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ORIGINAL ARTICLE

Ephemeral Wetland Macroinvertebrate Communities Across Climate Regions Share Similar Functional Trait Composition Despite Near-Total Taxa Replacement

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ABSTRACT

1. Community assembly in aquatic habitats is heavily influenced by hydrology, but understanding the influence of other habitat conditions is also critical. Most studies focus on comparisons of geographically close communities that exist under diverse hydrological regimes, but this framework limits our ability to understand how conditions other than hydrology shape ephemeral wetland communities. Here, we investigated how macroinvertebrate communities vary with local, landscape, and climate variables in ephemeral wetlands across a large geographic range with few geographic barriers.
2. We sampled ephemeral wetlands in North Dakota, New Mexico, and Texas (USA) in 2021 and in North Dakota and New Mexico in 2022. We used an array of hydrographic, climate, landscape, and spatial variables to relate taxonomic and functional macroinvertebrate community composition and diversity to habitat conditions.
3. Taxonomic composition was overwhelmingly different among states and between years: landscape-scale refuge availability explained variation in taxonomic composition, but local and climate-scale variables only explained variation within the context of other variables. Trait composition was similar between most sampling groups, but distinct trait assemblages occurred in the North Dakota 2021 communities. No predictor variable matrix explained trait composition alone, but local, climate, landscape, and spatial arrangement predicted composition when considering the overlapping influence of other variables. Taxa and trait diversity indices were associated with increased refuge habitat at landscape scale.
4. Our results show consistent trait structure across a large geographical scale in hydrologically similar wetlands, despite almost complete taxonomic turnover between regions. Patterns in taxonomic and functional composition imply that incorporating predictor variables at multiple scales is critical in understanding ephemeral wetland community composition.
5. Despite similar hydrological regimes and potential for connectivity via dispersal, taxa replacement is high in ephemeral wetlands across regions within a single grassland macrosystem. Taxonomic composition and overall diversity change with the

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context provided by a diverse suite of structuring variables. Further, we show that in most cases, ephemeral hydrology elicits a similar trait response across climate regions.

1 | Introduction

Hydrology is often touted as a "master variable" in aquatic habitats (Konar et al. 2013) and has received significant attention in scientific literature relative to other potential environmental filters (Resh et al. 1988). For an aquatic species to be successful, it must possess traits adapted to habitat-specific hydrological characteristics (i.e., the timing, frequency, flow, and/or amount of water present in a given habitat), and this trait variation is reflected at the community level (Poff 1997; Lamouroux et al. 2004; Schriever and Lytle 2016). Accordingly, wetland macroinvertebrate communities across the gradient of habitat permanence express vastly different characteristics. For example, permanent wetlands have substantially different assemblages and diversity levels compared to ephemeral wetlands (Whiles and Goldowitz 2001; Bonada et al. 2007; Dolédec et al. 2017; Hill et al. 2017; Patrick et al. 2019).

Many freshwater invertebrates found in ephemeral aquatic habitats are specially adapted to hydrological instability through dispersal away from a drying habitat or desiccation-resistance traits to ensure reestablishment once water returns (Boersma et al. 2014; Bogan et al. 2015; Schriever et al. 2015). Desiccation resistance traits can include behavioural (e.g., burrowing), reproductive (e.g., desiccation resistant eggs), or developmental adaptations (e.g., diapause) (Wiggins 1980; Poff 1997). In concert with dispersal and desiccation resistance, many taxa in ephemeral aquatic habitats can develop rapidly and may reproduce multiple times per year to capitalise on the presence of water (Lamouroux et al. 2004; Frazier and Schriever 2022). Both resident and transient taxa use ephemeral wetlands, and the degree to which they use ephemeral wetlands (spending whole life cycle vs. temporary use) often reflects how specialised their trait suites are (Hall et al. 2004).

The ecology of permanent aquatic systems has been well studied, and we currently have a broad understanding of differences between permanent and ephemeral wetland communities (e.g., Hill et al. 2017; Gleason and Rooney 2018). However, there is a gap in our ecological knowledge concerning which non-hydrology factors may affect assembly. The relative importance of other filters in influencing wetland assembly, including hydrography (e.g., temperature, dissolved oxygen, conductivity), landscape conditions (e.g., amount of nearby coloniser habitat), climate, and biotic interactions (e.g., predation, competition, and dispersal) is unclear. In permanent aquatic habitats, environmental conditions, landscape connectivity, and biotic interactions are known to be important in structuring communities (Viana et al. 2016; Pander et al. 2018). However, the roles of these factors for ephemeral systems are less understood. In particular, landscape connectivity has been implicated as critical in ephemeral wetland assembly (Gleason and Rooney 2018), but this factor has rarely been examined at large (e.g., macroecological) scales.

Studying assembly at large spatial scales introduces valuable variation in structuring variables but also often presents challenges, as dispersal limitation may drive community differences rather than measured predictor variables (Cañedo-Argüelles et al. 2015). The ephemeral wetlands of the central flyway across the Great Plains of North America constitute a macrosystem (Heffernan et al. 2014) that offers a unique opportunity to address the relative influence of non-hydrological variables along with the effects of connectivity.

Our study sites were in an almost universally flat and predominantly grassland landscape, with many ephemeral wetlands. Our sites occurred from the more temperate Prairie Pothole Region of the USA and Canada to the arid American Southwest. Variation in landscape configurations (e.g., regional wetland density), physicochemical features, and climate conditions is readily observable within the macrosystem. Flying aquatic insects are likely able to disperse between these aquatic habitat islands relatively easily (Townsend et al. 2003). Dispersal scale varies by taxon, with individuals of some species travelling as far as thousands of kilometres over supposed barriers (e.g., dragonflies; Kohli et al. 2018; Parr and Schmitz 2024), while other taxa may only travel within several hundred meters of where they emerged (e.g., chironomid midges; Vebrová et al. 2018; Medeiros et al. 2020). Passively dispersing animals may use other animals as vectors of transport, like birds migrating through the Great Plains American Central Flyway. External or internal transport of propagules by waterfowl and wading birds allows for dispersal across great distances (Vanschoenwinkel et al. 2008; Beladjal and Mertens 2009; Brochet et al. 2010; Green et al. 2023), while wind may offer local dispersal (Vanschoenwinkel et al. 2008; Parekh et al. 2014). Through these dispersal vectors, connection between habitat islands within the greater macrosystem should be possible.

