throughout the entire macroplot (707 m²). Microtopoghic range from plot center out along the cardinal transects was measured at 5-m intervals using a stadia rod (n = 12). Canopy cover was measured at 5-m intervals along cardinal and inter-cardinal transects using a densitometer (n = 24). Subplot placement employed a stratified random design. Understory wood stem density (DBH <2.5 cm; ht > 1 m) was measured in two subplots. Groundcover was estimated using modified Braun-Blanquet cover classes. Woody seedling recruit density of plants <1 m height were also counted in the m² subplots, as well as % bare soil, % leaf litter cover, and litter depth (cm).
Figure 3: Top graph: Sixty percent of the 286 plant species identified were classified as hydrophilic wetland plant species, which includes obligate (OBL), facultative wetland (FACW), and facultative (FAC) plant species (Lichvar et al., 2014). Bottom graph: species that usually occur in uplands, but occasionally can be found in wetlands accounted for 23% of the total flora (facultative upland: FACU), whereas upland species were relatively rare (UPL = 3% of the flora). Wetlands were placed into three size classes; large (>125 ha): DS (n = 15) and NL (n = 11); medium (<35 ha): NB (n = 3) and EV (n = 3); small (<15 ha): PP (n = 2) and TE (n = 2).
Figure 4: Medium-sized site Evergreen (EV) had the highest richness, averaging 46 plant species per macroplot; the two large sites, Dismal (DS) and Nomahengan/Lenape (NL), followed closely behind. North Brunswick (NB) was species poor, and was particularly lacking in herbaceous species. Plant richness in the two smallest wetlands, Polansky (PP) and Terrill (TE), was most similar to NB.
Figure 5: Species area curves for each of the six wetland sites: Dismal (DS = 15); NomLen (NL = 11); Evergreen (EV = 3); North Brunswick (NB = 3); Polansky (PP = 2); Terrill (TE = 2). Macroplot (707 m²) sample effort was scaled to wetland size class: large >125 ha (DS, NL); medium >25 ha (EV, NB); and small: >9 ha (PP, TE).
Figure 6: A) All macroplots contained nonnative plants species with the exception of those at NB. Small wetlands <15 ha in size did not differ significantly in the relative abundance of exotic species (PP vs. TE, p > 0.10). However, differences were observed between large wetlands DS and NL ($t_{15.825} = -2.221$, $p = 0.041$) and medium-sized wetlands EV and NB ($t_2 = 5.004; p = 0.038$). B) Macroplot exotic plant richness decreased with increasing leaf litter depth ($\beta = -0.486$). Dismal (DS), Lenape/Nomahegan (NL) (>100 ha); Evergreen (EV), North Brunswick (NB) (<35 ha); and Polansky (PP), Terrill (TE) (<12 ha).
Figure 7: A) Green (*Fraxinus pennsylvanica* Marsh.; FACW) and white ash (*F.* *Americana* L.; FACU) trees were abundant in three wetlands: DS (n = 15); NL (n = 11); and EV (n = 3). Ash relative Basal Area (BA) in small wetland site TE was <1% ( n = 2). Dashed line: mean; solid line: median; dots indicate outliers. B) When present (n = 12), green ash (FRPE) contributed a larger proportion of local macroplot basal area when the local terrain was relatively flat (Linear regression: $\beta = -0.720$, $t = -3.440$).
Figure 8: Relative histogram of tree DBH (cm) distributions among wetlands, binned into 5-cm size classes, with the smallest size class ranging 2.5-5 cm. Wetlands most vulnerable to invasive insects such as EAB and ALB are those with the strongest kurtosis (k), such as small-sized wetlands Polansky (PP, k = 0.08) and Terrill (TE, k = -0.46). Ash trees are present in the two large sites, Dismal (DS, k = 1.91) and NomLen (NL; k = 0.67), and medium site Evergreen (EV, k = 1.77). Oak and maple species dominated in North Brunswick (NB, k = 0.92). Total tree counts for each wetland: DS = 728; NL = 344; EV = 166; NB = 228; PP = 112; TE = 40.
Figure 9: Within groundcover subplots, the relative cover of hydrophytes decreased as within-plot microtopography increased ($\beta = -0.374$, $t = -2.354$). This significant trend also highlights a breakpoint: areas with <60 cm of topographic change within a 30-m diameter plot ($n = 24$) had significantly greater relative abundance of hydrophytes. Data points are coded by wetland sites: DS ($n = 15$); NL ($n = 11$), EV ($n = 3$); NB ($n = 3$); PP ($n = 2$); TE ($n = 2$). Linear regression line (grey) and 95% confidence intervals (dashed).
Figure 10: Cluster analysis of groundcover data collected at six wetland sites (DS, NL, EV, NB, PP, TE) revealed four distinct groups (chaining = 6.71%). Group descriptions include general plant assemblage traits, landscape setting, or local soil types. The first branching point created two clades that aligned with significant differences in sweetgum (S) and ash (A) tree basal area. Group 4 further divides into forested mineral flat headwater wetlands and riparian sites influenced by nearby (<75 m away) stream hydrology and overflow (subgroup G4). n = 36 macroplots.
Figure 11: Non-metric multidimensional (NMDS) ordination analysis of groundcover data supports the initial cluster analysis. This ordination further indicates that forested wetlands dominated by ash and sweetgum have unique groundcover assemblages. Second matrix vector (arrows) length/direction is proportional to the strength of correlation with the ordinal axes. Stream order (StrmOrd) was positively correlated with Axis 3 (Kendall $\tau = 0.417$). Indicator species analysis identified eight plant species (stars) (Table 3 for plant species). This ordination was resolved with three axes (n = 36).
Figure 12: Among the six wetland sites, four species produced more than 80% of the tree seedling recruits (height <1 m). Red maple (ACRU) and sweetgum (LIST2) seedlings occurred at all sites, respectively contributing 30 and 17%. Fraxinus recruits were counted in five sites, with an average relative density of 38%. Although only found in two sites, pin oak (QUPA2) accounted for 43% of recruits in medium-sized site EV.
CHAPTER 3

Wetland flooding limits the distribution and abundance of invasive Japanese stiltgrass (*Microstegium vimineum*)

Abstract

Ecosystem services provided by headwater wetlands in developed landscapes reflect the degree to which anthropogenic disturbances have altered hydrology and the expressed vegetation structure. The influence of flood duration and depth on the emergence and abundance of *Microstegium vimineum* (Japanese stiltgrass), an invasive annual shade-tolerant grass, was examined through a combination of field and greenhouse studies. Vegetation composition and environmental variables such as flood duration, leaf litter depth, and microtopography, were measured at six wetlands in the New York metro area. Seedling emergence was tested in a mesocosm experiment under eight flood treatment levels and compared to a saturated control. *Microstegium vimineum* dominance in wetland field surveys was negatively correlated with relative flood depth. Cover was greatest in areas experiencing little to no aboveground flooding, and in the presence of flooding, *M. vimineum* occurred on hummocks that served as topographic refuge. *Microstegium vimineum* seedling emergence was inhibited following four days of mesocosm flooding, an effect that lasted for the duration of the growing season. Only the control produced any seedlings for the duration of the mesocosm experiment. These results indicate that a few days of flooding prior to annual seedling emergence may significantly reduce the cover and distribution of this invasive in wetlands. Watershed managers and wetland restoration efforts should therefore consider the inherent resistance
that temporary spring flooding may provide against invasive establishment and dominance in forested headwater wetlands.

**Introduction**

Human-modified disturbance patterns and reduced environmental stress are thought to increase invasibility of a given habitat (Alpert et al., 2000; Price et al., 2011). The low tolerance of terrestrial invasive herbaceous plants to natural (more historical) flooding conditions (Price et al., 2011) and shade intolerance (Martin et al., 2009) may buffer forested wetlands against invasion. Natural flooding cycles during seedling emergence are therefore hypothesized to reduce the establishment, spread, and impact of some invasive plant species in the shaded understory of headwater swamps (Alpert et al., 2000; Lockwood et al., 2005; Simberloff, 2009). However, in the absence of historical abiotic stressors (e.g., anoxic soils), exotic invasive plant species are hypothesized to have a competitive advantage over native stress-tolerating wetland species (sensu Grime, 1977; Keddy, 1992). Previous research generally supports these hypotheses (Daehler, 2003), though a review by Lowry *et al.* (2013) highlights the need for invasive species research in wetland systems, particularly studies that combine field and greenhouse experiments. The extent to which short-term flooding may provide resistance to the establishment of exotic species has not been well studied in forested wetlands, though the management implications of such findings would be significant for large areas of North America.

Invasive plant species can alter soil properties that in turn have a significant effect on ecosystem structure and function (Ehrenfeld, 2010). Throughout the eastern United States, researchers have found reduced vegetation heterogeneity and lowered plant
biodiversity following invasion of *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass), an annual, shade-tolerate grass (Adams and Engelhardt, 2009; Flory and Clay, 2010). This structural shift is particularly important in partially closed canopy systems because sunflecks reaching the forest floor, not necessarily canopy gaps, play an important role in the presence and dominance of this C$_4$ invasive grass (Cheplick, 2010; Warren et al., 2011). Reduced vertical heterogeneity also will result in lower rates of water loss via evapotranspiration and interception, which increases precipitation throughfall and surface flow volume (Brown et al., 2005).

Floodwater storage and water quality protection are often cited reasons for conserving and restoring wetlands. Ecosystem services provided by wetlands play an integral role in water quality and water supply reliability, particularly within urbanized areas (Ehrenfeld, 2004). Preserving and restoring wetlands within headwater complexes may prove the most cost-effective for watershed managers and significantly reduce downstream flow (Brown et al., 2005). The ability of urban wetlands to buffer high water volumes and pollutant loads is a function of overall ecosystem health, or the level to which human modifications have affected system processes (Hogan and Walbridge, 2007). For example, water quality models have suggested that second-order streams receive approximately 65% of their nitrogen input from upper headwater streams (Alexander et al., 2007). However, these ecosystem services are compromised in developed landscapes where flooding duration and depth are often reduced, and frequency is increased (i.e., flashy hydroperiod) because of human interference. Ditching and subsequent lowering of the water table affects soil processes and plant species composition in wetland communities (Ehrenfeld et al., 2003; Groffman et al., 2003).
Habitat fragmentation can further alter system structure as smaller patches with greater edge habitat have been found to increase system invasibility (Vilà and Ibáñez, 2011). Invasive plant species dominance can also alter abiotic processes within wetlands, such as soil nutrient pools and water table levels (Ehrenfeld, 2010). Previous studies examining naturally occurring wetlands in developed landscapes highlights the variation among urban wetland structure (e.g., vegetation composition, woody stem density) and function (e.g., hydrology), emphasizing the need for research to understand mechanisms shaping these ecosystems (Woodward and Wui, 2001).

This study used a combination of field surveys and a greenhouse experiment to identify potential hydrology-mediated mechanisms driving invasive species dominance, using *M. vimineum* as a case study. Following vegetation surveys in forested headwater wetlands of New Jersey, I hypothesized that the spatial distribution and dominance of *M. vimineum* was limited by the presence of seasonal aboveground flooding. I specifically investigated if flood depth or duration had the greatest impact on rates of *M. vimineum* seedling emergence. Additional field research examined the explicit relationship between local wetland hydrology, microtopography, and *M. vimineum* abundance.

**Materials and methods**

*Study sites*

Research was conducted in six headwater mineral flat wetlands (Brooks et al., 2011) located in urban central New Jersey, USA (see Ch.2, Figure 1). Dominant wetland plant assemblages included deciduous swamps, scrub-shrub, and emergent (Cowardin et al., 1979). Post-agricultural land use legacies, such as ditching, and modern stormwater management infrastructure are present in or adjacent to all of these wetlands, though
much of the region became fallow by the mid-20th century. The regional temperate climate has annual average temperature and precipitation levels of 12°C and 124 cm year−1 (NOAA, 2011). Fifty-four percent of total rainfall occurs from April to September, which encompasses the majority of the average 180-day growing season (NOAA, 2011).

Seasonal patterns of flooding ranged from belowground soil saturation (hereafter, BG) to aboveground (hereafter, AG) seasonal/semi-permanently flooded (Cowardin et al., 1979) with predominantly sandy loam soils (NJDEP, 2012). A range of wetland sizes was surveyed in an effort to capture possible effects of patch size on floristic composition. Wetland patch sizes were categorized as large (>125 ha, n = 2), medium (<35 ha, n = 2), and small (<12 ha, n = 2). Macroplot sample points were regularly spaced along a 400-m grid within each wetland. Vegetation surveys were conducted during the 2008-2010 growing seasons. Within the smallest wetland, two additional radial macroplots were sampled 75 m from the center grid point, at 360°, and 240°. Vegetation from the radial sites is only presented in conjunction with the hydrology monitoring sites.

Field methods

To assess vegetation composition and environmental traits, 707-m² circular macroplots were divided into four quadrants along cardinal transects (Figure 1). Following a stratified random design, groundcover and midstory subplots were randomly distributed within quadrants. Tree species Diameter at Breast Height (DBH = 1.3 m) and total vascular plant species richness were quantified throughout each macroplot. Shrub and tree seedling species stem density (DBH <2.5 cm) were counted in two 88-m² midstory. Herbaceous species cover (%) was quantified in eight 1 m² groundcover
subplots using modified Braun-Blanquet cover classes (1 = <3 plants; 2 <5% cover; 3 = 5-25%; 4 = 25-50%; 5 = 50-75%; 6 = 75-90%; 7 = 90-100%). Each species’ cover class was converted to the median value for analysis. Leaf litter depth (cm) was measured at the center of each 1-m² groundcover subplot. Canopy (>15 m) and midstory (<10 m) cover were measured as a percent of 24 vertical projections, measured at 5 m intervals along cardinal and inter-cardinal transects using a densitometer (GRS, Arcata, CA). Data approximating macroplot topographic variance (cm) was gathered at 5-m intervals along cardinal transects using a stadia rod (n = 12). These topography data were converted to represent relative change in altitude from the plot center to the transect point, which served as a measure of macroplot topographic variance.

