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RESEARCH ARTICLE

Long-term monitoring shows that drought sensitivity and riparian land use change coincide with freshwater mussel declines

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Abstract

1. Freshwater mussels (Bivalvia: Unionoida) are globally imperilled and are the subjects of wide-ranging conservation initiatives. This study combined traditional species-monitoring surveys with a novel functional trait classification scheme and publicly available environmental data to assess potential environmental drivers of declining mussel abundance and species richness.
2. Surveys to document mussel abundance and assemblage composition in south-east Oklahoma, United States were conducted on the Glover, Mountain Fork and upper Little rivers. Present day survey results (2015–2021) were compared with those from previous studies (1993–1999, 2010) to document long-term changes in the species and functional composition of mussel assemblages and concurrent changes in climate and land use.
3. Mussel catch per unit effort declined by 71.5% between historical and present day surveys. Species richness declined by 44.4% over this same period. Using a novel classification of mussel drought sensitivity, it was found that the declines were associated with a disproportionate loss of drought-sensitive taxa (67.0% decline) – those classified as drought-tolerant did not decline in abundance. Mussel declines coincided with the loss of open surface waters (such as streams, ponds and lakes) and riparian wetlands, increased local air temperatures and longer and more intense hydrological drought.
4. These findings indicate that for a complete understanding of the causes and consequences of mussel declines, conservation biologists must not only monitor the species composition and abundance of threatened organisms, but also consider functional traits. The results further underscore the importance of long-term monitoring for long-lived organisms owing to the decadal time scales over which climate and land use change occur.

KEYWORDS

climate change, defaunation, functional trait, mussel survey, long-term monitoring, thermal tolerance, unionid

1 | INTRODUCTION

Fresh waters and freshwater biodiversity are among the world's most imperilled ecosystems (Strayer & Dudgeon, 2010). Among the myriad challenges to freshwater conservation, anthropogenic climate- and land-use change are perhaps the most pressing, because of their effects on hydrology, water temperatures and water quality (Martinuzzi et al., 2014; Reid et al., 2019). Freshwater ecosystems across the world are expected to suffer from more frequent and more intense periods of drought and continued loss of natural land cover such as wetlands and riparian forests that help buffer water quality and temperatures (IPCC, 2014; Martinuzzi et al., 2014). As a result of these interacting stressors, freshwater organisms are expected to decline in abundance and diversity (Spooner et al., 2011; Gill, Fovargue & Neeson, 2020). Predicting which species face the greatest threat from different stressors can guide conservation policy and focus decision-making, but such predictions require detailed knowledge of both the species composition and the functional ecology of threatened biological assemblages (Foden et al., 2013; Walls, 2018).

Freshwater mussels (Bivalvia: Unionoida) are filter-feeding bivalves that occur on every continent except Antarctica. These animals are globally imperilled (Strayer & Dudgeon, 2010; Böhm et al., 2021). For example, of 535 freshwater mussel species recently assessed by the International Union for the Conservation of Nature, 41% were categorized as Near Threatened, Vulnerable, Endangered or Critically Endangered, and insufficient data were available to assess the status of 17% of the species (Ferreira-Rodríguez et al., 2019). In North America, where the highest numbers of species have been documented (Graf & Cummings, 2007), the fauna has declined precipitously and ∼72% of species are considered imperilled (Williams et al., 2017). Although steep mussel declines documented in the twentieth century have been attributed primarily to large-scale hydrological changes from impoundments and channelization (Haag, 2012), more recent declines in some systems have been linked to changes in flow patterns stemming from drought and land use change (Golladay et al., 2004; Daniel & Brown, 2013; Randklev et al., 2018; Oosterhuis, Pardo & Ferreira-Rodríguez, 2021). Drought can create mass mortality events in mussel assemblages by elevating temperatures and reducing the available habitat area for mussels (Sousa et al., 2018; DuBose et al., 2019). Low water levels expose mussels both to desiccation and to increased predation from predators such as racoons and muskrats (Tyrrell et al., 1998; Sousa et al., 2018). Changes to local land use can also reduce mussel habitat if surface water withdrawals lead to a loss of wetted habitat in freshwater ecosystems (Randklev et al., 2018), or subject mussels to extreme high and low flows via the destruction of wetlands that act as hydrological buffers during precipitation events (Wang et al., 2010).

Mussel functional and life history traits make them highly susceptible to environmental changes. They are among the longest lived invertebrates, with lifespans ranging from 4 to >200 yr (Haag & Rypel, 2011). As a consequence of this long lifespan, and the corresponding time it takes individuals to reach sexual maturity, mussel populations are often slow to rebound reproductively (Haag, 2012). Mussels do show behavioural responses to elevated temperatures and low-water conditions, such as horizontal or vertical movement (burrowing) in the substrate (Newton, Zigler & Gray, 2015; Lymbery et al., 2021; Curley et al., 2022), but adults move slowly and thus are vulnerable to stream drying (Schwalb & Pusch, 2007; Allen & Vaughn, 2009). Movement behaviour is known to differ interspecifically but has yet to be investigated in many species. For example, broadly distributed species that can inhabit headwaters have been found to exhibit greater rates of movement than those that are restricted to larger, more stable streams (Daniel & Brown, 2014). Evidence also suggests that more drought-tolerant species burrow to greater depths to provide refuge from increased temperatures, whereas drought-sensitive species tend to display greater horizontal movement, in an effort to track the receding water levels and avoid emersion (Gough, Gascho Landis & Stoeckel, 2012). Even though mussels use these behavioural mechanisms to avoid stressors associated with stream drying, mussels are thermoconformers. Their metabolism is governed by water temperature, thus high water temperatures can lead to physiological stress and death prior to stream drying (Galbraith, Spooner & Vaughn, 2010; Atkinson, Julian & Vaughn, 2014; Ganser, Newton & Haro, 2015). Despite the evidence of varied mussel responses to stream drying, species monitoring protocols – which form the backbone of most conservation initiatives – do not typically account for the functional differences between species such as the thermal and behavioural traits described above. Rather, they focus primarily on taxonomic measurements (Vandewalle et al., 2010).

Monitoring shifts in the functional composition of assemblages may provide additional insights into the drivers of mussel defaunation. Mussel species vary in a wide range of functional traits, including body size and shell morphology, body stoichiometric composition, physiological tolerance and process rates, life history strategies, and fish host needs (Vaughn, 2010; Haag, 2012; Atkinson, van Ee & Pfeiffer, 2020). Body size, physiological temperature tolerance and life history strategy are three primary traits that influence how mussels respond to drought-related stressors. Thus, together, these three traits should be predictive of drought sensitivity in mussels.

Body size is important here because smaller mussels have higher mass-specific metabolic rates (Ismail et al., 2016), and thus are more easily physiologically stressed (Spooner & Vaughn, 2008) and more likely to be preyed upon (Tyrrell et al., 1998; Sousa et al., 2018). Physiological stress results in disruptions and alterations to metabolic pathways such as respiration, protein synthesis and gene expression (Roznere et al., 2017; Ferreira-Rodríguez et al., 2018; Curley et al., 2021), which in turn affect mussel body condition and growth. Thermal sensitivity is a functional trait that integrates a mussel species' behavioural and metabolic responses to increasing temperatures (Galbraith, Blakeslee & Lellis, 2012; Khan et al., 2019; Galbraith et al., 2020). Southern North American mussel species can generally be placed in two guilds based on their physiological tolerance to high water temperatures: thermally sensitive species that suffer decreased body condition and thermally tolerant species that continue to grow (Spooner & Vaughn, 2008). Previous studies have documented declines of thermally sensitive species following prolonged drought (Galbraith, Spooner & Vaughn, 2010; Atkinson, Julian & Vaughn, 2014). Life history strategies are likely to influence mussel recovery from drought losses (Tarter et al., 2022), as evidenced by Haag (2012). Here, mussels are considered to be either opportunistic (short lifespan, early maturity age and high reproductive rates), periodic (intermediate lifespan, maturity age and reproductive rates), or equilibrium strategists (long lifespan, high maturity age and low reproductive rates). Opportunistic species should recover more rapidly from drought losses compared with periodic or equilibrium species. Incorporating these trait classes into analyses should increase the ability of researchers to predict and manage drought sensitivity (Table 1) and help conservation agencies focus resources on vulnerable species.

