



# Impact of extreme climatic events on unionid mussels in a subtropical river basin

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**Abstract** An increase in extreme droughts and floods is expected with current and future climate changes. Such extreme climate events may have long-lasting impact on more sessile organisms, such as unionid freshwater mussels, which are highly imperiled. The objective of our study was to test specific predictions for the impact of an extreme drought in 2011/2012, extreme flooding in 2017, and long-term

changes by comparing recent and historical mussel community data from an understudied yet biodiverse region of Texas, USA. Drought had the most detrimental impact leading to community-wide declines, indicated by a significant decline of abundances, species richness and occupied sites. Flooding led to shifts in community composition and spatial distribution. Both severe declines and a distinct community shift occurred over the long-term, where the dominance of species shifted to those more tolerable of disturbance. Saltwater intrusion likely caused a significant increase post-flood of a species known to be tolerant of brackish water (*Glebulina rotundata*). The impact of flooding was likely buffered by connectivity with extensive backwater areas, forming large wetlands, which may act as crucial refuges for mussels during extreme climatic events. Thus, protecting wetlands is crucial to protect freshwater mussels and the ecosystem services they provide.

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## Introduction

Disturbance is a strong driver of community biomass and composition especially in rivers (Resh et al., 1988; Matthaei & Townsend, 2000; Urban, 2004), and spatial gradients in disturbance may be key in

sustaining biodiversity in river landscapes (Harvey et al., 2018). Disturbance in riverine systems is largely caused by extreme hydrological changes such as flooding and dewatering during drought. Greater disturbance intensity and frequency due to an increase in droughts and intense precipitation events are expected with current and future climatic changes (Kloesel et al., 2018; Lall et al., 2018).

The intensification of hydroclimatological dry-to-wet and wet-to-dry whiplashes may be especially detrimental for some groups of organisms. While many groups of aquatic macroinvertebrates are known to recover quickly from a disturbance, often within weeks or months following a disturbance (e.g., Fowler et al., 2004), extreme disturbances, especially those which would be rare under the historical natural flow regime, may have long-lasting impacts on longer-lived organisms, such as unionid mussels (e.g., Mitchell et al., 2019). Declines in mussels may strongly affect ecosystem processes and other species, because mussels are important ecosystem engineers providing important ecosystem services through biofiltration of water, nutrient cycling, and provision of habitat for other organisms (Vaughn, 2018). Riverine mussels (Family Unionidae) are among the most endangered organisms in North America (Strayer, 2008; Haag, 2012) and a better understanding of the impact disturbances have on their distribution is crucial to the development of effective conservation and recovery plans.

Several studies have examined the impact of drought on mussels, and have indicated that droughts can increase mortality, decrease diversity, and change community composition (Gagnon et al., 2004; Golladay et al., 2004; Haag & Warren, 2008; Galbraith et al., 2010; Sousa et al., 2018). Such changes can lead to losses in mussel provided ecosystem services (Vaughn et al., 2015). Mussels with different life history strategies were shown to respond differently to dewatering (Mitchell et al., 2018), but these differences may be irrelevant during severe droughts (Haag & Warren, 2008; Mitchell et al., 2019).

Major rainfall events are also increasing with climate change causing extreme flooding (Kloesel et al., 2018; Lall et al., 2018). For example, in 2017 Hurricane Harvey produced more rainfall than any tropical cyclone in United States' history (NOAA, 2018). Van Oldenborgh et al. (2017) concluded that global

warming made the precipitation about 15% more intense, and a similar study showed that extremely high ocean heat values, attributed to human-induced climate change, not only intensified the storm but also increased the rainfall amount (Trenberth et al., 2018). During flooding mussels can be washed out of suitable habitat and mortality often occurs when mussels are transported to shallow areas that desiccate during low flows (Hastie et al., 2001; Sousa et al., 2012). Transport of mussels into unsuitable or degraded habitat may lead to population declines and reduce population recovery (Karatayev et al., 2020). Flooding can also lead to mussels colonizing previously unoccupied habitat (Olson et al., 2018). It is possible that some species may have higher survival and a faster recovery after major flooding events, but this is not well understood.

The Big Thicket, including the Big Thicket National Preserve (BTNP), of Southeast Texas is known as one of the most extraordinarily biodiverse regions in North America (Moring, 2003). The Neches River Basin in this region, especially the Lower Neches River, downstream from the B. A. Steinhagen Reservoir, is considered to be the "hot spot" of Texas unionid diversity with 32 species, including five Texas state listed species, and two species which are under review for protections under the Endangered Species Act (Burlakova et al., 2011; Dascher et al., 2017; Walters et al., 2019). Because of the protection of the BTNP, much of the floodplain and riparian area in the Lower Neches Basin is heavily forested and undisturbed. Unfortunately, the BTNP is also recognized as the most at-risk of the "crown jewel" parks in the national parks system (Callicott et al., 2006). Threats to the availability and quality of aquatic habitat in the Big Thicket include loss of coastal wetlands, saltwater intrusion, and resource withdrawals (petrochemical, water, natural gas) contributing to wetland subsidence/compaction in combination with the stressors caused by global climate change.

