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Patterns of Rotifer Diversity in the Chihuahuan Desert

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Abstract: Desert aquatic systems are widely separated, lack hydrologic connections, and are subject to drought. However, they provide unique settings to investigate distributional patterns of micrometazoans, including rotifers. Thus, to understand rotifer biodiversity we sampled 236 sites across an array of habitats including rock pools, springs, tanks, flowing waters, playas, lakes, and reservoirs in the Chihuahuan Desert of the USA (n = 202) and Mexico (n = 34) over a period of >20 years. This allowed us to calculate diversity indices and examine geographic patterns in rotifer community composition. Of ~1850 recognized rotifer species, we recorded 246 taxa (~13%), with greatest diversity in springs (n = 175), lakes (n = 112), and rock pools (n = 72). Sampling effort was positively related to observed richness in springs, lakes, rivers, and tanks. Nestedness analyses indicated that rotifers in these sites, and most subsets thereof, were highly nested (support from 4 null models). Distance was positively correlated with species composition dissimilarity on small spatial scales. We predicted species richness for unsampled locations using empirical Bayesian kriging. These findings provide a better understanding of regional rotifer diversity in aridlands and provide information on potential biodiversity hotspots for aquatic scientists and resource managers.

Keywords: aridland; diversity indices; isolation by distance; Mantel tests; micrometazoans; nestedness; playas; rock pools; spatial scale; springs

1. Introduction

Delineating patterns of species distributions is important for understanding basic and applied questions in biogeography, ecology, and evolutionary biology [1,2]. Species distributions can be used in modeling current communities and in predicting outcomes to both short-term (e.g., acute pollution episodes) and long-term events (e.g., increases in temperature due to climate change). They also inform biogeography and macroecology [3]. Unfortunately, the biogeographic patterns of many small and understudied species have not been well-documented. As members of the Syndermata, rotifers offer a good example of this challenge. While they comprise an important component of freshwater ecosystems and contribute to both the microbial loop and typical aquatic food webs, it is unclear whether their distribution follows ubiquity theory [4,5], or whether they exhibit some level of endemicity [6–9]. Due to their ability to produce small resting stages that are easily transported by hydrochory [10], zoochory [11,12], or anemochory [13,14], it has been assumed that most rotifers were widely dispersed by passive means and that the majority of species would have cosmopolitan distributions [8,15,16]. However, recent studies have shown that the distribution of rotifer species encompasses the range from cosmopolitanism to biogeographies that are restricted to certain biogeographic realms, hotspots of biodiversity [7,17,18], or habitat types [4,17–19]. Two examples illustrate this point. (1) In his analysis of the genus *Trichocerca*, Segers [9] concluded that strict cosmopolitanism was evident in >1/3rd of the species analyzed, endemism was lacking in tropical regions but that it was strongly evident in the Northern hemisphere, and latitudinal variation was evident in >25% of the species. (2) Segers and De Smet [18] grouped species of *Keratella* into four categories: cosmopolitans (n = 8), Holarctic (n = 5), widespread (n = 3), and regional and local endemics, with seven subcategories: Afrotropical (n = 2), Australian (n = 6), Nearctic (n = 8), Neotropical (n = 8), Oriental (n = 2), Palearctic (n = 6), and marine (n = 5). To distinguish between the opposing views of cosmopolitanism versus endemism, additional studies are needed of larger geographic regions, with repeated sampling.

Since deserts contain waterbodies that are often widely separated, highly fragmented, possess limited hydrologic connections, and subject to unpredictable drought [20–22], they are ideal systems to determine patterns in aquatic species distributions. However, within a basin, assemblages of aquatic habitats can be quite complex. For example, a series of spring-fed pools can lead to a stream, each with its own edaphic conditions, that support a substantial number of species [22]; both can be hotspots of aquatic biodiversity, but maintain different arrays of species. Deserts also are considered ecological paradoxes. While generally low in terrestrial productivity, their varied habitats support striking levels of taxonomic diversity, often with a high degree of endemism. The Chihuahuan Desert of Mexico and the southwest USA is a prime example of such a system. This desert is a complex of intergrading plant communities arrayed across a broad series of elevational and latitudinal sequences [23]. It covers some 6.29×10^5 km^2, largely in the central Mexican plateau, but extending northward into west Texas, south-central New Mexico, and the southeastern Arizon. This well-defined ecoregion is the only desert system included in The Global 200 conservation priority listing as being recognized for its critical biodiversity values for both terrestrial and freshwater habitats [24].

An analysis specific to the Chihuahuan Desert [25] has designated 98 specific habitats or localities as priority sites for investigation and evaluation with respect to biodiversity resources; 37 are freshwater habitats. Of these, the highest priorities are assigned to systems with high intactness and high richness and/or endemism. An important array of these freshwater habitats is found in an arc from Big Bend National Park (BIBE, Texas) into Mexico, with the priority sites falling largely along the western boundary of the Sierra Madre Occidental, but extending as far south as the state of Hidalgo. A particularly important locality is the renowned Cuatro Ciénegas thermal spring system in Coahuila, perhaps the most studied of all Chihuahuan Desert aquatic systems [26–29]. This system of thermal springs, marshes, rivers, and large permanent lakes is home to a diversity of aquatic and mesic habitats that supports high levels of endemism in aquatic species [26,27,30]. Chihuahuan Desert springs and other water sources are recognized as sites of high biodiversity with high rates of endemism of macroinvertebrates, especially springsnails [31,32]. To complement that knowledge, more attention should be given to aquatic microinvertebrates of these systems.

While some aquatic sites in these deserts are relatively permanent over geologic time (playas and rivers), others are ephemeral over ecologic time (wet seasonally, monthly, weekly, even daily). Hydroregime (i.e., the duration, frequency, and timing of wet phases) is an important indicator of species richness, with increasing species diversity positively correlated with length of the filling cycle [33–35]. Connectivity among sites is also an important consideration, as connected sites will likely share large portions of their species pools. In the Chihuahuan Desert, connectivity among sites in different drainage basins is reduced by vast stretches of arid landscape [36]. Thus, system isolation may be a driving force in speciation and endemism. This certainly seems to hold true for fishes [37–40], springsnails [41–45], and amphipods [46,47]. In addition, communities may be structured through recent processes such as local and regional interactions (competition and dispersal) [48–50], habitat permanence [51,52], or local physiochemical conditions [48].

Prior to our work [53–57], there were few surveys of rotifers in the Chihuahuan Desert, with some notable exceptions. These mostly focused on smaller geographic areas and shorter time scales [58–63]. However, there have been numerous studies of rotifers from deserts and aridlands of the world, but in general, they have been limited to reports of species composition in specific habitats. These studies include the following: Sonoran [58,60,64–68], Algeria [69], Australia [70–81], Kalahari [82], Namib [83], Oman, Saudi Arabia, and Yemen [84], Spain [85], and Western Sahara [86]. The semi-arid regions in Mongolia also have been studied by several researchers [87].

Here we characterized patterns of rotifer species distribution in 236 aquatic systems that we sampled through a broad range of the Chihuahuan Desert. As appropriate to the system, we sampled the water column, sediments, and littoral vegetation during a period of ≥20 years. As part of our study, we tested the following hypotheses: (1) recovered richness will be positively correlated with sampling effort, (2) species are associated with particular habitats, (3) species composition will show nestedness, and (4) richness and assemblage composition possess a geographic pattern. In addition, using our dataset, we employed empirical Bayesian kriging to predict rotifer diversity across unsampled locations within the Chihuahuan Desert. Finally, we compared our results with those from five other desert systems and six studies from cool, temperate, and tropical systems. Our findings and analyses will help identify areas with high conservation value for zooplankton, including rotifers and add to our understanding of rotifer biogeography on a regional scale. They also inform the Baas-Becking (ubiquity) hypothesis in providing an indirect test of the assumption that for microinvertebrates, everything is everywhere [4,5].

2. Materials and Methods

2.1. Collection Sites

We collected samples from 236 sites, 202 USA and 34 Mexico during 1998–2020 (Figure S1; Appendix A). We sampled a variety of habitats including permanent lakes and reservoirs (n = 21), tanks (n = 11), temporary playas (n = 16), rock pools (n = 60) and artificial rock pools (n = 6), rivers and streams (n = 15), and springs (n = 95). Sampling effort varied among the sites from 1 visit to >20 visits; frequencies were used as ranks (1 = 1 sampling event; 2 = 2–5 events; 3 = 6–10 events; 4 = 11–20 events; 5 = >20 events), and at some sites only one type of sample was taken (e.g., plankton), while at others a variety of microhabitats were sampled. We compiled species lists at each site overall sampling dates using presence/absence criteria.

We described the sites at Big Bend National Park (BIBE) (Brewster Co., Alpine, TX, USA) in our previous work [53,54,88]. General characteristics for rock pools sites at Hueco Tanks State Park & Historic Site (HTSPHS) (El Paso Co., San Antonio, TX, USA) were provided by Schröder and colleagues [89] and springs in northern Mexico were described in detail by Ríos-Arana and colleagues [90].

Sampling techniques included using plankton nets (64 µm), aspirating samplers for flocculent bottom sediments, as well as taking grab samples (i.e., aquatic macrophytes for sessile species) [53,54]. We did not sample hyporheic habitats. The equipment was cleaned using distilled water rinses and, whenever possible, dried between uses in different systems. Although we usually took multiple samples at each site, we attempted to minimize environmental damage of the smaller systems by keeping the total amount of each sample to about 250 mL of source water. We recorded GPS coordinates using a Brunton Multi-Navigator® and used Google Earth to verify locations.

2.2. Species Identification

We identified morphospecies of rotifers (hereafter, species) primarily from live material using a Zeiss Axioscope with Neofluar objectives equipped with DIC, but when necessary, some specimens were preserved in 4% buffered formalin to view key taxonomic characters. For example, specimens of *Lecane* and *Lepadella* were fixed to view characteristics of the lorica, and in some cases trophi were examined using SEM. Keys to the Rotifera used in this study were as follows: Bdelloidea—[81,91,92]; Monogononta—[93–105]. We identified taxa to species or, if that was not possible, to genus: e.g., *Lecane* sp. We conducted all of the analyses using the lowest level of identification that we determined. For most specimens, we took voucher images with a SPOT camera and, when possible, voucher specimens were preserved in 70% ethanol and/or 4% buffered formalin. We housed all voucher specimens in UTEP's Biodiversity Collections.

2.3. *Diversity Indices*

To assess diversity of sites we calculated Hill numbers (q) of order 0 (richness, *S*), 1 (Shannon Index), and 2 (Simpson Index), and Sorensen's Index (SI). Species incidence was characterized at a variety of spatial grains by overlaying 0.1°, 0.25°, 1.0°, 1.25°, and 2.0° grids on the site map. We calculated incidence within these grids cell from presence/absence data from each collection site occurring within the boundaries of the grid cell.

2.4. *Sampling Effort*

We tested the relationship between species richness and sampling effort using linear regression in R version 4.0.2 (R Core Team, 2020) for all sites combined, as well as for each habitat type separately.

