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ECOLOGY OF SHALLOW LAKES

Processes contributing to rotifer community assembly in shallow temporary aridland waters

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Abstract Understanding how local conditions and dispersal dynamics structure communities of passively dispersing aquatic invertebrates remains uncertain, especially in aridland systems. In these systems, dispersal is irregular and successful colonization is subject to priority effects. To investigate these factors, we compared rotifer species composition from Chihuahuan Desert rock pools, playas, and tanks. (1) We found 132 species with high beta-dissimilarity among sites (> 0.8). (2) Correlation between species richness and habitat area was significant, but weak, for all sites. (3) Dissimilarity analyses, supported by negative Dispersal-Niche Continuum Index (DNCI) values, showed that stochastic processes dominate community assembly. (4) We examined influence of three important environmental variables on richness and community structure: hydroperiod, algal mat and macrophyte development, and conductivity; we also examined how rotifer trophi type (a functional trait) affected DNCI and identified indicator species. Hydroperiod was important for playas and tanks, but not rock pools. Conductivity had a strong influence. Richness was greatest in habitats with highest amounts of vegetation. Environmental factors explained ~12% of variation in community

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composition, indicating that while deterministic processes are significant, stochastic processes dominate in these systems. We provide a conceptual model that highlights the distinctive of nature aquatic communities in aridlands compared to temperate regions.

Keywords Deterministic processes · Playas · Rock pools · Species richness · Stochastic processes

Introduction

In one of her many insightful moments, Rachel Carson asked the questions "*Why does an animal live where it does? What is the nature of the ties that bind it to its world?*" This is a central goal of ecology: understanding biodiversity and how it is maintained, especially among a local suite of interacting communities comprising a metacommunity (Grainger & Gilbert, 2016; García-Girón et al., 2020). Recent advances in metacommunity theory have provided a scaffold against which we can frame questions regarding community assembly, priority effects, species functional trait distribution, area effects, dispersal, and speciation (Rizo et al., 2017; Valente-Neto et al., 2018; Gansfort et al., 2020). However, for aquatic systems most of our knowledge of community assembly comes from relatively stable (i.e., permanent) habitats. These possess long basin life, lasting centuries, or at least decades (Sferra et al., 2017), relatively high surface connectivity (Chaparro et al., 2018), and frequent attendance by a diverse bird fauna, many of which are capable of carrying dispersal stages of a rich biota (Meyer-Milne et al., 2021). But metacommunity theory should include the perspective of all habitat types, not just those with long basin life. The edaphic conditions of temporary habitats are strikingly different and this may lead to pronounced differences in community structure.

The differences between small, shallow basins of permanent habitats to those in aridlands are striking. First, the wet phase in aridland basins often persist perhaps for a month, but sometimes only weeks or even days (Walsh et al., 2014a; Kulkarni et al., 2019). Second, except for a few rivers and their flood plain basins, surface connectivity is limited for most aquatic habitats to small patches isolated by vast stretches of arid landscape (Kobayashi et al., 2015). Finally, while localized zoochory by residents is likely, long-distance dispersal to these isolated habitats along flyways is probably low, but possible (de Morais Jr. et al., 2019). In addition, aridland basins are highly dependent on seasonal rainfall. Thus, these basins are subject to cyclic disassembly (drying out) and reassembly (rehydration) (O'Neill, 2016). As a result, the current population in any system predominantly arises from hatchlings of diapausing stages deposited by previous populations and/or those that arrived via anemochory. Outflow and deflation have different outcomes in these basins. Outflow is a local phenomenon. Intense rains may overfill some smaller basins, especially rock pools. If transported to a nearby basin, viable adults may reproduce while diapausing stages may hatch or sink becoming part of the propagule bank. Deflation may have local or distant consequences; winds can entrain diapausing stages along with dust and carry them 10's to 1000's of meters where they may land in a suitable basin (Rivas Jr. et al., 2018; Rivas Jr. et al., 2019). Within a filling cycle, biotic interactions and selection pressures on life history features (e.g., high propensity for sex with concomitant ability to produce a dormant propagule) become intensified by the short hydroperiod (Schröder et al., 2007; Smith & Snell, 2012). Thus, being truly ephemeral systems, aridland basins provide exceptional opportunities to examine how communities of small-bodied, aquatic invertebrates (i.e., fairy-, clam-, tadpole shrimp, cladocerans, copepods, ostracods, rotifers) form and to test ecological theories without the confounding factors of permanence and connectivity (De Meester et al., 2005; Walsh et al., 2014a).

The Chihuahuan Desert is a large, well-defined ecoregion located in the southwest USA and northern Mexico, composed of a complex of intergrading communities arrayed across a broad series of elevation and latitudinal sequences. It is one of the few deserts recognized for its high biodiversity and high level of endemism (Dinerstein et al., 2001). This ecoregion also possesses a diverse array of aquatic habitats, including perennial and temporary waterbodies, as well as abandoned artificial basins (e.g., cattle tanks). Within this array of habitats our research has focused on rotifers for several reasons. (1) They contribute to both the food web and microbial loop (Wallace et al., 2015). (2) Habitats are usually rich in taxonomic diversity (Brown et al., 2020). (3) Rotifers produce small, desiccation resistant, propagules that resupply the sediment egg bank. These endure dry periods and yet can disperse via anemochory (Rivas Jr. et al., 2018, 2019). Thus, beginning with Rousselet (1909), researchers have argued that rotifers have a cosmopolitan distribution, following the 'everything is everywhere' model. Yet recent research indicates endemism for some species (Fontaneto et al., 2008a; Luo and Segers, 2020). We posit that examination of rotifer community assembly in shallow, temporary basins throughout the Chihuahuan Desert will improve our understanding of the processes that structure small passively dispersed aquatic invertebrate communities.

Our studies of aquatic habitats in the Chihuahuan Desert have shown that rotifer species diversity is high, with ~13% of all rotifer taxa occurring in this ecoregion, and that regional communities often comprise highly nested subsets of species, especially at small geographic scales (Walsh et al., 2014b; Ríos-Arana et al., 2019; Brown et al., 2020). We also have explored relationships between rotifer presence and environmental parameters for specific systems (i.e., saline systems) (Walsh et al., 2008), Mexican springs (Ríos-Arana et al., 2019), and selected aquatic sites at Big Bend (Walsh et al., 2014b). However, we still have a limited understanding of how rotifer species assembly takes place in temporary, aridland habitats across regional scales, nor do we have a firm appreciation of the relative contribution of stochastic versus deterministic processes in establishing rotifer communities in those habitats.