By leveraging the regional habitat diversity of the Great Plains, we sought to understand how wetland macroinvertebrate communities respond under different habitat conditions but within a similar hydrologic context. We analysed macroinvertebrate community composition in ephemeral wetlands in North Dakota, New Mexico, and Texas to understand how community composition differed and determine which taxa differed among communities. We predicted communities would have at least some degree of overlap by region because of potential dispersal and flexibility in habitat condition thresholds generally associated with taxa that predominantly use temporary wetlands (O'Neill et al. 2016; Bird et al. 2019). Given the potential for radically different environmental conditions throughout the year across these regions, we also compared community trait compositions to see if hydrology-associated traits were similar under different environmental conditions. We predicted differences in wetland abundance and hydroperiod associated with increasing latitude (Dodds et al. 2019) would result in different trait assemblages among

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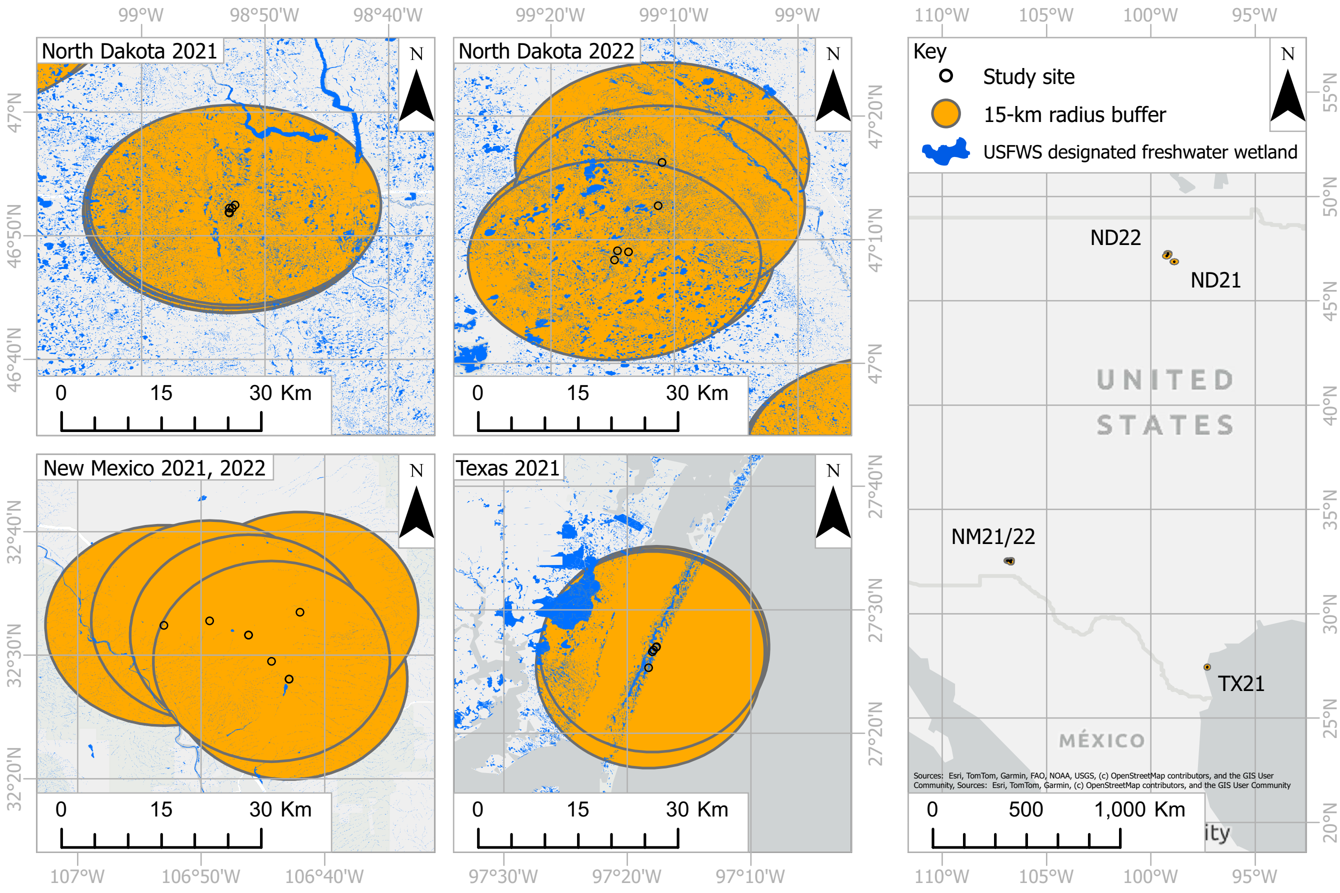

FIGURE 1 | Map of the surrounding area around each study location with USFWS-defined freshwater wetlands and 15-km radius buffers around each study wetland shown. Map of entire region displayed with sampled states named and sites shown.

regions based on variable selection pressure for ephemerality-adapted traits. We then used a wide array of local hydrographic, climate, and landscape variables to assess which conditions were associated with community trait and taxonomic identity. Finally, we examined the relationship between these habitat variables and overall community taxonomic and functional diversity metrics.

2 | Methods

2.1 | Study Sites

Replicate freshwater wetlands were selected in three regions within the central United States: eastern North Dakota, southcentral New Mexico, and the gulf coast of Texas (Padre Island) (Figure 1). These regions are separated by ~1000–2000 km stretches of plains, encompassing an area of roughly 1,000,000 km^2. The New Mexico sites are representative of Great Plains and Southwestern US playas, while the North Dakota sites are primarily shallow prairie potholes resulting from glaciation. The Texas wetlands are located within the dunes of a protected section of barrier island (Padre Island National Seashore). In North Dakota, ephemeral wetlands may be filled either by snowmelt in spring or heavy rains in summer, while other regions often experience filling via heavy summer rains associated with monsoons (New Mexico) or tropical systems (Texas; Table 1). These regions represent a range of climate conditions: North Dakota has a temperate climate with moderate rainfall, mild summers, and cold winters, New Mexico has hot summers, mild winters, and low precipitation, and the Texas sites have hot summers, warm winters, and high precipitation (Table 2). Seasonally cold temperatures in North Dakota mean most surface water freezes in winter. Wetland density varies at the landscape scale for each region as well, with very few wetlands in the area surrounding our New Mexico sites, many wetlands in North Dakota, and a moderate amount around our Texas sites, although these sites are on an island separated from the mainland by ~3 km of saltwater (Table 2, Figure 1). Given the geographic distance and climatic variation among regions, there is also considerable physicochemical variation among regions (Table 2).