In North America, mussel diversity is highest in the central and south-eastern portions of the USA (Graf & Cummings, 2007), which is also where significant extirpations of mussels are predicted to occur in the coming decades as a result of climate change, including more frequent and intense droughts (Spooner et al., 2011; Archambault, Cope & Kwak, 2018; Gill, Fovargue & Neeson, 2020). The mussels in this region are the foci of wide-ranging state and federal conservation initiatives owing to their vulnerability (Freshwater Mollusk Conservation Society, 2016; Oklahoma Department of Wildlife Conservation, 2016), and because they provide valuable ecosystem services such as water filtration and consumer-driven nutrient recycling (Vaughn, 2018). As such, long-term monitoring of freshwater mussel beds is necessary to understand temporal trends in mussel abundance and assemblage composition (Sanchez Gonzalez et al., 2021). Repeated sampling of sites over time can reveal declines in mussel abundance or species diversity and inform understanding of the causes and consequences of declines.

In this study, long-term trends in mussel assemblages and concurrent changes to climatic and landscape factors were assessed in three streams in the Ouachita Mountains of the US Interior Highlands biogeographical province. The goal was to assess: (i) how overall mussel abundance, species richness, and assemblage composition had changed over the course of three decades, dating from the present day back to the 1990s; (ii) whether changes in mussel assemblages coincided with changes in land use and local climate in the surrounding catchment; and (iii) how changes in mussel assemblages were related to their drought tolerance traits (Table 1). It was predicted that mussel declines would occur at sites where aquatic land cover (wetlands and open water such as streams, ponds or lakes) decreased, and temperatures and drought frequency increased. This region has experienced multiple periods of prolonged drought in the past few decades (Galbraith, Spooner & Vaughn, 2010; Atkinson, Julian & Vaughn, 2014; Vaughn, Atkinson & Julian, 2015). Thus, it was also predicted that the relative abundance of drought-tolerant species would increase or remain stable in contrast to drought-sensitive species, which were predicted to decline.

2 | METHODS

2.1 | Study rivers

The mussel fauna of the US Interior Highlands has high species richness ($S = 63$) and endemicity (14%; Haag, 2012), and includes streams draining the Ouachita and Ozark Mountains of eastern Oklahoma, Arkansas and south-west Missouri. The small to mid-sized rivers of the Ouachita Mountains in south-east Oklahoma support 16 mussel species that are listed as Species of Greatest Conservation Need by the Oklahoma Department of Wildlife Conservation (2016).

TABLE 1 Functional traits of a subset of mussel species found during historical and present-day surveys and their predicted response to drought. Mussels expected to increase in response to drought are classified as drought tolerant and mussels expected to decrease in response to drought are classified as drought sensitive. Species with an asterisk were found in historical surveys, but not in present-day surveys

Species	Tribe[a]	Adult size[b]	Thermal guild[c]	Life history strategy[d]	Predicted drought response
Amblema plicata	Amblemini	Large	Tolerant	Equilibrium	Tolerant
Actinonaias ligamentina	Lampsilini	Large	Sensitive	Equilibrium	Sensitive
Lampsilis cardium	Lampsilini	Large	Sensitive	Periodic	Sensitive
Lampsilis teres	Lampsilini	Large	Sensitive	Opportunistic	Tolerant
*Leptodea fragilis**	Lampsilini	Medium	Sensitive	Opportunistic	Tolerant
*Obliquaria reflexa**	Lampsilini	Small	Tolerant	Periodic	Tolerant
Potamilus purpuratus	Lampsilini	Large	Tolerant	Opportunistic	Tolerant
Ptychobranchus occidentalis	Lampsilini	Small	Sensitive	Periodic	Sensitive
Fusconaia flava	Pleurobemini	Small to medium	Tolerant	Equilibrium	Tolerant
Cyclonaias pustulosa	Quadrulini	Small to medium	Sensitive	Equilibrium	Sensitive
Tritogonia verrucosa	Quadrulini	Medium to large	Sensitive	Equilibrium	Sensitive

[a] From Williams et al. (2017).
[b] From Vaughn (2012) – small (length <60 mm), medium (60–100 mm), large (>100 mm).
[c] From Spooner & Vaughn (2008) and unpublished data.
[d] From Haag (2012).

The Glover River (catchment area = 828 km^2), the Mountain Fork (catchment area = 2240 km^2) and the Little River (catchment area = 4500 km^2) are part of the Arkansas–Red–White hydrological subregion. The three basins vary in their hydrology based on their size and the presence of impoundments. The Glover River is unimpounded, but Broken Bow Lake is a 57 km^2 reservoir on the Mountain Fork and Pine Creek Lake is a 15 km^2 reservoir on the Little River. The surveys in this study were restricted to the reaches upstream from the impoundments (Figure 1). The region is remote and has a sparse human population (U.S. Census Bureau, 2020). The land cover is primarily forest, although the Mountain Fork catchment has more agricultural and urban land cover than do the Glover River and upper Little River catchments (Atkinson, Julian & Vaughn, 2012). All three rivers feature similar substrates, with bedrock, boulder and cobble substrates in their headwaters, with a transition to cobble and gravel as they flow from the Ouachita Mountains to the West Gulf Coastal Plain (Oklahoma Department of Wildlife Conservation, 2016).

2.2 | Survey methods

Present-day mussel surveys were conducted at 33 sites on the Glover, Mountain Fork (above Broken Bow Lake) and upper Little River (above Pine Creek Lake) in 2019–2021. A subset of these sites was also surveyed historically – in 1993–1999, 2010 and 2015 – allowing an assessment of long-term trends in mussel abundance and assemblage composition (Vaughn & Taylor, 1999; Vaughn, 2003; Spooner & Vaughn, 2007; Atkinson, Julian & Vaughn, 2012; Hopper et al., 2018).

Present-day surveys were conducted between 10 July 2019 and 4 August 2021 (Figure 1). Sites were selected based on a combination of habitat characteristics, visual inspection of the river bottom and banks for shells, or using GPS coordinates, maps, field notes and site sketches from historical surveys. Timed searches were used because this technique is better for locating rare species and gives a more complete quantification of species richness than quadrat methods (Vaughn, Taylor & Eberhard, 1997; Strayer & Smith, 2003). Timed searches were also used in the previous surveys at these sites, which allowed comparisons with historical data. Surveyors canoed to the approximate location of each site and performed a reconnaissance snorkel search to locate the corresponding mussel bed. Once the bed was located, two to four surveyors systematically searched the entire area by snorkel. Searches were conducted in 15 min periods for a minimum of 0.5 person-h or until two successive 15 min periods failed to identify new species that were undetected in the previous ones. Mussels were located visually and by touch, placed in mesh

