Plant Species Richness Determinants in Ephemeral Ponds and Permanent Wetlands

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ABSTRACT
Ephemeral ponds (EPs) are wetlands that dry seasonally and are common in the forests of northern Wisconsin. We examined relationships between several environmental factors and plant species richness (number of species) in 43 EPs and 14 permanent wetlands (PWs) located in the Chippewa Moraine State Recreation Area. We used multiple linear regressions to identify significant relationships between environmental attributes and plant species richness. PWs had higher plant species richness than EPs, possibly due to their larger size and more stable hydrology. In EPs, chlorophyll-a was positively related to plant species richness, while pH and water depth were negatively related. In PWs, pH and SRP were strong negative predictors of plant species richness. Species richness may have been higher in low pH wetlands due to the addition of acid-loving species. High chlorophyll-a (algae) in EPs may have indicated a decrease in light limitation for vascular plants. In PWs, high SRP may have decreased species richness due to the dominance of competitive plant species. Plant species richness was significantly higher in wetlands dominated by dry hummock compared to wet pool/flat-type microtopography in both wetland types. The stable water levels in PWs make microtopographic variation more important for small-scale richness. Our results indicate that EPs may not be as important for vegetation conservation as PWs, and EPs may not be as susceptible to phosphorus pollution as PWs. With climate change causing less frequent but more intense precipitation events, more generalist species may increase in all types of wetlands, but especially EPs.

Keywords: Plant species richness, ephemeral ponds, wetlands

INTRODUCTION
Ephemeral ponds (EPs) are temporary wetlands that host a uniquely adapted flora and fauna. EPs are typically found in low forested areas that fill with water in the spring time and dry up sometime during the summer (Colburn, 2004). Although isolated from permanent water bodies and typically quite small, EPs still contain amphibians, including a variety of frogs and salamanders, as well as invertebrates and plants (Colburn, 2004). Drying prevents
fish colonization so that both amphibians and invertebrates can flourish. EPs have some species in common with permanent wetlands (PWs), but they also have their own distinct biota.

Few studies have been conducted on the effects of abiotic factors on plant community species richness (number of species) within ephemeral ponds. Abiotic factors are nonliving aspects of an environment, such as temperature, pH, salinity, or light. In general, wetland plant species richness can be affected by wetland microtopography (sub-meter variation in morphology and elevation), nutrient availability (i.e. N and P), levels of chlorophyll-a (a measure of algae growth), changes in pH (a measure of acidity) and conductivity (a measure of total ions) due to hydrosoil inundation in the spring, and wetland area (Colburn, 2004). Although this study is limited to investigation of the within-wetland environment, dispersal, or the ability to move across the landscape, also likely affects species richness in these isolated wetlands (Boughton et al., 2010).

Wetland plant species richness tends to be positively correlated with surface area (Nicolet et al., 2004). Habitat patches of larger area tend to have more resources and niches than those of smaller area (Cain, Bowman, & Hacker, 2011). Because EPs tend to be small (Colburn 2004), we expected PWs to have higher plant species richness than ephemeral ponds. In addition, the alternating flood-desiccation cycle may provide a more challenging environment for plant growth in EPs.

Higher levels of available phosphorus (P) can be associated with greater species richness in wetlands because P is often a limiting nutrient in freshwater systems (Xu et al., 2007). However, elevated phosphorus may lead to eutrophication in freshwaters and an increase in algae production, which can be detrimental to aquatic plants by blocking sunlight (Khan & Ansari, 2005). Johnston and Brown (2013) found that chlorophyll-a, P, and conductivity were among significant variables used to distinguish plant community assemblages. At the wetland scale, we hypothesized that as P and chlorophyll-a increased, there would be a decrease in species richness due to light attenuation from algal competition. In relatively unpolluted systems, conductivity is often indicative of the nutrient status of the wetland; higher conductivity means more nutrient ions (phosphates, nitrates, and ammonium) are present. Therefore, we hypothesized that increased conductivity would also lead to decreased plant species richness.

Johnston and Brown (2013) found that pH was a significant factor affecting plant community composition. Furthermore, pH is a vital determinant of the variation found in wetland plant functional groups (Sekulová et al., 2011). With decreasing levels of pH (increasing acidity), nutrient availability
decreases and only plants which are able to obtain nutrients in other ways will thrive (Mitsch & Gosselink, 2007). In conjunction with our hypotheses regarding P and chlorophyll a, we hypothesized that pH and plant species richness will have a negative relationship; less acidic (higher pH) environments will be dominated by competitive plant species due to increased nutrient levels, thereby reducing wetland species richness.