2.5. *Indicator Species Identification*

We determined indicator species for habitat types by testing for significant associations using the *indicspecies* package 1.7.8 version in R version 4.0.2 (R Core Team, 2020; https://cran.r-project.org/web/packages/indicspecies/indicspecies.pdf). This analysis calculates an Indicator Value (IndVal) index to measure the association between species and sites and combinations of sites based on the methods of Dufrene and Legendre [106] and De Caceres et al. [107]. The statistical significance is determined by permutation tests (n = 999).

2.6. *Nestedness*

We tested the hypothesis that smaller assemblages of rotifers are nested subsets of larger assemblages based on the habitats in which they are found by using the algorithms implemented in ANINHADO 3.0 (Bangu) [108–110]. In this program, the matrix is rearranged (packed) to achieve the densest grouping of species in the habitats [111]. We employed both the Temperature calculator ($T°$) and nestedness metrics based on overlap and decreasing fill (NODF) [109], but because the packing is only marginally different, here we report $T°$. We tested all packed matrices using the 4 null models described by Guimarães & Guimarães [110]. For comparison purposes we also included a meta-analysis of 11 published datasets of rotifers from other biomes including aridlands (n = 5), cold (n = 2), temperate (n = 2), and tropical regions (n = 2). In our previous nestedness study [90] we determined species or habitats to be idiosyncratic when their individual $T°$ was ≥1 SD than the mean of the matrix $T°$. Since species and site $T°$ often exhibit large variance, we decided to employ a more rigorous criterion, and here we note idiosyncratic species or habitats when their value is ≥2 SD of the mean of matrix $T°$.

2.7. *Relationship between Species Richness and Geographic Distance*

To determine whether distances between sites were contributing to differences in species composition, we conducted Mantel tests. Geographic distances between sites were estimated using Haversine distances based on GPS coordinates using the R package *geosphere* 1.5-10 [112]. Bray-Curtis dissimilarity matrices of species composition were constructed using the *vegdist* function from the R package *vegan* 2.5-6 [113]. We used Mantel tests, based on Spearman rank correlations, to determine whether species composition was related to (1) geographic distances between collection sites, (2) spatial scale (e.g., grid cells size), and/or (3) habitat type.

2.8. Prediction of Biodiversity Hotspots

Based on our survey data, we estimated richness throughout the Chihuahuan Desert using empirical Bayesian kriging [114]. Using kriging as a method to predict species richness in unsampled areas has the benefit of illustrating general trends in richness across broad geographic regions. This process uses a probabilistic predictor that models spatial dependence with functions (i.e., semivariograms). A semivariogram model was estimated from the species richness data we obtained in our surveys, and then used that estimate to simulate the richness in unsampled geographic areas. From these newly simulated data, another semivariogram was estimated and evaluated against previous models using Bayes' rule. This process was iterated (n = 100) and the simulated data were used to predict richness at unsampled locations. Richness values were log-empirically transformed (a multiplicative skewing normal score approximation based on the log of our survey richness data) prior to semivariogram fitting. This process ensures that negative richness values are not predicted. Kriging was conducted on species richness at each site and for each grain size.

3. Results

3.1. Species Composition

We identified 246 rotifer species, which represents a substantial portion of known rotifer species, genera, and families (~13, 50 & 77%, respectively) [17,115]. Given that the Chihuahuan Desert comprises only about 0.35% of the global landmass (excluding the poles), it includes a large percentage of known rotifer biodiversity. Species richness ranged from 1 to 44 at a given locality. The site with the highest richness was Laguna Prieta at HTSPHS (S = 44). This site was sampled >20 times during this study. The site with the second highest richness was Lago Colina located in Chihuahua, Mexico (S = 43), but this site was sampled only four times over a 2-year period. Species found in all habitat types (except rock pools) include *Brachionus quadridentatus, Cephalodella catellina, Cephalodella forficula, Cephalodella gibba, Colurella obtusa, Euchlanis dilatata, Lecane bulla, Lecane hamata, Lecane luna*, and *Platyias quadricornis*. *Lecane quadridentata* was found in all habitats except streams.

3.2. Diversity Indices

Of the five most common habitat types, springs had the highest richness (S = 175) while rock pools had the lowest (S = 53) (Figure 1A). Former cattle tanks also exhibited relatively low diversity (S = 53). In the few rivers (2 rivers, 26 sites) and streams (5 streams, 7 sites), sampled richness was 95 and 26, respectively. When compared to all other sites, springs also had the highest percentage of unique species (34.3%), followed by lakes and tanks (10.5%), playas (9.1%) and finally rock pools (5.7%) (Table 1). For these systems, Sorensen's Index ranged from 0.36 to 0.54, and most habitats share about 40% of their species (Table 1) with springs and lakes having the most divergent rotifer species communities. Diversity was highest at the largest spatial scale investigated, with the mean diversity for cells at the largest grid size being 48, 35, 27 for q = 0, 1, and 2, respectively. Diversity found for q = 0, 1, and 2 increased at higher spatial grains (r^2 = 0.16, 0.15, 0.12, respectively; p-value < 0.05 for each; Figure 1). The strength of this relationship decreased with increasing Hill number.

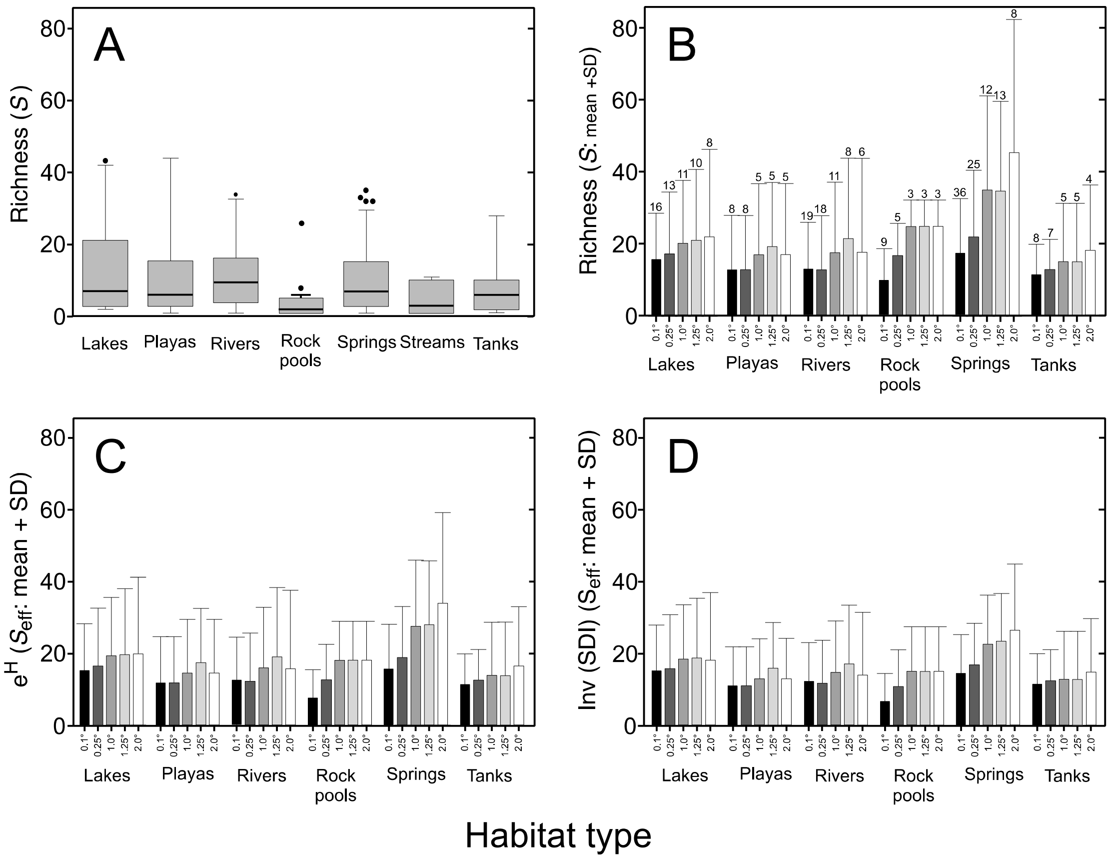

Figure 1. Observed species richness (*S*) of rotifers in 236 Chihuahuan Desert aquatic sites grouped by habitat type over >20 years. (**A**) Boxplots: horizontal lines indicate median, 95% confidence intervals are shown; dots represent outliers, (**B**) Richness at different geographic scales (grid cell sizes: 0.1°, 0.25°, 1.0°, 1.25°, 2.0°), numbers above bars are sample sizes, and are the same for panels C and D. (**C**) Effective richness e^H; Hill number, order q = 1. (**D**) Effective richness based on inverse (inv) of the Simpson's Diversity Index (SDI); Hill number, order q = 2.

Table 1. Species richness, unique species, and Sorensen's Index (below diagonal) and number of shared species (above diagonal) of rotifers from five selected habitat types in the Chihuahuan Desert.

Habitat Type	Species Richness (*S*)	Unique Species *	Versus Lake	Versus Playa	Versus Rock Pool	Versus Spring	Versus Tank
Lake	114	12 (10.5)	—	42	36	77	33
Playa	66	6 (9.1)	0.47	—	24	45	26
Rock pool	53	3 (5.7)	0.44	0.40	—	44	20
Spring	175	60 (34.3)	0.54	0.38	0.39	—	39
Tank	57	6 (10.5)	0.39	0.42	0.36	0.34	—

*—Number of species and percentage of *S* occurring only in this habitat type compared to all sampling sites.

3.3. Sampling Effort

There was a positive relationship between observed species richness and sampling effort when we included all sites in the analysis, although *S* is only weakly explained ($r^2 = 0.01$, $p < 0.05$; Figure 2). However, when analyzed by habitat type, the relationship was stronger (r^2 = 0.32, 0.17, 0.40, 0.56 for springs, lakes, rivers, and tanks, respectively). Although, in some cases, such as in rock pools, *S* was weakly explained by sampling effort ($r^2 = 0.02$, $p < 0.05$). Playas and streams did not show a significant relationship with sampling effort.