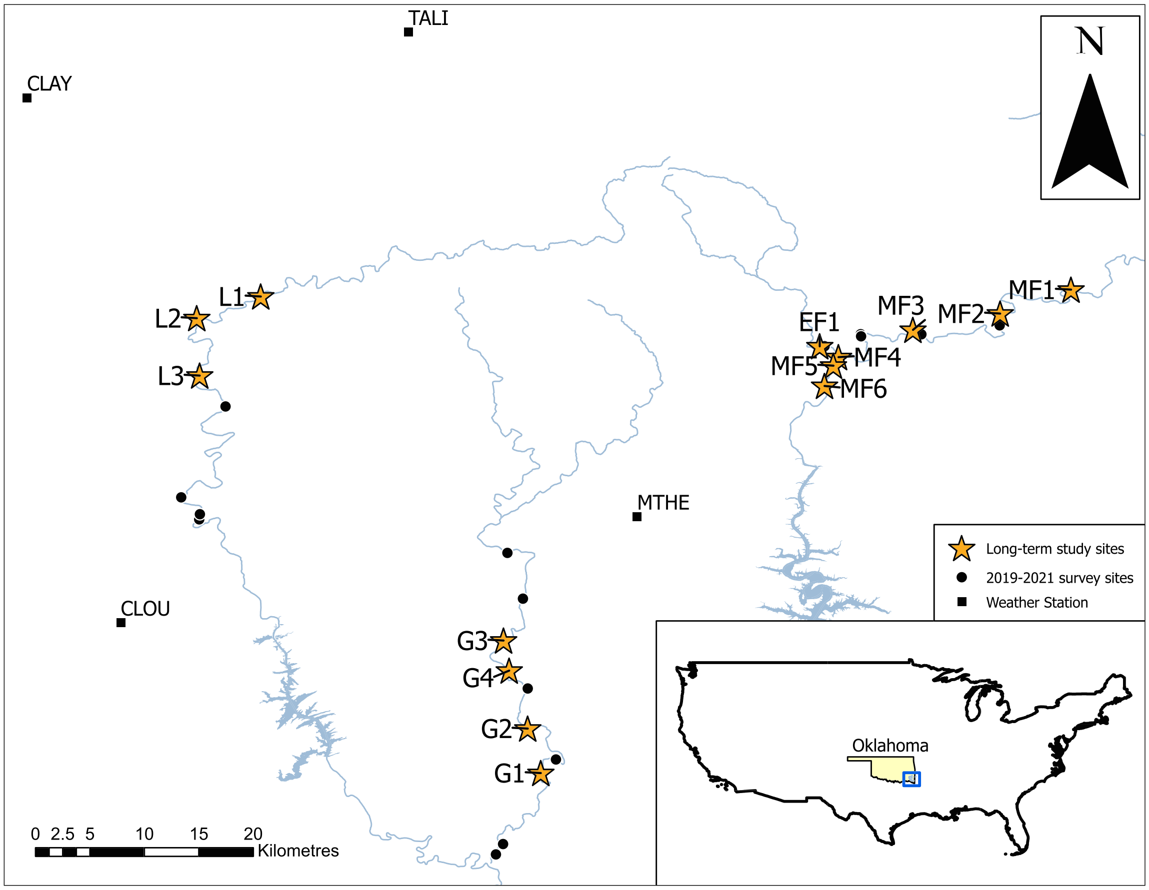

FIGURE 1 Map of the study region showing all survey sites, including those used for the long-term comparison of mussel assemblages, and the Mesonet weather stations used to collect climate data. Inset shows study catchment locations in south-east Oklahoma, USA, with the study region outlined in blue

bags, and subsequently identified to species following the search period. Only native unionid mussel species were counted, and all mussels were returned to the stream alive and placed firmly in the substrate. Although the introduced Asian clam *Corbicula fluminea* occurred at many sites, it was not quantified in some historical surveys and thus was not used in the analyses. These analyses do not consider the response of juvenile mussels because timed searches only effectively quantify adult mussels, and because other sampling methods that can quantify juveniles are destructive to mussel habitat.

2.3 | Mussel abundance, species richness and assemblage composition

To evaluate long-term trends in mussel abundance, data from 14 sites were compared across three survey periods (1993–1999, 2010 and 2015–2021). All of these sites were surveyed in 1993–1999 and four of the sites (MF4, MF5, L1 and L2) were also surveyed in 2010 (Vaughn & Taylor, 1999; Vaughn, 2003; Spooner & Vaughn, 2007; Atkinson, Julian & Vaughn, 2012). One site was also included that was surveyed in 2015 as part of the present day (2015–2021) surveys (Hopper et al., 2018). In total, four sites were on the Glover, seven in the Mountain Fork catchment (six on the mainstem and one on the Eagle Fork Creek tributary) and three on the upper Little River (Figure 1). The total number of mussels collected per person-h at each site during each of the three survey periods was standardized as catch per unit effort (CPUE). Total species richness at these sites in each of these periods was also quantified.

Changes to both species and functional composition between the sampling periods were also examined. For species composition analysis, the relative abundance (percentage of all mussels found at a given site) was quantified for each species at each site during each of the three survey periods. For functional composition analysis, mussels were classified as either drought tolerant or drought sensitive according to Table 1. The relative abundance of mussels in each of these two drought-tolerant categories was quantified at each site during each survey period. Only a subset of species – those for which there was enough information on the three component functional traits (body size, life history strategy and thermal tolerance) to make an accurate classification of their drought tolerance – were included in the functional composition analysis (i.e. species listed in Table 1).

2.4 | Local climate and land use

Changes in climatic and land use variables during the periods between surveys were analysed using publicly available data. The two inter-survey periods were 2000–2009 and 2011–2018, with the caveat that one site surveyed in 2015 (L3) overlaps the second interval. However, because this is only one of 14 sites, it should not unduly bias data interpretation. Summer (July–August) mean daily air temperature and mean maximum daily air temperature were calculated during the inter-survey periods using air temperature data from Oklahoma Mesonet weather stations. Air temperatures were used as a proxy because water temperature data were not available for all sites over the entire study period from 1993 to 2021, and air temperature has been shown to be highly predictive of water temperature in these streams (Vaughn & Julian, 2013). Data were gathered from four stations (Clayton (CLAY), Cloudy (CLOU), Mt Herman (MTHE) and Talihina (TALI); Figure 1), each of which was the geographically closest to at least one of the 14 sites. The frequency of hydrological drought conditions during the inter-survey periods for each river was also determined using data from United States Geological Survey (USGS) stream gauges. The Glover River (gauge 07337900) and the upper Mountain Fork above Broken Bow Lake (gauge 07338750) both have long-term discharge data for the duration of the three survey periods. The upper Little River has no gauge, so the first gauge below Pine Creek Lake (gauge 07338500) was used. Pine Creek has a one-to-one inflow-to-outflow ratio, so this gauge should reflect flow conditions in the upper Little River. The annual number of drought flow days was quantified as the average number of days per year below the 10th percentile of the flow–duration curve (Atkinson, Julian & Vaughn, 2014).

Because changes in land use might affect mussel assemblages by altering stream flows and thus mussel habitat conditions, national land use/land cover data from 2001 and 2019 were compared to assess land use change over the period of the surveys. The accuracy level for the 2001 land use/land cover data set is 79% (Wickham et al., 2013); accuracy assessment has not yet been completed for the 2019 land use/land cover dataset, but the 2016 dataset was accurate at 86.4% (Wickham et al., 2021), and a similar or higher accuracy level for the 2019 dataset is assumed here. For each site, land cover type was extracted from the appropriate land cover raster at three spatial scales: the entire catchment upstream of the site, a 100 m riparian buffer across all upstream tributaries and a 100 m riparian buffer extending only 1 km upstream from the site (Atkinson, Julian & Vaughn, 2012; package *FedData*, Bocinsky, 2021). Percentage land use was calculated at each scale by dividing the number of cells of each type by the number of cells extracted at that scale. To reduce the number of land use variables relative to the level of replication ($n = 14$ sites), the land cover types from the land use/land cover dataset were grouped into three categories (Supporting Information: Table S1): anthropogenic (agriculture and urban development), natural–terrestrial (forests and grassland or scrubland) and natural–aquatic (wetlands and open water such as streams, ponds, or lakes). Although grouping the variables inherently resulted in the loss of some information, the categorization simplified interpretation of the data and reduced the number of predictor variables in the models relative to the number of observations. Once grouped, net change in percentage land use at each scale was calculated.

2.5 | Statistical analyses

All statistical analyses were conducted in R v4.1.2 (R Core Team, 2021). Temporal trends in CPUE, species richness and the relative abundance of drought-sensitive and drought-tolerant species were analysed using linear mixed effects models with survey period as a fixed effect and site as a random intercept (package *lme4*, Bolker, 2022). To compare assemblage composition and reduce variation to two dimensions, non-metric multidimensional scaling was conducted with 100 iterations using a Bray–Curtis distance matrix based on the relative abundances for each species during each survey period (package *vegan*, Oksanen, 2022). Then the species scores from all sites were compared between survey periods using PERMANOVA (package *vegan*, Oksanen, 2022). One site on Eagle Fork Creek (EF1) had to be removed from the ordination because the only unionid collected there in the 2015–2021 period was not identifiable to species level.

Because local climate variables were collected from weather stations and USGS hydrological gauges, and thus not available at the site level, these data could not be used to predict site-level changes in mussel CPUE and species richness. Instead, temporal trends in mean temperatures and hydrological drought days during inter-survey periods were plotted to determine whether the timing of drought events was aligned with the timing of changes in mussel CPUE and species richness. To determine whether land use change was associated with changes in mussel abundance and species richness, Akaike Information Criterion corrected for small sample sizes (AIC_c) was used to compare regression models for predicting site-level changes in CPUE and species richness (e.g., $CPUE_{2015–2021}$ – $CPUE_{1993–1999}$) based on land use changes across all three spatial scales. Models with ΔAIC_c values ≤2 from the best model were considered equal. Linear regression statistics were used to assess the statistical significance and coefficients of determination of the models meeting this criterion.

