ORIGINAL ARTICLE

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# When rivers run dry: Perennial pools as ecological refuges for freshwater mussels during drought

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## Abstract

1. As the intensity and frequency of drought and drying events are predicted to increase globally with climate warming and increasing human water usage, there is an urgent need to understand what kind of habitats may serve as refuges for organisms to withstand adverse effects. When flows decrease in rivers, disconnected pools may provide critical habitat for survival of aquatic organisms such as freshwater mussels, a highly imperilled group for which drought and dewatering pose a major threat.

2. The objective of this study was to (1) examine whether pools serve as ecological refuges for freshwater mussels (Bivalvia: Unionidae) in drought-stricken streams by surveying mussel distribution in an intermittent section (i.e., a section that regularly goes dry) of the San Saba River, Texas, and (2) examine the habitat characteristics that influence whether a pool functions as a refuge.

3. We found that pool dimensions, thermal conditions, past dryness (number of years a pool was dry between 2004 and 2020), underlying geology, and aquatic and riparian vegetation influence the abundance and species richness of freshwater mussels in pools that may serve as important refuges for mussels to avoid desiccation and lethal high temperatures. Despite this, abundances and richness of mussels were low at all sites.

4. Our results suggest that pools that retain water during drought conditions (i.e., perennial pools) may serve as ecological refuges for globally imperilled organisms such as freshwater mussels on shorter timescales (e.g., days to years). Protection and prioritisation of maintaining suitable conditions in refuge pools may help mussels persist as drought and drying issues become more pervasive in aquatic ecosystems. However, if there is a limited number of isolated pools that only allow the survival of a small number of mussels, then these pools cannot prevent overall declines of mussels in drying rivers. Better management of surface water and groundwater in anthropogenically impacted systems could ensure the flowing conditions that are needed to protect mussels in the face of climate change.

**KEYWORDS**
dewatering, flow intermittency, habitat, thermal refuge, unionid

# 1 | INTRODUCTION

The frequency and intensity of drought and drying events are increasing globally as a result of human-induced climate change and growing agricultural and anthropogenic water demand (EPA, 2016; Lall et al., 2018; Mazdiyasni & AghaKouchak, 2015). This poses a major threat to freshwater organisms in rivers where intense droughts result in dry reaches, especially for organisms with lower mobility that depend on sustained flows (Haag & Warren, 2008).

Ecological droughts are episodes of periodic water scarcity that leave ecosystems vulnerable and result in loss of ecosystem services (Crausbay et al., 2017). Drought conditions are especially harmful in areas where flow intermittency is not part of the natural flow regime (Lytle & Poff, 2004). Drought may impact freshwater organisms by altering community composition (Attril et al., 1996), decreasing habitat connectivity and availability (Lennox et al., 2019), affecting recruitment success (Morrongiello et al., 2011), increasing disease transmission (Chiaramonte et al., 2016), and leading to local extirpation and even extinction of imperilled species (Vander Vorste et al., 2020). Many species are not well-adapted to the harsh environmental conditions such as high water temperatures and low dissolved oxygen that arise during drought or drying, and patches that remain wetted can be isolated. The shrinking water body size as a consequence of decreasing water levels creates not only harsh abiotic, but also biotic conditions with high competitive and predatory pressure (Humphries & Baldwin, 2003; Magoulick & Kobza, 2003).

Ecological refuges and evolutionary refugia in rivers and streams may buffer drying conditions and mitigate drought-related mortality and loss of ecosystem function (e.g., Magoulick & Kobza, 2003; Sedell et al., 1990). Ecological refuges are habitats that convey protection from or resistance to disturbances on shorter timescales (e.g., days, months or years; Sedell et al., 1990), resulting in higher survivorship for organisms that use them (Davis et al., 2013; Lancaster & Belyea, 1997). By contrast, evolutionary refugia contribute to organism persistence on longer timescales (e.g., millennia; Davis et al., 2013). Ecological refuges tend to occur in surface-water-dominated streams, whereas evolutionary refugia are most often associated with groundwater-dominated systems (Davis et al., 2013). Examples of potential ecological refuges include woody debris or algal mats that may dry more slowly than the rest of the streambed, as well as the hyporheic zone or remnant perennial pools that remain wetted as streams dry, including deep pools with groundwater inputs that maintain cooler temperatures (Arthington et al., 2005; Caldwell et al., 2020; Davis et al., 2013; Stubbington et al., 2017).

Refuges from drought and drying are especially important for imperilled organisms such as freshwater mussels (Bivalvia: Unionidae, hereafter termed mussels), which may have relatively long lifespans (sometimes >40 years) and limited mobility that can prevent them from escaping unfavourable conditions during drought (Haag, 2012; Lopes-Lima et al., 2018; Waller et al., 1999). Drought- and desiccation-tolerance among mussel species is variable, with a few exceptional species such as *Uniomerus tetralasmus* being able to persist during extended emersion and at high temperatures (Haag & Warren, 2008; Holland, 1991). However, most mussel species are unable to withstand desiccation for even relatively short time periods (Fogelman et al., 2023; Galbraith et al., 2012; Mitchell et al., 2018). Severe drought conditions can lead to mass mortality events for mussel populations (e.g., DuBose et al., 2019; Gagnon et al., 2004), as well as community-wide declines (Golladay et al., 2004; Haag & Warren, 2008; Mitchell et al., 2019; Tarter et al., 2022) and shifts towards more tolerant species (Lopez et al., 2022).

Because climate models predict global and local increases in drought and temperatures that may negatively impact already vulnerable mussel populations (e.g., Wootten et al., 2023), characterising potential drought refuges (i.e., areas that allow mussel survival during drought) provides essential information for managers seeking areas to restore or prioritise for mussel conservation in the face of climate change. Hence, the objective of our study was to better understand the role of pools as refuges for freshwater mussels during drought and drying conditions. Specifically, we investigated the presence, richness and abundance of mussels in pools during drought conditions in 2021 and 2022 in an approximately 75 km section of a historically perennial spring-fed river that has regularly become seasonally dry in the past 10 years, in part as a result of anthropogenic water use. We also examined the impact of different characteristics (abiotic and biotic conditions) of pools on mussel presence, richness and abundance. We hypothesised that variables related to the pool's ability to retain water and maintain cooler temperatures during drought would affect their capacity to act as ecological refuge for mussels. We therefore predicted that larger (e.g., deeper, longer or wider), dammed and perennial (i.e., permanently wet) pools with lower water temperatures would support greater species abundances and richness compared to smaller, natural and intermittent pools (i.e., pools that periodically go dry).