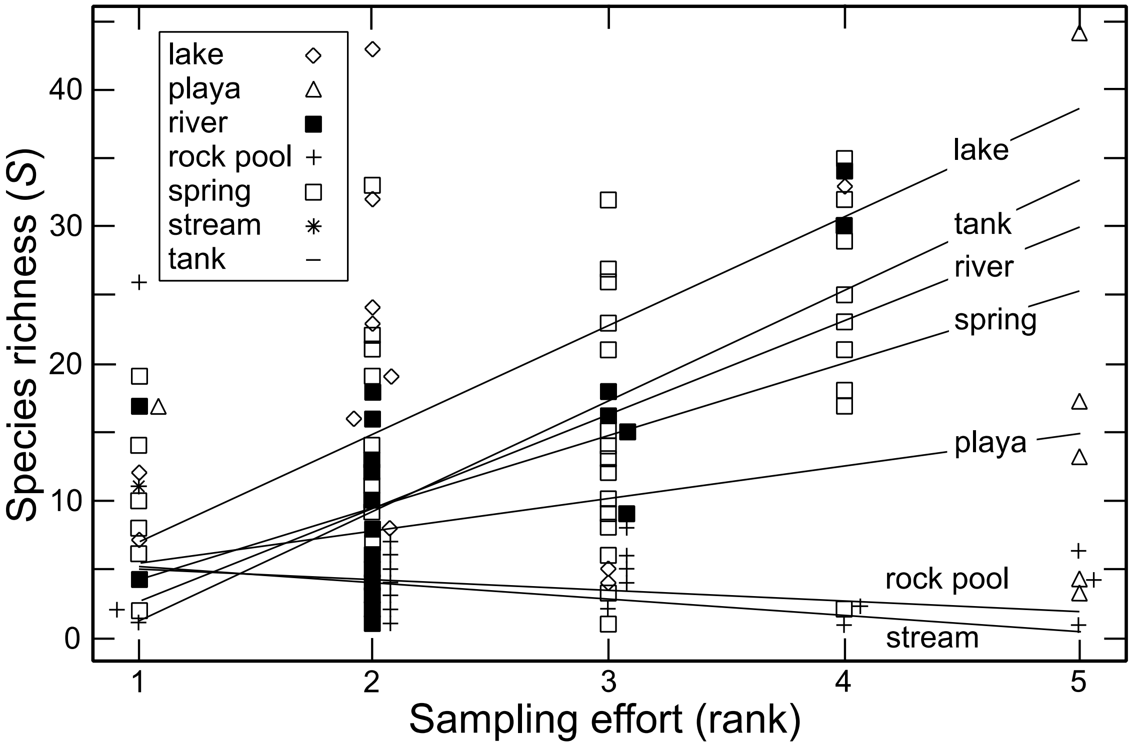

Figure 2. Observed species richness (*S*) as a function of sampling effort in 236 Chihuahuan Desert aquatic sites over 20 years. We shifted some of the data points to reveal their location; some remain obscured by other data points. Lines are linear regressions of the data analyzed separately for each site type. We ranked sampling effort as follows: 1 = 1 sampling event; 2 = 2–5 events; 3 = 6–10 events; 4 = 10–20 events; 5 = >20 events.

3.4. Indicator Species Identification

In the indicator species analysis, 144 species were associated with one habitat type, while only 4 species were associated with 6 of the 7 habitat types. Indicator species were identified for all habitat types and some combinations of habitat types (Table 2). Playas and Lake + Tanks had the most indicator species ($n = 5$). While two species (*C. gibba* and *L. luna*) were indicators of all habitat types except rock pools. Not surprisingly, *Hexarthra* n. sp. is an indicator species for rock pools. Indicator species with highly significant associations ($p < 0.001$) include *Hexarthra* n. sp. with rock pools, *Epiphanes brachionus* with playa habitats, *B. quadridentatus* with playa + river + tank habitats, *E. dilatata* with playa + river + stream + tank habitats, and *L. bulla* with lake + playa + river + spring + stream habitats. Species that were indicators of combinations of five habitat types include: *L. bulla*, *Philodina megalotrocha*, *L. luna*, and *C. gibba.*

Table 2. Rotifer indicator species by habitat type for 236 waterbodies in the Chihuahuan Desert. Only those combinations of habitat types with significant associations are reported. Indicator value (IndVal) is the test statistic and p values were calculated using permutation tests.

Habitat Type	Number of Associated Species	Indicator Species	IndVal	*p* Value
Lake	30	*Trichocerca pusilla*	0.483	0.003
		Asplanchna priodonta	0.378	0.008
Playa	16	*Epiphanes brachionus*	0.538	0.001
		Rhinoglena ovigera	0.458	0.011
		Filinia cornuta	0.433	0.002
		Asplanchna sieboldii	0.387	0.012
		Lacinularia flosculosa	0.354	0.048

Table 2. *Cont.*

Habitat Type	Number of Associated Species	Indicator Species	IndVal	*p* Value
Rock Pool	6	*Hexarthra* n. sp.	0.632	0.001
Stream	3	*Dicranophorus grandis*	0.378	0.027
		Wulfertia ornata	0.378	0.027
Tank	13	*Filinia* cf. *pejleri*	0.481	0.005
		Brachionus dimidiatus	0.360	0.018
Lake + River	5	*Keratella americana*	0.432	0.011
Lake + Rock Pool	1	*Trichocerca similis*	0.514	0.004
Lake + Stream	3	*Colurella adriatica*	0.423	0.014
Lake + Tank	6	*Asplanchna brightwellii*	0.433	0.013
		Brachionus caudatus	0.354	0.031
		Brachionus havanaensis	0.350	0.041
		Euchlanis calpidia	0.345	0.042
		Mytilina ventralis	0.332	0.042
Playa + Stream	1	*Trichocerca rattus*	0.445	0.004
River + Spring	2	*Dipleuchlanis propatula*	0.396	0.034
River + Tank	6	*Plationus patulus*	0.446	0.015
		Eosphora najas	0.397	0.022
		Brachionus bidentatus	0.364	0.026
Lake + Playa + Spring	3	*Lecane closterocerca*	0.439	0.049
Lake + Playa + Stream	2	*Brachionus plicatilis*	0.486	0.006
		Notommata glyphura	0.356	0.039
Lake + River + Spring	7	*Colurella uncinata*	0.482	0.010
Lake + River + Tank	4	*Keratella cochlearis*	0.467	0.003
		Brachionus variabilis	0.431	0.011
		Polyarthra dolichoptera	0.431	0.028
		Testudinella patina	0.403	0.040
Playa + River + Tank	3	*Brachionus quadridentatus*	0.674	0.001
		Brachionus angularis	0.439	0.019
Lake + Playa + River + Stream	1	*Cephalodella catalina*	0.455	0.019
Lake + Playa + River + Tank	4	*Brachionus calyciflorus*	0.432	0.026
		Epiphanes chihuahuaensis	0.368	0.036
Playa + River + Stream + Tank	2	*Euchlanis dilatata*	0.628	0.001
		Platyias quadricornis	0.462	0.012
Lake + Playa + River + Spring + Stream	2	*Lecane bulla*	0.668	0.001
Lake + River + Spring + Stream + Tank	1	*Philodina megalotrocha*	0.598	0.007
Lake + Playa + River + Spring + Stream + Tank	4	*Lecane luna*	0.564	0.008
		Cephalodella gibba	0.495	0.017

3.5. Nestedness

We evaluated nestedness in rotifers from the 236 Chihuahuan Desert aquatic habitats at several levels: (1) the completed dataset; (2) by habitat type (lakes, playas, tanks, springs, cascading pools, and rock pools); (3) by geospatial scale (0.1°, 0.25°, 1.0°, 1.25°, and 2.0°). As a comparison, we completed a meta-analysis on data from 11 published studies that examined rotifer assemblages from other biomes (see above). We report results of these analyses in Table 3 and summarized them below.

Table 3. Comparative statistics of nestedness among selected studies based on presence/absence data of rotifer species. (See Table A1 for an explanation of the sites, including the abbreviations used here.).

Regions Analyzed [1]	Number of Taxa	Number of Genera	Number of Families	Packed Matrix T°	Null Support [2]	Idiosyncratic Species [3]	Idiosyncratic Habitats [4]
Chihuahuan Desert (this study)							
All sites	246	59	25	2.4	4	*Hexarthra* n. sp.; *Trichocerca similis*	Caballo Reservoir, NM; Cattail Spring Pools C-D, BIBE, TX; Lake Lucero, WHSA, NM; Langford Hot Springs, BIBE, TX; Miller Ranch 2 (Spring), TX; Presa Chihuahua, MX; Rio Grande Village Cattail Pond, BIBE, TX; Rio Grande Village Upper Pond, BIBE, TX
By habitat type							
1. All lakes	112	38	24	14.2	4	*Encentrum* cf. *algente; Lecane arcula; Lecane quadridentata; Polyarthra vulgaris;* Synchaeta cf. *oblonga*	Presa Chihuahua, Chihuahua, MX
2. All playas	66	30	19	11.9	4	*Lecane hornemanni; Lecane thalera*	None
3. All tanks	57	27	14	11.1	4	*Brachionus durgae; Epiphanes brachionus; Lepadella patella*	Tule Cattle Tank, BIBE, TX
4. All springs	175	49	23	5.0	4	*Adineta vaga; Aspelta aper; Cephalodella catellina; Cephalodella tenuiseta; Colurella adriatica; Encentrum saundersiae; Filinia brachiata; Lepadella acuminata; Mytilina mucronata;* Notommata cf. *haueri*	Balmorhea State Park Main Pool, TX; Balmorhea Wetland 2, TX; Miller Ranch 96 Well, TX; Oak Creek BIBE, TX; Ojo de la Punta, ANPMS, MX; Sitting Bull Falls LNF, NM
Selected springs in Mexico	57	24	15	21.9	4	*Cephalodella* cf. *graciosa; Cephalodella megalocephala; Pleurotrocha petromyzon; Pleurotrocha sigmoidea*	One small, impounded spring: Ojo de en Medio, ANPMS
5. Cascading pools (BIBE)							
A. All rock pools	72	21	14	5.4	4	*Epiphanes daphnicola; Trichocerca similis*	Second pool of the flowage – surrounded by lush vegetation
B. Cattail Springs	65	19	11	23.7	4	*Colurella obtusa; Lecane pyriformis; Proales cryptopus; Tripleuchlanis plicata*	Small pool isolated from the main flowage at this site.
C. Ernst canyon	16	9	8	19.0	4	None	None

Table 3. *Cont.*

Regions Analyzed [1]	Number of Taxa	Number of Genera	Number of Families	Packed Matrix *T*°	Null Support [2]	Idiosyncratic Species [3]	Idiosyncratic Habitats [4]
D. Tuff canyon	4	4	3	11.7	0	None	Shallow rock pool (Tuff Canyon Site #4)
E. Window Trail canyon	16	7	6	23.3	2	*Lecane pyriformis*	Small tinaja nearly filled with small rocks and sediment, surrounded by plants
6. Rock pools at HTSPHS							
A. Isolated rock pools	14	11	9	4.9	4	None. However, *Hexarthra* n. sp. was found in all sites except for the two artificially enlarged, sheltered rock pools noted here	Two, artificially enlarged, rock pools sheltered by an overhanging shelf
B. Mesocosms: artificial rock pools	9	6	5	22.9	1	*Lecane nana*	None
By Geospatial scale (grid size)							
1. Grid 0.1°	246	59	25	4.4	4	*Adineta vaga; Brachionus plicatilis; Brachionus variabilis; Cephalodella* cf. *misgurnus/pachyodon; Lecane hornemanni; Lecane inermis; Synchaeta* cf. *oblonga; Trichocerca similis*	20755: Northern BIBE (Cattail Springs, Window trail, Croton spring) 29355:Caballo reservoir and Percha dam 30345:BLSP
2. Grid 0.25°	246	59	25	6.0	4	*Brachionus caudatus; Brachionus variabilis; Cephalodella* cf. *misgurnus/pachyodon; Epiphanes chihuahuaensis; Paradicranophorus sordidus; Polyarthra vulgaris; Trichocerca similis; Wulfertia ornata*	3310:Northern BIBE 4842:BLSP
3. Grid 1.0°	246	59	25	11.6	4	*Brachionus bidentatus; Brachionus plicatilis; Cephalodella calosa; Euchlanis triquetra; Filinia brachiata; Keratella americana; Keratella cochlearis; Philodina acuticornis; Philodina megalotrocha; Proales cognita; Wolga spinifera; Wulfertia ornata*	177: Delicias Beisbol field pool and Presa Francisco Ignacio Madero (southern pond and reservoir respectively) 298: BLSP

