

## AQUATIC MACROINVERTEBRATE DIVERSITY OF PLAYA WETLANDS: THE ROLE OF LANDSCAPE AND ISLAND BIOGEOGRAPHIC CHARACTERISTICS

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**Abstract:** Wetland habitats continue to be lost at a unsettling rate, especially freshwater emergent wetlands that are isolated geographically. These are the predominant wetlands found in arid and semi-arid environments, where they serve as foci of regional biodiversity. This is especially true of the playa wetlands of the Southern High Plains of Texas, USA. The factors that determine and maintain biotic diversity in these wetlands are understood poorly. Consequently, this study examined the effect of island biogeographic and landscape features on the diversity of aquatic macroinvertebrates in playa wetlands. Macroinvertebrates were collected from playas three times during the spring and summer of 1994 and categorized as resident or transient taxa based on life history strategies. Diversity was estimated using taxonomic richness (richness) and Fisher's log-series alpha ( $\alpha$ ). Surrounding land-use practices influenced resident richness, whereas playa surface area affected resident and transient richness, as well as resident  $\alpha$ . However, relationships differed among sampling dates. Regression analyses suggested that transient richness and  $\alpha$  were influenced more by insular characteristics than by landscape features. The converse was true for resident richness and  $\alpha$ . Therefore, both insular and landscape characteristics affected the diversity of macroinvertebrates in playa wetlands, but impacts were dependent on life-history strategy and time since inundation (i.e., sampling date). Consequently, conservation and management efforts targeting macroinvertebrates in playa wetlands will need to focus on the wetlands and characteristics of adjacent watershed features.

**Key Words:** playas, wetlands, aquatic macroinvertebrates, diversity, richness, theory of island biogeography, landscape ecology, Southern High Plains

### INTRODUCTION

Despite the increase in wetland conservation efforts over the past two decades (Emergency Wetlands Resources Act 1986), substantial losses of wetlands con-

tinue (Dahl 2000). This is especially true for freshwater emergent wetlands (Dahl 2000), particularly those that are geographically isolated (i.e., surrounded by uplands; Tiner et al. 2002). Between 1986 and

1997, approximately 486,000 hectares of freshwater emergent wetlands were converted to other uses (Dahl 2000). Such wetlands are common in arid and semi-arid regions and, consequently, are foci for biodiversity in these areas (Bolen et al. 1979, Holland and Jain 1981, Haukos and Smith 1994, Brendonck and Williams 2000, Tiner et al. 2002). Agriculture is one of the major threats to wetlands in these regions (Guthery and Bryant 1982, Grue et al. 1986), with 51% of the losses in emergent wetlands from 1986 to 1997 attributable to agriculture (Dahl 2000). Given the importance of these wetlands to regional biodiversity (Brendonck and Williams 2000), it is important to determine the factors that shape and maintain the biodiversity of these wetlands; otherwise, prudent policies for their conservation and management will remain illusive (Hughes and Hunsaker 2002).

Playas of the Southern High Plains, USA are examples of isolated, freshwater emergent wetlands that continue to be threatened by agricultural activities. These shallow basins are a conspicuous part of the landscape, with more than 19,000 playas occurring on the Llano Estacado or Southern High Plains region of Texas (Playa Lakes Joint Venture 1993). Playas are the predominant surface hydrologic feature and are important for ground-water recharge into the underlying Ogallala Aquifer (Zartman et al. 1994, 1996, Scanlon and Goldsmith 1997). The land around playas is among the most intensively cultivated areas in the United States (Bolen et al. 1979). Consequently, most of these wetlands are strongly modified by agricultural activities (Guthery and Bryant 1982, Bolen et al. 1989, Luo et al. 1997, Luo and Smith 1999).

As wetlands in a semi-arid environment, playas are the major habitat for a profusion of aquatic and wetland plants (Haukos and Smith 1997). They serve as breeding areas for numerous birds, amphibians, and macroinvertebrates (Bolen 1982, Seyffert 1985, Anderson et al. 1999, Hall et al. 1999) and are important as stopover points for migrating waterfowl, cranes, and shorebirds using the Central Flyway of the United States (U. S. Fish and Wildlife Service 1988, Haukos and Smith 1994, Davis and Smith 1998). Although less frequently studied than plants and birds, aquatic macroinvertebrates are one of the most diverse and abundant groups of organisms in these wetlands (Sublette and Sublette 1967, Parks 1975, Merickel and Wangberg 1981, Hall 1997, Hall et al. 1999, Anderson and Smith 2000). They appear in playas within days of inundation and quickly become abundant, occupying many trophic levels (Hall et al. 1999). Thus, macroinvertebrates are important trophic components of these ecosystems. Most research on aquatic macroinvertebrates in playas has focused on their importance as food resources for migrating waterfowl and shore-

birds (Baldassarre and Fischer 1984, Sheeley 1988, Davis and Smith 1998). Given their abundance and diversity in these wetlands, it is surprising how little is known about the factors that affect macroinvertebrates.