Several extreme climatic events may have affected the distribution and diversity of mussels in the Big Thicket during the last two decades (Table 1). The objective of this study was to examine the impact of extreme disturbance events on mussel communities in the Big Thicket, including the extreme drought in 2011/2012 and the extreme

**Table 1** Extreme climate events that occurred in the study region between 2002 and 2018. Flow data from United States Geological Survey gauge 08,041,500 Village Creek near Kountze, Texas

Year	Extreme climate event
2008	Hurricane Ike, breach of saltwater barrier and inundation of Lower Neches and Pine Island Bayou
2010–2012	Severe drought, minimum discharge 2.4 m <sup>3</sup> /s in Village Creek compared to a mean discharge of was 25.5 m <sup>3</sup> /s in Village Creek from 1940 to 2017
2016	Heavy rainfall, maximum discharge 697 m <sup>3</sup> /s in Village Creek
2017	Hurricane Harvey, discharge increased from 7.6 m <sup>3</sup> /s on August 24 to 5,154 m <sup>3</sup> /s on August 30, 2017

flooding in 2017 as a consequence of Hurricane Harvey's record-breaking rain amounts (Trenberth et al., 2018) by testing specific hypotheses and predictions (see below). We compared surveys conducted during this study with past survey data (Bordelon & Harrel, 2004; Ford, 2015). To the best of our knowledge, only one freshwater mussel survey was carried out within the past ten years within the region by Ford (2015). Karatayev and Burloкова (2007) attempted to survey the area but were unable to complete their work due to unsafe hydraulic conditions (velocities) from flooding. The most intensive pre-drought survey of the Big Thicket sub-basin was conducted by Bordelon & Harrel (2004).

We expected to see different changes after different kind of disturbances (i.e., drought vs flood events) and over a longer time period.

**Hypothesis 1** Previous studies have shown that relative abundances after a severe drought depend on pre-drought community composition (Haag & Warren, 2008; Mitchell et al., 2019); hence our hypothesis was that severe droughts impact different species similarly, resulting in a *community-wide decline* (and not a community shift, Table 2).

**Hypothesis 2** Changed habitat conditions due to flooding has detrimental effects on some species while benefiting others, causing a *community shift* (but not a community decline, Table 2). Equilibrium species (a life history strategy group characterized by long life spans, later maturity and lower fecundity) are believed to favor stable productive habitats (Haag, 2012), and should be most impacted by disturbance, whereas opportunistic species (characterized by traits

that facilitate colonization, such as early maturity and higher fecundity), and probably some periodic species (intermediate in their traits) should benefit the most.

**Hypothesis 3** Over the long term the combined effects of different disturbances (both drought and flooding) result in a *community-wide decline and a community shift*.

We assumed that community-wide declines would lead to several changes; (A) significant declines of abundances (measured as catch-per unit effort, CPUE); (B) rare species would be extirpated and result in a decline of species richness, and (C) previously widespread species would occupy fewer sites and more species would occupy a smaller fraction of sites. We expected that a community shift would cause (A) declines in CPUE mostly by equilibrium species and increases in CPUE mostly by opportunistic and periodic species; (B) significant changes (magnitude > 25%) in the relative abundance of tribes; specifically, a significant decline in the relative abundance of Pleurobemini (almost exclusively equilibrium species, Table 3) and Quadrulini (all equilibrium species), and an increase in Lampsilini (opportunistic and periodic species). Note that the results showed that Anodontini contributed < 2% to the community composition and *Amblemini* was only represented by one species, *Amblema plicata* (Say, 1817).

In addition, we examined whether changes in species abundance were associated with certain mussel life history traits such as maximum size, host specificity, number of known host fish, main host fish family and infection strategy.