Table 3. *Cont.*

Regions Analyzed [1]	Number of Taxa	Number of Genera	Number of Families	Packed Matrix $T°$	Null Support [2]	Idiosyncratic Species [3]	Idiosyncratic Habitats [4]
4. Grid 1.25°	246	59	25	10.5	4	*Dicranophorus mesotis; Euchlanis calpidia; Hexarthra* n.sp.; *Lacinularia flosculosa; Lecane aeganea; Lecane undulata; Paradicranophorus sordidus; Polyarthra vulgaris; Proales* cf. *halophila; Squatinella lamellaris* f. *mutica; Testudinella patina; Trichocerca similis*	El Paso area including HTSPHS
5. Grid 2.0°	246	59	25	9.5	4	*Encentrum* cf. *cruentum; Euchlanis calpidia; Paradicranophorus sordidus; Plationus patulus; Polyarthra vulgaris; Trichocerca similis*	64: El Paso/Juarez area including ANPMS, HTSPHS, IMRS 65: GUMO and Balmorhea SP
				Other aridland biomes			
1. Billabongs (Australia)	52	25	18	39.3	2	*Mytilina mucronata; Epiphanes daphnicola; Trichocerca rattus*	None
2. Various habitats (Oman)	66	20	12	45.9	3	*Cephalodella gibba; Colurella obtusa; Trichocerca tenuior*	Ravine (Wadi O7)
3. Various habitats (Saudi Arabia)	19	10	7	11.1	3	*Lecane ungulata*	Brackish water lagoon (Sabkhat S7)
4. Various habitats (Yemen)	74	26	16	11.3	4	*Brachionus urceolaris; Cephalodella forficula; Colurella adriatica; Lophocharis salpina*	Wet Wadi (Y30) with *Phragmites*
5. Dune pools (Spain)	34	18	12	16.5	4	*Lophocharis salpina; Trichocerca bidens; Trichocerca rattus*	Two pools: (1) mobile dune region; (2) stable dune region and close to a salt marsh
				Tropical biomes			
1. Costa Rican habitats	105	33	17	10.1	4	*Ascomorpha klementi; Keratella americana; Lecane nana; Lepadella patella; Resticula melandoca; Trichocerca dixonnuttalli*	Artificial Lake; *Bromelia*; Lake Turrialba
2. Eutrophic tropical fish ponds	57	22	15	61.8	0	None	None

Table 3. *Cont.*

Regions Analyzed [1]	Number of Taxa	Number of Genera	Number of Families	Packed Matrix T°	Null Support [2]	Idiosyncratic Species [3]	Idiosyncratic Habitats [4]
Temperate biomes							
1. North Island, NZ	79	32	20	26.3	4	*Filinia* cf. *pejleri; Keratella australis; Keratella tropica; Lecane flexilis; Lepadella acuminata; Trichocerca longiseta*	Lake Okaro; Lake Ototoa; Lake Tutira
2. Develi Plain, Turkey	84	33	17	31.6	3	*Lecane quadridentata; Lepadella biloba; Scaridium longicauda*	None
Cold biomes							
1. Antarctica & sub-Antarctica	24	6	3	22.7	2	*Brachionus quadridentatus; Notholca hollowdayi*	None
2. Canadian High Arctic	70	26	16	29.5	4	*Collotheca* sp. 2; *Cephalodella catellina; Squatinella* sp.; *Trichocerca* sp.	Small pool, 8 (P208)

[1]—Partitioning of the dataset. To run the nestedness analyses, we partitioned our Chihuahuan Desert dataset into units as follows. Chihuahuan Desert: All sites (n = 236). By habitat type: 1. Lakes (n = 21). 2. Playas (n = 16). 3. Tanks (n = 11). 4. Springs (n = 95). Selected springs in Mexico (n = 7) in Samalayuca, Chihuahua, Mexico; these data were previously published by Ríos-Arana, Agüero-Reyes, Wallace and Walsh [90]. 5. Cascading Pools: A. All pool habitats at Big Bend National Park (BIBE) (n = 40). B. Cattail Spring (BIBE) (n = 11). C. Ernst Canyon (BIBE) (n = 12). D. Tuff Canyon (BIBE) (n = 6). E. Window Trail (BIBE) (n = 10). 6. Isolated pools: A. Isolated rock pools (n = 27) at Hueco Tanks State Park and Historical Site (HTSPHS) (El Paso, TX). B. Mesocosms–Artificial rock pools (n = 6) developed over 9 weeks at HTSPHS [20]. By scale (grid size): 1. Gridded at 0.1° (n = 83 designations). 2. Gridded at 0.25° (n = 55 designations). 3. Grid 1.0° (n = 23 designations). 4. Gridded at 1.25° (n = 21 designations). 5. Gridded 2.0° (n = 14 designations). Other aridland biomes: 1. Billabongs (oxbows, cut–off meanders) (n = 13) in River Murray (southeastern Australia) [116]. 2, 3, 4. Various habitats ranging from permanent lakes and rivers to temporary pools in Oman (n = 9), Saudi Arabia (n = 19), and Yemen (n = 33), respectively [84]. 5. Ephemeral dune pools (n = 32) in Doñana National Park (Spain) [85]. Tropical biomes: 1. Costa Rica—various habitats including puddles, phytotelmata, ditches, and lakes (n = 29) [117]. 2. Eutrophic, tropical fish ponds (n = 5) in Darbhanga City (Bihar, India) [118]. Temperate biomes: 1. Lakes on North Island, New Zealand (n = 31) [119]. 2. Develi Plain (n = 8) Middle Anatolia, Kayseri, Turkey [120]. Cold Biomes: 1. Antarctica and sub-Antarctica—various habitats (n = 14) [121]. 2. Canadian High Arctic (Devon Island, Northwest Territories)—pools, ponds, and a small lake (n = 8) [122]. [2]—Number of null models supporting nestedness. [3]—Comments on species with individual T° ≥ 2 SD of the mean matrix T°. [4]—Comments on sites or gridded regions with individual T° ≥ 2 SD of the mean matrix T°.

The complete dataset exhibited nestedness, with support from 4 null models ($p < 0.001$). At this scale, only two idiosyncratic species (identified as those with a $T° \geq 2SD$ above the mean matrix $T° = 2.55$): *Hexarthra* n. sp. and *Trichocerca similis*. Of these two species, *Hexarthra* n. sp. [89] had the most restrictive distribution. It was confined to a group of 25 isolated rock pools at HTSPHS, indicating that it is a rock pool specialist. (See also the discussion below on rock pools.) The other idiosyncratic species, *T. similis*, was present in 24 habitats (~10% of all the sites we studied), including rock pools ($n = 18$), lakes ($n = 4$), one pond, and one spring. However, while it also seems to be a rock pool specialist, it was not present in the HTSPHS system. We found *T. similis* in two rock pool systems of BIBE possessing very different edaphic conditions. In our analysis of the complete dataset several sampling sites ($n = 8$) were identified as idiosyncratic habitats, but there was no common feature among them: springs ($n = 2$); lakes and reservoirs ($n = 3$); ponds ($n = 2$); cascading pools ($n = 1$).

We subdivided the dataset by habitat type to examine the distribution of rotifers separately in lakes, playas, tanks, springs, cascading pools, and isolated rock pools at HTSPHS. Lakes and reservoirs ($n = 21$) possessed five idiosyncratic species (*Encentrum* cf. *algente; Lecane arcula; L. quadridentata; Polyarthra vulgaris; Synchaeta* cf. *oblonga*), but only one idiosyncratic reservoir, Presa Chihuahua. Playas ($n = 16$) possessed two idiosyncratic species (*Lecane hornemanni* and *L. thalera),* but no idiosyncratic habitats. There were three idiosyncratic species in the tanks ($n = 11$) (*Brachionus durgae*, *E. brachionus*, and *Lepadella patella* and one idiosyncratic habitat, Tule Cattle Tank (BIBE). The spring habitats exhibited more diversity with 10 idiosyncratic species (*Adineta vaga, Aspelta aper, C. catellina, Cephalodella tenuiseta, Colurella adriatica, Encentrum saundersiae, Filinia brachiata, Lepadella acuminata, Mytilina mucronata,* and *Notommata* cf. *haueri*). Six of the spring habitats ($n = 95$) idiosyncratically distinct ($n = 6$); these included Balmorhea Main Pool, Balmorhea wetland 2, Miller Ranch 96 Well, Oak Creek BIBE, Ojo de la Punta ANPMS, and Sitting Bull Falls LNF. In a previous study of 7 springs in Mexico [90] we found four idiosyncratic species *Cephalodella cf. graciosa* and *Cephalodella megalocephala, Pleurotrocha petromyzon,* and *Pleurotrocha sigmoidea* and one small, idiosyncratic habitat: Ojo de en Medio.

We also examined a portion of the dataset that included only BIBE habitats in which one pool cascaded into another ($n = 40$). In that analysis two species (*Epiphanes daphnicola* and *T. similis*) and one habitat (a pool surrounded by lush vegetation) possessed idiosyncratic $T°$. Since the edaphic conditions of these pool habitats are different, we separated them by location ($n = 5$) to explore whether they exhibited unique species distributions. In the Cattail Spring pools ($n = 12$) four species (*C. obtusa, Lecane pyriformis, Proales cryptopus,* and *Tripleuchlanis plicata*) and one small pool isolated from the main flowage yielded idiosyncratic $T°$. Surprisingly in Ernst canyon, none of the 16 species or 12 rock pools proved to be idiosyncratic. Tuff canyon pools ($n = 6$) also possessed no idiosyncratic species and only one idiosyncratic habitat (one small pool). In the rock pool flowage of the Window Trail pools ($n = 10$ sites) one species (*L. pyriformis*) and one habitat (a small tinaja nearly filled with small rocks and sediment, surrounded by plants) possessed idiosyncratic $T°$. The rock pools at HTSPHS yielded no idiosyncratic species. However, as noted above *Hexarthra* n. sp. was found in all sites except for two artificially enlarged, sheltered rock pools. Those rock pools were also possessed idiosyncratic $T°$. In a separate study of six artificial rock pools (mesocosms) placed at HTSPHS, only one species (*Lecane nana*) had an idiosyncratic $T°$. Interestingly, this species was not found in natural habitats of HTSPHS during our extensive sampling effort ($n > 20$ for most sites over 20 years).

