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THE SPATIAL DISTRIBUTION OF, AND UPLAND IMPACTS ON, PLAYA WETLAND INVERTEBRATES

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THE SPATIAL DISTRIBUTION OF, AND UPLAND IMPACTS ON, PLAYA WETLAND INVERTEBRATES

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF BIOLOGY

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For my family, specifically my parents, Kenneth and Mary Bright. They may not understand what I do but they are still proud of me.

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ABSTRACT

Playa wetlands are a type of temporary wetland that are numerous in the Great Plains of the United States. Playa wetlands offer a unique habitat within semiarid grassland ecosystems. My research on the invertebrates of playa wetlands centered on two topics: (1) the distribution of invertebrates in and around playa wetlands and (2) whether playa resident invertebrates are affected by the surrounding landscape (sediment movement from uplands into wetlands).

In the first chapter, I examined whether the invertebrate community of the uplands influences the dry playa wetland invertebrate community. I used colored pan traps, pitfall traps, and aerial insect traps to sample the invertebrates within dry playas and in their surrounding uplands. There was no difference in abundance, richness, or overall community composition among flying insects captured with aerial traps between upland and dry wetland habitats. Invertebrates captured in colored pan traps (which tend to catch insects attracted to flowers), differed from upland to playas in abundance, but the overall invertebrate community was similar between locations. The pitfall traps, which tend to catch ground-dwelling invertebrates, showed similar invertebrate abundance and richness but different invertebrate composition between playa and upland. The invertebrates of the dry playas showed a high degree of nestedness within the upland assemblage. However, because of soil size composition and vegetational differences, some taxa (i.e. ants, thrips, megachilids) were better adapted to either the dry playa wetland or the surrounding uplands. Therefore, protecting playa wetlands will help conserve two distinct invertebrate communities, the dry playa and terrestrial communities.

The second chapter covers a survey of the location of aquatic invertebrate resting stages within playas and the surrounding uplands. I collected two soil cores from the surrounding uplands, at the edge, and in the center of the playa from four playa wetlands in western Oklahoma, United States. The soil cores were rehydrated in a greenhouse for two weeks under ambient temperature and light. Data from two soil cores from each location (i.e. upland, edge, and center) within each playa were pooled. Invertebrate richness, abundance, and overall community were calculated for each location. Aquatic taxa richness and abundance were higher in the center and edge locations than the upland locations. The overall invertebrate communities of the wetland soil and upland soil differed from each other while the edge community shared characteristics of both the upland and wetland communities. The differences in resting stages were likely due to environmental and behavioral factors that concentrate the resting stages into the center of the playa wetland. Therefore, the center of playa wetlands is probably the most critical area for conserving aquatic taxa species richness and abundance.

The third chapter deals with conservation issues involving uplands and wetlands. Here, I examined whether the resident invertebrate community was susceptible to landscape effects in the form of sedimentation and also considered a mechanism that may cause a decrease in invertebrate hatching from added sedimentation. Soil collected from four playas was homogenized to account for differences in invertebrate communities across locations within the playa. Sterilized upland soil of three different depths (0.25 cm, 0.5 cm, and 1.0 cm) was added on top of playa soil, and a fourth control treatment had no added sediment. The soil was

rehydrated for two weeks under a 12:12-hour light:dark regime at room temperature. Sedimentation affected invertebrate hatching, with the addition of 0.5 or 1.0 cm of sediment decreasing invertebrate hatching. Because sediments affect light attenuation, I examined whether light was a necessary cue for invertebrate hatching. To do so, I rehydrated homogenized soil under three light treatments (24-hour light, 12:12-hour light:dark, and 24-hour dark regimes). Very few invertebrates hatched in the dark; hatching was greater in the lighted treatments, with no differences between the 12:12-hour light:dark and 24-hour light treatments. Finally, I examined whether buried invertebrate resting stages could hatch if exposed to the correct environmental cues. I collected two soil cores from the center of each of the four playa wetlands and divided the soil cores into three different soil levels (0-2 cm, 2-5 cm, and 5-20 cm). The soil levels were rehydrated for two weeks in environmental chambers (12:12-hour light:dark regime at 25°C). There were more invertebrates in the two top layer of soils (0-2 cm and 2-5 cm) than the 5-20 cm layer. However, some invertebrates hatched from deeper layers, so some buried crustaceans can hatch when exposed to the correct environmental cues. Sedimentation affects invertebrate hatching from playa wetlands, in part by limiting light reaching the invertebrate resting stages. Buried resting stages can hatch even after sedimentation, once they are exposed to the correct environmental cues. Thus, sedimentation may be of great concern to playa wetlands conservation because overlaying sediment affects crustacean hatching, which might cause a decrease in invertebrate prey for higher trophic levels.

CHAPTER 1

Dry playa wetland invertebrate community is a natural subset of the surrounding upland invertebrate community

ABSTRACT

1. Temporary wetlands (i.e. Carolina Bays, prairie potholes and playa wetlands) exist along a continuum of inundation and dryness with different invertebrate communities inhabiting each stage. The invertebrate community of the aquatic phase differs from the invertebrate community of the surrounding terrestrial landscape, but the invertebrate composition of the dry phase is largely unstudied.
2. We used three different trap types to sample the terrestrial invertebrate community of dry playa wetlands in Oklahoma, USA, to determine whether the terrestrial invertebrate community of dry wetlands differed from that of the surrounding uplands.
3. Differences in the invertebrate assemblages of the dry playa wetland and the surrounding upland were detected with colored-pan and pitfall traps. These differences in invertebrate assemblages are consistent with differences in vegetation and soil composition.
4. We conclude that the terrestrial invertebrate community of dry playa wetlands is a natural subset of the surrounding upland invertebrate community but environmental filters (i.e. soil composition and vegetation) prohibit some invertebrates from inhabiting dry wetlands, while other invertebrates have greater success inhabiting dry wetlands.

INTRODUCTION

When inundated, temporary aquatic habitats, such as ephemeral wetlands and temporary rivers and streams, offer different habitats from their surrounding terrestrial habitats. However, when these habitats dry, terrestrial invertebrates can immigrate into the recently dried habitat. Therefore, the invertebrate community of dried aquatic temporary habitats might resemble the surrounding uplands (high degree of nestedness) or might not resemble the surrounding uplands (low degree of nestedness). For example, Steward *et al.* (2011) examined the invertebrate community of dry riverbeds and found that they differed from the surrounding uplands because the dry riverbeds were a unique habitat.

Several hypotheses have been suggested to explain species nestedness among habitats. Selective colonization occurs when species are added to biotas in a relatively deterministic order (Darlington, 1957; Simberloff & Abele, 1976; Patterson & Atmar, 1986; Ryti & Gilpin, 1987; Cook & Quinn, 1995), so as the wetland dries, invertebrates from uplands move into the dry wetlands, in a similar pattern to the movement of invertebrates into northern Minnesota seasonal ponds (Batzer, 2004). An alternative possibility is the selective extinction hypothesis, which proposes that nestedness is caused when species are lost in a regular, deterministic order (Patterson & Atmar, 1986; Patterson 1987; Patterson, 1990; Blake, 1991; Bolger *et al*., 1991; Soulé *et al*., 1992; Cook & Quinn. 1995). In this case, specific upland organisms would be absent because they are unable to survive in the dry playa lake habitats. The third process that may result in a high degree of nestedness is habitat nestedness based on habitat size; for example, larger islands allow for greater habitat diversity thus more species being able to coexist on the islands (Simberloff & Martin, 1991; Cook & Quinn, 1995).

Wetland research has mainly focused on survival strategies in response to habitat loss - either the strategies of terrestrial invertebrates to survive inundation or the strategies of aquatic invertebrates during the dry phase - and not the relationship of the invertebrate community of a dried wetland to that of the upland community. Terrestrial invertebrates that inhabit wetlands move out of the wetlands when they become inundated (Zulka, 1994; Bonn, 2000; Adis & Junk, 2002) and move into wetlands when they dry (Batzer, 2004). When wetlands dry, aquatic organisms either emigrate to other water sources (Corbet, 1980; Sheldon, 1984; Batzer & Wissinger, 1996) or remain through the dry phase in a diapausing or aestivating life stage (Wiggins *et al*., 1980; De Stasio, 1989; Hairston *et al*., 1995).

Playa wetlands are shallow, ephemeral wetlands that are found in prairie, semiarid, and arid environments worldwide. However, playa wetlands have their greatest abundance in the Southern High Plains ecosystem of the USA. Playas are depressional wetlands that probably formed from land subsistence and aeolian processes (Osterkamp & Wood, 1987). Hydrologically isolated, playas are not connected to another water source. They become inundated from storm precipitation, which occurs mainly in late spring or early summer, but they sometimes can become inundated in winter months (Johnson *et al*., 2011). Dry playa wetlands have distinct vegetation communities (Hoagland & Collins, 1997) and soil composition (Osterkamp & Wood, 1987) compared to the surrounding landscape. Inundated playa wetlands increase the biodiversity of the Southern High Plains (Haukos & Smith, 1994; Smith *et al*. 2011) and act as important stopover locations for migrating birds using the Central Flyway (Davis & Smith, 1998; Haukos et al. 2006). In addition to providing habitat and increasing biodiversity, playa wetlands also provide ecosystem services such as floodwater conveyance and aquifer recharge (Osterkamp & Wood, 1987; Gurdak & Roe, 2009). Although playa wetlands are both ecologically and hydrologically important, they are under severe threat from dredging or filling from sedimentation, with most impacts resulting from agricultural practices (Bolen *et al*., 1989; Luo *et al*., 1997; Luo *et al*., 1999; Johnson *et al*., 2011).

Even though unmodified playa wetlands typically are dry for most or all of the year, invertebrate studies have primarily focused on the aquatic phase (Anderson *et al*., 1999; Anderson & Smith, 2000; Smith, 2003; Anderson & Smith, 2004). This study examined the terrestrial invertebrate assemblage of dry playa wetlands and their surrounding uplands to determine if the dry playa wetland invertebrate community was a natural subset of the surrounding uplands. We hypothesized that the terrestrial invertebrate abundance, richness, and assemblage composition of dry wetlands will differ from the surrounding uplands because of differences of abiotic factors such as soil composition or disruption of the terrestrial environment by flooding.

METHODS

Site description

We surveyed four playa wetlands monthly in the summer of 2010 (Table 1.1). The selected wetlands were in the Oklahoma panhandle in Texas County (Lunceford Playa, McKinley Playa, and Balzer Playa) and in Beaver County (Oklahoma Wildlife and Prairie Heritage Alliance (OWPHA) Playa); Fig. 1.1). All wetlands were privately owned and enrolled in a land conservation program (Playa Lake Joint Venture or the Landowner Incentive Program), which mandated at least a 50-m buffer zone separating the conserved land from the surrounding agricultural land. Except for the Lunceford Playa, the playas had not been inundated for several years. The Lunceford Playa undergoes moist soil management by the Oklahoma Department of Wildlife Conservation, and is therefore periodically and artificially inundated throughout the year. We sampled during the dry periods. The four playas ranged in size from approximately 20,000 m^2 to 300,000 m^2 (Table 1.2). We defined the playa wetland as the area with hydric soils that was delineated by a break in the elevation from the surrounding landscape.

Invertebrate sampling

Three types of invertebrate traps were used to sample the invertebrate community in the dry playa wetland and the surrounding upland (Fig. 1.1). These trap types targeted different groups of invertebrates (Bartholomew & Prowell, 2005; Campbell & Hanula, 2007; Missa *et al*. 2009). The traps within the playa wetland were located near the center of the playa while the upland traps were deployed throughout the upland but no closer than 10 m to the edge of the wetland. We deployed an aerial malaise-type trap (4-head SLAM traps, BugDorm, Taichung, Taiwan) in each playa and in the upland adjacent to it (Fig. 1.1). These traps target flying insects and were deployed for 24 hours (Cancelado & Yonke, 1970). We used pitfall traps to capture invertebrates moving across the ground surface (Corti *et al*., 2013). These were constructed by inserting a 120-ml specimen cup inside a 590-ml plastic cup (area of opening = 63.6 cm^2) and burying it flush with the top of the soil. When soil invertebrates encountered a pitfall trap, they were funneled into the specimen cup and drowned in a soapy-water solution. We deployed 10 pitfall traps in each dry playa and 10 traps in each adjacent upland and collected them after 24 hours (House & Stinner, 1983). Pitfall traps were spaced approximately 10 m apart in a ring 10 m away from the aerial traps (Fig. 1.1) (Ward *et al*., 2001). We used colored-pan traps (yellow, green, red and blue) to capture invertebrates that are attracted to color. These consisted of 400-ml plastic bowls (surface area = 176.7 cm^2) filled with soapy water. We positioned 10 pan traps in each playa and 10 in each adjacent upland, aligned in transects with pans approximately 10 m apart (Fig. 1.1). Due to evaporation, pan traps were sampled after 2 hours.

Captured invertebrates were preserved in 70% ethanol until they were counted and identified. Invertebrates were identified to the lowest possible taxonomic level (usually family) using keys in Triplehorn and Johnson (2005) and Dindal (1990). After ensuring the different traps caught different numbers of invertebrates and unique invertebrate communities (Figs. 1.2 and 1.3), all analyses and data depictions were an average of invertebrates from each trap type (aerial vs. pitfall vs. pan) and each sampling location (wetland vs. upland) to generate a richness value, an abundance value, and overall assemblage for each trap type at each location for each sampling event.

Soil and vegetative sampling

During the June sampling, we haphazardly collected 10 soil sub-samples from near the center of each wetland and 10 soil sub-samples from each upland to a depth of

10 cm. The soil sub-samples were combined, resulting in one aggregated sample for each playa and upland. Samples were analyzed for pH, lime requirement (using Sikora Buffer), NO_3-N, P and K (by Mehlich 3 method) at the Oklahoma State University Soil, Water, and Forage Analytical Laboratory. The Mehlich 3 method uses the Mehlich 3 Extractant reagent to extract macro- and micronutrients from soil samples. After filtering the soil samples and Mehlich 3 Extractant through a 15-cm filter paper with medium porosity, the filtrate was analyzed via inductively coupled plasma mass spectrometry (ICP) (Mehlich, 1984; Hanlon & Johnson, 1984). Soil texture was calculated using the hydrometer method at the Oklahoma State University Soil, Water, and Forage Analytical Laboratory and percent soil particle size was calculated. The hydrometer method uses sodium hexametaphosphate to aggregate different particles, which then settle out of the solution at different times. At each time period, a hydrometer is used to read the density of the soil suspended in the solution (Bouyoucos, 1962).

In May, we took vegetative cover measurements at each of the four playas. At each playa, we haphazardly threw a 0.25 m^2 square quadrat five times in both the uplands and dry wetlands. At each throw, we calculated the vegetative cover percentage within the quadrant.

Statistical analyses

We used univariate and multivariate approaches to analyze the invertebrate data. First, richness (number of identified taxa) and abundance (average number of invertebrates caught for each trap type) were analyzed using analysis of variance (ANOVA), with trap type, geographic location, and location (wetland versus upland) as main effects (SigmaStat, Systat Software Inc., Chicago, Illinois) and only main effects and two-way interactions were analyzed. Abundance data were normalized to homogenize the variance by a log + 1 transformation (Zar, 1996). Transformed data are graphed. The effect of trap type was significant, so we analyzed the data from each trap type separately using a two-way repeated measure ANOVA with month and location as independent main effect variables. Tukey *post hoc* tests were used to determine differences within each main effect for significant repeated measure ANOVA results.

A second statistical approach used community composition data to determine if the overall invertebrate community of the dry playa wetland differed from that of the surrounding upland. We used non-metric multidimensional scaling (NMDS) (PRIMER 6, Primer-E Ltd, Ivybridge, United Kingdom) with Bray-Curtis similarity index to ordinate results, and analysis of similarity (ANOSIM) to determine if there were differences among clusters. We used two-way ANOSIM using month and location as main effects. Only invertebrates that were found in at least 20% of all samples were included in the non-metric multidimensional scaling and ANOSIM (Gauch, 1982; McCune *et al*., 2002). In addition, indicator species analyses were used to determine if particular species were more prevalent in a particular location (dry wetland vs. upland) (Dufrêne & Legendre, 1997) (PC-ORD 6, MJM Software Design, Gleneden Beach, OR). Statistical significance of indicator species was tested using a Monte Carlo test with 4999 permutations with a random number seed.

Soil size composition was analyzed with a multivariate analysis of variance (MANOVA) (SigmaStat, Systat Software Inc, Chicago, Illinois) after being arcsine-square root transformed to normalize the percentage data (Zar, 1996). The transformed soil percentages were treated as dependent factors while geographic location (playa identification) and location (dry wetland and upland) were independent variables. The effect of geographic location was not significant so only location was analyzed. Soil nutrients were analyzed using paired t-tests (SigmaStat, Systat Software Inc., Chicago, Illinois) where the location was the independent variable.

Vegetative cover data were analyzed with a two-way ANOVA after being arcsine-square root transformed to normalize the percentage data (Zar, 1996). The transformed percentage data were treated as dependent factors while geographic location (playa) and location (dry wetland and upland) were independent variables.

RESULTS

Trap types

We caught and identified 99,255 invertebrates from 23 orders and 175 taxa (Table 1.3). Invertebrate samples from the three different trap types differed in richness ($F_{2,89} = 89.2$, $p < 0.001$ (Fig. 1.2a), abundance ($F_{2,91} = 46.7$, $p < 0.001$) (Fig. 1.2b) and overall community composition (Global R = 0.89, p = 0.001) (Fig. 1.3a). Aerial insect traps caught almost twice the number of invertebrate taxa over the course of the study as the other types of traps, whereas the colored-pan traps caught the fewest (Fig. 1.2a). Abundance followed a similar trend, with aerial traps capturing the most invertebrates and the pan traps catching the fewest (Fig. 1.2b). Each trap type sampled a different invertebrate assemblage (Fig. 1.3a). Aerial traps chiefly caught species in the insect orders Diptera, Lepidoptera, Hymenoptera, and Coleoptera. The organisms associated with pitfall traps were in the order Collembola, in the class Arachnida (Acari and Lycosidae), and the family Gryllidae. The taxa associated with colored-pan traps were two families of Hymenoptera, Thysanoptera (thrips), and Salticidae. In addition, invertebrate richness ($F_{3,89} = 19.9$, $p < 0.001$) (Fig. 1.2a) and abundance ($F_{3,91} = 22.2$, $p < 0.001$) (Fig. 1.2b) declined across the sampling season. Invertebrate communities also differed across the sampling season (Fig. 1.3b).

Pitfall traps

Invertebrate taxa richness ($F_{3,31} = 2.50$, $p = 0.13$) and abundance ($F_{3,31} = 3.30$, $p = 0.07$) in pitfall traps did not change significantly over the sampling season (Figure 1. 2a,b). Pitfall traps caught an intermediate number of invertebrate taxa and intermediate number of invertebrate individuals compared to the other two trap types. Pitfall traps in dry wetlands and uplands had similar richness ($F_{1,31} = 0.35$, $p = 0.60$) and abundance of invertebrates ($F_{1,31} = 1.91$, $p = 0.26$) (Fig. 1.4a,b). However, pitfall traps in the dry wetlands caught a different invertebrate community than did the pitfall traps in the uplands (Global R = 0.14, $p = 0.006$) (Fig. 1.5a). Indicator species analysis showed that five invertebrate taxa differed between the two habitats (Fig. 1.6). More thrips (Thysanoptera; $p = 0.04$), ants (Formicidae; $p = 0.002$), and unidentified coleopterans ($p = 0.05$) were found in the uplands than in the dry wetlands. Scelionid wasps ($p = 0.05$) and noctuid moths ($p = 0.04$) were captured more frequently in the dry playa wetlands than the uplands (Fig. 1.6).