2.2 | Sampling Design and Methods

We sampled all sites (individual ephemeral wetlands, $n = 21$) approximately 2 weeks after inundation. Time and personnel constraints limited our sampling to a single timepoint, but after 2 weeks all wetlands sampled maintained large branchiopod (fairy, clam, and/or tadpole shrimp) populations, suggesting at least similar assembly states across wetlands (O'Neill 2016; O'Neill et al. 2016). In 2021 sampling occurred in North Dakota (mid-June, $n = 5$), New Mexico (late July, $n = 4$), and Texas (late May, $n = 5$), and during 2022 sampling occurred in North Dakota (early May, $n = 5$) and New Mexico (late July, $n = 4$). Immediately

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TABLE 1 | Sampling and habitat characteristic information for each sampling event. "Nearby permanent wetland cover" refers to the area of permanent wetlands (as defined by USFWS) within a 15 km radius buffer from the study wetlands. Values in parentheses represent standard deviations. Full environmental data is available at https://doi.org/10.5063/F1KH0KS7.

State-year	Sampling period	Typical hydroperiod	Average depth (m)	Water source	Water temperature (°C)	Dissolved oxygen (mg/L)	pH	Specific conductance (µS/cm)	Surface area (m^2)	Nearby permanent wetland cover (km^2)	Anthropogenic pressures
New Mexico 21	July 2021	Weeks	0.3 (0.1)	Rainfall	25.8 (4.0)	4.9 (2.6)	8.0 (0.3)	237.1 (68.9)	499.0 (446.4)	0.5 (0.1)	Cattle
New Mexico 22	July 2022	Weeks	0.2 (0.2)	Rainfall	26.0 (2.5)	4.5 (1.5)	7.3 (0.9)	241.0 (56.6)	859.4 (+/− 358.7)	0.4 (0.3)	Cattle
North Dakota 21	June 2021	Months	0.3 (0.1)	Rainfall	22.2 (3.0)	5.5 (2.1)	7.6 (0.4)	504.6 (264.3)	NA	66.9 (33.1)	Cattle, agriculture
North Dakota 22	May 2022	Months	0.6 (0.1)	Rainfall, snowmelt	15.3 (2.2)	8.2 (3.5)	7.8 (0.4)	375.8 (262.9)	NA	16.7 (3.9)	Cattle, agriculture
Texas	May 2021	Weeks	0.2 (0.1)	Rainfall	27.0 (1.1)	3.2 (2.0)	8.0 (0.2)	450.7 (203.5)	6007.9 (6808.4)	0.7 (0.7)	Anthropogenic litter

following snowmelt or substantial rainfall in each sampling region, sampling teams selected wetlands to include and waited 2 weeks post-inundation to sample communities. While the limited number of sites we sampled does not represent the entire range of conditions present within each respective state, we refer to these regional groupings of wetlands by their state label for the sake of simplicity in this study. Wetlands did not consistently fill between years, leading to total replacement of the wetlands sampled in North Dakota and replacement of two wetlands sampled in New Mexico during 2022.

Macroinvertebrates were sampled by sweeping a ~500-µm mesh net along three 10-m transects for 5 min per transect. We then pooled each transect within a wetland into a single sample. Collected macroinvertebrates were rinsed in a 500-µm sieve to remove non-target taxa (e.g., small zooplankton) and sediment. Anuran tadpoles were manually removed. Samples were preserved in 70%–80% ethanol and shipped to the University of Kansas for identification. Upon receipt, the samples were transferred to 95% ethanol for storage.

Insects were identified to genus or species (for most taxa collected from multiple states) by using published taxonomic reference keys (Van Tassell 1966; Gundersen 1978; Check 1982; Smetana 1988; Thorp et al. 2015; Merritt et al. 2019; Van Vondel 2021). Non-insect macroinvertebrates were identified to species (Anostraca and Leptestheriidae), genus (Cyzicidae, Limnadiidae, Physidae, Triopsidae, and Lynceidae), subfamily (Planorbidae), family (Trombidiformes), or higher taxonomic level (Oligochaeta) depending on taxonomic group according to Thorp et al. (2015). Most Trombidiformes collected were members of Arrenuridae and treated as such for trait data collection. Trait data (taxon-level trait assignments and references available online at https://doi.org/10.5063/F1KH0KS7) were collected for four traits: feeding guild, dispersal mode, voltinism, and desiccation resistance (Table S1). These traits are known to be associated with hydrologic variability and other general habitat conditions (Poff 1997; Statzner and Bêche 2010; Schriever et al. 2015). These data were obtained from multiple sources including existing trait datasets, primary literature, and books. We interpreted trait assignments from the literature by assigning each taxon to a single, binary trait modality within each trait category. When trait information was gathered from sources providing modality preferences or use frequency (i.e., fuzzy coded traits; e.g., Tachet et al. 2002), we used the dominant modality for each trait category in our dataset. Once trait assignments were gathered, we created a trait abundance by site matrix by cross-multiplying our binary trait by taxa matrix with our taxa abundance by site matrix.

We collected three categories of predictor variables: local environmental variables, climate data, and landscape wetland mosaic data. Local environmental variables included water temperature (°C), dissolved oxygen (mg/L), pH, specific conductivity (µS/cm), turbidity (NTU), average water column depth, time since wetland filling, submerged vegetation cover, emergent vegetation cover, and total vegetation cover. Hydrographic local environmental variables [water temperature (°C), dissolved oxygen (mg/L), pH, specific conductivity (µS/cm), and turbidity (NTU)] were measured at the time of sampling (typically afternoon) using multiparameter probes.

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TABLE 2 | Mean climate conditions for each region included in this study from 2000 to 2024. Data from the U.S. National Weather Service (US Department of Commerce n.d.).

State	Mean annual rainfall (cm)	Minimum monthly mean temperature (°C)	Maximum monthly mean temperature (°C)	Annual mean temperature (°C)
New Mexico	21.7	8.0	29.4	19.2
North Dakota	48.1	−11.4	21.7	5.4
Texas	77.3	14.4	29.9	22.9

In New Mexico, a Hydrolab MS 5 Sonde (OTT HydroMet, Sterling, VA, USA) was used. In North Dakota and Texas, YSI ProDSS water quality meters (YSI Inc., Yellow Springs, OH, USA) were used. Depth (m) was measured at the deepest point of each wetland and halfway to the water's edge in each cardinal direction (N, E, S, W) and then averaged. We visually estimated absolute emergent, submerged, and total (sum of emergent and submerged cover) percent vegetation cover in X% increments, in 5 equally spaced 1 m^2 quadrats along a transect spanning the longest length of each wetland. These coverage estimates were averaged across quadrats for all analyses and include both living, dead, and senescent plant material. Additionally, we estimated the number of weeks passed since the initial fill at sampling based on examining satellite imagery (Planet Labs 2021–2022) of sites preceding sampling.

