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Effect of Fire Suppression on Aquatic Invertebrates in Ephemeral Wetlands Embedded in Longleaf Pine Forests

An Honors Thesis submitted in fulfillment of the requirements for Honors in Biology

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Honors Director: Dr. Steven Engel

Abstract

It has been established for many years that longleaf pine forests require the ecological disturbance of fire in order to maintain a balanced ecosystem. However, a crucial part of these forests has become nearly excluded from prescribed burning. Ephemeral wetlands embedded within longleaf pine forests are a unique and dynamic seasonal habitat that provide homes, refuge, and breeding grounds for a large array of taxa. Past research suggests that fire suppression around ephemeral wetlands is causing harm to many species of amphibians and other herpetofauna, especially threatened species like the flatwoods salamander. However, other species have not been as well studied. This paper takes a deeper look into the impacts of fire suppression on wetlands by trying to understand how it affects a staple of the pond food chain: aquatic invertebrates. This experiment examined the decomposition rate by aquatic invertebrates of different types of leaf packs, including longleaf pine (Pinus palustris), wiregrass (Aristida stricta), and black gum (Nyssa sylvatica), as well as the different effects between an open canopy, representing a fire sustained ecosystem, and a closed canopy, representing a fire suppressed ecosystem. Although the decomposition rates were unaffected, invertebrate abundance and diversity were higher in the plots with open canopies, showing that more research needs to be conducted in order to understand proper fire management strategies for ephemeral wetlands.

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Introduction

Ecological disturbance plays a significant role in shaping the overall health of an ecosystem. According to the intermediate disturbance hypothesis, with the presence of some disturbance a single species cannot dominate, and species richness and diversity are at their peaks (Townsend et al., 2003). In the southeast United States, many forests rely on the disturbance of fire that occurs naturally every one to ten years (Chandler et al., 2017). In longleaf pine forests, fire reduces competition, controls disease, stimulates succession and production, and releases nutrients back into the soils (Outcalt, 2008). However, due to the poor connotation of fire, suppression of fire became popular in the 1900s. The effects of fire suppression on upland forests have been well-documented since then, but other effects have been far less studied. Pine flatwoods are a type of longleaf pine forest that are found in low-lying areas with poor drainage, resulting in shallow temporary wetlands (Means 1996). Little is currently known about how fire suppression has affected these wetland ecosystems.

A history of fire suppression has caused altered vegetation structures in upland forests surrounding ephemeral wetlands. Historically, wetlands had a relatively open canopy due to most of it being burned away, as well as a high density of herbaceous vegetation as a result of ecological succession and sunlight availability (Bishop and Haas, 2005). The lack of fire creates a dense woody midstory, causing an increase of canopy cover and a decrease of herbaceous vegetation (Kirkman, 1995). This change of leaf litter input could potentially affect aquatic invertebrates that act as the base of the food web and are the main decomposers of the ecosystem (Wiggins et al., 1980). The effect of the alteration of leaf litter on aquatic invertebrates has not been well studied (Jones et al., 2010), so it is important to determine this impact (Chandler et al., 2017).
To understand how ephemeral wetlands are affected by fire suppression, this paper will begin by reviewing past literature about why ephemeral wetlands and fire management are important. Much research has been conducted on fire suppression and upland forests, but more research needs to be done on how it affects wetlands. An experiment was conducted using aquatic invertebrates, different types of leaf packs including longleaf pine (Pinus palustris), wiregrass (Aristida stricta), and black gum (Nyssa sylvatica), and different canopy levels to demonstrate if there is a direct impact of fire suppression on ephemeral wetlands.

A previous study showed that invertebrates may be more abundant in areas with less canopy coverage and higher herbaceous vegetation, characteristics of an ecosystem managed with fire (Chandler et al., 2015). Therefore, it is hypothesized that there will be a higher abundance and diversity of aquatic invertebrates and a higher decomposition rate in the litter packs located in the open canopy coverage plots, showing that they respond positively to fire management and are negatively impacted in a long-term fire suppressed habitat.