Colored-pan traps

Colored-pan traps caught the fewest invertebrate taxa and individuals (Fig. 1.2). We saw decreases in both abundance ($F_{3,31} = 21.5$, $p <0.001$) and richness ($F_{3,31} = 29.88$, $p < 0.001$) of invertebrates caught as the season progressed (Figs. 1.2a,b). There was no difference in richness between the upland and dry wetland ($F_{1,31} = 5.14$, p =

0.11) (Fig. 1.3a) but wetland traps caught more invertebrates ($F_{1,31}$ = 16.8, p = 0.03) than did the dry wetland traps (Fig. 1.3b). The invertebrate communities were similar between locations (Fig. 1.5b). Indicator species analysis indicated that perilampids (p = 0.02) and psocopterans (p = 0.03) were caught more frequently in dry wetlands than uplands (Fig. 1.6). Other invertebrates that showed trends towards being indicator species included phorid flies (p = 0.09), cicadellids (p = 0.08), ants (p = 0.06), and leaf-cutter bees (p = 0.08). Phorid flies and cicadellids were more abundant in the dry wetlands, whereas ants and megachilid bees were more abundant in the uplands (Fig. 1.6).

Aerial traps

Four aerial traps were unrecoverable during the course of the study so aerial trap sample size was decreased to 28. Aerial traps caught the most invertebrates and most taxa of the three trap types (Fig. 1.2). Taxa richness ($F_{1,27}$ = 0.67, p = 0.42) and abundance ($F_{1,27}$ = 0.43, p = 0.52) of invertebrates caught by aerial traps did not differ between the dry wetland and upland sites (Fig. 1.4a,b). The dry wetland and upland sites shared similar aerial invertebrate assemblages (Fig. 1.5c). Indicator species analysis showed that more perlampids were caught in the surrounding uplands than in the dry wetlands (p=0.05) (Fig. 1.6). Taxa richness and abundance in aerial traps did not vary much across the summer (Fig. 1.2a,b).

Soil and Vegetation

Soil size composition (clay ($F_{1,7}$ = 7.58, p = 0.03) versus sand ($F_{1,7}$ = 6.18, p = 0.05)) differed between the upland and the wetland. Clay made up around 42% of the soil of the dry wetland and sand comprised around 24%. The upland had the opposite pattern, with around 40% of the soil composed of sand and 25% composed of clay. Soil from the two locations had similar amounts of silt. Potassium concentration of the dry wetlands soil (range: 400-1024 ppm) was greater than that in the uplands (range: 369-733 ppm) ($t = -2.54$, $p = 0.04$). There was a trend of higher phosphorus concentration in the dry wetlands (range: 86-119 ppm) than uplands (range: 52-67; 118 ppm), and removing an outlier yielded a significant difference between the dry wetlands and uplands ($t = -3.78$, $p = 0.01$). Amount of nitrogen did not differ between the dry wetlands (range: 4.5–23.5 kg/ha) and uplands (range: 19.1–28.0 kg/ha) ($t = 0.71$, $p = 0.50$).

There were no difference in the amount of vegetative cover among the four playas ($F_{3,7} = 0.18$, $p = 0.90$) or between locations (upland vs. dry wetland) ($F_{1,7} = 0.18$, $p = 0.11$).

DISCUSSION

Invertebrate community structure and abundance differed between the dry wetland and the upland. This difference was most apparent in the pitfall traps and, to a lesser extent, in the colored-pan traps. Pitfall traps are well-suited to capture invertebrates associated with soils and soil composition of the dry wetland does differ from the uplands (Allen *et al.*, 1972; Bolen, 1989; this study). The dry wetland soil is composed primarily of clay whereas the uplands are composed of relatively less clay and more sand. Additionally, we found differences in soil nutrients, with wetland soils having higher potassium and phosphorus concentrations. Soil composition affects soil invertebrate community structure (Curry, 1987; McCracken, 1994; Sanderson *et al.* 1995) and soils augmented with nutrients (fertilizers and manure) have higher abundances of non-insect invertebrates (Luizão, 1985, as cited by Stork & Eggleton, 1992).

In addition to the direct influence of soil characteristics of soil on invertebrates, soil composition and nutrient concentration influences vegetation composition and indeed vegetation composition differs between playa wetlands and the surrounding uplands (Hoagland & Collins, 1997; our observations). Differences in vegetation in dry wetlands and uplands are associated with the differential invertebrate catch (abundance) caught by the colored-pan traps. Colored-pan traps especially capture insects searching for plants – in our case, differences were found in pollinators, such as megachilids and noctuids, and plant-feeding thrips. Vegetation composition has been shown to affect the invertebrate community of other systems (Janzen, 1973; Southwood *et al*., 1979).

We did not see a location difference in invertebrate community structure caught by aerial traps, probably because flying insects, in general, are less affected by ground-level changes in habitat than are ground-associated invertebrates. Although the lack of significance could be the result of small sample sizes and thus low power.

The distribution of individual taxa, as highlighted by indicator species analysis, supported our conclusion that dry wetlands have a different invertebrate community from the uplands. Uplands had more ants, thrips, and megachilid bees, whereas dry wetlands had more scelionid wasps, noctuids moths, phorid flies, and leaf hoppers. Differential catches among trap types indicated that perilampid hymenopterans were actively flying in the dry wetlands (high aerial trap catches), but were attracted to vegetation in the uplands, where catches were greater in colored-pan traps. In contrast, ants (Formicidae) were active on the surface in uplands, where there were high counts in both pitfall and colored-pan traps.

Some taxa were differentially distributed with differing habitat conditions between wetland and upland areas. For example, we found that ants were more abundant in the uplands, where the soil is sandier, than they were in the dry wetlands. Johnson (2000) reported that some species of ants prefer sandier substrates to clay substrates. We found a similar trend of higher abundance of megachilid bees in the surrounding uplands, and Eickwort *et al*. (1981) found that megachilids preferred to nest in areas with sandier substrates. In addition, several studies have shown that the local composition of leafhopper assemblages varied with vegetation composition and soil type (Novotný, 1990, Brown *et al*., 1992; Hollier *et al*., 1994; Eyre *et al*., 2001). This differential distribution of specific taxa has been shown in other systems (Murakami and Hirao, 2010).

Even though most of these playa wetlands did not become inundated during the study, other factors associated with periodic inundation and unknown biotic interactions might affect invertebrate distributions. We found higher invertebrate abundance in ephemeral dry wetlands than in the uplands. Similarly, Novotny (1990) showed that leafhoppers had higher species richness in ephemeral habitats than in permanent habitats. In contrast, ground-nesting insects, such as some bees and ants, may prefer to nest in drier areas where the threat of inundation is lower and, indeed, ground-nesting bees and ants were more common in the uplands than in the wetland bottoms.

We found that dry wetlands have greater richness than were reported from Hall *et al.* (2004) of inundated playas. We found more than 175 taxa families in 23 orders in dry playa wetlands while Hall *et al.* (2004) found only 47 families in 13 orders in inundated playas. However, many of the taxa found in the dry wetland were also found in the surrounding uplands; hence, dry playa wetlands do not increase the biodiversity of the total ecosystem as much as do inundated playa wetlands, which contain many aquatic and semi-aquatic taxa that are not active in the dry phase.

This research showed that there are some differences in invertebrate assemblage composition and soils between dry playa wetlands and the surrounding uplands. However, dry wetland playa habitats are nested within the wider short-grass prairie uplands and the dry phase invertebrate community within playas demonstrate both the high colonization influx of terrestrial invertebrates and differential success in establishment and population growth among species. When playas are disturbed or destroyed (e.g., by draining, filling, or dredging), both the aquatic and terrestrial invertebrate communities within playas are impacted. The dry phase of other temporary wetlands (i.e. vernal pools, prairie potholes, and Carolina bays) should also be studied to determine whether these habitats support unique terrestrial invertebrate communities.

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APPENDIX

Table 1.1. The dates when each playa was sampled in 2010.

	Dates Sampled in 2010			
Balzer Playa	25 - 26 May	22 - 23 June	20 - 21 July	19 – 20 August
McKinley Playa	24 - 25 May	21 - 22 June	19 - 20 July	18 – 19 August
Lunceford Playa	26 - 27 May	23 - 24 June	21 - 22 July	20 - 21 August
OWHPA Playa	27 - 28 May	24 - 25 June	22 - 23 July	21 - 22 August

Table 1.2. A site description of the four playas used in the study.

	Lunceford Playa	**Balzer Playa**	**McKinley Playa**	**OWPHA playa**
Location	36°50'37.64"N 100°59'51.89"W	36°47'0.09"N 101°12'12.87"W	36°51'30.21"N 101°19'8.9"W	36°50'32.10"N 100°0'21.94"W
Area (m^2)	20,000	150,000	300,000	110,000
Managed	Yes	No	No	No
Inundation	Every 3-4 months	Rare	Rare	Rare

Table 1.3 When (month), where (playa vs. upland vs. wetland) and by what trap type (pitfall vs. pan vs. aerial) of all the taxa caught during the 2010 sampling season. B = Balzer Playa, L = Lunceford Playa, M = McKinley Playa, and O = OWHPA.

	May						**June**					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
CHELICERATA												
Acari												
Non-orbatidae	B,L,M,O	B,L,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,O	B,L,M,O	B,L,O	B,O
Orbatidae	B,L,M,O	B,L,M,O	B,L,O	L	B,L,O	L,O	B,L,M,O	B,L,M,O	B,M,O			
Araneae												
Agelenidae							L					
Dictynidae										O	L	B
Erigonidae	B,L,M,O	B,O	O	L,O	B,L,U	O	B,L,M,O	B,L,M	L,O		L,B	O
Gnaphosidae	L											
Hahniidae		M					B					
Lycosidae	B,L,M,O	B,M,O	O	L,O	O	B,O	B,L,M,O	B,L,M,O	O	L,O	M	
Oonopidae												
Salictidae			B,O	O					B,L,M	L,M		
Tetragnathidae		B			B	B,M,O					B,M	
Thomisidae			B	M	M	O		O				
Opiliones												
Gagrellidae							O					
CRUSTACEA												
Ostracoda				B								
Isopoda												
Oniscidae	B,L,O	B,O					B,O	O				
MYRIAPODA												
Chilopoda		L										
HEXAPODA												
Blattodea												
Blattidae											M	
Coleoptera												
Anobiidae					B,O	L,O						B
Anthicidae								L			M,O	
Bostrichidae					L		L					

	July						August					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
CHELICERATA												
Acari												
Non-orbatidae	B,L,M,O	B,L,M,O	B,M	B,L,O	B,L,M,O	L,M,O	B,L,M,O	B,L,M,O	O	B	B,O	B,L,M
Orbatidae	B,L,M,O	B,L,M,O		B,LO			B,L,M,O	B,L,M,O	B	B	M	
Araneae												
Agelenidae							L					
Dictynidae	B					M				O	B	L
Erigonidae	M,B,OL	B,O,L	O		M,B	L,O					L,M	M
Gnaphosidae							B,L,M,O	B,L,O		L	L,M,O	B,L
Hahniidae							M	B,M				
Lycosidae	B,M,O	B,L,M,O		B,O	B,M		B,O	B,L,M	L	B,L	L,O	L
Oonopidae							B					
Salictidae	B,L,M	L,M,O	O	M			M	M,O	O	L,M		
Tetragnathidae						B			O			
Thomisidae	M	O		L		B	M,L				B,L	
Opiliones												
Gagrellidae								O				
CRUSTACEA												
Ostracoda		M										
Isopoda												
Oniscidae	O	O										
MYRIAPODA								L				
Chilopoda								L				
HEXAPODA												
Blattodea												
Blattidae	O											
Coleoptera												
Anobiidae												
Anthicidae	B,L	O			M	B					O	M,O
Bostrichidae	O										M	M

	May						**June**					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Byrrhidae											M	
Cantharidae					O	O						
Carabidae	B,L,M,O	B,L,M,O	L		L		B,M,O	B,L,M,O		O	L,M	O
Cerambycidae											B	
Chyrsomelidae	B,L,M	B,M	B,L,M,O	B,M,O	B,L,M,O	B,L,M,O	B	B,L,M		B,L	B,L,M,O	B,O
Cleridae				O							O	
Coccinellidae		B		B		B,L,M					B	
Corylophidae	L		L		B,L,O	M,O					M	B
Curculionidae	B,O	B	B	B,M	B,L,M,O	B,L,M,O	L	B,L		B,L	B,M,O	B
Dascillidae												
Dermestidae	B	B	L,M									
Dytiscidae												
Elateridae	B,O					M		B,L,M			B,L,M,O	B,O
Eucnemidae											B,L,M,O	B
Latridiidae	M	M,O	L		B,L,M	B,L,M,O		M			B,L,M,O	B,O
Lycidae												
Meloidae	B,L,M	L	M	L,M,O	L	B,L	B,M	B,L,M,O	B,M,O	B,L,M,O	B	B
Melyridae				L	M,O	M,O						
Monotomidae	B											
Mordellidae	M		M	B	B,L	B,O		B			O	
Mycetophagidae												
Nitidulidae	L	B							B			
Omethidae											M	O
Phalacridae												
Ptiliidae								B				
Ptilodactylidae											O	
Scarabaeidae	B,L,O	L,O	L,M,O	L,M,O	O	O		L	O	B		
Tenebrionidae	M							M				
Silvanidae												
Staphylinidae	B,L,M,O	B,M,O	M	L,M	B,L,M,O	B,L,M,O	B,M,O	B,L		O	B,L,M	B,M
Collembola												
Entomobryidae	B,L,M,O	B,L,M,O	B	B,L	B,M,O	L,O	L,M,O	B,L,M,O		L	L,O	

	July						**August**					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Byrrhidae												
Cantharidae						O						
Carabidae	B,L,M,O	M,O				B,L	B,L,M,O	B,L,M,O	O			
Cerambycidae												
Chyrsomelidae	O	M			B,M	B,L,M,O		B,M	L	L,O	B,L,M,O	B,L,M,O
Cleridae	O											
Coccinellidae												
Corylophidae	B,M					B,L					M,O	M
Curculionidae	O					B,L	O	B		B,L	L,M,O	B,L
Dascillidae											B,O	M
Dermestidae											L	O
Dytiscidae	L											
Elateridae		L,M				B,L,O	M	B				M
Eucnemidae	O				M	B,L					O	
Latridiidae		M			B	B,M,O	M			B,M	L,M	L,M
Lycidae												B
Meloidae	B,L,M,O	M,O	B,L,M	O		B	B,L,M,O	B,M,O	B,L,M,O	B,L,M,O		
Melyridae	M			O	M			L		M	B,L	B
Monotomidae												
Mordellidae						B					O	
Mycetophagidae					M	L						
Nitidulidae								M				
Omethidae												
Phalacridae						M						
Ptiliidae		B										
Ptilodactylidae												
Scarabaeidae	B							B				
Tenebrionidae	B,M							O				
Silvanidae								B				
Staphylinidae	B,L	L			B,M	B,L,M	B,M	B,L		M	B,L,M	B,M
Collembola												
Entomobryidae	B,L,M,O	B,L,M,O	B	O		B,M,O	B,L,M,O	B,L,M,O	B,O	B,L,M	M,O	O

	May						June					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Hypogasturidae												
Isomatidae	B,L,M,O	B,L,M,O	B,O	B,O,L			B,L,M,O	B,L,M,O	B,L	B		
Onychuridae	B,L,M,O	B,L,M,O	B,L,O	B,L,O			B,L,M,O	B,L,O	B,L,M	M		
Sminthuridae	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M	L,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O		O
Diptera												
Anisopodidae								M				
Asilidae								O		L		
Bombyliidae												
Calliphoridae		B	M					B				
Cecidomyiidae												
Ceratopogonidae	B,L,M,O	B,L,M	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,M	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,O
Chironomidae			B,O	L	B,L,M,O	B,L,M,O	B,L	B,L,M			B,L,M,O	B,O
Chloropidae	L,O	B,L	B,L,O	L,O	B,L,M,O	B,L,O			L	L	O	B
Conopidae	L,M	M	B,L,M,O	B,M,O	M,O	M,O	B,M	M,O	L,M,O	B,L,M,O	B,L,M,O	O
Culicidae	L	B,M			B,L,M,O	B,L,M,O	L	L		B,L	B,L,M,O	B,O
Curtonotidae												
Dolichopodidae	B,M,O	B,L,M	B,L,M,O	B,L,M,O	B,L,O	B,O	M	L,M		B,L	B,M,O	O
Drosophilidae						B						
Empididae	L,M,O	B,M	M,O	M,O	B,M,O	B,L,M,O	B,L,O	L,M,O		L	B,L	B,O
Fanniidae				B							B,M,O	
Heleomyzidae	B,L,M,O	B,L,O	L,O	M,O	B,L,M,O	B,L,M,O			M,O	M	B,L,M	O
Micropezidae						B						
Musicidae	B,L,M	B,L		L	B,M,O	B,L,O				L	B,L,M	B
Phoridae		B,M		B,L,M		B,M	O	B,L,M	O	L,O	B,L,O	O
Piophilidae	M	M		M								
Pipunculidae			B	B	O				L		L	
Psychodidae		M			B,L,O	B,L,O					B,L,O	B,O
Sarcophagidae	B,M	M	B,L,M	M,O	L,O	B,M,O	B,L	L	O	L	B,M	B,O
Scathophagidae												
Scatopsidae					B							
Sciaridae	B,L,M,O	B,L,M,O	B,M,O	B,M,O	B,L,M,O	B,L,M,O	L	O		L	B,L,M,O	B,O
Sepsidae					B,M	B,L,O						

	July						August					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Hypogasturidae							B,L,O	B,O				
Isomatidae	B	B,L	O	B,L,M			M	L	B,L,M,O	B,L,M,O		
Onychuridae		L,M,O					M	L,M		B,L		
Sminthuridae	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B	O	B,L,M,O	B,L,M,O			M	L
Diptera												
Anisopodidae												
Asilidae							L	L				
Bombyliidae						L	M			M		
Calliphoridae						B,M	B	B				
Cecidomyiidae												
Ceratopogonidae	B,L,M,O	B,L,M,O	L,M,O	L,M	B,M	B,L,M,O	B,M	L	B,LO	O	B,L,M,O	B,L,M,O
Chironomidae	O	L,M		B	B,M	B,L,M,O	L,M	B		L	B,L,M,O	B,L,M,O
Chloropidae			B,M	B	B,M	B,L,M			M	L	B,M	B,L,O
Conopidae	B	B,M,O	B,M,O	B,L,M,O	B,M	B,L,M,O	M	M		B,M	L	
Culicidae					B,M	B,L,M,O					B,L	B,L,O
Curtonotidae								L				
Dolichopodidae					B,M	L,M,O		B,L		B	B,L,O	B,L,M,O
Drosophilidae												
Empididae		L			B,M	B,L	B	B,L,O			L	L,O
Fanniidae						B	O					B,L
Heleomyzidae		L			B,M	B,L		L		L	L,O	
Micropezidae											B,L	B
Musicidae						O		L				
Phoridae	L,M,O	L,M,O			M	B,L,O	B,L,O	B,L		B		
Piophilidae										B		
Pipunculidae					M	L,M					M	L
Psychodidae					B,M	B,L					M,O	
Sarcophagidae	L	M			B,M	L,M	B	B,L			L,M	L.M.O
Scathophagidae			L	L		B					L	
Scatopsidae												B
Sciaridae	M	B,L,M,O	B		B,B	B,L,O	O	B		B	B,L,O	B,O
Sepsidae												