3 | RESULTS

3.1 | 2015–2019 mussel assemblages

In total, 866 individuals of at least 18 different species were collected across the entire 33-site survey (Table 2). *Amblema plicata* was the most common species, comprising 45.5% of individuals sampled, and occurred in all three catchments. Only three other mussel taxa comprised a significant proportion of the individuals sampled: *Fusconaia flava* (18.5%), *Cyclonaias pustulosa* (9.0%) and *Villosa* spp. (7.9%). All other species comprised <5% of the total assemblage (Table 2). The federally listed *Theliderma cylindrica* was detected in the

TABLE 2 Summary of full survey results for the Glover, Mountain Fork, and upper Little rivers, OK, USA. Values shown are the number of individuals found of each species listed, in each catchment. Surveys were conducted during 2019–2021

	Catchment				
Species	Glover River	Upper Little	Mountain Fork	All sites	Relative abundance (all sites)
Actinonaias ligamentina	24	0	0	24	2.8%
Amblema plicata	240	64	90	394	45.5%
Cyclonaias pustulosa	53	10	15	78	9.0%
Ellipsaria lineolata	2	0	0	2	0.2%
Fusconaia flava	36	107	17	160	18.5%
Lampsilis cardium	11	6	17	34	3.9%
Lampsilis siliquoidea	0	0	8	8	0.9%
Lampsilis teres	1	0	0	1	0.1%
Lasmigona costata	0	3	7	10	1.2%
Obovaria arkansasensis	8	0	3	11	1.3%
Potamilus purpuratus	7	0	0	7	0.8%
Ptychobranchus occidentalis	0	0	5	5	0.6%
Pyganodon grandis	1	0	0	1	0.1%
Quadrula quadrula	2	0	0	2	0.2%
Strophitus undulatus	4	0	14	18	2.1%
Theliderma cylindrica	3	0	0	3	0.3%
Tritogonia verrucosa	17	10	2	29	3.3%
Villosa spp.	3	1	64	68	7.9%
Unidentifiable	6	0	5	11	1.3%
Mean CPUE (range)	32 (0–116)	68 (0–114)	17 (0–84)	42	—
Species richness	15	7	11	18	—
Total live mussels	418	201	247	866	100.0%

Glover River, but not in the upper Little or Mountain Fork rivers. Two species found in historical surveys (*Leptodea fragilis* and *Obliquaria reflexa*) were not found in the present-day studies.

3.2 | Mussel declines are stronger among drought-sensitive species

Across the 14 sites with long-term survey data, total mussel abundance tended to decline over time ($\chi^2 = 18.97$, $P < 0.001$; Figure 2a–c). Average mussel abundance declined slightly at the four sites in both the 1993–1999 and 2010 surveys ($P = 0.076$), and more sharply in the 2015–2021 survey that included all sites ($P < 0.001$). There was a net 71.5% decline in mussel CPUE over the course of the three survey periods. Species richness also declined over time ($\chi^2 = 13.93$, $P < 0.001$; Figure 2d–f). However, species richness showed a different temporal trend, with similar species richness levels detected at the sites in both the 1993–1999 and the 2010 surveys ($P = 0.882$), then a sharp decline in species richness in the 2015–2021 survey ($P = 0.003$). There was a net decline of 44.4% in species richness across the three survey periods. However, the overall species composition of the mussel assemblages across sites did not change strongly over time ($F_{2,29} = 1.59$, $P = 0.100$; Supporting Information: Figure S1).

When changes in relative abundances of only the drought-tolerant and drought-sensitive functional groups were modelled, the relative abundance of drought-sensitive mussels underwent a net decline of 67.0% over time ($\chi^2 = 18.28$, $P < 0.001$; Figure 3a–c), with similar abundances at the four sites in both the 1993–1999 and the 2010 surveys ($P = 0.552$), followed by a stark decline detected in the full 2015–2021 survey ($P = 0.001$). In contrast, drought-tolerant mussels experienced no change in relative abundance over time ($\chi^2 = 0.77$, $P = 0.681$; Figure 3d–f). Of the 11 species classified in Table 1, six were found only in the Glover River, and many were uncommon (Table 2).

3.3 | Changing local climate coincides with mussel declines

Air temperatures and hydrological drought frequency both increased from the first inter-survey period (2000–2009) and the second inter-survey period (2011–2018; Figure 4). There were two major droughts, one during each of the inter-survey periods – in 2005–2006 and 2011–2013 (Supporting Information: Figure S2). The 2011–2013 drought tended to be longer and coincided with higher air temperatures than the 2005–2006 drought. Mean maximum July–August daily air temperatures increased by an average of 0.14°C between the two inter-survey periods, driven by increases at three of the four weather stations (Figure 4a). The mean July–August daily air temperatures at the four weather stations increased by an average of 0.26°C between the two inter-survey periods, driven by increases at all four of the weather stations (Figure 4b). The mean annual number of hydrological drought flow days across the three USGS gauges also increased by 37% between the two inter-survey periods, from 38 to 60 days per year; drought increases were larger in the Little River and Glover River than the Mountain Fork (Figure 4c).

3.4 | Loss of aquatic land cover is associated with mussel declines

All of the models describing mussel declines in response to land use changes included natural aquatic land cover (woody wetlands +

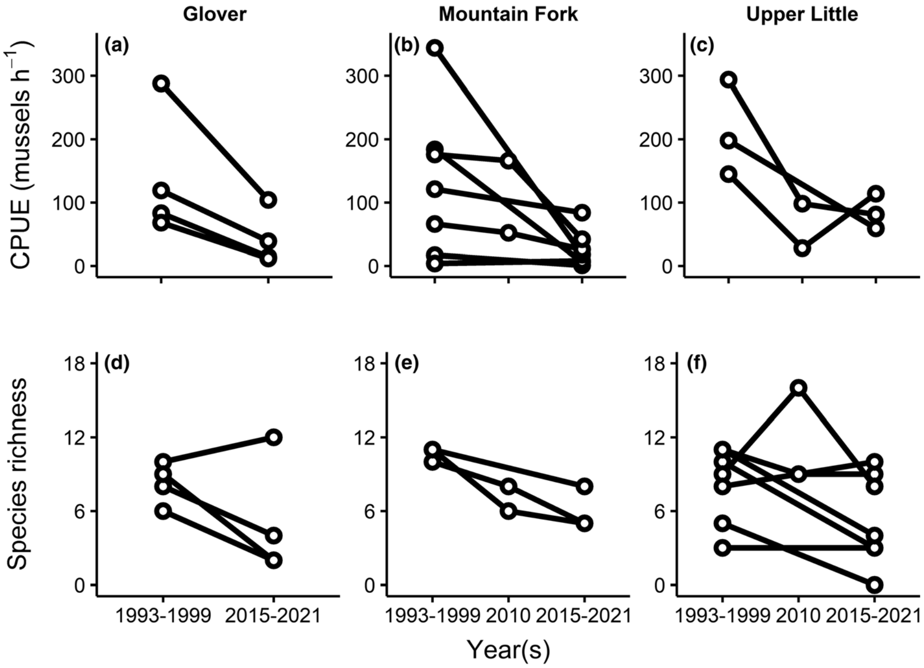

FIGURE 2 Freshwater mussel assemblage data collected from timed search surveys conducted over three decades in south-eastern Oklahoma, USA showing catch per unit effort (CPUE) on (a) the Glover River, (b) the Mountain Fork and (c) the upper Little River, and mussel species richness on (d) the Glover River, (e) the Mountain Fork and (f) the upper Little River. Each line connecting the time points when surveys were conducted represents the trend at an individual site