Literature Review

Importance of Ephemeral Wetlands

Ephemeral wetlands are a type of temporary, seasonal isolated wetland that develop in shallow topographic depressions surrounded by an otherwise flat landscape. These wetlands are a dynamic habitat that have both wet and dry periods, providing a unique aquatic community (Chandler et al., 2015). They rely on precipitation events in late winter and early spring to fill the depression with water, followed by a loss of water through evapotranspiration resulting in being completely dry by mid to late summer (Semlitsch et al., 1996). Wetlands are important features for both humans and the natural world. Some benefits include increased water quality
and pollutant removal, flood prevention, support of a high biodiversity, and linking aquatic and terrestrial environments (Mitsch and Gosselink, 2000). In the southeastern United States, isolated wetlands include: Carolina bays, pocosins, Coastal Plains ponds, gum ponds, cypress domes, sinkhole wetlands, woodland vernal ponds, inter- and intra-dunal wetlands, natural ponds, and excavated ponds (Tiner, 2003). Because there is a large variety of isolated wetlands, generalizations may not be completely applicable for all types of wetlands (Jones et al., 2010).

Many animals spanning across a large array of taxa rely on the presence of ephemeral wetlands for survival. Although not well represented in peer-reviewed studies, mammals and birds have been observed using temporary wetlands. Seasonal ponds can provide foraging areas for bats (Wilhide et al., 1998) and refuges for black bears (Richardson and Gibbons, 1993) and smaller mammals like bobcats and marsh rabbits (Monschein, 1981). Clark et al. (1985) detected 40 species of mammals in pocosins and Carolina bays. Seasonal drying of isolated wetlands concentrates prey (Ogden et al., 1976), attracting important waterfowl and other avian species, including the endangered wood stork (Coulter and Bryan, 1993). These wetlands can also often support large wading bird rookeries and can act as a place of refuge to bird species during periods of drought (Moler and Franz, 1987; Richardson and Gibbons, 1993). Mamo and Bolen (1999) estimated that approximately 70 percent of temperate forest avian species in North Carolina were observed in the Carolina bays.

Herptiles are the vertebrates that are most commonly associated with isolated wetlands. The rotation of wet and dry phases creates unique ecological challenges for aquatic species, and many have developed adaptations to persist through dry periods, such as retreating below ground, reaching a life stage that is resistant to desiccation, or simply leaving the wetland (Williams 1985). The dry periods cause seasonal ponds to lack large predatory fish, removing a
significant source of predation (Wilbur, 1980). This has led many amphibian species to adapt specifically to breed in temporary ponds where predation pressure on larvae is low (Wellborn et al., 1996). At least ten anuran and five salamander species located in the southeastern Coastal Plains rely on the presence of ephemeral wetlands for breeding (Moler and Franz, 1987; Russell et al. 2002) Past surveys have shown that herpetofaunal species in ephemeral wetlands embedded in longleaf pine forests have high species richness. Dodd (1992) demonstrated that at least 16 amphibian and 26 reptile species use temporary ponds in northern Floridian longleaf pine sandhills communities. A survey conducted by Wigley et al. (1999) examined 444 seasonally flooded ponds spanning over 35 counties in north Florida, south Alabama, and south Georgia, and identified a total of 16 salamander, 24 anuran, 34 reptile, and 37 fish species. This includes some species that are more fragile in number, such as the federally threatened flatwoods salamander that relies on ephemeral wetlands as a breeding ground (Bishop and Haas, 2005).

Aquatic invertebrate communities in ephemeral wetlands are often complex. They reach high densities and function at multiple trophic levels. Most invertebrates are near the base of the food web and are very important contributors to the ecosystem (Wiggins et al., 1980). Not only do they provide a food source for many species in the wetland and surrounding upland forest, but several also act as decomposers. Most primary consumer invertebrates consume the leaves that fall from the surrounding trees, which keeps the wetland clear of material and releases nutrients into the system (Wiggins et al., 1980). High population densities, a reduction in predation pressure, and the ecological challenges of living in a very dynamic environment can also lead to the development of a diverse amphibian/aquatic invertebrate community where they may compete with each other, or even prey on one another (Wiggins et al., 1980; Batzer and Wissinger, 1996). Even though they are a crucial part of the ecosystem, aquatic invertebrates are
not as well studied as other organisms in terms of longleaf pine forest disturbance. Aquatic invertebrates are critical components in ephemeral wetlands, and it is important to understand how this group responds to changes in their environment (Chandler et al., 2015).