	May						June					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Sphaeroceridae												
Syrphidae		B	L,O	B,L,M	B,L	B,L,M,O						
Tachinidae	M,B		M,O	L,M	B,L,M,O	B,L,M,O				L	B,L,M,O	B
Tephritidae					B	M,O					B	
Therevidae					B	O					B	B
Tipulidae												O
Hemiptera												
Aleyrodidae					L					O		
Alydidae						B						
Anthocoridae				M	M	B,M,O		B,L		B	B,L	O
Aphididae	B,M,L	L	M	B,M,O,L	B,L,M,O	B,L,M,O	M		B,O		B,L,M,O	
Aradidae								L				
Artheneidae				L				M				
Berytidae												
Cercopidae						B,M						
Cicadellidae	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,O
Cixiidae							L	L,O			B,L,O	B,O
Coccoidea			L	L,O	B	O	O	O	B	L		
Cydnidae	B,M							M				
Delphacidae	B,L,O	B	L,O	L,O	B,M	B,O				L	B,L	
Derbidae				L								
Dictyopharidae	B,M	O		M,O				O		B		O
Heterogastridae												
Lygaeidae	B,M	B,O	M	M,B	B,M,O		M	M		B,M,O	B,M,O	B,O
Miridae	B,M			B,M	B,L,M,O	B,L,M,O	B	B		L	B,L,M	B
Pentatomidae			L	L	B	O	B	M		M		
Psyllidae						B						
Reduviidae							L				L,M	B
Rhopalidae												
Rhyparochromidae												
Saldidae								M				
Scutelleridae												

	July						August					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Sphaeroceridae					M	O	L					
Syrphidae						L		L			L	L
Tachinidae						B,L,M				B	B	L,M
Tephritidae						B					B,O	L,O
Therevidae					M	O					O	
Tipulidae												
Hemiptera												
Aleyrodidae						O			M	L		
Alydidae											M	
Anthocoridae											L	
Aphididae					B,M	M,O	M	L		L	L,M,O	L,B,M
Aradidae												
Artheneidae												
Berytidae											B	B
Cercopidae												
Cicadellidae	B,L,M,O	B,L,M,O	B,L,O	B,L,M,O	B,M	B,L,M,O	B,M,O	B,L,M	B,L,M,O	B,L,M,O	B,L,O	B,L,M,O
Cixiidae		L			B,M	B,L,M,O					L,M,O	B,L,M,O
Coccoidea	B,M,O	B,M,O	O		B,M	B	L,M,O	L,M,O	L,O	B,L	L	B,M,L
Cydnidae		L										
Delphacidae	L	L		L		B,L,M	B	L,M		L	B,L	
Derbidae												
Dictyopharidae												
Heterogastridae												B
Lygaeidae				M	B,M	B					M	B
Miridae	B,M				M	B,L,O				O	B,M	M,O
Pentatomidae				M								
Psyllidae												
Reduviidae	O				M						L,M	
Rhopalidae								L		L		
Rhyparochromidae											L	
Saldidae												
Scutelleridae								B				

	May						**June**					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Tingidae						M					M	
Hymenoptera												
Andrenidae				M			L	L		M,O		
Apidae	B,M		O	M				L	B,L,M,O	B,L,M,O		
Argidae												
Bethylidae			M	L	B,L,M	B,M,O					B,L,M	B,O
Braconidae	B	O	M	L,M	B,L,M,O	B,L,M,O	L,O	B,M		L	B,L,O	B,O
Cephidae			L									
Chalcididae				O		M						
Colletidae				L,M								
Encyrtidae												
Eucharitidae											M	
Eulophidae					B,L,M,O	B,L,M,O				O		
Eupelmidae											B,L	B,O
Eurytomidae											B,L	
Figitidae						M					B	
Formicidae	B,M,O	B,L,O	B,L,M,O	O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,O	B,L,M,O	B,L,M,O	B,O
Halictidae	B,M,L	B,L,M,O	B,L,M,O	B,L,M,O			L,M,O	B,M	B,L,O	B,L		
Ichneumidae	B,M		M		B,M,O	B,M,O		M	B			
Megachilidae	B,M		M,O						M			
Melittidae			M	M								
Mutillidae											O	
Mymaridae	B,L,O	B,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,O	B,L,M	B,L,O	B,L,M,O	B,L,M,O	B,L,M,O	B,O
Perilampidae	B,M	B,M	B,M	B,L,M	B,L,M,O	B,L,M,O	B,L,M	B,L,M	O	B,O	B,L,M,O	B,O
Platygastridae												
Proctotrupidae												
Pteromalidae	M	M	B,M		B,L,M,O	B,L,M,O	B	O	B	M,O	L,O	B,O
Scelionidae	B,L,M,O	B,L,M,O	B	B,L	L,O	B,L,O	B,L,M,O	B,L,M,O			O	
Sphecidae			L,M,O	M,O				L,M	L	M	B,M,O	O
Torymidae			B									
Vesipidae				L,B								
Lepidoptera												

	July						August					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Tingidae					M	B,L						
Hymenoptera												
Andrenidae			O	O								
Apidae	O	M,O	B,L	B,O			B,O		B,L,O	B,L,M		
Argidae				L						L		
Bethylidae					B,M	O					B,L	L
Braconidae		B,M	B	B	B,M	B,L,M,O	L	B,O		B	B,L,M,O	B,L,M,O
Cephidae												
Chalcididae												
Colletidae					B			L			L	
Encyrtidae												B
Eucharitidae												
Eulophidae												
Eupelmidae					B,M	B,O		B				
Eurytomidae					B	B,M						
Figitidae												
Formicidae	B,L,M,O	B,O,L	B,L,O	L,O	B,M	B,L,M,O	B,L,M,O	B,M,O	B,L,M	B	B,L,M,O	L,M,O
Halictidae	L,M	O	B,L,M,O	B,L,O			M,L	B,O	B,L,O	B,L,M,O		
Ichneumidae				B		B,O						L
Megachilidae		B	B,M,O	B,L					O			
Melittidae												
Mutillidae						O						
Mymaridae	L,B,O	B,L,M,O	B	B,L,O	B,M	B,L,M,O	M	M		B,M,O	B,L,M,O	B,L,M,O
Perilampidae	L,M,O	L,M,O		B,M	B,M	B,L,M,O	B,L,M,O	B,L,M,O		B,O	B,L,M,O	B,L,M,O
Platygastridae							B					
Proctotrupidae							L	B				
Pteromalidae	B,M,L	B,L,M,O	B,O	B,M	B,M	B,L,M,O	B,M,O	B,M,O			B,L,M	M,O
Scelionidae	B,L,M	B,L,M,O		L			B,L	B,L,M,O	B	L		B
Sphecidae		O	O		B		L			L,M,O	B	L
Torymidae							M	B,M				
Vesipidae	B										O	
Lepidoptera												

	May						**June**					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Arctiidae											B	
Bucculatricidae												
Crambidae	M			M	M,B	B,L,O					B,L,M	
Coleophoridae								L				
Eriocraniidae						B					M	
Gelechiidae	M		L	O	B,L,M,O	B,O		B			B,L,M,O	
Geometridae	M	M			O	O					M,O	O
Gracillariidae	M,O	L,M		M	B,L,M,O	B,L,M,O					B,L,M,O	O
Heliodinidae												
Heliozelidae											B	
Hesperiidae								O	O,B	B,O		
Noctuidae		M,O	L	O	B,L,M,O	B,L,M,O		M			B,L,M,O	B
Opostegidae												
Pieridae	B,M	B,M	L,M					L	L	L		
Pterophoridae												
Pyralidae											M	
Sphingidae												
Tineidae	L		L,M,O	B,L	B,L,M,O	B,L,M,O					L,M,O	O
Zygaenidae												
Neuroptera												
Chrysopidae					B,L,M	B,L,M,O					L,M	
Hemerobiidae					M	B,O						
Orthoptera												
Acrididae	B,O		B,L,M,O	M,O			B,M	B,L	M,O	L,O	B	
Gryllidae	B,M,O	B,O	L	B,O			B,M,O	B,L,M,O	M			
Gryllacrididae	B							M,O				
Phasmatodea												
Heteronemiidae		O										
Psocoptera	L,O	M	M,O	B,L,M,O	B,M,L	B,M,O			L	B,L,M	B,L,M,O	B,O
Siphonoptera												
Pulicidae	L,O	M										
Thysanoptera	B,L,M,O	B,O	B,L,M,O	L,M,O	B,O	M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M,O	B,L,M	B,O

	July						**August**					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Arctiidae												
Bucculatricidae												L
Crambidae					B	B,L,M					L,M,O	L,M,O
Coleophoridae												
Eriocraniidae												
Gelechiidae					B	B,O					L,M,O	L,M,O
Geometridae			O			L,M,O					B,O	O
Gracillariidae		M			O	O						
Heliodinidae							B	B,O	M		L	
Heliozelidae												
Hesperiidae		L	O									
Noctuidae		O			B	L,M,B		M			B,O	L,O
Opostegidae											B,L,O	
Pieridae				L						L		
Pterophoridae						B					B	
Pyralidae								B				
Sphingidae						M,L					L	
Tineidae		B,O	B	B		B,M	B,L,M,O	M	O	M,O	L,O	M,O
Zygaenidae												L
Neuroptera												
Chrysopidae					B,M	B,L					B	M,O
Hemerobiidae						O						
Orthoptera												
Acrididae		B,L,M	O	B,L,O		M	B,M	L,M,O		B	B	L
Gryllidae	B,L,M,O	B,L,M,O					L,M	B,L,M,O		M		O
Gryllacrididae												
Phasmatodea												
Heteronemiidae												
Psocoptera	B,M,O	M		L,M,B	B,M	B,L,M,O	M	M	L	M	B,M,L	L,M,O
Siphonoptera												
Pulicidae	B,M,O	M					M	M				
Thysanoptera	L,M,O	L,O	B,M,O	B,L,O		O	L,M,O	B	B,L,M,O	B,L,M	M	

	May						June					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Trichoptera												
Hydroptilidae					M	O					B	
MOLLUSCA												
Bivalvia												
Sphaeridae	L											
Gastropoda												
Succineidae		O						O				

	July						August					
	Pitfall		Pan		Aerial		Pitfall		Pan		Aerial	
	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland	Upland	Wetland
Trichoptera												
Hydroptilidae	M										L	M
MOLLUSCA												
Bivalvia												
Sphaeridae												
Gastropoda												
Succineidae												

Figure 1.1 Map of sites and sampling schematic. The four playas were located in Beaver and Texas Counties of Oklahoma USA. The maps are to scale while the schematic design of the study is not to scale. The thicker black lines represent rivers found in the Oklahoman panhandle, while the triangles represent nearby towns. The sampling design was conducted at each of the four playas on the map.

Figure 1.2 Interaction plots for monthly invertebrate taxa richness (a) and abundance (b). Graphs show mean (± standard error) invertebrate richness and abundance captured each month in each trap type and the mean for all trap types.

Figure 1.3 Ordination of invertebrate abundance in each trap type (a) and caught in each month (b). Plots show non-metric multidimensional scaling results for samples pooled by date and trap type (colored-pan traps N = 32, pitfall traps N = 32, aerial traps N = 28). Analysis of similarity (ANOSIM) results are shown.

Figure 1.4 Invertebrate richness (a) and abundance (b) of the wetland and upland sites for each trap type. Statistical analyses tested each trap type (colored-pan traps N = 32, pitfall traps N = 32, aerial traps N = 28) using location (wetland versus upland) as the dependent factor. The line within each box represents the mean. The top and bottom of the box represents the 75th and 25th quartiles, respectively. The whisker bars represent the 90th and 10th deciles, and dots represent any outliers. Asterisks (*) denote that wetland and upland differed significantly.

Figure 1.5 Non-metric multidimensional scaling (NMDS) ordinations of the invertebrate assemblages caught in each trap type. The community caught by (a) pitfall traps (N=32), (b) colored-pan traps (N = 32) and (c) invertebrates caught in aerial traps (N = 28).

Figure 1.6 The eleven taxa identified by indicator species analysis that were located primarily in either the upland or the playa wetland. Asterisks denote statistical differences by location. The other taxa in the figure had p-values > 0.05 and < 0.10. The line within each box indicates the mean. The top and bottom of each box represent the 75th and 25th quartiles, respectively. The whisker bars represent the 90th and 10th deciles, and dots represent any outliers.

Figure 1.1

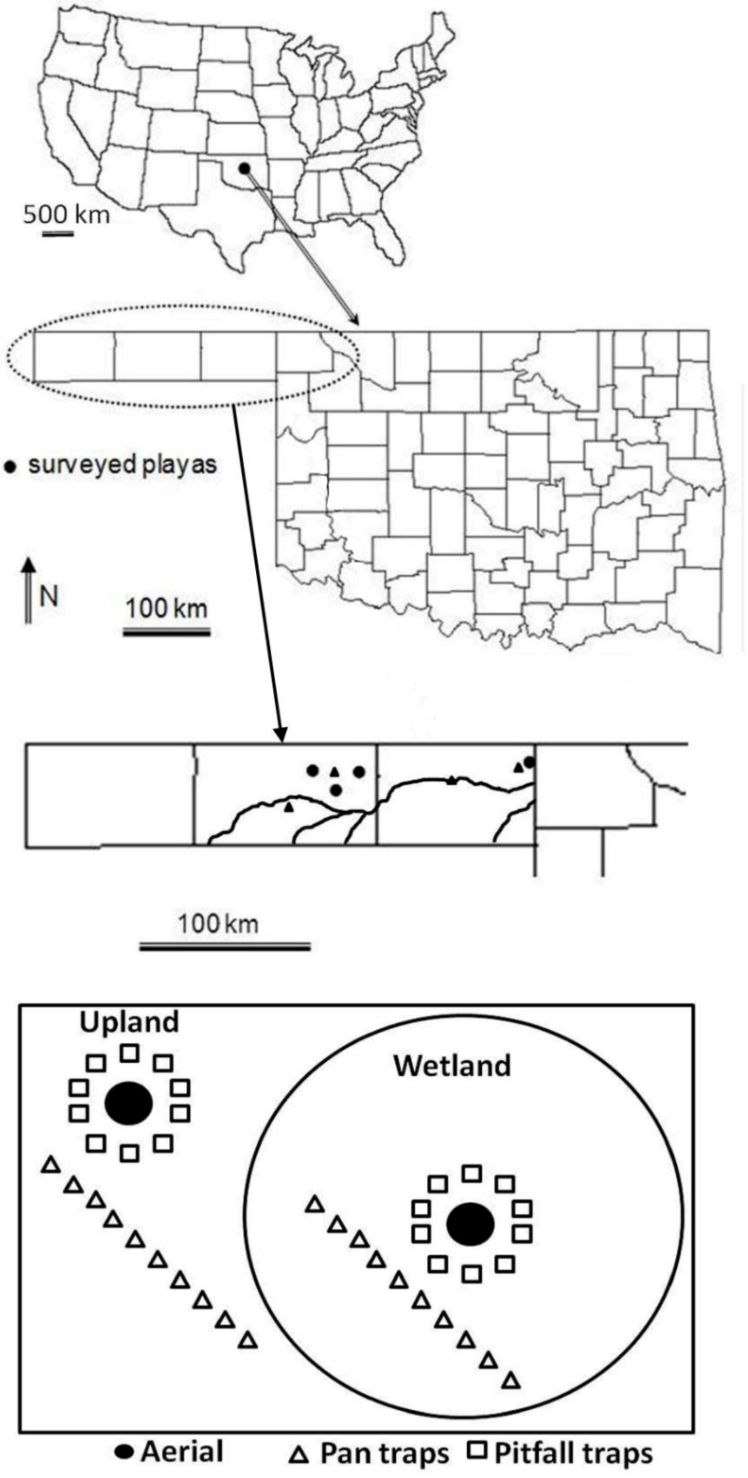

500 km
surveyed playas
N
100 km
100 km
Upland
Wetland
Aerial
Pan traps
Pitfall traps

Figure 1.2

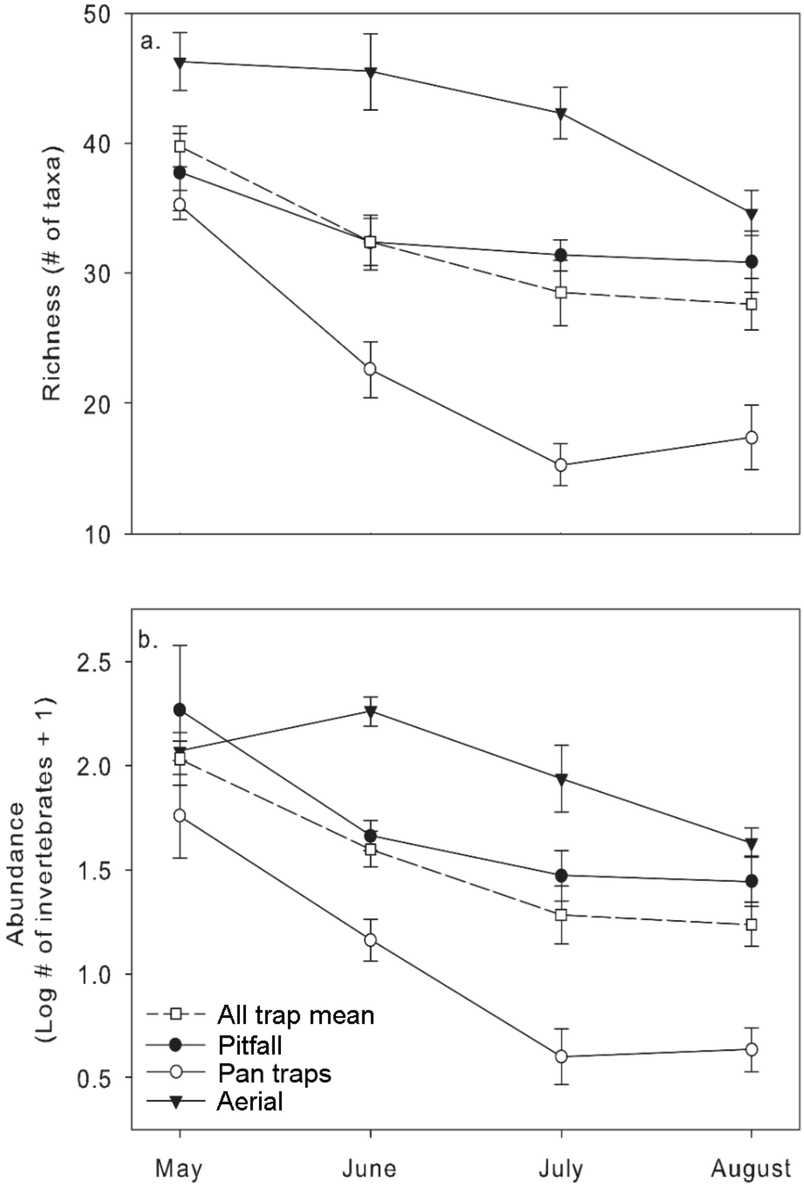

a.
Richness (# of taxa)
50
40
30
20
10
b.
Abundance
(Log # of invertebrates + 1)
2.5
2.0
1.5
1.0
0.5
All trap mean
Pitfall
Pan traps
Aerial
May
June
July
August