Because playas are aquatic islands within a terrestrial matrix, island biogeography (MacArthur and Wilson 1967) and landscape ecology (Naveh and Liberman 1983, Risser et al. 1984) provide conceptual bases for studying macroinvertebrate diversity and colonization. The theory of island biogeography predicts that size of an island and its proximity to a source of colonists determine the equilibrium number of species on an island, with larger islands and those nearer a source of colonists harboring more species than smaller or more distant islands. Although originally proposed to account for differences in species diversity on oceanic islands, the tenets of island biogeography have been used to explain successfully the differences in species diversity among mountain tops (Brown 1971), urban parks (Gavareski 1976), lakes (Fryer 1985), vernal pools (Ebert and Balko 1987), individual leaves (Andrews et al. 1987), and carrion (Doube 1987). Similarly, insular characteristics such as island area and proximity to sources of colonists that provide the basis for island biogeography theory could help explain differences in aquatic macroinvertebrate diversity among playa wetlands.

As a complementary view, landscape ecology emphasizes the influence of the surrounding matrix on species diversity of habitat islands (Harris 1984). Indeed, characteristics of the surrounding landscape often have a considerable effect on insular species diversity (Tilghman 1987, Green et al. 1994, Natuhara et al. 1999). In some instances, the surrounding landscape has been more important than the size of a habitat in determining its species diversity (Webb et al. 1984). The landscape perspective also may be relevant in determining the diversity of aquatic macroinvertebrates in playa wetlands because land-use characteristics can have profound effects on the biota of waterbodies (Newbold et al. 1980, Rundle and Ormerod 1991, Ormerod et al. 1993, Rundle and Attrill 1995, Townsend et al. 1997).

These two perspectives are not mutually exclusive. MacArthur and Wilson (1967) realized that differences in the matrices between islands, such as prevailing winds, water currents, and climate, affected species diversity. Similarly, landscape ecology (Forman 1995) recognizes the importance of habitat size and the spatial distribution of habitats. Species diversity likely results from a combination of insular and landscape factors. If landscape characteristics are most important, differences in diversity of aquatic organisms in playas should reflect surrounding land uses and watershed at-

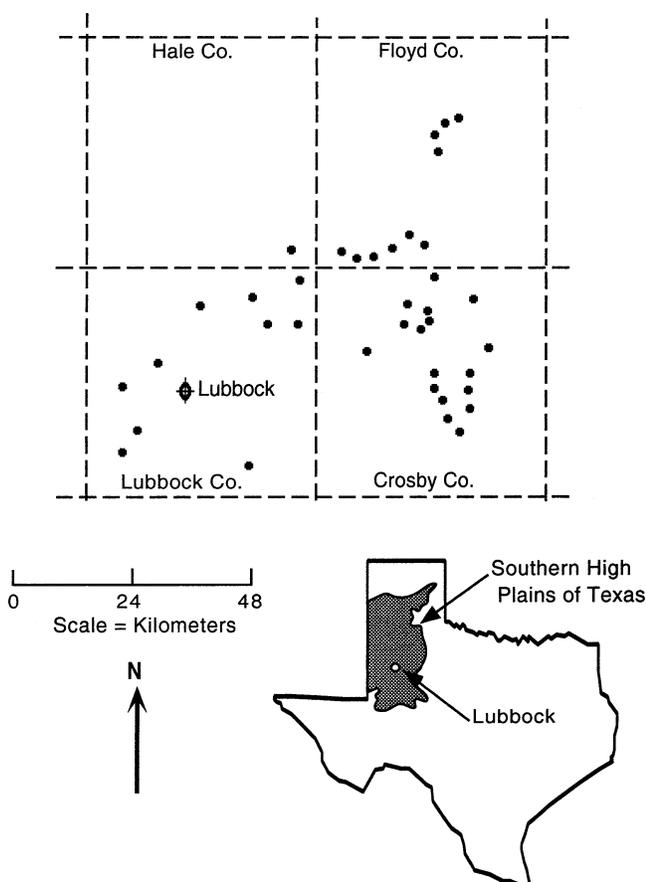


Figure 1. Locations of sampled playas on the Southern High Plains of Texas, USA.

tributes. However, if insular characteristics are more important, diversity should be influenced by “island” characteristics such as depth, areal extent of the surface water, and the number and proximity of surrounding playas. The objective of this study was to examine the effects of insular and landscape characteristics on two aspects of the diversity of aquatic macroinvertebrates in playa wetlands (taxa richness and Fisher’s log-series  $\alpha$ ) and thereby elucidate the determinants of macroinvertebrate diversity in playas.