**Table 2** Hypotheses, predictions, and results for responses of mussel communities to drought, flooding, and long-term changes

	Post-drought (2002 vs. 2014; n = 13 sites)	Post-flood (2014 vs. 2018; n = 16 sites)	Long-term (2002 vs. 2018; n = 10 sites)
<b>Hypothesis</b>	H1 Community-wide decline (no community shift)	H2 Community shift (no community-wide decline)	H3 Community-wide decline + community shift
<b>Results supported hypothesis?</b>	Partial support, also some indication for community shifts	Yes, but community shift mostly driven by increase of species tolerant of brackish water	Fully supported
<b>Community-wide decline predicted?</b>	<b>Yes</b>	<b>No</b>	<b>Yes</b>
Significant declines in CPUE?	Yes	No significant difference	Yes
Significant decline in species richness?	Yes	No significant difference	Yes
Less widespread species, more species with limited range	Yes, and abundance for similar occupancy slightly higher post-disturbance	Minor changes in occupancy patterns No significant relationship between occu- pancy and abundance post-disturbance	Yes, and abundance for similar occupancy slightly higher post-disturbance
<b>Community shift predicted?</b>	<b>No</b>	<b>Yes</b>	<b>Yes</b>
Significant (magnitude > 25%) decline in relative abundance of <i>Quadrulini</i> and <i>Pleurobemini</i> and increase in <i>Lampsilini</i>	Decline of <i>Quadrulini</i>	Decline of <i>Pleurobemini</i> and increase in <i>Lampsilini</i>	Shift from a dominance of <i>Pleurobemini</i> and <i>Quadrulini</i> to <i>Amblemini</i> and <i>Lamp- silini</i>
Declines in CPUE by equilibrium species. Increases, if present, by opportunistic and periodic species	Most species (12 of 18) declined, those showing increases were mostly oppor- tunistic and periodic species	Most species (15 of 23 species) showed smaller changes (magnitude < 10 ind./p- H). Equilibrium species experienced both larger increases and decreases; highest increases by <i>Glebulita rotundata</i> (periodic species)	A third (7 of 22) of the species declined or were not found. Declines were primarily equilibrium species. Most increases were fairly small

**Bold** is simply used to put emphasis on the main categories

**Table 3** Life history strategies and tribes for the 25 mussel species collected during all survey events, their maximum size and observed changes in their abundance. Mussels were assigned strategies based on Haag (2012) (pp. 208–210). For those species without a strategy assigned by Haag, we allo-

cated strategies based on members of the same genus and our knowledge of mussel traits. Size data was obtained from Haag (2012) and Howells (2014). Total CPUE is the sum of CPUEs of all sites

	Tribe	Max size (mm)	Changes in Total CPUE [ind/p-H]		
			Post-drought (2014 vs. 2002)	Post-flood (2018 vs. 2014)	Long-term (2018 vs. 2002)
<b>Equilibrium species</b>					
<i>Amblema plicata</i>	Amblemini	180	– 38.1	– 2.4	21.7
<i>Plectomerus dombeyanus</i>	Lampsilini	150	23.7	46.0	43.2
<i>Fusconaia askewi*</i>	Pleurobemini	80	– 108.1	– 127.6	– 177.2
<i>Pleurobema riddellii*</i>	Pleurobemini	62	– 4.0	–	– 2.6
<i>Cyclonaias nodulata</i>	Quadrulini	76	–	1.0	–
<i>Cyclonaias pustulosa</i>	Quadrulini	80	– 191.3	– 14.8	– 214.6
<i>Quadrula quadrula</i>	Quadrulini	120	–	74.2	1.0
<i>Quadrula</i> sp.	Quadrulini	120	–	83.0	32.0
<i>Tritogenia nobilis</i>	Quadrulini	114	–38.3	2.0	–36.1
<i>Tritogenia verrucosa</i>	Quadrulini	200	– 3.9	3.2	0.0
<b>Opportunistic species</b>					
<i>Pyganodon grandis</i>	Anodontini	200	1.8	8.2	4.0
<i>Utterbackiana suborbiculata</i>	Anodontini	100	–	2.0	2.0
<i>Lampsilis teres</i>	Lampsilini	185	– 12.2	5.7	14.1
<i>Leaunia lienosus</i>	Lampsilini	65	–10.5	–1.7	–5.4
<i>Potamilus fragilis</i>	Lampsilini	178	1.0	2.7	–2.3
<i>Potamilus purpuratus</i>	Lampsilini	200	– 0.5	24.0	16.1
<i>Sagittunio subrostratus</i>	Lampsilini	80	–	–	2.0
<i>Toxolasma</i> sp.	Lampsilini	75	12.2	–29.9	8.1
<b>Periodic species</b>					
<i>Strophitus undulatus</i>	Anodontini	100	–	– 1.0	–
<i>Glebula rotundata</i>	Lampsilini	150	–	392.0	2.0
<i>Lampsilis hydiana</i>	Lampsilini	127	– 25.3	– 5.7	1.1
<i>Lampsilis satura*</i>	Lampsilini	150	– 1.7	0.3	6.9
<i>Obliquaria reflexa</i>	Lampsilini	84	0.5	7.0	– 1.0
<i>Obovaria arkansasensis*</i>	Lampsilini	55	– 2.3	– 5.7	14.5
<i>Unio merus tetralasmus</i>	Pleurobemini	141	1.5	0.3	–