Figure 1.3

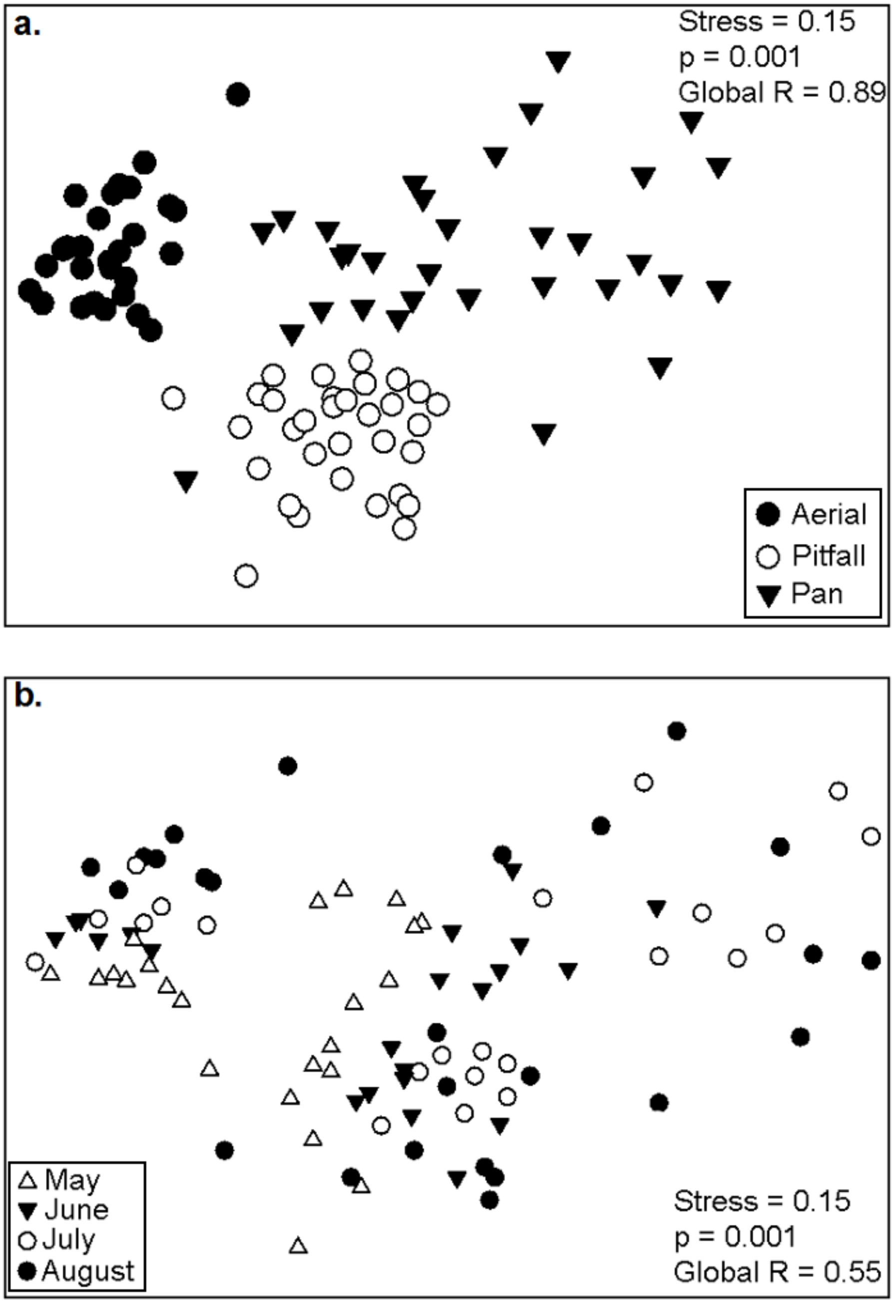

a.
Stress = 0.15
p = 0.001
Global R = 0.89
● Aerial
○ Pitfall
▼ Pan
b.
△ May
▼ June
○ July
● August
Stress = 0.15
p = 0.001
Global R = 0.55

Figure 1.4

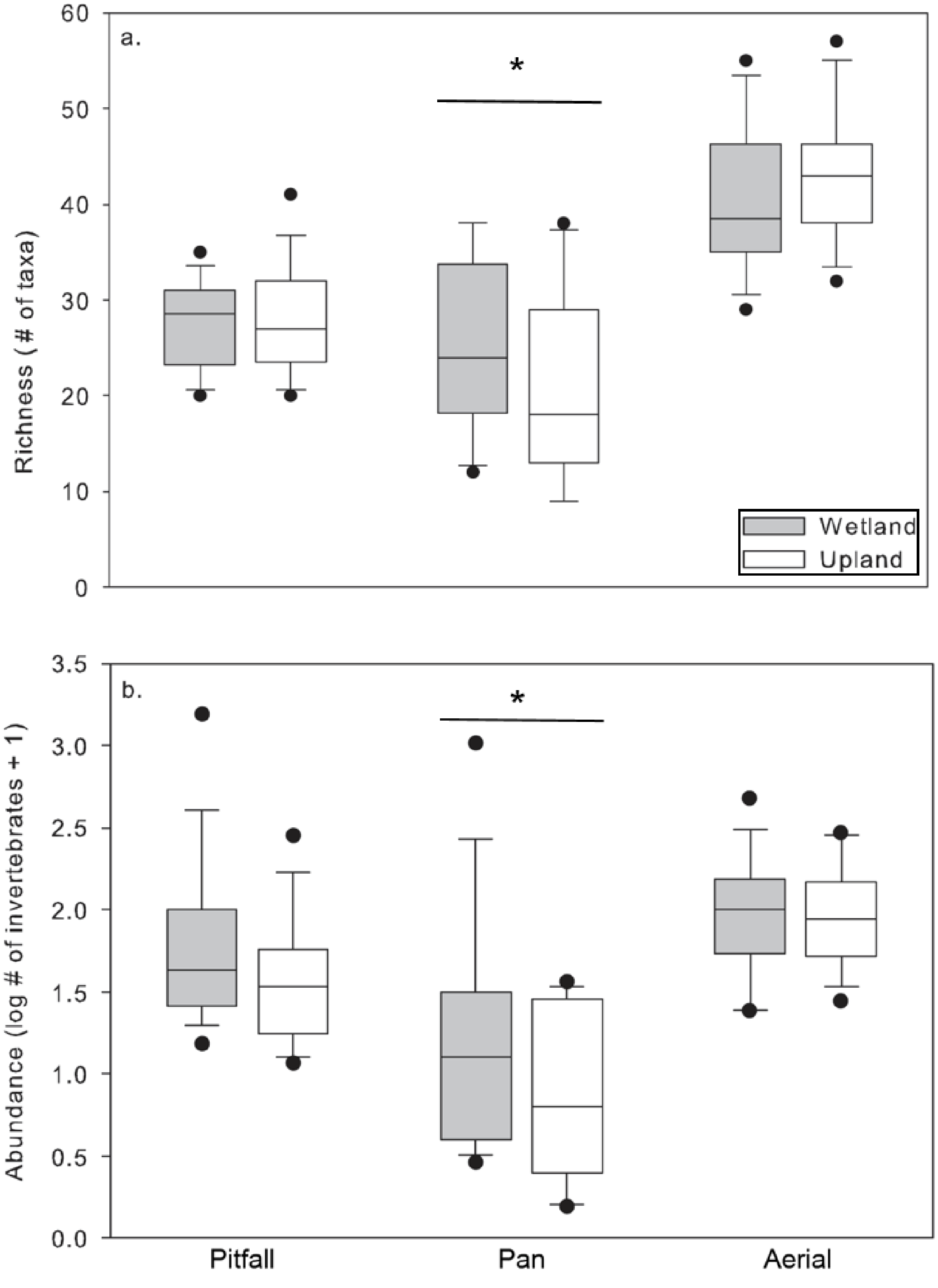

a.
*
Richness (# of taxa)
0
10
20
30
40
50
60
Wetland
Upland
b.
*
Abundance (log # of invertebrates + 1)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Pitfall
Pan
Aerial

Figure 1.5

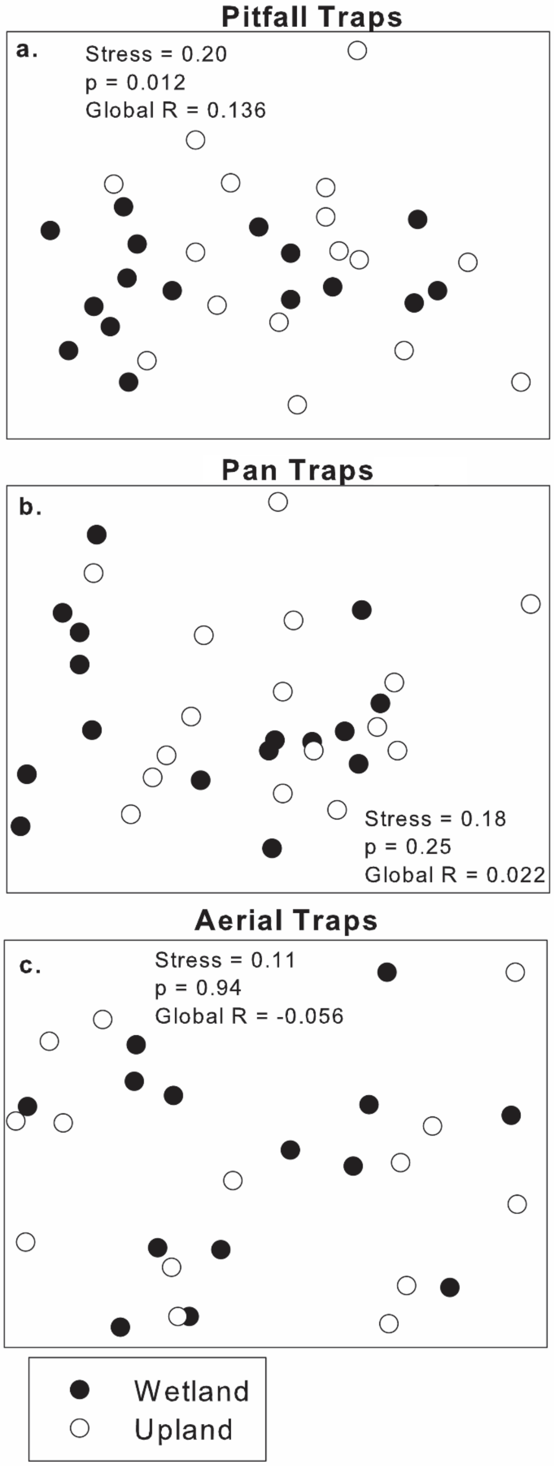
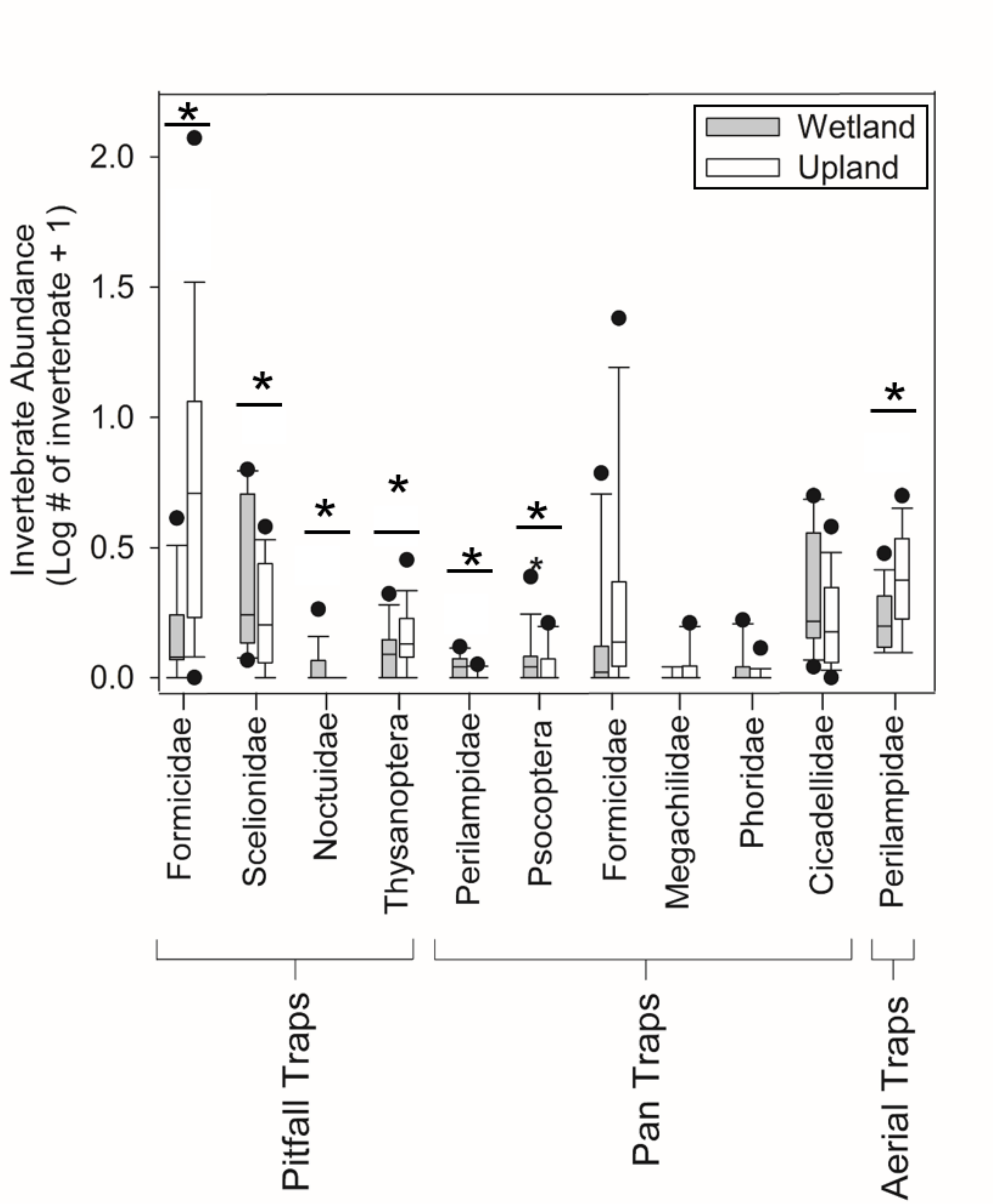

Pitfall Traps
a.
Stress = 0.20
p = 0.012
Global R = 0.136
Pan Traps
b.
Stress = 0.18
p = 0.25
Global R = 0.022
Aerial Traps
c.
Stress = 0.11
p = 0.94
Global R = -0.056
● Wetland
○ Upland

Figure 1.6


Wetland
Upland
Invertebrate Abundance (Log # of invertebrate + 1)
0.0
0.5
1.0
1.5
2.0
*
Formicidae
Scelionidae
Noctuidae
Thysanoptera
Perilampidae
Psocoptera
Formicidae
Megachilidae
Phoridae
Cicadellidae
Perilampidae
Pitfall Traps
Pan Traps
Aerial Traps

CHAPTER 2

Spatial distribution of resting stages of crustaceans and other aquatic invertebrates in playa wetlands

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ABSTRACT

Crustaceans in temporary wetlands have resting stages that allow them to persist in the soil during dry phases. We examined the spatial distribution of resting stages of invertebrates in the soil of playa wetlands. We took soil cores near the center and near the edge of the playas and in the surrounding upland of the dry playas. We then rehydrated the soil cores for two weeks. We found higher abundance and taxa richness, and a different taxonomic composition, in the playa center than in the upland. Invertebrate abundance and taxa richness were intermediate at the wetland edge and taxonomic composition overlapped with those from the center and upland. Crustaceans (e.g. tadpole shrimps and calanoid copepods) were more abundant in the wetland center than at the edge or upland. Environmental factors and invertebrate behavior may play a role in organizing the spatial distribution of aestivating stages of aquatic invertebrates.

INTRODUCTION

Temporary wetlands have unique aquatic invertebrate (Batzer *et al.*, 1999; Batzer & Wissinger, 1996) and vertebrate (Babbitt *et al.*, 2003) assemblages that can cope with the stresses involved with life in variable habitats. These aquatic animals have been classified as either transient species or resident species (Hall *et al.*, 1999). Transient species are highly-mobile taxa (e.g. flying insects) that can emigrate to other water bodies when their habitat becomes inhospitable (Wissinger, 1995) and return when conditions improve. Resident species tend to be less mobile taxa (e.g. crustaceans and molluscs) that cannot emigrate and must persist in the wetland throughout the inhospitable dry periods (Begon *et al.*, 1999).

Resident organisms use various life history strategies to survive dry periods (see reviews by Boulton & Suter, 1986; Wiggins *et al.*, 1980; Williams, 2005; Williams & Hynes, 1976). Some resident aquatic organisms use resting stages to persist in wetland soils through the dry phase (Williams, 1998; Williams, 2005). These resting stages include aestivating stages, resting eggs, cysts, and ephippia. The composition of resting stages in the soil has been termed the invertebrate seedbank (Boulton, 1989), which is analogous to the plant seedbank in soils. Resting stages in the invertebrate seedbank can remain viable for several years without inundation (Begon *et al.*, 1999; Boulton & Lloyd, 1992; Brock, 1998; Frouz *et al.*, 2003; Hildrew, 1985; Jenkins *et al.*, 1997). Once the correct environmental cues occur, organisms in the invertebrate seedbank hatch or break dormancy (Brewer, 1964; Broch, 1965, 1969; Brown & Carpelan, 1971; Gjullin *et al.*, 1941; Weissman-Strum & Kindler, 1963). The organisms that emerge from the invertebrate seedbank after inundation are some of the earliest and ecologically most important colonizers of temporary wetlands (Gleason *et al.*, 2004; McLachlan & Cantrell, 1980; Richardson *et al.*, 1972; Sublette & Sublette, 1967).

Anthropogenic modifications to temporary wetlands can decrease the abundance and diversity of invertebrates hatching from the seedbank. Shortening or lengthening the hydroperiod of temporary wetlands prevents some invertebrates from hatching or breaking dormancy (Golladay *et al.*, 1997; Merdic & Sudaric, 2003). In addition, pesticide and chemical use in nearby agricultural fields affects invertebrate emergence (Angeler & Moreno, 2007; Angeler *et al.*, 2006). Sedimentation of soil from the tilling of agricultural fields near wetlands decreases the abundance of invertebrates and plants that emerge from their respective seedbanks (Gleason *et al.*, 2003).

Playa wetlands continue to undergo severe anthropogenic modifications, especially hydroperiod alteration (Bolen *et al.*, 1989) and increased sedimentation (Luo, 1994; Luo *et al.*, 1997). We need more knowledge about the functioning of the invertebrate seedbank to better understand the effects of these perturbations on playa invertebrate ecology. Our objective was to examine the distribution of the invertebrate seedbank across playa wetlands based on emergence from wetted soils. Hydroperiod and the frequency of inundation may differ across a playa wetland, with the deepest portion having longer, more frequent inundation than the shallower edges. Consequently, we predicted higher invertebrate emergence and diversity from seedbanks near the center of playas than near the edge or in the upland soils. While other studies have examined the number of aestivating cysts across other types of temporary wetlands (e.g. Avery, 1940; Thiéry, 1997), our study differs because we rehydrated dry playa wetland soil and examined actual invertebrate emergence.