We retrieved climate data for the duration of the fill period and the year preceding the estimated fill date from Open-Meteo (Hersbach et al. 2023; Zippenfenig 2023) (https://doi.org/10.5063/F1KH0KS7). Data included average high and low temperatures, rainfall, snowfall, and total precipitation for both timeframes, as well as average wind speed during the fill period. Using this data, we also created new variables for each timeframe for the number of days below freezing and average degree day. Average degree day was calculated by summing averaged daily high and low temperatures across a given timeframe (fill period or year prior) and averaging this sum across the number of days a given wetland was filled prior to sampling.

Landscape-scale data included wetland counts and areal coverage classified by type and hydrology, as defined by the United States Fish and Wildlife Service, within a 15-km buffer of each study wetland. We extracted and mapped these data from the National Wetlands Inventory (NWI) Wetlands Data Layer (U.S. Fish and Wildlife Service 2018) by using ArcGIS (ESRI Inc. 2022). Using this data, we also created dummy variables for the proportion each hydroperiod type (permanent, semi-permanent, and ephemeral) contributes to total wetland area within the 15-km buffer.

2.3 | Data Analysis

Given the unique conditions before and during fill events and inconsistent overlap in site selection between years, we used state-year rather than state as a grouping variable (e.g., North Dakota 2021 and North Dakota 2022, which were different wetland sites, were treated as separate groups). Analyses were run in R statistical software (R Core Team 2021). Taxonomic and functional community compositions (as taxa abundance by site and trait modality abundance by site matrices, respectively, grouped by state-year) were visualised by using non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarities calculated from community abundance matrices. We tested for differences among communities grouped by state-year by using permutational multivariate analysis of variance (PERMANOVA, vegan package; Oksanen et al. 2022) on Bray–Curtis distances derived from Hellinger-transformed abundance data (taxa by site or trait modality by site) with pairwise PERMANOVA *post hoc* tests. Indicator species analyses (indicspecies package; De Caceres and Legendre 2009) were performed on raw abundance data to pinpoint specific taxa/trait modality differences between groups based on relative abundances of taxa/trait modalities.

To assess how taxonomic and functional community compositions vary with environmental variables, we performed variance partitioning with Hellinger-transformed abundance matrices and a subset of each environmental variable category (local, climate, landscape, and spatial categories) using the function *varpart* in the vegan library (Oksanen et al. 2022). Due to the large number of environmental variables recorded, we performed a multistep process to select the strongest variables for variance partitioning (Figure S1). First, we selected all non-spatial variables ($n = 49$) that were significantly correlated ($p < 0.05$) with patterns of community composition, determined by fitting linear environmental vectors onto an ordination of a given abundance matrix using the *envfit* function (Figures S2 and S3; Table S2) in the vegan library (Oksanen et al. 2022). We then manually removed variables that were highly correlated with one another (correlation coefficient > 0.50) to reduce potential overfitting and multicollinearity (Dormann et al. 2013; Figures S4 and S5), while retaining variables that may have ecological relevance. Spatial distance (Euclidean) among wetlands was transformed via Moran eigenvector mapping (MEM) for use in constrained analyses (package adespatial; Dray et al. 2023). For both taxa and trait abundance datasets, we used forward selection to include the best-structuring MEM eigenvectors. Environmental variables were sorted into their respective categories and sub-selected again for each category (local, climate, landscape, spatial) via stepwise model selection based on redundancy analysis (RDA) R^2 and p-value association with Bray–Curtis transformed abundance matrices (Oksanen et al. 2022). Use of MEM in RDA without correction has been shown to produce spurious results due to spatial autocorrelation (Gilbert and Bennett 2010). To detect potential spatial autocorrelation within each predictor category, local, climate, and landscape matrices, alongside respective selected

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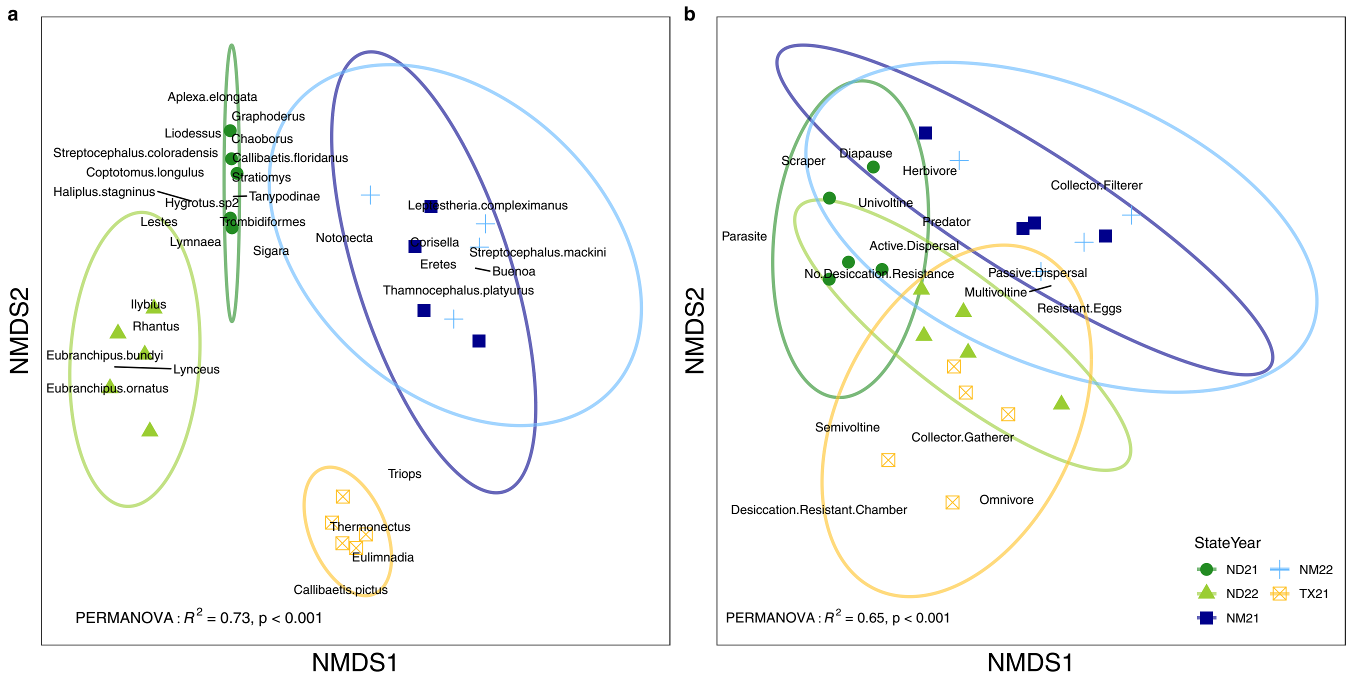

FIGURE 2 | NMDS ordinations of taxonomic (a) and functional (b) community structure by state-year with symbols representing community samples. For the taxa plot (a), significant indicator taxa are displayed, while all trait modalities are displayed in the functional trait plot (b). State-year designations include North Dakota 2021 and 2022 (ND21 and ND22), New Mexico 2021 and 2022 (NM21 and NM22), and Texas 2021 (TX21). Ellipses represent 95% confidence intervals by state-year grouping.