## 2 | METHODS

### 2.1 | Study area

The San Saba River is a tributary of the Colorado River that runs through the Edwards Plateau region in central Texas. Land use and land cover in the region are dominated by ranch land, agricultural land and shrubland (TPWD, 2018). Annually, the region receives between 559 and 864 mm of precipitation on average (Griffith et al., 2007), and the flow regime is characterised mostly by low flow periods with occasional (flash) flooding events that are usually short in duration (e.g., days; Austin-Bingamon, 2023; Blum et al., 1994). The San Saba River is spring- and groundwater- fed, but both the surface water and the connected aquifer have been subjected to agricultural pumping, which has contributed to flow intermittency in some sections of the river (Carollo, 2015; RPS Espey, 2013). Before 2000, the San Saba River was not known to go dry (Young et al., 2018). This study focused on an approximately

75 km stretch of the middle San Saba River (Figure 1), which is prone to drying during the summer months and has experienced flow intermittency during at least 5 years in the last decade (RPS Espey, 2013; Young et al., 2018).

## 2.2 | Recent and historical drought conditions in the San Saba River

Texas experienced an unprecedented drought beginning in late 2010 and carrying into 2012 (Nielson-Gammon, 2012). Below-average rainfall and above-average temperatures led to what was categorised as an exceptional drought (≤−2.0 on the Standardised Precipitation index [SPI] and ≤−5.0 on the Palmer Drought Severity Index [PDSI];

Nielson-Gammon, 2012). Between October 2010 and December 2012, the USGS gauge in the middle San Saba River recorded 105 days of zero flow (USGS 08144600), and extensive portions of the middle section dried partially or completely (USDA, 2012). The 2011 drought was categorised as the most severe one-year drought on record for Texas (Nielson-Gammon, 2012).

Since the 2011 drought, the San Saba River has experienced periodic drought conditions ranging from abnormally dry to exceptional drought (U.S. Drought Monitor, 2023; Figure 2), including during 2021 and 2022 when data for this study were collected (www.drought.gov; PDSI of −1.0 to −1.9 in December 2021; U.S. Drought Monitor 2023; Figure 2). By mid-March 2022, portions of the catchment sub-basin began to transition to extreme drought (PDSI −4.0 to −4.9), which persisted in more than 50% of the sub-basin until early
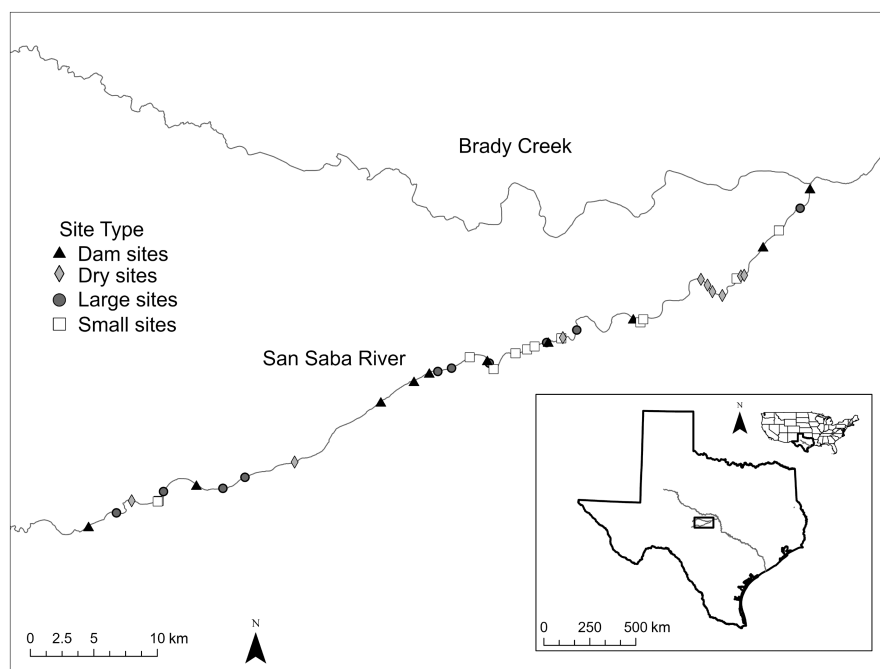


**FIGURE 1** Location and type of 41 pool sites in the intermittent middle section of the San Saba River, TX, USA. Sites were sampled from 2021 to 2022. Large pools had a length greater than the median pool length of 115 m, whereas small pools were shorter than 115 m. Dry sites dried completely more than twice based on aerial imagery from select years between 2004 and 2021. Triangles represent dam sites, diamonds represent dry sites, circles represent large sites and squares represent small sites.
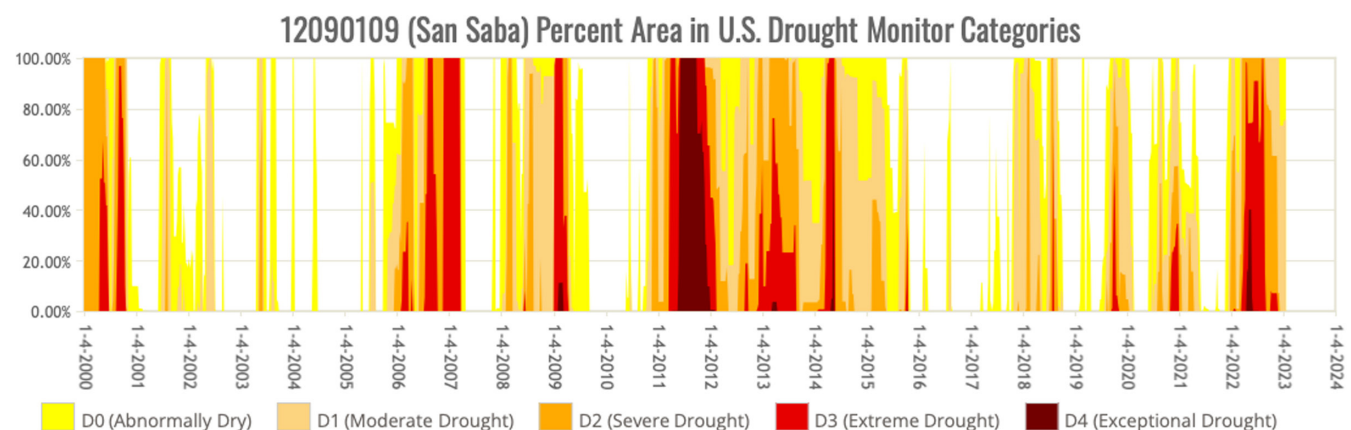


**FIGURE 2** Temporal patterns in drought conditions in the San Saba River sub-basin based on U.S. Drought Monitor categories from January 2000 to January 2023. The U.S. Drought Monitor is jointly produced by the National Drought Mitigation Center (NDMC) at the University of Nebraska-Lincoln, the United States Department of Agriculture, and the National Oceanic and Atmospheric Administration. Figure courtesy of NDMC.