METHODS

We collected dry soil cores monthly between May and August (Table 2.1) (half of the total annual rainfall normally occurs during these months) (Brock *et al.*, 1995; McPherson *et al.*, 2007) in 2010 from four playas in western Oklahoma (Table 2.2). At each dry playa, we collected two soil cores at least 10 m apart from three different locations: the upland; the edge of the playa; and the center of the playa. Although playas were dry, vegetational differences between the playas and upland were apparent and allowed delineation of playa edges. The upland soil was collected at least 15 m from the edge of the wetland. The edge soil was collected within the playa near the elevation break and vegetation change. The center soil was collected near the center of the playa. Each soil core was 42 cm x 33 cm, with a depth of 10 cm.

We transported the soil to a greenhouse at the Aquatic Research Facility at the University of Oklahoma in Norman, Oklahoma USA. The following day, we rehydrated the soil with unsterilized and untreated well water to a water depth of approximately 5 cm in plastic microcosms. We covered the mesocosms with a mesh net to prevent any aerial insect colonization. If needed, water was added throughout the experiment to maintain a depth of 5 cm. The mesocosms were exposed to ambient photoperiod and similar seasonal temperatures. After two weeks, we collected the invertebrates by pouring the water column and the uppermost layer of soil through a 250-µm sieve. We then did a visual check of the mesocosm to ensure that no macroinvertebrates were left on the soil surface. The samples were then preserved in 70% ethanol until sorted in the laboratory. The use of 250-µm sieve did exclude the collection of some microinvertebrates (e.g. rotifers, microcrusteans). Invertebrates were identified to the lowest practical taxonomic level using keys found in Smith (2001), Merritt *et al.* (2008), and Thorp and Covich (2009). Due to the fact that most of the invertebrates were still in the immature stage of development, taxonomic resolution was limited in the study.

To reduce variability, the invertebrates collected from the two soil cores from each location (center, edge, and upland) of a given playa were pooled and averaged for each playa. Richness (the number of invertebrate taxa) and abundance (# of invertebrate/m^2) were calculated for each location for all playa lakes. Since taxa richness data did not meet all of the assumptions for ANOVA, taxa richness was analyzed with a Kruskal-Wallis rank test (SigmaStat, Systat Software Inc.). Abundance data were log + 1 transformed and analyzed using a three-way ANOVA with soil location, playa/wetland, and month as classification variables (i.e. “treatments) (SigmaStat, Systat Software Inc., Chicago, Illinois), followed by Tukey’s *post hoc* test. Because we were unable to collect all samples at once and sampling extended over a 3-month period, we treated month of collection as a block effect variable. (De Szalay and Resh, 2000; Gleason *et al.*, 2003).

Community assemblages were compared by ordination using non-metric multidimensional scaling (NMDS, Primer v6, Primer-E Ltd). To test for significant differences among soil locations and among playas, we used an analysis of the similarity (ANOSIM) test with the Bray-Curtis similarity metric option on assemblages pooled across months. We examined the assemblages using the entire invertebrate assemblage and again with only the aquatic (and semi-aquatic) taxa. In addition, an indicator species (taxa that appear in high abundance and high frequency) analysis was conducted on both sets of data (entire and aquatic) to identify taxa that were more likely found in the center, edge, and upland of playas (Dufrêne & Legendre, 1997). Significance was determined in the indicator species analysis by a Monte Carlo test with 4999 random permutations (PC-ORD 6, MJM Software Design). All taxa identified as an indicator taxon were then analyzed using a one-way ANOVA to determine any abundance differences among the different playa locations (Bright *et al.*, 2010).

RESULTS

We identified 32,425 organisms that emerged from 42 soil cores. The range of invertebrate abundance was 310 to 7,222 invertebrates/m^2 with a mean of 1,685.7 ± 266.8 SE individuals/m^2. These invertebrates included representatives from 27 aquatic taxa. The most common crustaceans, which were found in more than half of the samples, were Ostracoda (Latreille, 1802) and Cladocera (*Streblocerus* sp.) (G.O. Sars, 1862), while the other common invertebrate taxa included Chironomidae (two sub-families, Chironominae and Tanypodinae), Nematoda (Rudolphi, 1808), and *Psychoda* (moth flies) (Table 2.3).

Aquatic-taxa richness varied only with sampling location ($H_{2,48} = 11.60$, $p = 0.003$; Fig. 2.1a). The center of the dry playas had the greatest number of aquatic taxa emerging after rewetting. The upland had approximately 40% fewer aquatic invertebrate taxa emerging than did the center of the playa, and the edge of the dry playa lakes had intermediate richness that did not differ significantly from the soil from either the center of the playas or the upland.

The abundance of aquatic invertebrates emerging from the rehydrated soil differed among sampling locations ($F_{2,48} = 3.42$, $p = 0.06$; Fig. 2.1b). The abundance data were more variable than the richness data but mirrored the pattern of the richness data, with the greatest number of invertebrates emerging from the center of the playa and the lowest number emerging from the upland. Samples taken near the edge of the playa lakes had an intermediate number of emerging invertebrates. In addition to the difference among locations, invertebrate abundance differed among sampling dates. Abundance varied by month ($F_{3,48} = 4.08$, $p = 0.02$; Fig. 2.2). Peak abundance occurred in June and July, with about twice as many invertebrates present than in May and August.

Community analysis showed similar trends to the taxa richness and abundance analyses. Different aquatic communities developed among the playa locations (ANOSIM: Global R = 0.201, $p = 0.01$; Fig. 2.3a). The invertebrate assemblages from the upland soil differed from the assemblages from the center, and the assemblages from the edge of the playa did not differ from assemblages from either the upland or the center of the playa. In the NMDS ordination, these edge samples were interspersed between both the upland and center samples. In addition, community analyses showed that one playa wetland had a different invertebrate community than the rest of the playa wetlands (Fig. 2.3b; Global R = 0.18, $p = 0.007$).

Indicator species analysis of aquatic taxa identified only one taxon that differed among the sample locations. Ostracods emerged in significantly greater numbers from soil from the center and edge of the playas than from soil from the uplands ($F_{2, 48}$ = 8.68, $p < 0.001$; Fig. 2.4a). Inclusion of terrestrial and aquatic invertebrates in the analysis identified more indicator species ($p < 0.01$; Fig. 2.4b). Cladocerans (*Streblocerus* sp.), nematodes, ostracods, clam shrimps (*Lynceus* sp.), tadpole shrimps (*Triops longicaudatus*), calanoid copepods and snails (*Radix* sp.) were more likely to be found near the center, while psycodids, cecidomyiids, and oribatid mites were more likely to found in upland soils (Fig. 2.5a,b). Indicator taxa for the center of playas were mostly aquatic or semi-aquatic and indicator species from the uplands were primarily terrestrial, although nematodes (playa center) and psycodids (uplands) include both aquatic and terrestrial species.

DISCUSSION

Taxonomic richness, abundance, and assemblage composition of invertebrates that emerged from rewetted dry playa soil showed a clear transitional pattern from the center of playas to the uplands. This distributional pattern is illustrated by branchiopods (clam shrimps, fairy shrimps, cladocerans, and tadpole shrimps), which were the most abundant organisms found in the center of the playa wetlands and decreased in abundance at playa edges. Branchiopods are crustaceans with low dispersal abilities that are generally adapted to life in temporary habitats, surviving dry periods in resting stages. Our research with emerging invertebrates corroborates the distributional pattern of previous studies, showing more brachiopod cysts in the center than near the edge of non-playa wetlands (Mura, 1991; Thiéry, 1997). Branchiopods play a vital role in playa lake ecology because they are early playa wetland colonizers (Moorhead *et al.*, 1998; Williams, 1998) and contribute a significant portion to invertebrate biomass in playa wetlands. These invertebrates also comprise a significant component of waterfowl diets in playas (Bergman & Derksen, 1977).

Environmental factors could drive the spatial distributional pattern of aestivating stages of playa invertebrates. Hydroperiod exerts a strong influence on the ecology and life history strategies of temporary wetland invertebrates (Darby *et al.*, 2002; Tronstad *et al.*, 2005). The hydroperiod at any particular location varies around and within the playa wetland. The surrounding upland has little or no hydroperiod because of water removal as runoff and a higher soil permeability (Osterkamp & Wood, 1987), whereas hydroperiods in playas are longer due to lower soil permeability. Additionally, hydroperiod can vary within a playa. The edge of the playa dries faster than the center of the playa because of shallower depths of standing water at playa edges relative to playa centers (Grubb & Parks, 1968). Because of unequal drying times across temporary wetlands, organisms are concentrated in the center as the wetlands dry (Khalaf & Hall, 1975; McLachlan & Ladle, 2001; Mura, 1991), where they can complete their life cycle. In addition to the central concentration of invertebrate abundance, resting eggs located near the edges can be transported with sediment towards the playa center during inundation (Davis *et al.*, 1984; Lehman, 1975; Likens & Davis, 1975).

Invertebrate behavior might explain the differences in spatial distribution of resting stages in playa wetlands (Thiéry, 1997). For example, we found the highest abundance of cladocerans in the center of the playa because these species might prefer the open water to the littoral zones. The cysts and ephippia of planktonic cladocerans were found in higher abundances in the profundal zone of wetlands (Herzig, 1985) and permanent ponds (De Stasio, 1989) than the littoral zones. Futhermore, we found higher abundances of calanoids near the center, which could be attributed to calanoids' preference for open water (Hutchinson, 1967; Wetzel, 2001). In addition, many species of fairy shrimp regularly drop cysts from a brood pouch (Avery, 1940; Murugan *et al.*, 1996), hence more cysts might be dropped in the center of playas because of the higher concentration of these relatively long-lived organisms towards the center as the playas dry.

Whereas crustaceans use resting eggs and cysts, other types of aquatic organisms survive periods of drought and drying by burrowing into the soil. When the soil becomes inundated after a dry period, these organisms emerge from the soil to complete their life cycle. Some organisms that aestivate in the soil are amphibians (Smith *et al.*, 2012) and snails (Heckman, 1979). Although we did not find any vertebrates that emerged from the soil in the playas that we sampled, we did find snails. We found higher abundance of *Radix* in the soil from the center of the playas. These snails burrow and aestivate within wetland soil to survive dry periods (Brown, 1979; Eisenberg, 1966; McMahon, 1983), which corresponds to the pattern we found in this study.

In addition to environmental and behavioral factors, the characteristics of the resting cysts could contribute to the spatial distribution within a playa. Cysts can differ in buoyancy (Broch, 1969; Hajirostamloo, 2008; Sorgeloos, 1997). Wind and water currents primarily determine the distribution of buoyant cysts, whereas adult behavior and location determine the distribution of sinking cysts. Different egg characteristics (i.e. water content, ultrastructure) affect the buoyancy of cysts and ephippia.

Indicator taxa from upland soils are generally associated with moist terrestrial habitats. When all taxa were included in the analyses, we saw higher abundance of the cecidomyiids in the upland soil. Tronstad *et al.* (2005) found a similar trend of cecidomyiids in rehydrated higher-elevated floodplain soil. Furthermore, *Psychoda* sp. were found in greater abundance in upland soil than playa wetland soil. Psychodids prefer to breed and lay eggs in damp, but not flooded, decaying matter, which is more likely found on the upland than within inundated playa lakes (Satchell, 1947).

Some aquatic species emerged from upland soil. These organisms were typically cladocerans or ostracods, which have resting stages that can be passively dispersed via winds (Bilton *et al.*, 2001; Dahms, 1995; Dodson & Frey, 1991; Smith, 2001), in digestive tracts of birds (Proctor, 1964; Proctor *et al.*, 1967; Swanson, 1984), or on other animals (Havel & Shurin, 2004; Swanson, 1984). Passive dispersal may be an important dispersing mechanism for aquatic organisms in ephemeral aquatic communities (Vanschoenwinkel *et al.*, 2008). For example, some cladoceran behaviors and ephippia characteristics can increase the chance of passive dispersal (Cáceres *et al.*, 2007; Fryer, 1996; Green & Figuerola, 2005; Schultz, 1977). Wind dispersal would also allow for dispersal among different playas and provide a mechanism for recolonization of invertebrates in playa lakes.

Although wind dispersal is likely the cause of aquatic organisms located in upland soils, aquatic invertebrates might also have dispersed to the upland sites through inundation. Wetlands in cropland have greater fluctuations in water levels than wetlands in grasslands (Euliss & Mushet, 1996), so inundation that overtops the playa lake edges are more likely and such inundated upland areas may have deposited resting stages.

Some aquatic invertebrates purposely lay eggs near or above the water's edge – possibly a mechanism to ensure adequate water depth for their life cycles before emergence. For example, female *Aedes* mosquitoes prefer to lay their eggs above the waterline of wetlands so that when the wetland fills their eggs will hatch (Merritt *et al.*, 2008). Although *Aedes* larvae did not emerge from our samples, this species has emerged from other soil samples from playas (Bright and Bergey, unpublished), indicating that the edge is not a static location, but varies with each inundation. Other species (i.e. *Triops numidicus* (Grube, 1865)) may similarly lay their eggs near the edge to ensure that the wetland hydroperiod will be sufficient to complete their life cycle (Thiéry, 1997).

Results of this study indicate that the central, deepest area of playas is critical to maintaining biodiversity and abundance of playa invertebrates. This central area is also the area most susceptible to sediment deposition when sediments are mobilized from disturbed uplands during heavy rains. To develop effective management strategies, further studies are needed to examine the interactions among upland disturbance, rainfall patterns, sediment mobilization and settlement, and effects of sedimentation on resting stage emergence across playas.

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APPENDIX

Table 2.1. The dates when soil was collected from each playa in 2010.

	Dates Soil was Collected in 2010			
Lunceford Playa	26 May	23 June	21 July	20 August
Balzer Playa	25 May	22 June	20 July	19 August
McKinley Playa	24 May	21 June	19 July	18 August
OWHPA Playa	27 May	24 June	22 July	21 August

Table 2.2 Site descriptions of the four playas used in this study.

	Lunceford Playa	Balzer Playa	McKinley Playa	OWPHA Playa
Location	36°50'37.64"N 100°59'51.89"W	36°47'0.09"N 101°12'12.87"W	36°51'30.21"N 101°19'8.9"W	36°50'32.10"N 100°0'21.94"W
County	Texas	Texas	Texas	Beaver
Area (m^2)	20,000	150,000	300,000	110,000
Managed	Yes	No	No	No
Inundation	Every 2 or 3 months	Rare	Rare	Rare

Table 2.3 Location of taxa found in each of the four playas (C = center, E = edge, U = upland, and N/F not found).

	Lunceford Playa	Balzer Playa	McKinley Playa	OWPHA Playa
Aquatic or Semi-Aquatic Invertebrates				
Hydrachnidae	C, E	C, E	C, E	C
Streblocerus sp.	C, E, U	C, E, U	C, E, U	C, E, U
Daphnia sp. (O. F. Müller, 1785)	C	C, E	E	C, E
Entomobryidae	C, E, U	E, U	U	C, E
Isotomidae		E, U	E	U
Sminthuridae	C, E, U	C, E	C, E, U	C, E, U
Oligochaeta	C, E, U	C, E, U	C, E, U	C, E, U
Nematoda	C, E, U	C, E, U	C, E, U	C, E
Ostracoda	C, E, U	C, E, U	C, E, U	C, E, U
Triops longicaudatus (LeConte, 1846)	N/F	C	C, E	N/F
Lynceus brachyrus (O. F. Muller, 1776)	U	C, E	C, E	C
Radix sp.	N/F	C	N/F	N/F
Cyclopoida (Burmeister, 1834)	C, E, U	C, E, U	E	C, U
Calanoida (G. O. Sars, 1903)	N/F	C	C	N/F
Psychoda	C, E, U	C, E, U	C, E, U	C, E, U
Chironominae	C, E, U	C, E, U	C, E, U	C, E, U
Tanypodinae	C, E, U	C, E, U	C, E, U	C, E, U
Dolichopodidae	C	U	N/A	U
Cecidomyiidae	C, E, U	E, U	C, E, U	C, U
Sciaridae	C	E	C	N/A
Terrestrial Invertebrates				
Aranae	N/F	C	U	C
Orbatidae	C, E, U	E, U	E, U	C, E, U
Onscidae	C, E, U	C, E, U	C, E, U	C, U
Thysanoptera	U	E	E, U	C, E, U
Latriidae	U	N/F	N/F	U
Cydnidae	N/F	N/F	E, U	N/F
Immature Hemiptera	C, E	U	N/F	C, U

Figure 2.1. Taxonomic richness (a) and abundance (number of invertebrates per m^2) (b) of aquatic invertebrates emerging from rehydrated playa soil taken from three locations: near the playa center, near the edge, and from the surrounding upland (N = 4 playas), with four monthly samples from each playa. The line within each box represents the mean. The top and bottom of each box represents the 75th and 25th quartile, respectively. The whisker bars represent the 90th and 10th deciles, and dots represent any outliers. Different letters denote significant differences.

Figure 2.2. Monthly total abundance (number of invertebrates per soil core) of invertebrates emerging from rehydrated soil from four playa lakes in the summer of 2010. Untransformed data are shown. The top and bottom of each box represent the 75th and 25th quartiles, respectively. The line within each box represents the mean. The whisker bars represent the 90th and 10th deciles, and dots represent any outliers. Different letters denote significant differences.

Figure 2.3. Non-metric multidimensional ordination (X and Y axis plots) of abundance data for invertebrates emerging from rehydrated playa soils. Data points are samples and are coded by (a) playa location (center, edge, and upland) and (b) playa (N = 4 playas). The ordination shows the differences of the assemblages among the different locations in and around the dry playa lakes.

Figure 2.4. Distribution of indicator species across playas. The top graph (a) shows invertebrates more likely to be found in the upland than the wetland center. The bottom graph (b) shows invertebrates that are more likely to found in the soil from the playa center than the surrounding uplands. Graphs show means ±1 standard error.