_Hydrology methods_

Monitoring occurred at macroplots located within two to four of the largest subareas of each wetland during the 2012 and 2013 growing season (June-November). To balance the sampling effort, half of the selected sites contained _M. vimineum_ in the prior richness surveys and half did not. Ecotone water level digital loggers (RDS Inc., North Carolina, USA) collected data hourly on the depth (cm) of flooding at or above ground level (AG). These data were used to calculate flood duration (total % days flooded, average duration of standing water) and frequency (# AG flooding events). Peak flood depth data were combine with the absolute topographic variance to obtain relative peak flood depth (relative peak flood = absolute topographic variance – peak flood depth). This relative flood depth represents whether the entire plot was submerged at any point during the flood monitoring season (AG = negative value), or whether portions of the macroplot were perhaps dry hummocks above the peak flood line (i.e., BG). In
conjunction with hydrology monitoring, *M. vimineum* cover was estimated again in September 2013 within four 1-m² groundcover subplots. Soil samples were also collected at this time from within 1 m of the Ecotone water well. After scrapping leaf litter from the soil surface, a soil core was taken from the first 10 cm of the soil profile. Soil samples were transported on ice and frozen prior to nutrient and soil texture analysis conducted by Rutgers’ Soil Testing Lab, New Brunswick, New Jersey, USA.

**Greenhouse methods**

*Microstegium vimineum* seeds were collected from plants at Terrill (TE) in October 2010 in preparation for the mesocosm experiment. Seeds were collected from terminal inflorescences because the species produces cleistogamous (self-pollinated) and chasmogamous (out-crossing) inflorescences; the latter are terminal on each culm. Following collection, seeds were cold stratified for three months at 4°C to mimic overwintering conditions.

This mesocosm experiment focused on two of the most prominent factors influencing floristic dominance in wetlands: flood duration and flooding depth. Because this experiment targeted simple effects, only one factor, depth or duration, was manipulated. Field observation informed the selection of four levels of each factor, as illustrated in Figure 2. Therefore, flood depth was maintained at 2 cm above the soil surface for the duration treatment (4, 8, 12, 21 days) and duration was kept constant for 21 days for the depth levels at or above the soil surface (0 cm and 1, 3, 5 cm, respectively). Seven randomized blocks were used to replicate the experimental and control treatments (n = 63). Two holes in each mesocosm pail ensured flood height was maintained within each mesocosm, as maintained via drip irrigation. The greenhouse
experiment took place in the Floriculture Greenhouse, Rutgers University, New Brunswick, New Jersey, USA. Greenhouse conditions mimicked those of regional summer daytime (21 –26 °C) and nighttime (18–24 °C) temperatures. Fifty percent shade cloth blanketed the greenhouse ceiling to mimic forest understory conditions.

Five days prior to seeding, 10 cm square plastic pots were filled with a *Sphagnum*-based potting soil mix (Fafard/Sun Gro Horticulture, Agawam, MA), placed on a mist bench, and watered daily to increase sorption and decrease flooding rejection. Gravimetric soil moisture at seed set was 68% (105° C drying oven, >48 hours). Thirty seeds were distributed on the soil surface of each pot in July 2011 (Day 1) and covered with a thin layer of dampened sand. The sand served to mimic fall leaf litter following *M. vimineum* seed set and more importantly, to prevent the seeds from floating, as observed in pilot studies. Data were collected at 4-day intervals during the first three weeks of the experiment, in conjunction with duration treatment manipulations. Seedlings were counted as present when the coleoptile fully unrolled. The first three seedlings in each experimental unit (pot) remained for the duration of the experiment, while additional seedlings were removed once counted.

Following flood manipulations, all remaining units were drawn down (day 4-21 depending on manipulation) to maintenance (control) watering level. Seedling counts continued every eight days after drawdown. The sand surface was scarified to encourage seedling emergence at weeks five and six. Longest tiller length of each plant was measured at week 7, and flagged for re-measurement at experiment’s end. Plants exhibited signs of nutrient stress at week six, at which time each pot received 1.25 ml of Osmocote 14-14-14 slow release fertilizer (The Scotts Company, Marysville, OH),
followed by 4 oz of dilute Scotts Soluble Trace Element Mix. The experiment ended November 2011 (day 106), approximately the latest local frost date. Upon completion, tiller density and length (cm) were measured, terminal inflorescence spikelets were counted, and aboveground biomass was collected and dried prior to weighing.

For each of the nine treatments, soil from two randomly selected experimental units were homogenized and analyzed for soil moisture and nutrients. Potassium chloride extractions performed <12 hours following experiment’s end were submitted to Rutgers’ Soil Testing Lab (New Brunswick, NJ) for major- and micro-nutrient analysis.

*Statistical Analyses*

For simple comparisons t-tests were used with a $\alpha = 0.05$ (e.g., *M. vimeineum* abundance in AG vs. BG sites). Kruskal-Wallis (K-W) or Mann-Whitney Rank nonparametric analyses were used when data violated t-test assumptions. Spearman’s rank nonparametric correlation analysis was used to examine trends among vegetation and environmental variables, using a significance level per Rohlf and Sokal (Rohlf and Sokal 1981). When applicable, partial correlation analysis was used to account for two correlating independent variables. Linear regression was used to analyze trends between *M. vimeineum* cover and flooding (Quinn and Keough, 2002). All data summaries are presented as mean $\pm$ standard error of the mean (SEM) unless otherwise stated. Statistical analyses were conducted with SPSS, version 17.0 (SPSS Inc 2008). Figures were created in SigmaPlot version 11.0 (Systat Software Inc 2008), Adobe Illustrator CS5 (Adobe Systems 2010), and ArcGIS version 10 (Esri 2012).

**Results**

*Wetland vegetation*
Tree canopies were predominantly composed of *Acer rubrum* L., *Liquidambar styraciflua* L., *Quercus palustris* Münchh. and *Fraxinus pennsylvanica* Marshall. Median canopy cover was 88%, with an average of 76% (SEM = 4.6%), which was skewed by four non-forested, emergent assemblages characterized as having basal area of <3 m² ha⁻¹. In woodland sites (n = 31), tree canopy basal area ranged from 12.8 to 54.8 m² ha⁻¹, with an average of 30.3 m² ha⁻¹ (± 1.7 m² ha⁻¹). As expected, canopy closure exhibited a strong positive correlation with basal area (Spearman’s: n = 35, r = 0.471, p = 0.004). Common shrub and thicket-forming species included *Vaccinium corymbosum* L., *Viburnum dentatum* L., *Rosa multiflora* Thunb., *Rubus allegheniensis* Porter. Woody midstory density varied within wetlands and among size classes, ranging from 0 to 347 stems 100 m⁻² (102 ± 51 stems 100 m⁻²).

Pervasive groundcover species included *Pilea pumila* (L.) A. Gray and *Boehmeria cylindrica* (L.) Sw. Non-flowering plant species such as *Thelypteris noveboracensis* (L.) Nieuwl., *Onoclea sensibilis* L., and graminoids such as *Leersia virginica* Willd., *M. vimineum*, and *Carex lurida* Wahlenb. were common. Macroplot herbaceous ground cover averaged 63% (± 7%) per m², and leaf litter depth ranged from 0.6 to 6 cm (3 ± 0.2 cm). Topography expressed a tenfold difference (12-122 cm) in absolute range among sites, with an average altitudinal change of 52 cm (± 5 cm) over a 15-m distance (Figure 3). The relative contribution of silt to local soil conditions (Appendix 3.1) was positively correlated with topographic range (Spearman’s r = 0.567, p = 0.028). Even when accounting for topography, *M. vimineum* cover was still strongly correlated with soil textured that had a high silt content (Partial correlation: df = 12, r = 0.612, p = 0.02); when sand was substitute for the same analysis no significant trends were detected (r = -
0.455, p = 0.102. When soil texture was ≥25% loam, *M. vimineum* average cover was 3.5x higher than when loam was <25% (32 vs. 9%). None of the other soil parameters presented as significant correlates for this exotic species. In areas where *M. vimineum* was present, I found no correlation between the species’ cover and macroplot structure, including variables such as basal area, shrub density, total species richness, or litter depth (all variables, Spearman’s r < 0.481, p > 0.05).

*M. vimineum* abundance and flooding

*Microstegium vimineum* abundance, as measured in the groundcover subplots, was captured in 46% (n = 16) of the 35 macroplots (Figure 4a). Comparing sites based on BG and AG demonstrated that frequency of *M. vimineum* occurrence was not significantly reflective of flood classification (t-test, df = 14, t = 2.019, p = 0.063) (Fig 5b). However, *M. vimineum* cover was five times greater in sites with BG (Md = 15, N = 9) flood classification than in sites with AG flooding (Md = 3, N = 7) (Mann-Whitney Rank: U = 8.50, z = -1.23, p = 0.012).

As predicted, there was a strong positive correlation between mean macroplot *M. vimineum* cover in 2013 and mean relative peak flood depth (Figure 5a; Table 4). Hydrology data from the water wells demonstrated a positive relationship between average flood duration and peak flood depth (Figure 5b; Spearman’s: N = 15, r = 0.764, p = 0.001). Wetlands were flooded at or above the soil surface for an average of 35-85% of the monitoring period, with an average standing duration of 3-63 days (Figure 6, Table 2).

Flooding mesocosm

Only the control treatment, which did not receive flooding at or above the soil
surface at any time, produced *M. vimineum* seedlings. Seedlings emerged in the control treatment 8-20 days following seed set (Figure 7). *Microstegium vimineum* seed germination and seedling production did not occur under flooded soil conditions (K-W, df = 8, H = 61.740, p <0.001). Because none of the 56 flooded mesocosms produced seedlings, even following drawdown and scarification of the soil surface, only control treatment plant growth data could be measured (Table 3). Soil analysis results did not indicate large difference among the treatments (Appendix 2).

**Discussion**

This study demonstrates that the establishment and spatial distribution of a pervasive invasive, Japanese stiltgrass *M. vimineum*, is inhibited by the occurrence of flooding prior to seedling emergence. Distribution and dominance of plants in wetlands are determined by species’ plasticity and possession of traits available to cope with the physiological stressors of flooding (Pezeshki, 2001; Magee and Kentula, 2005). Headwater wetlands therefore have a strong abiotic resistance to this invasive species that may readily colonize drier adjacent uplands (D'Antonio et al., 2001; Price et al., 2011). For annual plants such as *M. vimineum*, the persistence of patchy populations in interior areas with low propagule pressure is largely dependent on successful seed bank recruitment (Turnbull et al., 2000). Results presented here demonstrate that flooding significantly reduces seed viability of this invasive plant.

Hypotheses formed from the initial field surveys were supported by the mesocosm results and reinforced by subsequent field and hydrology surveys. *Microstegium vimineum* dominance is strongly reduced by the presence of short-term seasonal aboveground flooding, an effect that persisted for the entirety of the growing
season. These results further demonstrate that flood depth and duration have a great capacity to mitigate invasive dominance in the shaded understory of forested wetlands. However, the truncated flood duration observed here is typical of urban wetlands with flashy hydroperiods and may have a greater impact on other aspects of community composition (Ehrenfeld et al., 2003; Price et al., 2011).

In field surveys, *M. vimineum* dominance reflected relative flood depth. That is, topographic areas above the relative peak flood line served as refugium for localized populations. Mesocosm germination rates were low (7-20%), though within reason given the stressors of the system and previous findings (e.g., Cheplick, 2010; Droste et al., 2010). These stark experimental results provided strong support for the field observation that *M. vimineum* did not colonize areas that experienced seasonal aboveground flooding, despite established *M. vimineum* plants’ ability to withstand shallow flooding (Barden, 1987; Touchette and Romanello, 2010).

These results have important management implications as much of the wetland area in this urban study region is second growth, post-agricultural preserved greenspace. Historic anthropogenic use and hydrologic modifications (e.g., ditching that lower the water table) alter the expressed vegetation structure (Yepsen et al., 2014). Human modifications therefore negatively affect wetlands’ innate resistance to invasive plants and their capacity to reduce downstream flood surges following heavy rains. These modifications ultimately reduce ecosystem services provided by headwater complexes relative to stormwater retention, water quality and groundwater infiltration (He et al., 2000; Alexander et al., 2007; Lassaletta et al., 2010; Hill et al., 2014). Unlike other studies (Kourtev et al., 1999; Ehrenfeld, 2008), I found no correlation between soil
nutrient content or pH and *M. vimineum* occurrence and cover. When marginal trends were observed in my dataset, accounting for stream proximity significantly reduced the strength of the interaction. This result suggests that in wetland systems, teasing apart correlations between nutrients and stream transport may be difficult, and even misleading in the absence of a manipulative experiment. Instead of nutrients, soil texture appeared to be of greater importance to *M. vimineum* dominance in these wetland systems.

Many invasive herbaceous species are heliophilic and possess life-history traits that make them superior competitors in novel, mesic environments (Daehler, 2003). In contrast, shade-tolerate invasives are likely to progress at a slower rate that is in line with succession and possess physiological traits that aid in resource acquisition (Von Holle et al., 2003; Martin et al., 2009). Research in upland forests by Warren et al. (2011) indicates that *M. vimineum* grows best in open woodlands, and suggests that the species may become a poor competitor, or be excluded, when in deep shade. However, no significant trends were observed between *M. vimineum* cover, basal area, shrub density, and vertical midstory or canopy cover in these forested wetland systems.

In summary, through a combination of field and experimental mesocosm studies, I have demonstrated that *M. vimineum* seedling production is significantly reduced in the wake of seasonal flooding prior to seedling emergence. These results have important implications for managed wetlands and creation or restoration projects in topographically low-lying areas. Flooding at or above the soil surface for less than five days prior to spring emergence can significantly reduce invasive dominance. Because of reduced seed viability, the effect of seasonal flooding may last the entire growing season, even after drawdown of temporarily flooded areas. If implemented, these management methods may
increase native species biodiversity, habitat heterogeneity, ecosystem function, and reduce the ecological impact of Japanese stiltgrass *M. vimineum* invasions.
References


Table 1: Wetland site descriptions and sampling intensity of the six research wetlands.