MEM eigenvectors, were analysed via Moran spectral randomisation (MSR)-corrected variance partitioning (function msr.varipart: adespatial; Dray et al. 2023) (Clappe et al. 2018). MSR-corrected variance partitioning is currently restricted to include only two explanatory matrices, so each variable group matrix was run separately with the appropriate spatial data (sensu Loewen et al. 2020). We chose to report some variance partitioning results despite spatial autocorrelation detection via the MSR approach, as these spatially autocorrelated environmental variables still co-occur with our study communities and offer insight into assembly under those conditions. Given our study is observational, reporting and discussing results in this context still shows valuable insight into which conditions are associated with specific communities.

We compared locations with large differences in abundance by calculating abundance-based rarefied Shannon diversity and taxa richness by using the iNEXT package (Hsieh et al. 2022). We also calculated Pielou's evenness by using the vegan package (Oksanen et al. 2022), and functional richness and functional dispersion with the FD package (Laliberte et al. 2014) in R. We performed all community-level diversity index calculations at the community sample level. Here we also reduced our number of predictor variables using the same variable sets as we did for variance partitioning, to reduce overfitting and multicollinearity. From this subset, we used a stepwise, Akaike information criterion (AIC) based process to select the most informative environmental variables for inclusion in linear models for each diversity index (Table S5; stepAIC function, MASS package; Ripley et al. 2023). If the best-fit model failed to meet the assumptions of a standard linear model, we used generalised linear models.

3 | Results

We collected and identified a total of 18,615 invertebrates representing 84 unique taxa, 37 families, and 15 orders. Communities across state-year sampling events showed an overall difference in taxonomic composition (Figure 2a; PERMANOVA, $p<0.001$). Further, we observed differences in taxonomic composition in 9 of 10 pairwise comparisons between state-year groupings (pairwise PERMANOVA, Table 3). The only nonsignificant comparison was between New Mexico 2021 and 2022 ($p_{\text{BH-adjusted}}=0.062$). Strong indicator taxa for each group were typically species of large branchiopods (Spinicaudata, Laevicaudata, Anostraca, and Notostraca) or predaceous diving beetles (Dytiscidae) (Figure 2a). The only genera collected in multiple regions were *Streptocephalus* fairy shrimp (Anostraca: Streptocephalidae), *Triops* tadpole shrimp (Notostraca: Triopsidae), and *Callibaetis* mayflies (Ephemeroptera: Baetidae). Within these three genera, only one species, *Streptocephalus texanus*, was collected in multiple regions. It is possible that one species of tadpole shrimp (*Triops longicaudatus*) was collected in multiple regions, but this genus is currently in need of revision, and there is not an adequate key for species-level identification based on morphology (Thorp et al. 2015). At a lower resolution, all wetlands shared similar groups of dominant taxa, with each region having their own representatives of the clam shrimp, fairy shrimp, and predacious diving beetle groups.

Functional trait composition also differed overall among state-year groupings (Figure 2b; PERMANOVA, $p<0.001$). Relative to taxonomic communities, functional trait communities overlapped more in ordination space across state-years and tended to have less "species" level separation. We found that 5 of the

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TABLE 3 | Pairwise PERMANOVA results by state-year for taxonomic and functional trait composition of macroinvertebrate communities sampled. State-year designations include North Dakota 2021 and 2022 (ND21 and ND22), New Mexico 2021 and 2022 (NM21 and NM22), and Texas 2021 (TX21). Provided *p*-values have been corrected via Benjamini–Hochberg procedure (false discovery rate).

State-year comparison	Community type compared	R^2	$p_{\text{BH-adjusted}}$
ND21-ND22	Taxonomic	0.598	0.014*
ND21-NM22		0.365	0.014*
ND21-NM21		0.512	0.018*
ND21-TX21		0.488	0.014*
ND22-NM22		0.499	0.014*
ND22-NM21		0.664	0.014*
ND22-TX21		0.674	0.014*
NM22-NM21		0.288	0.057
NM22-TX21		0.396	0.014*
NM21-TX21		0.573	0.018*
ND21-ND22	Trait	0.743	0.030*
ND21-NM22		0.641	0.030*
ND21-NM21		0.699	0.030*
ND21-TX21		0.724	0.030*
ND22-NM22		0.231	0.178
ND22-NM21		0.471	0.030*
ND22-TX21		0.249	0.120
NM22-NM21		0.064	0.876
NM22-TX21		0.234	0.178
NM21-TX21		0.398	0.051

Note: * indicates statistically significant comparisons ($p < 0.05$).

10 pairwise comparisons of trait composition showed significant differences in trait–state abundances between state-year groupings, including all community comparisons with the North Dakota 2021 group (pairwise PERMANOVA, Table 3). North Dakota 2021 had seven trait modalities associated as indicators, while New Mexico 2022 had two, and Texas had one (Table 4).

Overall, our best predictor variable subset (Table S3) explains ~26% of the total variance of ephemeral wetland taxonomic composition (variance partitioning, $p < 0.001$) (Figure 3a). Our landscape-scale variables (number of riverine wetlands, area of lacustrine wetlands within a 15-km buffer) explain a modest amount of variance alone ($R^2_{\text{adj.}} = 0.09$, $p = 0.014$), but our climate (average high air temperature during the fill period, rain accumulation in the year preceding sampling) and local (average wetland depth) partitions failed to explain significant portions of variation alone while controlling for other predictors ($R^2_{\text{adj.}} = 0.04$, $p = 0.095$; $R^2_{\text{adj.}} = -0.01$, $p = 0.526551$, respectively). However, within the context of other predictors, landscape-scale ($R^2_{\text{adj.}} = 0.14$, $p = 0.002$), climate ($R^2_{\text{adj.}} = 0.18$, $p < 0.001$), and local ($R^2_{\text{adj.}} = 0.09$, $p < 0.001$) variables each explain significant portions of the total compositional variance. Our spatial variables failed to explain composition and were eliminated from model consideration during forward selection of MEM variables ($p_{\text{MEM1}} = 0.054$). The nonsignificant spatial component implies there is no spatial autocorrelation with these communities.