## METHODS

### Study Area

Playas from a four-county area adjacent to and including Lubbock County, Texas, USA (latitude, 33° 20′ N to 34° 20′ N; longitude, 102° 45′ W to 101° 00′ W) were sampled for macroinvertebrates three times over an eight-week period, the approximate duration of inundation, during the spring and summer of 1994 (Figure 1). Classification of playas was based on size of basin (i.e., extent of the underlying layer of Randall

clay) and surrounding land use. Geographic information for each playa basin and watershed was developed by digitizing the playas from Natural Resource Conservation Service county soil survey maps (GIS; ARC/INFO, Environmental Systems Research Institute, Inc. Redlands, CA). United States Geological Survey 7.5-minute topographic quadrangle maps were used for geographic control. Land-use information was obtained from aerial photographs, taken twice a year for crop evaluation purposes, and data from the Farm Service Agency offices in each county. This information was then ground-truthed to verify the interpretation of the imagery.

Three main types of land use predominate on the Southern High Plains: agricultural crops (AGR), rangeland (RNG), and grasslands in the Conservation Reserve Program (CRP). Agricultural practices consist of crops such as sorghum, cotton, and wheat. The Conservation Reserve Program (Food Security Act 1985) was established to encourage farmers to remove highly erodible soil from agriculture and to plant native vegetation in its place. On the Southern High Plains of Texas, the native vegetation is grassland. However, grazing is prohibited on CRP grasslands. Because of the unpredictable flooding of playas, many farmers have entered lands surrounding playas into the CRP.

Playas were classified based on the predominant ( $\geq 50$  percent of area) land use (AGR, RNG, CRP) within 100 m of the perimeter of the basin. Three size categories were distinguished within each land-use group: small playa basins were  $\leq 10$  ha, medium basins ranged from  $>10$  to  $\leq 20$  ha, and large basins were  $>20$  and  $\leq 33$  ha. These size categories encompassed approximately 98 percent of playas in the four-county area of this study. Playas also were classified by size according to water surface area at each time period. Because the areal extent of water and the number of sampled playas changed with time, playas were assigned to one of three groups (small, medium, and large) based on their position in the overall size distribution of playas within each sampling period (i.e., lower, middle, or upper third, respectively; Table 1).

Estimation of playa surface area was based on the position of the water’s edge, marked with stakes placed at each cardinal point soon after initial inundation. Playas were assumed to dry uniformly. Because most playas are slightly elliptical (Reeves 1966), surface area was calculated as the area of an ellipse,

$$A = \Pi \times L \times W/4$$

where  $L$  is the length of the longest axis of the playa and  $W$  is the length of the perpendicular axis. Surface area was calculated for each playa at each sampling period. In addition, average water depth and a visual

Table 1. Areal extent (\*hectares) of playa surface water used to categorize playas as small, medium, and large in each sampling period. The number of playas in each category is enclosed by parentheses. Sampling period 1, May 26–June 7; period 2, June 20–28; period 3, July 11–14 (1994).

Period	Size Categories		
	Small	Medium	Large
1	3.31–6.34 (13)	6.49–10.01 (12)	11.58–23.44 (13)
2	2.23–3.76 (9)	3.95–6.16 (8)	7.22–18.15 (8)
3	0.98–2.48 (4)	3.39–4.62 (3)	4.87–9.82 (3)

estimate of the percentage of the playa surface covered by emergent vegetation were recorded during each sampling period. An estimate of emergent vegetative cover was used because a quantitative floristic survey of these wetlands was beyond the scope of this project (Wood et al. 2001).

#### Invertebrate Collection and Identification

Sampling began approximately three weeks after playas were inundated by spring storms (Hall 1997). At each sampling, 50 points were located at random within each playa using random number tables to indicate the direction of the transect and the distance between consecutive samples. At each point, two surface, six subsurface, and five benthic samples were taken, resulting in 100 surface, 300 subsurface, and 250 benthic samples per playa. This protocol was based on preliminary sampling of a playa not included in this study. An aquatic D-net was used for surface and subsurface samples, and a single-bore corer (2'' inner diameter) was used for benthic samples (Hall 1997).

Initially, macroinvertebrates from surface and subsurface samples were preserved in 95 percent ethanol, whereas benthic samples were preserved in 10 percent formalin. After macroinvertebrates were separated from debris and sediment, all specimens were transferred to 80 percent ethanol. Individuals were identified to the specific level when possible (Appendix 1). Voucher specimens were deposited in the Enns Entomology Museum, University of Missouri-Columbia, the Illinois Natural History Survey Annelida Collection, Champaign (Oligochaeta), and the Aquatic Insect Collection of the Kansas Biological Survey, Lawrence (Chironomidae).

#### Statistical Analyses

Because playa lakes are ephemeral, their aquatic inhabitants have developed strategies for enduring or avoiding periods of desiccation (Wiggins et al. 1980). Macroinvertebrate inhabitants were categorized into two groups based on these strategies. Residents are

organisms with drought-resistant life stages that usually have no autonomous means of emigration or immigration. In contrast, transients are organisms that, for the most part, have limited or no drought-resistant life stages and are capable of active movement between playas during their life cycle, usually as flying adults. Because these differences in dispersal ability could be paralleled by differences in response to insular or landscape characteristics (Batzer and Wissinger 1996), resident and transient taxa were analyzed separately. To avoid problems associated with successional changes in macroinvertebrate composition (Moorhead et al. 1998), separate statistical analyses were conducted for each sampling date.