Researchers have recognized that both stochastic and deterministic processes are important drivers in establishing community composition (Valente-Neto et al., 2018). However, understanding their relative importance remains elusive even as researchers continue to refine these concepts (Fukami, 2015; Brown et al., 2017; Suzuki & Economo, 2021). Stochastic processes include ability to disperse, successful colonization (including overcoming priority effects), and random extirpation. Deterministic processes include species sorting and niche availability (Wedderburn et al., 2013; Lopes et al., 2014).

Stochastic processes appear to become more pronounced as dispersal becomes more difficult either due to low dispersal ability and/or increased distance between sites (De Meester et al., 2016). This may be related to increased invasibility of sites after a disturbance (Symons & Arnott, 2013; Symons and Arnott, 2014). For example, initial dispersers may become established in a community, but long-term success becomes less likely over time (De Meester et al., 2016; Medeiros et al., 2021). If many species arrive approximately at the same time, such as during an intense wind event, the final assembly may include these species. However, longer time intervals between arriving colonists reduces the likelihood that a species will become established, unless it quickly adapts (Stroud et al., 2019; Medeiros et al., 2021). If species have enough time to adapt to local edaphic conditions before the arrival of subsequent immigrants, they may be able to competitively exclude newcomers, thereby creating a monopolization effect (De Meester et al., 2002). Thus, priority effects can create patchiness in species presence among sites over time. This can lead to higher beta-diversity among systems where priority effects are important (De Meester et al., 2002; Fukami, 2015).

Many deterministic processes influence rotifers and other aquatic invertebrate community structure in shallow aridland waters. Among the most important of these are hydroperiod, conductivity, and productivity. Hydroperiod causes strong species sorting in habitats, becoming progressively stronger with shorter hydroperiods (Wellborn et al., 1996; Vanschoenwinkel et al., 2010; Sim et al., 2013; Kulkarni et al., 2019). This occurs due to the difficulty of completing a life cycle in habitats with short hydroperiods; that is, selection will exclude species with life cycles longer than the basin's hydroperiod. Thus, species sorting can create strong nestedness among assemblages, especially among those with short hydroperiods (Kulkarni et al., 2019; Brown et al., 2020). Conductivity also can create a species sorting effect by excluding species incapable of survival in certain salinity ranges (Jocque et al., 2010; Echaniz et al., 2013); this is particularly important in structuring rotifer community composition (Walsh et al., 2008; Kaya et al., 2010). Not surprisingly halophilic rotifers dominate many saline aridland systems (Walsh et al., 2008; Nandini et al., 2019). In many aquatic systems, rotifer population levels and biomass are positively correlated with productivity (Yoshida et al., 2003); however, Dodson et al. (2000) found no significant relationship of primary productivity with rotifer species richness in a survey of 33 well-studied lakes. In addition, Chase (2010) and Lopes et al. (2014) reason that regions with higher productivity are more vulnerable to priority effects, which results in greater species turnover, i.e., higher beta-diversity. However, in their study of > 100 permanent and temporary lakes and ponds, Lopes et al. (2014) reported that beta-diversity was lower in the temporary habitats.

Habitat features often constrain community development such that the species assemblages are unique or contain one or more species that are indicative of the habitat. Aquatic habitats are replete with examples of indicator species (e.g., Karpowicz & Ejsmont-Karabin, 2021). The presence of indicator species likely implies that deterministic processes are important drivers of community composition.

Here, we compared rotifer species assemblages in three distinct types of shallow, temporary waters in the Chihuahuan Desert: rock pools ($n = 60$), playas ($n = 17$), and abandoned cattle tanks ($n = 13$). Specifically, we (1) assessed species richness among the three habitat types, (2) tested the hypothesis that species richness is determined by habitat area, (3) used an index to determine the relative strength of stochastic versus deterministic factors in the three habitat types, (4) examined relationships between three known important environmental drivers of species assemblages (hydroperiod, conductivity, and macrophyte/algae presence) and the functional trait of rotifer jaw (trophi) structure, and (5) identified indicator species for these temporary habitats.

Materials and methods

Sample collection

In a large-scale survey of Chihuahuan Desert aquatic systems (2005–2020), we sampled rotifer communities in over 230 sites (Brown et al., 2020); here we analyze data from rock pools ($n = 60$), cattle tanks ($n = 13$), and temporary playas ($n = 17$) from the survey and with a few additional sites (Fig. 1). Although we usually took multiple samples at each site, we attempted to minimize environmental impact to smaller systems by keeping the total amount of each sample to about 250 ml of source water. We sieved all source water through netting of 64 µm. Sampling effort varied among the sites (from 1 to > 20 collections) and at some sites only one type of sample was taken (e.g., plankton), while at others a variety of microhabitats were sampled. The unbalanced effort was a result of logistical constraints of sampling a large number of sometimes widely separated

