Environmental factors influencing amphibian community assemblage in dune wetlands on the Lake Michigan coast

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Appendix D: Thesis Final Approval Form

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The signatures of the committee members below indicate that they have read and approved the thesis of <your full legal name> in partial fulfillment of the requirements for the degree of <Master of XXXX>.

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Abstract

Wetlands in dune landscapes provide important breeding habitat for amphibians along the Lake Michigan Coast. Unfortunately, these unique habitats and the corresponding amphibian metapopulations are understudied and threatened. We assessed amphibian species richness and terrestrial habitat type in 16 permanent and ephemeral wetlands along the coast of Lake Michigan in Grand Haven, MI. Wetland area, terrestrial habitat type, depth, hydroperiod, shade, and degree of isolation were measured from April to September of 2017. Nine species of amphibian were found; Green Frog (*Rana clamitans melanota*) and Spring Peepers (*Pseudacris crucifer crucifer*) were most abundant and Fowlers Toad (*Anaxyrus fowleri*) was rarest. Non-metric multidimensional scaling (NMDS) revealed that wetlands in open dunes and great lake barrens were more likely to contain American Toad (*Anaxyrus americanus*), and Leopard Frog (*Rana pipiens*) while forested wetlands were more likely to contain Wood Frog (*Rana sylvatica*), and Gray Tree Frog (*Hyla versicolor*). Least cost modeling (LCM) was used to determine the shortest path through navigable habitat between wetlands and provided an associated isolation score for each wetland ranging from 243—least isolated, to 928—most isolated. Isolation was significantly negatively correlated with species richness ($r = -0.29$), $p = 0.02$). There was also a positive correlation between hydroperiod, area, and depth (PCA, scaling =2). Non-parametric correlation testing showed a strong positive correlation between species richness and area ($r = 0.6$, $p = 0.014$) and hydroperiod ($r = 0.86$, $p < 0.001$). However, some small temporary wetlands situated in the open dunes harbored rare species not found in other wetlands. These findings highlight the importance of protecting all of these habitats from land development, fragmentation and degradation in order to conserve multiple species, as well as overall landscape connectivity of the system.

Table of Contents

List of Tables

List of Figures

Chapter 1 - Introduction

Introduction

Amphibians are currently the most threatened group of vertebrates on the planet (Cushman 2006, Wake and Vredenberg 2008) primarily due to habitat destruction, fragmentation, disease and global climate change (Sodhi et al. 2008). Amphibians have a fragile lifecycle with specific environmental requirements; habitat loss and fragmentation have forced a disconnect between habitat types required for different life stages, which results in higher risk breeding migration—specifically for amphibians with aquatic larvae (Becker et al. 2007). Due to their threatened status, amphibians are now the target of many conservation efforts, the bulk of which are centered around protecting and conserving vital breeding habitat, such as wetlands. Ecologically intact wetlands with low anthropogenic disturbance are positively correlated with amphibian species richness, but the habitat matrix around the wetland is also quite important. Fragmentation in wetland complexes can drastically reduce amphibian vagility and increases the chances of juvenile mortality during post-metamorphosis dispersal (Rothermel 2004, Becker et al. 2007, Sodhi et al. 2008). Wetlands are critical habitat for many species of amphibians, allowing for breeding and larval growth, via abundant food resources, but can also host amphibian predators (Babbit et al. 2003, Hecnar 2004). Ephemeral wetlands are only inundated for part of the year and provide a unique habitat to amphibians. Being generally free of fish predators due to periodic drying, these wetlands are ideal habitat for juvenile amphibians (Hecnar 2004).

The recent push for wetland protection has helped to slow the habitat destruction, but unfortunately over half of the wetlands in the world have been drained or converted for other uses since 1900 (Davidson 2014). In the United States, large wetlands are significantly more protected than smaller, isolated wetlands due to the legislative bias assuming that large, hydrologically connected wetlands are more biodiverse (Babbit 2005, Copeland 2016). Further understanding of how amphibians use ephemeral and permanent wetlands will aid in their conservation, and the future of wetland protection legislation.

Ephemeral dune wetlands are naturally highly disturbed habitats and can have unique community assemblages due to periodic drying. The relative abundance and diversity of amphibians found in these habitats varies based on a number of variables, both abiotic and biotic. Although biotic factors such as predation and competition play a role in shaping amphibian diversity, abiotic factors are generally regarded as being more influential (Hecnar 2004). Amphibian species richness in ephemeral wetlands is influenced by many variables, including wetland area, hydroperiod, spatial configuration and isolation, adjacent habitat type, and water quality which will affect wetlands differently depending on the regional climate and habitat type (Hecnar 2004). Dunes dominate the landscape along the Lake Michigan coast in West Michigan, providing a large area of habitat for a variety of organisms. Within these dune ecosystems low points of the parabolic dune structure will seasonally reach the water table and wetlands will form in the dunes. These ecosystems are usually free of fish as they are almost always groundwater fed and detached from lakes and streams. The surrounding habitat is mostly arid, and many are only seasonally inundated, however during the spring and summer months the vegetation and wildlife becomes quite diverse and abundant. The surrounding arid habitat makes amphibian mobility between wetlands difficult and transforms the wetland complex into a matrix of habitat patches and corridors. Unfortunately, ephemeral dune wetlands in West Michigan are understudied in the context of amphibian metapopulation dynamics and movement patterns. To our knowledge, this study is the first of its kind in West Michigan and represents a starting point in regard to amphibian conservation in Michigan dune habitats. Our study site, the Kitchel-

Lindquist-Hartger Dunes Preserve and surrounding area in Grand Haven, MI is an excellent example of ecologically intact dunes, that harbor many ephemeral wetlands. The close proximity to both the Grand River, and Lake Michigan also make it a unique system to study, and further research at this site and similar sites can help to verify the findings of this research.

Purpose

The purpose of this study is to assess amphibian species richness in a series of interdunal wetlands at Kitchel-Lindquist-Hartger Dunes Preserve and surrounding area, then correlate those findings with abiotic data gathered from the wetlands. Abiotic data analyzed included wetland area, depth and hydroperiod; terrestrial habitat type and associated wetland isolation specific to amphibian dispersal and migration capabilities; percentage of shaded habitat, and water quality. This study helps inform wildlife and land management on amphibian dispersal capabilities and movement patterns in a dune wetland complex and the associated effects of the landscape and wetland characteristics on amphibian biodiversity.

Scope

The scope of this study is limited to naturally occurring freshwater dune systems in West Michigan, and the species associated with the region. The results of this study may be used to infer amphibian behavior and community assemblage based on a host of abiotic variables that can be measured rapidly. The goal is to use this study as a framework for amphibian conservation and wetland protection in dune systems in West Michigan. Although directed at Michigan dune systems, the concepts of this research can be applied more broadly to freshwater dunes around the world.

Assumptions

Amphibians have the capability to move between the wetlands studied at least in some capacity, and that their ability to move through the habitat is directly controlled by the habitat type. In our isolation analysis within ArcGIS, we classified each cover type with a resistance value associated to amphibian dispersal capability. The ratio of these values was determined by expert opinion (via personal communication with Jennifer Moore, PhD). Multiple scales were tested to determine an isolation score using the Least Cost Modeling tool in ArcGIS before settling on the most conservative scale, 1-10. The isolation score was an average of the cost-distance values of each wetland to its nearest three neighbors in order to provide a more complete view of relative isolation in regard to the complex.

If amphibian larvae are present in the wetland, breeding population presence of that species is inferred. If amphibian calls are heard at a wetland, it is inferred that there is some sort of breeding population there.

The effects of certain variables were negligent on amphibian species richness and thus were not included in the analysis. pH was omitted from this analysis due to the low standard deviation of pH values between wetlands, as well as the range of values being within normal levels for Michigan amphibians. Water quality measurements including dissolved oxygen (%), turbidity, orthophosphate, and conductivity were also omitted from this analysis as there was no significant sources of pollution at any of the sites, and eutrophication was not present in any sites.