September 2022 (U.S. Drought Monitor, 2023; Figure 2). In April and May 2022, as much as 40% of the San Saba River was experiencing exceptional drought, and dry conditions persisted into 2023 (U.S. Drought Monitor, 2023; Figure 2). From late March 2022 into December 2022, the entire sub-basin was experiencing moderate drought conditions or worse (U.S. Drought Monitor, 2023; Figure 2). A flow gauge operated by the Lower Colorado River Authority within the middle San Saba recorded 21 days with zero flow during the study period, spanning from 30 July to 19 August 2022 (LCRA gauge 1563; hydromet.lcra.org).

## 2.3 | Site selection

We selected sites in the middle San Saba River using a stratified random sampling design. We assumed that pools that retained water during the exceptional drought in 2012 according to National Agriculture Inventory Program (NAIP) imagery were perennial given the exceptionally dry conditions during the 2011–2012 drought (Figure S1A; USDA, 2012). We identified any stretch of water greater than 5 m in length and not clearly exhibiting riffle-like conditions (e.g., flowing water as evidenced by rough or broken texture indicating turbulence) as a pool. We determined the approximate length (m) of each pool in the middle San Saba during 2012 and recorded whether pools were above low-head dams or low water crossings.

In order to capture a range of pool sizes, we randomly selected a subset of 10 pools that were longer than the median pool length of 115 m and 10 pools that were smaller than the median pool length using ARCGIS PRO (version 2.50; ESRI). In addition, we selected 10 perennial sites located above low-head dams or low water crossings. To characterise intermittent pools in the section, we used available NAIP imagery, collected between April and October between 2004 and 2020 to determine how often pools historically went dry (Figure S1C; USDA, 2004, 2005, 2006, 2008, 2010, 2012, 2014, 2016, 2018, 2020). When cloud cover made it more difficult to determine whether a few sites were dry (approximately four pools in 2016), we consulted local landowners on pool conditions and supplemented their recollection with typical drying patterns (i.e., NAIP imagery from other years). The number of times a pool went dry during this time was retained as a "times dry" variable for future analysis. We then selected a subset of 10 intermittent pools that dried more than twice during this time period. We also included one additional pool that was sampled previously in 2021 and had live mussels present. Thus, we sampled a total of 41 sites, including 31 perennial and 10 intermittent sites. Ten of the perennial pools above were dams or low-water crossings and 18 perennial sties were larger (>115 m) pools, whereas none of the intermittent pools were larger or above a man-made structure (Figure 1). To the best of our knowledge, some of our sites in the lower 20 km of the section represent the first reported mussel sampling in the section of the San Saba River just upstream of the confluence of Brady Creek.

## 2.4 | Data collection

We collected abiotic and biotic characteristics that may affect mussel survival during drought conditions for all 41 pools between September 2021 and October 2022 (Table 1). Pools were also evaluated for dryness or partial dryness (i.e., reduction of water level leading to isolated remnant pools) during the summer of 2022. We deployed temperature loggers (HOBO; Onset Corporation, Bourne, MA, USA) at the approximate centre of each pool in summer 2021 or spring 2022 that collected temperature data near the channel bed every 2 h for at least one summer season. We retained data collected at each site between June and September 2022 for analysis. Temperature loggers at five sites either malfunctioned or were not retrievable during summer 2022, so we estimated temperature data using linear regression with water temperatures available for previous seasons at missing sites and the nearest site where data were available (Figures S2–S6) or with an AIC model based on data from all sites (*MuMIn* package; Barton, 2022; Figure S7).

In order to collect mussels, we used timed searches, which have been shown to be effective in areas where few mussels occur, because of the low densities of mussels that can be found in the study section (Sanchez & Schwalb, 2021). To account for variation in pool size (~8 to ~1150 m), we varied search effort according to pool length, and searched each pool for between 2.5 and 10 person hours (p-h). Larger pools were divided into roughly equally sized areas and each area was searched for 2.5 p-h. If we found a new species in the last person hour of searching, we conducted an additional 1 p-h search until no new species were discovered. We used tactile and visual search methods to search for mussels in all pools, and we sampled four pools using SCUBA gear as a consequence of depths >2 m. We collected all live specimens, identified them to species and measured each individual (lengthwise, from anterior end to posterior end). In addition, 3–12 0.5-m$^2$ quadrats (depending on pool length) were excavated at equal intervals along the width of the river to determine approximate density estimates of *Corbicula* spp. at sites. We used *Corbicula* per m$^2$ (live plus total number of valves divided by two) to quantify density because there was much greater variation in overall (live and dead) *Corbicula* density across sites compared to live density alone. Furthermore, density of both live and dead *Corbicula* spp. has been suggested as representative of live *Corbicula* density at sites in other studies, and high densities of dead valves could represent past mass die-offs that negatively impacted water quality and freshwater mussel survival (Cherry et al., 2005; Ring & Woolnough, 2022).

Because no aerial imagery was available for the summer of 2022 at the time of analysis, we estimated the minimum surface area of all 41 pools by digitising the perimeter of pools during the 2011–2012 drought using NAIP imagery projected using the Universal Transverse Mercator (UTM) Zone 14N coordinate system (USDA, 2012). In the absence of other data, we assumed that surface area during the 2011–2012 drought was similar to the minimum pool surface area, given that it has been characterised as the most severe one-year drought

**TABLE 1** Abiotic and biotic characteristics collected for each sampling site or sub-site in the middle San Saba River, TX, USA, grouped for multiple factor analysis (MFA).

| Group | Type | Variables included | Collection method |
|---|---|---|---|
| Temperature | Quantitative | (1) Maximum temperature<br>(2) Mean temperature<br>(3) Median temperature<br>(4) Number of days >30°C<br>(5) Number of days >35°C<br>(6) Average daily variation in temperature<br>(7) Overall range in temperature | HOBO temperature loggers |
| Pool size | Quantitative | (1) Log($x+1$) surface area<br>(2) Pool length<br>(3) Pool depth<br>(4) Pool width | (1) 2012 NAIP imagery<br>(2) Field measurements<br>(3) Field measurements<br>(4) Field measurements |
| Substrate | Quantitative | (1) % clay<br>(2) % silt<br>(3) % sand<br>(4) % gravel<br>(5) % pebble<br>(6) % cobble<br>(7) % boulder<br>(8) % bedrock<br>(9) % leaf litter | Visual estimates averaged across researchers |
| Invasive species | Quantitative | (1) Overall *Corbicula* spp. density | Quadrat searches |
| Water quality | Quantitative | (1) Conductivity<br>(2) Turbidity | (1) YSI 556 MPS<br>(2) HACH portable turbidimeter |
| Riparian and aquatic vegetation | Quantitative | (1) % canopy coverage<br>(2) % aquatic vegetation coverage | Visual estimates averaged across researchers |
| Times dry | Qualitative | (1) Number of years a pool was dry 2004–2022 | NAIP imagery |
| Thermal difference | Qualitative | (1) >2°C vertical temperature difference | Thermal time series |
| Geology | Qualitative | (1) Underlying geology | Horton (2017); GIS analysis |
| Vegetation | Qualitative | (1) Vegetation presence<br>(2) Vegetation type (emergent/submergent) | Field observations |

on record for Texas. Because pool surface area varied widely across sites, we used log($x+1$) surface area for analyses following Bogan et al. (2019).