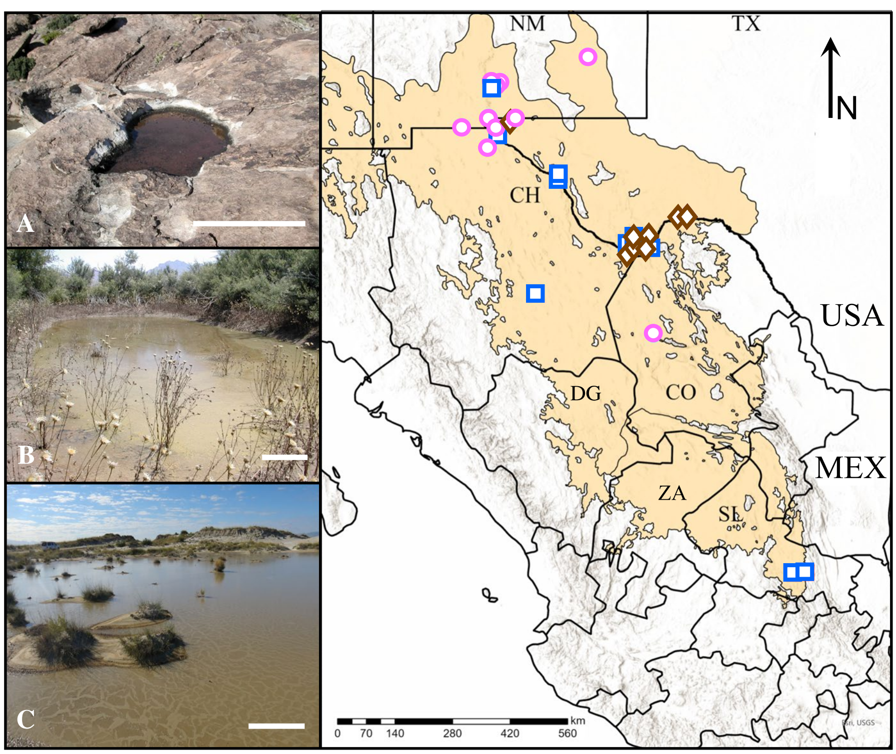

Fig. 1 Sampling sites in the USA and Mexican Chihuahuan Desert ($n = 90$). Rock pools ($n = 60$), diamonds; cattle tanks ($n = 13$), squares; temporary playas ($n = 17$), circles. Many symbols overlap with one another. State name abbreviations in México (MEX): *CH* Chihuahua, *CO* Coahuila, *DG* Durango, *SL* San Luis Potosí, *ZA* Zacatecas; in USA: *NM* New Mexico, *TX* Texas. **a** A representative rock pool, Hueco Tanks State Park & Historic Site; **b** abandoned cattle tank, Big Bend National Park, **c** temporary playa, southern New Mexico. (Bars = – 1 m)

temporary habitats. However, as noted in Brown et al (2020), sampling effort was not an important determinant of species richness. A rarefaction analysis was conducted on the current dataset and is included in Supplemental Information, Table S1. For each site we compiled a species list of presence/absence data over all sampling dates (Brown et al., 2020). Species were identified using the keys listed in Brown et al. (2020), Except for two sampling sites (San Francisco tank [$S = 7$; 22.0529200 N, − 99.8474700 W] and Presa De La Vaca tank [$S = 10$; 22.0678055 N, − 99.5843333 W]) all the sites we examined here are noted in Brown et al. (2020). Species lists for these sites and others are available by request.

Habitat characterization

We analyzed selected physical and environmental parameters including habitat type and size (area), hydroperiod, conductivity, and productivity to determine relative contribution of stochastic and deterministic processes that shaped the rotifer communities. We also recorded latitude and longitude for all sites; these are given in Brown et al. (2020), except for those noted above. We measured conductivity with a pre-calibrated YSI model 556 multiprobe meter. Categorical variables included habitat type (rock pool, playa, tank), hydroperiod (ranked 1–3 [short = 1, intermediate = 2, and long = 3] based on volume and shading), and presence and relative abundance of algae, as visible mats (0 = none, 1 = some, 2 = abundant) and macrophytes (0 = none, 1 = rare, 2 = abundant, 3 = dominant). Macrophytes comprised mostly submerged cattails, grasses, and mosses. We used the level of algae and macrophytes as an indirect proxy for habitat productivity (Juračka et al., 2019). If a site had more than one sampling event, we averaged the values of the environmental parameters. We estimated area as the product of the maximum length and maximum width.

Data analysis

We used R version 4.0.2 for statistical analyses (R Core Team, 2020). The correlation between the log area (m^2) of the habitat and log species richness (S) was determined using linear regression. We tested different models of species-area relationships using the R-package *sars,* comparing models based on Akaike's information criterion (Matthews et al., 2019). To model the influence of spatial distribution, we created distance-based Moran's eigenvector maps (dbMEMs) from the latitude and longitude of our sites with the package *adespatial* (Dray et al., 2021). Nearest neighbor trees and weights used in constructing these dbMEMs were done with the R- package *spdep* (Bivand and Wong, 2018). We calculated variance partitioning between our environmental predictors and significant dbMEMs with significant spatial autocorrelation using the *vegan* 2.5–6 package (Oksanen et al., 2019). To determine relationships between species distributions and environmental factors and habitat area we used partial Canonical Correspondence Analysis (pCCA) implemented in the *vegan* 2.5–6 package after removing the influence of dbMEMs with siginificant spatial autocorrelation. We decided on this unimodel approach by inspecting the first axis of a Detrended Correspondence Analysis (DCA) of our species assembly data conducted with the *vegan* package. We tested specific environmental factors for autocorrelation with dbMEMs using a Moran's I test in R. For this analysis, we excluded sites with incomplete data; after this reduction, we retained 58 rock pools, 14 playas, and 12 tanks in the dataset. Prior to running the pCCA, we tested for multicollinearity and conducted an F test (ANOVA) to determine significance of predictor variables. We used Sørensen's Dissimilarity Index as a measure of beta-diversity (Baselga, 2012). Further, we used general linear modeling with a Poisson distribution to test for a relationship between algae/macrophytes and species richness in R version 2.5–6.

To further investigate the relative contribution of stochastic and deterministic factors on community assembly, we calculated the PER-SIMPER and Dispersal Niche Continuum Index (DNCI) (Vilmi et al., 2021) using the *DNCImper* 1.0 package with 1 000 permutations in R (Gibert et al., 2020). To account for the asymmetry in site number between habitat types (we have > 50% the number of rockpool sites than other habitat types) and hydroperiods, sites of each habitat type and hydroperiod were randomly resampled to equalize the number of sites per habitat. The more negative the value of the DCNI, the more likely that stochastic processes dominate community structure. We calculated DNCI values for differences between habitat type, habitat hydroperiod, and the functional trait of rotifer jaw structure (trophi) type.

Rotifers differ in how they consume food. Raptorial species with trophi of virgate, cardate, incudate, forcipate, and uncinate types tend to process one large item at a time; microphagous species with malleate, malleoramate, and ramate trophi tend to process many small particles in a short period of time (Obertegger et al., 2011). We implemented an indicator species analysis using the *indicspecies* 1.7.9 package and SIMPER analysis in Community Analysis Package (CAP) version 6.2.4.

Results

Species diversity

Species richness (S) among all the sites we sampled ranged from 1 to 44 with a total of 132 species in all sites. However, within each category ranges and means ($\bar{x}$ ± 1SD) varied widely: playas (1–44; $\bar{x}$ = 9.5 ± 9.8); tanks (1–28; $\bar{x}$ = 8.5 ± 7.8); rock pools (1–26; $\bar{x}$ = 3.2 ± 3.6) (Fig. 2). With the exception of one site, rock pools were relatively depauperate with S ranging from 1 to 8. The two playas with the highest richness, Laguna Prieta (S = 30) and Mescalero Canyon (S = 44), are located at Hueco Tanks State Park & Historic Site. The other playas examined in this study had wide ranging richness (S = 1–23). The two tanks with the highest richness were located in Big Bend National Park. A recently constructed tank at Rio Grande Village had S = 28. The other site (Tule Tank; S = 21) is an artificially enhanced, natural low-lying basin near a spring and a historic settlement.