Nestedness was evident across all five geospatial scales (0.1°, 0.25°, 1°, 1.25°, and 2.0°), with support from 4 null models ($P < 0.001$) at each scale. A total of 38 idiosyncratic species were identified in the geospatial analysis and of these eight were identified at more than one spatial scale: *Brachionus plicatilis; Brachionus variabilis; Cephalodella* cf. *misgurnus/pachyodon; Euchlanis calpidia; Paradicranophorus sordidus; P. vulgaris; T. similis;* and *Wulfertia ornata*. Ten regions were identified as idiosyncratic across the five geospatial grids. No obvious pattern of habitats emerged from the scale analysis.

Of the 246 species identified in this study, 59 possessed idiosyncratic $T°$ in one or more of the analyses. Of that set we recorded 10 species twice (*A. vaga*, *B. plicatilis*, *B. variabilis*, *C.* cf. *misgurnus/pachyodon*, *E. calpidia*, *F. brachiata*, *L. hornemanni*, *L. pyriformis*, *S.* cf. *oblonga*, and *W. ornata*), while three other species occurred more often: three (*P. sordidus*), four (*P. vulgaris*), and five (*T. similis*) times.

For comparison purposes we reviewed published datasets from four other biomes, including aridland (*n* = 5), tropical (*n* = 2), temperate (*n* = 2), and cold (*n* = 2) biomes. In 13 billabongs of Australia three species (*M. mucronata*; *E. daphnicola*; *Trichocerca rattus*), but no habitats, possessed idiosyncratic *T*°. Similar results were found in the desert habitats of Oman (*n* = 9 sites) (*C. gibba; C. obtusa; Trichocerca tenuior*), Saudi Arabia (*n* = 23 sites) (*Lecane ungulata*), and Yemen (*n* = 12 sites) (*Brachionus urceolaris; C. forficula; C. adriatica; Lophocharis salpina*). In each of these datasets, a single habitat possessed an idiosyncratic *T*°: Ravine (Wadi O7), Sabkhat (S7), and Wet Wadi (Y30) with *Phragmites*, respectively. An analysis of 32 dune pools in Spain also yielded similar results: three idiosyncratic taxa (*L. salpina; Trichocerca bidens; T. rattus*) and two idiosyncratic habitats: mobile dune region; stable dune region and close to a salt marsh. The two tropical datasets we evaluated offered very different results. In 29 Costa Rican habitats we found six idiosyncratic species (*Ascomorpha klementi; Keratella americana; L. nana; L. patella; Resticula melandoca; Trichocerca dixonnuttalli*) and three idiosyncratic habitats (an artificial Lake; Lake Turrialba; bromeliads). On the other hand, no idiosyncratic taxa or habitats were present in five tropical fishponds. We found similar results in two temperate regions. In 31 sites on the North Island of New Zealand six species (*Filinia* cf. *pejleri; Keratella australis; Keratella tropica; Lecane flexilis; L. acuminata; Trichocerca longiseta*) and three lakes (Lake Okaro; Lake Ototoa; Lake Tutira) yielded idiosyncratic *T*°. In seven habitats of the Develi Plain (Turkey) three species (*L. quadridentata; Lepadella biloba; Scaridium longicauda*), but no habitats with idiosyncratic *T*°. We examined published data from two habitats in cold biomes: one each in the Antarctica (*n* = 14) and Arctic (*n* = 8 sites). These habitats yielded a moderately rich fauna of 24 and 70 taxa, with two (*B. quadridentatus; Notholca hollowdayi*) and four (*Collotheca* sp. 2; *C. catellina; Squatinella* sp.; *Trichocerca* sp.) idiosyncratic taxa, respectively.

Of the 246 taxa identified in our Chihuahuan Desert dataset, 114 were also reported in the four comparison biomes: Aridlands (5 studies; n = 89 species); Tropical (2 studies; n = 63 species)*;* Temperate (2 studies; n = 72 species)*;* and Cold (2 studies; n = 30 species). In spite of this overlap, fewer species with idiosyncratic *T*° were found among all datasets. Of the 59 idiosyncratic species identified from the Chihuahuan Desert, only 11 also were identified as being idiosyncratic in the comparison biomes: Aridlands (n = 5) (*C. adriatica, C. obtusa, L. ungulata, M. mucronata,* and *E. daphnicola);* Tropical (n = 3) (*K. americana, L. nana,* and *L. patella);* Temperate (n = 2) (*L. quadridentata* and *L. acuminata);* Cold (n = 1) (*C. catellina*). None of those 11 species were present in more than one of the comparison biomes.

3.6. Relationship between Species Richness and Geographic Distance

Mantel tests showed a significant correlation between distance and species composition for grid cell sizes below 1.25°. The effect became progressively larger at smaller grid cell size, being the most substantial at cell size 0.1° (*p* = 0.01) and the least significant at the largest grid cell size (2°; *p* = 0.1). Species composition in springs demonstrated no significant correlation with distance at any spatial scale investigated. In contrast, playa species composition showed significant correlations with distance at all grain sizes. Tank composition was significant at all grain sizes with the exception of 0.25°. All other habitats showed significant correlation at small grain sizes, but little correlation at large grain sizes (See Table 4). Stream sites were too few (n = 3) to adequately assess using Mantel tests, and thus were not analyzed as a separate habitat.

Table 4. Mantel correlation coefficients (r) between Haversine geographic distances and Bray-Curtis dissimilarity values for rotifer communities between sites (n) at each grid size investigated. Habitat types were then analyzed separately, with the exception of streams due to low number of samples (n = 3 at grid size 0.1°).

Region	**Mantel r Statistic**	***P*-Value**	**n**
All sites			
sites	0.12	<0.001	236
0.1°	0.12	0.01	84
0.25°	0.14	0.02	55
1°	0.03	0.22	24
1.25°	0.20	0.08	21
2°	0.20	0.10	14
By habitat			
Lakes			
sites	0.30	0.001	21
0.1°	0.25	0.044	16
0.25°	0.20	0.105	13
1°	0.31	0.048	11
1.25°	0.32	0.085	10
2°	0.35	0.095	8
Playas			
sites	0.55	<0.001	16
0.1°	0.60	0.009	8
0.25°	0.62	0.002	7
1°	0.74	0.008	5
1.25°	0.58	0.083	5
2°	0.80	0.008	5
Rivers			
sites	0.27	<0.001	26
0.1°	0.41	<0.001	19
0.25°	0.48	<0.001	18
1°	0.42	0.012	11
1.25°	0.13	0.271	8
2°	0.13	0.350	6
Rock pools			
sites	0.12	<0.001	60
0.1°	−0.16	0.696	9
0.25°	0.61	0.133	5
Springs			
sites	0.02	0.334	95
0.1°	−0.06	0.752	36
0.25°	−0.05	0.663	25
1°	0.06	0.321	12
1.25°	0.02	0.406	13
2°	0.16	0.253	8
Tanks			
sites	0.41	0.012	11
0.1°	0.35	0.063	8
0.25°	0.28	0.147	7
1°	0.60	0.017	5
1.25°	0.67	0.008	5
2°	0.77	0.083	4

3.7. Prediction of Biodiversity Hotspots

Generally, patterns of predicted species richness were similar among the spatial scales investigated (Figure 3). At smaller scales, localized hotspots of richness are apparent within the Chihuahuan Desert.

At the site level, 0.1° and 0.25° grid cell sizes, predicted species richness was highest in a band spanning from the southern Chihuahuan Desert northward along the western border to the El Paso/Juarez area, and a band spanning from Guadalupe Mountains National Park (TX) to Balmorhea State Park (TX), with low predicted richness along the Rio Grande in this area. When we excluded the site level, a band of high predicted richness exists from Samalayuca across the Rio Grande to Balmorhea State Park, each with localized hotspots (Figure 3B,C). Cuatro Ciénegas showed high richness at most scales (Figure 3B–D). At grid cell sizes >0.25°, distinct hotspots are less apparent (Figure 3D). At these higher scales, local hotspots are more difficult to resolve due to the lower number of grid cells present within the Chihuahuan Desert (n = 24 for 1° grid cells).

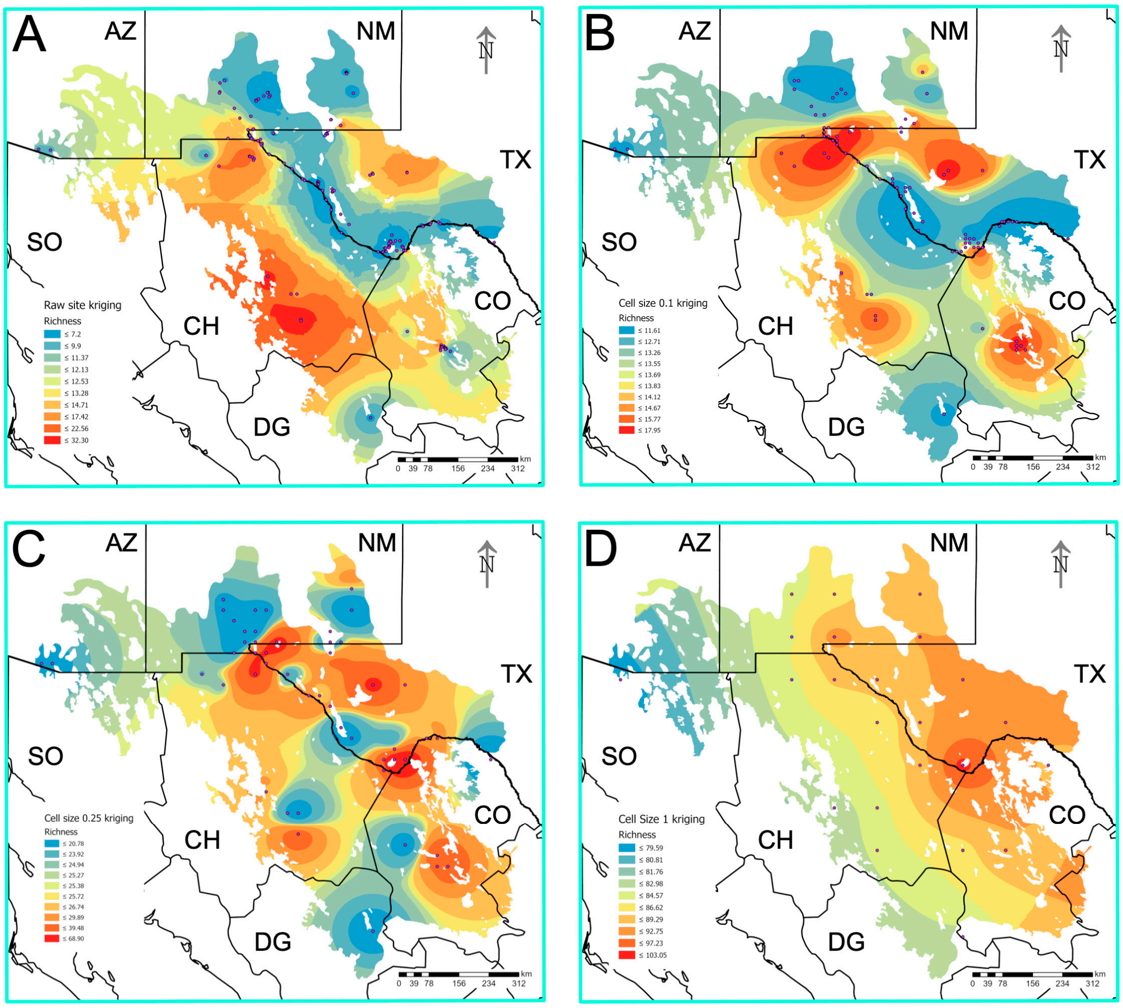

Figure 3. Empirical Bayesian kriging of predicted rotifer species richness within the Chihuahuan Desert ecoregion [123] interpolated from all sites (n = 236) and at a variety of spatial scales. (**A**) All collection sites (**B**) 0.1° grid cells, (**C**) 0.25° grid cells, and (**D**) 1° grid cells. Sites (panel A) and grid cell centroids (panels B–D) are represented by purple dots. We obtained state boundaries from the USGS and ArcGIS online [124]; ArcGIS Mexican state boundary shapefile courtesy of M. Hoel (www.arcgis.com).