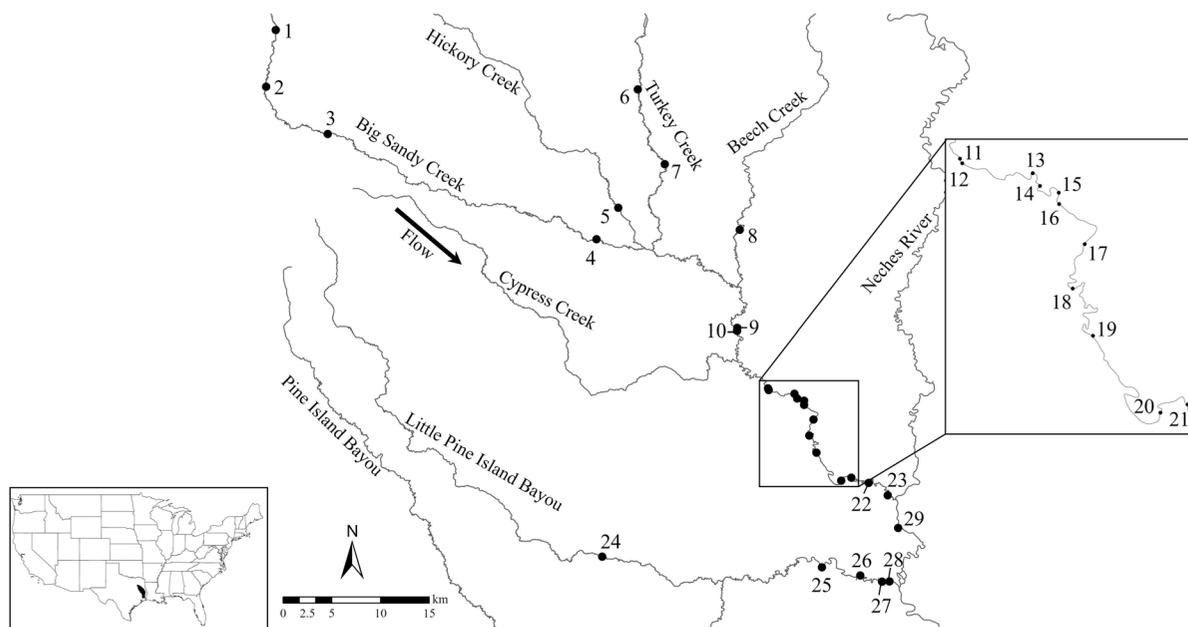
Species with an asterisk are listed as threatened in Texas

## Methods

### Study area

The study area encompassed ~7.4 km of the Neches River upstream of the confluence with Village Creek to ~18.2 km downstream to the

confluence of Pine Island Bayou. The study area also included ~137.4 km of the Village Creek sub-basin (including Big Sandy Creek, Hickory Creek, Beech Creek and Cypress Creek), ~23.4 km of Pine Island Bayou and ~11.0 km of its tributary, Little Pine Island Bayou (Fig. 1). Streams in this region generally have soft, acidic, slow-moving waters surrounded by predominantly forested watersheds



**Fig. 1** The study region and our 29 sampling sites in the Lower Neches River basin. See Table 4 for which sites were utilized for comparisons

(> 60%) that contain moderate (< 8%) urbanization (Burlakova et al., 2011).

#### Survey sites and sampling of mussels

Data from 29 survey sites in different part of the BTNP (Fig. 1; Table 4) was used for comparisons of historical and pre–post-disturbance data in this study. The data was collected by different teams of researchers in different years (Table 4) ranging from 2002 (Bordelon & Harrel, 2004) and 2014 (Ford, 2015) to our most recent survey efforts in 2018. In 2018, sites for which historical survey data were available were sampled if they were within the BTNP and were accessible (21 sites, Table 4). The length of each sample site varied between 50 and 140 m and depended on the extent of the uniform mesohabitat type.