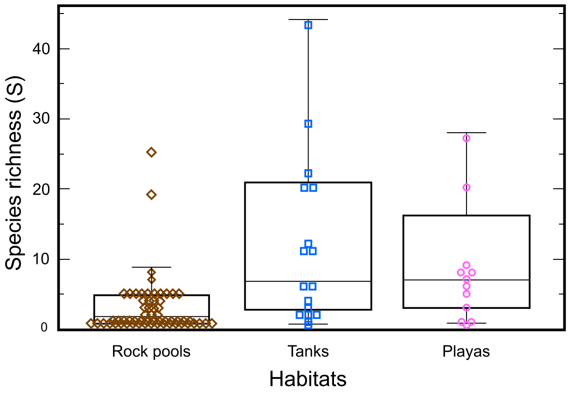

Fig. 2 Rotifer species richness (S) in selected habitat types in the Chihuahuan Desert. The horizontal lines within the boxes indicate their respective medians; the boxes indicated the range of lower (Q_1) and upper quartiles (Q_3); dots outside the boxes indicate outlying datapoints; error bars represent 2 standard deviations above the mean

Playas had the greatest gamma-diversity (S = 81), with tanks and rock pools having similar levels of gamma-diversity (n = 65 and 61, respectively). Sørensen's dissimilarity values for our study sites are similar to those from other habitats (Table 1).

Habitat area

We found that a persistence model best described our data. For each habitat type individually, we found that a negative exponential model best described rockpools, a logarithmic function best described playas and a linear function best described tanks when compared by Akaike's information criterion. We found a significant but weak relationship (R^2 = 0.15; P < 0.001) between site area and species richness when we analyzed all habitat types together. However, when we examined the habitats separately, the sites no longer showed a significant relationship between area and species richness (P > 0.05) regardless of the model (Fig. 3).

PER-SIMPER and DCNI

Stochastic models most closely align with our empirical results. Models with both sites and species constrained showed the smallest deviation from our data, while constraining only sites showed the highest deviation (Fig. 4, Table 2). The mean DNCI value (± 1SD) was − 6.49 ± 0.57. When we analyzed by trophi type among habitat types, raptorial feeders possessed a less negative DNCI value (− 3.80 ± 0.46) than microphagous feeders (− 5.42 ± 1.34). The pairwise habitat comparisons were similar to the overall results.

Beta-diversity

Dissimilarity among the three habitat types was quite high (> 0.8). These values were similar to those for most of the habitats used as representatives (Table 3).

Table 1 Rotifer species diversity among selected sites

Region	Habitat	# Sites examined	Diversity			References
			Alpha	Beta	Gamma	
Aridlands						
Chihuahuan Desert	Playas	17	1–44	0.83 (0.18)	81	1
Chihuahuan Desert	Rock pools	60	1–26	0.81 (0.30)	61	1
Chihuahuan Desert	Tanks	13	1–28	0.84 (0.13)	65	1
Chihuahuan Desert	Springs	95	1–35	0.85 (0.14)	175	2
Australia	Billabongs (River Murray)	13	8–13	0.77 (0.13)	52	3
Oman	Lakes, rivers, pools	9	10–25	0.61 (0.14)	66	4
Saudi Arabia	Lakes, rivers, pools	19	1–15	0.73 (0.26)	40	5
Spain	Dune pools	32	1–14	0.68 (0.21)	34	6
Yemen	Lakes, rivers, pools	35	1–29	0.84 (0.18)	74	7
Temperate/tropical						
India	Eutrophic fish ponds	5	14–25	0.71 (0.21)	57	8
Subtropical China	Shallow lakes	5	26–30	0.20 (0.06)	39	9
Temperate Portugal	Eutrophic lakes	3	16–31	0.42 (0.19)	40	10
Cryogenic Arctic	Permafrost thaw waters	5	14–19	0.23 (0.19)	24	11
High Arctic, Canada	Pools, ponds, small lake	8	8–27	0.64 (0.12)	70	12

Diversity calculated for all sites examined in the study: alpha = species richness (ranges); beta = mean species turnover based on Sørensen's Index (± 1SD); gamma = total regional species richness

Datasets used: 1—This study; 2—Brown et al. (2020); 3—R.J. Shiel, pers. commun.: discussed in Shiel and Koste(1983); 4—Segers and Dumont (1993); 5—Segers and Dumont (1993); 6—Mazvelos et al. (1993); 7—Segers and Dumont (1993); 8—Sharma and Dudani (1992); 9—Wen et al. (2011); 10—Castro et al. (2005); 11—Bégin and Vincent (2017); 12—(De Smet and Beyens 1995)

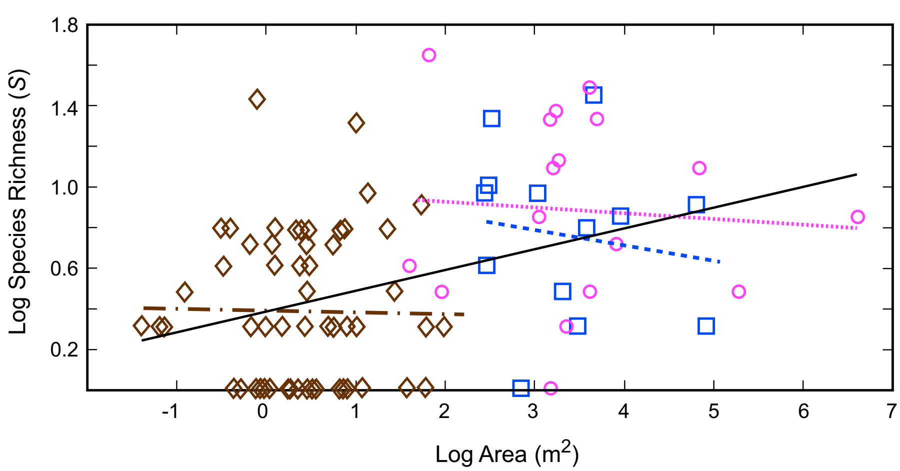

Fig. 3 Area-species richness (S) relationships of rotifers in selected habitat types in the Chihuahuan Desert. Some symbols overlap in their location. Symbols are as follows. Playas ($n = 17$) circles, dotted line: $S = -0.027$ Area + 0.9862; $R^2 = 0.0054$; $P > 0.05$; Cattle tanks ($n = 13$) squares, dashed line: $S = -0.0776$ Area + 1.0288; $R^2 = 0.025$; $P > 0.05$; Rock Pools ($n = 60$) diamonds, alternating dash-dotted line: $S = -0.0085$ Area + 0.3904; $R^2 = 0.0003$; $P > 0.05$; All sites combined (n = 90) solid line: $S = 0.103$ Area + 0.3871; $R^2 = 0.1514$; $P = 1.46 \times 10^{-4}$