4. Discussion

Comprehensive studies of rotifer distributions are common, but vary widely in their focus. For example, many emphasize long-term, ecological questions across several water bodies [125–128], the dynamics in a particular lake [129–134] or region [13,14,117,135–140], or examine a single taxon [141–148]. Collectively, such studies provide insight into the biogeography of the phylum. However, to obtain a thorough understanding of the biogeography of rotifers, long-term, systematic survey data is required. Unfortunately, that level of effort is difficult to accomplish, so most studies provide a short-term, snapshot of a region or of a particular habitat [149–155]. On the other hand, extensive regional studies have been published, which illustrate the diversity of rotifers that may be present in one area: three studies illustrate this point. (1) The study by Segers and Dumont [84] of >110 sites across the Arabian Peninsula, which included five countries, yielded >115 species. (2) In examining 33 lakes on the North Island of New Zealand, Duggan and his colleagues [135] reported 79 species. (3) In a long-term study (1982 onward) of the zooplankton of seven water bodies in the Trout Lake LTER [140], ~75 species have been recorded.

While our choice of collection sites was pragmatic and based on accessibility, sampling >225 diverse habitats over a 20-year period, with many sites visited multiple times, this study comprises an extensive survey. Due to its thorough nature, our analysis of Chihuahuan Desert aquatic systems offers additional insight to the understanding diversity of rotifers in aridlands, and it offers testable predictions regarding the presence of biodiversity hotspots at a regional level.

Among habitats, rotifer species richness was highest in springs (n = 175) and lowest in rock pools (n = 53) followed closely by tanks and playas (n = 57, 66, respectively). This difference in diversity may reflect the relative stability of these habitats in terms of hydroperiod and/or connectivity with other sites. For example, the ephemeral rock pools at HTSPHS are unique in character from all other rocky basins examined in our study. All of the HTSPHS rock pools have nearly identical edaphic conditions, and the *Hexarthra* found in these pools was identified as a strong indicator species for rock pools (Table 2). For rotifers, the use of the indicator species concept has been used mostly in regard to water quality [99]; thus, our application is somewhat unique. It should be noted that some species have been highly associated with acidic habitats (e.g., *Cephalodella hoodi* [156], *Cephalodella acidophila* [157], *Keratella taurocephala* [158]), and function as indicators. The five species with significant indicator values associated with a combination of five habitat types (*L. bulla*, *P. megalotrocha*, *L. luna*, and *C. gibba*) possess wide ecological tolerances. Another implication is that these morphospecies likely represent cryptic species complexes [159,160] (see below).

Locations we identified possessing high predicted richness generally overlap the proposed wetland priority sites for the Chihuahuan Desert [25]. However, we found low richness in the Rio Grande and at aquatic sites in White Sands National Park (NM). Several priority areas were sparsely sampled in our study (i.e., the Apachean and the Meseta central subregions); making the predicted richness within these regions less reliable. However, some unusual outcomes occurred at various spatial scales. At our smallest scale (e.g., site level;) some areas that contain highly sampled locations yielded low overall predicted richness. For example, at HTSPHS large numbers of ephemeral rock pools are in close proximity to more speciose playas such as Laguna Prieta, the site with the highest richness in our survey (n = 44). The low diversity of these rock pools decreased our predicted richness for the entire area at the smallest spatial scale. At the 0.1° grid size, the low diversity rock pools and high diversity playas of HTSPHS are combined, resulting in a hotspot on the kriging map. We found similar scenarios at Cuatro Ciénegas (Mexico), BIBE (TX) and Bottomless Lakes State Park (NM). At the largest spatial scale (grid size 1°), the pattern seemed to be more influenced by sampling intensity.

Of the 17 different ways we examined nestedness in the Chihuahuan Desert sites, only three did not exhibit nestedness. The rock pools of Tuff Canyon had no support from the null models; Window Trail Canyon had support from only two; and the artificial rock pools (mesocosms) had support from only one model. These results are not surprising as the basins within of each of these systems are quite similar: Tuff Canyon (basalt larva and tuff deposits); Window Trail (limestone); Mesocosms (plastic basins filled with artificial pond water). This indicates that, for nestedness to be present, the inclusive habitats must possess environmental heterogeneity, and if nestedness were not present, we would expect the species assembly to be random within the habitats [161,162].

In the 18 ways that we analyzed nestedness in our Chihuahuan Desert dataset, we recorded a large number of species to be idiosyncratic (n = 59; ~24%). These species are those, that within the context of the data, contributed disproportionately to the overall matrix temperature; i.e., their occurrence is, therefore, unexpected in that nested group (Table 3). It is notable that most of the idiosyncratic species are generally considered cosmopolitan or having broad environmental tolerances. Our analyses also show that rotifer assemblages are correlated with distance at smaller spatial scales but are more homogenous at the regional level (Table 4). Other papers have reported similar patterns in multiple studies analyzing species assemblages or populations of a single species [147,160,163–167]. Thus, our results seem to support the Baas Becking Principle—"*Everything is everywhere*, but, *the environment selects*"—the ubiquity hypothesis [168]. That is, organisms with small dispersal stages (<1 mm) are easily, and widely, dispersed, but arrival does not necessarily guarantee persistence in a habitat [169].

We know that in rotifers, community structure may result from a combination of their high dispersal capacity and their ability to create resting egg banks [5,170]. These two traits can lead to the monopolization of local habitats if the initial colonization and subsequent production of an egg bank leads to rapid adaptation and then to the exclusion of other species. This construct has been named the monopolization hypothesis [171,172]. Thus, at small spatial scales, monopolization leads to high dissimilarity among sites, as may be the case of rock pools and springs in our study (lowest v. highest species richness). However, the high dispersal capability of rotifers may lead to increasing community similarity at larger spatial scales. In general, community composition of organisms with high dispersal ability are less impacted by geographic distances than those with low capacity. Local edaphic conditions, including the arrival sequence, ultimately selects the composition of assemblages that endures.

At larger spatial scales, a greater degree of habitat heterogeneity is present within each region, resulting in a reduction of assemblage differences among regions because of shared habitat types occurring within the larger geographic areas. We have previously reported that rotifer assemblages are more homogenous at the regional level, thereby supporting the relative cosmopolitan nature of dominant rotifer species [57]. However, there can be significant associations between local environmental parameters and species assemblages [53]. Here we report that Chihuahuan Desert spring assemblages were not correlated with distance at any spatial scale investigated. This may be due to the unique edaphic conditions present in each habitat. This was seen in *T. similis,* which was found in a series of small to large rock pools lying along an erosional channel of Cretaceous limestone in Ernst canyon (n = 12 sites) [173], as well as in Tuff canyon (n = 6 sites) where the rocks pools are arrayed in a channel of eroded basalt lava and tuff deposits [174].

We note that our estimate of richness is likely underestimated, as we could not identify some specimens to species; this is especially true for the Bdelloidea. In addition, it is well known that many traditional species of rotifers are, in fact, complexes of cryptic species [175,176]. For example, two species common in our samples, *E. dilatata* and *B. plicatilis,* are comprised of at least 4 and 15 separate lineages, respectively [145,147]. Two of the four newly described species of the *E. dilatata* complex occur in the Chihuahuan Desert [147]. During the surveys undertaken for this study, they were all recorded as *E. dilatata.* Finally, several new species are pending formal description.

Our research identified rotifers that exhibited distribution patterns at two extremes: either widely or narrowly distributed. Five species were widely distributed: i.e., being present in 50 or more of the sites we sampled. These species were *E. dilatata*, *L. bulla*, *L. luna*, *L. patella*, and *P. megalotrocha*. The perception in the literature is that species with wide distributions have few specific growth requirements. However, as noted above some of these species may represent cryptic species complexes: *E. dilatata* [147], *L. bulla* [56], *P. megalotrocha* [177], and *L. luna* (Walsh, unpubl. data). On the other hand, some species were narrowly distributed. In our collections we found 70 species only once (e.g., *Asplanchna intermedia, Brachionus rotundiformis, Cephalodella dentata, Filinia limnetica, Synchaeta tremula*). These species may possess rigorous requirements for growth, be poor dispersers, and/or poor competitors, in each case restricting their distributions.

In addition, we did not sample all sites evenly. We sampled some sites only once at one station, while we sampled others >20 times and from multiple stations/microhabitats within the waterbody. We showed that for sites at BIBE, increased sampling effort increased the number of species recovered even up to seven collections [88]. Similarly, among all sampled habitat types, sampling effort increased richness found, although this relationship was weakest in rock pools, possibly due to their low diversity.

5. Conclusions

Understanding the biogeography of rotifers remains an important problem. Indeed, the general perception that they do not have a biogeography remains largely untested. Rousselet was the first to pose this idea; he argued that " … the Rotifera enjoy a cosmopolitan distribution which is not limited to continents, but extends to all places on the surface of the earth where suitable conditions prevail" [15]. This view, which presaged that of Baas Becking, had been the prevailing view until challenged by several researchers [4,8,169,178]. Yet a large part of the question of whether rotifers possess a biogeography remains rooted in three issues. (1) There is a rotiferologist effect—that the distribution of rotifers indicates more the distribution of researchers, and the habitats that they survey, than the rotifer species themselves [179]. (2) Currently, there are few venues where researchers can receive training in rotifer taxonomy and identification [180]. Thus, identification is often limited to easily recognized species. (3) Recently researchers have come to the realization that cryptic speciation is widespread within the phylum [145,147,181,182] (see also above). Thus, reports of a species from distant locations that are identified based solely by morphological characters may be insufficient to consider them as identical. Emerging science on cryptic speciation suggests that they may be genetically distinct enough to warrant the designation of separate species. Examples of previously unrecognized morphological and ecological differences in the *B. plicatilis* complex [145], among other species [159], support this contention. Until these issues are, to a large degree, settled, an adequate test of whether rotifers fit the ubiquity hypothesis is not possible.