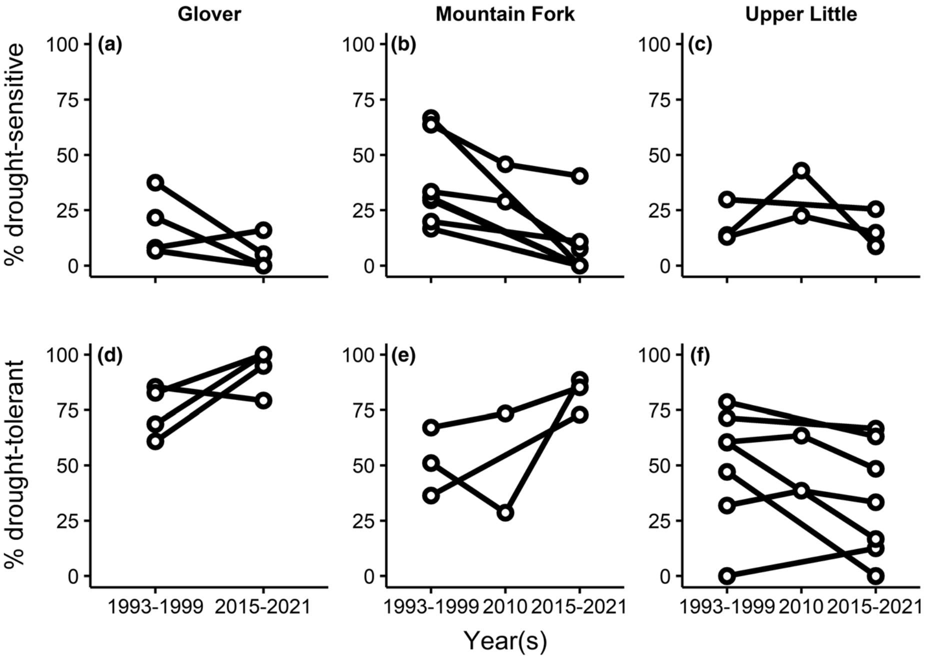

FIGURE 3 Freshwater mussel drought sensitivity data collected from timed search surveys conducted over three decades in south-eastern Oklahoma, USA showing relative abundances of drought-sensitive mussels on (a) the Glover River, (b) the Mountain Fork and (c) the upper Little River, and of drought-tolerant mussels on (d) the Glover River, (e) the Mountain Fork and (f) the upper Little River. Relative abundances shown are percentages of all individuals collected at each site, and mussels without sufficient data for classification by drought sensitivity are not included. Thus, abundances do not sum to 100%. Each line connecting the time points when surveys were conducted represents the trend at an individual site

emergent herbaceous wetlands + open water) at the 1 km riparian buffer scale (Table 3). Models at the larger spatial scales (all upstream tributaries and whole catchment) were not statistically significant and explained little variance in mussel CPUE and species richness over time. Changes to CPUE and species richness were best described by two candidate models each (Table 3). The simplest model for each of these two responses included a positive association between change in natural aquatic land cover and the associated mussel response (CPUE model: $P = 0.031$, adj. $R^2 = 0.28$; species richness model: $P = 0.057$, adj. $R^2 = 0.21$). The second model describing CPUE included positive associations between both change in natural aquatic and change in anthropogenic land cover ($P = 0.048$, adj. $R^2 = 0.32$). The second model describing species richness included positive associations between both change in natural aquatic and change in natural terrestrial land cover ($P = 0.070$, adj. $R^2 = 0.27$). The regression parameters for each of the four models suggested that change in aquatic land cover was positively related to CPUE and species richness (Supporting Information: Tables S2–S5). Thus, these models suggest that decreasing natural aquatic land cover in riparian buffers at the 1 km reach scale were associated with declines in mussel CPUE and species richness.

4 | DISCUSSION

The results of mussel surveys conducted across three decades suggest that declines in abundance and species richness in this region's mussel assemblages are disproportionately associated with the loss of drought-sensitive mussel species. The largest observed declines in both mussel abundance and species richness occurred following a period in which the highest observed air temperatures and the longest observed hydrological drought in the study area coincided. These findings align with research from the region that shows a loss of thermally sensitive species and associated ecosystem functions in previous years (Galbraith, Spooner & Vaughn, 2010; Allen et al., 2013; Atkinson, Julian & Vaughn, 2014). Mussel declines were also associated with a loss of natural aquatic habitat, including both riparian wetlands and open surface waters, over the course of the surveys.

Three functional traits (body size, thermal tolerance and life history strategy) were synthesized into a single functional index of drought sensitivity, which was used to determine changes in the functional composition of mussel assemblages. The loss of drought-sensitive species coincided with elevated air temperatures and increases in hydrological drought frequency and duration. However, the inclusion of life history traits for which the drought sensitivity index could be used was limited to species for which accurate thermal tolerance data could be obtained. Five of seven thermally sensitive species for which these data were available were also classified as drought sensitive, and all four thermally tolerant species were classified as drought tolerant. This raises the question of whether the inclusion of life history traits and body size in our drought classification index improves the ability of conservation biologists to make more accurate predictions of mussel responses to drought over the use of thermal tolerance data alone.

Improving the drought classification index used in this study would start with the inclusion of additional species and survey data with a finer temporal resolution and the addition of other mussel traits such as morphology and movement. Although annual sampling may be too frequent owing to the stress that sampling induces for mussels, sampling on a rotating basis every 2–5 years rather than decadal mussel sampling would allow a more specific drought sensitivity index to be developed beyond the binary 'sensitive vs. tolerant' scheme used here. Sampling juvenile mussels, although

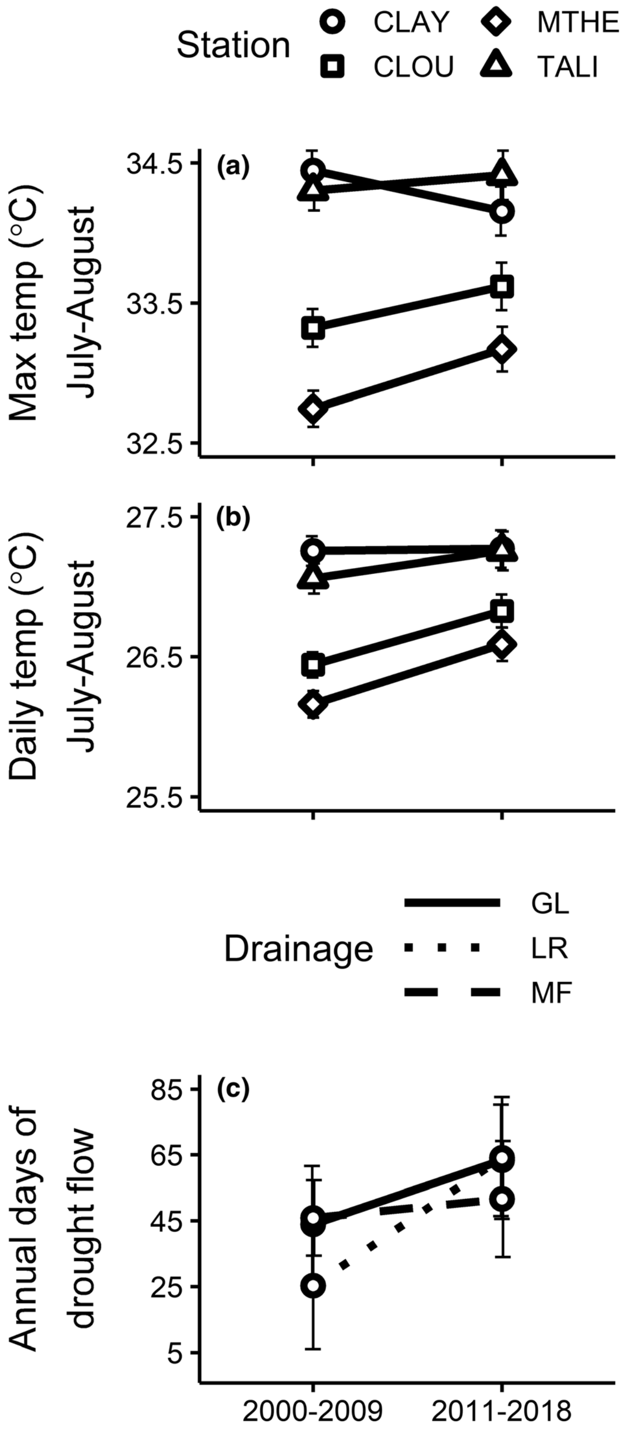

FIGURE 4 Temperature and hydrological drought data for the inter-survey periods. (a) Mean maximum daily air temperatures in July–August increased at three of four weather stations in the study region, and (b) mean daily air temperatures in July–August increased at all four weather stations. (c) The average number of drought flow days per year increased at USGS gauges on the Glover, Mountain Fork and Little rivers

destructive, may also yield additional insights into mussel drought sensitivity, as trends in juvenile abundances over time are indicative of recruitment, and thus the speed at which populations may rebound from drought disturbances (Ćmiel et al., 2020). The functional traits used in this study – thermal sensitivity and body size – were selected as predictors of decreases in mussel abundance because they predict mussel responses to heat stress (Spooner & Vaughn, 2008; Vaughn, Atkinson & Julian, 2015; DuBose et al., 2019) and to desiccation and predation during drought (Tyrrell et al., 1998; Sousa et al., 2018). Life history strategies were selected because they may also dictate how rapidly a mussel population can recover from losses. For example, equilibrium life history strategists are likely to be at the greatest risk of extirpation and extinction owing to the length of time their populations need to recover. Opportunistic or periodic life history strategists should rebound more rapidly because of their faster life cycles and earlier reproductive maturity. However, integrating additional traits into the index could improve its predictive capacity. Traits that could be added to the index are shell morphology and thickness, which affect a mussel's ability to burrow in the sediment to escape low water (Allen & Vaughn, 2009; Levine, Hansen & Gerald, 2014), and traits related to recolonization ability such as regional abundance and fish–host relationships (Vaughn, 2012). We propose that functional traits can be a useful tool in freshwater conservation programmes and species monitoring protocols in regions at increased future risk of drought.