<table>
<thead>
<tr>
<th>Wetland</th>
<th>Longitude (N)</th>
<th>Wetland size (ha)</th>
<th>Vegetation macroplot n</th>
<th>Water well points n</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Latitude (W)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dismal (DS)</td>
<td>40° 33' 12&quot; N</td>
<td>225</td>
<td>15</td>
<td>4</td>
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<tr>
<td></td>
<td>-74° 23' 33&quot; W</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nomahegan Lenape (NL)</td>
<td>40° 40' 40&quot; N</td>
<td>130</td>
<td>11</td>
<td>3</td>
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<tr>
<td></td>
<td>-74° 19' 02&quot; W</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Evergreen (EV)</td>
<td>40° 33' 40&quot; N</td>
<td>31</td>
<td>3</td>
<td>2</td>
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<tr>
<td></td>
<td>-74° 20' 00&quot; W</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North Brunswick (NB)</td>
<td>40° 27' 25&quot; N</td>
<td>28</td>
<td>3</td>
<td>2</td>
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<tr>
<td></td>
<td>-74° 27' 50&quot; W</td>
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<td></td>
<td></td>
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<td>Terrill (TE)</td>
<td>40° 37' 46&quot; N</td>
<td>11.5</td>
<td>2</td>
<td>2</td>
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<td></td>
<td>-74° 23' 15&quot; W</td>
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<td></td>
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<td>Polansky (PP)</td>
<td>40° 34' 53&quot; N</td>
<td>9</td>
<td>1 (2)*</td>
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<td></td>
<td>-74° 21' 24&quot; W</td>
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</tr>
</tbody>
</table>

* To capture hydrologic subareas in the smallest site, two radial macroplots were sampled 75 m from the center point at 360° N and 240° SSW
Table 2: Hydrologic descriptive metrics for investigated wetland sites are summarized in the table below. The number of Ecotone water well monitoring points is included in parentheses next to each site name. Flooding depth data were calibrated to equate the soil surface to zero. Data are presented as 2012-2013 mean ± standard error of the mean and range (minimum – maximum). DS (2) and EV (1) each had site(s) with aboveground flooding that last for the duration of monitoring, resulting in a skewed flood frequency of “1”.

<table>
<thead>
<tr>
<th>Site</th>
<th>Days monitored</th>
<th>Total days flooded (%)</th>
<th>Flood duration</th>
<th>Flood frequency</th>
<th>Peak flood depth (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DS</td>
<td>129 ± 8</td>
<td>66 ± 15</td>
<td>30 – 100</td>
<td>38 ± 31 3 - 136</td>
<td>7 ± 2 1 - 14</td>
</tr>
<tr>
<td>NL</td>
<td>146 ± 6</td>
<td>36 ± 6</td>
<td>7 – 61</td>
<td>4 ± 0 2 - 8</td>
<td>13 ± 1 9 - 15</td>
</tr>
<tr>
<td>EV</td>
<td>134 ± 15</td>
<td>58 ± 23</td>
<td>29 – 99</td>
<td>12 ± 9 3 - 23</td>
<td>9 ± 4 1 - 16</td>
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<tr>
<td>NB</td>
<td>141 ± 16</td>
<td>35 ± 17</td>
<td>7 – 63</td>
<td>3 ± 2 1 - 7</td>
<td>15 ± 2 6 - 19</td>
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<tr>
<td>TE</td>
<td>153 ± 0</td>
<td>85 ± 10</td>
<td>62 – 100</td>
<td>63 ± 50 9 - 157</td>
<td>5 ± 4 1 - 11</td>
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<tr>
<td>PP</td>
<td>135 ± 9</td>
<td>19 ± 4</td>
<td>12 – 29</td>
<td>4 ± 3 1 - 8</td>
<td>8 ± 3 3 - 12</td>
</tr>
</tbody>
</table>

DS, Dismal (n = 4); NL, Nomahegan Lenape (n = 3); EV, Evergreen (n = 2); NB, North Brunswick (n = 2); TE, Terrill (n = 2); PP, Polansky (n = 2).
Table 3: Mean ± SEM plant growth measurements four weeks after flood drawdown (day 52). In addition to culm height (culm ht) and tiller density, density of terminal inflorescences per plant (term inflor plant$^{-1}$) and aboveground biomass were measured at experiment’s end. $n = 7$.

<table>
<thead>
<tr>
<th></th>
<th>Week 7</th>
<th>Week 15</th>
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<tr>
<td>Culm ht (cm)</td>
<td>21.3 ± 2.6</td>
<td>60.6± 4.9</td>
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<tr>
<td>Tillers plant$^{-1}$</td>
<td>4.7 ± 0.6</td>
<td>10.5± 1.3</td>
</tr>
<tr>
<td>Term inflor plant$^{-1}$</td>
<td>24.2± 2.9</td>
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</tr>
<tr>
<td>Plant Biomass (mg)</td>
<td>720.0 ± 9.0</td>
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</tr>
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</table>
Table 4: Linear regression results for *M. vimineum* cover relative to peak flood line. $R^2 = 0.400$.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
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<tr>
<td>Regression</td>
<td>1</td>
<td>2517.4</td>
<td>2517.4</td>
<td>8.672</td>
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<tr>
<td>Residual</td>
<td>13</td>
<td>3773.6</td>
<td>290.3</td>
<td></td>
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</tr>
<tr>
<td>Total</td>
<td>14</td>
<td>6291.0</td>
<td>449.4</td>
<td></td>
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</table>
Figure 1: Schematic of 15-m radius macroplot sampling design, including cardinal transects, and 1-m² groundcover subplots ($n = 8$). Macroplot topography was measured at 5-m intervals along the transects, relative to plot center. This figure illustrates Ecotone water well placement at the lowest altitude within a macroplot.
Figure 2: Mesocosm experiment included a three-week manipulation, after which all were maintained at the control depth (dotted line). Flood duration treatments (4) were flooded 2 cm AG until drawdown date, denoted by an “X”. The experiment ran for 15 weeks.
Figure 3: Relationship between *M. vimeineum* dominance and hydrologic classification. a) *Microstegium vimeineum* was greatest in saturated sites (BG). Macroplot $n = 35$. b) When present in groundcover subplots, mean (± SEM) percent cover was significantly greater in BG sites than AG sites, $n = 9$ and $n = 7$, respectively. Different letters indicate significant differences at $P < 0.05$. 
Figure 4: Macroplot topography varied within wetlands and among size classes, as illustrated by sites where flood monitoring occurred. Zero represents plot center; each boxplot contains 12 data points that are relative to each plot’s center altitude. a) Data from large wetlands DS, Dismal Swamp, and NL, Nomahegan Lenape. b) Data from medium sized wetlands: EV, Evergreen; NB, North Brunswick; and small wetlands: TE, Terrill; PP, Polansky.
Figure 5: a) *Microstegium vimineum* cover increased with distance above the relative peak flood line (0 cm). The shaded area highlights points where aboveground standing water covered the entire macroplot. b) Relationship between flood duration and peak flood depth. Large: DS, Dismal Swamp; NL, Nomahegan Lenape; Medium: EV, Evergreen; NB, North Brunswick; Small: TE, Terrill; PP, Polansky Park.
Figure 6: Average relative duration of flooding at or above the soil surface during the 2012 and 2013 monitoring seasons. Stage duration varied greatly within and among wetlands and size classes. DS, Dismal Swamp; NL, Nomahegan Lenape; EV, Evergreen; NB, North Brunswick; TE, Terrill; PP, Polansky Park
Figure 7: Average cumulative *M. vimineum* seedling production from the control treatment (*n* = 7). The cumulative proportion of germinated seeds ranged from 7 to 20 %. 
CHAPTER 4

Vegetation structure shapes competent West Nile virus host and vector abundance in urban wetlands

Abstract

The effects of urbanization significantly influence the structure and function of remnant natural areas. Biodiversity loss is one of the strongest impacts of landscape fragmentation. Vector-borne disease systems that encompass multiple host and vector species may be strongly influenced by these community shifts because biodiversity may increase infection rate due to decreased host diversity (the “dilution effect”). Here we focus on West Nile virus disease risk as it relates to habitat structure, amplifying avian hosts (e.g., American Robin, Blue Jay, and Common Grackle), and competent mosquito vectors (e.g., Culex pipiens, Cx. restuans). This study took place in six forested freshwater wetlands ranging in size from large (>125 ha) to small (<15 ha), located in the New York City metropolitan region. We identified 287 plant, 68 bird, and 29 mosquito species; while bird species richness increased with plant richness, mosquito richness declined. Interannual variation of competent WNV hosts was five times higher in small wetland patches compared to large. Relative abundance of competent vectors reflected climatic variation rather than the effects of wetland patch size. Both hosts and vectors were positively correlated with maple tree basal area, a habitat trait that was associated with exotic plant richness. Unexpectedly, competent vectors were not associated with trash density. Non-competent floodwater mosquito species (e.g., Aedes vexans) accounted dominated these wetlands (>70% relative abundance) and their distribution
reflected local habitat structure and hydrology. As the most abundant host species in these forested wetland sites, American Robin density may be a useful metric for monitoring WNV risk. Restoring the forested understory and natural flooding conditions of these wetlands will promote non-competent host and vector diversity.

Introduction

Our understanding of the connections between biodiversity and the risk of transmission and infection of zoonotic diseases has increased drastically in the past two decades, particularly in urban regions (Johnson et al., 2015b). This trend is especially true for diseases that are multi-host vector-borne pathogens because some host species serve to amplify virulence and transmission, while others have a diminishing effect (Keesing et al., 2006; Keesing et al., 2010). The foundational work of Ostfeld and colleagues (Ostfeld and Keesing, 2000a; Ostfeld and Keesing, 2000b; Schmidt and Ostfeld, 2001) demonstrated that a loss of biodiversity within the host community can increase disease transmission if vectors become more likely to encounter a competent reservoir host (i.e., the “dilution effect”).

West Nile virus (WNV) is a mosquito-borne flavivirus that causes illness and death in a range of vertebrates, including humans (Colpitts et al., 2012; Petersen et al., 2013). Wild bird populations are the primary host of WNV, though some species have a greater capacity to serve as amplifying hosts for this disease (Kilpatrick et al., 2007). Komar et al. (2003) developed a WNV competency index (CI) for bird species that are common in the New York metropolitan area. Bird species with a CI >1 are generally considered to be highly competent hosts (hereafter, “competent”) because they demonstrated high susceptibility, infectiousness, and duration of infectious viremia.
Following emergence of WNV in 1999, New York City served as a metropolitan epicenter for the 2000 season (Bernard et al., 2001). During that season, Bernard et al. (2001) observed that 67% of wild American Crows (Corvus brachyrhynchos) and 40% of Blue Jays (Cyanocitta cristata) from the epicenter tested positive for WNV. These two species, as well as American Robin (Turdus migratorius), Common Grackle (Quiscalus quiscula), House Finch (Haemorhous mexicanus), and House Sparrow (Passer domesticus) have also been identified as competent amplifying host species for WNV (hereafter, the "competent host" guild. Komar et al., 2003; Kilpatrick et al., 2007).

The importance of habitat area and heterogeneity in shaping bird assemblages has long been studied (e.g., MacArthur and MacArthur, 1961; Boecklen, 1986). In urbanized landscapes, vegetation structure and fragment patch size play an important role in attracting and sustaining diverse avian assemblages (Findlay and Houlahan, 1997). Additionally, although housing density has been shown to correlate positively with forest bird species richness, this variation was connected to a greater number of species characterized as year-round residents (Pidgeon et al., 2007). In creating an index of biological integrity for wetland birds, a generalists guild composed of year-round residents characterized as edge species corresponded positively to the estimated disturbance gradient (e.g., buffer width, altered flooding. Veselka et al., 2010). The competent WNV hosts mentioned earlier are included in the generalist guild.

At a broader scale, land cover or general community type is an important predictor for avian biodiversity during breeding (MacFaden and Capen, 2002; Riffell et al., 2006) and migration (Rodewald and Matthews, 2005). Microhabitat composition, such as understory density, is also important for supporting a diverse avian assemblage,
particularly during the breeding season (MacFaden and Capen, 2002; Mabry, 2013; Reidy et al., 2014). Given some species’ territory requirements or sensitivity to conditions indicative of unnatural habitat edges, a minimum patch area may also be required to ensure nest success (Tilghman, 1987; Smith and Chow-Fraser, 2010). For example, Smith and Chow-Fraser (2010) found that obligate marsh-nesting birds were significantly less likely to occur in wetland patches <5.5 ha. Tilghman (1987) observed a similar pattern in urban woodland patches where interior species, such as Canada Warbler (*Cardellina canadensis*), occurred only in fragments >5 ha in size.

Mosquito species also have specific habitat requirements, reproductive cycles, and varying competency for transmitting WNV. Within the northeastern U.S., *Culex restuans* and *Cx. pipiens* (hereafter, “*Culex*”) are similar in their appearance and ecology, and both may act as bridge vectors between avian hosts and humans (i.e., takes blood meals from both birds and humans). However, recent research has identified temporal differences in the *Culex* species’ activity (Egizi et al., 2014; Johnson et al., 2015a). In addition to *Culex*, *Aedes albopictus*, *Ae. japonicus*, and *Ae. triseriatus* are also considered competent WNV vectors for this region (hereafter, "competent vector"). Johnson et al., 2015a). These competent vector species are multivoltine (2+ broods/year), and are generally considered to be urban generalists that breed in artificial and natural container habits, such as stormwater basins and used car tires (Crans, 2004). Previous research by Johnson et al. (2012) suggests that the proportion of competent vectors within urban wetland patches is significantly lower than adjacent residential areas. Instead, riparian floodwater mosquito species tend to dominate, in particular *Ae. vexans*, which is not considered a competent vector for WNV.
As with birds (Boecklen, 1986; Tilghman, 1987), urban habitat heterogeneity has been positively correlated with increased mosquito species richness (Chaves et al., 2011). Unlike birds, few studies have quantified relationships between habitat structure and mosquito biodiversity, though mechanisms influencing larval development have been tested (e.g., food source, competition). For example, Fish and Carpenter (1982) suggest that growth of tree-hole mosquito larvae (*Ae. triseriatus*) in an oak-based substrate is significantly lower than in a maple (*Acer* spp.) leaf substrate. Attributing the results to tannic acid in oak leaves, David et al. (2000) found similar results for *Ae. aegypti*, *Ae. albopictus*, and *Cx. pipiens* larvae. Water quality in stormwater basins has also been shown to influence larval development, with *Culex* complex larvae responding positively to higher levels of ammonia (Gardner et al., 2013).