Thus, our research effort addresses three important aspects in understanding species distributions and biogeography. We covered a broad geographic range, provided a long-term study, and used repeated sampling of sites. Thus, it is not surprising that our study yielded a large number of species. Supporting our previous study that focused on a smaller geographic region (i.e., BIBE), here, we found that sampling effort was positively correlated with rotifer richness in more permanent habitats (e.g., lakes, springs, rivers) and in anthropogenic tanks. In addition, for some sites our efforts spanned seasons and years. Our predictive maps show that it is probable that additional rotifer species remain undiscovered in the Chihuahuan ecoregion. They also give guidance for focusing efforts, as well as for conservation prioritization. Additional diversity also may be revealed by molecular applications such as DNA sequencing to delineate cryptic species and environmental sequencing of water and sediments to find rare species and/or to sample habitats during desiccated periods. In conjunction with environmental data (e.g., water quality data, land use patterns), our findings also can be used to determine ecological drivers of rotifer species assemblages.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/12/10/393/s1, Figure S1: Examples of Chihuahuan Desert aquatic systems.

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Appendix A

Table A1. Site name, locations, habitat types, and sampling intensities for waterbodies included in this study. APFFC = Área de Protección de Flora y Fauna Cuatrociénegas, ANPMS = Área Natural Protegida Médanos de Samalayuca, BANWR = Buenos Aires National Wildlife Refuge, BIBE = Big Bend National Park, CAVE = Carlsbad Caverns National Park, GUMO = Guadalupe Mountains National Park, HTSHPS = Hueco Tanks State Park and Historic Site; WHSA = White Sands National Park. Sampling effort: 1 = 1 sample date only, 2 = 2–5 sampling dates, 3 = 6–10 sampling dates, 4 = 11–20 sampling dates, 5 = >20 sampling dates.

Site Name/Location	Habitat Type	Latitude	Longitude	Species Richness	Sampling Effort
Arizona					
Triangle Pond, BANWR	spring	31.55	−111.533889	6	2
Lake Arivaca, BANWR	lake	31.531896	−111.253136	6	1
New Mexico					
Lazy Lagoon, BLSP	playa	33.3541666	−104.3417666	3	2
Cottonwood Lake, BLSP	lake	33.3388666	−104.3340277	6	2
Mirror Lake, BLSP	lake	33.3363666	−104.3327333	2	2
Figure Eight Lake, BLSP	lake	33.3339333	−104.3324666	2	2
Pasture Lake, BLSP	lake	33.3310666	−104.3295666	16	2
Lea Lake, BLSP	lake	33.3170833	−104.3303666	8	2
Elephant Butte Reservoir	lake	33.1607361	−107.1885194	2	2
Rio Grande, Williamsburg	river	33.10335	−107.293983	12	2
Caballo Reservoir	lake	32.8977222	−107.2985583	13	1
Dune Pond 1, WHSA	playa	32.7243	−106.393367	1	1
Dune Pond 3, WHSA	playa	32.72365	−106.394917	3	1
Lost River, WHSA	stream	32.8802	−106.1708833	3	1
Lower Lost River Pool, WHSA	stream	32.8775333	−106.1789333	1	1
Lake Holloman	lake	32.80745	−106.1227833	6	1
Backcountry Trailhead, WHSA	playa	32.797	−106.26965	2	1
Garton Spring, WHSA	spring	32.775067	−106.145267	1	2
Lake Lucero, WHSA	playa	32.6976333	−106.4511666	7	2

Table A1. *Cont.*

Site Name/Location	Habitat Type	Latitude	Longitude	Species Richness	Sampling Effort
Cattle Tank, WHSA	tank	32.67485	−106.44345	4	2
Dripping Springs	spring	32.3231888	−106.5725138	6	2
La Mancha Wetlands	river	32.278092	−106.828626	13	2
Red Lake	lake	32.8615027	−104.1771791	2	
Sitting Bull Falls, LNF	spring	32.243666	−104.696599	7	1
Sitting Bull Falls, LNF	spring	32.2434916	−104.6962916	19	2
Sitting Bull Falls Pool 1, LNF	spring	32.2390333	−104.7025333	19	1
Sitting Bull Falls Pool 2, LNF	spring	32.2385	−104.702667	3	1
Rattlesnake Spring, CAVE	spring	32.1097	−104.471625	33	2
404A Playa	playa	32.0125844	−106.523427	16	
404B Playa	playa	32.022586	−106.508957	17	1
McKittrick Creek, GUMO	stream	31.985783	−104.769383	1	2
Smith Spring, GUMO	spring	31.9186111	−104.806667	3	1
Manzanita Spring, GUMO	spring	31.9103194	−104.79855	23	3
Chosa Spring south side, GUMO	spring	31.9065333	−104.7821166	5	2
Chosa Spring north side, GUMO	spring	31.906397	−104.782996	4	2
Upper Pine Spring Pool #1, GUMO	spring	31.9032666	−104.81785	4	2
Upper Pine Spring Pool #2, GUMO	spring	31.9029666	−104.81765	7	2
Guadalupe Canyon Seepage 1, GUMO	spring	31.869527	−104.8380166	3	1
Guadalupe Canyon Seepage 3, GUMO	spring	31.8696	−104.8377833	5	1
Columbus Playa, NM	playa	31.805433	−107.103833	12	1
NM Highway 180	river	32.508553	−106.957176	10	2
Rio Grande, Percha Dam	river	32.868149	−107.304454	5	2
Rio Grande, Anthony	river	32.005933	−106.639733	9	3
Texas					
BRH, HTSPHS	playa	31.927081	−106.041142	4	5
Heart, HTSPHS	rock pool	31.924848	−106.042467	2	5
Hex, HTSPHS	rock pool	31.924734	−106.04221	2	5
Stacia, HTSPHS	rock pool	31.924685	−106.042592	1	5
North Temp, HTSPHS	rock pool	31.924682	−106.042347	4	5
Vero, HTSPHS	rock pool	31.924675	−106.042662	2	5
Boo’s Pond, HTSPHS	playa	31.9246611	−106.045825	3	5
South Temp, HTSPHS	rock pool	31.924658	−106.042285	6	5
Cammie, HTSPHS	rock pool	31.924642	−106.042669	1	5

Table A1. *Cont.*

Site Name/Location	Habitat Type	Latitude	Longitude	Species Richness	Sampling Effort
Laguna Prieta, HTSPHS	playa	31.9246388	−106.046675	17	5
Al, HTSPHS	rock pool	31.924634	−106.042674	1	5
Walsh, HTSPHS	rock pool	31.924628	−106.042628	2	5
Julie, HTSPHS	rock pool	31.924622	−106.042497	1	5
Luisa, HTSPHS	rock pool	31.924768	−106.042617	1	5
Jamie, HTSPHS	rock pool	31.92456	−106.042433	1	5
Behind East, HTSPHS	playa	31.919195	−106.041106	13	5
Mescalero Canyon, HTSPHS	playa	31.9188166	−106.040366	44	5
Clammation, HTSPHS	rock pool	31.922556	−106.042508	1	4
Shelby, HTSPHS	rock pool	31.924622	−106.042668	1	5
Pia, HTSPHS	rock pool	31.924544	−106.042239	1	4
Monica, HTSPHS	rock pool	31.925051	−106.045727	1	4
Kettle 1, HTSPHS	rock pool	31.918455	−106.040106	2	4
Kettle 2, HTSPHS	rock pool	31.918455	−106.040107	2	4
Kettle 3, HTSPHS	rock pool	31.918455	−106.040101	2	4
Kettle 4, HTSPHS	rock pool	31.918446	−106.040105	4	5
Kettle 5, HTSPHS	rock pool	31.918484	−106.040087	2	4
Behind Picnic, HTSPHS	rock pool	31.924831	−106.045855	2	3
1 of 4, HTSPHS	rock pool	31.924826	−106.045663	2	4
2 of 4, HTSPHS	rock pool	31.92482	−106.04567	1	4
3 of 4, HTSPHS	rock pool	31.924813	−106.045669	1	4
4 of 4, HTSPHS	rock pool	31.924799	−106.045673	1	4
Abelex, HTSPHS	rock pool	31.924624	−106.042526	1	3
Iceskating Pond, HTSHPS	playa	31.924729	−106.045909	4	3
Rio Grande, Borderland	river	31.8859527	−106.5988777	12	1
Crossroads Pond	lake	31.836988	−106.580518	4	2
Keystone Heritage Park Wetland	spring	31.8224694	−106.5642444	5	2
Rio Grande, American Dam	river	31.786506	−106.526992	15	3
Ascarate Lake	lake	31.7501777	−106.4047527	33	4
Ascarate Duck Pond	lake	31.7473027	−106.4035527	7	1
Feather Lake	lake	31.6890972	−106.305	24	2
Rio Bosque Wetland Cell 1	tank	31.64202	−106.315503	2	1
Rio Bosque Wetland Cell 2	tank	31.636467	−106.310833	8	2
Rio Grande, San Elizario	river	31.669737	−106.337114	18	3
Rio Grande, Fort Quitman	river	31.087533	−105.60933	4	2
Rio Grande, Presidio	river	29.60365	−104.45197	2	2
Rio Grande, C 50	river	30.585217	−104.892833	5	2
Rio Grande, C 20	river	30.36695	−104.8118	3	2