**Importance of Fire**

According to the intermediate disturbance hypothesis, all communities are subject to disturbances that exhibit different frequencies and intensities (Townsend et al., 2003). As the name implies, an intermediate amount of disturbance should allow a community to be at its highest biodiversity and species richness (Townsend et al., 2003). Longleaf pine forests in the southeast require the occasional presence of fire in order to stay balanced (Christensen, 1981). Early historical records indicate a high frequency of fire in the southeastern United States, which was most likely contributed from Native American activity and lightning (Christensen, 1981). Although fire suppression was once popular during the 1900s, the importance of fire in longleaf pine forests has since been widely recognized across the scientific community, and prescribed burnings have since been established. Most longleaf pine forests in the southeast are now regularly burned approximately every 1-4 year(s) (Clewell, 1989). Prescription burning often takes place during the winter and spring months because it is easier to keep the fire contained (Bishop and Haas, 2005). Although this takes care of the upland forest, burning during the colder months presents a problem for ephemeral wetlands. Naturally, a higher number of fires would typically occur in a forest during peak lightning season, from May to August (Robbins and Myers, 1992). During the summer, ephemeral wetlands are dry and the vegetation surrounding the basin can be burned. However, winter prescription burning takes place when wetlands are in the wet phase and burning becomes much more difficult. Managers and fire personnel may be reluctant to include the burning of wetlands into their fire-management plans due to the
misconception that not burning them is a form of protection and conservation, or possibly because of the desire to avoid muck fires. When loose, organic material under the top layer of soil ignites, it produces muck fires, which can burn for weeks at temperatures of more than 500 degrees Fahrenheit and produce noxious fumes, making them difficult to extinguish (Watts and Kobziar, 2012). To avoid producing muck fires, firebreaks often being plowed around the perimeters of wetlands, causing fire to never reach the wetlands. Ultimately, many ephemeral wetlands often end up going years without getting the burning they need.

After years of fire suppression, many wetlands in the southeast are likely now very overgrown (Huffman and Blanchard, 1991). According to Skelly et al. (1999), canopy overgrowth can lead to local population extinctions and loss of diversity in aquatic ecosystems. Closed canopies create shade, which decreases the amount of understory vegetation, dissolved oxygen concentration, and water temperature. This can diminish growth, development, and survivorship of many species.

It is very important to understand the impacts that this accidental fire suppression has on ephemeral wetlands and the organisms that reside in them so that we can make the proper conservation approaches in the future. An experiment was conducted to examine the decomposition rate by aquatic invertebrates of different leaf pack types, including longleaf pine, wiregrass, and black gum, as well as the different effects between an open canopy, representing a fire sustained ecosystem, and a closed canopy, representing a fire suppressed ecosystem. It is hypothesized that there will be a higher decomposition rate of litter packs and aquatic invertebrates will be more abundant and diverse in open canopy coverage plots, showing that they respond positively to fire management and are negatively impacted in a long-term fire suppressed habitat.
Experimental Design

Study Sites

Three wetlands were chosen at random on Eglin Air Force Base in Okaloosa County, Florida (Figure 1). Eglin AFB contains over 146,000 hectares of actively managed longleaf pine forests. It was important to conduct this experiment during the winter months so the wetlands would be filled in order for aquatic invertebrates to be present. Areas of open and closed canopy were chosen, and canopy cover was estimated by measuring a grid of points on the survey plot with a Cajanus tube. All leaf packs were deployed in November 2015. Early retrieval of leaf packs at 24 days from one pond occurred in December 2015. All other packs were removed after 104 days in February 2016.

Figure 1. General location of studied wetlands located on Eglin Air Force Base.

Leaf Litter Pack Decomposition

To determine how a change in leaf litter input affects aquatic invertebrate communities, three types of leaf litter packs were used containing 15.0g of either dried longleaf pine (*P. palustris*) needles, wiregrass (*A. stricta*), or black gum (*N. sylvatica*). All three wetlands received a set of three leaf litter packs, one of each type, in both open and closed canopy coverage plots.
One of the wetlands received a second set of litter packs that was removed after only 24 days, whereas all other litter packs were removed 104 days after insertion (Figure 2). Once removed, all litter packs were washed with ethanol to displace and remove aquatic invertebrates. The packs were then dried and burned for one hour at 500°C. The ash-free dry mass of each was then determined.