Figure 2.1

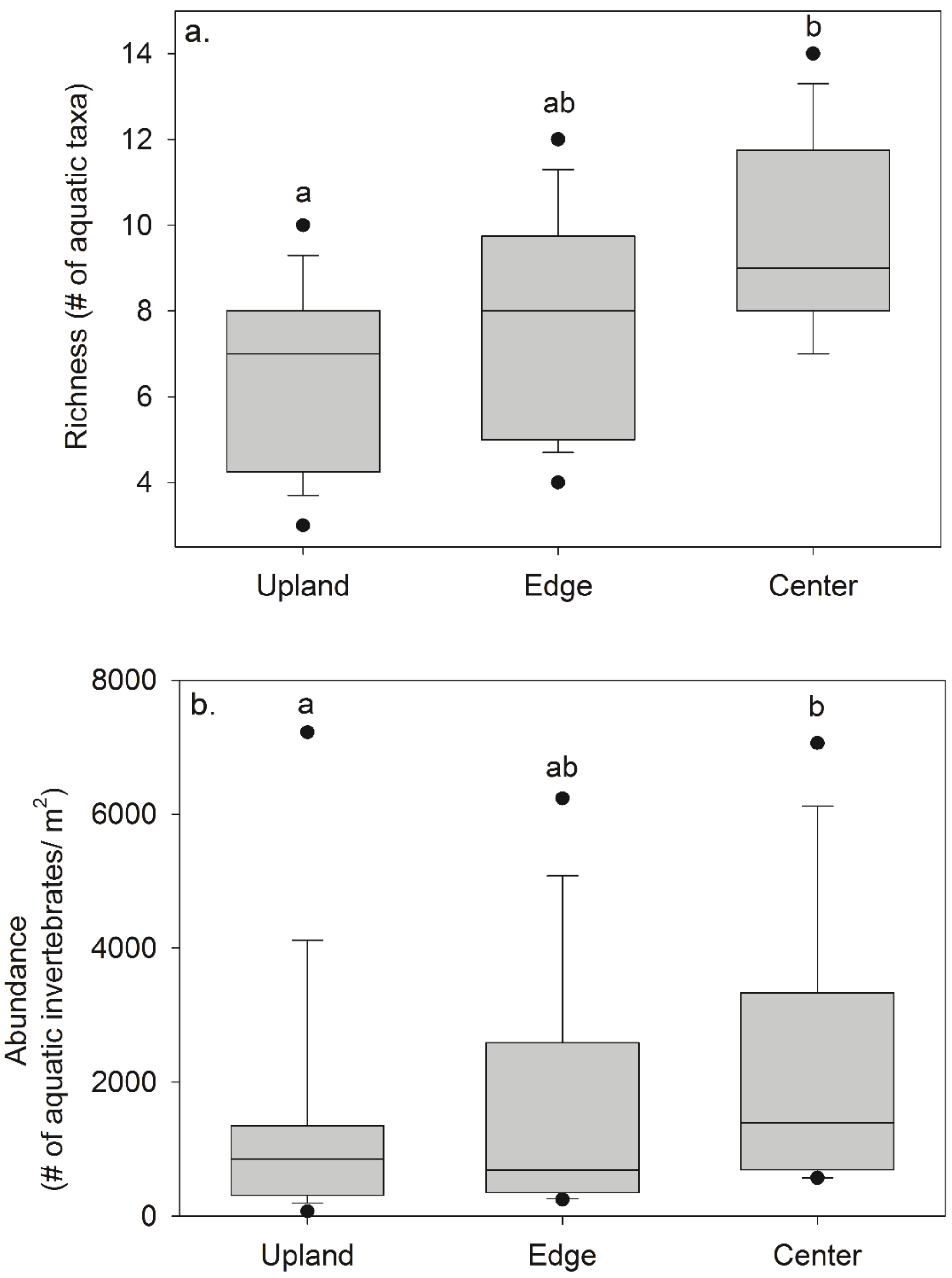
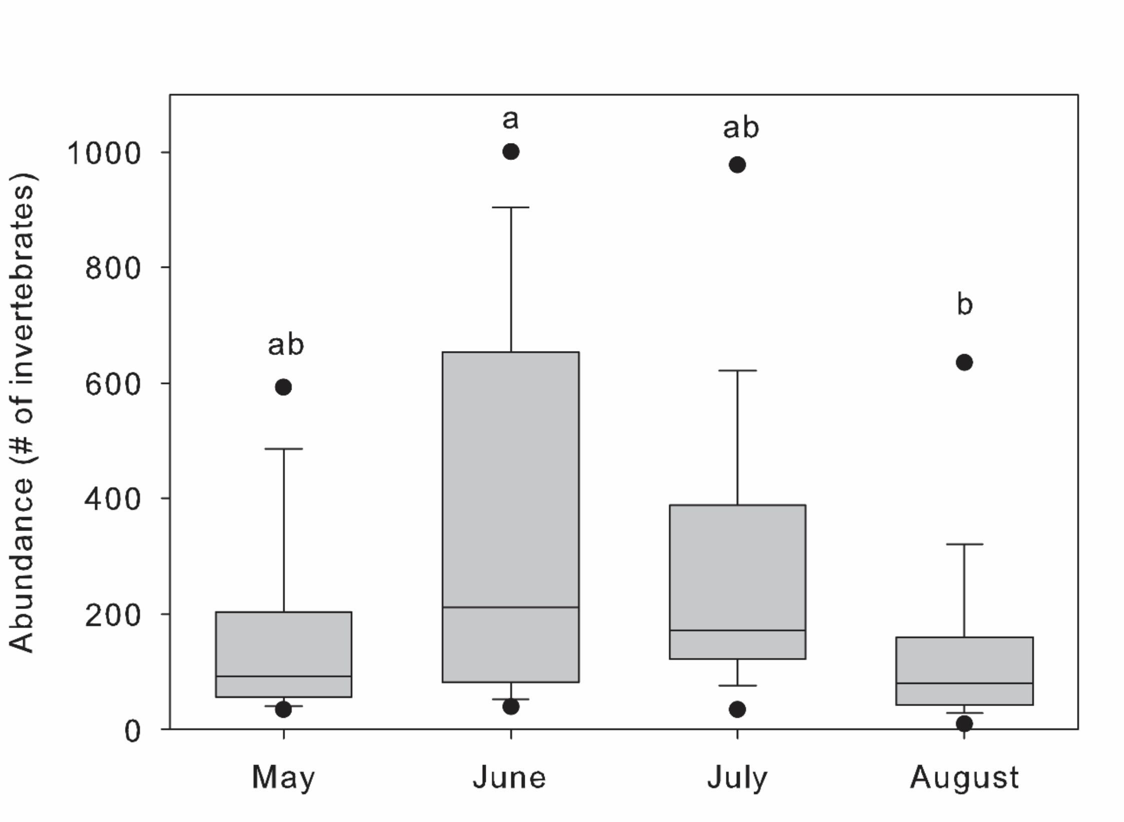

a.
Richness (# of aquatic taxa)
14
12
10
8
6
4
a
ab
b
Upland
Edge
Center
b.
Abundance
(# of aquatic invertebrates/ m^2)
8000
6000
4000
2000
0
a
ab
b
Upland
Edge
Center

Figure 2.2



Abundance (# of invertebrates)
0
200
400
600
800
1000
May
June
July
August
ab
a
ab
b

Figure 2.3

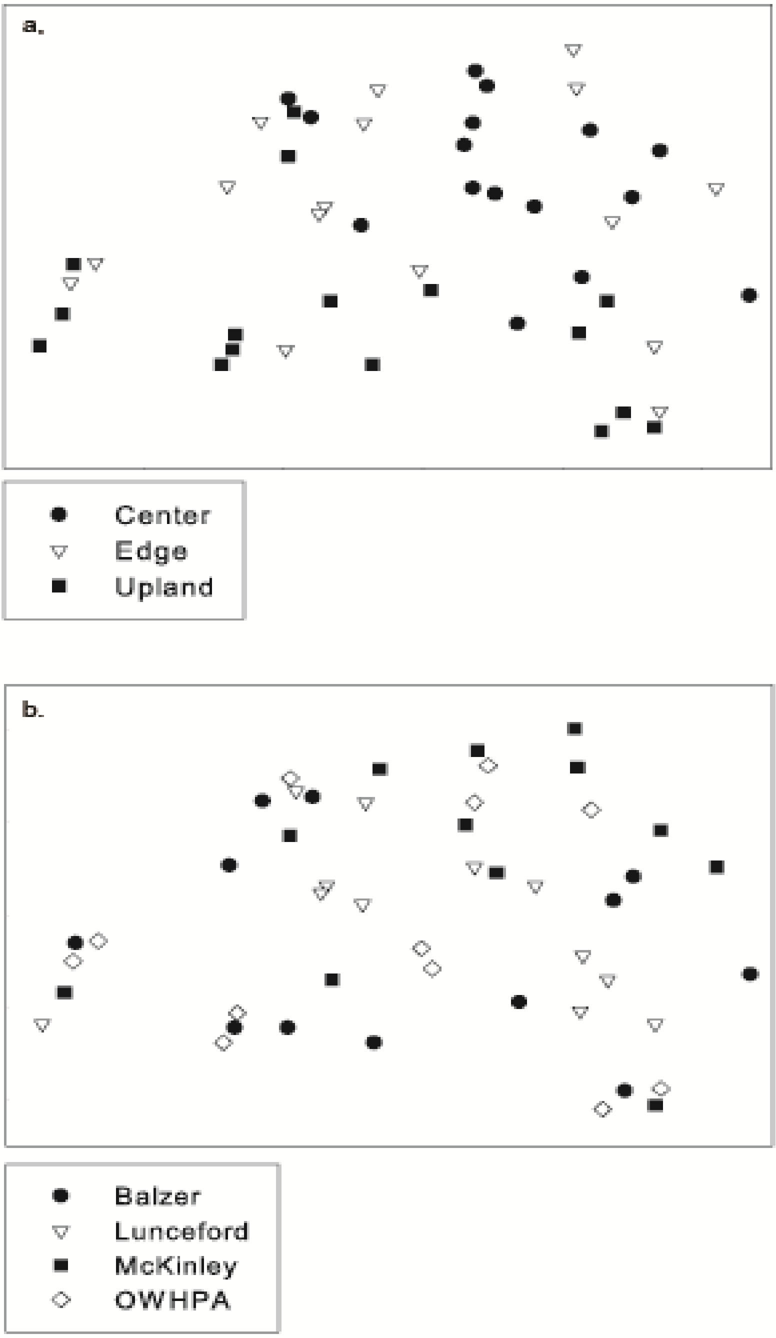
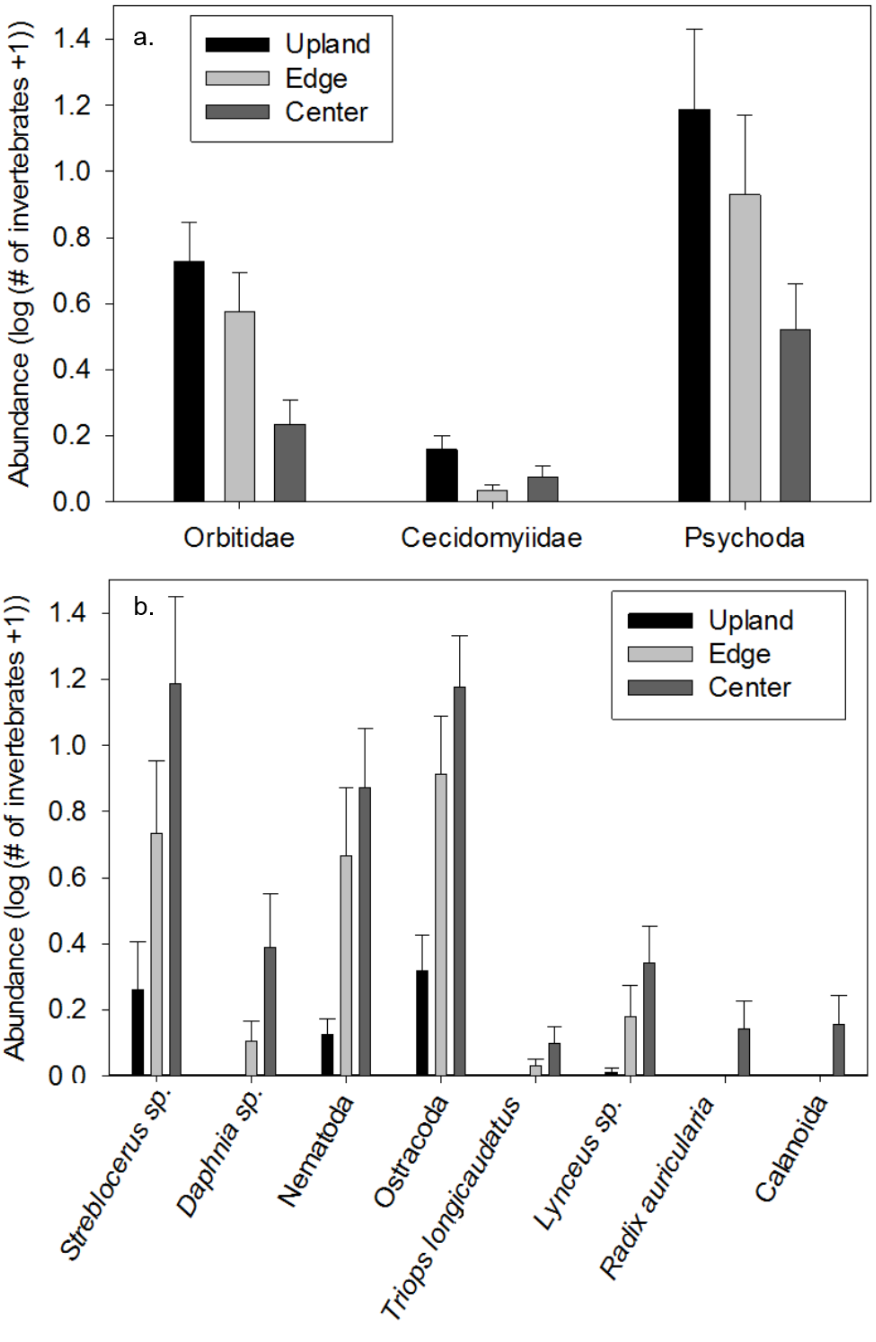


Figure 2.4


a.
Upland
Edge
Center
Abundance (log (# of invertebrates +1))
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Orbitidae
Cecidomyiidae
Psychoda
b.
Upland
Edge
Center
Abundance (log (# of invertebrates +1))
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Streblocerus sp.
Daphnia sp.
Nematoda
Ostracoda
Triops longicaudatus
Lynceus sp.
Radix auricularia
Calanoida

CHAPTER 3

Resident aquatic taxa of isolated, temporary wetlands are susceptible to sedimentation from surrounding uplands

ABSTRACT

The theories of island biogeography, metapopulation dynamics, and landscape ecology attempt to explain the diversity, abundance, and richness of organisms in isolated habitats. Understanding organismal diversity in isolated, temporary wetlands is best approached through metapopulation dynamics within the local landscape context because these wetlands are low points in the landscape, into which nutrients and pollutants flow. A current environmental concern for isolated, temporary wetlands is pollution in the form of sediments from the surrounding uplands, which can flow into wetlands during rain-induced overland flow of water. We examined the susceptibility of the resident taxa of isolated, temporary wetlands to sedimentation. Specifically, we examined whether differing sedimentation depths affect hatching of the resting stages of crustaceans. The addition of sediment on top of the wetland soil decreased both abundance and richness of hatching invertebrates. We then examined a possible mechanism for the decreased hatching rate under increased sedimentation. Because sedimentation affects light penetration in soil, we tested the effect of light on invertebrate hatching and found that light is a necessary environmental cue for hatching. Finally, we examined the location of resting stages in the soil profile and whether buried eggs could hatch if exposed to the correct environmental cues. We concluded that resting eggs were most numerous near the soil surface but some deeper eggs were still able to hatch after exposure the environmental cues. Our experiments demonstrate that burying the resting stages of aquatic invertebrates reduces hatching, in part due to lack of proper environmental cues (light). This burial of invertebrate resting stages by

sediment and the resulting reduction in hatching success might influence prey availability for amphibians and migrating birds that use playa wetlands.

INTRODUCTION

Three current theories attempt to explain the biodiversity of isolated habitats (e.g., oceanic islands, fragmented forests): (1) the theory of island biogeography (MacArthur & Wilson, 1967); (2) metapopulation dynamics (Hanski, 1999); and (3) landscape ecology (Harris, 1984). The theory of island biogeography states that, at equilibrium, islands that are more isolated should have a lower species diversity than less-isolated islands and larger islands should have more species than smaller islands. Metapopulation dynamics theory states that populations of isolated habitats are interconnected via dispersal. Landscape ecology theory states that the species diversity of isolated habitats is influenced by the structure of the surrounding landscape.

Geographically isolated, temporary wetlands can be considered to be similar to oceanic islands (Holland & Jain, 1981; Ebert & Balko, 1987; Hall *et al.*, 2004). When the wetlands become inundated, these habitats become suitable habitats for aquatic taxa while surrounded by an inhospitable landscape. However, there are some distinct differences between isolated wetlands and oceanic islands or fragmented forests. Unlike islands and forests, wetland size does not appear to influence the diversity of organisms inhabiting the wetland (Hall *et al.*, 2004). Additionally, whereas oceanic islands are relatively stable habitats (equilibrium conditions are possible), temporal variation in frequency and duration of available habitat is common in temporary wetlands (Ebert & Balko, 1987). Consequently, aquatic organisms that inhabit temporary wetlands have been selected to exhibit various life histories to survive the variability of their habitats (Lahr, 1997).

The life history strategies that aquatic taxa use to survive in temporary habitats depend on their ability to disperse (Hall *et al.*, 1999). Aquatic taxa able to disperse over great distances (e.g., by flying) are generally transient taxa or non-resident taxa. Non-resident taxa immigrate to inundated wetlands from other waterbodies and emigrate to other waterbodies when the wetland dries. The majority of non-resident taxa are insects. Taxa that cannot disperse persist in the dry wetlands as resting stages (i.e. eggs or aestivating stages). These organisms are considered resident taxa and are mainly crustaceans and gastropods.

Temporary wetlands that are dominated by resident organisms are usually more geographically isolated and, as a consequence, the invertebrate community structure should be dominated by metapopulation dynamics however local landscape affects within wetland conditions (Hall *et al.,* 2004; Angeler & Alvarez-Cobelas, 2005). Therefore, any environmental pollution from the uplands surrounding an isolated wetland may have a greater impact on the invertebrate community than would be the case in a highly-connected wetland system. The invertebrate communities of less geographically isolated wetlands show less impact from anthropogenic stressors because new taxa and organisms can re-colonize faster. Sedimentation from the surrounding upland is an example of such a pollutant and is a great concern for isolated wetlands, especially for possible effects on the resident aquatic taxa that reside in the wetland during dry periods (Angeler & Alvarez-Cobelas, 2005).

Playa wetlands are under severe threat from sediments that enter the system from the surrounding uplands (Luo, 1994; Luo *et al.*, 1997; Luo *et al.*, 1999; Burris & Skagen, 2013; Daniel *et al.*, 2015). Added sediments change the vegetative (Dittmar & Neely, 1999; O'Connell *et al.*, 2013) and zooplankton communities (Euliss & Mushet, 1999; Gleason *et al.*, 2003). We examined the susceptibility of the playa wetland crustacean community to sedimentation. We predicted that as sedimentation increases, the richness and abundance of crustaceans hatching from playa soil should decrease. Since sedimentation affects light penetration into native playa soils, we also examined whether light was a necessary environmental cue for invertebrate hatching or for ending diapause. Finally, to determine whether buried resting stages remain could hatch, we exposed the resting stages from various depths in the playa soil column to the correct environmental cues. We predicted that there would be a greater abundance, richness and of resting stages nearer the soil surface than at deeper depths since eggs nearer the surface will more likely receive the correct environmental cues, for instance light, than eggs at deeper depths.

METHODS

We conducted a series of mesocosm experiments using wetland and upland soils collected from four playas in Texas and Beaver Counties in western Oklahoma, USA. Three of the four playas were probably historically farmed, but currently all of them are enrolled in land conservation programs. Each of the playas has a natural grass buffer to minimize the effects of sedimentation from the surrounding agricultural fields. Additionally, all but one playa are under a natural hydroperiod regime. The managed playa is under moist soil management by the Oklahoma Department of Wildlife Conservation to promote playa use by migrating waterfowl.