Taxonomic diversity was evaluated in two ways: as taxonomic richness (the number of distinguishable species, morphospecies, or higher taxonomic groups; Appendix 1) and as Fisher's log-series  $\alpha$  (Fisher et al. 1943), which is sensitive to richness and the abundance of species. The latter index assumes an underlying log-series species abundance distribution but is robust with respect to deviations from that distribution (Taylor 1978). Fisher's log-series  $\alpha$  (Magurran 1988) is calculated as

$$\alpha = [N(1 - x)] / x,$$

where  $x$  is estimated by the iterative solution of

$$S / N = \{ (1 - x) / x \} \{ -\ln(1 - x) \}$$

and  $S$  is the number of species, morphospecies, or higher taxa, with  $N$  equal to the number of individuals. Fisher's log-series  $\alpha$  is not unduly influenced by sample size, and an underlying log-series distribution is more applicable than others, given the ephemeral nature of playa lakes and the resultant adaptations of their faunas (Hall 1997). Nevertheless, the species abundance distribution of each playa in each time period was tested for deviations from a log-series distribution via Chi-square goodness of fit analysis to verify the appropriateness of Fisher's log-series  $\alpha$  as an index of macroinvertebrate diversity in playa lakes (Magurran 1988).

Several multivariate analyses were used to elucidate the effect of insular and landscape characteristics on

Table 2. Insular and landscape characteristics used in multiple regression analyses.

<i>Insular Characteristics</i>	
Average size of the playas within a three km radius	
Average water depth	
Distance to the nearest playa	
Number of excavated pits in the playa	
Percent of the playa surface area with emergent vegetation	
Size of the nearest playa (based on basin size)	
Total number of playas in a three km radius	
Total area of playas (based on basin sizes) within a three km radius	
<i>Landscape Characteristics</i>	
Number of culverts draining into the playa	
Number of roads in the watershed	
Percent of the watershed in cotton	
Percent of the watershed in the Conservation Reserve Program	
Percent of the watershed in rangeland	
Percent of the watershed in sorghum	
Percent of the watershed in wheat	
Size of the watershed	
Slope of the watershed	

taxonomic richness and Fisher's log-series  $\alpha$  (hereafter referred to as richness and  $\alpha$ , respectively) The effects of playa size and surrounding land use (AGR, CRP, RNG) on richness or  $\alpha$  were assessed separately during each time period using analysis of covariance (Procedure ANOVA, SPSS Inc. 1990). Covariates (surface area of the playa and basin size) were used because resident and transient taxa have disparate colonization abilities. Because resident taxa withstand periods of desiccation and do not emigrate when playas dry, the size of the basin (i.e., the extent of the available refuge) might be important. However, most transient taxa must immigrate to a playa after the playa fills; consequently, the areal extent of the surface water might be an important cue for these taxa (Fernando 1959).

Stepwise multiple regression was used to assess the combined effects of insular and landscape characteristics on richness and  $\alpha$  (Procedure REGRESSION, SPSS Inc. 1990). Eight insular and nine landscape characteristics (Table 2) were used as independent variables. Insular characteristics included those variables concerned with physical aspects of the playa or the distribution and size of surrounding playas that might affect macroinvertebrate colonization. Conversely, landscape characteristics were attributes of the intervening matrix surrounding each playa (i.e., the playa's watershed).

An increased probability of committing a Type I error occurs when considering multiple statistical tests. To minimize this likelihood, Bonferroni's sequential adjustment (Rice 1989) was used to evaluate the sig-

nificance of independent variables in determining the factors associated with variation in dependent variables (e.g., resident or transient richness).

## RESULTS

### Richness

Approximately 190,000 individuals representing 107 taxa were collected in this study. These taxa represented 81 genera, 47 families, 13 orders, 7 classes, and 3 phyla (Appendix 1). Richness differed over time and with life history strategy. Overall macroinvertebrate richness ranged from 23.6 to 32.6, depending on sampling period, with the greatest values achieved during the second sampling period. Richness of resident taxa ranged from 7.2 to 9.8, and was greatest during the first and second sampling periods. Richness of transient taxa ranged from 13.8 to 22.8 and was greatest during the second and third sampling periods. These trends in taxa richness generally were consistent regardless of land use or size of playas.

The effects of land use, basin size, and surface area on richness varied over time and between resident and transient faunas. Differences in surrounding land use accounted for significant variation in resident richness after the effects of playa area and basin size were removed but only during the first sampling period (ANCOVA;  $F = 4.306$ ;  $P = 0.022$ ;  $df = 2,33$ ). Average resident richness was greatest in playas surrounded by rangeland and lowest in playas surrounded by agriculture. Transient richness was not associated significantly with surrounding land use in any sampling period.