**Figure 2.** Three different types of leaf packs, represented by the three colors light blue, royal blue, and orange, placed in three wetlands in areas of both open (white) and closed (grey) canopy coverage. Leaf packs remained for either 24 or 104 days.

**Aquatic Invertebrate Sampling**

All aquatic invertebrates were removed from the leaf litter packs before the packs were dried. The invertebrates were kept in ethanol and then organized and totaled taxonomically based on appearance under a microscope. Once totaled, the data was used for further statistical analysis to determine species abundance and diversity.

**Statistical Analysis**

The ash-free dry mass was determined by subtracting the mass of the ash from the total final dry mass. The percent remaining/g was divided by the number of days the pack was in the wetland to find the rate constant k. The days to 99% loss was found by dividing the natural log of
0.01 by k. ANOVA and ANCOVA models were used to examine how the two treatments, litter type and habitat, affect decomposition rates and invertebrate communities. Species abundance was determined, and the Shannon-Weaver Index was used to calculate the diversity of invertebrate communities. The invertebrate abundance was corrected by dividing the total number of individuals by the grams of ash-free dry mass.

**Results**

Canopy cover averaged 73.76% in closed canopy plots and 30.10% in open canopy plots. After 24 days, *N. sylvatica* had a faster average decomposition rate (–0.015±0.002) than both the *P. palustris* (–0.010±0.001) and *A. stricta* (–0.008±0.001) regardless of fire history ($F_{(2,14)} = 65.7$, $P = <0.001$). This trend was still seen after 104 days with 53% of black gum remaining compared to 76% and 77% of pine and wiregrass, respectively ($F_{(2,50)} = 127.2$, $P = <0.001$). Canopy cover appeared to have an effect on decomposition after 24 days ($F_{(1,14)} = 7.2$, $P = 0.018$) but that effect was greatly diminished after 104 days ($F_{(1,50)} = 0.49$, $P = 0.49$) (Table 1).

**Table 1.** Estimated number of days until 99% decomposition of 15.0 g leaf litter packs containing three different litter species and placed in two habitat types in wetlands on Eglin AFB after 24 and 104 days.

<table>
<thead>
<tr>
<th>Litter Species</th>
<th>After 24 Days</th>
<th>After 104 Days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Closed Canopy</td>
<td>Open Canopy</td>
</tr>
<tr>
<td>N. sylvatica</td>
<td>332</td>
<td>284</td>
</tr>
<tr>
<td>A. stricta</td>
<td>573</td>
<td>534</td>
</tr>
<tr>
<td>P. palustris</td>
<td>505</td>
<td>448</td>
</tr>
</tbody>
</table>

After both 24 and 104 days, the average number of colonized invertebrates was highest in the gum leaf packs for both open and closed canopies, followed by wiregrass and then pine. The
closed canopy sections had more invertebrates on average after 24 days, but far fewer than the open canopy sections after 104 days (Table 2).

Table 2. Mean number of invertebrates (±SD) colonized three different leaf litter packs after 24 and 104 days. The total number of invertebrates was standardized by the ash free dry mass remaining from each leaf pack.

<table>
<thead>
<tr>
<th></th>
<th>After 24 Days</th>
<th>After 104 Days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Closed Canopy</td>
<td>Open Canopy</td>
</tr>
<tr>
<td><em>N. sylvatica</em></td>
<td>18.53 ± 12.35</td>
<td>10.15 ± 3.43</td>
</tr>
<tr>
<td><em>A. stricta</em></td>
<td>15.71 ± 5.40</td>
<td>3.46 ± 2.57</td>
</tr>
<tr>
<td><em>P. palustris</em></td>
<td>10.74 ± 6.80</td>
<td>5.31 ± 4.43</td>
</tr>
</tbody>
</table>

After 24 days, over 90% of the aquatic invertebrates found in the leaf packs was spread among four orders: Isopoda, Diptera, Acari, and Amphipoda. Overall, more total invertebrates were found in closed canopy areas with organisms, such as Acari being much more abundant than in open canopy areas. The invertebrates preferred different types of leaf litter inputs as well, with the greatest amount of Isopoda being found in the gum packets, Diptera in gum and pine, Acari in wiregrass and pine, and Amphipoda being fairly evenly distributed in all three. In closed canopy, Isopoda dominated in gum packs, but fell in wiregrass and pine, which were both heavily dominated by Acari. In open canopy, Isopoda was most dominant in both gum and wiregrass packs, but Diptera was much more highly abundant in the pine (Figure 3).
Figure 3. Mean abundance with standard error (individuals/pack) (top) and relative contributions (bottom) of the top four invertebrate groups including Isopoda, Diptera, Acari, and Amphipoda, that colonized leaf packs in closed canopy (left) and open canopy (right) in pine flatwood wetlands after 24 days.