In addition to data collected during site visits, we evaluated surficial geology for each pool using data from Horton (2017). The primary underlying geology at 18 sites throughout the section was limestone and dolostone (Horton, 2017; Figure 3a; Table S1). Six sites were primarily dolostone, five sites were primarily sandstone and mudstone, four sites were fine and coarse detrital alluvium, and fewer than three sites each were sand, paragneiss, sand and sandstone, limestone-sand-mudstone, or limestone (Horton, 2017; Figure 3a; Table S1).

In order to better understand the thermal characteristics in our study pools, we collected thermal time series based on methods from Vaccaro and Maloy (2006). After a minimum 10–15 min equilibration period at the furthest upstream part of pools, three researchers in kayaks (positioned in the centre and on either edge of the stream) towed two HOBO temperature loggers, one at the surface of the water, and one near the streambed, downstream until the end of the pool was reached. Temperature loggers collected data at 1 s intervals, and GPS coordinates along the length of the pool were measured using a Forerunner 645 (Garmin International). We constructed thermal time series using the temperature data obtained and assessed differences in surface and bottom temperature for their potential as cold patches, possibly as a result of groundwater discharges. We considered sites that had an average temperature difference greater than 2°C to have cold patches that thermally buffered external conditions (Sullivan et al., 2021). We collected data once in February and once between July and October 2022, except at a subset of sites that dried during summer 2022, where no data were collected. Data collection occurred on cloudless days whenever possible to avoid cloud interference with solar radiation that could potentially influence water temperatures.

## 2.5 | Data analysis

We conducted all analyses in R software (version 4.2.2; R Core Team, 2022). Data did not meet all the assumptions of parametric tests, so we assessed differences in catch per unit effort (CPUE; number of mussels per p-h) and species per unit effort (SPUE; species per p-h) of freshwater mussels in natural versus dammed pools and intermittent versus perennial pools using randomisation tests. A randomisation test is a nonparametric, distribution-free alternative
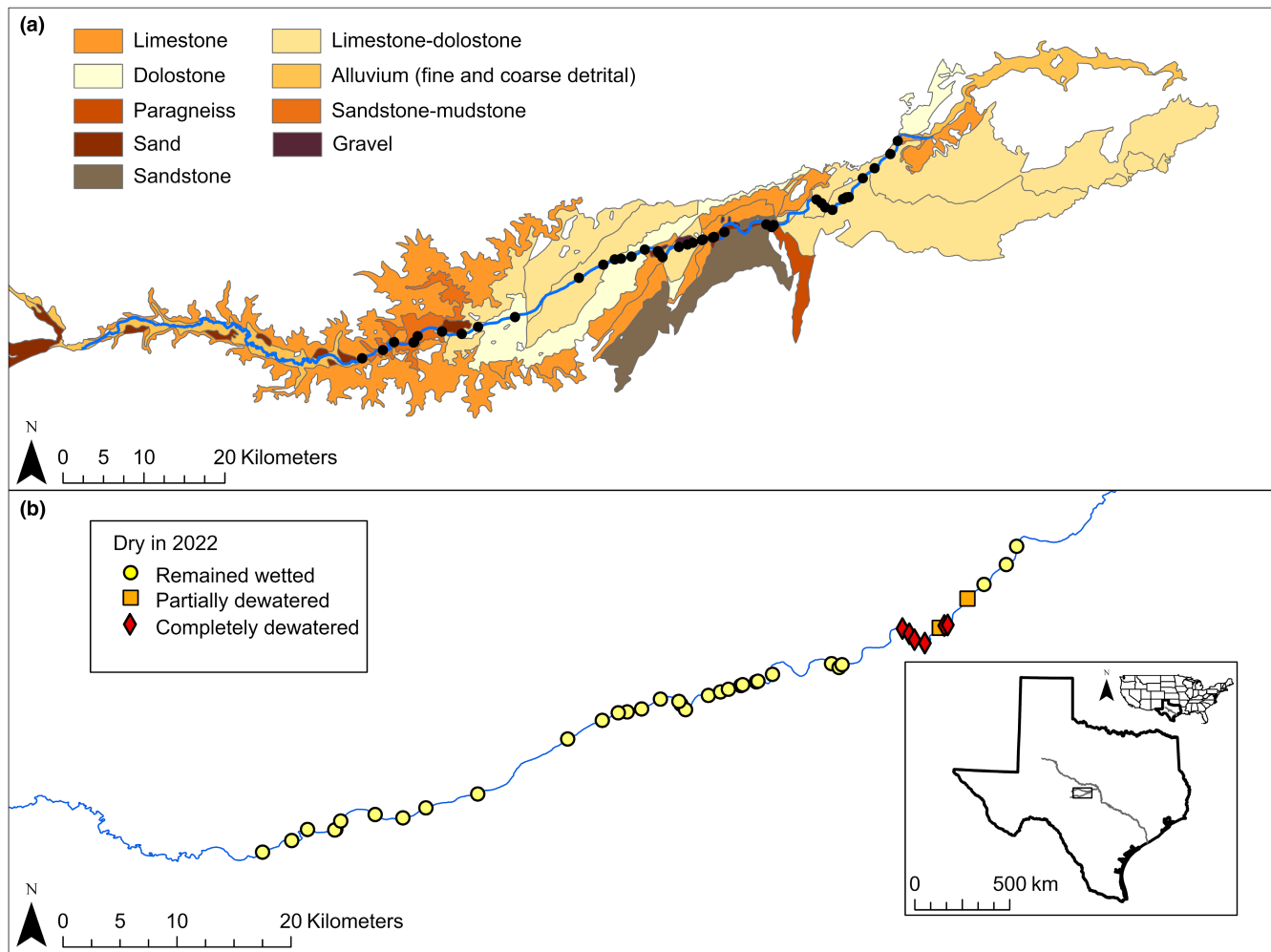
**FIGURE 3** Characteristics of pools in an intermittent reach of the San Saba River, including (a) underlying geology and (b) whether pools remained wetted, dried partially or dried completely in summer 2022. Circles represent sites that sustained water in 2022, squares represent sites that were partially dewatered and diamonds represent sites that were completely dewatered.

to analysis of variance (ANOVA) that assesses the statistical significance of an *F* statistic (from ANOVA) by repeatedly randomly resampling data without replacement for *n* permutations to determine the probability that an observed difference is not the result of random chance (Hooton, 1991). We conducted randomisation with 10,000 permutations to obtain a *p*-value to assess the null hypotheses that there were no differences in CPUE or SPUE between different pool types. To get an initial understanding of the environmental and biotic relationships observed in pools, we also conducted Spearman correlations of pool size with pool temperature and CPUE or SPUE.