The negative relationship between loss of riparian wetlands and associated open surface waters to mussel abundance and to a lesser extent species richness is probably explained by the loss of the hydrological buffering that wetlands provide, and by the loss of habitat area caused by declines in open surface water area. It is more likely that the loss of aquatic land cover was driven by the loss of riparian wetlands because the resolution of the land use/land cover dataset in the analysis is 30 × 30 m. At this resolution, it would be difficult to detect changes in the wetted area of the stream; however, this possibility cannot be ruled out as the sites in the present study are at relatively shallow upper-catchment locations. Here, minor decreases in flow as a result of increasing drought frequency could result in substantial changes to surface water area by exposing shallow stream beds. Such reductions in the wetted habitat area of freshwater ecosystems, which may be caused by increased evaporative stress or water withdrawals elsewhere in the catchment (Crausbay et al., 2017), will inherently reduce the amount of habitat available to mussels and other aquatic organisms (Randklev et al., 2018). Mussels are also more likely to experience extreme high and low flows without the retention services provided by wetlands and other surface waters (Wang et al., 2010). Extreme flows tend to limit mussel abundances and distributions because at low flows mussels require enough hydraulic force for food and oxygen delivery, whereas at high flows mussels require forces to be low enough that they are not displaced downstream (Lopez & Vaughn, 2021). Alternative explanations for the adverse effect of lost riparian wetlands and surface waters on mussels could include the correlation of wetland loss with decreases in landscape-level nutrient and sediment retention (Wang, Yang & Melesse, 2008; Wang et al., 2010). However, there were no symptoms of eutrophication or sedimentation observed at the study sites, so nutrient and sediment pollution are unlikely culprits for the declines observed in this study.

TABLE 3 Model selection results using Akaike's Information Criterion with adjustment for small sample sizes (AIC_c) to select the best linear models relating land use change (between 2001 and 2019) to mussel community changes in abundance (catch per unit effort, CPUE) and species richness (between surveys in 1993–1999 and 2015–2021)

Response	Scale	Model terms	K	AIC_c	Δ_i	w_i	F	P	Adj. R^2
CPUE	1 km buffer	Natural-aquatic	3	168.337	0.000	0.357	5.99	0.031	0.28
		Anthropogenic + natural-aquatic	4	170.297	1.960	0.134	4.07	0.048	0.32
Species richness	1 km buffer	Natural-aquatic	3	74.829	0.000	0.362	4.45	0.057	0.21
		Natural-terrestrial + natural-aquatic	4	76.509	1.680	0.156	3.43	0.070	0.27

Note: See Methods and Supporting Information: Table S1 for definitions of the land use categories listed as model terms.

The south-eastern USA and the Interior Highlands are expected to experience significant reductions in flow, increases in temperature, more variable precipitation and increased extirpations of aquatic organisms over the coming decades as a result of climate change (Spooner et al., 2011; IPCC, 2014). Flow reductions may be further exacerbated by human land use changes. For example, forestry and timber are dominant economic forces in south-eastern Oklahoma, as are pasture and agriculture, driving the conversion of riparian wetlands into additional space for timber and grazing land. These climate and land use changes may create positive feedback loops of mussel declines that result in long-term losses of mussel biomass and diversity and play out over many years owing to the relatively long lifespans of most mussels (DuBose et al., 2019). However, land use conversion also provides opportunities for cooperation between conservation organizations and other stakeholders. Programmes in the USA and Europe have been established to assist landowners with implementing best management practices on behalf of freshwater mussels, including the planting of riparian buffers and livestock exclusion fences that preserve riparian habitat (Blevins et al., 2019; Bleasdale et al., 2020). In some cases, landowners can even be compensated by the government as an incentive for ecological responsibility (Crausbay et al., 2017; Blevins et al., 2019).

The decadal scales over which both mussel assemblage dynamics and anthropogenic change tend to occur highlight the importance of long-term monitoring of freshwater mussel populations. Here, it has been shown that analysing temporal changes in both the species and functional composition of mussel beds yields further insights into the potential adverse effects of anthropogenic change on mussels. Mussel declines threaten both biodiversity and the roles that mussels play in driving ecosystem functioning and generating ecosystem services (Atkinson, Julian & Vaughn, 2014; Vaughn, 2018; DuBose et al., 2019; Atkinson & Forshay, 2022). Even remote natural catchments are vulnerable to human changes, but repeated sampling at appropriate time scales and functional classifications can provide additional biological insights that may help decision-makers prioritize freshwater mussel conservation.

4.1 | Implications for conservation

The findings in the present study support two broadly applicable conservation recommendations. First, longer-lived species require longer-term monitoring programmes and repeated sampling to understand the causes and consequences of changes in their populations and assemblages (Sanchez Gonzalez et al., 2021). We suggest that conservation agencies should emphasize the importance of long-term monitoring and repeated sampling when evaluating the status of imperilled freshwater mussel species and assemblages, and in planning their protection. Second, the use of functional trait classifications during conservation assessments provides additional information that can help clarify the response of organisms to their environment in a changing world (Vandewalle et al., 2010; Foden et al., 2013; Crabot et al., 2021). Here, we advocate for conservation assessments to include functional classifications in conjunction with the traditional taxonomic classifications that are typically collected. Analysing functional changes in biological assemblages may yield insights into the mechanisms driving assemblage change that remain unclear when focused solely on taxonomic changes.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Allen, D.C., Galbraith, H.S., Vaughn, C.C. & Spooner, D.E. (2013). A tale of two rivers: implications of water management practices for mussel biodiversity outcomes during droughts. *Ambio*, 42(7), 881–891. https://doi.org/10.1007/s13280-013-0420-8

Allen, D.C. & Vaughn, C.C. (2009). Burrowing behavior of freshwater mussels in experimentally manipulated communities. *Journal of the North American Benthological Society*, 28(1), 93–100. https://doi.org/10.1899/07-170.1

Archambault, J.M., Cope, W.G. & Kwak, T.J. (2018). Chasing a changing climate: reproductive and dispersal traits predict how sessile species respond to global warming. *Diversity and Distributions*, 24(7), 880–891. https://doi.org/10.1111/ddi.12740

Atkinson, C.L. & Forshay, K.J. (2022). Community patch dynamics governs direct and indirect nutrient recycling by aggregated animals across spatial scales. *Functional Ecology*, 36(3), 595–606. https://doi.org/10.1111/1365-2435.13982

Atkinson, C.L., Julian, J.P. & Vaughn, C.C. (2012). Scale-dependent longitudinal patterns in mussel communities. *Freshwater Biology*, 57(11), 2272–2284. https://doi.org/10.1111/fwb.12001

Atkinson, C.L., Julian, J.P. & Vaughn, C.C. (2014). Species and function lost: role of drought in structuring stream communities. *Biological Conservation*, 176, 30–38. https://doi.org/10.1016/j.biocon.2014.04.029

Atkinson, C.L., van Ee, B.C. & Pfeiffer, J.M. (2020). Evolutionary history drives aspects of stoichiometric niche variation and functional effects within a guild. *Ecology*, 101(9), 1–12. https://doi.org/10.1002/ecy.3100

Bleasdale, A., Browne, A., Byrne, D., Cronin, P., Dunford, B., Finn, J.A. et al. (2020). The KerryLIFE freshwater pearl mussel conservation project. In: O'Rourke, E. & Finn, J.A. (Eds.) *Farming for nature: The role of results-based payments*. Wexford, Ireland: Teagasc and National Parks and Wildlife Service, pp. 148–183.

Blevins, E., McMullen, L., Jepsen, S., Blackburn, M., Code, A. & Black, S.H. (2019). Mussel-friendly restoration: a guide to the essential steps for protecting freshwater mussels in aquatic and riparian restoration, construction, and land management projects and activities. The Xerces Society for Invertebrate Conservation.