Sampling methods were generally kept consistent between years and mussels were searched with timed searches that included tactile searches of the substrate (see details below). Timed searches can be better at detecting rare species and species richness compared to quantitative methods and are widely used in surveys of river mussels, but they can also be biased toward larger individuals (e.g., Sanchez & Schwalb, 2021). Sampling in 2018 proceeded from

the shoreline outward until either the opposite bank was reached, or water depths exceeded 3 m. All specimens were identified, counted, and returned to the stream. In addition, genetic samples were collected by brush-swabbing the mantle and foot of live mussels (Henley et al., 2006), which is a non-lethal, non-consumptive method, and stored in ethanol. DNA was extracted from those swabs using the GeneJet DNA extraction kit (ThermoFisher, Inc.) and samples were analyzed to inform identification of species that were difficult to distinguish by external morphology (Schwalb et al., 2019). The analysis of DNA from 97 mussels informed the identification of ten species. In 2018 tactile searches of soft substrate (most sites) were conducted to a depth of approximately 15–20 cm. To facilitate the detection of smaller individuals and monitor recruitment, softer substrate was rinsed through a mesh of 500  $\mu\text{m}$  in areas with high mussel densities (average: 45 individuals per p-H). Exceptionally small (< 5 mm) individuals were detected including several that appear to be the smallest documented specimens of *Potamilus amphichaenus* (Frierson, 1898, Note: *P. amphichaenus* was found at sites not included in the analyses of this study (see Tarter, 2019)) and *Lampsilis hydiana* (Lea, 1838). In addition, juvenile mussels of some species

**Table 4** Sites used in the different historical comparisons. Drought sites consisted of areas surveyed in 2002 and 2014, flood sites consisted of sites surveyed in 2014 and 2018, and long-term sites consisted of those surveyed in 2002 and 2018

Site no.	Location	Drought	Flood	Long-term
1	Big Sandy Creek	–	X	–
2	Big Sandy Creek	X	X	X
3	Big Sandy Creek	–	X	–
4	Village Creek	–	X	–
5	Hickory Creek	X	–	–
6	Turkey Creek	X	–	–
7	Turkey Creek	X	–	–
8	Beech Creek	X	–	–
9	Village Creek	X	–	–
10	Village Creek	X	–	–
11	Village Creek	X	–	–
12	Village Creek	X	X	X
13	Village Creek	–	X	–
14	Village Creek	–	X	–
15	Village Creek	X	X	X
16	Village Creek	X	X	X
17	Village Creek	–	–	X
18	Village Creek	–	–	X
19	Village Creek	X	X	X
20	Village Creek	X	–	–
21	Village Creek	–	–	X
22	Village Creek	–	–	X
23	Village Creek	–	–	X
24	Little Pine Island Bayou	–	X	–
25	Little Pine Island Bayou	–	X	–
26	Pine Island Bayou	–	X	–
27	Pine Island Bayou	–	X	–
28	Pine Island Bayou	–	X	–
29	Neches River	–	X	–
Total number		13	16	10

were occasionally found attached by byssal threads to larger woody debris [e.g., *P. amphichaenus*, *Unio tetralasmus* (Say, 1831), *Pyganodon grandis* (Say, 1829)] or empty shells of dead mussels (*Toxolasma* sp.).

Sieves were not used in 2014 or 2002, but tactile searches that included searching the substrate to a depth of at least 6 cm were carried out consistently in all survey years. Both the 2002 and 2014 surveys recorded small species like *Toxolasma* and small individuals of several larger species. Thus, we are confident the loss of smaller species were not due to differences in search methods.

Sampling efforts for the surveys, in 2002, 2014 and 2018 ranged between 1 to 3 person-hours (p-H) per site, averaging  $2.2 \pm 0.16$ ,  $1.2 \pm 0.05$ ,  $1.1 \pm 0.12$  p-H respectively. All surveys were carried out at or below median flow conditions. Average search times in 2018 were kept consistent with 2014, but both were slightly lower compared to 2002, partly because mussels were no longer present at several sites. Sampling effort was consistent with other surveys in this region (Neches and Sabine Rivers), where large numbers of mussels can be found within a rather short time (Ford et al., 2014, 2016; Howells, 2014). During both the 2014 and 2018

search efforts, rare species such as *P. amphichaenus*, *Pleurobema riddellii* (Lea, 1862), and *Obovaria arkansasensis* (Lea, 1862) and juveniles of numerous species including *P. amphichaenus* were collected (data from sites without historical data not used in this study) suggesting that search time and methodology were adequate to capture rare species, and individuals of all size classes. Species nomenclature follows Williams et al. (2017) and the Freshwater Mollusk Conservation Society 2021 update ([https://molluskconservation.org/Library/Committees/Names/Appendix\\_1\\_Bivalves\\_Revised\\_Names\\_List\\_20210825.pdf](https://molluskconservation.org/Library/Committees/Names/Appendix_1_Bivalves_Revised_Names_List_20210825.pdf)), which included synonymization of the following taxa in this study (*Cyclonais mortoni* to *C. pustolosa*, *Leptodea* to *Potamilus*, *Quadrula apiculata* to *Q. quadrula*), and re-assignments of *Ligumia subrostrata* to *Sagittunio subrostratus*, *Villosa lienosa* to *Leaunio lienosus*, and *Quadrula nobilis* to *Tritogenia nobilis*.