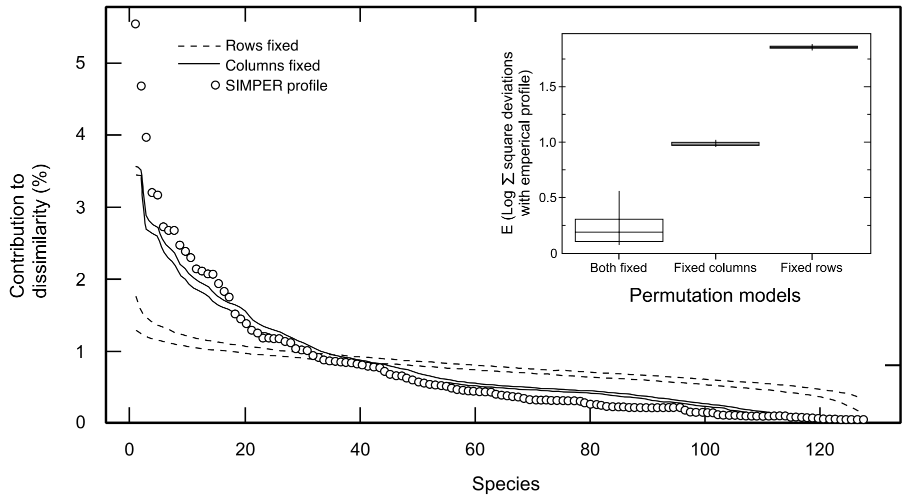

Fig. 4 Comparison of SIMPER profiles created from our empirical data (rotifer species assemblages) with permutation models representing niche-controlled distribution (rows/sites fixed, dotted lines, deterministic) and dispersal-controlled distribution (columns/species fixed, solid lines, stochastic). Inset: Box plots for the E metric of these comparisons is in the upper right corner of the graph

Table 2 Dispersal-Niche Continuum Index (DNCI) for selected rotifer communities in the Chihuahuan Desert categorized by habitat type, hydroperiod, and rotifer trophi type

Comparison	DNCI	SD
Habitat overall	−6.17	0.57
Rock pools vs. playas	−5.18	0.95
Rock pools vs. tanks	−6.91	0.92
Playas vs. tanks	−7.47	1.16
Hydroperiod overall	−7.20	0.93
Short vs intermediate	−5.77	0.31
Short vs long	−6.65	1.01
Intermediate vs long	−7.33	2.03
Rotifer trophi type		
Raptorial feeders	−3.80	0.46
Microphagous feeders	−5.42	1.32

Also included is an analysis based on food preference of species within a habitat. A negative value indicates the dominance of dispersal or other stochastic processes in community assembly (Vilmi et al., 2021)

Table 3 Effects of algae and macrophyte presence and abundance on rotifer species richness in desert ephemeral waters using Generalized Linear Modeling based on a Poisson distribution in R

Coefficients	Estimated standard error	z value	Pr(>|z|)	Significance
Intercept	0.923	0.099	9.28	< 0.001
Algae	0.731	0.102	7.15	< 0.001
Macrophytes	0.690	0.071	9.67	< 0.001

Partial Canonical Correspondence Analysis

The length of the first axis of our DCA analysis was 6.8, suggesting that a unimodal approach was appropriate for our data (ter Braak & Prentice, 1988). The ANOVA indicated that all predictor variables were significant at the 0.05 level. The pCCA explained ~12% (R^2 adjusted) of the variance observed in our species presence/absence data. The first constrained component was negatively associated with conductivity and site area, and to a lesser extent, positively associated with algal mat development (Fig. 5). The second constrained component was negatively associated with habitat type, hydroperiod, and presence of macrophytes. Several rotifer species were negatively correlated with the first constrained component (*Proales similis* Beauchamp, 1907, *Proales halophila* Remane, 1929, *Hexarthra polyodonta* (Hauer, 1957), *Encentrum putorius* Wulfert, 1936, *Brachionus plicatilis* Müller, 1786) or the second constrained component (*Euchlanis calpidia* (Myers, 1930), *Lindia torulosa* Dujardin, 1841, *Cephalodella panarista* Myers, 1924, *Sinantherina socialis* (Linnæus, 1758), *Filinia novaezealandiae* Shiel & Sanoamuang, 1993, *Cephalodella poitera* Myers, 1934, and *Brachionus havanaensis* Rousselet, 1911). On the other hand, two species (*Epiphanes macroura* (Barrois & Daday, 1894) and *Hexarthra* sp.) were positively correlated with the second constrained component. Of our predictor variables, only the presence of

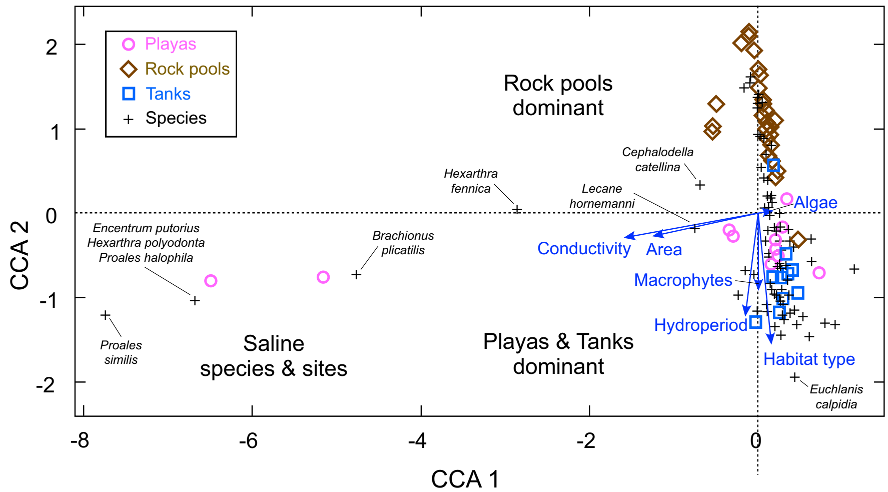

Fig. 5 Partial Canonical Correspondence Analysis (pCCA) of environmental correlates of rotifer species richness in selected Chihuahuan Desert aquatic habitats with variation due to spatial autocorrelation removed. Note that some symbols overlap and for plotting purposes the species and sites were scaled by eigenvalue

algal mats was significantly autocorrelated with the dbMEMs (Moran I statistic standard deviate: 5.57, $P<0.01$). Variance was partitioned by individual fraction with environmental predictors accounting for 17% of the variance, whereas the significant dbMEMs accounted for ~2% of the observed variance (R^2 adjusted).