Although I was responsible for the collection of vegetation and habitat structure data and all analyses and text presented here, this research was conducted as part of an interdisciplinary team funded by EPA grant R833777, P.I. Joan Ehrenfeld. Nellie Tsipoura and Kristin Mylecraine-Munafo of NJ Audubon orchestrated the avian surveys. Rutgers’ vector biologists Mike Sukhdeo and Brian Johnson were responsible for the mosquito surveys. Our goal was to assess the potential for urban wetlands to facilitate the dilution effect for the WNV disease system. Research questions diving this study include: 1) To what extent do competent WNV hosts and vectors reflect wetland habitat structure?; and 2) How do wetland and patch size influence the biodiversity of these taxa and the relative abundance of competent hosts and vectors? To answer these questions, we sampled the plant, mosquito, and avian assemblages of six forested headwater wetlands ranging from small (<15 ha) to large (>125 ha) in urban central New Jersey,
Within each taxonomic group, I first assessed overall species richness and assemblage composition relative to each wetland and wetland patch size. Second, I examined correlations between habitat structure and fauna composition. These methods were then used to identify correlates between habitat structure and the relative abundance of competent WNV hosts and vectors.

**Materials and methods**

**Study sites**

The study region is located in urban central New Jersey, <50 km from New York City. Six wetland patches, ranging from small <15 ha, to large >225 ha were sampled during the 2008-2011 growing seasons. All of the wetlands fell within the Piedmont physiographic province, within the Arthur Kill (409.7 km²), or Lower Raritan (910.7 km²) water management areas (WMAs). Urban lands cover 83% of Arthur Kill and 58% of the Lower Raritan WMA while wetlands cover approximately 4.5% and 18%, respectively (NJDEP, 2007). Wetland sites discussed here are the same as those detailed in Chapter 2. Vegetation, bird, and mosquito survey intensity varied across years and wetland sites, as outlined in Table 1.

**Vegetation methods**

The same vegetation sample points and methods outlined in Chapter 2 were used for the floristic data described here. However, metrics relevant to bird and mosquito habitat requirements were also measured. Within each macroplot, areas that flooded intermittently (hollows) were mapped and their cumulative area was measured (hereafter, “larval area”). These subtle depressions are ideal for “floodwater” mosquitoes that lay desiccation-resistant eggs on moist surfaces (e.g., *Aedes* spp.). In contrast, species that lay
eggs on the surface of standing water (e.g., *Culex* spp.) often lose viability if they become dry (Crans, 2004; Rey et al., 2012). Bottles/cans, small trash (<1 m²), and large trash were also tallied within each macroplot. To identify “pan” habitats in which treehole mosquito species may oviposit in the woody understory (sensu Kitching, 1971), the number of stems that branched below the 1.3 m diameter at breast height were also noted. Coarse woody debris (CWD), which is important for some mosquito and bird species, was tallied along macroplot cardinal transects. A caliper was used to place CWD into one of three size classes (7.5-15, 15-25, >25 cm), and level of decay was also qualified for pieces >25 cm diameter (bark on, no bark wood hard, wood soft).

Coarse vegetation structure and habitat heterogeneity was measured along three 50-m transects that extended beyond the macroplot, creating a 100-m diameter sample area (Figure 1). Along each transect, changes in groundcover (e.g., native, exotic, emergent, streams), understory composition (e.g., dense native, exotic, sparse/deer browsed), and canopy cover (e.g., open, partially closed, closed) were noted as distance along the transect (cm); the values were converted to a percent of the total 150 m transect distance (e.g., percent open canopy). An index of sample area heterogeneity was measured by tallying the number of changes within the 150 m transect. Because three transects were surveyed, the minimum heterogeneity score is three (3), which would indicate that the sample area is uniform around the macroplot.

*Fauna methods*

Avian sample points coincided with all of the vegetation macroplot locations with the exception of the smallest wetland, Polansky (PP), which could only support one avian point in the center of the patch. Sample points were visited 2-3 times during the breeding
season and surveyed between one half hour prior to sunrise and four hours after sunrise on days without precipitation and wind speeds <12 mph (Ralph et al., 1993). Observers recorded all bird species that they heard or observed during ten one-minute intervals.

Mosquito methods are outlined in detail in Johnson et al. (2012) and Johnson and Sukhdeo (2013). Briefly, mosquito collection occurred at 2-4 sample points located 100 m from the wetland patch edge. The number of wetlands surveyed and sampling intensity varied from 2009 to 2011 (Table 1). During 2009-2010, CO₂ baited CDC Miniature Light Traps (John W. Hock Company) were used to attract host-seeking mosquitoes. CDC Gravid Traps (John W. Hock Company) were added in 2011 to attract gravid (pregnant) females seeking to lay eggs in the baited hay infusion. Both trap types were set at least one hour prior to sunset and collected the following morning. Mosquitoes were identified to species, with the exclusion of Cx. pipiens and Cx. restuans, which are notoriously difficult to distinguish morphologically (Harrington and Poulson, 2008). These two mosquito species were grouped as Culex for statistical analyses. One additional Culex species was captured, Cx. territans. This native wetland mosquito is ecologically and morphological distinct from Cx. pipiens and Cx. restuans, and was therefore not included in the Culex group.

Statistical Analyses

Analyses used here follow those outlined in Chapter 2. Relative abundance (RA) values were used to describe composition of the bird and mosquito assemblages. Avian data were averaged across years (2-3), with the exception of medium-sized wetlands EV and NB that were added during the final survey year. When variance values are presented with sample averages they represent the standard error of the mean (SEM). Life history
guilds, such as nesting location (Cornell Lab of Ornithology, 2015), and functional
groups such as RA of edge + year-round resident species, or RA of wetland species were
also used to characterize wetland avifauna. Bird species of Regional Priority or Special
Concern (hereafter referred to as RPSC. ACJV, 2008; Partners in Flight Science
Committee 2012) were pooled to examine trends between their RA and habitat structure.
Yearly mosquito data were analyzed for trends relative to habitat variables, but averages
were also used to describe general composition.

Prior to analysis with the fauna data, Spearman’s correlation analysis was used to
identify unique habitat structure variables, and reduce occurrence of autocorrelation ($\alpha >$
0.10, $r_s < 0.279$). Analysis of trends between faunal data and habitat data were assessed
with Spearman’s correlation and linear regression analysis. All univariate analyses
employed followed a significance threshold of $\alpha = 0.05$; $r_s$ for the avian dataset was
0.335 ($n = 35$), while the mosquito dataset varied according to sampling effort: 0.738
(2009, $n = 8$), 0.648 (2010, $n = 10$), 0.886 (2011, $n = 6$) (Zar, 1999). Pearson’s partial
correlation ($r_p$) analysis was used when a second mediating factor was suspected. Where
linear regression analyses are significant ($p < 0.05$), the $r^2$ value and regression equation
are given, in addition to the supporting ANOVA results. Friedman repeated measures
ANOVA on ranks (RM ANOVA) was used to test for differences among years ($\geq 3$ years)
for the temperature and precipitation data (May-Oct, 2008-2011; $df = 3$). Tukey Test was
used to reduce Type 1 error during pairwise RM ANOVA comparisons.

No bird or mosquito species were removed prior to hierarchical cluster analysis
and Non-metric multidimensional scaling (NMDS) ordination. As in Chapter 2, all
second matrix variables were log transformed. NMDS stress values $<20$ were deemed
significant for the avian data set, while stress <15 was appropriate for the mosquito data given the smaller sample sizes (McCune and Grace, 2002). Multiple Response Permutation Procedure (MRPP) analysis was used to test uniqueness of groups identified via cluster analysis. When groups were significantly different (A > 0.1, p < 0.05), indicator species analysis was used to identify species that were emblematic of a given group (Dufrêne and Legendre, 1997; McCune and Mefford, 1999). Kendall’s rank correlation was used to describe correlations within the ordinal space (α < 0.05).

Significant values for Kendall’s tau were \( \tau > 0.234 \) and \( \tau > 0.407 \) for the avian (n = 35) and mosquito (n = 14) datasets, respectively (Rohlf and Sokal, 1981). SPSS (2008) and PCORD (McCune and Mefford, 1999). Supporting graphics were created in SigmaPlot (Systat Software Inc., 2008) and Adobe Illustrator (CS5).

**Results**

A total of 384 species were identified in this study, including 287 species of plants, 68 bird species, and 29 mosquito species. When compared among the three wetland size classes, no differences were observed for the fauna data, but large wetlands (>125 ha) contained significantly more plant species than small (<15 ha) patches (Figure 3). Interestingly, avian and mosquito species richness increased and decreased, respectively, as floristic richness increased (Figure 4). When only native plants were included, this pattern held for birds \( (r_S = 0.335, p = 0.049) \), but not for mosquitoes \( (r_S = -0.333, p = 0.252) \).

This study spanned four years, which encompassed record-breaking weather events (Figure 2). The 2009 season began unusually cool and wet, while Tropical Storm Irene brought historical levels of precipitation when it made landfall in the New York
Metropolitan region on August 28, 2011. Repeat measures analysis on ranks suggests that the differences in precipitation (May-Oct) were highly different during our study ($\chi^2 = 7.80, p = 0.050$). Temperature differed significantly among years ($\chi^2 = 9.102, p = 0.028$). Pairwise comparisons revealed that 2010 ranked significantly higher than 2009 ($q = 3.637, p < 0.05$).

**Avian assemblage composition**

A total of 68 bird species were observed during the 2008-2010 breeding seasons, including 22 species considered to be facultative or obligate wetland birds (Appendix 4.1). The annual total bird count for Polansky (PP) sequentially decreased from 2008 to 2010, at which point the population was 60% lower than when this study began (48 vs. 29 birds/3 surveys). Relative abundance (RA) of wetland associated birds was positively correlated with the proportion of hydrophytes present in the local flora (Figure 7a). In contrast, bird species classified Regional Priority or Special Concern (RPSC) were negatively correlated with inundation depth (Figure 7b). RPSC species accounted for a third of the total bird species richness. Of the 23 RPSC species, only eight were facultative wetland associates or obligate wetland species such as Traill's Flycatcher (*Empidonax traillii*), Wood Duck (*Aix sponsa*), and Green Heron (*Butorides virescens*).

Wetland patch size did not appear to influence the diversity of avian life history traits (Figure 5). The majority of species were insectivorous ($78 \pm 1\%$ RA) and the only secondary carnivore observed were Red-tailed Hawks (*Buteo jamaicensis*). Tree nesting species were the most common ($39 \pm 2\%$ RA), and many of these species included year-round birds that live in edge habitats. Species that nest in shrubs were the second most represented nesting strategy.
Avian assemblages reflected different aspects of the canopy structure. Species typical of open woodlands and forests predominated in all wetlands (52 and 35% RA, respectively). In canopies where green ash was present, shrub-nesting species were significantly more abundant (Figure 6). Unexpectedly, shrub stem density was only indirectly correlated with green ash dominance, as both green ash ($r_S = 0.423, p = 0.013$) and shrubs ($r_S = 0.432, p = 0.010$) were independently, positively correlated with thicket area. The ground cover of these ash swamps were dominated by hydrophytes ($r_S = 0.397$), and contained areas of bare exposed soil ($r_S = 0.374$). Snag density was negatively correlated with green ash dominance ($r_S = -0.382, p = 0.026$), which may explain the negative correlation between shrub and cavity nesting birds ($r_S = -0.835, p < 0.01$).

As expected, mature forest stands contained more interior forest birds compared to early- and mid-successional stands (Figure 6). Year-round species typical of edge habitats were positively correlated with tree BA ($r_S = 0.534, p = 0.001$); competent WNV hosts accounted for 42 to 63% of the RA of this category ($60 \pm 2\%$). Higher BA was associated with more leaf litter cover ($r_S = 0.376$), and open understories in the surrounding 50-m sample area ($r_S = -0.319$).

Hierarchical cluster analysis identified four distinct assemblages; each group contained sample points from at least three wetlands (Figure 8). The four distinctive groups were reinforced by MRPP analysis ($A = 0.198, p < 0.001$). Group B1 included open woodland forest stands that are considered mid successional ($n = 5$; Table 2). Sixteen of the 35 survey points fell within group B2. Forest interior species were at their highest RA in B2, averaging 15% compared to other groups, which averaged $\leq 5\%$ RA.
However, this group also contained the highest RA of year-round species typical of edge habitats (Table 2). Three of the four indicator species associated with this group were classified as RPSC (Figure 9). Wetland and wetland associated birds common in open woodland and freshwater marsh habitat were in greatest numbers in group B3, comprising 51% of the average RA. Interestingly, the relative abundance of wetland birds was significantly different among all four cluster groups (Table 2). This assemblage also had the highest average avian species richness (20 spp.), and significantly more shrub nesting species (Table 2). Group B4, the sister group to B1, was defined last in the hierarchal analysis. All four sites in B4 are characterized as mature forest stands with open understories. As expected given the open understory structure, this group contained the fewest shrub nesting species (Table 2). Competent WNV hosts were found in greatest numbers in the smallest group (B4).