Resident and transient richness were associated significantly with covariates during the second and third sampling periods, respectively. During the second sampling period, resident richness was associated negatively with playa surface area ( $F = 7.033$ ;  $P = 0.015$ ;  $df = 1,20$ ); the positive relationship between transient richness and basin size was intriguing but was not significant ( $F = 3.902$ ;  $P = 0.062$ ;  $df = 1,20$ ). During the third sampling period, transient richness was related negatively to playa surface area ( $F = 10.559$ ;  $P = 0.023$ ;  $df = 1,5$ ), but resident richness showed no relationship to either covariate.

A combination of insular and landscape characteristics contributed to variation in richness. During the first sampling period, a significant amount of variation in transient richness was attributed positively to the amount of emergent playa vegetation ( $r^2 = 0.35$ ) and negatively to the number of culverts ( $r^2 = 0.11$ ) draining into the playa (Model  $R^2 = 0.46$ ,  $P < 0.001$ ). In contrast, resident richness was not significantly related to any of the insular or landscape characteristics during

Table 3. Significant relationships between diversity variables and variables used in ANCOVA and stepwise multiple regression analyses in each sampling period. (IB = island biogeographic variable; L = landscape variable).

Diversity Variable	Sampling Period	ANCOVA Variables				Multiple Regression Variables					
		L Land use	IB		Avg. Playa Size in 3 km Radium	Average Water Depth	Distance to Nearest Playa	Number of Pits in Playa	% Emergent Vegetation	Size of Nearest Playa	
			Basin Size	Playa Area							
Resident richness	1	x									
	2									x	
	3										
Resident $\alpha$	1										
	2										
	3										
Transient richness	1								x		
	2					x			x		
	3					x					
Transient $\alpha$	1			x					x		
	2					x			x		
	3					x					

the first sampling period. During the second sampling period, transient richness was associated positively with the amount of playa vegetation ( $r^2 = 0.08$ ) and negatively to average water depth and the abundance of roads ( $r^2 = 0.16$ ) in the watershed (Model  $R^2 = 0.76$ ,  $P < 0.001$ ). Examination of partial correlation coefficients revealed a significant positive correlation between water depth and the amount of the watershed planted in winter wheat. However, depth accounted for over twice the amount of unique variation in transient richness compared to winter wheat during this period ( $r^2 = 0.52$  and  $0.24$ , respectively). Resident richness was affected positively by the size of the nearest playa (Model  $R^2 = 0.22$ ,  $P = 0.018$ ). During the third sampling period, transient richness was associated negatively with average water depth (Model  $R^2 = 0.56$ ,  $P = 0.013$ ), whereas resident richness showed no significant relationship with insular or landscape characteristics.

### Diversity

Chi-square analyses revealed that Fisher's log-series  $\alpha$  was an appropriate diversity index to characterize playa lakes. Depending on sampling period, 90–96% of playas had taxon abundance distributions that were not significantly different from a log-series distribution ( $P > 0.05$ ).

Fisher's log-series  $\alpha$  varied over time and differed between resident and transient faunas. Overall macroinvertebrate  $\alpha$  ranged from 4.2 to 5.6 and was greatest during the second sampling period. Resident  $\alpha$

ranged from 1.4 to 2.2 and was greatest during the second sampling period. In contrast, transient  $\alpha$  remained essentially constant, between 3.9 and 4.0 across sampling periods.

Even after the removal of variation due to playa size, differences in surrounding land use never accounted for significant variation in  $\alpha$ , based on analysis of covariance. During the first sampling period, resident  $\alpha$  (after Bonferroni adjustment) approached significance with playa surface area ( $F = 4.936$ ;  $P = 0.033$ ;  $df = 1,33$ ; adjusted  $P$  must be  $\leq 0.025$  to be considered significant) and the relationship was positive. However, this relationship was not found in the second or third sampling periods. Similarly, transient  $\alpha$  was not associated with either covariate in any sampling period.

Variation in  $\alpha$  usually was attributed to a combination of insular and landscape characteristics based on stepwise multiple regression analyses. In the first sampling period, resident  $\alpha$  was associated positively with the percent of the watershed containing sorghum (Model  $R^2 = 0.36$ ,  $P < 0.001$ ), whereas transient  $\alpha$  was related positively to the amount of emergent playa vegetation (Model  $R^2 = 0.25$ ,  $P = 0.002$ ). During the second sampling period, resident  $\alpha$  again was associated positively with the percentage of the watershed planted in sorghum (Model  $R^2 = 0.31$ ,  $P = 0.004$ ), whereas transient  $\alpha$  was related positively to the amount of emergent playa vegetation ( $r^2 = 0.43$ ) and negatively with average water depth ( $r^2 = 0.12$ ) in the playa (Model  $R^2 = 0.55$ ,  $P \ll 0.001$ ). As was seen