Poisson GLM of macrophytes and algal mat influence on species richness returned the following formula: $S=0.73\ \mathrm{M}+0.69\mathrm{A}+0.92$ where M is macrophyte presence, and A is algal mat presence. All coefficients and the intercept were highly significant ($Z=9.67$, 7.15, and 9.28, respectively; all had $P<0.01$) (Table 3). Linearity of our residuals was checked by visual inspection of Q–Q plots.

Indicator species

We determined 29 taxa to be indicator species (*indval.g*, $P<0.05$; Table 4). Of these, one was an indicator of rockpools (*Hexarthra* sp., $P<0.01$), 19 were indicators of playas, 6 were indicators of tanks, 5 were indicators of tanks and playas, and one was an indicator of rock pools and tanks (*Trichocerca similis* (Wierzejski, 1893)). Several species were significant indicator species ($P<0.005$) including: playas, *Cephalodella megalocephala* (Glasscott, 1893), *Epiphanes brachionus* (Ehrenberg, 1837), *Lecane bulla* (Gosse, 1851), *Lecane luna* (Müller, 1776); tanks, *Polyarthra dolichoptera* Idelson, 1925; playas and tanks, *Brachionus angularis* Gosse, 1851, *Brachionus quadridentatus* Hermann, 1783, *Euchlanis dilatata* Ehrenberg, 1830 and *Platyias quadricornis* (Ehrenberg, 1832). SIMPER analysis also indicated that *Hexarthra* sp. was the species that most associated with rock pools but also showed *Trichocerca similis* and *Lepadella patella* (Müller, 1773) made substantial contributions to differences in communities among rock pools and other habitat types. Similarly, for the other habitat types, there was some overlap with the indicator species analyses (Table 4).

Discussion

In our previous study of rotifers in the Chihuahuan Desert we showed that (1) rotifer species composition is very diverse, (2) species dissimilarity among sites was correlated with distance, and (3) localized hotspots of richness are predicted across several scales of analysis (Brown et al., 2020). Here, we found that rotifer species richness varies greatly among habitat types and that stochastic processes dominate in determining community assembly for shallow ephemeral systems. While stochastic processes contribute the most to species composition, we found a small influence of deterministic effects on community assembly (i.e., hydroperiod and conductivity). Differentiating among stochastic effects could lead to further insights into community assembly in these systems. In addition, deterministic effects are more localized, so repeated sampling of individual sites may provide further support for their role in determining community structure.

Table 4 Rotifer species with highest contributions to the average between-group Sorensen dissimilarity among rotifer communities in select aquatic habitats in the Chihuahuan Desert as a function of habitat according to SIMPER analyses (species contributing at least 10% to similarity; % contribution in parentheses) and Indicator Species analyses (*indval.g P* value)

Habitat	Species with high SIMPER contributions	Indicator species	*P* value
Rock pools	*Hexarthra* sp. (58%), *Trichocerca similis* (15.4%), *Lepadella patella* (10.1%)	*Hexarthra* sp.	0.01
Tanks	*Euchlanis dilatata* (50.3%), *Polyarthra dolichoptera* (14%), *Brachionus angularis* (13%)	*Polyarthra dolichoptera*	0.005
		Asplanchna brightwellii, Brachionus bidentatus, Filinia pejleri, Eosphora najas, Polyarthra vulgaris	< 0.05
Playas	*Brachionus quadridentata* (24%), *Epiphanes brachionus* (10%)	*Asplanchna seiboldii, Cephalodella megalocephala, Epiphanes brachionus, Lecane bulla, Lecane luna*	0.005
		Asplanchnopus hyalinus, Brachionus calyciflorus, Brachionus plicatilis, Cephalodella gracilis, Cephalodella sterea, Filinia cornuta, Lacinularia flosculosa, Lecane thalera, Lepadella rhomboides, Notommata glyphura, Rhinoglena ovigera, Squatinella rostrum, Trichocerca rattus, Trichocerca cf. *vernalis*	< 0.05
Rock pools & Tanks	N/A	*Trichocerca similis*	< 0.05
Rock pools & Playas	N/A	N/A	
Tanks & Playas	N/A	*Brachionus angularis, Brachionus, quadridentatus, Euchlanis dilatata, Platyias quadricornis*	0.005
		Cephalodella gibba	< 0.05

We found high beta-diversity, and when compared to rotifer assemblages in other localities, they were among the highest in dissimilarity (Table 1). In our past analyses, we found that species assemblages were highly nested (Ríos-Arana et al., 2019; Brown et al., 2020), which may contribute to the high beta-diversity we observed. Nestedness may reflect the portion of beta-diversity that is structured by deterministic effects. For example, nestedness in rock pools may be due to strong species sorting by hydroperiod, in which case it should reflect the influence of deterministic effects on the assembly (Ripley & Simovich, 2009). We also found that as spatial grain increases, distance influences the species assemblage less for rock pools than for other habitats (Brown et al., 2020). At larger spatial scales richness of rock pools may be more representative of the regional species pool available to these sites, leading to lower beta-diversity. Additionally, at small scales rock pools may have significant hydrological connections with nearby rock pools, increasing similarity among them. Our current study supports the conclusions of Lopes et al. (2014) that species similarity should be lower in temporary habitats than in those with longer basin life. However, one should undertake comparisons among studies with caution for several reasons. (1) Sampling efforts differed among the published studies we included in Table 1. (2) Grouping sites by habitats can conflate habitats with very different edaphic conditions. For example, the rock pools comprised three different bedrocks: syenite porphyritic granite, limestone, and pyroclastic-flow deposits. (3) Studies may miss important suites of species by using snapshot datasets of communities.

Unlike Juračka et al. (2019) we found no relationship between habitat area and *S* when examining the three habitat types separately. However, when combined, there was a weak, but significant correlation. This species-area effect seems to be due to intrinsic differences in habitat size and richness between rock pools, which are smaller with relatively low diversity, and the playas and tanks which are larger with higher diversity. We sampled smaller sites (i.e., rock pools) much more frequently than the other habitats.