Bocinsky, K.R. (2021). FedData: functions to automate downloading geospatial data available from several federated data sources.

Böhm, M., Dewhurst-Richman, N.I., Seddon, M., Ledger, S.E.H., Albrecht, C., Allen, D. et al. (2021). The conservation status of the world's freshwater molluscs. *Hydrobiologia*, 848(12–13), 3231–3254. https://doi.org/10.1007/s10750-020-04385-w

Bolker, B. (2022). lme4: Linear Mixed-Effects Models using 'Eigen' and S4.

Ćmiel, A.M., Strużyński, A., Wyrębek, M., Lipińska, A.M., Zając, K. & Zając, T. (2020). Response of freshwater mussel recruitment to hydrological changes in a eutrophic floodplain lake. *Science of the Total Environment*, 703, 135467. https://doi.org/10.1016/j.scitotenv.2019.135467

Crabot, J., Mondy, C.P., Usseglio-Polatera, P., Fritz, K.M., Wood, P.J., Greenwood, M.J. et al. (2021). A global perspective on the functional responses of stream communities to flow intermittence. *Ecography*, 44(10), 1511–1523. https://doi.org/10.1111/ecog.05697

Crausbay, S.D., Ramirez, A.R., Carter, S.L., Cross, M.S., Hall, K.R., Bathke, D.J. et al. (2017). Defining ecological drought for the twenty-first century. *Bulletin of the American Meteorological Society*, 98(12), 2543–2550. https://doi.org/10.1175/BAMS-D-16-0292.1

Curley, E.A.M., Thomas, R., Adams, C.E. & Stephen, A. (2021). Behavioural and metabolic responses of Unionida mussels to stress. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(11), 3184–3200. https://doi.org/10.1002/aqc.3689

Curley, E.A.M., Thomas, R., Adams, C.E. & Stephen, A. (2022). Adaptive responses of freshwater pearl mussels, *Margaritifera margaritifera*, to managed drawdowns. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 32(3), 466–483. https://doi.org/10.1002/aqc.3759

Daniel, W.M. & Brown, K.M. (2013). Multifactorial model of habitat, host fish, and landscape effects on Louisiana freshwater mussels. *Freshwater Science*, 32(1), 193–203. https://doi.org/10.1899/12-137.1

Daniel, W.M. & Brown, K.M. (2014). The role of life history and behavior in explaining unionid mussel distributions. *Hydrobiologia*, 734(1), 57–68. https://doi.org/10.1007/s10750-014-1868-7

DuBose, T.P., Atkinson, C.L., Vaughn, C.C. & Golladay, S.W. (2019). Drought-induced, punctuated loss of freshwater mussels alters ecosystem function across temporal scales. *Frontiers in Ecology and Evolution*, 7(July), 1–13. https://doi.org/10.3389/fevo.2019.00274

Ferreira-Rodríguez, N., Akiyama, Y.B., Aksenova, O.V., Araujo, R., Christopher Barnhart, M., Bespalaya, Y.V. et al. (2019). Research priorities for freshwater mussel conservation assessment. *Biological Conservation*, 231, 77–87. https://doi.org/10.1016/j.biocon.2019.01.002

Ferreira-Rodríguez, N., Fernández, I., Cancela, M.L. & Pardo, I. (2018). Multibiomarker response shows how native and non-native freshwater bivalves differentially cope with heat-wave events. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28(4), 934–943. https://doi.org/10.1002/aqc.2884

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.-C., Akçakaya, H.R., Angulo, A. et al. (2013). Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians, and corals. *PLoS ONE*, 8(6), e65427. https://doi.org/10.1371/journal.pone.0065427

Freshwater Mollusk Conservation Society. (2016). A national strategy for the conservation of native freshwater mussels. *Freshwater Mollusk Biology and Conservation*, 19(1), 1–21. https://doi.org/10.31931/fmbc.v19i1.2016.1-21

Galbraith, H.S., Blakeslee, C.J. & Lellis, W.A. (2012). Recent thermal history influences thermal tolerance in freshwater mussel species (Bivalvia: Unionoida). *Freshwater Science*, 31(1), 83–92. https://doi.org/10.1899/11-025.1

Galbraith, H.S., Blakeslee, C.J., Spooner, D.E. & Lellis, W.A. (2020). A weight-of-evidence approach for defining thermal sensitivity in a federally endangered species. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(3), 540–553. https://doi.org/10.1002/aqc.3287

Galbraith, H.S., Spooner, D.E. & Vaughn, C.C. (2010). Synergistic effects of regional climate patterns and local water management on freshwater mussel communities. *Biological Conservation*, 143(5), 1175–1183. https://doi.org/10.1016/j.biocon.2010.02.025

Ganser, A.M., Newton, T.J. & Haro, R.J. (2015). Effects of elevated water temperature on physiological responses in adult freshwater mussels. *Freshwater Biology*, 60(8), 1705–1716. https://doi.org/10.1111/fwb.12603

Gill, K.C., Fovargue, R.E. & Neeson, T.M. (2020). Hotspots of species loss do not vary across future climate scenarios in a drought-prone river basin. *Ecology and Evolution*, 10(17), 9200–9213. https://doi.org/10.1002/ece3.6597

Golladay, S.W., Gagnon, P., Kearns, M., Battle, J.M. & Hicks, D.W. (2004). Response of freshwater mussel assemblages (Bivalvia: Unionidae) to a record drought in the Gulf coastal plain of southwestern Georgia.

Journal of the North American Benthological Society, 23(3), 494–506. https://doi.org/10.1899/0887-3593(2004)023%3C0494:ROFMAB%3E2.0.CO;2

Gough, H.M., Gascho Landis, A.M. & Stoeckel, J.A. (2012). Behaviour and physiology are linked in the responses of freshwater mussels to drought: differential mussel responses to drought. *Freshwater Biology*, 57(11), 2356–2366. https://doi.org/10.1111/fwb.12015

Graf, D.L. & Cummings, K.S. (2007). Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies*, 73(4), 291–314. https://doi.org/10.1093/mollus/eym029

Haag, W.R. (2012). *North American freshwater mussels: natural history, ecology, and conservation*. New York, NY, USA: Cambridge University Press.

Haag, W.R. & Rypel, A.L. (2011). Growth and longevity in freshwater mussels: evolutionary and conservation implications. *Biological Reviews*, 86(1), 225–247. https://doi.org/10.1111/j.1469-185X.2010.00146.x

Hopper, G.W., Gido, K.B., Vaughn, C.C., Parr, T.B., Popejoy, T.G., Atkinson, C.L. et al. (2018). Biomass distribution of fishes and mussels mediates spatial and temporal heterogeneity in nutrient cycling in streams. *Oecologia*, 188(4), 1133–1144. https://doi.org/10.1007/s00442-018-4277-1

IPCC. (2014). *Climate Change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*.

Ismail, N.S., Tommerdahl, J.P., Boehm, A.B. & Luthy, R.G. (2016). *Escherichia coli* reduction by bivalves in an impaired river impacted by agricultural land use. *Environmental Science and Technology*, 50(20), 11025–11033. https://doi.org/10.1021/acs.est.6b03043

Khan, J.M., Hart, M., Dudding, J., Robertson, C.R., Lopez, R. & Randklev, C.R. (2019). Evaluating the upper thermal limits of glochidia for selected freshwater mussel species (Bivalvia: Unionidae) in central and East Texas, and the implications for their conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(8), 1202–1215. https://doi.org/10.1002/aqc.3136

Levine, T.D., Hansen, H.B. & Gerald, G.W. (2014). Effects of shell shape, size, and sculpture in burrowing and anchoring abilities in the freshwater mussel *Potamilus alatus* (Unionidae): burrowing and anchoring in mussels. *Biological Journal of the Linnean Society*, 111(1), 136–144. https://doi.org/10.1111/bij.12178

Lopez, J.W. & Vaughn, C.C. (2021). A review and evaluation of the effects of hydrodynamic variables on freshwater mussel communities. *Freshwater Biology*, 66(9), 1665–1679. https://doi.org/10.1111/fwb.13784

Lymbery, A.J., Ma, L., Lymbery, S.J., Klunzinger, M.W., Beatty, S.J. & Morgan, D.L. (2021). Burrowing behavior protects a threatened freshwater mussel in drying rivers. *Hydrobiologia*, 848(12–13), 3141–3152. https://doi.org/10.1007/s10750-020-04268-0

Martinuzzi, S., Januchowski-Hartley, S.R., Pracheil, B.M., McIntyre, P.B., Plantinga, A.J., Lewis, D.J. et al. (2014). Threats and opportunities for freshwater conservation under future land use change scenarios in the United States. *Global Change Biology*, 20(1), 113–124. https://doi.org/10.1111/gcb.12383

Newton, T.J., Zigler, S.J. & Gray, B.R. (2015). Mortality, movement and behaviour of native mussels during a planned water-level drawdown in the upper Mississippi River. *Freshwater Biology*, 60(1), 1–15. https://doi.org/10.1111/fwb.12461

Oklahoma Department of Wildlife Conservation. (2016). Oklahoma Comprehensive Wildlife Conservation Strategy: a strategic conservation plan for Oklahoma's rare and declining wildlife.