#### Comparison with historical data

To examine historical changes in mussel communities in our study area survey data was compared for sites which were sampled in at least two different years (Table 4). Surveys in 2014 and 2018 were conducted in the Village Creek sub-basin, Pine Island Bayou sub-basin and the Lower Neches River (Fig. 1; Table 4). Surveys in 2002 were from the Village Creek sub-basin (Big Sandy Creek and its tributaries along with mid and lower Village Creek) only (Fig. 1; Table 4). Several assessments were carried out: (1) to assess potential impacts of drought, survey data from 13 sites that were surveyed both in 2002 and 2014 were compared (available sites were restricted to the Village Creek sub-basin); (2) to assess the impact of severe flooding in 2017 due to Hurricane Harvey, survey data from 16 sites that were surveyed both in 2014 and 2018 were compared; (3) to assess long-term changes (including impacts of drought and flooding events) survey data from 10 sites that were surveyed both in 2002 and 2018 were compared (available sites were restricted to the Village Creek sub-basin).

The following analyses were done to examine whether community-wide declines and/or community shifts had occurred. The total CPUE at each site and for each species, computed as the number of mussels per person hour (p-H), were compared between

surveys using paired *T*-test and log transformed CPUE data. Species richness was also calculated and compared with paired *T*-tests. In addition, due to some potential historical misidentifications between *Toxolasma parvum* (Barnes, 1823) and *Toxolasma texasiense* (Lea, 1857), both species were combined into *Toxolasma* sp. for data analysis. Occupancy was computed as the percentage of sites where a species was present. Widespread species were defined as those occupying >60% of all sites and species with a limited range those occupying ≤20%. The relationship between occupancy and log (abundance + 1) was examined with a linear regression for different years.

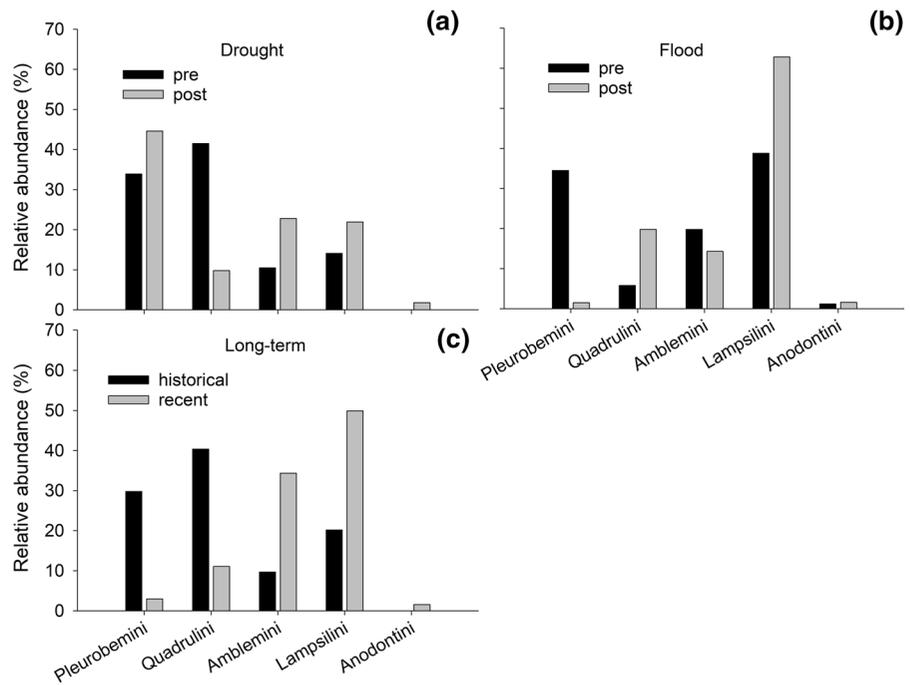
In addition, the relative abundance of different species and tribes as percentage of the total CPUE was compared between different years. Mussels were assigned an opportunistic, periodic, or equilibrium life history strategies, following Haag (2012). For those species that were not allocated a strategy by Haag, we assigned strategies based on similar species (members of the same genus) and our knowledge of their behaviors (Table 3). We also gathered available data on number of host fish, the known or likely main host family, infection strategy, and shell length (Ford & Oliver, 2015; Freshwater Mussel Host Database, 2020; Haag, 2012; Howells, 2014; Landis et al., 2012; Marshall et al., 2018).