TABLE 4 | Indicator analysis results for functional traits of macroinvertebrate communities grouped by state-year sampling group. Only significant results are shown. State-year designations include North Dakota 2021 (ND21), New Mexico 2022 (NM22), and Texas 2021 (TX21).

	Trait category	IV value	*p*
ND21			
Predator	Feeding guild	0.831	0.0002
Univoltine	Voltinism	0.831	0.0004
Scraper	Feeding guild	0.749	0.0001
No desiccation resistance	Desiccation resistance	0.719	0.0042
Active dispersal	Dispersal	0.677	0.0112
Parasite	Feeding guild	0.659	0.0122
Herbivore	Feeding guild	0.631	0.0092
NM22			
Multivoltine	Voltinism	0.635	0.0054
Passive dispersal	Dispersal	0.618	0.0088
TX21			
Omnivore	Feeding guild	0.684	0.0044

A similar total proportion of variation in trait composition to that of taxonomic composition was explained by the analysis ($R^2_{\text{adj.}} = 0.22$, $p = 0.023$) (Figure 3b). Of the local-scale variables considered, dissolved oxygen concentration, total vegetation cover, and average wetland depth influenced trait assemblages after model selection. For climate variables, total precipitation during the fill period alone was the strongest predictor of trait assemblages. The number of riverine wetlands and total wetland area within a 15 km radius were the strongest landscape variables, while the spatial matrix was composed of a single MEM vector (MEM 4). Including the overlapping influence of other variable groups, climate variables showed the strongest influence on trait composition ($R^2_{\text{adj.}} = 0.19$, $p = 0.007$), followed by local conditions ($R^2_{\text{adj.}} = 0.15$, $p = 0.003$), landscape variables ($R^2_{\text{adj.}} = 0.12$, $p = 0.032$), and our spatial matrix ($R^2_{\text{adj.}} = 0.12$, $p = 0.016$). When controlling for the overlapping influence of other variable groups, none of the local scale, climate, landscape, or spatial variables were still associated with trait composition ($R^2_{\text{adj.}} = -0.01$, $p = 0.499$; $R^2_{\text{adj.}} = 0.04$, $p = 0.185$; $R^2_{\text{adj.}} = 0.03$, $p = 0.242$; $R^2_{\text{adj.}} = -0.03$, $p = 0.749$, respectively). Spatial autocorrelation contributed to the capacity for our environmental

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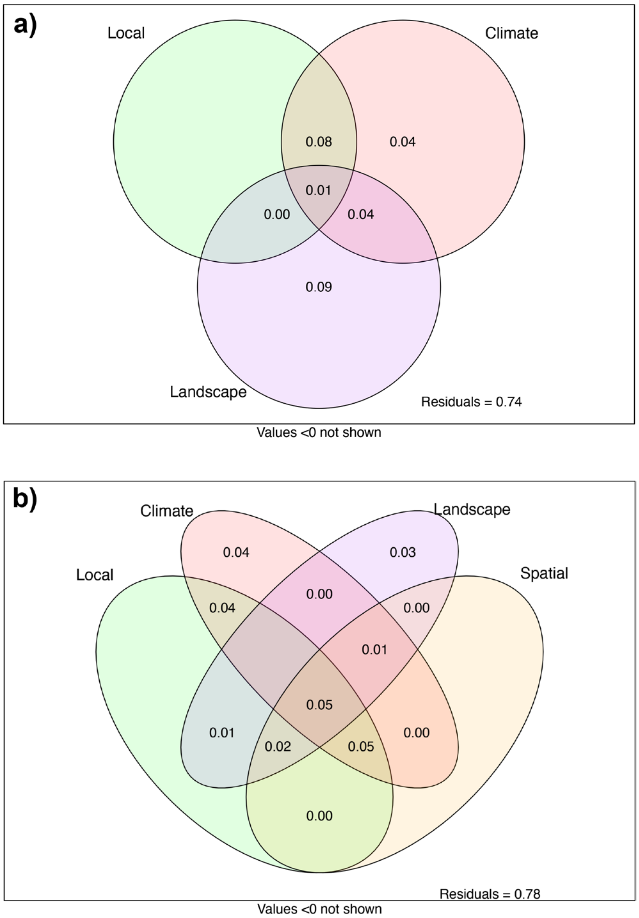

FIGURE 3 | Variance partitioning results for (a) taxonomic and (b) trait compositions of ephemeral wetlands. Values represent adjusted R^2, with higher values showing stronger influence on community composition by individual partitions or the overlap of multiple partitions. Only values >0 are displayed. For the taxa-based model (a), the local variable group includes wetland depth, climate includes average high temperature during the fill period and rainfall in the year preceding the fill period, landscape includes lacustrine wetland area and the number of riverine wetlands within a 15 km buffer of each study wetland. The spatial component failed to predict taxonomic composition. The trait-based model (b) included dissolved oxygen concentration, total aquatic vegetation cover, and wetland depth for local variables, total precipitation during the fill period for climate variables, the number of riverine wetlands and total wetland area within a 15 km buffer of each study wetland for landscape variables, and a single eigenvector (MEM 4) for spatial variables.

variables to explain variance in trait composition (Table S4). For our local and landscape matrices, this contribution was enough to make the single-matrix partitioning models nonsignificant after MSR correction, despite only modest changes in $R^2_{adj.}$ values. We chose to retain the local and landscape variables in our overall partitioning model despite the spatial autocorrelation given their nonsignificance when controlling for other matrices and to still report relationships these variables have within the context of the other matrices.

We found some combination of environmental variables that explains each of our diversity indices (Table 5). Rarefied Shannon diversity increased with the area of lacustrine wetlands within a 15 km buffer (GLM, $p=0.028$) (Table 5). Rarefied taxa richness was also associated with lacustrine wetland area, but was also explained by rainfall within the previous year (GLM, $p<0.001$). Pielou's evenness increased with higher average air temperature during the fill period and with nearby lacustrine wetland area (LM, $p=0.030$, $R^2=0.23$). Functional richness increased with higher average windspeed during the fill period, the number of nearby riverine wetlands, and lower average wetland depth and nearby total wetland area (GLM, $p<0.001$). Functional dispersion increased with fewer nearby riverine wetlands and lower total nearby wetland area (LM, $p=0.021$, $R^2=0.25$).

4 | Discussion

The American Great Plains present a large network of ephemeral wetlands under diverse physicochemical, climatic, and landscape conditions with perceivably few strong geographic dispersal barriers. With this in mind, we sought to assess differences among regions within this macrosystem in terms of taxonomic and functional composition. We found these diverse conditions foster communities of different taxa, despite the potential for movement among regions. However, when comparing trait composition in these communities, the overarching pressure of intermittent hydrology remains evident, with most communities following similar functional strategies to cope with periodic drying.