Hypothesis

We hypothesized that species richness would correlate positively with hydroperiod, depth and area; isolated wetlands will have lower species richness; and wetlands surrounded by forest, or close to the forest edge, will have greater richness.

Significance

This research is, to our knowledge, the first of its kind in Michigan and will help local agencies and land managers to make conservation decisions directed toward wetland protection and amphibian biodiversity. The study also lays the methodological framework for similar research to be done in other systems and our results point to a number of suggestions for additional follow-up research. Long term goals include using information from this study and future studies to build a case for legislative action for the protection of ephemeral wetlands along the lakeshore and in dune habitats.

Chapter 2 - Manuscript

Environmental factors influencing amphibian community assemblage in dune wetlands on the Lake Michigan coast

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Abstract

Wetlands in dune landscapes provide important breeding habitat for amphibians along the Lake Michigan Coast. Unfortunately, these unique habitats and the corresponding amphibian metapopulations are understudied and threatened. We assessed amphibian species richness and terrestrial habitat type in 16 permanent and ephemeral wetlands along the coast of Lake Michigan in Grand Haven, MI. Wetland area, terrestrial habitat type, depth, hydroperiod, shade, and degree of isolation were measured from April to September of 2017. Nine species of amphibian were found; Green Frog (*Rana clamitans melanota*) and Spring Peepers (*Pseudacris crucifer crucifer*) were most abundant and Fowlers Toad (*Anaxyrus fowleri*) was rarest. Non-metric multidimensional scaling (NMDS) revealed that wetlands in open dunes and great lake barrens were more likely to contain American Toad (*Anaxyrus americanus*), and Leopard Frog (*Rana pipiens*) while forested wetlands were more likely to contain Wood Frog (*Rana sylvatica*), and Gray Tree Frog (*Hyla versicolor*). Least cost modeling (LCM) was used to determine the shortest path through navigable habitat between wetlands and provided an associated isolation score for each wetland ranging from 243—least isolated, to 928—most isolated. Isolation was significantly negatively correlated with species richness ($r = -0.29$), $p = 0.02$). There was also a positive correlation between hydroperiod, area, and depth (PCA, scaling =2). Non-parametric correlation testing showed a strong positive correlation between species richness and area ($r = 0.6$, $p = 0.014$) and hydroperiod ($r = 0.86$, $p < 0.001$). However, some small temporary wetlands situated in the open dunes harbored rare species not found in other wetlands. These findings highlight the importance of protecting all of these habitats from land development, fragmentation and degradation in order to conserve multiple species, as well as overall landscape connectivity of the system.

Keywords: metapopulations, wetland conservation, dune ecosystem, landscape connectivity, community ecology

Introduction

Amphibian biodiversity is of increasing conservation concern due to the rapid decline in global amphibian species richness (Sodhi et al. 2008, Wake and Vredenburg 2008). Wetlands are critical habitat for many species of amphibians, allowing for breeding and larval growth, via abundant food resources, but can also host amphibian predators (Babbit et al. 2003, Hecnar 2004). Ephemeral wetlands are depressed areas in a landscape that become seasonally inundated with water and are home to a wide variety of plants and animals (Grootjans et al. 2008), these wetlands are only inundated with water for a portion of the year and serve an important role in maintaining amphibian populations. Periodic drying of these wetlands and pools creates a fish-free environment for amphibians, which allows for greater juvenile success due to the lack of predation (Hecnar 2004, Lowe et al. 2015). While steps are being taken now to protect amphibian habitat to prevent further loss of these organisms, over half (64-71%) of the wetlands in the world have been drained or converted for other uses since 1900 (Davidson 2014). Understanding and protecting remaining wetlands is now of critical importance to the survival of remaining amphibian populations.

The correlation between ecologically intact wetlands (low anthropogenic disturbance) and amphibian species richness is significant, and a fragmented habitat drastically reduces dispersal capability (Rothermel 2004, Becker et al. 2007, Sodhi et al. 2008). Ephemeral dune wetlands are naturally highly disturbed habitats and can have unique community assemblages due to periodic drying. Amphibian species richness in ephemeral wetlands is influenced by many variables, including wetland area, hydroperiod, spatial configuration and isolation, adjacent habitat type, and water quality which will affect wetlands differently depending on the regional climate and habitat type (Hecnar 2004). Ephemeral, and hydrologically isolated wetlands provide amphibians with important breeding habitat free from fish predators (Werner et al. 2007), and further understanding of these complex and chaotic environments will allow us to identify knowledge gaps and simplify interactions into a subset of predictive variables (Dale 2006). Despite mounting evidence that these habitats are of ecological importance to amphibians, research on populations in freshwater ephemeral dune wetlands, specifically in North America is lacking.

In the United States, large wetlands are significantly more protected than smaller, isolated wetlands due to the legislative bias assuming that large, hydrologically connected wetlands are more biodiverse (Babbit 2005, Copeland 2016). The relationship between habitat area and species richness is called the species-area effect (Wilson and MacArthur 1967) and is generally applied over wide spatial scales. The theory operates under the assumption that larger habitats promote greater species richness because these areas have greater habitat diversity. In wetlands, habitat area is a fundamental factor influencing amphibian community composition and significantly correlates with amphibian species richness in non-permanent wetlands (Hecnar and M'Closkey 1998, Babbit 2005). However, recent studies suggest that smaller, isolated wetlands tend to support a unique group of amphibians that are generally not found in larger wetlands, and also serve as important sources for recolonization in the event of a local extinction (Semlitsch et al. 1998, Snodgrass et al. 2000, Babbitt 2005).

Hydroperiod is another factor that can affect species richness and has been shown to be weakly correlated with wetland area, this is not a strong relationship however, and exceptions often exist to this (Snodgrass et al. 2000). Hydroperiod affects amphibian species richness and assemblage in wetlands because of the interspecies variation in amphibian larval development times, which can range from a few weeks to multiple years, and depends heavily on hydrologic regime (Pechmann et al. 1989). Wetlands with shorter hydroperiods tend to contain amphibians that develop rapidly and have a low tolerance for predation, resulting in a wetland with lower richness, but a unique assemblage not found in long hydroperiod wetlands (Baldwin et al. 2006). But, wetlands with shorter relative hydroperiods also tend to have lower species richness than permanent wetlands due to fewer species being able to fully develop in the shorter time frame. In this context, hydroperiod can have an even greater influence on species assemblage and richness than wetland area (Babbitt et al. 2003). This contrasts with the legislative view that permanent, hydrologically connected wetlands will contain species present in smaller, ephemeral, or isolated wetlands. However, to our knowledge, studies assessing the effect of hydroperiod on amphibian species richness have never been done in a freshwater dune system where the hydrologic regime tends to be more variable. Hydroperiod is also directly related to fluctuating water levels and increased occurrences of drought due to climate change, which can also strongly influence species composition in temporary wetlands (Croley et al. 1998).

In addition to hydroperiod, terrestrial habitat type can significantly influence amphibian community composition, dispersal and distribution (Dodd and Cade 1998, Marsh and Trentham 2001). Amphibians use both aquatic and terrestrial habitat, so landscape variation and barriers between wetlands are very important to distribution (Pope et al. 2000). Barriers to dispersal can increase mortality rates as well as decrease connectivity between populations of amphibians (Gibbs 1998, Hels and Buchwald 2001). Barriers can exist in many forms and can have a wide range of implications due to amphibian reliance on ecological connectivity (Hecnar and

M'closkey 1997). Species richness is positively correlated with canopy cover, number of nearby wetlands, and wetland area (Houlehan and Findlay 2003), providing further support the importance of connectivity. All amphibians have species-specific dispersal capabilities that can influence assemblage in wetland ecosystems, and juvenile dispersal is the primary driver of population connectivity in amphibians, so breeding site choice can have profound impacts on landscape connectivity (Preisser et al. 2001, Cushman 2006, Rothermel 2004). Regional forest cover has a strong correlation with amphibian species richness in wetlands within a larger forested landscape, the forest floor provides safe passage between wetlands and increases connectivity of amphibian populations (Findlay et al. 2001, Karraker 2009).