## Results

### Post-drought survey

Consistent with our first hypothesis, there were significant declines in CPUE and species richness post-drought, indicating a community-wide decline. In 2014 no mussels were found at two sites, while mussels were present at all 2002 sites and CPUE per site decreased significantly from  $47.3 \pm 11.7$  to  $16.9 \pm 11.7$  ( $n=13$ ) mussels per p-H, (paired *T*-test,  $T_{12} = 1.78$ ,  $P < 0.001$ ). CPUE per species was also significantly lower (64%) in 2014 compared to 2002 (paired *T*-test,  $T_{17} = 1.73$ ,  $P = 0.01$ ). A total of 18 species were found (2002: 17 species, 2014: 16 species). Species richness per site was significantly lower in 2014 ( $3.9 \pm 0.8$ , range 0–10) compared to 2002 ( $7.9 \pm 0.8$ , range 1–12; paired *T*-test,  $T_{12} = 1.8$ ,  $P < 0.0001$ ). Two species, *Tritogenia nobilis* (Conrad, 1854) and the Texas state listed *P. riddellii* were found in 2002 but not in 2014,

**Fig. 2** Changes in relative abundance (%) by tribe for **a** pre (2002) and post (2014) drought, **b** pre (2014) and post (2018) flooding, and **c** long-term change between historical (2002) and more recent surveys (2018)



whereas the opportunistic species *P. grandis* was only found in 2014. Overall, of the 18 species collected, most declined in CPUE (12 species, including 2 that were absent in 2014) or showed a slight increase ( $<2$  mussels per p-H all sites combined, 4 species). Only two taxa *Toxolasma* and *Plectomerus* showed increases  $>12$  mussels per p-H with all sites combined (Table A2).

In contrast to our prediction, there were also some indications of community shifts post-drought, most notably a decline in the relative abundance of Quadrulini (Table 2). Pleurobemini (34% of total CPUE) and Quadrulini (42% of CPUE) were the most dominant tribes ( $>75\%$  of CPUE) in 2002. Both included almost exclusively equilibrium species, except *Unio*, which contributed  $\leq 1\%$  to all mussels surveyed in both years. While Pleurobemini remained dominant (45% of CPUE), Quadrulini declined, mostly due to a decline of *Cyclonaias pustulosa* (Lea, 1831) ( $-32\%$  in relative abundance). In contrast, Lampsilini and Amblemini increased by 8 and 12% in relative abundance respectively (Fig. 2), mostly due to the above-mentioned increase of the opportunistic taxa *Toxolasma* and equilibrium taxa *Plectomerus*. An opportunistic Anodontini species (*P. grandis*) was only present in 2014 but contributed  $<2\%$  to the total CPUE.

#### Post flooding survey

As predicted (Table 2) no community-wide decline was detected and no significant differences were found in CPUE per site (2014:  $24.9 \pm 23.1$ ; 2018:  $54.3 \pm 23.1$  per p-H;  $n=16$ ; paired *T*-test,  $T_{15}=1.75$ ,  $P=0.4$ ) and species richness ( $4.1 \pm 1.2$ , range 0–10) to 2018 ( $3.6 \pm 1.2$ , range 0–16;  $n=16$ ; paired *T*-test,  $T_{15}=1.75$ ,  $P>0.02$ ) pre- and post-flood (Table 2). However, species richness increased at the six most downstream sites. In accordance with hypothesis 2 several indications for a community shift were found, most notably a decline in Pleurobemini and an increase in Lampsilini (Fig. 2). This was mostly due to the high abundance of *Glebulina rotundata* (Lamarck, 1819), which only occurred at the five most downstream sites, and was not collected in 2014.

The tribes with higher relative abundance in 2014 were Amblemini (20%, mostly *Plectomerus*, equilibrium species), Pleurobemini (35%, mostly *Fusconaia askewi* (Marsh, 1896), equilibrium species) and Lampsilini (39%, mostly *Toxolasma*, opportunistic species, (Fig. 2; Table 3). In 2018, the mussel community was dominated by Lampsilini (63%). The relative importance of Quadrulini (equilibrium species) increased (+14%) in 2018 together with an increase