General experimental methods

We ran our mesocosms experiments in 34.6 x 21 x 12.4 cm plastic boxes in a laboratory at the University of Oklahoma. Dry soil was collected from the four playas in western Oklahoma in May 2012 and stored covered in plastic tubs in a greenhouse at the Aquatic Research Facility until use (see below). Between 0.75 and 1.0 kg of soil was added to mesocosms; however, the top soil layers (0-2 cm) and (2-5 cm) from the soil depth experiment were closer to 0.5 kg because we used smaller soil cores to collect this soil. We rehydrated the soil in each mesocosm to a 5-cm depth with unsterilized well water. After a two-week rehydration period for each trial, we sampled invertebrates by pouring the water column and the uppermost soil layer through a 250-µm sieve. Invertebrates and other captured materials were preserved in 70% ethanol. We identified the invertebrates to the lowest practical taxonomic resolution with the aid of a stereomicroscope and identification keys in Smith (2001).

Sedimentation depth experiment

Soil collected from the center of four dry playas was pooled and homogenized to decrease variablity of resting stages and added to mesocosms in May 2014 (methods similar to Bright & Bergey, 2015). Since sedimentation comes from the upland, we used addition of upland soil to test the effects of sedimentation on invertebrate hatching. Ten mesocosms were randomly assigned to each of four sedimentation treatments. Three of the sedimentation treatments consisted of adding a 0.25-, 0.50-, or 1.0-cm layer of upland soil, collected near one of the dry playas, over the playa soil; the fourth treatment was a control with no added upland sediment. To avoid hatching of any resting stages in the upland soil, we sterilized the upland soil in an autoclave for two hours (Wolf & Skipper, 1994) before adding it to mesocosms. This trial used a 12-hour light:dark cycle with six 40-watt florescent lights (Phillips™ T12 High CRI C50 Supreme) per treatment, with lights positioned 60 cm above the mesocosms (60 µmol m^{-2} s^{-1} of light at the top of each mesocosm), and ambient room temperature (21.5-23.0°C).

Light experiment

We randomly assigned 30 different mesocosms to three different light treatments in October 2013. Light treatments consisted of 24-hour dark, 12-hour light:dark (control) and 24-light cycles. The dark treatment was covered with an opaque black plastic that inhibited any light from reaching the samples. As in the sediment experiment, light was provided by six 40-watt florescent lights (Phillips™ T12 High CRI C50 Supreme) per treatment, with lights positioned 60 cm above the mesocosms (60 µmol m^{-2} s^{-1} of light at the top of each mesocosm), and temperature was ambient room temperature (21.5-23.0°C).

Depth profile survey

We collected two soil cores from the center of each of the four playas. Each core was divided into three different layers, 0-2 cm, 2-5 cm, and 5-20 cm, for a total of 24 samples. The samples were rehydrated and kept in environmental chambers (25°C; 12-hour light:dark cycle) for two weeks in February 2013. After two weeks, invertebrates were collected and preserved in ethanol. Taxa richness and abundance were calculated for each treatment.

Algae and nutrients

In each experiment (sedimentation, light, and soil depth), we collected water samples to filter algae to quantify the planktonic algal biomass of each treatment, measured as chlorophyll *a* concentration (Aloi, 1990; Stevenson, 1996). Approximately 400 ml water were collected before invertebrate collection from each mesocosm and stored in small, plastic bottles and iced until analyzed. Water samples were filtered through glass fiber filters and chlorophyll *a* on the filter was extracted via the ethanol method (Sartory & Grobbelaar, 1984). After calculation of chlorophyll *a* concentration, any sample that resulted in a negative value were excluded from any further statistical analyses (four samples from the study and eight from the soil depth study).

Water was also collected from the sedimentation and light experiments to examine the nutrient levels from each of the treatments. We used a Hach DR/890 Colorimeter (Hach Company, Loveland, CO, USA) to test for nitrate (cadmium reduction method) and reactive phosphorus (ascorbic acid method) (Rice *et al.*, 2012). The appropriate chemical packets were added to 10 ml of water. After the required time, the light absorption through the chemical and water was recorded and chemical concentration was calculated.

Light transmission through soil

Because sediments in playas come from the uplands, we measured light transmission though upland soil to measure the effects of sediment depth on light penetration to resting stages because light can impact invertebrate hatching. A quantum meter (Apogee Instruments Inc., Logan, UT, USA) was placed within a cardboard box. A circular opening slightly smaller than a petri dish was cut in the box. Light reaching the quantum meter had to pass through the petri dish. Pre-weighed soil samples were added to the petri dish and exposed to an overhead light. We measured the amount of light that passed through the empty petri dish and through the combined soil and petri dish. The soil in the petri dish was gently redistributed twice and light measurements retaken, and the mean percent transmitted light was recorded for each soil sample (N = 28). We calculated soil depth using soil density, soil weight, and the area of the petri dish.

Statistical analyses

The number of hatched invertebrates and number of taxa per kilogram of soil were calculated for each experiment. Abundance data were log + 1 transformed to normalize the data, as needed. Transformation was not needed for the other data (richness, nutrients, and chlorophyll). One-way analysis of variance (ANOVA) was used to test for statistical differences across treatments in the sedimentation, light, and sediment depth experiments. If statistical significance was found, Tukey *post hoc* tests were run to determine differences among treatments.

We used multivariate statistics (Primer v6, Primer-E Ltd, Plymouth, UK) to determine whether the hatched invertebrate community differed among treatments, using the log (x + 1) transformed data. We ran an analysis of similarity (ANOSIM) on the Bray-Curtis similarity matrix to determine whether the invertebrate communities differed across treatments. If communities differed, we used SIMPER analysis to determine species' contributions to the dissimilarity between pairs of different treatments. We then ran a one-way ANOVA on the species that contributed most to the differences in each experiment to determine whether there were statistically significant differences. Light penetration through soil was analyzed using non-linear regression.

RESULTS

Sediment depth experiment

As sedimentation increased, fewer total invertebrates hatched from rehydrated playa wetland soil ($F_{3,39}$= 7.38, p = <0.001) (Fig. 3.1a). The addition of 1 cm soil resulted in a 25% reduction in the number of invertebrates hatching relative to the control. Abundance in all of the sedimentation treatments had a higher standard deviation than the control treatment.

Taxa richness showed a strong pattern of reduction with increasing sedimentation ($F_{3,39}$= 16.57, p = <0.001) (Fig. 3.1b). Mean richness decreased from six to two taxa with the addition of 1 cm of sediment. Invertebrate community composition differed among treatments (Global R = 0.19, p = 0.001); specifically, communities differed among all treatments except between the 1-cm and 0.5-cm sediment depths and the 0.5-cm and 0.25-cm sediment depths. The species contributing the most to differences among the treatments were cladocerans, clam shrimps, and ostracods, which had lower hatching rates with added sediment (Table 3.1).

We found no difference in the amount of chlorophyll *a* ($F_{3,39}$= 0.48, p = 0.70) (Table 3.2) or nutrient levels (nitrate: $F_{3,8}$ = 3.24, p = 0.08; phosphorus: $F_{3,8}$ = 1.09, p = 0.41) (Table 3.3) among the sedimentation treatments.

Light experiment

The number of invertebrates ($F_{2,29}$= 55.61, p = <0.001) (Fig. 3.2a), number of taxa hatching ($F_{2,29}$= 34.93, p = <0.001) (Fig. 3.2b), and chlorophyll *a* levels ($F_{2,25}$ = 10.54, p = <0.001) (Fig. 3.2c) differed among light treatments. The numbers of invertebrates and taxa hatching from the dark treatment were an order of magnitude lower than in the 12-hour light:dark (control) and the 24-hr light treatments. Taxonomic composition of the invertebrate communities differed among treatments (Global R = 0.44, p = 0.001). The invertebrate community that hatched from the dark treatment differed from the light and control treatments, whereas the light and control treatments had similar invertebrate communities. Cladocerans and clam shrimp were found in higher numbers in treatments with light than in the dark treatment (Table 3.4).

Chlorophyll *a* levels were higher in the light treatment than in both the dark and control treatments ($F_{2,25}$ = 10.54, p < 0.001) (Table 3.1; Fig 3.2 c). There was no difference in nutrient levels among treatments (nitrate: $F_{2,8}$ = 2.12, p = 0.20; phosphorus: $F_{2,8}$ = 1.96, p = 0.22) (Table 3.3).

Light transmission through soil declined rapidly and exponentially (regression R^2 = 0.95; Fig. 3.3). A soil layer of 0.02 cm decreased light level passing through soil almost 50% and as soil depth approached 0.08 cm, percent transmission approached zero.

Depth Profile Survey

The two most abundant taxa were macrothricid cladocerans and ostracods (Table 3.5). We found differences in the abundance ($F_{2,23}$= 3.83, p = 0.04; Fig. 3.4a), richness ($F_{2,23}$ = 3.74, p = 0.04; Fig. 3.4b), and chlorophyll *a* biomass ($F_{2,15}$= 5.09, p = 0.02; Fig. 3.4c) among playa soil depths. Both abundance and richness were higher in the shallower soils (the 0-2 and 2-5 cm depths) than at 5-20 cm. Depth profile differences were largely the result of cladocerans, clam shrimps, and ostracods, which hatched less frequently at deeper depths. Chlorophyll *a* concentration was higher in the 0-2 and 5-20 cm depths than in the 2-5 cm depth ($F_{2,15}$ = 5.09, p = 0.02) (Table 3.1).

DISCUSSION

We found that resident taxa of isolated, temporary wetlands were susceptible to landscape effects of pollution in the form of upland sediments. Sedimentation exhibited a strong inverse relationship with invertebrate hatching success; even the addition of 0.5 cm of soil significantly decreased both invertebrate abundance and richness, which resulted in differences among invertebrate communities across the depth treatments in our study. During intense rain storms, sediments carried by the overland flow of water may enter playas, especially playas in plowed landscapes. As hydrologically closed systems, playas will retain the sediments that enter them and sedimentation has indeed been identified as a problem in these ecosystems (Burris & Skagen, 2013). Our experiments indicate that such added sediments affect not only the physical structure of playas, but also playa biota.

The impacts of sedimentation on the hatching of invertebrate resting stages occurs not only in playas but also in other types of isolated, temporary wetlands and for other tpyes of organisms. Sediment decreases invertebrate hatching in prairie potholes (Gleason *et al.,* 2003) and buries the seed bank and decreases seed germination in temporay wetlands (Jurik *et al.,* 1994; Wang *et al.,* 1994; Gleason *et al.,* 2003; Chen *et al.,* 2014). Sedimentation also can alter the vegetative growth and influence the mode of reproduction of some wetland plants (Chen *et al.*, 2014).

Disruption of environmental cues affects hatching from crustacean resting stages (Cáceres & Tessier, 2003; Allen, 2010) and sedimentation may disrupt these cues. Known environmental cues associated with hatching include light (this study; Wiggins *et al,*. 1980; Mitchell, 1990), temperature (Uye *et al.,* 1979; Brendonck *et al.,* 1998; Brendonck & Riddoch, 2002; Vandekerkhove *et al.,* 2005), conductivity (Sam & Krishnaswamy, 1979; Brendonck *et al,*. 1998) and dissolved oxygen (Moore, 1967; Uye *et al.,* 1979).

To test the effects of sedimentation on light as a hatching cue, we first confirmed that light influenced hatching. The presence of light strongly affected hatching crustaceans, with higher diversity and abundance of hatching crustaceans under both the 24-hr light and the 12-hr light:dark treatment in comparison to the dark treatment. The 12-hr light:dark treatment closely resembles the light regime in western Oklahoma in spring, when playas most commonly fill. In contrast, few invertebrates hatched without light in the 24-hr dark treatment. Therefore, playa crustaceans have a minimum light threshold to induce hatching. The requirement for the presence of light has been found for individual taxa from temporary wetlands (i.e. clam shrimp (Bishop, 1967), fairy shrimp (Sorgeloos, 1980; Mitchell, 1990) and rotifers (Minkoff *et al.*, 1983)) and is generally applicable to playa crustaceans.

Light attenuation through upland soil, the source of playa sedimentation, was rapid, confirming that overlaying sediment can reduce crustacean hatching by affecting light cues. A layer of upland soil of only 0.10 cm blocked nearly all light. Light transmission varies among soils and is affected by soil properties such as soil color (Kasperbauer & Hunt, 1988) and soil composition (Bliss & Smith, 1985). Additional evidence for the interaction among sedimentation, light attenuation, and crustacean hatching was that sedimentation and lack of light in our studies impacted the same two taxa: cladocerans and clam shrimp.

Although we did not specifically test cues other than light, our light experiment was not confounded by variation in temperature, conductivity, and oxygen. We ran the trial at room temperature, which is similar to mean temperature in spring. We used well water to fill the mesocosms, so conductivity was similar among treatments. Water in the mesocosms was shallow and algal biomass was low, so oxygen levels would not have differed much across the different treatments, although we did not measure them.

Despite the apparent loss of light cues in the sedimentation study, invertebrates still hatched from the 0.25-cm sediment treatment. Some shallowly buried resting stages may have been unburied by pertubation in the process of adding water to the mesocosms, similar to the effect of water moving into the playa wetland during inundation. Because playa wetlands fill from overland runoff from precipitation, some buried resting stages could become unburied and float (Broch, 1969; Sorgeloos, 1997; Hajirostamloo, 2008). Once floating, resting stages would be exposed to the suitable environmental cues that induce hatching (Cáceres *et al.,* 2007). In our experiment, the unburying of resting stages might have led to the larger variation in invertebrate abundance that hatched from the sedimentation treatments in comparison to the control.

The presence of light was a hatching cue when combined with inundation. The soil used in our study was stored under a natural light regime, but this light pre-treatment alone did not cue hatching, just as subsequent darkness with inundation did not cue hatching. Instead, the presence of light was needed concurrently with water to break diapause.

Although crustacean resting stages may not hatch if covered by sediment or deprived of light, we tested whether such buried resting stages could hatch if exposed to the environment. The depth profile survey confirmed our predictions that the abundance and richness of invertebrates decreases as playa soil depth increases. Laying eggs near the soil surface provides greater access to environmental cues for breaking dormancy. Eggs occurring in deeper soil depths would be less likely to break dormancy and hatch successfully.

Eggs hatched from all the tested playa soil depths. Because diapausing crustacean eggs from temporary wetlands can remain viable more than 20 years (Brock *et al.,* 2003), the age of buried eggs was unknown, especially as resting stages may be buried in a number of ways. Dry temporary wetlands are often used as cropland (Euliss & Mushet, 1999) and at least three of the four playas wetlands in our study had a history of being farmed. During tillage, eggs were likely displaced to other soil depths. Past sedimentation also might have buried some eggs. In addition, as playa wetlands dry, cracks form in the wetland bottom and eggs might be transported by wind into these cracks, displacing eggs downward. Many crustaceans drop eggs that settle on the playa bottom, but tadpole shrimp forage and burrow into wetland soil and may bury eggs in the process (Croel & Kneitel, 2011). In addition, many invertebrates use a bet-hedging strategy when it comes to hatching, such that not all eggs hatch when conditions are appropriate and these unhatched eggs are more likely to be buried than eggs that hatch during the first inundation (Brendonck, 1996; Brendonck & Riddoch, 2002; Hotovy & Petrusek, 2007).

We found that playa wetland communities (particularly the resident invertebrate community) can be greatly impacted by landscape effects. In addition, other wetland processes are affected by the surrounding landscape. Sedimentation rates are greater in playa wetlands that occur in cultivated agricultural lands than those that occur in range lands because tilled soil is loosened and more of it flows into playa wetlands during overland water flow than does from untilled playas (Luo *et al.,* 1997). Playas with cultivated uplands also have more exotic plant species, higher plant diversity, and fewer perennial plant species than playas in uncultivated wetlands, factors that may affect water infiltration and increase disturbance of the natural hydroperiod (Smith & Haukos, 2002). Cultivated uplands around playas also influence dynamics of the amphibian community and decrease postmetamorphic body size of amphibians (Gray *et al.,* 2004). Playa wetland organisms that are greatly affected by the surrounding uplands are organisms that are poor colonizers, such as crustaceans and amphibians. In contrast, organisms that can colonize from other wetlands are more affected by island biogeographic or metapopulation dynamics. For example, the avian community (e.g., geese, diving and dabbling ducks, and shorebirds) in the Rainwater Basin were less likely to affected by landscape effects than by within playa wetland conditions (Webb *et al*., 2010).

Prevention of sedimentation and other environmental pollution from the surrounding uplands is crucial to conserving temporary wetland ecosystems. Sedimentation can be reduced by planting a buffer zone of native plants around the wetlands (Skagen *et al.*, 2008; Cariveau *et al.*, 2011; Daniel *et al.*, 2015). Direct restoration of playa wetlands by removing sediments to the underlying clay layer did not restore the plant community (Beas *et al.,* 2013). Complete sediment and soil removal would likely remove resident taxa resting stages and likewise impact crustaceans. Our study indicates that partial or staged removal of sediments, combined with protection from future sedimentation, is preferred to complete sediment removal as a means to re-establish playa morphology without loss of resident biota.

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APPENDIX

Table 3.1. Untransformed mean number (± SE) of organisms per kilogram of soil and ANOVA results (df = 3, 39 N = 40) for the organisms found in each sedimentation treatment level. Different letters denote differences between treatments.

	Control	0.25 cm sediment	0.50 cm sediment	1.0 cm sediment	F-statistic	P-value
Cladocera	107.7 ± 19.6^{a}	927.1 ± 201.9^{b}	290.6 ± 131.4^{a}	105.4 ± 70.6^{a}	9.6	<0.001
Ostracoda	13.0 ± 3.8^{a}	3.0 ± 0.7^{b}	1.1 ± 0.4^{bc}	0.5 ± 0.2^{c}	9.0	<0.001
Clam shrimp	34.0 ± 8.3^{a}	1.7± 0.4^{b}	0.5 ± 0.1^{bc}	0.1 ± 0.1^{c}	15.9	<0.001
Fairy shrimp	0.1 ± 0.1	0.3 ± 0.2	0.5 ± 0.4	0.1 ± 0.1	0.7	0.54
Tadpole shrimp	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	1.0	0.40

Table 3.2. Mean chlorophyll *a* concentration levels (µg/ml) (± SE) and ANOVA results (Sediment study: df = 3, 39; Light study: df = 2, 27; Soil depth study: df = 2, 15) for the sediment, light, and soil depth studies. Different letters within each study denote difference between treatments.

	Chlorophyll *a* (µg/ml)	**F-statistic**	**p-value**
Sediment study			
Control (N=10)	0.92 ± 0.14	0.48	0.70
0.25 cm added (N=10)	0.65 ± 0.40		
0.50 cm added (N=10)	0.83 ± 0.16		
1.0 cm added (N=10)	1.06 ± 0.40		
Light study			
24-hr light (N=8)	3.69 ± 2.51[a]	10.54	<0.001
12:12-hr light:dark (N=10)	0.92 ± 0.14[b]		
24-hr dark (N=8)	0.81 ± 0.21[b]		
Soil depth study			
0-2 cm layer (N = 5)	0.80 ± 0.19 [a]	5.09	0.02
2-5 cm layer (N = 6)	0.19 ± 0.05 [b]		
5-20 cm later (N = 5)	0.29 ± 0.19 [a]		

Table 3.3 Mean nutrient (nitrate and phosphorus) levels (mg/L) (± SE) and ANOVA results (Sediment study: df = 3, 11, N = 9; Light study: df = 2, 8, N = 9) for the sediment and light studies.