In order to understand the variables driving variation at sites (Table 1) and to reduce the dimensionality of the dataset, we conducted multiple factor analysis (MFA) using the *FactoMineR* package in R Studio (Lê et al., 2008). MFA functions in a similar way to principal component analysis (PCA) and multiple correspondence analysis (MCA) but allows the use of both quantitative and qualitative variables that are grouped (Table 1; Escofier & Pagès, 1994). MFA allowed us to reduce the number of variables we used to explain

variation in CPUE and SPUE of mussels across pools to avoid issues of multi-collinearity. Missing values (for conductivity at sites that dried and turbidity data for one site) were estimated before analysis using a regularised iterative PCA algorithm in the *missMDA* package in R (Josse & Husson, 2013, 2016).

We grouped variables into 10 groups and standardised quantitative variables (based on their unit variance; Table 1). We visualised and interpreted results of the MFA using the *factoextra* package in R STUDIO (Kassambara & Mundt, 2020). We determined whether the contribution of groups to a given dimension was greater than the average contribution if all components contributed uniformly to that dimension (Kassambara, 2017). Next, we used linear regression to examine how the environmental conditions captured by MFA dimensions influenced abundance and species richness of mussels in pools. To identify informative variables based on the MFA results, we used a broken stick model and performed bootstrap selection with the *FWDselect* package in R (Frontier, 1976; Jackson, 1993; Sestelo et al., 2015, 2016).

**TABLE 2** Species, number of individuals found, relative percent abundance, and number of sites present for freshwater mussels surveyed from 2021 to 2022 in 41 pools in the middle San Saba River, TX, USA.

| Species | n | Percent of total (%) | Number of sites |
|---|---|---|---|
| *Amblema plicata* | 2 | 1.03 | 2 |
| *Pustulosa petrina* | 4 | 2.05 | 3 |
| *Pustulosa pustulosa* | 1 | 0.51 | 1 |
| *Lampsilis bracteata* | 90 | 46.15 | 11 |
| *Potamilus fragilis* | 37 | 18.97 | 9 |
| *Potamilus purpuratus* | 28 | 14.36 | 4 |
| *Quadrula quadrula* | 3 | 1.54 | 3 |
| *Tritogonia verrucosa* | 4 | 2.05 | 4 |
| *Utterbackia imbecillis* | 26 | 13.33 | 8 |

*Note*: A total of 195 mussels were collected at 21 of the 41 surveyed sites.

## 3 | RESULTS

### 3.1 | Survey results

We collected a total of 195 live mussels of nine species during surveys, and we found live mussels at 21 sites (Table 2). Catch per unit effort ranged from 0 to 8 mussels/p-h and on average, CPUE was 0.8 mussels/p-h (Figure 4a). Species per unit effort ranged from 0 to 0.8 species/p-h, with an average of 0.2 species/p-h (Figure 4b). *Lampsilis bracteata*, a threatened species proposed for listing as federally endangered, was the most abundant and widespread species, contributing more than 46% of mussels found, followed by two lentic species *Potamilus fragilis* and *P. purpuratus* (Table 2). We found a few individuals of *Pustulosa petrina* (Neemuchwala et al., 2023, formerly named *Cyclonaias petrina*), another species proposed for endangered species listing, at three sites throughout the reach (USFWS, 2021). No mussels were found at sites that dried more than two times
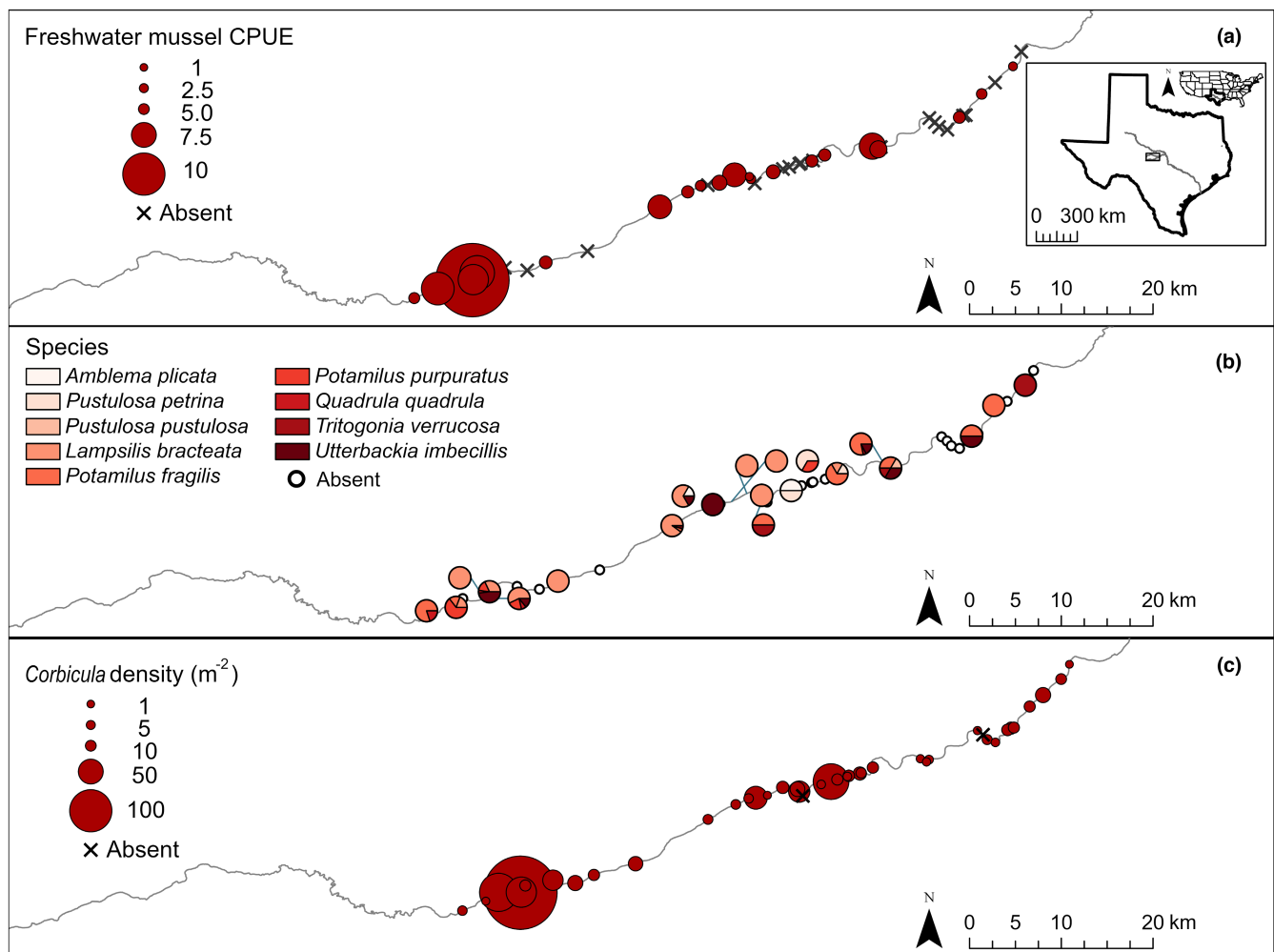