**Mosquito assemblage composition**

During the 2009-2011 trapping seasons, a total of 22 native mosquito species were identified. Three nonnative exotic species considered to be competent WNV vectors were also surveyed (*Aedes albopictus*, *Ae. japonicus*, and *Cx. pipiens*). Competent native vectors in our survey pool included *Cx. restuans* and *Ae. triseriatus*. With an average relative abundance (RA) of 63 ± 4%, *Ae. vexans* (AEVE), a common wetland floodwater species, was the most pervasive. However, AEVE RA was comparatively low in the North Brunswick wetland (36 ± 2%). The relative abundance of AEVE was inversely related to oak tree basal area, as well as habitat heterogeneity (Figure 10). For all macroplots sampled, herbaceous groundcover was also lower in oak-dominated canopies. Where oak was a dominant or co-dominant (>20%), groundcover averaged only 30%,
while the groundcover of non-oak stands averaged 71%/m² ($F_{1,34} = 9.279, p = 0.004$).

Two generalists, *Culex* and *Anopheles punctipennis* were respectively the second (11 ± 1%) and third (6 ± 1%) most sampled mosquito species. Five species occurred at fewer than 25% of the sample points (Appendix 4.2).

Cluster analysis identified three distinct groupings (16% chaining), which were validated by MRPP ($A = 0.302, p < 0.001$). NMDS ordination provided further support for these groupings (Figure 11). The three dimensional solution explained 92% of the variance observed in the data (stress = 1.72). From the second matrix, larval area (i.e., hollows) positively correlated with Axis 3 ($\tau = 0.541$) towards group M1 for which *Ae. vexans* (AEVE) is the indicator species. Correlation analysis also found a positive trend between AEVE RA and larval area ($r_s = 0.477, p = 0.081$). These results align with the ecology of this floodwater species, which is common in forested swamps (Appendix 4.2). Larval area was positively correlated with snag density ($r_s = 0.544, p = 0.0429$), a trait that could potentially increase habitat for tree hole-breeding mosquito species.

Sample area habitat heterogeneity was negatively correlated with Axis 3 ($\tau = 0.512$), toward the direction group M1, which included the two NB wetland sample points. These points are characterized as having a very dense woody understory and hydroperiods classified as saturated to temporarily flooded. Indicator species identified for group M1 are diverse in their ecology; *Ae. canadensis* (AECAT) is a freshwater wetland generalist, while *Coquillettidia perturbans* (COPE) is typical of semipermanent/permanently flooded swamps and marshes. *Aedes japonicus* is an exotic species that breeds in container habitats. Group M2 falls in the center of the ordination and is characterized by *Culex*, urban generalists that breed in containers. *Culex* was most
strongly correlated with Axis 2 (not shown, $\tau = -0.758$), which explained 13.3% of the variance. None of the three habitat variables included in this ordination were significantly correlated with Axis 2 ($\tau < 0.407$).

Previously discussed mosquito results represent data collected with Light Traps. The addition of Gravid Traps in 2011 added a new layer of information regarding the relative abundance of pregnant mosquitoes looking to oviposit in the baited traps (Figure 12). Species’ relative abundance from the Gravid Trap dataset reveals that unlike the other sample points, EV2 and PP3 are dominated by gravid AEVE. Both of these sample points occur near a semi-permanent/intermittently exposed wetland – prime larval habitat for AEVE. In contrast, EV1 and PP2 occur <100 m from a stormwater retention pond and ditch, respectively.

*Competent West Nile virus hosts and vectors*

The relative abundance of competent WNV hosts and vectors demonstrated slight annual variations within and among the six wetlands (Figure 13). Although a positive correlation was expected between WNV host and vector abundance, no such trend was observed (Figure 14). Within-year comparisons of wetland size classes identified differences that did not necessarily carry across years (Figure 15). No differences in host RA were detected in 2009. In contrast, 2009 vector abundance was significantly lower in small wetlands compared to large ($F_{1,6} = 13.057, p = 0.011$), but no differences were observed for the subsequent seasons.

Competent host abundance was lower in large wetlands compared to small wetlands in 2008 ($F_{1,27}: 16.312, p < 0.001$), and compared to medium wetlands in 2010 (K-W: $H = 4.589, p = 0.032$). At the species level, American Robins were the most
common WNV host and occurred in the greatest numbers, averaging 5 birds/year (RA: 13 ± 1%). Blue Jays were the second most frequently surveyed (n = 33; 3 birds/year; RA = 8 ± 1%). Relative abundance of Common Grackle (8 ± 2%) was similar to Blue Jay, but Grackles occurred less frequently and occasionally in flocks (n = 23; 4 birds/year). Each with an average relative abundance of <2%, American Crow (n = 10; RA), House Finch (n = 1), and House Sparrow (n = 2) were minor contributors to the WNV host composition in these wetlands. Based on these results, it would be expected that population dynamics of American Robin, Blue Jay, and Common Grackle would shape the proportion of competent to non-competent hosts.

WNV host populations experienced the greatest inter-annual population fluxes in small wetlands (Polansky and Terrill), while large wetlands appeared relatively unchanged (Figure 14). American Robins accounted for 60 of the total 116 birds surveyed in Polansky, which amounted to half of the total host RA for that site. Host population declines from 2008 to 2009 in Terrill (TE) reflect Common Grackle population shifts from 11 ± 6 birds/season to 1 individual. More broadly, early successional stands contained significantly fewer competent birds compared to late successional stands (md RA: 18 vs. 30%; K-W: H = 9.833, p = 0.002; Figure 16a). However, adjusting for wetland site effects weakened this trend (df = 32, rp = 0.312; Figure 16b). WNV host RA was negatively associated with understory density within the 50-m sample area (rs = -0.362, p = 0.033), but this habitat variable was also negatively correlated with macroplot BA. Maple, the most abundant genera of trees in this study, was positively associated with WNV host RA (F1,33 = 8.172, p = 0.007; Figure 16c).
Further, maple dominance was positively correlated with the proportion of exotic plant species present (Figure 16d).

Two of the most abundant WNV hosts were highlighted as indicator species for group B4 in the cluster analysis (Figure 9; AMRO, BLJA). Three of the survey points in this cluster group were within 50 m of a human-created or natural edge (i.e., stream), while the fourth point was in the smallest wetland patch, Polansky (PP). In large wetlands (n = 26), the dominance of competent hosts declined as the number of wetland-obligate and wetland associated birds increased ($r_S = 0.514$, $p = 0.007$).

Evergreen (EV) and North Brunswick (NB) contained sample points that had fewer than 14 mosquito species, however, lower richness did not translate to a difference in relative abundance of competent West Nile virus (WNV) vectors ($F_{1,12} = 1.865$, $p = 0.197$). The number of WNV competent mosquitoes increased with the density of AEVE (Figure 17); however, the relative abundance of AEVE and WNV vectors often exhibited opposing responses to habitat variables. For example, WNV vector RA increased with increasing tree sapling density ($r_S = 0.606$, $p = 0.033$), a habitat variable that was negatively correlated with larval area ($r_S = -0.554$, $p = 0.0373$).

Patterns were observed between canopy composition and WNV vector relative abundance. In contrast with AEVE (Figure 10a), high oak tree basal area (BA) was positively correlated with vector RA (Figure 18a/c). In these wetlands, areas dominated by oak contained a greater proportion of upland plant species ($r_S = 0.453$, $p = 0.006$), which may suggest that fewer floodwater mosquito species would be present. Leaf litter cover was also characteristic of upland-dominated areas ($r_S = 623$, $p < 0.001$), and vector RA increased in kind (Figure 18e).
Although no trends were observed between maple dominated stands and wetland plant status, a positive trend was seen with WNV vector RA, though a point from wetland site NB obscured the significance (Figure 18b/d). Removal of that NB point did reveal a significant positive correlation ($r^2 = 0.332, \beta = 0.576; F_{1,11} = 5.460, p = 0.039$). Total tree BA area showed no significant trends with WNV vector RA. Competent vectors were not correlated with the density of human trash ($r_S = 0.020, p = 0.940$; Figure 18f). More so than the 2010 or 2011 vector datasets, site effects appeared to weight more heavily in 2009 (e.g., Figure 18b).

The addition of gravid traps in 2011 highlighted the differences between the two methods (light vs. gravid) and variation among the three wetlands sampled that year (Figure 19). In Dismal (DS), the RA of gravid competent WNV hosts was very high and little variation was observed between the two points in that wetland. In contrast, medium-sized wetland EV and small wetland Polansky (PP) captured a much wider within-wetland range. The low competent vector abundance at these points may indicate that individuals are not finding blood meals within the trapping range, or the local habitat is not suitable for depositing eggs. Unlike Aedes, Culex eggs are not resistant to desiccation.

**Discussion**

This study examining wetland plant, bird, and mosquito assemblage composition in urban wetlands suggests that competent WNV hosts and vectors respond similarly to some habitat variables. In mature forest stands (BA$>$30 m$^2$/ha), the minimum relative abundance (RA) of competent hosts was 15%, which was more than 7x the 2% minimum observed in early/mid-successional woodlands. Avian host abundance responded positively to maple dominance, a trait that was highly correlated with exotic plant
richness. WNV vectors also increased with maple BA, as well as oak; the latter was associated with increased upland plant richness and a sparse herbaceous layer.

Wetland fragment size as well as sample year had important implications for WNV host and vector relative abundance (Johnson et al., 2012). In 2009, a fairly wet and cool season, competent vector RA was nearly twice as high in large fragments compared to small (19 vs. 11%). This trend reversed for the following two years with vector RA slightly lower in large sites compared to medium or small; the magnitude of change within wetlands across years was consistent for vectors (<9%). Previous research conducted in New Jersey observed significantly higher WNV infection rates during the drier, 2010 season, compared to the wet sampling season of 2011 (Johnson and Sukhdeo, 2013). Also in New Jersey, Egizi et al. (2014) found that mosquito feeding behavior in the spring may include fewer competent host species, an important factor in curbing seasonal WNV amplification.

Decreases in host biodiversity have been suggested to increase the success of pathogen transmission and cause areas with species-poor host communities to experience greater variance in epidemic size (Johnson et al., 2015b). The magnitude of change in WNV hosts among years was minor (<3%) for large wetlands. However, the two small fragments Polansky (PP) and Terrill (TE), respectively experienced 22 and 16% host population shifts during the three-year study period. Shifts in PP reflected the population dynamics of American Robin, while the decline in host RA observed in TE was attributed to reduced Common Grackle density. In New Jersey where these two species are temperate migrants, their population shifts likely reflect minor seasonal differences between their breeding and non-breeding distributions (Cornell Lab of Ornithology,
Because American Robin and Common Grackle were the most abundant competent hosts, these interannual differences could have significant implications for local WNV disease risk. American Robin, in particular, has been identified as a “super spreader” because even when the species occurs at low densities, they have served as the blood meal for ≥40% of WNV-infectious mosquitoes (Marm Kilpatrick et al., 2006; Egizi et al., 2014).

Avian assemblages in small forest fragments may experience more interannual variation than those in large simply because fluctuations in resource availability are felt more acutely in small patches, particularly if they are highly isolated and of low quality (MacArthur and Wilson, 1963; Andrén, 1994; Prugh et al., 2008). A review of urban avifauna diversity by Chase and Walsh (2006) suggests that urban environments favor seed eating birds, omnivores, and ground foragers. The competent WNV hosts presented here support their assessment, as all six species are ground-foraging omnivores or seedeaters. Chase and Walsh (2006) further identify traits that urbanization selects against, such as high canopy and foliage gleaners, bark gleaners, insectivores, and drillers. However, research by Rush et al. (Rush et al., 2014) highlights the importance of vegetation structure in supporting a diverse avian assemblage. Total richness between their study and ours was similar (65 vs. 68), but unlike their study, we found American Robin to be associated with shade-tolerant maple dominated canopies (Rush et al., 2014).

Habitat composition appeared to play a large role in shaping mosquito assemblage composition. The most abundant species, *Ae. vexans*, responded positively to hollow microtopography in areas that experience seasonal to semi-permanent inundation. Unlike competent WNV vectors, *Ae. vexans* relative abundance decreased with oak tree
dominance. For both groups, trends between mosquito composition and canopy structure were only apparent for dominant tree genera, not for stand basal area as a whole. In this respect, both competent vectors and hosts responded similarly.

The negative correlation between competent WNV vectors and *Ae. vexans* is intriguing and may suggest fundamental differences in niche requirements, or potentially interspecific interactions. Data collected with gravid traps further highlights their patterns of occurrences (Durland Fish and Carpenter, 1982; Crans, 2004; Schäfer and Lundström, 2006; Juliano, 2009; Rey et al., 2012). Total mosquito species richness observed here (29 spp.) was much higher than those reported by Chaves et al. (19 spp. 2011) or Wagner et al. (14 spp. 2007). The former study found that mosquito species richness was positively associated with habitat heterogeneity and noted that climatic variability appeared to have a negligible effect on mosquito richness. However, my results suggest that the interactions between mosquito richness and habitat structure are more complex in these urban wetlands.

**Conclusion**

The effect of urban wetland habitat structure can greatly influence the relative abundance of competent West Nile virus vector and host species. Wetland patch size appeared to have no significant effect on competent vector abundance, while interannual variance in hosts was more striking in small patches (<15 ha). In this system, American Robins were the most abundant competent hosts, and as a temperate migrant, this species’ abundance may be an important monitoring metric for WNV disease risk. In particular, competent hosts were more abundant in mature woodlands with open understories, which in this region, does not necessarily reflect patch size, but rather stand
age and the impact of over browsing by white-tailed deer. Human-modified flooding conditions have likely caused shifts in mosquito relative abundance, though more research is needed to understand how floodwater (e.g., *Ae. vexans*) and permanent standing water-breeding mosquitoes (e.g., *Culex*) respond to these perturbations.
References

ACJV. 2008. New England/Mid-Atlantic coast bird conservation region (BCR 30) implementation plan. Atlantic Coast Joint Venture (ACJV), Laurel, MD.