After the full 104 days, many changes had occurred since the first 24 days. Overall, far more aquatic invertebrates were found in open canopy plots totaling 9932 individuals, compared to only 6750 total individuals for closed canopy plots. Three of the top four orders maintained their position from the 24 day mark, including Isopoda, Diptera, and Acari, but small Cladocera replaced Amphipoda. These four orders contained approximately 92.4% of the total invertebrates. On average, Isopoda and Diptera remained relatively the same in abundance between closed and open canopy, but Acari was higher in closed canopy, and small Cladocera was much higher in open canopy. Standard error was also less variable after 104 days compared to that of after 24 days. In closed plots, Isopoda was most dominant in gum packs, but was outcompeted by small Cladocera in open plots. In wiregrass and pine leaf packs, Isopoda and
Diptera remained similar, but Acari dominated in closed areas, and small Cladocera was highest in open areas (Figure 4).

Figure 4. Mean abundance with standard error (individuals/pack) (top) and relative contributions (bottom) of the top four invertebrate groups including Isopoda, Diptera, Acari, and Cladocera (small), that colonized leaf packs in closed canopy (left) and open canopy (right) in pine flatwood wetlands after 104 days.

All of the aquatic invertebrates were split into 6 different taxonomic groups: crustaceans (Isopoda, Amphipoda, Anostraca, Cladocera, Cladocera (small), Copepoda, and Decapoda), insects (Diptera, Hemiptera, Coleoptera and larvae, Odonta, Tricheptera, Anisoptera, and Zygoptera), arachnids including Acari, Collembola, Gastropoda including limpets, and unknown invertebrates. Of these groups, crustaceans had the highest abundance in both closed and open canopy coverage, comprising of 53.9% and 73.2% of total invertebrates, respectively.
Gastropoda had a slight increase from closed to open plots, whereas insects and arachnids both had slightly higher abundances in closed coverage areas. Collembola and unknown invertebrates remained mostly unchanged (Figure 5).

![Graph showing total abundance of six taxonomic groups](image)

**Figure 5.** Total abundance of the six taxonomic groups found in leaf litter packs of ephemeral wetlands after 104 days in areas with closed and open canopy coverage.

Aquatic invertebrate diversity, calculated by the Shannon-Weaver Diversity Index, can be seen in Table 3. The overall diversity was higher in closed plots after 24 days, but the overall, as well as all three leaf packs, were much higher in open plots after the full 104 days. Both time periods showed the highest diversity in gum packs for closed canopies, and wiregrass in open canopies. Both canopy coverage types had a higher diversity after 104 days than 24 days (Table 3).
Table 3. Average Shannon-Weaver Diversity Index values (±SD) for invertebrate communities colonizing leaf packs in ephemeral wetlands embedded in longleaf pine forests after 24 and 104 days.

<table>
<thead>
<tr>
<th></th>
<th>After 24 Days</th>
<th></th>
<th>After 104 Days</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Closed Canopy</td>
<td>Open Canopy</td>
<td>Closed Canopy</td>
<td>Open Canopy</td>
</tr>
<tr>
<td><strong>N. sylvatica</strong></td>
<td>1.04 ± 0.15</td>
<td>0.46 ± 0.09</td>
<td>1.09 ± 0.29</td>
<td>1.22 ± 0.20</td>
</tr>
<tr>
<td><strong>A. stricta</strong></td>
<td>0.78 ± 0.18</td>
<td>0.73 ± 0.39</td>
<td>1.03 ± 0.31</td>
<td>1.35 ± 0.21</td>
</tr>
<tr>
<td><strong>P. palustris</strong></td>
<td>0.92 ± 0.22</td>
<td>0.69 ± 0.09</td>
<td>0.96 ± 0.19</td>
<td>1.23 ± 0.21</td>
</tr>
<tr>
<td><strong>Overall</strong></td>
<td>0.91 ± 0.20</td>
<td>0.62 ± 0.24</td>
<td>1.03 ± 0.31</td>
<td>1.27 ± 0.35</td>
</tr>
</tbody>
</table>