This may account for the lack of correlation between habitat area and richness in this study. Recent studies that controlled for species abundance concluded that island species-area effects are likely a sampling bias (e.g., Gooriah & Chase, 2019; Gooriah et al., 2021). Alternatively, some studies have found that large regional species pools can cause richness scaling with habitat area due to deterministic processes (Spasojevic et al., 2018).

Our comparisons of overall DNCI scores for habitat type indicated a predominance of stochastic processes in structuring rotifer community assembly. Our values are similar to those found for passive dispersers and macroinvertebrate communities in streams by Vilmi et al. (2021). Although stochastic forces dominated overall, in our pairwise comparisons by habitat type we found slightly more deterministic indices for rock pools when compared with either playas or tanks than for tanks compared with playas. This is what we would expect to see; rock pools have multiple etiologies and their edaphic conditions differ substantially from the other habitat types. In addition, tanks and playas are separated by greater distances than rock pools which are typically clustered. Rotifer trophi structure, a functional trait, affected the DNCI scores of rotifer habitat comparisons, with raptorial feeders having a more deterministic score than microphagous feeders. Microphagous feeders are generalists relative to raptorial feeders that rely on larger prey. We speculate that reliance on particular food sources may make raptorial feeders more prone to species sorting and other deterministic processes.

Our multivariate analysis showed a small, but significant, influence of deterministic processes in shaping rotifer community assembly. Several rotifer species were highly correlated with conductivity and hydroperiod. We expected this result because hydroperiod and salinity influence rotifer richness through species sorting (Walsh et al., 2008; Montero-Pau et al., 2011). For example, several rotifers aligned to the first component are known to be halophilic species (*B. plicatilis, E. putorius, H. polyodonta, P. halophila, and P. similis*) (Green, 1986; Fontaneto et al., 2008b). Spatial characteristics accounted for a very small portion of the variation (~2%) observed in rotifer species assemblages. One explanation for this small contribution may be the high passive dispersal capacity of aquatic species that inhabit temporary habitats or alternatively the relative homogeneity of these habitats. This likely leads to high stochasticity in colonists and the resulting species assemblages.

Habitat area and conductivity were both negatively aligned along the first component of the pCCA. Several of our larger playas, in particular Lake Lucero, are in locales with high water tables. When the water table is high it is more likely to interact with the playa, potentially increasing salinity (Rodríguez-Rodríguez, 2007). Additionally, Lake Lucero is located in a hot low-lying basin, so evaporites build up in the playa causing increased salination (Weir Jr., 1965). The relatively large size of playas coupled with their ground water interaction may explain the relationship we saw between conductivity and area. We also saw similar negative relationships between macrophytes and habitat type, which is likely due to the fact that most rock pool habitats lack macrophytes. We found only a small influence (~12% R^2 adjusted) of our constraining variables in structuring variation in rotifer community assemblages. This low explanatory power may indicate that deterministic effects have a relatively small role in determining community assembly in these systems or that there are other important factors that we did not measure. Despite this, given the strong gradient in conductivity found in some of these habitats, we suggest that apart from hydroperiod, salinity is the most important deterministic variable that is influencing community assembly in these habitats.

SIMPER species contributions and indicator species analysis showed overlap in species habitat associations. Indicator species analysis identified *Hexarthra* sp. as an indicator of rock pool habitats. This species is known to be adapted to short hydroperiod; it has a truncated lifecycle and is immediately capable of mixis rather than going through several amictic cycles first, the usual path for monogonont rotifers (Schröder et al., 2007). Indicator species have been reported for other specialized habitats such as acidified lakes where rotifers may occur, *e.g., Cephalodella acidophila* Jersabek, Weithoff & Weisse, 2011 (Weithoff et al., 2019) and *Keratella taurocephala* Myers, 1938 (Yan & Geiling, 1985).

Community development in shallow, aridland waters

While aridland basins may appear superficially similar to those in temperate systems, we have posited that constructs based on long-lived basins are insufficient to describe development of the aquatic invertebrate communities in the shallow water basins of aridlands. Nor do these basins resemble dry riverbeds that after decades of drought may receive flow from upstream (Urban et al., 2020). Thus, we need a refined conceptual model to focus attention on the processes driving habitat colonization and species assemblage in these habitats.

In our conceptual model (Fig. 6) we note that the distinctive factors of these aridland habitats fall into three broad categories: basin properties, sediment egg banks, and dispersal, all of which have important consequences to their invertebrate inhabitants. (1) These basins have a hydroperiod that involves stochastic filling during the wet season, followed by inevitable drying that lasts for uncertain duration. (2) Sediment depths and degree of their exposure to environmental stresses differ widely among sites. (3) Dispersal that transport propagules to or away from basins (i.e., anemochory/deflation, hydrochory/overflow, and zoochory, including anthropogenic movement) are inherently unequal and vary among habitats.

Our conceptual model also focuses on the primary difference between shallow desert basins and those in temperate regions — ephemerality. Regardless of the edaphic conditions, shallow basins in the Chihuahuan desert possess short hydroperiods; they fill with monsoonal rains and then lose water through evaporation and/or seepage (Scuderi et al., 2010). Thus, over the seasonal life of an aridland basin they fill rapidly and just as quickly their abiotic properties change; water temperature, conductivity, dissolved oxygen, pH, and the concentration of dissolved materials vary continuously over a short time frame. Nevertheless, the aridland basin ultimately ends in a return to dryness. Concomitant with variations in abiotic factors, biotic factors (e.g., food, competitors, and predators) also change during the basin life, reflecting the idiosyncratic nature of each basin (Fig. 6, lower left).