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with the New York 1999 strain of West Nile virus. Emerging Infectious Diseases 9:311-322.


with housing and landscape patterns across the USA. Ecological Applications 17:1989-2010.


Systat Software Inc. 2008. SigmaPlot. 11.2.0.5. San Jose California USA.


Table 1: Sampling intensity across years and fauna groups for each of the six wetland patches, which were grouped into three size classes: large; medium; and small. Avian surveys took place during the June-July breeding season, while mosquito surveys were conducted June through September. Calendar week numbers in brackets indicate the start and end of fauna sampling [start-end]. Wetland plant surveys were conducted during the 2008-2010 growing seasons.

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Large (&gt;125 ha)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dismal (DS)</td>
<td>15</td>
<td>45</td>
<td>15</td>
<td>15</td>
<td>2</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>Nomahegan/ Lenape (NL)</td>
<td>11</td>
<td>33</td>
<td>11</td>
<td>11</td>
<td>2</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td><strong>Medium (35-25 ha)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Evergreen (EV)</td>
<td>3</td>
<td>9</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>North Brunswick (NB)</td>
<td>3</td>
<td>9</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td><strong>Small (&lt;15 ha)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polansky (PP)</td>
<td>2</td>
<td>6*</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Terrill (TE)</td>
<td>2</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><strong>Total points</strong></td>
<td>36</td>
<td>108</td>
<td>29</td>
<td>29</td>
<td>8</td>
<td>22</td>
<td>10</td>
</tr>
</tbody>
</table>

*These data were averaged or comparisons with avian data.
Table 2: Avian species richness and relative abundance (% RA) of select categories of the avian assemblage were assessed for differences among the four groups. Macroplot tree basal area was significantly different among the groups, but no pairwise differences were observed. Guilds examined included year-round resident species that are also considered edge species (Edge + yr resident); bird species of conservation importance (RPSC: Regional Priority or Special Concern); Shrub nesting species; and RA of wetland and wetland associated birds (obligate, facultative wetland, facultative). Data are present as group means and standard error of the mean (SEM). See Appendix 4.1 for the full species list.

<table>
<thead>
<tr>
<th></th>
<th>B1: Open woodland</th>
<th>B2: Mature forest</th>
<th>B3: Open woodland/ freshwater marsh</th>
<th>B4: Mature forest</th>
<th>ANOVA F_{3,31}</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree basal area m^2/ha</td>
<td>Mean 23 SEM 6</td>
<td>Mean 31 SEM 9</td>
<td>Mean 20 SEM 13</td>
<td>Mean 38 SEM 6</td>
<td>3.604</td>
<td>0.024</td>
</tr>
<tr>
<td>Bird species richness</td>
<td>Mean 19 SEM 1</td>
<td>Mean 17 SEM 1</td>
<td>Mean 20 SEM 1</td>
<td>Mean 16 SEM 2</td>
<td>2.620</td>
<td>0.068</td>
</tr>
<tr>
<td>WNV hosts % RA</td>
<td>Mean 28^{ab} SEM 4</td>
<td>Mean 24^{a} SEM 2</td>
<td>Mean 17^{a} SEM 6</td>
<td>Mean 43^{b} SEM 3</td>
<td>10.255</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Edge + yr resident % RA</td>
<td>Mean 35^{ab} SEM 4</td>
<td>Mean 38^{a} SEM 2</td>
<td>Mean 26^{b} SEM 2</td>
<td>Mean 33^{ab} SEM 3</td>
<td>4.873</td>
<td>0.007</td>
</tr>
<tr>
<td>RPSC % RA</td>
<td>Mean 14^{a} SEM 3</td>
<td>Mean 31^{b} SEM 1</td>
<td>Mean 19^{a} SEM 1</td>
<td>Mean 11^{a} SEM 2</td>
<td>26.071</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Shrub nesters % RA</td>
<td>Mean 32^{a} SEM 15</td>
<td>Mean 26^{ab} SEM 6</td>
<td>Mean 55^{c} SEM 17</td>
<td>Mean 12^{d} SEM 6</td>
<td>37.106</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Wetland spp % RA</td>
<td>Mean 28^{a} SEM 4</td>
<td>Mean 17^{b} SEM 2</td>
<td>Mean 51^{c} SEM 3</td>
<td>Mean 6^{d} SEM 4</td>
<td>40.421</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Shared superscript letters indicate no difference (p > 0.05) between groups (ANOVA, Bonferroni adjustments).
Table 3: Mosquito species indicator values (IV) and Monte Carlo significance levels for five mosquito species identified as emblematic for their designated group using Indicator Species Analysis. AEVE was associated with group M1, CULEX with M2, and the remaining species were affiliated with M3 (Figure 11). The full species list is in Appendix 4.2.

<table>
<thead>
<tr>
<th>Code</th>
<th>Scientific name</th>
<th>Common name</th>
<th>Habitat</th>
<th>Uni-or multivoltine</th>
<th>IV</th>
<th>Monte Carlo p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>AECAT</td>
<td><em>Aedes canadensis</em></td>
<td>Woodland Pool</td>
<td>Wetland generalist</td>
<td>uni</td>
<td>95.5</td>
<td>0.016</td>
</tr>
<tr>
<td>AEJA</td>
<td><em>Aedes japonicus</em>&lt;sup&gt;1,2&lt;/sup&gt;</td>
<td>Rockpool</td>
<td>Container breeder, wetland or urban generalist</td>
<td>multi</td>
<td>83.2</td>
<td>0.012</td>
</tr>
<tr>
<td>AEVE</td>
<td><em>Aedes vexans</em>&lt;sup&gt;2B&lt;/sup&gt;</td>
<td>Floodwater &quot;Vexans&quot;</td>
<td>Freshwater swamp/ riparian</td>
<td>multi</td>
<td>44.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>COPE</td>
<td><em>Coquillettidia perturbans</em></td>
<td>Cattail</td>
<td>Freshwater swamp/ marsh</td>
<td>uni, but has multiple broods/year</td>
<td>85.5</td>
<td>0.087</td>
</tr>
<tr>
<td>CULEX</td>
<td><em>Culex complex</em>&lt;sup&gt;1&lt;/sup&gt;</td>
<td>White-dotted Northern House</td>
<td>Container breeder, urban generalist</td>
<td>multi</td>
<td>46.8</td>
<td>0.0618</td>
</tr>
</tbody>
</table>

<sup>1</sup>Competent vectors for West Nile virus disease transmission to humans.  
<sup>2A</sup>Nonnative invasive species;  
<sup>2B</sup>Naturalized nonnative species (Chaves et al., 2011).  
Figure 1: Three 50-m transects extending beyond the macroplot characterized coarse vegetation structure for the sample area. Cardinal directions were used for transect placement, north (solid line) or south (dashed line), which was alternated between macroplots.
Figure 2: Monthly precipitation and average temperature for the state of New Jersey for the duration of this study (ONJSC, 2015). Departure from normal represents departure from the *annual* normal, relative to data collected from 1981 to 2010.
Figure 3: Among the wetland size classes, plant species richness was the only study group to show significant differences (K-W: $H = 6.827$, $p = 0.033$). Large wetlands (>125 ha) contained greater plant richness compared to small patches (<15 ha), while medium wetlands (25-35 ha) did not differ significantly from either size class.
Figure 4: Avian richness was positively correlated with macroplot floristic richness ($F_{1,33} = 4.966, p = 0.033$). When wetland class size was taken into account, the positive correlation between bird and total plant richness was still present ($r_p = 0.346, p = 0.045$). In comparison, mosquito richness showed a negative trend with plant species richness ($F_{1,12} = 6.009, p = 0.031$). Symbols identify large (>125 ha), medium (25-35 ha), and small-sized (<15 ha) wetland fragments.
Figure 5: Life history traits for bird assemblages within six urban wetlands fragments that ranged by size class from large (>125 ha) to small (<15 ha). Dismal (DS, n = 15), the largest wetland, was sampled during the 2008-2010 breeding bird seasons, which Nomahegan/Lenape (NL, n = 11) was sampled 2008-2009. Medium sized wetlands (25-35 ha) were added to this study in 2010: Evergreen (EV, n = 3) North Brunswick (NB, n = 3). The smallest site, Polansky (PP, n = 1), was sampled all three years, and Terrill (TE, n = 2) in 2008-2009. Life history traits follow the Cornell Lab of Ornithology (2015) database (herbivorous = seed eaters).
Figure 6: Avian assemblages strongly reflected woodland canopy structure.  a) shrub nesting species were significantly more abundant when green ash trees were present (n = 13) in the canopy compared to areas lacking (n = 22) green ash trees (F$_1$,$_{33}$ = 5.259, p = 0.028).  b) as expected, forest interior birds’ relative abundance (RA) was significantly higher in mature forest stands (Basal area > 30 m$^2$/ha, n = 17) compared to early/mid successional stands (n = 18; Kruskal-Wallis: H = 5.730, p = 0.017). Within each graph, different letters indicate significant differences between the populations (p < 0.05).
Figure 7: a) The relative abundance (RA) of wetland associated birds was positively correlated with hydrophyte richness. b) In contrast, bird species of Regional Priority/Special Concern (RPSC) were negatively correlated with the local mean peak inundation depth (positive SEM lines are shown for both the y and x-axis). Wetland patches ranged in size: large (>125 ha): Dismal (DS) and Nomahegan/Lenape (NL); medium: Evergreen (EV) and North Brunswick (NB); and small (<15 ha): Polansky (PP) and Terrill (TE).
Figure 8: Cluster analysis of avian species’ relative abundance using Sorensen’s distance metric and flexible beta linkages ($\beta = -0.35$). Two large (>125 ha) wetlands were sampled: Dismal (DS, 2008-2010); Nomahegan/Lenape (NL, 2008-2009); and two small: (<15 ha) Polansky (PP, 2008-2010); Terrill (TE, 2008-2009). Two medium (<35 ha) wetlands Evergreen (EV) and North Brunswick (NB) were added in 2010, the last year the bird surveys were conducted. When applicable, relative abundance values were averaged across years.
Figure 9: Indicator species associated with levels of the avian hierarchical cluster analysis. Observed indicator values are in parentheses beside each species’ code. See Appendix 4.1 for the full species list.
Figure 10: *Aedes vexans* (AEVE) had the highest overall relative abundance (RA) of any mosquito species surveyed in this study. If multiple years were sampled at a given point, standard error of the mean (SEM) is presented with the mean value. a) AEVE relative abundance was negatively correlated with the relative dominance of oak tree basal area (BA; $F_{1,12} = 5.057, p = 0.044$). When mediated by wetland, the trend was still marginally significant (Pearson’s partial correlation: $r_p = -0.501, p = 0.081$). b) Although AEVE appeared to decrease with increasing habitat heterogeneity, this variable was heavily weighted by differences among wetlands. Wetland fragments ranged in size: large (>125 ha): Dismal (DS) and Nomahegan/Lenape (NL); medium: Evergreen (EV) and North Brunswick (NB); and small (<15 ha): Polansky (PP) and Terrill (TE).
Figure 11: NMDS ordination, combined with cluster and indicator species analysis were used to identify three distinctive mosquito assemblage groups. Plotted variables from the second axis include larval area (Axis 3: $\tau = 0.541$), green ash basal area (FRPE BA; Axis 1 ($\tau = 0.541$), and sample area habitat heterogeneity (Axis 3 $\tau = 0.512$). Significant indicator species identified included floodwater species *Aedes vexans* (AEVE), *Culex* (CULEX), *Ae. canadensis* (AECAT), and *Coquillettidia perturbans* (COPE). *Aedes japonicus* is an exotic species that breeds in container habitats. Group M3 includes the two sample points for wetland site North Brunswick (NB).
Figure 12: A second trap type was added for the 2011 mosquito trapping season. Baited gravid traps attract pregnant mosquitoes looking for an ideal habitat in which to deposit their eggs. Three wetlands were sampled during the 2011 season: Dismal (DS); Evergreen (EV); and Polansky (PP). Data represent species’ relative abundance (RA).