Discussion

It was found that black gum leaves had a faster decomposition rate than either wiregrass or pine, regardless of fire history or days left to decompose. Black gum also had the highest average number of invertebrates across all canopy coverages and lengths of time (Table 2). This may suggest that the most successful ephemeral wetland ecosystems have a relatively high abundance of *N. sylvatica*. Although black gum had the highest Shannon-Weaver diversity for closed canopies, it possessed the lowest diversity in open canopies. Pine had the highest diversity after 24 days, but wiregrass became the most diverse at the end of the experiment (Figure 5).

Although canopy cover appeared to affect decomposition rates after 24 days, this correlation faded as time went on (Table 1), refuting the hypothesis that open canopies would support a higher rate of decomposition. This could have been affected by the study sites having varying differences of canopy cover, allowing varying temperatures from sunlight to possibly impact the decomposition process.
Interestingly, the data taken on invertebrates after 24 days showed that diversity and abundance were higher in closed canopy plots. However, after the full 104 days, invertebrate diversity and abundance were both higher in open canopy sections (Figure 4, Table 3), supporting the original hypothesis. This is also consistent to past research. A study conducted by Chandler et al. (2015) showed that invertebrate abundance was lower in pine flatwoods wetlands with higher, or more closed canopy coverage, as well as with more shrubbery and less herbaceous vegetation. These are all characteristics of a fire-suppressed wetland. The results suggest that aquatic invertebrates thrive better in an environment that has been treated with fire, resulting in open canopies.

Different aquatic invertebrate species preferred different leaf types and canopy coverages. For instance, crustaceans were much more successful in open canopy plots, but other groups, such as insects and arachnids were more abundant in closed canopy plots. Isopoda showed the highest abundance in gum litter packs under all studied circumstances. Acari, on the other hand, was the highest in pine and wiregrass. Diptera and Amphipoda were both relatively close in abundance in each of the leaf packs. Small Cladocera was highest in gum under open canopy coverage but were more abundant in wiregrass under closed canopy. This shows that the healthiest ecosystem may have a mixture of leaf types and litter input rather than being dominated by one (Huffman and Blanchard, 1991). This could represent the time after the upland forest has had some time to regrow after a fire, but not enough time to result in abundant overgrowth. Future research should investigate to see what percentage of each leaf type in litter produces the most diverse ephemeral wetland ecosystem.

Further research still needs to be conducted in the future in order to fully understand the full effects of fire on ephemeral wetlands and the organisms that reside in them. Studies could
examine the proper amount of canopy coverage and percent leaf litter input that encourages the healthiest, most balanced ecosystem. Habitat degradation can result in changes in community structure, which can negatively impact the function of an ecosystem (Bishop and Haas, 2005). These results, as well as results from other studies (Chandler et al., 2015), demonstrate that aquatic invertebrate communities in ephemeral wetlands embedded in longleaf pine forests may generally respond poorly to environmental conditions resulting from long-term fire suppression. Therefore, in order to promote a healthy and high-quality habitat, managers should focus on periodically burning wetland basins rather than ignoring their need for fire (Bishop and Haas, 2005). Studies in the future should also examine the possible impacts of new and different management strategies. A mixed strategy could be used that alters frequency and seasonality of fires, rather than only burning during the winter months. Drought years could also be utilized to successfully burn wetlands during the months where they would otherwise usually be filled and unable to burn (Chandler et al., 2015). Others have suggested combining regular burning events with mechanical and herbicide treatments in order to reduce woody vegetation and prevent overgrowth (Martin and Kirkman, 2009).

Ephemeral wetlands are an important and unique ecosystem and should be a management priority as they support high diversity across several species and taxa that may not be able to live elsewhere. Until data suggests otherwise, it appears that wetlands may need to be burned periodically like their surrounding uplands and not be neglected during prescription burnings in order to maintain a healthy and balanced ecosystem.

References