	Nitrate (mg/L)	Nitrate F-statistic	Nitrate p-value	Phosphorus (mg/L)	Phosphorus F-statistic	Phosphorus p-value
Sediment study						
Control	0.07 ± 0.03	3.24	0.08	2.66 ± 1.26	1.09	0.41
0.25 cm added	0.07 ± 0.03			4.07 ± 0.79		
0.50 cm added	0.30 ± 0.06			4.11 ± 0.59		
1.0 cm added	0.10 ± 0.06			2.66 ± 0.21		
Light study						
24-hr light	0.0 ± 0.0	2.12	0.20	3.43 ± 0.53	1.96	0.22
12:12-hr light:dark	0.07 ± 0.03			2.66 ± 0.21		
24-hr dark	0.70 ± 0.46			5.10 ± 1.44		

Table 3.4. Untransformed mean number (± SD) of organisms per kilogram of soil and ANOVA results (df = 2, 29 N = 30) for the organisms found in each light treatment level. Different letters denote differences between treatments.

	24 hr Light	12:12 hr Dark:Light	24 hr Dark	F-statistic	P-value
Cladocera	191.0 ± 45.1^{a}	107.8 ± 24.2^{a}	0.42 ± 0.6^{b}	15.7	<0.001
Ostracoda	7.1 ± 2.8	12.8 ± 5.2	6.3 ± 2.6	1.6	0.22
Clam shrimp	32.1 ± 10.3^{a}	34.0 ± 11.0	0.0 ± 0.0^{b}	8.7	0.001
Fairy shrimp	0.4 ± 0.3	0.1 ± 0.2	0.0 ± 0.0	2.5	0.08
Tadpole shrimp	0.1 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	1.0	0.38
Collembola	0.6 ± 0.3	0.4 ± 0.3	0.0 ± 0.0	3.3	0.052
Acari	0.0 ± 0.0	0.1 ± 0.2	0.5 ± 0.6	1.3	0.30
Psychoda	1.2 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	2.2	0.13
Nematoda	0.0 ± 0.0	0.1 ± 0.2	0.0 ± 0.0	1.0	0.38

Table 3.5 Untransformed mean number (± SE) of organisms per kilogram of soil and ANOVA results (on log (x + 1) transformed data) (df = 3, 23 N = 24) for the organisms found in each tested soil depth.

Taxon	0-2 cm	2-5 cm	5-20 cm	F-statistic	P-value
Cladocera	19.7 ± 8.0	0.8 ± 0.3	0.5 ± 0.1	0.9	0.41
Ostracoda	6.7 ± 1.5	1.6 ± 0.3	0.0 ± 0.0	2.8	0.08
Clam shrimp	4.0 ± 0.9	0.4 ± 0.2	0.2 ± 0.1	2.8	0.08
Fairy shrimp	0.3 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	1.0	0.39
Tadpole shrimp	0.3 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.5	0.60
Radix sp.(snail)	0.7 ± 0.2	0.9 ± 0.4	0.2 ± 0.1	0.3	0.75

Figure 3.1 The number of invertebrates per kilogram of soil (a) and taxa (b) that hatched from the different sedimentation treatments. The line within each box is the median, the box represents the 25 and 75 quartiles, the whisker plots represent the 10 and 90 deciles, and the dots represent any outliers. Letters denote significant differences among treatments. N = 10.

Figure 3.2 The number of invertebrates per kilogram of soil (a) and taxa (b) that hatched and chlorophyll *a* concentration (c) from the different light treatments. The line within each box is the median, the box represents the 25 and 75 quartiles, the whisker plots represent the 10 and 90 deciles, and the dots represent any outliers. Letters denote significant differences among treatments. N = 10.

Figure 3.3 The percentage light transmission through different depths of soil. Each point is a mean of three measurements. The best-fit regression line shows an exponential decline of light transmission with increasing soil depth.

Figure 3.4 The number of invertebrates per kilogram of soil (a) and taxa (b) that hatched and chlorophyll *a* concentration (c) from different soil depths. The line within each box is the median, the box represents the 25 and 75 quartiles, the whisker plots represent the 10 and 90 deciles, and the dots represent any outliers. Letters denote significant differences among treatments. N=8.

Figure 3.1

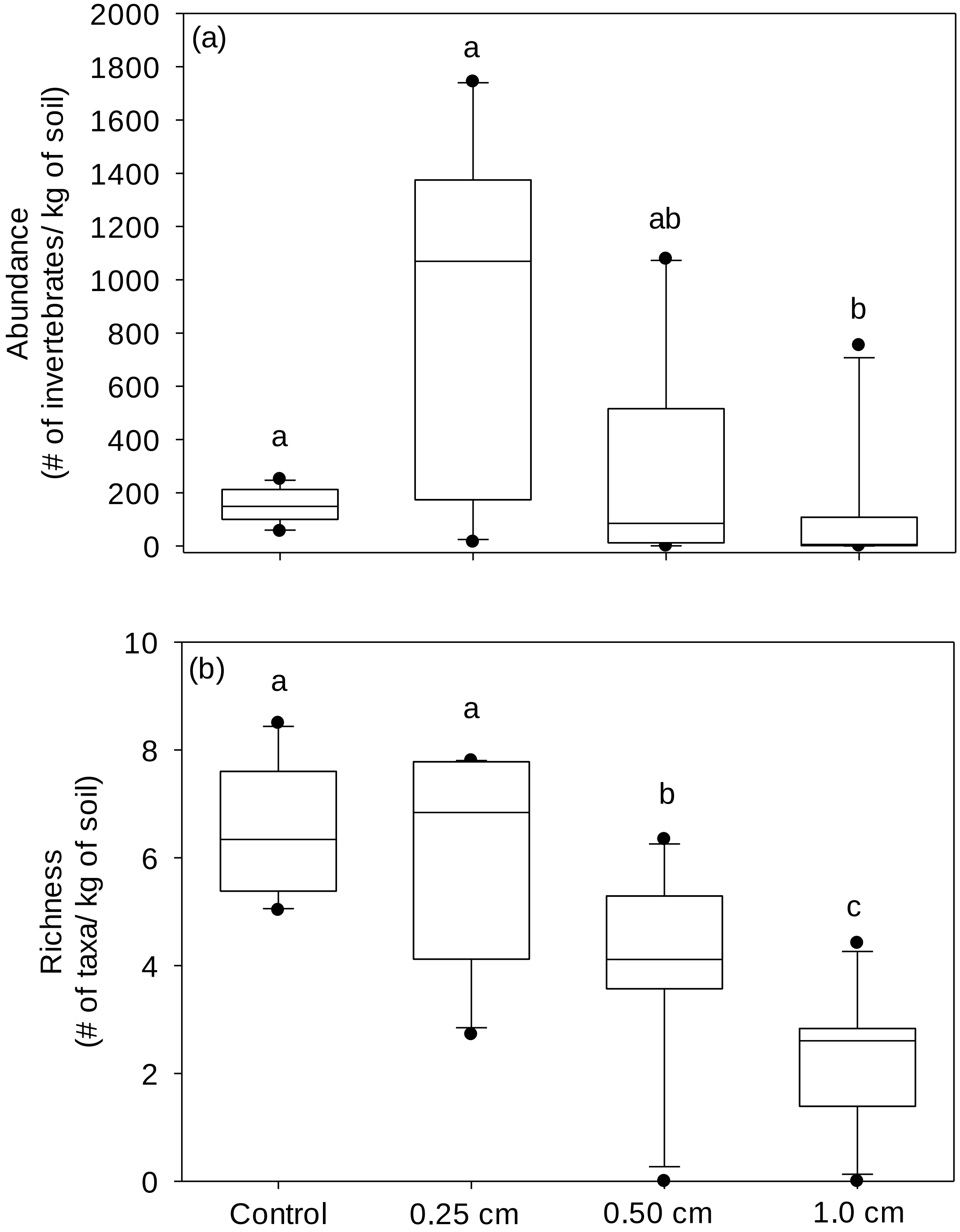
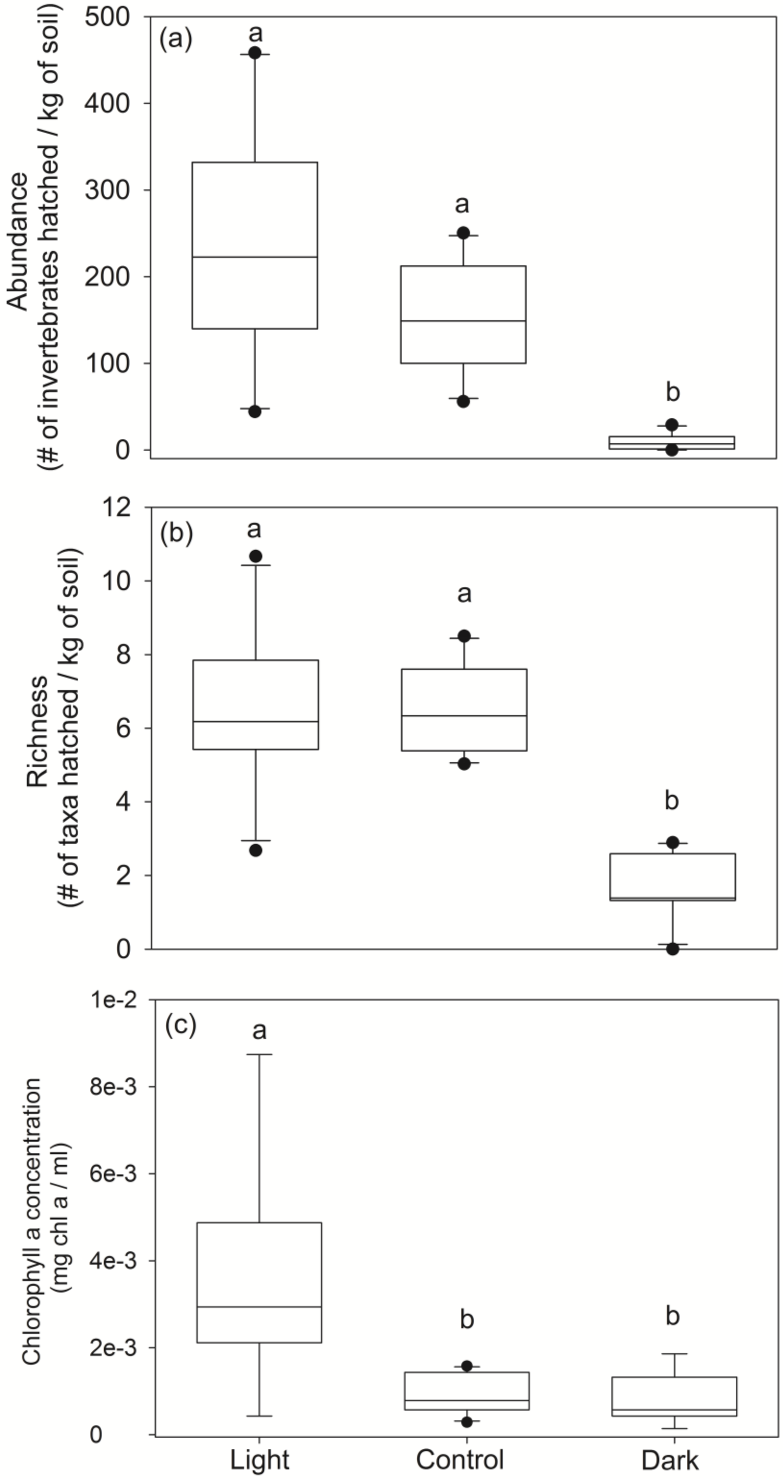

(a)
Abundance
(# of invertebrates/ kg of soil)
2000
1800
1600
1400
1200
1000
800
600
400
200
0
a
a
ab
b
(b)
Richness
(# of taxa/ kg of soil)
10
8
6
4
2
0
a
a
b
c
Control
0.25 cm
0.50 cm
1.0 cm

Figure 3.2



(a)
Abundance
(# of invertebrates hatched / kg of soil)
500
400
300
200
100
0
a
a
b
(b)
Richness
(# of taxa hatched / kg of soil)
12
10
8
6
4
2
0
a
a
b
(c)
Chlorophyll a concentration
(mg chl a / ml)
1e-2
8e-3
6e-3
4e-3
2e-3
0
a
b
b
Light
Control
Dark

Figure 3.3

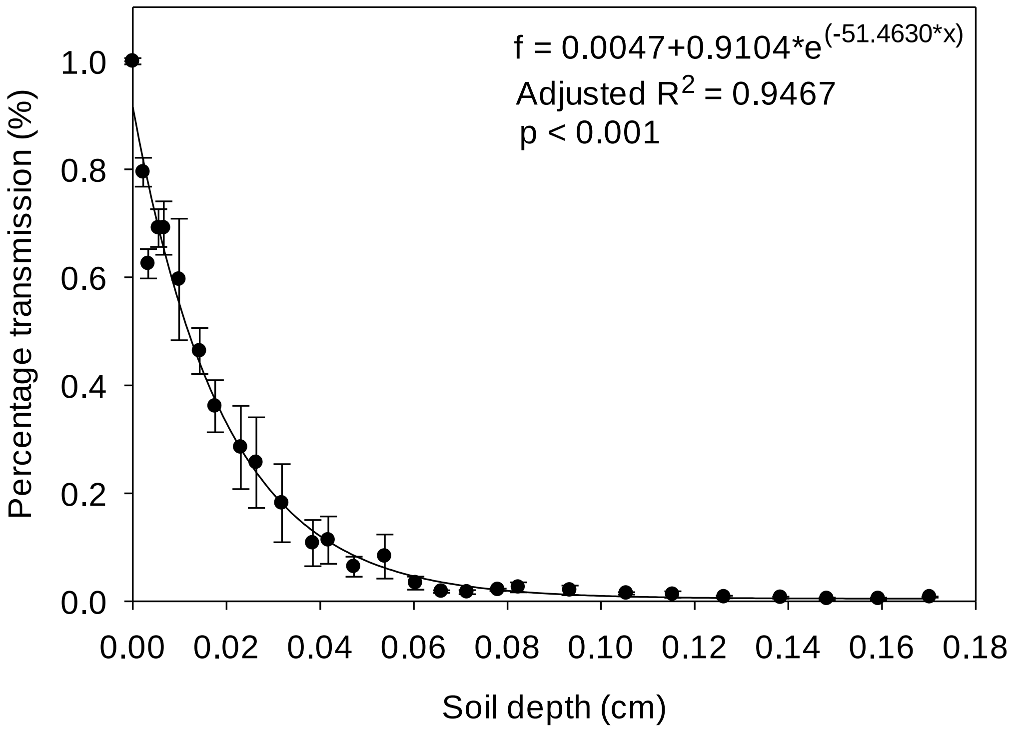
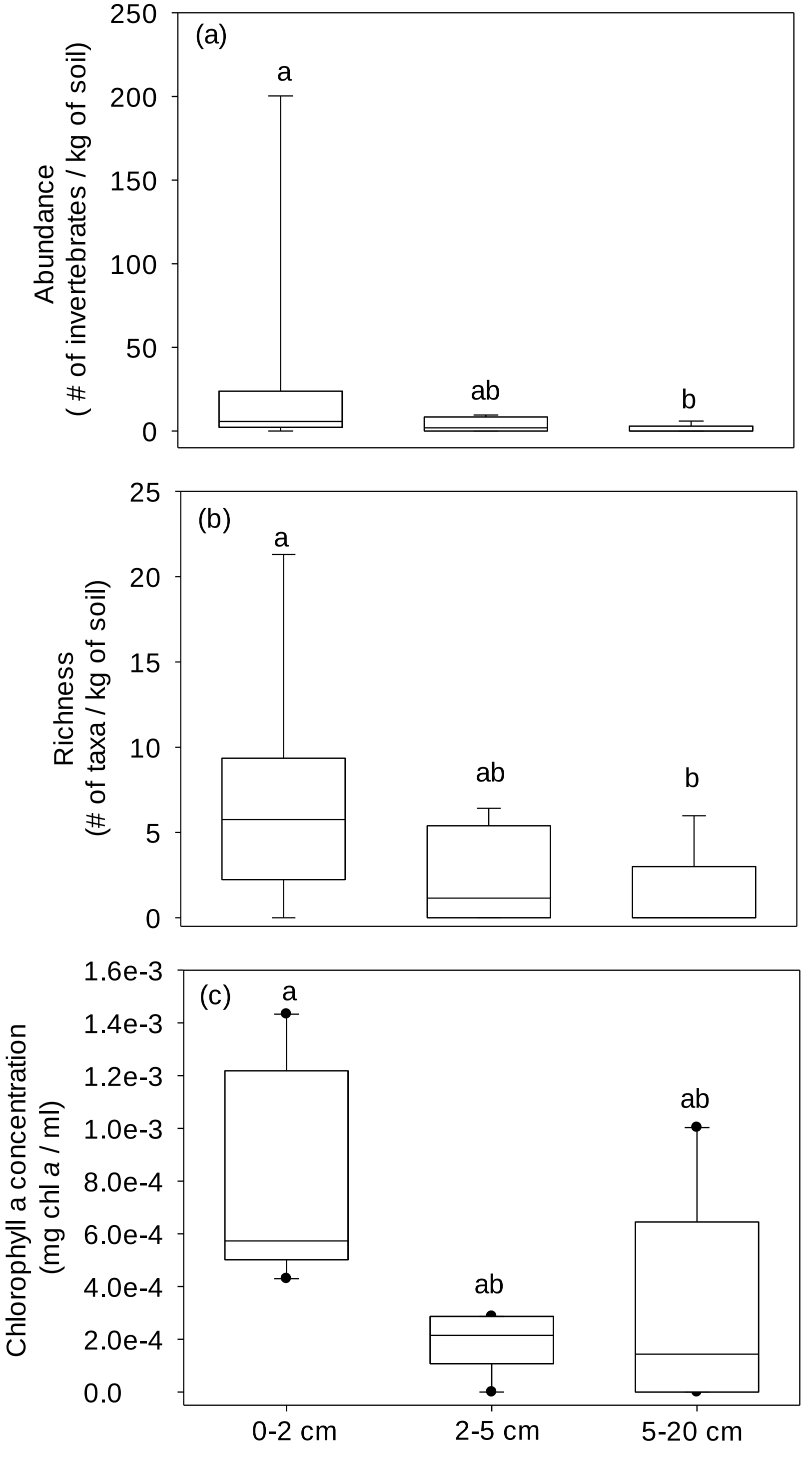

f = 0.0047+0.9104*e^(-51.4630*x)
Adjusted R^2 = 0.9467
p < 0.001
Percentage transmission (%)
1.0
0.8
0.6
0.4
0.2
0.0
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0.18
Soil depth (cm)

Figure 3.4


(a)
a
ab
b
Abundance
(# of invertebrates / kg of soil)
0
50
100
150
200
250
(b)
a
ab
b
Richness
(# of taxa / kg of soil)
0
5
10
15
20
25
(c)
a
ab
ab
Chlorophyll a concentration
(mg chl *a* / ml)
0.0
2.0e-4
4.0e-4
6.0e-4
8.0e-4
1.0e-3
1.2e-3
1.4e-3
1.6e-3
0-2 cm
2-5 cm
5-20 cm