*Culex*: *Cx. pipiens* + *Cx. restuans*; AEVE: *Ae. vexans*; ANPU: *Anopheles punctipennis*. 
Figure 13: The relative abundance (RA) of competent West Nile virus (WNV) vectors (mosquitoes) and hosts (birds) varied annually within and among the six wetland patches. Each patch was placed into one of three size classes: large (>125 ha: DS, NL); medium (<35 ha: EV, NB); and small (<15 ha: PP, TE). Competent avian hosts included here were classified as having a reservoir competency index of >1 by Komar et al. (2003). Competent vector species included the *Culex* complex (*C. restuans* and *C. pipiens*), *Aedes albopictus*, *Ae. japonicas*, and *Ae. triseriatus*. Number of sample sites within each wetland (Avian n | Mosquito n): DS: 15|2*; NL: 11|2; EV: 3|2; NB: 3|2; PP: 1|2; TE: 2|2 (*In 2010, DS n = 4). Note the y-axes have different scales.
Figure 14: Unexpectedly, no trends were observed between WNV host and vector RA (i.e., a positive correlation). Wetland patch appeared to play a larger role in the RA of these groups. Data presented here are the sample points for which bird and mosquito sampling coincided (2009-2011); where multiple years were sampled, standard error of the mean is indicated (grey lines). Wetland fragments: large (>125 ha): Dismal (DS) and Nomahegan/Lenape (NL); medium: Evergreen (EV) and North Brunswick (NB); and small (<15 ha): Polansky (PP) and Terrill (TE).
Figure 15: Relative abundance (RA) of competent West Nile virus (WNV) amplifying hosts and vectors when grouped by wetland size classes: large (>125 ha: DS, NL); medium (<35 ha: EV, NB); and small (<15 ha: PP, TE). Data represent size class averages ± standard error of the mean (SEM); medium sites were added in 2010. Top: Avian data were collected 2-3 times within the breeding season (2008-2010). Bottom: Mosquito data shown here were collected weekly, June-Oct, using light traps, with an average of 17.6 ± 0.4 collections per year (2009-2011). See Appendices 4.1 and 4.2, respectively, for the full lists of bird and mosquito species considered competent hosts and vectors.
Figure 16: a) Relative abundance (RA) of West Nile virus (WNV) hosts relative to forest stand development. Early/mid: basal area (BA) <30 m²/ha; Late: BA > 30 m²/ha. b) When wetland site was accounted for, the trend between BA and host RA lessened. c) WNV host relative abundance increased with maple tree BA (note data transformations), β = 0.446. d) The proportion of exotic species in the local flora increased with increased maple dominance, β = 0.488. Dashed lines represent 95% confidence intervals. Wetland fragments (same symbols/colors used for b-d): Dismal (DS); Nomahegan/Lenape (NL); Evergreen (EV); North Brunswick (NB); Polansky (PP); and Terrill (TE). Where multiple years were sampled (Table 1), data represent sample point averages.
Figure 17: Top (log$_{10}$ scale): Even when the effects of wetland site were accounted for, a positive correlation was observed between the number of *Ae. vexans* mosquitoes and competent WNV vectors (See Appendix 4.2 for full list of species). Bottom: This trend was reversed, however, when data were converted to relative abundance (RA). Pearson’s partial correlation ($r_p$) was used to account for site effects.
Figure 18: Competent WNV vector relative abundance as related to tree canopy composition and habitat variables. a) 2010 data only; b) 2009 data only; c-f) if multiple years were sampled, data were averaged ± standard error of the mean (SEM). Line of best fit was included for $p < 0.10$ and 95% confidence intervals (dashed lines) were added where linear regression analysis was significant ($p < 0.05$). Pearson’s partial correlation analysis ($r_p$) was used where other effects appeared significant; b) controlled for site ($df = 5$); e) controlled for Site + Herbaceous cover, the latter was correlated with leaf cover ($df = 10$). Dismal (DS); Nomahegan/Lenape (NL); Evergreen (EV); North Brunswick (NB); Polansky (PP); and Terrill (TE). Data were collected using CDC Mini Light Traps.
Figure 19: The 2011 mosquito sampling season included large wetland DS (Dismal), medium-sized wetland EV (Evergreen), and small wetland PP (Polansky). Two styles of traps were deployed at two sample sites within each wetland: a light trap (also used 2009-2010) and a gravid trap (new for 2011). Gravid traps were designed to attract and trap *Culex* Complex species that have had a blood meal and are looking to oviposit (positive trap bias). Light traps present as a negative bias for host-seeking (not-yet-fed) individuals from the *Culex* Complex. No significant difference was detected in WNV RA between light (n = 6) and gravid (n=6) methods (Wilcoxon Rank: Z = -1.782, p = 0.094)
Appendix 3.1: Soil analysis from samples collected at the hydrology sampling points. Data represent wetland mean with standard error of the mean indicated in parentheses. Dismal (DS) = 4; NomLen (NL) = 3; Evergreen (EV) = 2; North Brunswick (NB) = 2; Polansky (PP) = 2; Terrill (TE) = 2. Macroplot site numbers are indicated in brackets [#] beside each soil texture class.

<table>
<thead>
<tr>
<th>Soil composition</th>
<th>pH</th>
<th>Elec conduct</th>
<th>% Organic carbon</th>
<th>% Sand</th>
<th>% Silt</th>
<th>% Clay</th>
<th>% OM</th>
</tr>
</thead>
<tbody>
<tr>
<td>DS</td>
<td>5.11 (0.18)</td>
<td>0.25 (0.06)</td>
<td>8.2 (2.2)</td>
<td>57 (7)</td>
<td>22 (5)</td>
<td>21.0 (4)</td>
<td>14 (4)</td>
</tr>
<tr>
<td>EV</td>
<td>5.05 (0.16)</td>
<td>0.27 (0.03)</td>
<td>9.6 (0.5)</td>
<td>48 (20)</td>
<td>40 (18)</td>
<td>13.0 (2)</td>
<td>17 (1)</td>
</tr>
<tr>
<td>NB</td>
<td>4.49 (0.14)</td>
<td>0.18 (0.02)</td>
<td>37.8 (7.4)</td>
<td>87 (8)</td>
<td>13 (8)</td>
<td>0.8 (0.3)</td>
<td>65 (13)</td>
</tr>
<tr>
<td>NL</td>
<td>5.40 (0.14)</td>
<td>0.32 (0.08)</td>
<td>13.8 (6.5)</td>
<td>63 (6)</td>
<td>27 (5)</td>
<td>10.3 (3)</td>
<td>24 (11)</td>
</tr>
<tr>
<td>PP</td>
<td>4.49 (0)</td>
<td>0.16 (0)</td>
<td>8.8 (0.4)</td>
<td>51 (6)</td>
<td>35 (7)</td>
<td>14.0 (1)</td>
<td>15 (1)</td>
</tr>
<tr>
<td>TE</td>
<td>5.43 (0.07)</td>
<td>0.28 (0.13)</td>
<td>10.5 (1.3)</td>
<td>49 (10)</td>
<td>37 (5)</td>
<td>14.0 (5)</td>
<td>18 (2)</td>
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</table>

<table>
<thead>
<tr>
<th>Macronutrients</th>
<th>P kg/ha</th>
<th>K kg/ha</th>
<th>% Total Kjeldahl N</th>
<th>NH₄⁺ mg/L</th>
<th>NO₃⁻ mg/L</th>
<th>Ca kg/ha</th>
<th>Mg kg/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>DS</td>
<td>45 (9)</td>
<td>189 (13)</td>
<td>0.41 (0.14)</td>
<td>29 (9)</td>
<td>12.0 (7.9)</td>
<td>3647 (1574)</td>
<td>513 (157)</td>
</tr>
<tr>
<td>EV</td>
<td>56 (10)</td>
<td>209 (3)</td>
<td>0.44 (0.01)</td>
<td>17 (5)</td>
<td>1.5 (0.5)</td>
<td>2614 (445)</td>
<td>495 (19)</td>
</tr>
<tr>
<td>NB</td>
<td>89 (2)</td>
<td>158 (6)</td>
<td>1.20 (0.26)</td>
<td>42 (3)</td>
<td>1.0 (0)</td>
<td>265 (68)</td>
<td>95 (7)</td>
</tr>
<tr>
<td>NL</td>
<td>64 (14)</td>
<td>133 (15)</td>
<td>0.54 (0.17)</td>
<td>28 (9)</td>
<td>8.3 (3.4)</td>
<td>3943 (167)</td>
<td>396 (54)</td>
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<tr>
<td>PP</td>
<td>115 (42)</td>
<td>154 (43)</td>
<td>0.43 (0.01)</td>
<td>32 (17)</td>
<td>15.5 (9.5)</td>
<td>712 (220)</td>
<td>176 (37)</td>
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<tr>
<td>TE</td>
<td>98 (16)</td>
<td>150 (17)</td>
<td>0.46 (0.08)</td>
<td>43 (22)</td>
<td>8.5 (6.5)</td>
<td>2167 (278)</td>
<td>258 (39)</td>
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<table>
<thead>
<tr>
<th>Micronutrients (mg/L)</th>
<th>B</th>
<th>Cu</th>
<th>Fe</th>
<th>Mm</th>
<th>Zn</th>
<th>Soil texture classifications [associated plot number]</th>
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</thead>
<tbody>
<tr>
<td>DS</td>
<td>0.83 (0.39)</td>
<td>8.12 (1.12)</td>
<td>268 (28)</td>
<td>20.8 (10.5)</td>
<td>22.2 (8.3)</td>
<td>Sandy clay loam [11,7], Loam [9], Sandy loam [4]</td>
</tr>
<tr>
<td>EV</td>
<td>0.60 (0.08)</td>
<td>9.45 (2.67)</td>
<td>445 (63)</td>
<td>70.1 (50.8)</td>
<td>43.5 (1.9)</td>
<td>Sandy loam [1], Silt loam [2]</td>
</tr>
<tr>
<td>NB</td>
<td>0.26 (0.01)</td>
<td>11.22 (1.41)</td>
<td>47 (23)</td>
<td>2.9 (0.3)</td>
<td>8.4 (0.3)</td>
<td>Loamy sand [1], Sand [2]</td>
</tr>
<tr>
<td>NL</td>
<td>1.01 (0.23)</td>
<td>13.05 (3.20)</td>
<td>356 (39)</td>
<td>52.7 (15.4)</td>
<td>29.0 (3.1)</td>
<td>Sandy loam [3, 5, 11]</td>
</tr>
<tr>
<td>PP</td>
<td>0.27 (0)</td>
<td>13.29 (2.58)</td>
<td>273 (47)</td>
<td>10.1 (2.8)</td>
<td>12.9 (3.9)</td>
<td>Loam [2], Sandy loam [3]</td>
</tr>
<tr>
<td>TE</td>
<td>0.65 (0.23)</td>
<td>7.97 (5.22)</td>
<td>416 (27)</td>
<td>25.1 (2.0)</td>
<td>29.1 (14.8)</td>
<td>Loam [1], Sandy loam [2]</td>
</tr>
</tbody>
</table>
Appendix 3.2: Soil analysis of potting soil and sand collected prior to the experiment as well as samples from the experimental treatments, which were all collected on the final day of the experiment. Electrical conductivity and potassium values are not reported because the KCl extraction invalidated the data. All nutrients are presented as ml/L.

<table>
<thead>
<tr>
<th>Initial</th>
<th>pH</th>
<th>P</th>
<th>NH$_4^+$</th>
<th>NO$_3^-$</th>
<th>Ca</th>
<th>Mg</th>
<th>B</th>
<th>Cu</th>
<th>Fe</th>
<th>Mn</th>
<th>Zn</th>
</tr>
</thead>
<tbody>
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<td>Sand</td>
<td>4.44</td>
<td>0.0231</td>
<td>0.129</td>
<td>0.303</td>
<td>6.123</td>
<td>1.1637</td>
<td>0.0183</td>
<td>0.0081</td>
<td>0.0393</td>
<td>0.0156</td>
<td>0.0024</td>
</tr>
<tr>
<td>Potting soil</td>
<td>4.08</td>
<td>3.795</td>
<td>16.055</td>
<td>31.346</td>
<td>317.10</td>
<td>175.74</td>
<td>0.0150</td>
<td>0.0093</td>
<td>0.3981</td>
<td>1.3380</td>
<td>0.3114</td>
</tr>
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<td>Experimental</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Control</td>
<td>4.46</td>
<td>2.6283</td>
<td>0.147</td>
<td>1.019</td>
<td>172.35</td>
<td>63.99</td>
<td>0.0981</td>
<td>0.0024</td>
<td>0.0525</td>
<td>0.2154</td>
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<tr>
<td>0 cm</td>
<td>4.82</td>
<td>2.0937</td>
<td>0.994</td>
<td>2.733</td>
<td>175.59</td>
<td>65.94</td>
<td>0.0039</td>
<td>0.006</td>
<td>0.0351</td>
<td>0.5931</td>
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<tr>
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<td>5.40</td>
<td>2.1261</td>
<td>1.076</td>
<td>3.462</td>
<td>171.42</td>
<td>63.78</td>
<td>0.0096</td>
<td>0.0021</td>
<td>0.0504</td>
<td>0.5571</td>
<td>0.0588</td>
</tr>
<tr>
<td>3 cm</td>
<td>4.22</td>
<td>1.3125</td>
<td>0.592</td>
<td>1.841</td>
<td>170.40</td>
<td>66.63</td>
<td>0.0048</td>
<td>0</td>
<td>0</td>
<td>0.6045</td>
<td>0.0258</td>
</tr>
<tr>
<td>5 cm</td>
<td>4.45</td>
<td>1.3113</td>
<td>0.185</td>
<td>1.822</td>
<td>169.14</td>
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<td>0.0009</td>
<td>0.0804</td>
<td>0.5205</td>
<td>0.1077</td>
</tr>
<tr>
<td>4 days</td>
<td>4.45</td>
<td>2.2605</td>
<td>0.389</td>
<td>3.496</td>
<td>166.68</td>
<td>64.50</td>
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<td>0.0012</td>
<td>0.1623</td>
<td>0.5322</td>
<td>0.0939</td>
</tr>
<tr>
<td>8 days</td>
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<td>1.6887</td>
<td>0.378</td>
<td>2.602</td>
<td>172.05</td>
<td>67.11</td>
<td>0.0054</td>
<td>0.0015</td>
<td>0.1200</td>
<td>0.6672</td>
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<td>0.0021</td>
<td>0.0105</td>
<td>0.6096</td>
<td>0.0546</td>
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Appendix 4.1: 2008-2010 breeding bird species list and life traits (Sensu Cornell Lab of Ornithology, 2015). Species considered competent host species for this study are indicated in bold. RPSC = regional priority concern; inc/dec indicates population trends. *Exotic nonnative species. Wetland use: obligate (OBL); facultative wetland (FACW); facultative (FAC); facultative upland (FACU); upland (UPL). Range: breeding (b); migration (m); wintering (w). Range: breeding (b); migration (m); and wintering (w).