Sediments in desert basins also vary, ranging from nearly absent in rock pools (a few mm) to substantial (ca. 10 cm or greater) in cattle tanks and playas (authors, pers. obs.). Thus, in rock pools the diapausing stages of aquatic invertebrates experience extremes in temperature and ultraviolet radiation (Jocque et al., 2010). While sediment depth in cattle tanks and playas are more substantial, they dry to significant depths during the dry season. However, while lying deeper in the sediment may afford diapausing rotifer embryos some protection from

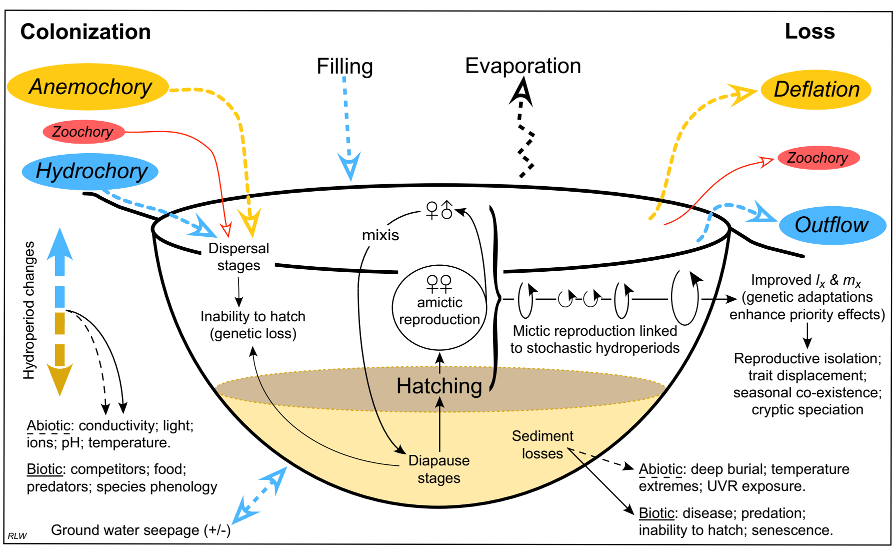

Fig. 6 Generalized conceptual model of important factors influencing community assembly of small-bodied, aquatic invertebrates including rotifers found in the isolated, temporary, shallow water basins of aridlands (e.g., playas, rock pools, tanks). Larger font size of colonization and loss processes indicates their relative importance (see text for details). Size of the circular arrows (in mictic reproduction) indicates that the length of the hydroperiods varies among filling cycles. Ground water seepage (+/−) is of minor importance in rock pools. Symbols: Biotic processes = solid lines (—), abiotic processes = dashed lines (---); filled arrowheads = processes within the basin

drying, García-Roger et al. (2006) reported that percent hatching decreased as a function of sediment depth. Thus, lying deeper in the sediment probably means greater age and with that increased susceptibility to loss via abiotic and biotic processes. Collectively, these factors may impact the viability of propagules unequally in the three habitat types (Fig. 6, lower right).

Dispersal of propagules among a group of closely opposed, shallow basins can involve both gains and losses of propagules (Fig. 6, upper left and right). However, these differ among the basins we studied. Local fauna (insects and vertebrates) probably comprises the scope of zoochory, especially at the smallest sites. This is due to the fact that most of these habitats are too small and too isolated, and also because they fill during the monsoon season, which is outside the period of normal migration for avifauna. Hydrochory and outflow varies among the three habitats in our study. For cattle tanks and playas surface flow only brings in materials and potentially propagules from the surrounding landscape; water does not flow from these systems to other sites, unless it is through ground water seepage: an unknown factor in our study sites. In contrast, in rock pools hydrochory is site specific. Inter-basin connectivity between rock pools at Hueco Tanks State Park & Historic Site occurs only as sheet-flow across a rocky surface; at best channels in these systems are poorly defined. However, connectivity among basins in the other regional rock pools we examined is much more well-defined. During monsoonal rains in those systems, upstream basins systems overtop their margins and flow to the next basin in well-defined channels. Thus, they form true dispersal networks (Brown & Swan, 2010).

The construct that emerges from our studies of isolated desert basins is one of the extremes. Once the basin has refilled, rotifers may begin to hatch from diapause and increase their population size, but due to an uncertain hydroperiod, mixis (which replenishes the sediment egg bank) must occur before the basin dries. This sequence repeats, but filling-drying cycles are stochastic. Therefore, because occurrence, extent, and duration of hydroperiod is not predictable, there must be a tight coupling between reproduction and short hydroperiod. As illustrated in the center of the model (Fig. 6), this process begins with amictic reproduction, but as species go through several mictic reproductive cycles each becomes genetically more well adapted to the basin's conditions. The outcome of this is a progressive genetic refinement (improved survivorship and reproduction), which enhance the resident's priority effects (De Meester et al., 2002, 2016). Over many mixis cycles this should lead to trait displacement, reproductive isolation, seasonal co-existence, and ultimately cryptic speciation (Kordbacheh et al., 2017; Mills et al., 2017).

Conclusion and perspectives

While our understanding of aquatic invertebrate community assembly in aridland ephemeral systems is improving, we suggest that attention to the following points will advance it further. (1) While we visited many of the sampling sites repeatedly, this research only provides a snapshot survey of the rotifer fauna of these habitats. Thus, we should not construe the fact that we did not find specific species to indicate that they are not present at some other time during the hydroperiod. To circumvent this limitation, we suggest using the technique of resurrection ecology—hatching dispersal stages by rehydrating dry sediments—to assess the zooplankton fauna from the sediments of ephemeral habitats (Pinceel et al., 2017; Vargas et al., 2019) and/or by applying environmental DNA sequencing to water and sediment samples (Yang & Zhang, 2020; Zawierucha et al., 2021). (2) To differentiate impacts of stochastic effects in structuring community assembly, we recommend that researchers perform a series of mesocosm experiments in which they vary the arrival sequence of diapausing stages. That protocol could add a complicating factor of providing a sediment egg bank to some mesocosms (Langley et al., 2001; Nielsen et al., 2002). (3) To expand our understanding of community assembly we recommend the study of other aquatic invertebrates (Juračka et al., 2019), in aridland ephemeral systems, and to compare our systems to that of vernal pools (Kneitel, 2014) and prairie-potholes (McLean et al., 2020) in temperate zones. (4) The analysis of rotifer trophi should be refined by using more than two categories (Palazzo et al., 2021). (5) Additional functional traits of rotifers should be examined (Obertegger & Flaim, 2018; Goździejewska et al., 2021). (6) An evaluation of the relative importance of zoochory versus anemochory would help further elucidate the processes structuring community assembly (Moreno et al., 2019). (7)

Finally, a challenging, but next logical step would be to parameterize our conceptual model and compare its processes to that of other ephemeral systems, using microbes, protists, and other invertebrates.

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Declarations

Conflict of interest The authors have no conflicts of interest/competing interests. The sponsors had no role in the design, execution, interpretation, or writing of the study.

Ethical Approval The appropriate agencies provided collecting permits (see acknowledgments). None of the specimens that we collected are endangered or threatened. Sampling and processing protocols followed appropriate guidelines established by state and federal parks.

Availability of data and material Data are available from the corresponding author, but most species data and site coordinates are available in Brown et al. (2020). Metadata are available at: https://datarepo.bioinformatics.utep.edu/getdata?acc=9UX5TMO7PXAMPZK

Code availability Not applicable.

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