Transient taxa were more influenced by insular characteristics than were residents (Table 3), possibly because transient taxa are true colonists (*sensu* MacArthur and Wilson 1967). Nonetheless, neither playa basin size nor surface area was the predominant factor influencing transient diversity. Instead, the amount of emergent vegetation, one likely dimension of habitat heterogeneity, and playa water depth were the most influential factors. The relationship between emergent vegetation and aquatic macroinvertebrates has been noted in many studies of wetlands (Krull 1970, Voigts 1976, Neck and Schramm 1992, Ward and Blaustein 1994, Streever et al. 1995, Leslie et al. 1997, Brendonck and Williams 2000, de Szalay and Resh 2000, Zimmer et al. 2000, Battle and Golladay 2001, Wood et al. 2001) and is not surprising given that vegetation is used by wetland invertebrates for food, ovipositioning sites, and as refuges from predators. In addition, increased vegetative cover is important for other playa fauna, including amphibians (Anderson et al. 1999) and birds (Haukos and Smith 1991, Anderson and Smith 1999). Similarly, water depth is an important factor determining the abundance and community structure of aquatic macroinvertebrates in wetlands (Voigts 1976, Riley and Bookout 1990, Magee et al. 1993, Leslie et al. 1997, Zimmer et al. 2000). It was not surprising to see a consistent effect of vegetation and water depth on the diversity of aquatic macroinvertebrates regardless of sampling period.

A critical prediction of the theory of island biogeography is that richness increases with island size. However, this relationship remains equivocal for temporary environments. Several studies of temporary ponds do not support this relationship (Driver 1977, Garcia-Valdecasas et al. 1984, Lake et al. 1989, Schneider and Frost 1996), nor does this investigation. Yet, other studies do (Stout 1964, Reisen 1973, Ebert and Balko 1987, Spencer et al. 1999, Brooks 2000). The ephemeral nature of temporary ponds may preclude the attainment of an equilibrium between extinction and immigration (Wiggins et al. 1980, Lake et al. 1989, Moorhead et al. 1998). When the assumption of equilibrium conditions cannot be met, predictions concerning species-area relationships may not be valid (Simberloff and Abele 1976). For this reason, playa size may not be a useful characteristic in the conservation or management of aquatic macroinvertebrate diversity in these wetlands.

Southwood (1977) suggested that time (flood duration *sensu* Mitsch and Gosselink 2000) is the limiting resource in ephemeral environments, with biotic interactions of secondary importance. This hypothesis has been supported by many studies of temporary waterbodies (Wiggins et al. 1980, Jefferies 1989, Boulton and Lake 1992, Boulton and Lloyd 1992, Schneider

and Frost 1996). However, as has been pointed out by Wissinger et al. (1999), duration is often positively related to wetland size. Therefore, studies relating richness to either size or duration must be aware of the confounding effects of such a relationship. In fact, several studies of macroinvertebrates in temporary habitats show a positive correlation between habitat size and duration (Stout 1964, Reisen, 1973, Nolte 1989, Brooks 2000, Boix et al. 2001), leaving it unclear as to whether the macroinvertebrate richness is a function of area or habitat duration.

In this study, there was no significant relationship between playa surface area and duration ( $r = -0.08$ ,  $P = 0.319$ ). In contrast, there was a positive correlation between depth and duration ( $r = 0.81$ ,  $P < 0.000$ ). However, there was either no correlation (1<sup>st</sup> period) or a negative correlation between depth and species richness ( $r = -0.70$ ,  $P < 0.000$ ;  $r = -0.71$ ,  $P = 0.021$ ; 2<sup>nd</sup> and 3<sup>rd</sup> periods, respectively). This is not to say that habitat duration has no effect on macroinvertebrate diversity in playa wetlands as richness was greatest during the second sampling period. However, habitat duration was not examined as a structuring factor in this study because of the confounding effect of localized rainfall events which are common to this region. More specifically, playas with increased macroinvertebrate diversity resulting from the retention of water for longer periods of time (i.e., there is a longer period for colonization for transient taxa) could not be distinguished from playas with increased macroinvertebrate diversity due to a rewetting of dry perimeter soils and the concomitant re-emergence of resident taxa.

The shape of species abundance distributions (log-series) suggests that the organization of communities within these wetlands is dominated by one or only a few factors (May 1975, Magurran 1988). Moreover, previous studies on the vegetation of playas (Haukos and Smith 1993, 1994) and phyllopods of other temporary habitats (Donald 1983) suggest that macroinvertebrate communities of playa lakes may be controlled by unpredictable precipitation events. Haukos and Smith (1993, 1994) have shown that playa vegetation depends, in part, on the timing and frequency of inundation in preceding years. If transient macroinvertebrate taxa select habitats based on vegetational characteristics, the presence of transient taxa similarly should reflect historic inundation regimes or basin cultivation history (Euliss et al. 2002). Moreover, resident assemblages may reflect interactions of land use and inundation history because the development of some resident taxa is related to the moisture regime of the preceding year (Donald 1983).