The local habitat type and vegetation at each wetland can have a significant effect on community composition as well. The extent and type of emergent vegetation and debris provides specific microhabitats for certain species, and higher variation in this debris and vegetation—usually associated with larger habitats—will provide for a wider range of species (Hecnar and M'closkey 1998, Bunnell and Zampella 1999). Connectivity is closely related to terrestrial habitat type, and also plays an important role in community assemblage and species richness. Habitats with a higher degree of connectivity will likely have higher species richness than more isolated habitats (Wilson and MacArthur 1967). Amphibian populations in wetland complexes are functionally connected, and permanent wetlands often serve as refugia for amphibians during the dry season and serve as important sources for recolonization of wetlands that have experienced a local extirpation (Marsh and Trentham 2001). This phenomenon, known as meta-population dynamics, is responsible for the regional persistence of many amphibians even with local extirpations from single wetlands.

Dunes dominate the landscape along the Eastern Lake Michigan coast. Within these dune ecosystems low points of the parabolic dune structure will sometimes reach the water table and wetlands will form in the dunes. These ecosystems are unique for a number of reasons; there are usually no fish in them as they are almost always groundwater fed and detached from lakes and streams, the surrounding habitat is mostly arid, and many are only seasonally inundated. The results from this study provide important information on how amphibians use wetlands in a dune habitat, and the influence of area, hydroperiod, terrestrial habitat type, and isolation on species assemblage. In this study, we assess amphibian species richness within a series of dune wetlands and correlate the findings with data gathered from the wetlands on hydroperiod, depth, spatial area, surrounding terrestrial habitat type, degree of isolation, and shade. We hypothesized that species richness would correlate positively with hydroperiod and area; isolated wetlands will have lower species richness; and wetlands surrounded by forest, or close to the forest edge, will have greater richness. The results from this study show a clear relationship between a variety of wetland variables and amphibian species richness. These findings can be used to inform amphibian conservation decisions in Michigan as well as potentially alter wetland protection legislation to include a variety of wetland types.

Methods

Study Area

This study was conducted from April to September 2017 at Kitchel-Lindquist-Hartger Dunes Preserve and adjacent land owned by the city—an area of roughly 150 acres in Grand Haven, Michigan (Fig 1). The study area is approximately 100m from Lake Michigan at its westernmost point and borders the Grand River on the southeastern edge. There is an abandoned sand mining pit that has flooded to create a large inland lake approximately 500m north of the sampling area. We sampled 18 seasonal and permanent dune wetlands, two of which were omitted from this study due to extremely short hydroperiod, and lack of amphibians, 16 wetlands were included in this analysis. The wetlands vary in size greatly (3-4800 m^2), are free from fish predation, usually contain water from early spring to late fall, and are all groundwater fed and hydrologically isolated from rivers and lakes. The sites have a variety of surrounding terrestrial habitat types including pine plantation, deciduous forest, open dunes, great lakes barrens (GL barrens) or a combination of habitat types.

Species Richness

Amphibian species richness was assessed in each of the wetlands using multiple methods. Call surveys were performed throughout the sampling period and carried out for 5-10 minutes upon arriving at each wetland, before doing anything else, to determine the presence of male frogs before physical sampling occurred, this typically took place early in the morning or at dusk. Visual surveys were done by a single researcher walking along the perimeter of the wetland and searching the riparian and emergent vegetation around them in a 2-m radius, with equal time being given to every 2-m stretch of wetland perimeter. Amphibians found during the visual surveys were captured by hand or dip net when possible unless positive identification was made without capture. Due to the disruptive nature of dip netting the perimeter of a wetland, and the high probability that the samplers actions will affect call frequency and sight survey results, the sampling of larval amphibians was done using dip nets at 2-m increments around the wetland perimeter *after* call and visual surveying had occurred. In addition to this, transects put in place through the longest part of the wetland were used for netting and visual encounter surveys in a 2-m zone around the transect in all directions, with equal time being given to each 2-m stretch. Larval amphibians unable to be identified in the field were anesthetized using clove oil and later identified in the lab using a taxonomic key (Altig and McDiarmid 2015). All sight surveying was coupled with pictures of each amphibian when possible for further review in the lab. In addition to call surveys conducted on site, a call monitor was placed at a subset of wetlands (7) that had the most activity based on preliminary sight surveys. Access was limited to one monitor for the sampling period, so it was moved between wetlands every 2-3 weeks in order to evaluate whether other monitoring techniques were missing any amphibians. The call monitor was programmed to record for 5 minutes at 7AM, 7PM, and 11PM in order to capture calls during active times. Egg mass sampling was also used in conjunction with call surveying to evaluate breeding activity. When found, egg masses were photographed and later identified in the lab using a taxonomic key (Altig and McDiarmid 2015). Presence/absence was determined at the end of the sampling season, and included amphibians found with all sampling methods used. All methods were carried out in accordance with Wilkinson's *Amphibian Survey and Monitoring Handbook* (2015).

Abiotic Factors

Staff gages were installed before the seasonal inundation occurred in each of the wetlands and were subsequently checked at every sampling event to monitor depth fluctuations throughout the sampling period. Hydroperiod was monitored throughout the year (April 2017-March 2018) and quantified as number of months inundated. Due to a drought in June of 2017 when many wetlands dried up temporarily, a subset of these wetlands have shorter hydroperiods than they would in a typical season. The area of each wetland was measured by walking the perimeter of the open water using the polygon function on a Garmin GPSmap 62sc handheld GPS receiver. Since the area was variable throughout the sampling period, measurements were taken during each sampling event which resulted in multiple area measurements comprising a range of values for each wetland.

Isolation Analysis

Wetland polygons were imported into ArcGIS from the GPS unit and terrestrial habitat type surrounding each of the wetlands was determined using the classify land cover features in ArcGIS via a high-resolution satellite map of Michigan. This provided the location and area of certain habitat types in relation to wetlands. Inspection of each wetland directly prior to sampling further validated habitat type surrounding the wetlands. The isolation analysis was done using least cost modeling (LCM) in ArcGIS 10.5.1. LCM works by assigning resistance values to habitat matrix cover types within ArcGIS and calculating the lowest cost route for an organism to travel between wetlands.

Resistance values range from 1-10 and are based on the habitat preference of amphibians. The higher the value the more difficult it is to for the organism to traverse a particular habitat type. All resistance values were obtained via expert opinion (personal communication, Jennifer Moore): deciduous forest = 1, pine forest = 3, great lake barrens = 8, and open dunes = 10. These resistance values were tested at multiple scales, using the same ratio (1:10, 1:100, 1:1000) with the least cost function in ArcGIS before settling with the most conservative scale, 1:10. Land cover data was obtained using the “classify land cover” feature in ArcMaps on our high-resolution satellite map: a computer training module was then used to identify exemplary areas of each habitat so that the program could recognize the habitat types based on reflectance of each pixel. The program was run after the training modules were completed and constructed a land cover map (Figure 1), in all cases terrestrial habitat type was ground truthed at wetlands.

In order to summarize the variable connectivity of each of our wetlands into one value, the distance (m) from each wetland to its nearest three neighbors if traveling through habitat corridors/navigable areas was averaged and used as an isolation score in statistical analysis (Snodgrass 2000, Bossuyt et al. 2003). Isolation scores were calculated; higher scores indicated a more isolated wetland, while lower scores were representative of a well-connected wetland (Table 2). All isolation scores are based on probability and further research is needed to confirm accuracy compared to actual amphibian dispersal.