**FIGURE 4** (a) Abundance (catch per unit effort) and (b) species richness of freshwater mussels and (c) density of invasive *Corbicula* spp. at 41 sites in the intermittent middle section of the San Saba River, TX, USA during surveys in 2021 and 2022.

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between 2004 and 2020, but we found very low abundances of mussels at sites that dried partially in summer 2022. *Corbicula* spp. densities ranged from 0 to 189 individuals/m², with an average of 20.8 individuals/m² (Figure 4c).

## 3.2 | Drought conditions

All but one of the pools that were classified as perennial based on 2012 imagery were wetted or partly wetted according to NAIP aerial imagery from 2004 to 2020. One site appeared to dry completely in 2014 but remained at least partially wetted in all other years. Extensive drying was observed at some other sites in 2005–2006 and 2016, but isolated pools remained in portions of each site. In August 2022, we observed six study pools that dried completely, and two pools that experienced extensive drying resulting in isolated pools, one of which was a dam site (Figures 3b and 5). All of these pools occurred in a stretch of the river over 10km long that ceased flowing completely for a portion of the summer (Figure 5a,b). The exact dates that flow ceased and returned in this reach are unknown, but local residents indicated that flows ceased for several weeks during late July and August 2022 (Los Valles Ranch, personal communication). To the best of our knowledge, all other sites remained wetted throughout the study period.

Between June and September 2022, temperature loggers recorded maximum water temperatures between 29.5°C and 45.2°C at sites that retained water, and as high as 60.9°C at dry sites (Figure 6; Table S2). Nineteen sites experienced temperatures greater than 35°C, with a range of 21–83days above 35°C at dry sites and 0–72days above 35°C at sites that remained wetted (Table S2). Six drying sites and three wetted sites experienced temperatures above 40°C, although it should be noted that two of the wetted sites were estimated based on temperatures at nearby sites and were not directly observed reaching this temperature. There were one to four days above 40°C at wetted sites and 17–70days above 40°C at dry sites.

## 3.3 | Environmental data

Temperatures near the riverbed ranged from 3.4°C colder to 6.6°C warmer than surface temperatures in the winter months and 2.1°C warmer to 8.9°C cooler than surface temperatures in the summer, with an average difference of 0.6°C warmer than the surface in the winter and 2.0°C cooler in the summer across all sites. Of the 41 sampled sites, 13 experienced average temperature differences greater than 2.0°C, our defined threshold for thermal buffering. Across sites, the average temperature difference at the surface versus the riverbed was positively related to pool length, width, depth and log-transformed surface area, whereas maximum daily temperature and average daily variation in temperature were inversely related to all four aspects of pool size (Table S3). Perennial pools had significantly ($p < 0.001$) lower mean ($28.7 \pm 0.2$°C) and maximum temperatures ($34.3 \pm 0.7$°C) than intermittent pools ($30.3 \pm 0.2$°C and $48.8 \pm 3.2$°C, respectively). Likewise, maximum temperatures were lower in natural ($33.8 \pm 1.1$°C) versus dammed ($39.1 \pm 1.7$°C) pools, but the difference was not statically significant ($p = 0.08$), and there was no significant difference in mean temperatures ($p = 0.49$).

## 3.4 | Mussel abundance and richness in relation to pool characteristics

In accordance with our prediction, we found no mussels in pools categorised as intermittent, although we found a single mussel in a pool
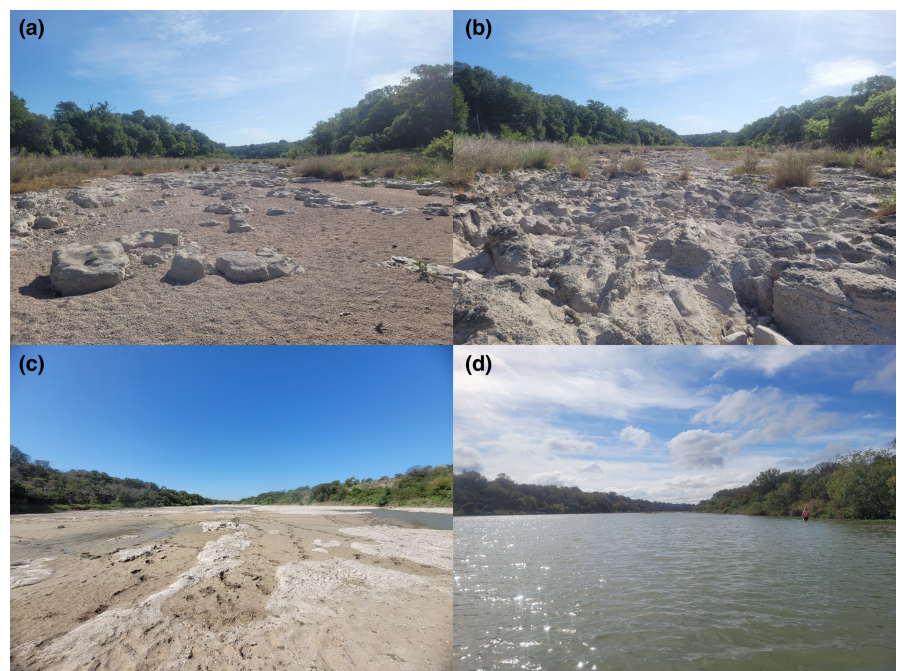