Table A1. *Cont.*

Site Name/Location	Habitat Type	Latitude	Longitude	Species Richness	Sampling Effort
Rio Grande, Candelaria	river	30.133417	−104.69	1	2
Rio Grande, Guadalupe POE	river	31.431854	−106.148343	4	2
Rio Grande, Montoya Drain	river	31.799933	−106.556490	11	3
Montoya and Doniphan	river	31.873037	−106.592262	4	2
Rio Grande Fabens	river	31.430277	−106.14222	18	2
Album Park	playa	31.783419	−106.346349	5	3
McNary Reservoir	lake	31.2242138	−105.7890083	12	1
Diamond Y Roadside	spring	31.0088	−102.922533	13	2
Diamond Y Spring	spring	31.0010666	−102.9242833	18	2
East Sandia Flow	spring	30.9910833	−103.7286	10	2
East Sandia Spring	spring	30.9909666	−103.7288666	22	2
Balmorhea Lake	lake	30.9663333	−103.7134	5	2
Balmorhea Main Pool	spring	30.9445833	−103.7876666	5	2
Balmorhea Wetland 1	spring	30.9449166	−103.7835	27	3
Balmorhea Wetland 2	spring	30.945413	−103.785982	5	2
Balmorhea Canal	spring	30.9444472	−103.7851583	32	3
Roadside Wetland	river	30.8551333	−105.3608833	17	1
Soda Spring	spring	30.8276388	−105.3173055	10	1
Beauty Spring B	spring	30.8243333	−105.3148611	2	2
Stump Spring A	spring	30.8225883	−105.3151466	7	1
Masims Spring	spring	30.8219666	−105.314733	2	1
Dynamite Spring	spring	30.8218833	−105.31545	6	1
Squaw Spring	spring	30.7972166	−105.0111833	2	2
Corral Tank, IMRS	tank	30.785263	−104.984084	9	2
Peccary Tank, IMRS	tank	30.755556	−105.004167	3	1
Rattlesnake Tank, IMRS	tank	30.743611	−105.008333	1	1
Red Tank, IMRS	tank	30.7303083	−104.9891083	2	2
Miller Ranch 96 Well	spring	30.6238533	−104.6739988	9	2
Miller Ranch 2 (Spring)	spring	30.55025	−104.66645	13	1
Miller Ranch Glidewell	spring	30.571483	−104.657317	8	1
Pinto Canyon Stream	stream	30.0308666	−104.468433	10	1
Kimball Hole Miller Ranch	spring	30.585278	−104.626667	5	1
Sanderson Canyon	rock pool	29.8472	−102.1837055	6	1
La Mesa Canyon Tule 2	rock pool	29.829091	−102.360993	26	1
Rio Grande, Above Dryden	river	29.8090277	−102.1481138	1	1
Lower Madison Falls Seep 1	spring	29.7967666	−102.3779333	7	2
Silber Hotspring 2	spring	29.76835	−102.5635833	2	1
Below Hotsprings Texas	spring	29.7484	−102.5406833	3	1
Fuentes Ranch Shafter	stream	29.7936833	−104.27665	11	1

Table A1. *Cont.*

Site Name/Location	Habitat Type	Latitude	Longitude	Species Richness	Sampling Effort
Buttrill Springs, BIBE	spring	29.54585	−103.2738	6	2
McKinney Spring 1, BIBE	spring	29.4090166	−103.08715	3	1
Grapevine Spring, BIBE	spring	29.4075666	−103.19085	1	1
McKinney Wall Spring, BIBE	spring	29.407466	−103.0885166	1	1
McKinney Tinaja, BIBE	rock pool	29.4073666	−103.0886833	1	1
Dripping Spring Cliff, BIBE	spring	29.4066833	−103.3103166	1	1
Dripping Spring, BIBE	spring	29.4049666	−103.3078583	1	2
Dripping Spring Upper, BIBE	spring	29.4049491	−103.3078470	1	1
Onion Tinaja, BIBE	rock pool	29.4014	−103.32585	1	1
Paint Gap Tank, BIBE	tank	29.3878555	−103.302675	10	3
San Felipe Creek Del Rio	stream	29.36985	−100.8838166	1	1
Croton Spring, BIBE	spring	29.3446166	−103.3471166	10	3
Croton Stream, BIBE	spring	29.3437833	−103.3465	4	2
Government Spring 2, BIBE	spring	29.3406167	−103.2559833	2	2
Government Spring 1, BIBE	spring	29.3405666	−103.2560833	2	4
Oak Creek, BIBE	spring	29.2828666	−103.3421833	6	3
Window Trail Pool A, BIBE	rock pool	29.28003	−103.3299472	2	2
Window Trail Pool B, BIBE	rock pool	29.28003	−103.33	4	2
Window Trail Pool C, BIBE	rock pool	29.28009	−103.33018	1	2
Window Trail Pool D, BIBE	rock pool	29.2802	−103.33038	2	2
Window Trail Pool E, BIBE	rock pool	29.28025	−103.33043	6	3
Window Trail Pool F, BIBE	rock pool	29.28031	−103.3305	6	3
Window Trail Pool G, BIBE	rock pool	29.28035	−103.3305388	4	3
Window Trail Pool H, BIBE	rock pool	29.2804138	−103.3305388	4	2
Window Trail Pool I, BIBE	rock pool	29.2804611	−103.3305388	6	2
Window Trail Pool Donut, BIBE	rock pool	29.2802722	−103.330475	5	2
Carlota Tinaja, BIBE	rock pool	29.2790833	−103.0354166	1	1
Cattail Spring A, BIBE	spring	29.2731805	−103.3355138	35	4
Cattail Spring B, BIBE	spring	29.2731833	−103.33555	25	4
Cattail Spring C, BIBE	spring	29.2731833	−103.3355861	17	4
Cattail Spring C′, BIBE	spring	29.2731833	−103.3356305	9	3
Cattail Spring C″, BIBE	spring	29.2731833	−103.335675	8	3
Cattail Spring C-D, BIBE	spring	29.2731555	−103.3357336	13	3
Cattail Spring D, BIBE	spring	29.2731527	−103.3358277	17	4
Cattail Spring E, BIBE	spring	29.2731444	−103.3359666	18	4
Cattail Spring F, BIBE	spring	29.2731333	−103.3360833	21	4
Cattail Spring G, BIBE	spring	29.2731666	−103.3361638	29	4
Cattail Spring H, BIBE	spring	29.2731694	−103.3362388	23	4
Ernst Tinaja 1, BIBE	rock pool	29.2568666	−103.0100833	6	3

Table A1. *Cont.*

Site Name/Location	Habitat Type	Latitude	Longitude	Species Richness	Sampling Effort
Ernst Tinaja 2, BIBE	rock pool	29.2567416	−103.0103583	5	3
Ernst Tinaja 3, BIBE	rock pool	29.2567415	−103.0104	6	2
Ernst Tinaja 4, BIBE	rock pool	29.2562666	−103.0112916	2	2
Ernst Tinaja 4A, BIBE	rock pool	29.2563611	−103.0111083	6	2
Ernst Tinaja 5, BIBE	rock pool	29.2560416	−103.0117361	8	3
Ernst Tinaja 6, BIBE	rock pool	29.2559972	−103.0119166	6	3
Ernst Tinaja 7, BIBE	rock pool	29.2559944	−103.01195	5	3
Ernst Tinaja 8, BIBE	rock pool	29.2559888	−103.0119694	1	2
Ernst Tinaja 9, BIBE	rock pool	29.2559805	−103.0119972	5	3
Ernst Tinaja 10, BIBE	rock pool	29.255975	−103.0120138	3	2
Ernst Tinaja Hueco, BIBE	rock pool	29.2551	−103.0148833	6	1
Ward Spring 2, BIBE	spring	29.24445	−103.3505833	1	1
Tule Cattle Tank, BIBE	tank	29.2424333	−103.4438305	21	3
Tule Spring A, BIBE	spring	29.2422833	−103.4426666	6	3
Tule Spring B, BIBE	spring	29.24155	−103.4428333	3	3
Burro Spring, BIBE	spring	29.2373	−103.4259	14	3
Rio Grande Village Cattail Pond, BIBE	tank	29.189	−102.9716166	28	3
Rio Grande Village Canal, BIBE	river	29.18615	−102.97225	6	2
Rio Grande Rio Grande Village, BIBE	river	29.18555	−102.979666	16	3
Langford Hot Springs, BIBE	spring	29.1794944	−102.995466	3	2
Rio Grande Village Pump House, BIBE	river	29.17945	−102.95325	16	2
Rio Grande Village Upper Pond, BIBE	river	29.1785472	−102.9531833	30	4
Rio Grande Village Lower Pond, BIBE	river	29.1785166	−102.95375	34	4
Glenn Springs, BIBE	spring	29.1744166	−103.1575	21	3
Trap Spring, BIBE	spring	29.1636333	−103.4194166	3	2
Mule Ears Spring (Middle), BIBE	spring	29.1624	−103.4082666	2	1
Mule Ears Spring (Lower), BIBE	spring	29.16235	−103.4082833	5	2
Rio Grande, Santa Elena	river	29.15415	−103.598683	4	1
Tuff Canyon Falls (wall), BIBE	rock pool	29.15115	−103.4855	2	1
Tuff Canyon 1, BIBE	rock pool	29.1507666	−103.48605	1	2
Tuff Canyon 3, BIBE	rock pool	29.1507666	−103.4859	2	2
Tuff Canyon 4, BIBE	rock pool	29.15077	−103.4857666	3	2
Tuff Canyon 5, BIBE	rock pool	29.1509	−103.48575	2	2

Table A1. *Cont.*

Site Name/Location	Habitat Type	Latitude	Longitude	Species Richness	Sampling Effort
Tuff Canyon 6, BIBE	rock pool	29.15095	−103.485389	1	1
Mexico					
Presa Chihuahua	lake	28.5762166	−106.1711833	32	2
Delicias Beisbol Field Pool	tank	28.1648166	−105.498500	6	1
Presa Francisco Ignacio Madero	lake	28.1626166	−105.6321833	19	2
Lago Colina	lake	27.5724	−105.4004666	43	2
Presa de la Boquilla	lake	27.5361333	−105.4011333	23	2
Laguna La Leche	playa	27.2860833	−102.9161666	7	1
San Jose del Anteojo, APFFC	spring	26.9693166	−102.1208166	21	2
Tio Julio, APFFC	spring	26.9462833	−102.0592	10	1
Poza Tortugas, APFFC	spring	26.93145	−102.1247	27	3
Poza Azul, APFFC	spring	26.9226666	−102.1226333	3	2
Rio Mesquites, APFFC	river	26.9222222	−102.1083333	8	2
Poza Marcelo, APFFC	spring	26.9104	−102.0363166	6	2
Las Playitas, APFFC	spring	26.9085166	−102.01745	7	2
Los Gatos, APFFC	spring	26.88875	−101.9980333	14	2
Poza la Becerra, APFFC	spring	26.8784166	−102.1377666	13	2
Los Hundidos Main pool, APFFC	spring	26.8711666	−102.0204166	13	2
La Campana, APFFC	spring	26.8683666	−102.0278333	3	1
Poza El Arco B, APFFC	spring	26.8683333	−102.0228	6	1
Poza Churince, APFFC	spring	26.8404166	−102.1342333	15	3
Ejido El Venado Entrance, APFFC	spring	26.9146333	−102.047	14	1
Ejido El Venado Grande, APFFC	spring	26.8199	−101.904833	1	1
Ejido El Venado A, APFFC	spring	26.8194666	−101.9053166	7	1
Presa Francisco Zarco Durango	lake	25.2693055	−103.7727222	2	1
Ojos Altos A	spring	31.40685	−107.6181833	1	3
Ojos Altos B	spring	31.4068	−107.6179666	1	2
Ojos Altos C	spring	31.4035166	−107.616	12	3
Ojos Altos D	spring	31.4032666	−107.6163	9	3
Ojo de la Punta, ANPMS	spring	31.3859166	−106.6022666	32	4
Ojo de en Medio ANPMS	spring	31.37885	−106.5877833	26	3
Ojo de la Casa ANPMS	spring	31.3656166	−106.5322333	21	3
DunasCampestre ANPMS	spring	31.335967	−106.491333	8	3
El Huerfano ANPMS	spring	31.294817	−106.511017	10	3
Ojo de Santa Maria	spring	31.1552777	−107.3172222	22	2
Upper Mexican Hotsprings	spring	29.7460833	−102.5455666	11	2

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