Statistical Analysis

All data were tested for normality using the Shapiro-Wilk test, and transformed as necessary. In all cases the statistical program "R" was employed (R 3.3.1 Development Core Team 2016). Multivariate principle components analysis (PCA) was used to explore patterns in abiotic data collected throughout the sampling period (April-September). Non-metric multidimensional scaling (NMDS) using the Bray-Curtis distance metric, allowed us to explore degree of similarity or dissimilarity in amphibian community composition between the different wetlands and terrestrial habitat types. An analysis of similarities (ANOSIM) was used to determine if clusters were statistically different based on terrestrial habitat type, and SIMPER identified which species contributed most to differences in community structure between wetlands. Spearman's Rank-Order Correlation test was used to assess the relationship between wetland area and depth, wetland area and hydroperiod, hydroperiod and species richness, and isolation and species richness. Pearson's Product-Moment Correlation was used to analyze the relationship between area and species richness. Spearman's correlation was used for data that did not meet parametric assumptions, and Pearson's was used for data that did meet parametric assumptions. Welch's 2-samples t-test was used to assess whether species richness was higher in sites surrounded by or touching forest (n = 7), than in open dune or barrens sites (n = 9).

Results

Nine Anuran species were found throughout the sampling period, and no salamanders were found. The most common species found were Spring Peeper *(Pseudacris crucifer crucifer),* Green Frog *(Rana clamitans melanota),* Gray Tree Frog *(Hyla versicolor),* and Wood Frog *(Rana sylvatica)*. The rarest species found was Fowler's Toad *(Bufo fowleri)*, found at only one wetland (Table 1).

Output from the LCM analysis provide maps of the study site in relation to each wetland and show habitat resistance from the origin point. Isolation scores ranged from least isolated (243) to most isolated (928) (Table 2). Isolation was significantly negatively correlated with species richness (r = -0.29, p = 0.02).

A Sheppard diagram illustrated the relationship between observed dissimilarity and ordination distance, and determined it was significantly linear (R^2=0.99), allowing us to make strong assumptions regarding ordination distance at multiple scales. Sites were clustered into two main groups and several smaller groups based on amphibian species assemblage (Figure 2). These clusters were determined to be statistically significant (ANOSIM R = 0.7859, p = 0.03) with the right cluster dominated by sites in open dunes and the left in primarily forested or mixed habitat. Wetlands with the same species assemblage appear in figure 2 overlaid (wetlands GLB1, GD1, and PP1). Open dune, and GL barrens sites were typically lacking wood frog, and gray tree frog in comparison to deciduous and pine forest wetlands, as well as wetlands that bordered forest habitat. In contrast, American toad (*Bufo americanus americanus)* and leopard frog (*Rana pipiens)* were more likely to be found in open dune, and GL barrens sites than in forested habitat.

Although community assemblage between wetlands was significantly different, Welch's two sample t-test determined that there was no significant difference in species richness between forested sites and dune/GL barrens sites ($t = 0.51$, $df = 14$, $p = 0.62$).

The principle components analysis showed that hydroperiod, depth, and area were closely related to each other, while shade and isolation were mostly independent. Multiple points representing each site show the leftward trend along PC2 showing the increase in area and depth throughout the sampling period. Spearman's rank order test found a significant positive correlation between hydroperiod and species richness ($r = 0.86$, $p < 0.001$), and area and species richness ($r = 0.60$, $p = 0.014$).

Discussion

Out of the nine-species found at the dunes preserve during this study, only four were found at more than half of the sites (Table 1). These species are some of the most common amphibians in Michigan and it is not surprising that they were the most widely dispersed. Green Frog, Spring Peeper, Gray Tree Frog and Wood Frog dominated in wetlands that were well connected, as well as some of the more isolated wetlands. Spring peepers were found in the most habitat types, while Fowler's Toad preferred a relatively isolated open dune wetland with a short hydroperiod. This preference could be due to the lack of predation in these types of wetlands by more competitive species such as Green and Wood Frogs, which tended to be absent in open dune wetlands and are known to prey upon toad tadpoles (Petranka and Thomas 1995). All wetlands studied produced juvenile anurans, though limited numbers were seen and not all species breeding were accounted for as post-metamorphosis juveniles. No salamanders were found during this study, or in the past two years at the study area in related research. This is could be due to the low soil moisture content throughout the study area, as well as local habitat constraints and time of sampling.

Fowler's Toad, which is a species of special concern in Michigan, has only been reported to the Michigan DNR three times since 2011, and none of these locations were classified as supporting breeding populations. During this study we found a robust population of Fowler's Toad at one isolated wetland in the dunes preserve, with larval specimens as well as adults in large numbers. Finding a breeding population of these toads along the lakeshore was unexpected and represents a rare opportunity to conserve breeding habitat. Future surveys should be done to determine whether or not there are more breeding populations within the greater west Michigan dune systems, and if so, start to put protections in place in order to prevent further loss. These findings were reported to the Michigan DNR once confirmation of Fowler's Toad presence was officially made and represent a major finding in Ottawa county that could help protect these fragile ecosystems.

Isolation scores revealed that many of the wetlands that were spatially close, were functionally disconnected. For example, most of the open dune wetlands had higher isolation scores than their forested counterparts, despite being closer together. Seasonality and annual variances impose a temporal variability to isolation, and some wetlands will only be connected during certain times of the year and rely heavily on local climate and hydrology (Euliss et al. 2004). The higher isolation scores of open dune wetlands are due to the higher habitat resistance values for open dunes compared to forested habitat, these resistance values were based on expert opinion (via personal communication with Jennifer Moore, PhD), and are primarily based on assumptions of amphibian mobility through various habitat types. In nearly all isolation studies using least cost modeling, resistance values are estimated based on local landscape conditions and target organisms, as the analysis itself is probability based and needs genetic data and species-specific dispersal capabilities in order to be confirmed (Adriaensen 2003). However, least-cost modeling can still be an important tool to understand general landscape permeability and amphibian usage patterns, with this in mind we minimized our potential error by running the analysis at three scales using the same ratio and chose the most conservative scale to include in our multivariate analysis. Amphibians have highly permeable, moist skin that is sensitive to desiccation, which makes open dunes a barrier to their dispersal. Thus, open dunes represent the lowest quality amphibian habitat found in this study area with a resistance value of 10. Amphibians prefer more shaded or vegetated habitat instead, such as deciduous forests, pine forests, and even some parts of great lake barrens corridors, which are much more suited to amphibian movement due to the higher amounts of shade and moisture present in these habitat types (Marsh and Trentham 2001). Although no significant difference existed in species richness between terrestrial habitat types ($t = 0.51$, $df = 14$, $p = 0.62$), there were significant differences in community composition between terrestrial habitat types (Figure 2). Wetlands in the open dunes tended to be more ephemeral, but also contained significantly different assemblages that contribute to the overall amphibian biodiversity of the study area. Thus, these ephemeral wetlands must be considered for protection in both the context of increased habitat connectivity in high resistance habitat, as well as maintaining a diverse amphibian meta-community.

Michigan dune systems experience natural disturbance regularly due to their migrating nature and related successional pathways. Constantly shifting water levels near the lake cause ephemeral wetlands in the dunes to get larger and deeper, or dry up completely based on seasonality as well as annual variances. This constant disturbance and change opens up many ecological niches that are both temporally and spatially variable and are vital to maintaining regional biodiversity (Southwood 1977). Habitat type and variability can provide a templet for evolutionary change, that can help maintain genetic diversity within metapopulations and dispersed populations. T.R.E. Southwood developed a comprehensive theory on how habitat variability can drive evolution of life history characteristics and maintain genetic diversity. In this model, habitat is measured by the frequency of disturbances and the general level of adversity, all relative to a target organism—both in regard to generation time (temporal) and dispersal capability (spatial) (Southwood 1988). Since the dunes are constantly changing, ecological niches can be seasonal, and can also drive organisms to adapt to multiple life history strategies to take full advantage of a dynamic environment. In an environment where patchy distribution of organisms is common there are likely spatial variances in niche partitioning, highlighting the importance of microhabitat type and connectivity to overall persistence of amphibian populations, and their related genetic diversity.