**FIGURE 5** Examples of (a) and (b) dry riverbed observed in the middle section of the San Saba River, TX, USA in August 2022, (c) a site that was reduced to three isolated pools in August 2022, and (d) the same site after flow returned in November 2022. Extensive drying was observed in a >10-km reach in the lower section of the middle San Saba River in August 2022. Picture credits: Kiara Cushway and Tara Lanzer.
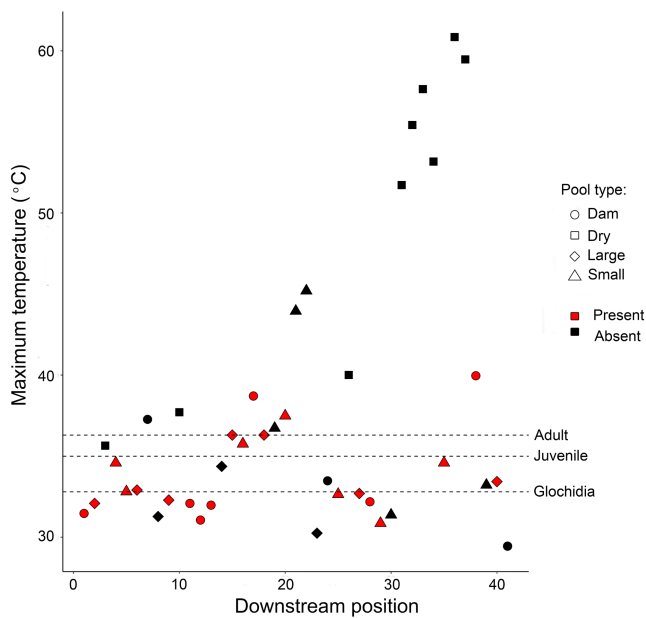
**FIGURE 6** Maximum temperatures at different pool types in the middle San Saba River, TX during summer 2022. Red shapes indicate mussel presence and black shapes indicate mussel absence at sites. Dotted lines represent the average acute median lethal tolerance of mussel species with known thermal tolerances in North America during the glochidial, juvenile and adult life stages (Fogelman et al., 2023). Downstream position references the order of pool sites in the downstream direction. Circles represent dam sites, squares represent dry sites, diamonds represent large sites and triangles represent small sites.



**FIGURE 7** Dimensions one and two of multiple factor analysis (MFA) run for 10 groups of variables explaining variation in environmental characteristics in 41 pools in an intermittent section of the San Saba River, TX, USA, based on data collected in 2021 and 2022. A group's position in space reflects its correlation with a given dimension. Contribution to dimension one increases from left to right in the plot, and contribution to dimension two increases from bottom to top.

initially categorised as perennial, but which dried once in 2014 according to aerial imagery (USDA, 2014). By contrast, perennial pools had an average CPUE of $1.0 \pm 0.3$ mussels/ p-h and an average SPUE of $0.2 \pm 0.1$ species/ p-h. Catch per unit effort and SPUE were significantly positively correlated with aspects of pool size such as length, width, depth and log($x + 1$) surface area, with the strongest correlation between CPUE and width ($r = 0.57$, $p < 0.001$; Figures S8 and S9; Table S4). Average CPUE and SPUE was similar between natural and dammed pools and no significant differences were found based on randomisation tests (Table S5). Mussel CPUE tended to be highest when the underlying geology consisted primarily of sandstone and mudstone, or sandstone, mudstone, and limestone, and lowest at sites that were primarily limestone, or limestone and dolostone (Table S1). Species per unit effort tended to be highest when the underlying geology consisted mainly of paragneiss or sandstone and mudstone (Table S1).

By conducting multiple factor analysis, we were able to group the variables driving variation across pool sites into dimensions and determine what variables contributed the most to those dimensions. Based on the broken stick model, we retained 12 MFA dimensions that explained 83.6% of the total variation in site characteristics, with the first and second dimensions explaining 18.1% and 10.1% respectively (Table S6; Figure 7). Dimension one was most related to pool size (21.5% contribution to the first dimension), temperature (19.3%), past dryness (12.3%), aquatic and riparian vegetation
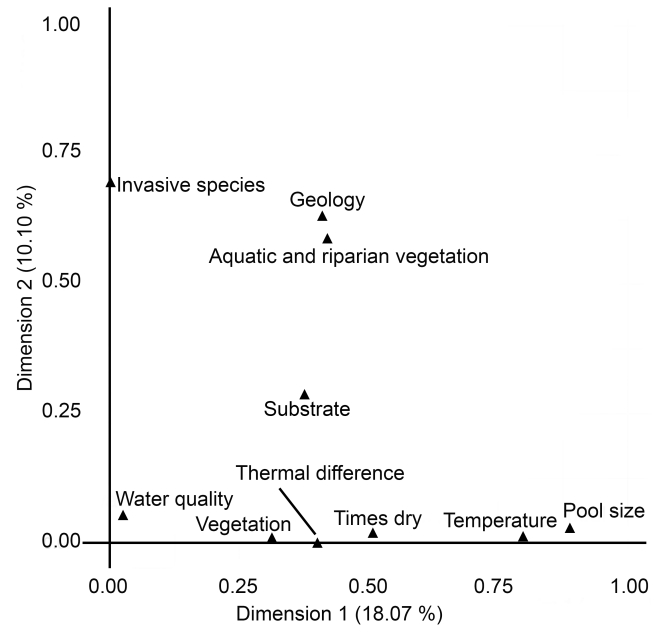
(10.1%), and geology (10%; Table S6; Figure 7). Dimension two was most related to invasive species, geology, aquatic and riparian vegetation, and substrate (Table S6; Figure 7). Much of the variation in other MFA dimensions was explained by differences in geology across sites (Table S6). Bootstrap variable selection indicated that one variable was sufficient for explaining variation in log-transformed CPUE ($q = 1$, $T = 5.84$, $p = 0.26$, deviance $= 2.13$) and log-transformed SPUE ($q = 1$, $T = 1.13$, $p = 0.71$, deviance $= 0.22$), which resulted in regression models that used MFA dimension one as the sole predictor for both regressions. MFA dimension one was able to explain approximately 26% of the variation in log-transformed CPUE (multiple $R^2 = 0.26$, $F_{1,39} = 13.4$, $RSE_{39} = 0.47$, $p < 0.001$; Table S7). MFA dimension one was able to explain approximately 24% of the variation in log-transformed SPUE (multiple $R^2 = 0.24$, $F_{1,39} = 12.5$, $RSE_{39} = 0.16$, $p < 0.01$; Table S7).

## 4 | DISCUSSION

The ability of pools to retain water during drought affected their capacity to act as refuges, as we only found mussels at sites categorised as perennial. Hence, perennial pools were important refuge habitats in the intermittent segment of the San Saba River. Across perennial pools, habitat gradients such as water temperature, aspects of pool size (e.g., depth, width, surface area), geology, and amount of aquatic

and riparian vegetation influenced mussel abundance and species richness in refuge pools.

Studies of other organisms have emphasised the importance of pools as refuges (Bogan et al., 2019; Davis et al., 2013; Magoulick & Kobza, 2003), but perennial pools may be especially important for freshwater mussels because of their relatively sedentary lifestyle, long lifespan and limited ability to escape drying conditions (Gough et al., 2012; Haag, 2012; Waller et al., 1999). Pre- and post-drought comparisons of mussel populations in the San Saba River after the exceptional drought in 2011 indicated that drought conditions led to significant declines in CPUE and species richness (Mitchell et al., 2019). Another study in the San Saba River found that riffle specialist species were mostly absent in intermittent reaches (Randklev et al., 2018). In addition, surveys conducted in the middle section of the river in 2018 found few live mussels in riffles, with most individuals restricted to deeper pools or runs (Mitchell, 2020).