4.1 | Community Composition

Despite the large observed differences in community composition, we recorded comparatively high trait convergence among state-year sample groups. This relationship implies that strong regional factors structure communities, despite the potential for dispersal, but ephemeral hydrology dictates the specific traits taxa must possess to be successful in these habitats. Literature specifically comparing ephemeral wetlands across large spatial gradients is sparse, but Schriever and Lytle (2016) found a similar pattern of trait convergence between ephemeral wetlands in temperate Canada and intermittent streams in the arid American Southwest. While not directly addressing hydrology as the primary structuring variable, other studies have found communities under similar environmental conditions show trait convergence in stream fish (Lamouroux et al. 2002) and macroinvertebrates (Statzner et al. 2004) at macrosystem scale.

Most communities in this study fall within the established trait-based ecology context of ephemeral aquatic habitats, with many other studies presenting similar trait assemblages to ours based on hydrologic regime (Bogan and Lytle 2011; Rosset et al. 2017; Frazier and Schriever 2022). Representatives of most trait modalities are present within each of our sample groups, but they occur at drastically different ratios. Most noticeable is the relative dominance of organisms with univoltine reproduction and no desiccation resistance in the North Dakota 2021 sample group. Initially, this seems counter-intuitive given the ephemeral nature of these habitats, as success in temporary aquatic habitats is typically the result of adaptations to the eventual absence of water (Wiggins 1980; Poff 1997; Carvallo et al. 2022). The taxa that dominate these communities are active dispersers,

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TABLE 5 | Linear model results for sampled community diversity indices. If model assumptions were met after variable selection, linear regression (LM) was used; if the model failed to meet the assumptions of LM, generalised linear models (GLM) were used. Assumed error distribution for each GLM is shown in parentheses.

Diversity index	Model type	Overall *p*	Overall $R^2_{adj.}$	Predictor variable/ intercept	Estimate	Std. error	*p*
Rarefied Shannon diversity	GLM (Gamma)	0.028	NA	Intercept	0.982	0.152	< 0.001*
				Nearby lacustrine wetland area (km^2)	0.566	0.155	0.002*
Rarefied taxa richness	GLM (Gaussian)	< 0.001	NA	Intercept	10.868	2.592	< 0.001
				Nearby lacustrine wetland area (km^2)	0.241	0.044	< 0.001*
				Rainfall within the last year (cm)	−0.003	0.005	0.580
Pielou's evenness	LM	0.030	0.23	Intercept	0.211	0.127	0.113
				Avg. high air temperature during fill period (°C)	0.007	0.005	0.151
				Nearby lacustrine wetland area (km^2)	0.004	0.001	0.014*
Functional richness	GLM (Gaussian)	< 0.001	NA	Intercept	−17.935	7.008	0.020
				Avg. wetland depth (m)	−23.652	9.800	0.027*
				Avg. windspeed during fill period (km/h)	1.767	0.347	< 0.001*
				Number of nearby riverine wetlands	0.028	0.007	0.001*
				Total nearby wetland area (km^2)	−0.047	0.021	0.038
Functional dispersion	LM	0.021	0.25	Intercept	4.729	0.208	< 0.001*
				Number of nearby riverine wetlands	−0.001	0.0002	0.011*
				Total nearby wetland area (km^2)	−0.002	0.001	0.071

* indicates statistical significance ($p < 0.05$).

which may imply facultative or temporary use of these wetlands by organisms that can move to permanent water bodies when drying occurs, enabled by the comparatively dense landscape–wetland mosaic in North Dakota, similar to facultative use and dispersal in streams (Chester and Robson 2011). These organisms may find that these ephemeral habitats are sinks where they cannot complete their life cycles, but their presence may still be functionally important for overall community dynamics. Alternatively, some active dispersers may reproduce in smaller, ephemeral habitats and return to permanent waters as adults (Batzer and Resh 1992). North Dakota's cooler climate allows longer hydroperiods for ephemeral wetlands compared to drier and hotter locations like New Mexico, making facultative use a more practical strategy at northern latitudes. Drier climates ultimately result in fewer permanent habitats in the landscape, resulting in reduced capacity for facultative use and dominance by species with opportunistic, rapid life histories. Despite receiving higher annual rainfall than North Dakota, our study sites in coastal Texas are isolated from other wetlands similarly to New Mexico (and thus less favourable as facultative habitat), as they are located on a narrow island with ~5 km of unsuitable saltwater habitat between the barrier island and mainland and mostly ephemeral freshwater habitat on the island itself. Interestingly, the wetlands sampled in North Dakota in 2022 were generally more similar in trait composition to the other, more isolated regions sampled, possibly due to isolation caused by the timing of this fill cycle in early spring, before flying insect populations were abundant (Miller et al. 2008; Bischof et al. 2013).

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Differences in overall trait assemblages were the result of differences in feeding guild trait prevalence, with North Dakota 2021 presenting strategies indicative of more complex food webs and longer food chains, as would be expected with longer hydroperiods (Schriever and Williams 2013; O'Neill and Thorp 2014). Longer hydroperiods and lower evaporation rates also allow for more persistent wetland vegetation in North Dakota relative to other regions (Dodds et al. 2019), providing broader trophic niche availability (Céréghino et al. 2008; Frazier and Schriever 2022). This relationship is likely reflected by the relatively strong association of dissolved oxygen concentration and total vegetation cover and trait assemblages we observed. Higher dissolved oxygen values may be the result of highly abundant live vegetation (Reeder 2011), while our total vegetation metric includes living and senescent vegetation, implying the influence of these two energy pathways influences trophic niche availability and diversity.