Microtopographic features, such as small pools, logs, or hummocks, affect plant microhabitats (climate, sunlight, moisture availability, and organic matter) within wetlands and, in turn, influence species persistence. Studies on restored wetlands suggest that those with more microtopographic variation had higher species richness (Tweedy et al., 2001). Variation in microtopography leads to more niches being available for plant species and a wider variety of microenvironmental conditions. Plant diversity in created wetlands was positively related to tortuosity (amount of bend or twist) and elevation difference, both measures of microtopography (Moser, Ahn, & Noe, 2007). These studies support the hypothesis that microtopography (created by hummocks, logs, and stumps) will increase species richness in ephemeral ponds.

Water depth and hydroperiod (the duration of water in the wetland) also affect species richness. Shallower wetlands tend to have more species than deep wetlands (Cherry & Gough, 2006), perhaps due to more microtopographic variation. In addition, only specialized aquatic plant species can tolerate deep water environments (Mitsch & Gosselink, 2007). We hypothesized that wetland water depth would have a negative effect on plant species richness.

Although substantial work has been done on plant species richness-environment relationships in wetlands, little has been done in ephemeral ponds. We were particularly interested in the effects of environmental factors on plant species richness and whether EPs or PWs have higher species richness. Because little is known about EP plant communities, a multiple scale, multiple factor study was needed. Our study had multiple objectives. We aimed to determine 1) which type of wetland had higher species richness, permanent or ephemeral, 2) the important environmental predictors of plant species richness within EPs and PWs, and 3) the effects of microtopography on species richness at multiple scales.

**Methods**

**Study Site**

This study was conducted in 57 wetlands (39 EPs and 18 PWs) in the 1,856 ha Chippewa Moraine State Recreation Area of Chippewa County,
The region is part of a terminal glacial moraine (Syverson, 2007), and contains numerous kettles that support wetlands of different sizes and depths (Figure 1). EPs ranged in size from 0.03 to 0.51 ha with a mean size of 0.09 ha. PWs ranged in size from 0.15 to 3.7 ha with a mean size of 1.6 ha. The region is heavily forested with mid-successional Quercus spp. (oak) and Acer rubrum (red maple).

Vegetation Sampling

Plant surveys were conducted using quadrats (1 m²) sampled in a stratified random manner within each wetland. Quadrat spacing ranged from 3 to 30 meters and transect spacing ranged from 5 to 30 meters. The number of plots per wetland varied from 9 to 47 (depending upon wetland size), with a mean of 18.2 plots per wetland. Transect lines were arranged perpendicular to the hydrologic gradient or in a ring around larger, deeper wetlands. Plant surveys were conducted during the latter part of the growing season from late July through early September, 2013. In northern latitudes, wetland plant sampling typically occurs during this time period in order to capture maximum plant growth and number of species in both EPs and PWs. Within each plot, all plant species were identified to species. The total species richness for each wetland was calculated as the total number of different species identified in the quadrats.
Environmental Sampling

In the same quadrats as the plant surveys, we sampled environmental variables, including woody, litter, moss and bare ground percent-cover. Microtopography was assessed using quadrat microtopographic score (QMS). QMS was categorized 0 through 5 (Table 1), according to topographic position, which included a gradient from high hummocks to pools (Figure 2).

**TABLE 1**

<table>
<thead>
<tr>
<th>Quadrat Microtopographic Score</th>
<th>Structural Featured Represented</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Pool</td>
</tr>
<tr>
<td>1</td>
<td>Flat</td>
</tr>
<tr>
<td>2</td>
<td>Low Hummock</td>
</tr>
<tr>
<td>3</td>
<td>Hummock</td>
</tr>
<tr>
<td>4</td>
<td>High Hummock</td>
</tr>
<tr>
<td>5</td>
<td>Stump</td>
</tr>
</tbody>
</table>

**FIGURE 2**

Canopy cover was measured using a convex spherical densitometer. Water depth, peat depth, litter depth, and litter type (deciduous or graminoid) data were also collected in each quadrat. Nutrient levels and water chemistry parameters were assessed four times per growing season between May and early August, 2013. Conductivity and pH data were collected using a field Oakton PCTestr 35® meter at water surface in the three different locations of each wetland. In the same locations, mid-depth water samples were collected and processed in the laboratory for chlorophyll-a, total and soluble reactive phosphorus (SRP), ammonium, and nitrate concentrations. Samples for chlorophyll determination were filtered onto glass fiber filters (Gelman...
A/E, 2 µm nominal pore size) and extracted in 90% alkaline acetone. Viable chlorophyll and pheopigment concentrations estimated used the trichromatic equation (APHA 1999). Total and soluble reactive phosphorus were also processed according to APHA (1999) protocols, and nitrate and ammonium were sampled using ion-specific probes.