Several factors influencing temperature are likely to serve as important components of a pool's ability to provide ecological refuge. As predicted, aspects of pool size such as length, depth, width and surface area were all positively correlated with mussel abundance and richness, and pool size contributed the most to the MFA dimension selected as the best predictor of mussel abundance and richness. Water temperature near the streambed was the second most important variable in the MFA analysis. Water temperature can be associated with pool size but also may be controlled by other factors such as channel characteristics or hyporheic flow and groundwater discharges, the latter two of which have been linked to summer thermal regime and habitat suitability for mussels in other rivers of the United States (Briggs et al., 2013; Klos et al., 2015). Thermal refuges, provided by groundwater input, serve as important habitats that are buffered from extreme variations in temperature, which may be harmful for ectothermic organisms such as mussels (Sullivan et al., 2021). High temperatures are harmful to mussels because they increase metabolic demands while decreasing the resources required for metabolism (e.g., oxygen), impacting the amount energy available for survival and reproduction (Ganser et al., 2015; Vaughn et al., 2015). Increased canopy coverage and aquatic and riparian vegetation, another important group contributing to MFA dimension one, can also help buffer the effects of solar radiation on water temperatures (Bogan et al., 2019; Vaughn & Julian, 2013) and contribute to the effectiveness of the thermal refuge.

Although the thermal tolerances of many mussel species remain unknown, average acute median lethal temperatures for mussels at different life stages tend to fall between 32.7 and 36.3°C (Fogelman et al., 2023). More than half the pools in the middle San Saba where mussels were present exceeded at least one of these median lethal temperatures during summer 2022, indicating that mussels already may be living at or above their thermal tolerances. Because mussels are ectothermic, high water temperatures can alter metabolic rates and lead to decreases in survival, growth and reproductive success, which can have individual and population-level effects (Ganser et al., 2015; Khan et al., 2020). Hence, areas that provide relief or refuge from high temperatures are important for mussels, especially

given their limited ability to escape unfavourable temperatures via horizontal movement (Haag, 2012; Waller et al., 1999).

Many studies have cited dams (especially larger dams regulating water releases) and low water crossings as negatively impacting mussel species as a result of factors such as increased siltation, alteration of flow regimes, and barriers to host fish and mussel dispersal (Dean et al., 2002; Levine et al., 2003; Watters, 1996). However, a few studies have recognised the potential role of low-head dams and other anthropogenic structures to act as refuges for mussels (Sousa et al., 2021; Sullivan & Littrell, 2020), which is in accordance with our results that mussel abundance and richness did not differ between dammed and natural pools. Low-head dams may help retain water, decreasing the risk of drying, but high temperatures may be detrimental if groundwater input is lacking. More research is needed to better understand the role of dammed pools as refuges and the potential for low-head dams to also serve as ecological traps, where mussels preferentially select habitats that can decrease survival if conditions change (Sousa et al., 2019, 2021).

Geology affects the permeability of substrate and the subsequent potential for groundwater–surfacewater interactions, which can influence factors such as baseflow that contribute to sustaining flows (Falke et al., 2011). Geology also appeared to be an important factor for mussel abundance and richness, with intermittent pools and pools that dried being primarily in areas with limestone-dolostone. Likewise, Haag and Warren (2008) found that streams in Alabama and Mississippi flowing primarily through limestone seemed to be disproportionately affected during drought conditions compared to streams with underlying shale or sandstone.

The density of invasive *Corbicula* did not seem to be an important factor in refuge pools in this study, possibly because most sites harboured relatively low densities of *Corbicula*, which may limit the impact of factors such as mass die-off events or interspecific competition. While not important in this study, the potential role of invaders in influencing the suitability of habitat refuges should be considered, as the presence of invasive species, especially in high densities, may contribute to degradation of refuge potential or suppress behavioural adaptations in native mussels (Cherry et al., 2005; Ferreira-Rodríguez, 2019).

Our study did have some limitations that may have influenced the results. Firstly, the identification of perennial pools was based on limited aerial imagery and not continuous measurements of water levels, but pools being wet during the exceptional drought of 2011–2012 seemed to be a good predictor of mussel presence. Secondly, summer 2022 pool temperatures estimated with regression of 2021 data may underestimate actual temperatures observed in pools given the more extreme weather conditions in 2022, but estimates fell within the ranges observed at other sites. Thirdly, we also were unable to definitively identify areas of groundwater discharge throughout the segment using thermal time series data alone, which remain to be studied. Instead, we identified pools that may serve as thermal refuges as a first step in understanding the spatial and temporal dynamics of thermal conditions across pools. Finally, although some of the variables collected during this study provided

important insight into factors controlling mussel abundance and richness in pools, other unmeasured factors such as increased risk of predation during drought and host fish presence also may be important (Gascho Landis et al., 2012; Walters & Ford, 2013).

In our system, pools are likely serving as ecological refuges for mussels, but may not be sufficiently permanent to serve as evolutionary refugia. The presence of mussels in perennial pools suggests that pools are helping mussels persist on short timescales (e.g., days to years), but extremely low abundances suggest that local populations may be remnant survivors of drought-related declines. This is especially concerning given that nearly half of the mussels found during surveys were *L. bracteata*, a Texas endemic that is found only in the Colorado River drainage and is a candidate for endangered species listing (USFWS, 2021). Catch per unit effort in the middle segment of the San Saba during our study (0.8 mussels/ p-h) was much lower than in the upper and lower segments of the river, where CPUEs of 7–20 mussels/ p-h have been noted (Mitchell et al., 2023; Randklev et al., 2018).

Unfortunately, depauperate communities and declines in mussel populations in response to drought and drying are not isolated conditions or events. Across the globe, mass mortality events and population declines are being reported as the consequence of droughts, heatwaves and water abstraction (e.g., Jones, 2007; Kakino et al., 2011; Mouthon & Daufresne, 2010; Paschoal et al., 2020; Sousa et al., 2018). Our case study in the middle San Saba River may portend a grim global trend, where droughts and increasing human water consumption result in declines of already imperilled mussel species (e.g., Mitchell et al., 2019) and only low abundances of mussels are able to survive in isolated perennial pools. Hence, understanding how refuge areas can influence mussel persistence during drought and drying is important for informing management actions and policy decisions such as establishment of environmental flows, water abstraction limits and localised management. Without proper management actions that protect both mussels and their habitats, imperilled areas such as the middle San Saba River may quickly become incapable of supporting freshwater mussel populations.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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