Oksanen, J. (2022). vegan: Community Ecology Package.

Oosterhuis, D., Pardo, I. & Ferreira-Rodríguez, N. (2021). How does summer environmental degradation influence native mussels in *Corbicula* invaded rivers? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(6), 1245–1256. https://doi.org/10.1002/aqc.3547

R Core Team. (2021). R: a language and environment for statistical computing.

Randklev, C.R., Tsakris, E.T., Johnson, M.S., Popejoy, T., Hart, M.A., Khan, J. et al. (2018). The effect of dewatering on freshwater mussel (Unionidae) community structure and the implications for conservation and water policy: a case study from a spring-fed stream in the southwestern United States. *Global Ecology and Conservation*, 16, e00456. https://doi.org/10.1016/j.gecco.2018.e00456

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J. et al. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873. https://doi.org/10.1111/brv.12480

Roznere, I., Watters, G.T., Wolfe, B.A. & Daly, M. (2017). Effects of relocation on metabolic profiles of freshwater mussels: metabolomics as a tool for improving conservation techniques. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(5), 919–926. https://doi.org/10.1002/aqc.2776

Sanchez Gonzalez, I., Hopper, G.W., Bucholz, J. & Atkinson, C.L. (2021). Long-term monitoring reveals differential responses of mussel and host fish communities in a biodiversity hotspot. *Diversity*, 13(3), 122. https://doi.org/10.3390/d13030122

Schwalb, A.N. & Pusch, M.T. (2007). Horizontal and vertical movements of unionid mussels in a lowland river. *Jounral of the North American Benthological Society*, 26(2), 261–272. https://doi.org/10.1899/0887-3593(2007)26[261:HAVMOU]2.0.CO;2

Sousa, R., Ferreira, A., Carvalho, F., Lopes-Lima, M., Varandas, S. & Teixeira, A. (2018). Die-offs of the endangered pearl mussel *Margaritifera margaritifera* during an extreme drought. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28(5), 1244–1248. https://doi.org/10.1002/aqc.2945

Spooner, D.E. & Vaughn, C.C. (2007). Mussels of the mountain Fork River, Arkansas and Oklahoma. *Publications of the Oklahoma Biological Survey*, 8, 14–18.

Spooner, D.E. & Vaughn, C.C. (2008). A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling. *Oecologia*, 158(2), 307–317. https://doi.org/10.1007/s00442-008-1132-9

Spooner, D.E., Xenopoulos, M.A., Schneider, C. & Woolnough, D.A. (2011). Coextirpation of host-affiliate relationships in rivers: the role of climate change, water withdrawal, and host-specificity. *Global Change Biology*, 17(4), 1720–1732. https://doi.org/10.1111/j.1365-2486.2010.02372.x

Strayer, D.L. & Dudgeon, D. (2010). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, 29(1), 344–358. https://doi.org/10.1899/08-171.1

Strayer, D.L. & Smith, D.R. (2003). *A guide to sampling freshwater mussel populations*. Bethesda, Maryland, USA: American Fisheries Society.

Tarter, A.A., Ford, D.F., Symonds, D.E., Ford, N.B. & Schwalb, A.N. (2022). Impact of extreme climatic events on unionid mussels in a subtropical river basin. *Hydrobiologia*, 1–16. https://doi.org/10.1007/s10750-022-04819-7

Tyrrell, M., Hornbach, D.J., Tyrrell, M. & Hornbach, D.J. (1998). Selective predation by muskrats on freshwater mussels in 2 Minnesota rivers. *Journal of the North American Benthological Society*, 17(3), 301–310. https://doi.org/10.2307/1468333

U.S. Census Bureau. (2020). State profiles: 2020 Census. https://www.census.gov/library/stories/state-by-state/oklahoma-population-change-between-census-decade.html

Vandewalle, M., de Bello, F., Berg, M.P., Bolger, T., Doledec, S., Dubs, F. et al. (2010). Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and*

Conservation, 19, 2921–2947. https://doi.org/10.1007/s10531-010-9798-9

Vaughn, C. (2003). The mussel fauna of the Glover River. Oklahoma. *Proceedings of the Oklahoma Academy of Science*, 83, 1–6.

Vaughn, C.C. (2010). Biodiversity losses and ecosystem function in freshwaters: emerging conclusions and research directions. *Bioscience*, 60(1), 25–35. https://doi.org/10.1525/bio.2010.60.1.7

Vaughn, C.C. (2012). Life history traits and abundance can predict local colonisation and extinction rates of freshwater mussels. *Freshwater Biology*, 57(5), 982–992. https://doi.org/10.1111/j.1365-2427.2012.02759.x

Vaughn, C.C. (2018). Ecosystem services provided by freshwater mussels. *Hydrobiologia*, 810(1), 15–27. https://doi.org/10.1007/s10750-017-3139-x

Vaughn, C.C., Atkinson, C.L. & Julian, J.P. (2015). Drought-induced changes in flow regimes lead to long-term losses in mussel-provided ecosystem services. *Ecology and Evolution*, 5(6), 1291–1305. https://doi.org/10.1002/ece3.1442

Vaughn, C.C. & Julian, J.P. (2013). *Incorporating ecological costs and benefits into environmental flow recommendations for Oklahoma rivers: phase I, southeastern Oklahoma*.

Vaughn, C.C. & Taylor, C.M. (1999). Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conservation Biology*, 13(4), 912–920. https://doi.org/10.1046/j.1523-1739.1999.97343.x

Vaughn, C.C., Taylor, C.M. & Eberhard, K.J. (1997). A comparison of the effectiveness of timed searches vs. quadrat sampling in mussel surveys. In: Cummings, K.S., Buchanan, A.C. & Koch, L.M. (Eds.) *Conservation and management of freshwater mussels II: initiatives for the future*. Rock Island, Illinois: Upper Mississippi River Conservation Committee, pp. 157–162.

Walls, S.C. (2018). Coping with constraints: achieving effective conservation with limited resources. *Frontiers in Ecology and Evolution*, 6, 24. https://doi.org/10.3389/fevo.2018.00024

Wang, X., Shang, S., Qu, Z., Liu, T., Melesse, A.M. & Yang, W. (2010). Simulated wetland conservation-restoration effects on water quantity and quality at watershed scale. *Journal of Environmental Management*, 91(7), 1511–1525. https://doi.org/10.1016/j.jenvman.2010.02.023

Wang, X., Yang, W. & Melesse, A.M. (2008). Using hydrologic equivalent wetland concept within SWAT to estimate streamflow in watersheds with numerous wetlands. *Transactions of the ASABE*, 51(1), 55–72. https://doi.org/10.13031/2013.24227

Wickham, J., Stehman, S.V., Sorenson, D.G., Gass, L. & Dewitz, J.A. (2021). Thematic accuracy assessment of the NLCD 2016 land cover for the conterminous United States. *Remote Sensing of Environment*, 257, 112357. https://doi.org/10.1016/j.rse.2021.112357

Wickham, J.D., Stehman, S.V., Gass, L., Dewitz, J., Fry, J.A. & Wade, T.G. (2013). Accuracy assessment of NLCD 2006 land cover and impervious surface. *Remote Sensing of Environment*, 130, 294–304. https://doi.org/10.1016/j.rse.2012.12.001

Williams, J.D., Bogan, A.E., Butler, R.S., Cummings, K.S., Garner, J.T., Harris, J.L. et al. (2017). A revised list of the freshwater mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada. *Freshwater Mollusk Biology and Conservation*, 20(2), 33. https://doi.org/10.31931/fmbc.v20i2.2017.33-58

SUPPORTING INFORMATION

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

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