**ANALYSIS**

We used Welch’s t-test to compare plant species richness between PWs and EPs. Stepwise multiple linear regression was used to narrow down the suite of environmental variables that affect species richness, and then multiple linear regression was used to create models. We conducted regression analyses for EPs and PWs separately in order to determine whether the importance of different factors differed between the two wetland types. Linear regressions modeling the effects of microtopography on species richness were conducted at both the quadrat scale and the wetland scales. All statistical tests were completed using Minitab (2010).

**RESULTS**

**Richness in Ephemeral Ponds versus Permanent Wetlands**

PWs had a significantly higher mean richness of 32.9 (SE = 2.0) species, while EPs had 23.5 species (SE = 1.0, Figure 3). These means were significantly different (P = 0.001, t = 3.32, df = 29).

**FIGURE 3**

![Graph showing plant species richness in Ephemeral Ponds and Permanent Wetlands](image-url)
Predictors of Species Richness in Ephemeral Ponds and Permanent Wetlands

The best model for predicting species richness in EPs was richness = 142 - 18.4 pH + 0.342 chla - 0.207 depth (P < 0.001, F3,23 = 11.95, R2 = 60.9%). The best model for predicting species richness in PWs was richness = 139 - 17.2 pH - 24.2 SRP (P < 0.001, F2,12 = 16.66, R2 = 73.5%). pH was the only variable that significantly affected species richness in both EPs and PWs. Note that peat depth was significantly correlated with pH (r = -0.362, P = 0.006). In EPs, chlorophyll-a and water depth were also important. In PWs, SRP was also important (Figure 4). Although we measured both nitrate and ammonium forms of nitrogen, neither of these were important predictors for plant species richness in either EPs or PWs.

Microtopography Effects on Species Richness at Multiple Scales
The relationship between mean QMS and species richness among both EPs and PWs was significant and positive (in EPs, P = 0.007, richness = 7.0 + 10.5QMSmean, F1,37 = 8.03, R2 = 17.8%; in PWs, P = 0.002, richness = 12.5 + 14.2QMSmean, F1,13 = 14.44, R2 = 52.6%). There was a similar
relationship between QMS and species richness in both wetland types, as indicated by a similar slope to the regression models (Figure 5), although the QMS explained more species richness variability in PWs than in EPs.

**FIGURE 5**

Within-wetland QMS showed significant positive relationships with plant species richness in 37% of all wetlands. A higher proportion of PWs compared to EPs had significant within-wetland relationships between QMS and richness (Fisher’s Exact Test: \( P = 0.022 \), Figure 6).
SUMMARY

While QMS had significant positive relationships with species richness in both EPs and PWs, these relationships were stronger in the PWs. In addition, QMS was more important to species richness within PWs than EPs. The only environmental variable that was a significant predictor of species richness in both EPs and PWs was pH (Table 2).

<table>
<thead>
<tr>
<th>Factor</th>
<th>Effect on EPs</th>
<th>Effect on PWs</th>
</tr>
</thead>
<tbody>
<tr>
<td>QMS (among wetlands)</td>
<td>Significant positive</td>
<td>Significant positive</td>
</tr>
<tr>
<td>QMS (within wetlands)</td>
<td>Significant positive less often</td>
<td>Significant positive more often</td>
</tr>
<tr>
<td>Chlorophyll-a</td>
<td>Significant positive</td>
<td>n.s.</td>
</tr>
<tr>
<td>pH</td>
<td>Significant negative</td>
<td>Significant negative</td>
</tr>
<tr>
<td>SRP</td>
<td>n.s.</td>
<td>Significant negative</td>
</tr>
<tr>
<td>Water Depth</td>
<td>Significant negative</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

Discussion: Richness relationships between EPs and PWs.

PWs had higher mean plant species richness than EPs. This result was likely due to the smaller size of the EPs. Alternatively, their more ex-
treme environmental conditions may cause lower species richness. Generalist species may be the only plants that can tolerate the extreme hydrologic fluctuations in EPs. In an experimental study by Warwick and Brock (2003), amphibious plant species were found in all types of water regimes, but submerged and terrestrial plants only grew under specific conditions. Terrestrial plants did not grow well when subjected to long periods of submergence, while aquatic plants cannot tolerate prolonged desiccation (Warwick and Brock 2003). PWs may host all types of plants, whereas EPs host only tolerant plant species (i.e., amphibious generalist species). EPs may provide a poor habitat for submerged plants due to annual drying, as well as a poor habitat for terrestrial plants that germinate early in the spring before drying occurs.