Despite seeing relatively similar functional structure, we observed almost no shared taxa between any regions and within North Dakota between years. Most taxa distinct to sample groups are hypothetically able to readily disperse long distances (e.g., Dytiscidae; Schäfer et al. 2006) or are reportedly dispersed by animal vectors or wind (e.g., large branchiopods: Anostraca, Spinicaudata, Laevicaudata, and Notostraca) (Vanschoenwinkel et al. 2008; Beladjal and Mertens 2009; Rogers 2014b; Parekh et al. 2014). We predicted this potential for dispersal would result in greater overlap in distributions and a more similar taxonomic community structure than we observed. For the large branchiopods, distributions could be determined in part by their dispersal vectors themselves. Species or populations of migrating birds consistently using similar routes and pools during migration between years (Tedeschi et al. 2020) with little crossover may have created distinct branchiopod communities based on longitudinal position along the Central Flyway (Muñoz et al. 2013). If this is the case, climate change-mediated shifts in avian migratory routes (Andersson et al. 2022) may alter distributions of large branchiopod species across the central US. Conversely, the distribution patterns we observed may suggest that invertebrate dispersal among wetlands via migrating birds is not as widespread as others suggest (Schwentner et al. 2012; Rogers 2014b; Martín-Vélez et al. 2022), and/or establishment upon arrival at a new habitat is difficult and infrequent. There are potential environmental filters for large branchiopods that we did not measure in this study, principally substrate geochemistry, that have been implicated in structuring assemblages (Rogers 2014a; Frisch et al. 2021) and could further explain the patterns found here. The taxonomic disparity among regions in non-branchiopod taxa can be partially explained by North Dakota, with higher colonisation potential (via longer hydroperiods and higher wetland density within the landscape), habitat complexity due to persistent wetland vegetation, and assumed food web diversity, with different taxonomic groups potentially able to use these habitats compared to other regions (Vanschoenwinkel et al. 2010; Frazier and Schriever 2022). The role of colonisation in determining community composition is especially evident comparing North Dakota community composition between years, with the 2021 filling and sampling taking place during summer when coloniser populations are high and readily seeking new habitat, while the 2022 filling and sampling was in the spring, before coloniser populations had become reestablished following ice thaw and the community was characterised by those with resistant life stages (Miller et al. 2008).

Community composition varies with changes in habitat, climate, and landscape-scale variables, but only when taking into account the combined influence of all variables. We note that the number of wetlands examined in this study may limit habitat condition diversity, potentially obscuring the strength of these variables in structuring communities. To address this, future studies should sample across finer spatial scales and create a continuous study area that avoids large geographic gaps and create finer gradients of habitat conditions, which would better illustrate spatial patterns or dispel their influence on community composition. This framework has been used in some studies at large geographic scales (e.g., Gleason and Rooney 2018; Daniel et al. 2019; Atkinson et al. 2021), but not yet at the scale studied here. Additionally, establishing diel physicochemical profiles may show patterns not detectable by point measurements through analysis of the magnitude of daily variation and/or daily maxima and minima that may act as habitat filters (see Emery-Butcher et al. 2024). Alternatively, dispersal limitation could be directly addressed by employing a common garden study design with large branchiopod resting eggs from disparate locations rewetted under similar ambient conditions.

4.2 | Community Metrics

Climatic differences among regions appear to drastically impact the characteristics of ephemeral wetland communities, beyond the extent portrayed by climate-specific variables in our analyses. As discussed earlier, lower evaporative pressure in northern climates results in different long-term conditions in these habitats, with soil staying saturated longer than in arid climates, ultimately facilitating the persistence of wetland vegetation through dry periods and providing invertebrates more time to prepare for extended dry periods. These conditions also result in higher landscape cover/frequency of various refuge habitats (e.g., lake- and river-associated wetlands), which we found associated with higher taxonomic and trait diversity. The density of ephemeral wetlands in the landscape was not associated with diversity and richness. Similar relationships have been seen in smaller, regional systems (Hall et al. 2004), exemplifying the importance of permanent/semi-permanent refuge habitat as it relates to diversity in ephemeral wetland habitat.

The increase in niche breadth associated with higher refuge habitat availability is also reflected in taxonomic breadth. Regions with greater niche availability see higher rarefied Shannon diversity and taxa richness, a pattern also seen in other habitats (Heino 2000; Schriever et al. 2015). Conversely, Heino et al. (2008) found no relationship between landscape-scale variables and functional diversity, taxonomic richness, or Shannon diversity in a boreal stream network, suggesting the relationship we found may not be generalisable outside of ephemeral wetland habitat.

Our evenness metrics, functional dispersion and Pielou's evenness, were most strongly associated with landscape-scale

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conditions. We found higher refuge habitat availability increased taxonomic evenness but decreased functional evenness (functional dispersion). In refuge-scarce landscapes, few taxa may have the opportunity to effectively colonise a newly wetted habitat, resulting in numerical dominance by a small subset of the taxa that may be present in a community. When refuges are abundant, there is a higher likelihood for competition between coloniser taxa, creating more even relative abundance patterns (Seymour and Altermatt 2014). Successful competition would necessitate similar suites of functional traits for colonising taxa, thus skewing the community trait assemblage toward that suite and driving down functional dispersion through increased redundancy (Townsend et al. 1997). Daniel and Rooney (2022) found functional dispersion of wetland macroinvertebrate communities to be negatively associated with wetland permanence within the Prairie Pothole Region of Canada. Given our refuge-dense sites (in North Dakota) also have longer hydroperiods, our data imply extension of this trend across regions within wetlands of similar hydrology. Further, higher habitat availability increases regional species richness, subsequently increasing potential for taxonomic evenness in wetlands within these habitat matrices (Dehling et al. 2010).

5 | Conclusion

Our data show the structuring potential of ephemeral hydrology reported by others (Schriever et al. 2015; Schriever and Lytle 2016) persists across climate regions, but there is potential for variation in trait assemblages due to external context surrounding a wetland community. Ephemeral wetland communities in different climate zones find themselves within very different landscape wetland mosaics, and these differences create variation in potential life history and trophic strategies for colonising macroinvertebrates based on refuge availability and persistence; the relationships between communities, climate, local, and landscape conditions are closely intertwined. Different landscape conditions shape taxonomic and functional diversity, likely due to spillover and facultative use of temporary wetlands by permanent wetland residents, but no variable group examined here adequately explains taxonomic composition alone. Further, at least in temperate zones, temporal conditions dictate coloniser population state and by extension colonisation species pool diversity, abundance, and characteristics, leading to substantially different communities occupying superficially similar wetlands when wetlands fill at different points in the year. The strong pattern of unique local community composition seen here implies a great importance of local habitat protection for the sake of preserving greater regional biodiversity, despite the potential for many taxa to travel between localities.

Author Contributions

Conceptualization: C.F.F., C.J.P., K.E.M., J.D.H., and J.H.T. Developing methods: C.F.F., J.H.T., J.D.H., W.J.B., J.B., K.E.M., and C.J.P. Conducting the research: C.F.F., A.T.K., J.D.H., J.B., W.J.B., and E.B. Data analysis: C.F.F. Data interpretation: C.F.F. and A.T.K. Preparation of figures and tables: C.F.F. Writing: C.F.F., A.T.K., J.H.T., J.D.H., W.J.B., C.J.P., J.B., K.E.M., and E.B.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Trait database, environmental, and invertebrate abundance data available online at https://doi.org/10.5063/F1KH0KS7.

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