Hydroperiod and area were found to be strongly correlated at the study site, which is partially due to the majority of larger wetlands occurring in the northern part of the study area, where the parabolic low points of the dunes tend to be much larger and more exaggerated resulting in deeper wetlands that are more likely to last through the drying period in the late summer and fall/winter. The relationship between hydroperiod and area also has an effect on species presence. When larval amphibians are able to overwinter at these sites it allows them to become larger and more competitive the following year, as well as being more likely to return to breed there again as adults due to relatively high site fidelity and low dispersal rates in temperate amphibians (Sinsch 1989, Blaustein et al. 1994). Second year larval amphibians were common in the larger northern wetlands and were primarily Green and Bull Frog tadpoles. Larger amphibian tadpoles are known to prey upon smaller tadpoles, and this could influence an adult amphibians' decision to breed at a wetland, as well as the viability of the first-year offspring (Petranka and Thomas 1995). In addition, the longer hydroperiod allows for more species to breed at these sites, due to the lack of temporal larval development constraints. Both hydroperiod and area were significantly positively correlated with species richness, which corroborates the results of past studies (Snodgrass 2000, Findlay et al. 2001, Babbitt et al. 2003, Babbitt 2005). However, hydroperiod was more strongly associated with species richness than area, suggesting that smaller wetlands with long hydroperiods can maintain a high species richness, comparable to that of large permanent wetlands. Although smaller, these long hydroperiod wetlands likely serve as refugia for amphibians during times of drought. This would serve to naturally increase species richness, based on immigration of species in need of habitat. Wetland DEC2 (Table 2) represents an ideal example. Species richness was higher in this relatively small wetland than in all wetlands except the largest northern wetlands in the study. In addition, DEC2 was also less isolated than many other wetlands which would allow for migration between sites in the event of a drought. Due to greater connectivity and longer hydroperiod, this small wetland served as an integral part of the wetland complex at the study site and highlights the importance of smaller wetlands with long hydroperiods in addition to large wetlands. In more isolated wetlands such as OD1, the effect of a longer hydroperiod on species richness was evident. This wetland had higher than average species richness, despite being the second most isolated wetland in the study (Table 2). Due to longer hydroperiod at this wetland which allowed for almost year-round access to food resources, it is likely that amphibians here are permanent residents of the immediate surrounding area since the cost of traversing between this wetland and other habitat types is likely extreme. Future research could address this and our assumptions of a metapopulation by quantifying gene flow between adjacent wetlands.

Conclusion

The results of this study show the importance of all of these wetlands to the overall health of the amphibian populations in the study area. These results are reminiscent of Wilson and MacArthur's results in their study of mangrove islands and the resulting conclusions in their Island Biogeographical Theory (1967). Although their theory was marine based, the same principles have been shown to apply to certain terrestrial systems as well using patch dynamics and ecological disturbance theory (Southwood 1977, Rozenweig 1995, Semlitsch et al. 1998, Snodgrass 2000, Hecnar 2004). A constantly changing and dynamic habitat, exemplified here in Michigan dune systems, is directly related to maintaining a variety of ecological niches, which in turn increase overall biodiversity (Southwood 1977). Large, permanent wetlands were shown to have the highest species richness, however rare species that were absent from these wetlands tended to occupy smaller, more ephemeral wetlands. In addition, small, long hydroperiod wetlands had higher species richness than many other wetlands of greater size, and likely serve as refugia to amphibians during periods of drought when other ephemeral wetlands are dry. This highlights the importance of protecting multiple types of wetlands to ensure conservation of many amphibian species, not just the most common. Current legislation would only protect three wetlands in this study, all due to their proximity to Lake Michigan or the Grand River, and none of the wetlands would be protected based on size (Natural Resources and Environmental Protection Act 1994). We propose that wetland protection regulations should include smaller, and ephemeral wetlands in addition to large, hydrologically connected wetlands in order to help conserve amphibian biodiversity. Freshwater dune ecosystems are a relatively rare type of habitat, and highly variable from year to year which leads to unique ecological communities in these areas. Michigan's dunes are among the most pristine in the world and should be conserved and protected for future generations to enjoy. Results from this study should help to inform conservation efforts for amphibians, by emphasizing the importance of preserving a complex and dynamic habitat mosaic overlooked by current laws and regulations. Future studies should be aimed at understanding gene flow and population connectivity in the context of immigration and emigration between breeding sites and measuring site fidelity of larval amphibians when they return to breed. This future research will help to confirm the existence of these organisms as a metapopulation rather than just a dispersed population. Dunes are dynamic ecosystems that change annually, and results from future research can provide a better understanding of habitat corridor uses in amphibians that are migrating to breeding sites and could also influence conservation efforts aimed at increasing landscape connectivity for target organisms.

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Table 1. Species found and frequency of occurrence during wetland sampling at Kitchel-Lindquist-Hartger Dunes Preserve and surrounding area from April-September 2017.

Species	# of wetlands present
Spring Peeper (*Pseudacris crucifer crucifer)*	14
Green Frog (*Rana clamitans melanota)*	13
Gray Tree Frog (*Hyla versicolor)*	11
Wood Frog (*Rana sylvatica)*	10
American Toad (*Anaxyrus americanus americanus)*	7
Chorus Frog (*Pseudacris triseriata triseriata)*	3
Leopard Frog (*Rana pipiens)*	3
Bull Frog (*Rana catesbeiana)*	2
Fowlers Toad (*Anaxyrus fowleri)*	1

Table 2. Abiotic variables and species richness in wetlands at Kitchel-Lindquist-Hartger Dunes Preserve during sampling from April-September 2017. Hydroperiod values reflect one year of observation April 2017 – April 2018. Isolation was rounded to the nearest whole number and is the average of the least cost distance from each wetland to its nearest three neighbors. Area was averaged throughout the sampling period and rounded to the nearest whole number.

Wetland	Terrestrial Habitat	Average Area (m^2)	Isolation score	Hydroperiod (months)	Shade %	Species Richness
OD1	Open Dune	910	895	9	0	5
OD2	Open Dune	467	928	6	0	2
OD3	Open Dune	143	648	3	0	3
OD4	Open Dune	197	581	6	0	3
GO1	GL Barrens/Open Dune	4259	642	12	5	7
GLB1	GL Barrens	439	291	8	10	4
GLB2	GL Barrens	134	880	3	70	2
GLB3	GL Barrens	96	446	3	40	2
GLB4	GL Barrens	2896	556	12	5	7
GD1	GL Barrens/Deciduous	266	243	8	70	4
GD2	GL Barrens/Deciduous	16	495	3	30	1
GD3	GL Barrens/Deciduous	123	572	3	20	4
DEC1	Deciduous	1161	442	12	5	4
DEC2	Deciduous	67	359	12	90	6
DEC3	Deciduous	2896	355	12	90	8
PP1	Pine Plantation	21	281	8	90	4

Fig 1. A map of wetland study sites and habitat types at Kitchel-Lindquist-Hartger Dunes Preserve and surrounding area, Grand Haven, MI.