Given the appreciable diversity of aquatic macroinvertebrates in playa wetlands and their importance to the foodweb of these ecosystems (Davis and Smith

1998, Anderson and Smith 1998, Anderson and Smith 1999, Hall *et al.* 1999), prudent management is necessary for the maintenance of regional biodiversity. However, given the differences in life history strategies among playa macroinvertebrates and their different sensitivities to environmental factors, policies that focus solely on playa basins themselves will not be sufficient to conserve macroinvertebrate diversity. Meaningful management strategies and conservation efforts must also address anthropogenic disturbances in the surrounding watershed of these isolated and imperiled wetlands.

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## Appendix 1.

Phylum	Subphylum	Class	Subclass	Order	Family
Annelida		Oligochaeta		Opisthopora Tubificida	Lumbricidae Tubificidae
		Hirudinea		Rhynchobdellida Pharyngobdellida	Glossiphoniidae Erpobdellidae
Mollusca		Gastropoda	Pulmonata	Basommatophora	Lymnaeidae Physidae Planorbidae
Arthropoda	Cheliceriformes	Chelicerata	Arachnida	Acari	Arrenuridae Eylidae Hydrachnidae
	Uniramia	Insecta	Pterygota	Ephemeroptera Odonata	Pionidae Baetidae Aeshnidae Lestidae Coenagrionidae Libellulidae
				Hemiptera	Belostomatidae Corixidae
					Gerridae Mesoveliidae Notonectidae
				Coleoptera	Saldidae Veliidae Haliplidae
					Dytiscidae
					Gyrinidae
					Helophoridae Hydrophilidae

## Appendix 1. Extended.

Genus	Specific Epithet	Authority	Designation
<i>unknown</i>			resident
<i>Limnodrilus</i>	<i>hoffmeisteri</i>	Claparède	resident
<i>Limnodrilus</i>	<i>sp.</i>		resident
<i>unknown</i>			resident
<i>Helobdella</i>	<i>triserialis</i>	(Blanchard)	resident
<i>Erpobdella</i>	<i>punctata</i>	(Leidy)	resident
<i>Fossaria</i>	<i>cockerelli (bakerilymnaea)</i>	Pilsbry & Ferriss	resident
<i>Physella (Costatella)</i>	<i>bottimeri</i>	(Clench)	resident
<i>Planorbella (Pierosoma)</i>	<i>tenuis</i>	(Dunker)	resident
<i>Arrenurus</i>	<i>dentipetiolatus</i>	Marshall	resident
<i>Arrenurus</i>	<i>undescribed sp.</i>		resident
<i>Eylais</i>	<i>sp.</i>		transient
<i>Hydrachna</i>	<i>sp.</i>		transient
<i>Piona</i>	<i>floridana</i>	Cook	resident
<i>Callibaetis</i>	<i>sp.</i>		transient
<i>Anax</i>	<i>junius</i>	Drury	transient
<i>Lestes</i>	<i>disjunctus</i>	Selys	transient
<i>Enallagma</i>	<i>civile</i>	(Hagen)	transient
( <i>Tramea, Pantala, Sympetrum</i> )			transient
<i>Belostoma</i>	<i>flumineum</i>	Say	transient
<i>Corisella</i>	<i>edulis</i>	(Champion)	transient
<i>Corisella</i>	<i>tarsalis</i>	(Fieber)	transient
<i>Rhamphocorixa</i>	<i>acuminata</i>	(Uhler)	transient
<i>Sigara</i>	<i>alternata</i>	(Say)	transient
<i>Trichocorixa</i>	<i>reticulata</i>	(Guérin-Méneville)	transient
<i>Trichocorixa</i>	<i>verticalis</i>	(Fieber)	transient
<i>Gerris</i>	<i>marginatus</i>	Say	transient
<i>Mesovelis</i>	<i>mulsanti</i>	White	transient
<i>Buenoa</i>	<i>margaritacea</i>	Torre-Bueno	transient
<i>Notonecta</i>	<i>undulata</i>	Say	transient
<i>Saldula</i>	<i>pallipes</i>	(Fabricius)	transient
<i>Microvelia</i>	<i>sp.</i>		transient
<i>Haliplus</i>	<i>triopsis</i>	Say	transient
<i>Haliplus</i>	<i>tumidus</i>	LeConte	transient
<i>Brachyvatus</i>	<i>sp.</i>		transient
<i>Copelatus</i>	<i>sp.</i>		transient
<i>Cybister</i>	<i>fimbriolatus</i>	(Say)	transient
<i>Eretes</i>	<i>sticticus</i>	(Linnaeus)	transient
<i>Hygrotus</i>	<i>nubilus</i>	(LeConte)	transient
<i>Laccophilus</i>	<i>fasciatus terminalis</i>	Aubé	transient
<i>Laccophilus</i>	<i>quadrilineatus quadrilineatus</i>	Horn	transient
<i>Neobidessus</i>	<i>sp.</i>		transient
<i>Thermonectus</i>	<i>nigrofasciatus ornaticollis</i>	(Aubé)	transient
<i>Uvarus</i>	<i>lacustris</i>	Say	transient
<i>Dineutus</i>	<i>sp.</i>		transient
<i>Gyrinus</i>	<i>sp.</i>		transient
<i>Helophorus</i>	<i>linearis</i>	LeConte	transient
<i>Berosus</i>	<i>exiguus</i>	(Say)	transient
<i>Berosus</i>	<i>infuscatus</i>	LeConte	transient
<i>Berosus</i>	<i>miles</i>	LeConte	transient
<i>Berosus</i>	<i>styliferus</i>	Horn	transient
<i>Enochrus</i>	<i>hamiltoni</i>	(Horn)	transient
<i>Hydrophilus</i>	<i>triangularis</i>	Say	transient
<i>Paracymus</i>	<i>confusus</i>	Wooldridge	transient