<table>
<thead>
<tr>
<th>Bird Code</th>
<th>Common name</th>
<th>Scientific name</th>
<th>RPSC</th>
<th>Wetland use</th>
<th>Habitat</th>
<th>Diet</th>
<th>Foraging behavior</th>
<th>Nesting</th>
<th>Range</th>
<th>Edge inter</th>
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</thead>
<tbody>
<tr>
<td>AMCR</td>
<td>American Crow</td>
<td>Corvus brachyrhynchos (Brehm)</td>
<td>FACU</td>
<td>open woodland</td>
<td>omnivore</td>
<td>ground</td>
<td>tree</td>
<td>bw</td>
<td>both</td>
<td></td>
</tr>
<tr>
<td>AMGO</td>
<td>American Goldfinch</td>
<td>Spinus tristis (L.)</td>
<td>inc</td>
<td>UPL</td>
<td>open woodland</td>
<td>seeds</td>
<td>foliage gleaner</td>
<td>shrub</td>
<td>bmw</td>
<td>edge</td>
</tr>
<tr>
<td>AMRO</td>
<td>American Robin</td>
<td>Turdus migratorius (L.)</td>
<td>FACU</td>
<td>open woodland</td>
<td>insects</td>
<td>ground</td>
<td>tree</td>
<td>bmw</td>
<td>both</td>
<td></td>
</tr>
<tr>
<td>BAOR</td>
<td>Baltimore Oriole</td>
<td>Icterus galbula (L.)</td>
<td>RP</td>
<td>FACU</td>
<td>open woodland</td>
<td>insects</td>
<td>foliage gleaner</td>
<td>tree</td>
<td>bm</td>
<td>edge</td>
</tr>
<tr>
<td>BARS</td>
<td>Barn Swallow</td>
<td>Hirundo rustica (L.)</td>
<td>FACU</td>
<td>towns</td>
<td>insects</td>
<td>aerial</td>
<td>buildings</td>
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<tr>
<td>BEKI</td>
<td>Belted Kingfisher</td>
<td>Megaceryle alcyon (L.)</td>
<td>OBL</td>
<td>Lake/Pond</td>
<td>fish</td>
<td>aerial dive</td>
<td>burrow</td>
<td>bmw</td>
<td>NS</td>
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<tr>
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<td>bmw</td>
<td>both</td>
<td></td>
</tr>
<tr>
<td>BLPW</td>
<td>Blackpoll Warbler</td>
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<td>m</td>
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<td>Blue Jay</td>
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<td>ground</td>
<td>tree</td>
<td>bw</td>
<td>edge</td>
</tr>
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<td>BGGN</td>
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<td>foliage gleaner</td>
<td>tree</td>
<td>bm</td>
<td>edge</td>
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<tr>
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<td>Brown Thrasher</td>
<td>Toxostoma rufum (L.)</td>
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<td>shrub</td>
<td>bmw</td>
<td>edge</td>
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<tr>
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<td>Brown-headed Cowbird</td>
<td>Molothrus ater (Boddart)</td>
<td>UPL</td>
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<td>seeds</td>
<td>ground</td>
<td>tree</td>
<td>bmw</td>
<td>edge</td>
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<td>Canada Goose</td>
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<td>OBL</td>
<td>marsh</td>
<td>seeds</td>
<td>ground</td>
<td>ground</td>
<td>bmw</td>
<td>NS</td>
</tr>
<tr>
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<td>SC</td>
<td>UPL</td>
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<td>insects</td>
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<td>ground</td>
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<td>ground</td>
<td>ground</td>
<td>bmw</td>
<td>NS</td>
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<tr>
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<td>Cedar Waxwing</td>
<td>Bombycilla cedrorum (Vieillot)</td>
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<td>tree</td>
<td>bmw</td>
<td>edge</td>
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<tr>
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<td>Chipping Sparrow</td>
<td>Spizella passerina (Bechstein)</td>
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<td>bmw</td>
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<td>Quiscalus quiscula (L.)</td>
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<td>FACU</td>
<td>open woodland</td>
<td>omnivore</td>
<td>ground</td>
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<td>bmw</td>
<td>edge</td>
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<tr>
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<td>Common Yellowthroat</td>
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<td>shrub</td>
<td>bm</td>
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<td>NS</td>
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<td>insects</td>
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<td>bm</td>
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<tr>
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<td>Scientific name</td>
<td>RPSC</td>
<td>Wetland use</td>
<td>Habitat</td>
<td>Diet</td>
<td>Foraging behavior</td>
<td>Nesting</td>
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<td>insects</td>
<td>ground</td>
<td>cavity</td>
<td>bmw</td>
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<tr>
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<td>Fish Crow</td>
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<td>FACW</td>
<td>shore-line</td>
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<td>ground</td>
<td>tree</td>
<td>bmw</td>
<td>NS</td>
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<td>RP</td>
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<td>insects</td>
<td>shrub</td>
<td>bmw</td>
<td>edge</td>
<td></td>
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<tr>
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<td>Great Blue Heron</td>
<td><em>Ardea herodias</em> (L.)</td>
<td>SC</td>
<td>OBL</td>
<td>marsh</td>
<td>fish</td>
<td>Stalking</td>
<td>tree</td>
<td>bmw</td>
<td>NS</td>
</tr>
<tr>
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<td>Great Crested Flycatcher</td>
<td><em>Myiarchus crinitus</em> (L.)</td>
<td>RP</td>
<td>UPL</td>
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<td>insects</td>
<td>flycatching</td>
<td>cavity</td>
<td>bm</td>
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<tr>
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<td>Green Heron</td>
<td><em>Buto rides virescens</em> (L.)</td>
<td>RP</td>
<td>OBL</td>
<td>marsh</td>
<td>fish</td>
<td>Stalking</td>
<td>tree</td>
<td>bm</td>
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<tr>
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<td>Hairy Woodpecker</td>
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<td>cavity</td>
<td>bw</td>
<td>both</td>
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<td>HOFI</td>
<td>House Finch</td>
<td><em>Haemorhous mexicanus</em> (Statius Müller)</td>
<td>UPL</td>
<td>towns</td>
<td>seeds</td>
<td>ground</td>
<td>tree</td>
<td>bw</td>
<td>edge</td>
<td></td>
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<tr>
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<td>House Sparrow*</td>
<td><em>Passer domesticus</em> (L.)</td>
<td>UPL</td>
<td>towns</td>
<td>seeds</td>
<td>ground</td>
<td>cavity</td>
<td>bw</td>
<td>edge</td>
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<tr>
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<td>House Wren</td>
<td><em>Troglo dyes aedon</em> (Vieillot)</td>
<td>UPL</td>
<td>open woodland</td>
<td>insects</td>
<td>foliage gleaner</td>
<td>cavity</td>
<td>bm</td>
<td>NS</td>
<td></td>
</tr>
<tr>
<td>INBU</td>
<td>Indigo Bunting</td>
<td><em>Passerina cyanea</em> (L.)</td>
<td>RP</td>
<td>FACU</td>
<td>open woodland</td>
<td>insects</td>
<td>foliage gleaner</td>
<td>shrub</td>
<td>bm</td>
<td>edge</td>
</tr>
<tr>
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<td>Killdeer</td>
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<td>FAC</td>
<td>Grassland/shore</td>
<td>insects</td>
<td>ground</td>
<td>ground</td>
<td>bmw</td>
<td></td>
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<tr>
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<td>Mallard</td>
<td><em>Anas platyrhynchos</em> (L.)</td>
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<td>UPL</td>
<td>LakePond</td>
<td>seeds</td>
<td>dabbler</td>
<td>ground</td>
<td>bmw</td>
<td>NS</td>
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<td>Mourning Dove</td>
<td><em>Zenaida macroura</em> (L.)</td>
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<td>UPL</td>
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<td>seeds</td>
<td>ground</td>
<td>tree</td>
<td>bmw</td>
<td>edge</td>
</tr>
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<td>Northern Cardinal</td>
<td><em>Cardinalis cardinalis</em> (L.)</td>
<td>inc</td>
<td>UPL</td>
<td>open woodlands</td>
<td>seeds</td>
<td>ground</td>
<td>shrub</td>
<td>bw</td>
<td>edge</td>
</tr>
<tr>
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<td><em>Mimus polyglottos</em> (L.)</td>
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<td>UPL</td>
<td>towns</td>
<td>omnivore</td>
<td>ground</td>
<td>shrub</td>
<td>bmw</td>
<td>NS</td>
</tr>
<tr>
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<td>Northern Parula</td>
<td><em>Setophaga americana</em> (L.)</td>
<td>SC</td>
<td>FACW</td>
<td>forest</td>
<td>insects</td>
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<td>tree</td>
<td>bm</td>
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<td>NOWA</td>
<td>Northern Waterthrush</td>
<td><em>Parke sia noveboracensis</em> (Gmelin)</td>
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<td><em>Icterus spurius</em> (L.)</td>
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<td>insects</td>
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<td>bm</td>
<td>NS</td>
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<td>OVEN</td>
<td>Ovenbird</td>
<td><em>Seiurus aurocapilla</em> (L.)</td>
<td>dec</td>
<td>UPL</td>
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<td>ground</td>
<td>bm</td>
<td>interior</td>
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<tr>
<td>RBWO</td>
<td>Red-bellied Woodpecker</td>
<td><em>Melanerpes carolinus</em> (L.)</td>
<td>inc</td>
<td>UPL</td>
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<td>cavity</td>
<td>bw</td>
<td>both</td>
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<td>REVI</td>
<td>Red-eyed Vireo</td>
<td><em>Vireo olivaceus</em> (L.)</td>
<td>UPL</td>
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<td>foliage gleaner</td>
<td>tree</td>
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<td>interior</td>
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<td>RTHA</td>
<td>Red-tailed Hawk</td>
<td><em>Buteo jamaicensis</em> (Gmelin)</td>
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<td>UPL</td>
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<td>shrub</td>
<td>bmw</td>
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<td>RODO</td>
<td>Rock Pigeon*</td>
<td><em>Columbia livia</em> (Gmelin)</td>
<td>UPL</td>
<td>towns</td>
<td>seeds</td>
<td>ground</td>
<td>buildings</td>
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<td><em>Phoenicus ludovicianus</em> (L.)</td>
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<td>Common name</td>
<td>Scientific name</td>
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<td>Wetland use</td>
<td>Habitat</td>
<td>Diet</td>
<td>Foraging behavior</td>
<td>Nesting</td>
<td>Range</td>
<td>Edge inter</td>
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<td>tree</td>
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<td>NS</td>
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<td>cavity</td>
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<td>Meleagris gallopavo (L.)</td>
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<td>Worm-eating Warbler</td>
<td>Helmitheros vernivorum (Gmelin)</td>
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<td>bm</td>
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<td>Yellow Warbler</td>
<td>Setopha petechia (L.)</td>
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<td>edge</td>
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<td>Coccyzus americanus (L.)</td>
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<td>tree</td>
<td>bm</td>
<td>NS</td>
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<td>Yellow-shafted Flicker (N flicker)</td>
<td>Colaptes auratus (L.)</td>
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<td>edge</td>
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<td>Setopha dominica (L.)</td>
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<td>bark</td>
<td>tree</td>
<td>bm</td>
<td>NS</td>
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Appendix 4.2: List of observed mosquito species and their life history traits (sensu Crans, 2004; Chaves et al., 2011; Rey et al., 2012).

<table>
<thead>
<tr>
<th>Known common name</th>
<th>Species</th>
<th>Code</th>
<th>Environment</th>
<th>Wetland obligate</th>
<th>Habitat</th>
<th>WNV Competent</th>
<th>Reproduction</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Ae. abserratus (Felt &amp; Young)</td>
<td>AEAB</td>
<td>Natural</td>
<td>Yes</td>
<td>Swamp</td>
<td>Uni</td>
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<tr>
<td>Asian Tiger</td>
<td>Ae. albopictus (Skuse)</td>
<td>AEBL</td>
<td>Urban</td>
<td>No</td>
<td>Container</td>
<td>Yes</td>
<td>Multi</td>
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<tr>
<td>Brown Saltmarsh</td>
<td>Ae. cantator (Coquillett)</td>
<td>AECAT</td>
<td>Natural</td>
<td>Yes</td>
<td>Salt Marsh</td>
<td>Multi</td>
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<tr>
<td>Woodland Pool</td>
<td>Ae. canadensis (Theobald)</td>
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<td>Natural</td>
<td>Yes</td>
<td>Wetland</td>
<td>Uni</td>
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<tr>
<td>Little Smokey</td>
<td>Ae. cinereus (Meigen)</td>
<td>AEIC</td>
<td>Natural</td>
<td>Yes</td>
<td>Bog, Swamp</td>
<td>Uni</td>
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<tr>
<td></td>
<td>Ae. grossbecki (Dyar &amp; Knab)</td>
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<td>Natural</td>
<td>Yes</td>
<td>Swamp</td>
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<td>Ae. japonicus (Theobald)</td>
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<td>Ae. stimulans (Walker)</td>
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<tr>
<td>Black Salt Marsh</td>
<td>Ae. taeniorhynchus (Wiedemann)</td>
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<td>Salt Marsh</td>
<td>Multi</td>
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<td>Eastern Treehole</td>
<td>Ae. triseriatus (Say)</td>
<td>AETRS</td>
<td>Both</td>
<td>No</td>
<td>Container/Tree holes</td>
<td>Yes</td>
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<tr>
<td>Three Striped</td>
<td>Ae. trivittatus (Coquillett)</td>
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<td>Riparian, Swamp, Full/part forested</td>
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<td>Floodwater (&quot;Vexans&quot;)</td>
<td>Ae. vexans (Meigen)</td>
<td>AEVE</td>
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<td></td>
<td>Anopheles bradleyi (King)</td>
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<td>Brackish swamps</td>
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<td>Mottled-winged Anopheles</td>
<td>An. punctipennis (Say)</td>
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<td>Common Malaria</td>
<td>An. quadrimaculatus (Say)</td>
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<td>Bog, Swamp</td>
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<td></td>
<td>An. walkeri (Theobald)</td>
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<td>Swamp</td>
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<tr>
<td>Cattail</td>
<td>Coquillettidia perturbans (Walker)</td>
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<td>Marsh, Swamp</td>
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<td></td>
<td>Culiseta inornata (Williston)</td>
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<td>Cedar Swamp/Black-tailed</td>
<td>Cs. melanura (Coquillett)</td>
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<td>Bog, Swamp</td>
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<td>Cx. territans (Walker)</td>
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<td>Multi*</td>
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<td>Orthopodomyia signifya (Coquillett)</td>
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<td>Both</td>
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<td>Container/Tree holes</td>
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<td>Psorophora ciliata (Fabricius)</td>
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<td>Dark Ricefield</td>
<td>Ps. colombiae (Dyar &amp; Knab)</td>
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<td>White-footed Woods</td>
<td>Ps. ferox (von Humboldt)</td>
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1 Occurred at <25% of sample points.