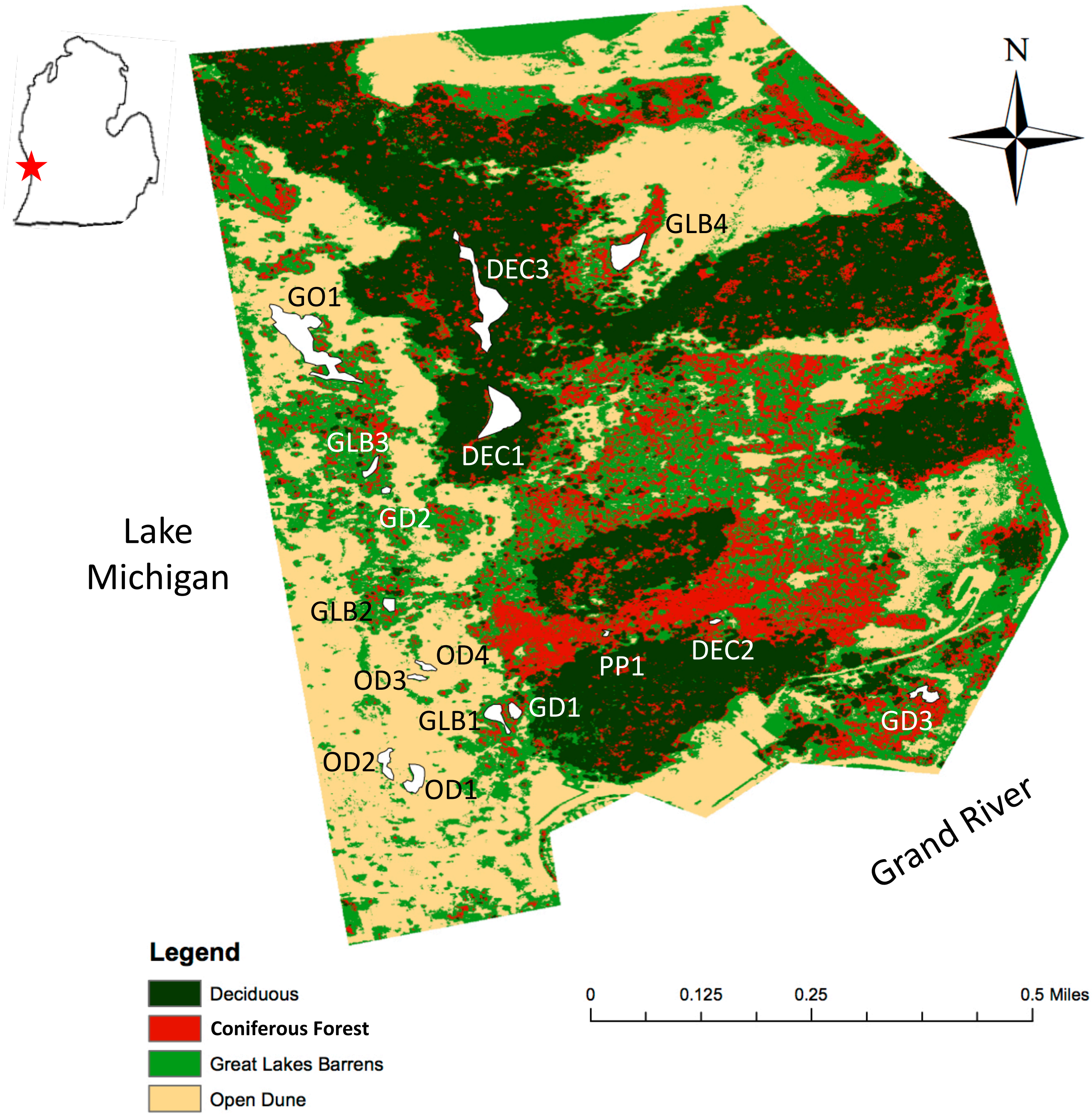


Fig 2. Non-metric multidimensional scaling of community assemblage in wetlands, scaling = 2. Sites spatially close to one another represent similar species assemblages. Habitat type clusters were significant and are delineated by symbol: X = open dune, O = great lake barrens, ◊ = great lake barrens/open dune, ∇ = great lake barrens/deciduous, + = deciduous, Δ = pine plantation. (*) denotes three wetlands with the same species assemblage: GLB1, GD1, PP1.

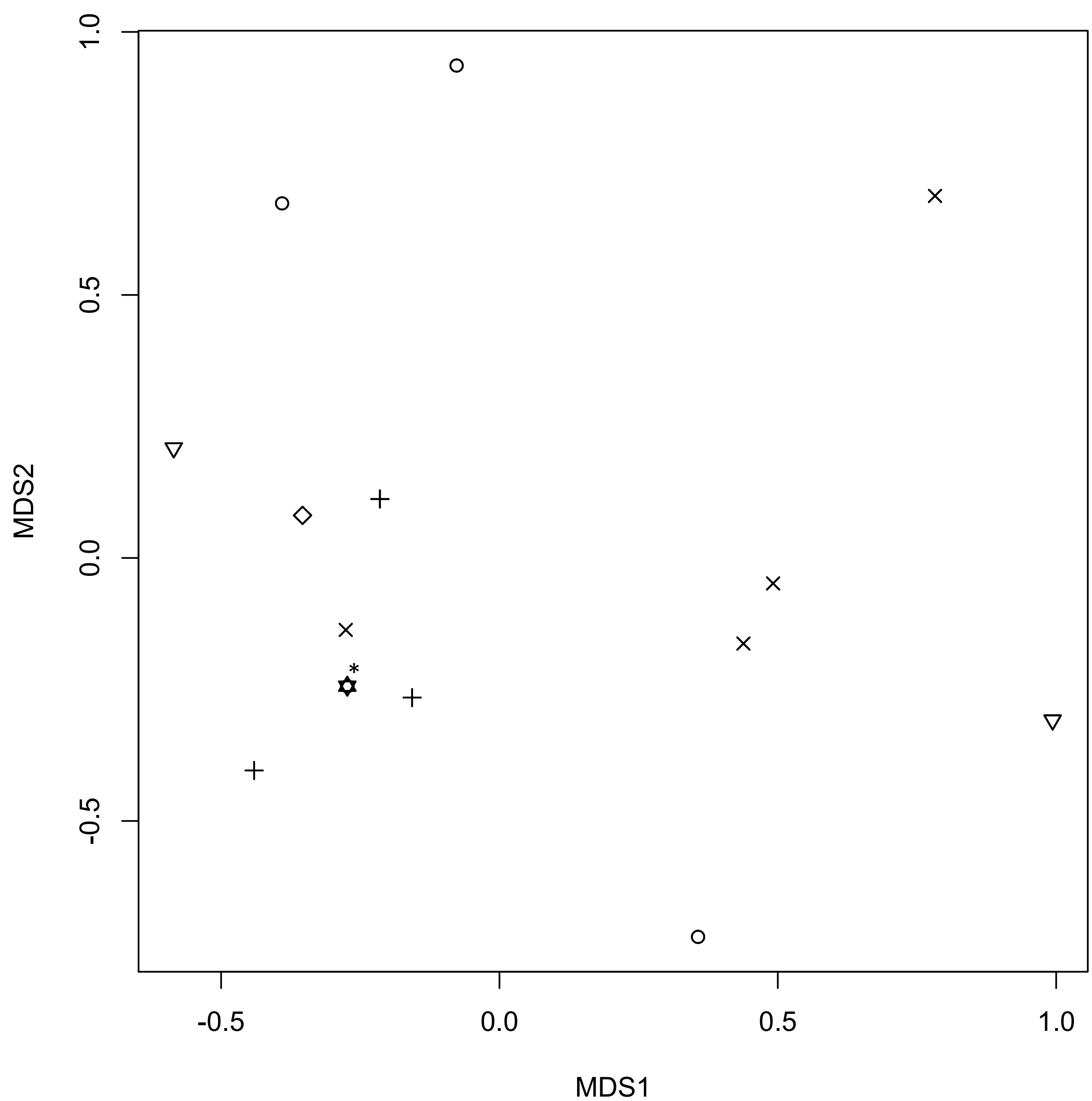


Fig 3. PCA of abiotic variables in relation to wetland sampling events. PC1 variance explained = 39.7%, PC2 variance explained = 31.9%. Points represent abiotic sampling events at wetlands, and vectors represent abiotic variables measured. There is a general leftward trend of sites through time, indicating that throughout the sampling period, wetlands tended to get larger and increase in depth. Overlapping site designations on the right hand side of the plot represent wetlands that experienced some abiotic change, but otherwise were fairly stable throughout the sampling period.