## Appendix 1. Extended. Continued.

Phylum	Subphylum	Class	Subclass	Order	Family
					Curculionidae
				Diptera	Ceratopogonidae
					Chironomidae
					Culicidae Dolichopodidae Ephydriidae
					Psychodidae
					Stratiomyidae Syrphidae Tabanidae Branchinectidae
	Crustaceae	Branchiopoda		Anostraca	Streptocephalidae
				Conchostraca	Thamnocephalidae Caenestheriidae Leptestheriidae Lynceidae Triopsidae Cyprididae
		Ostracoda		Notostraca Podocopida	Ilyocyprididae

## Appendix 1. Extended. Continued.

Genus	Specific Epithet	Authority	Designation
<i>Tropisternus</i>	<i>lateralis</i>	(Fabricius)	transient
<i>Bagous</i>	<i>sp.</i>		transient
<i>Lissorhoptrus</i>	<i>simplex</i>	(Say)	transient
<i>Listronotus</i>	<i>grypidioides</i>	(Dietz)	transient
<i>Listronotus</i>	<i>filiformis</i>	(LeConte)	transient
<i>Listronotus</i>	<i>scapularis</i>	(Casey)	transient
<i>Notiodes</i>	<i>aeratus</i>	(LeConte)	transient
<i>Forcipomyia</i>	<i>sp.</i>	Coquillett	transient
	morphospecies 1		transient
	morphospecies 2		transient
	morphospecies 3		transient
<i>Ablabesmyia</i>	<i>sp.</i>		transient
<i>Apedilum</i>	<i>sp.</i>		transient
<i>Chironomus</i>	<i>sp. 1</i>		resident
<i>Chironomus</i>	<i>sp. 2</i>		resident
<i>Clinotanypus</i>	<i>sp.</i>		resident
<i>Cricotopus</i>	<i>sp.</i>		resident
<i>Cryptochironomus</i>	<i>sp.</i>		transient
<i>Dicrotendipes</i>	<i>sp.</i>		resident
<i>Endochironomus</i>	<i>nigricans</i>	(Johannsen)	resident
<i>Labrundinia</i>	<i>sp.</i>		transient
<i>Parachironomus</i>	<i>sp.</i>		resident
<i>Polypedilum</i>	<i>sp.</i>		resident
<i>Procladius</i>	<i>bellus</i>	(Loew)	transient
<i>Procladius (Holotanypus)</i>	<i>sp.</i>		transient
<i>Tanypus</i>	<i>sp.</i>		resident
<i>Tanytarsus</i>	<i>sp.</i>		resident
<i>Culex</i>	<i>tarsalis</i>	Coquillett	transient
	morphospecies 1		transient
<i>Notophila</i>	<i>sp.</i>		transient
	morphospecies 1		transient
	morphospecies 2		transient
	morphospecies 3		transient
	morphospecies 4		transient
	morphospecies 1		transient
	morphospecies 2		transient
<i>Odontomyia</i>	<i>sp.</i>		transient
<i>Eristalis</i>	<i>sp.</i>		transient
<i>Tabanus</i>	<i>prob. subsimilis</i>	Bellardi	transient
<i>Branchinecta</i>	<i>lindahli</i>	Packard	resident
<i>Branchinecta</i>	<i>packardi</i>	Pearse	resident
<i>Streptocephalus</i>	<i>dorotheae</i>	Mackin	resident
<i>Streptocephalus</i>	<i>texanus</i>	Packard	resident
<i>Thamnocephalus</i>	<i>platyurus</i>	Packard	resident
<i>Caenestheriella</i>	<i>setosa</i>	(Pearse)	resident
<i>Leptestheria</i>	<i>compleximanus</i>	(Packard)	resident
<i>Lynceus</i>	<i>brevifrons</i>	(Packard)	resident
<i>Triops</i>	<i>longicaudatus</i>	(LeConte)	resident
<i>Megalocypris</i>	<i>gnathostomata</i>	(Ferguson)	resident
<i>Cyprinotus</i>	<i>antillensis</i>	(Broodbakker)	resident
<i>Pelocypris</i>	<i>tuberculatum</i>	(Ferguson)	resident