**Environment-richness relationships**

The negative relationship observed between richness and pH for both EPs and PWs in this study may be due to pH effects or it may be a coincidental correlation. More flooded, deep ponds may have a higher pH due to dilution of hydrogen ions. Our study demonstrated a decrease in species richness with increased water depth, and these more pH-neutral ponds may have fewer plants because they are deeper water, not due to any specific effects of pH. A real effect of pH may have been seen because wetlands with lower pH had more peat accumulation, leading to the addition of more acid-loving species to the assemblages of plants.

Previous studies have reported positive feedback between SRP and chlorophyll-a in fresh waters, as P-limited algal growth increases with higher phosphorus concentrations (Mitsch & Gosselink, 2007). In the PWs from this study, SRP had a significant negative relationship with species richness. Phosphorus can limit rare species in wetlands (Venterink et al., 2003). The majority of wetlands in our research area had abundant phosphorus for plant growth. High phosphorus levels may encourage the growth of competitive species and discourage specialist, stress tolerant species (Güsewell et al., 2005).

In EPs, a significant positive relationship was observed between chlorophyll-a and species richness. This finding is atypical for freshwater lakes (Khan & Ansari, 2005), but may be explained by the characteristics of our particular system of wetlands. Chlorophyll-a increases with light and nutrient availability (Mitsch & Gosselink, 2007), which may be limiting in our system of EPs. The ponds are in a heavily forested setting and many have high canopy cover. Similar to water depth, light may not be limiting in PWs due to their larger size and lower canopy cover.

Water depth predicted richness in EPs only. Similar to Cherry and
Gough (2006), we found that mean seasonal water depth was significantly negatively correlated with plant species richness. The lack of relationship in PWs may be due to their lack of seasonal drying and the establishment and persistence of submerged and amphibious plants in these wetlands. For a deep-water-adapted plant to colonize and establish in an EP, we speculate that the pond would need to be flooded for several years. It is also possible that water depth indirectly affects plant species richness through other factors. For example, deeper ponds may dilute pH and SRP, provide a longer water column for light attenuation to occur, and would need more dramatically variable microtopography in order to create microhabitats of dry and wet areas.

Like other studies, we found that microtopography increased species richness (Tweedy et al., 2001; Okland at al., 2008). Microtopography creates a variety of microenvironments in which a variety of different plants can survive. A mixture of dry and wet areas in a wetland provides places in which plant species with a variety of life strategies (terrestrial, aquatic, or amphibious) can germinate and grow (Vivian-Smith, 1997). Due to light attenuation and gas exchange limitations, submerged aquatic plants need specialized adaptations (Mitsch and Gosselink 2007). At a certain depth, amphibious plants no longer survive, and only submerged plants remain. In our study, the deepest areas of ponds had no emergent plants, and occasionally were devoid of vegetation. Microtopography is critical for providing germination safe sites in PWs, but may not be as important within EPs due to their fluctuating water levels that provide a variety of habitats. PWs may depend more on microtopography to increase plant richness because their water levels do not fluctuate as much.

Implications and future directions

From the perspective of vegetation quality, EPs may not be as important to conserve as PWs. Their real value is likely in sustaining macroinvertebrate and amphibian populations. Harsh conditions in EPs may allow for only generalist, “weedy” plant species to persist. Richer plant communities may not be as viable in EPs due to interval drying and flooding. However, because EPs did not show a significant relationship with SRP, they may have a higher conservation value where flood mitigation is desired and fertilizer runoff from agriculture is present. The nature of EPs provides flood water catchments in the spring, but their natural plant communities are less affected by high phosphorus levels.

PWs’ significant negative relationship with both pH and SRP may make them more susceptible to effects from agricultural runoff. For this reason, PWs in areas with less surrounding agricultural land should have a
higher conservation value. In areas where agricultural runoff surrounds PWs, EPs could serve as a buffer to nutrient enrichment.

The flashy weather events predicted to increase with current climate change (IPCC, 2013) may lead to increased dominance of generalist species in EPs. It may also lead to generalist species invasion around the fluctuating edges in PWs. More intense but infrequent precipitation may cause more area in the wetlands to be suitable only for generalist species. Changes in weather patterns and consequently the hydrology of these systems may cause their plant community assemblages to change.

Future research will continue to examine plant species richness and how it is affected by additional factors, such as hydroperiod length or regional topography. There may also be plant species that are unique to EPs. The Chippewa Moraine Ephemeral Ponds Project is an ongoing five-year study. Field research, along with experimental research, is needed to more closely understand the nature of these systems. It is likely that a combination of multiple factors has strong relationships with plant species richness.
REFERENCES


Plant Species Richness Determinants in Ephemeral Ponds and Permanent Wetlands