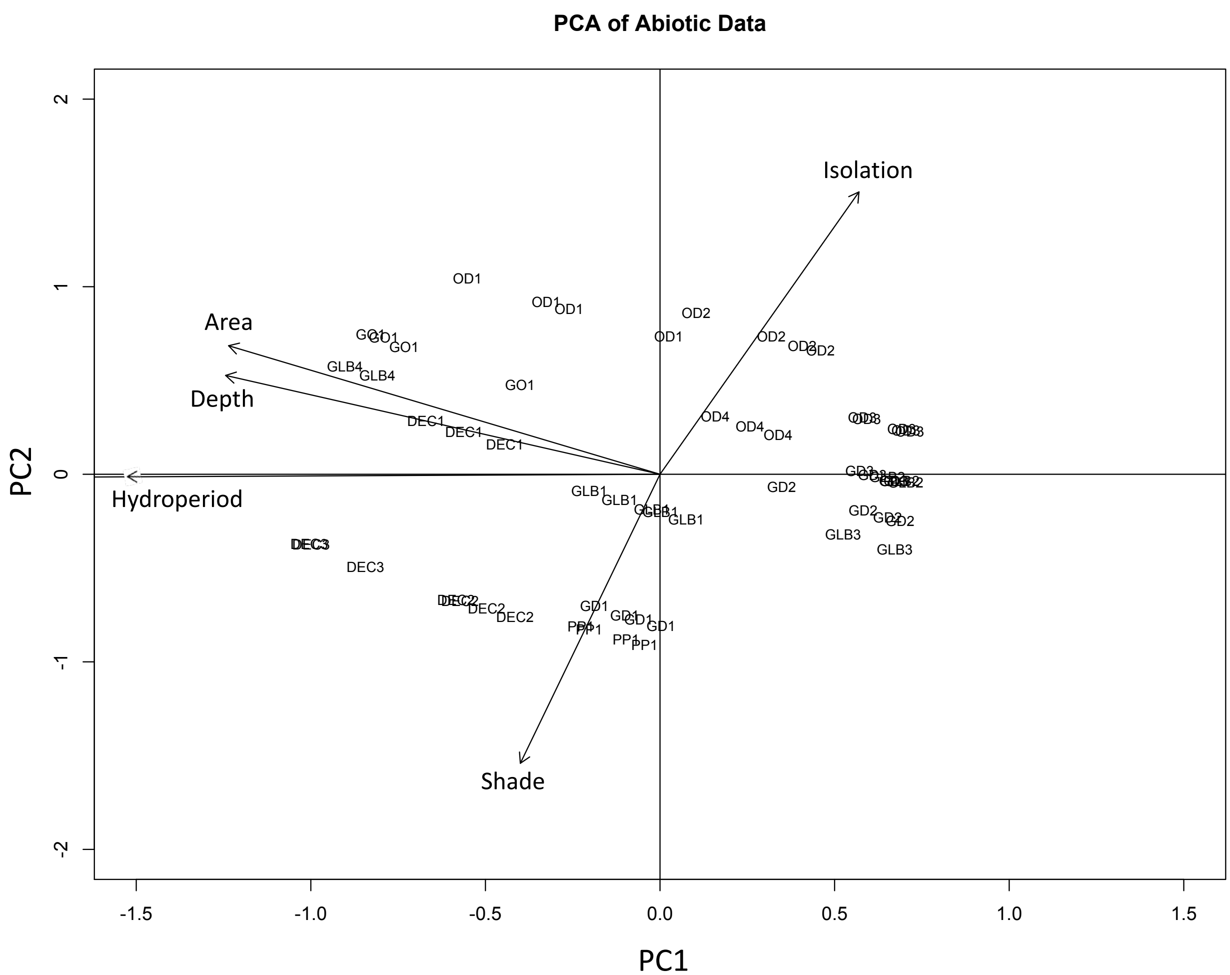
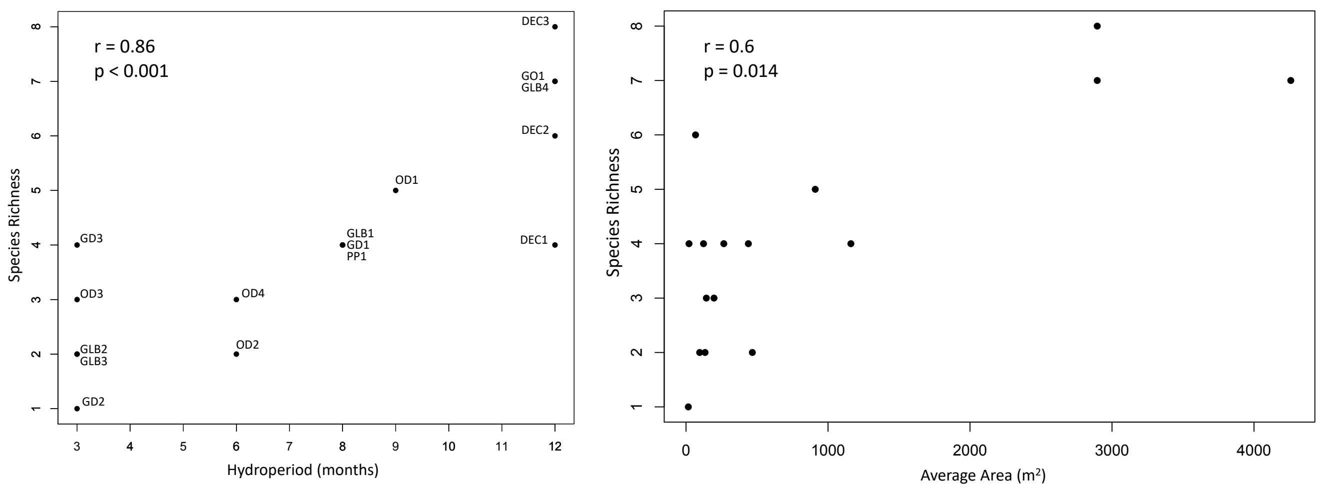


Fig 4. Relationship between species richness and hydroperiod, and species richness and average area at Kitchel-Lindquist-Hartger Dunes Preserve and surrounding area in Grand Haven, MI



Chapter 3 – Literature Review

Introduction

Amphibians are currently the most threatened group of vertebrates on the planet (Cushman 2006, Wake and Vredenberg 2008) primarily due to habitat destruction, fragmentation, disease and global climate change (Sodhi et al. 2008). Habitat destruction and fragmentation, combined with the naturally restricted ranges of amphibians has only further exacerbated the problem. Most of the habitat destruction that occurs in amphibian habitat is anthropogenic, and human population density positively correlates with a higher threat risk to amphibians (Sodhi et al. 2008). Ephemeral wetlands are only inundated with water for a portion of the year and serve an important role in maintaining amphibian populations due to the fish free environment that they provide for tadpoles (Hecnar 2004). However, over half of the worlds wetlands have been drained or converted for other uses since 1900 (Davidson 2014), which leaves the vast majority of amphibian breeding habitat under threat of destruction and degradation.

Amphibians have a fragile lifecycle with specific environmental requirements; habitat loss and fragmentation have forced a disconnect of habitat types required for different life stages, which results in higher risk breeding migration—specifically for amphibians with aquatic larvae (Becker et al 2007). Post-metamorphic dispersal contributes more to regional population persistence than adult dispersal does in amphibians (Sinsch and Seidel 1995, Preisser et al. 2000), and fragmentation causes juvenile dispersal to be limited, decreasing population connectivity in areas where landscape complementation between aquatic and terrestrial habitats is not strong (Rothermel 2004). Global climate change is one of the largest threats facing amphibians due to the indirect and direct effects that it has on the ecosystem (Hof 2011). Range shift, habitat alteration, food availability and local climate changes indirectly increase susceptibility of high risk species to go extinct (Sodhi et al. 2008).

Wetlands

Wetlands are excellent habitat for amphibians and are often clustered into a system of connected habitats, called a wetland complex. Isolated wetlands also exist and are important breeding habitats for some species (Semlitsch et al 1998). Wetland communities are essential to maintaining biodiversity because they tend to be hotspots for many species, amphibians included (Euliss et al. 2004). Ephemeral wetlands are depressed areas in a landscape that become seasonally inundated with water and are home to a wide variety of plants and animals (Grootjans et al. 2008). Amphibians are often found in seasonal wetlands and vernal pools, which provide excellent habitat at the right time of the year due to the lack of predation usually associated with temporary wetlands (Lowe et al. 2015). The relative abundance and diversity of amphibians found in these habitats varies based on a number of variables, both abiotic and biotic. Although biotic factors such as predation and competition play a role in shaping amphibian diversity, abiotic factors are generally regarded as being more influential (Hecnar 2004).

The correlation between ecologically intact wetlands (low anthropogenic disturbance) and amphibian species richness is significant, and a fragmented habitat drastically reduces dispersal capability (Rothermel 2004, Becker et al. 2007, Sodhi et al. 2008). Amphibian species richness in ephemeral wetlands is influenced by many variables, including: wetland area, hydroperiod, spatial configuration and isolation, adjacent habitat type, and water quality (Hecnar 2004). These variables affect wetlands differently depending on the regional climate and habitat type and unfortunately, research on amphibian populations in freshwater ephemeral dune wetlands in North America is lacking.

Wetland Protection

Wetland protection legislation in Michigan applies only to certain wetlands, the current criteria for protection and regulation apply if the wetland is any of the following: hydrologically connected or within 1000 feet to one of the Great Lakes or Lake St. Clair; connected to or within 500 feet of an inland lake, pond, river or stream; greater than five acres in size; or determined by the DEQ to be essential to the preservation of the state's natural resources (State and Federal Wetland Regulations, 2018). Even with these minimal protections in place, the property owner can still get a permit to drain and build on the wetland if the DEQ approves the permit, which leaves the vast majority of wetlands in Michigan under threat of destruction and degradation.

Spatial Area

The species-area effect has its roots in Island Biogeographical Theory (IBT), first described by Wilson and Macarthur in 1967. The theory center around islands and proposes that the number of species found in an undisturbed insular habitat or island, is determined by immigration and extinction/emigration on the simplest level. Immigration and emigration are dependent on barriers to dispersal, and distance to the source of colonization—known as the distance effect. Once an island is colonized, the species-area effect is what determines how many species can exist in the habitat. The species-area effect describes species diversity within a habitat based on the size of the habitat: larger areas of habitat will promote greater species richness and larger populations due to greater habitat heterogeneity (Wilson and MacArthur 1967). Although these concepts and the theory itself center around islands, it can also be applied to habitat patches in a matrix of inhospitable habitat as well (Rozenweig 1995). Emergent vegetation and shoreline features can also function to increase the area of hospitable habitat in a wetland by providing habitat that otherwise would be normal shoreline (Bunnell and Zampella 1999). Once considered to be the main factor attributing to species richness in wetlands, studies are now showing that there many more variables that affect ecological communities within wetlands. This being said, habitat area remains a fundamental factor influencing community composition in wetlands (Semlitsch et al. 1998, Hecnar 2004).

Hydroperiod

Seasonal wetlands can last less than a month, or most of the year (Babbit et al. 2000, 2003, 2005). The length of time that the wetlands are inundated with water is known as the hydroperiod, which can vary based on hydrology, geomorphology, and climate. Hydroperiod does not necessarily correlate with size (Snodgrass et al. 2000), and can be treated as a separate variable affecting amphibian species diversity. Hydroperiod has been shown by multiple studies to be as important, or more important than wetland size in determining species richness and abundance (Pechmann et al. 1989, Snodgrass et al. 2000, Babbit et al. 2003). Shorter hydroperiod usually favors species with rapid development and a low tolerance for predation—which tends to be lower in wetlands with shorter hydroperiod (Baldwin et al. 2006, Lowe et al. 2015). Longer hydroperiod is generally associated with greater species richness due to the range of developmental times for amphibian larvae while the wetland is inundated (Baldwin et al. 2006). Wetlands with a relatively shorter hydroperiod constrain amphibians to a narrow timeframe for breeding which only promotes certain species (Snodgrass et al. 2000, Babbit et al. 2003). In a study done in Ann Arbor, Michigan researchers found that wetlands with a shorter hydroperiod that are also hydrologically connected to a wetland with longer hydroperiod, will have a population that is represented in the wetland with longer hydroperiod (Werner et al. 2007).

Spatial dynamics and Isolation

The species-area effect tells us that a habitat in isolation will have less biodiversity than a habitat that is relatively closer to a source of recolonization, while maintaining the idea that isolated populations will usually have unique evolutionary assemblages due to the lack of immigration and emigration (Wilson and Macarthur 1967). Isolation, which decreases connectivity can be dependent on distance to other wetlands but also barriers to dispersal—such as inhospitable habitat, or areas with high predator density (Hels and Buchwald 2001). In wetlands, local extinctions are fairly common and organisms rely on recolonization from other wetlands in order to persist regionally (Hecnar 2004). Metapopulation spatial dynamics are of particular importance when assessing amphibian species richness in wetlands, due to the high rate of species turnover—especially seasonal wetlands (Hecnar 2004). Isolation from wetlands, and other bodies of water decrease the likelihood that fish will be present in the wetland, and fish presence greatly reduces amphibian species richness due to the high rate of predation (Werner et al. 2007). Isolation can serve an important role in amphibian species richness by allowing organisms to thrive under unique conditions partially removed from the threats that predation and competition pose (Snodgrass et al. 2000). Large isolated wetlands have also been shown to have an abundance of amphibian biomass, which challenges the idea of IBT that isolation decreases abundance (Gibbons et al. 2006). In isolated interdunal wetlands, the successional pathway moves slower, which can lead to a unique community assemblage in some cases (Bossuyt et al. 2003). Seasonality imposes temporal variability to isolation, some wetlands will only be connected during certain times of the year, these types of systems rely heavily on local climate and hydrology (Euliss et al. 2004).

Terrestrial Habitat Type

Terrestrial habitat type is important in temporary wetlands due to the impacts it has on dispersal and connectivity in an area that is only seasonally inundated (Dodd 1998, Houlehan 2003, Machado 2012). Amphibians are not uniformly distributed in the terrestrial environment around wetlands, instead they are more often found in habitat corridors or navigable areas that connect wetlands (Rittenhouse and Semlitsch 2007). Forested landscapes tend to be more friendly to amphibian dispersal than dry/arid habitat (Karraker 2009), and distance to forest edge, or upland type habitat from a wetland will have a profound impact on dispersal capabilities (Dodd and Cade 1998). In amphibians, population connectivity is primarily affected through juvenile dispersal (Cushman 2006), in a fragmented landscape terrestrial ecosystem type is very important to juvenile dispersal. One study found that fewer than 15% of all juveniles leaving a pond and traversing a pasture made it to the forest edge 50m away (Rothermel 2004). If distances are greater than this through inhospitable terrain, the percentage of juveniles reaching safe habitat would greatly decrease, emphasizing the importance of terrestrial and aquatic ecosystem connectivity in relation to dispersal.

Water Quality

General water quality effects both aquatic plants and animals, amphibians in particular have a unique relationship to the water they inhabit, due to their extremely permeable skin. Eutrophication, caused by nutrient enrichment, can be very problematic for amphibians indirectly. Eutrophication causes dissolved oxygen to decrease in the water and discourages biodiversity of invertebrates, which comprise a significant portion of amphibian diet (Boyer and Grue 1994). Embryo development is also inhibited by high levels of N and P in the water (Boyer and Grue 1994). Levels of NH3 are directly related to amphibian mortality, and pose a threat in wetlands where acid-base interactions favor that form of nitrogen (Boyer and Grue 1994). Amphibians are surprisingly tolerant of acidic conditions, with observed mortality increasing only below pH 4 (Pierce 1985). Alkaline conditions have been shown to have serious implications in larval development, or simply block larval development from occurring in some cases (Fominykh 2008). A lot of variation still exists on a species level though, and further research is needed in order to understand the complex relationships between various species and acidity in the environment. For example, the effects of pH could be subtle and have implications within amphibian food webs that are not readily apparent (Sadinski and Dunson 1992).

Conclusion

Amphibian diversity, and abundance are correlated with a number of environmental variables within wetlands, both biotic and abiotic. These variables account for differences in the way amphibians interact with their environment in the form of dispersal, breeding, and competition. Seasonal wetlands in particular are more dynamic than their permanent counterparts; terrestrial habitat type and isolation, wetland area, and hydroperiod account for most of the variation seen within amphibian community assemblages. Future studies should take a multi-method approach to obtain useful data on the factors controlling amphibian distribution and community assemblages within seasonal wetlands.

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