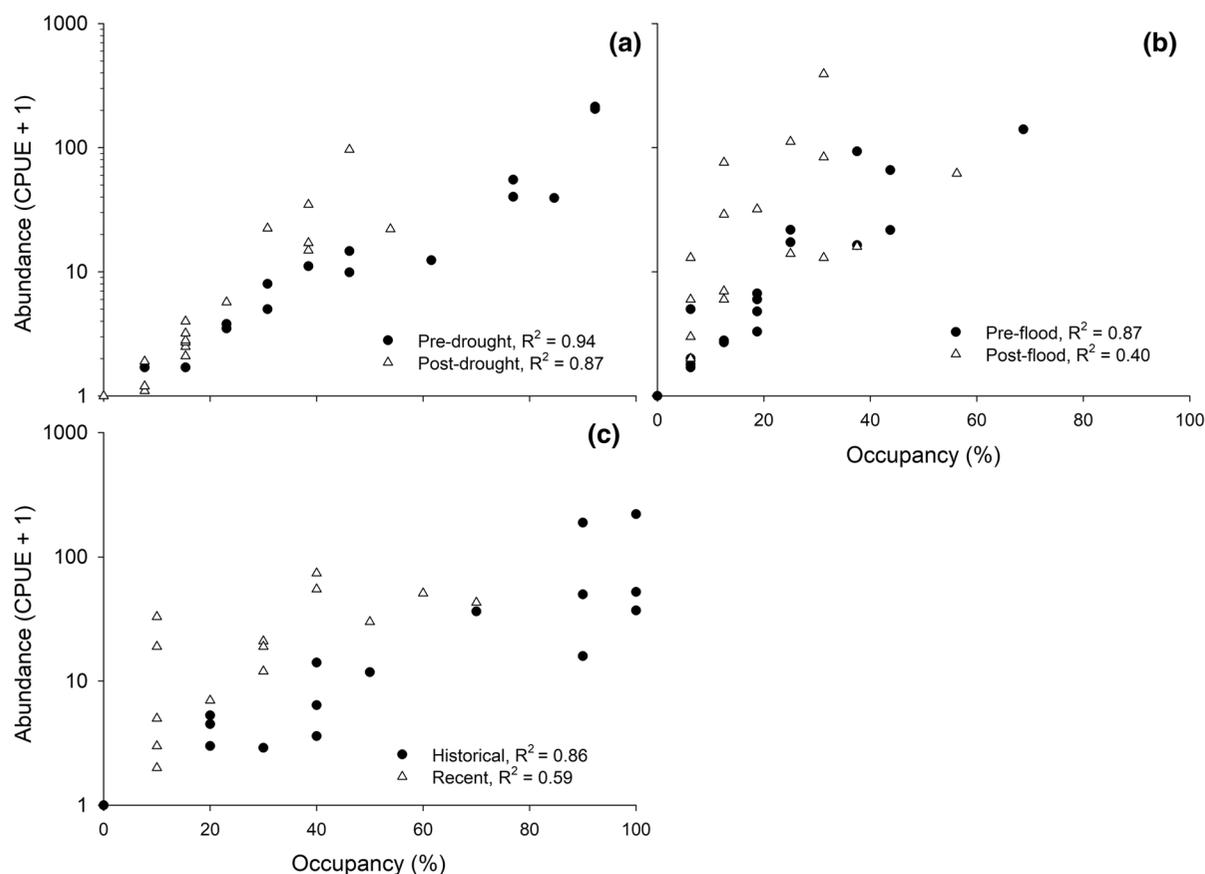
in Quadrulini species (from 3 to 6 species). The opportunistic Anodontini contributed <2% in both years.

CPUE per species was significantly higher (118%) in 2018 than 2014 (paired  $T$ -test,  $T_{22}=1.72$ ,  $P=0.04$ ). Of the 23 species collected, most (15) showed smaller changes ( $\pm 10$  mussels per p-H for all sites combined), whereas three species showed declines (between -15 [*C. pustulosa*] and -128 [*F. askewi*] mussels per p-H for all sites combined), and five species showed increases (between +24 [*Potamilius purpuratus* (Lamarck, 1819)] and +392 [*G. rotundata*] mussels per p-H, Table A2).

#### Long-term changes

In accordance with hypothesis 3 a combination of a community-wide decline and a community shift was

detected over the longer-term. Significant declines were detected in both CPUE (from  $64.1 \pm 25.1$  to  $37.1 \pm 25.1$  mussels per p-H,  $n=9$ , paired  $T$ -test  $T_9=1.8$ ,  $P < 0.01$ ) and species richness (significantly lower in 2018 ( $4.8 \pm 2.0$ , range 0–13) compared to 2002 ( $9.2 \pm 2.0$ ,  $n=9$ , range 6–12; paired  $T$ -test,  $T_9=1.8$ ,  $P < 0.03$ ). No mussels were found at two sites in 2018. A larger community shift was observed in the long-term dataset compared to the pre- and post-flood data. The dominance of Pleurobemini and Quadrulini (70% of the total CPUE in 2002) shifted to Amblemini and Lampsilini (84% in 2018, Fig. 2). This was mostly driven by declines of *F. askewi* and *C. pustulosa* and higher relative abundance of opportunistic taxa such as *Lampsilis teres* (Rafinesque, 1820), *P. purpuratus* and *Toxolasma* species but also taxa considered equilibrium species (*A. plicata* and *Plectomerus dombeyanus* (Valenciennes, 1827),



**Fig. 3** Relationship between abundance (total CPUE) and occupancy (proportion of sites a species was found at) for **a** pre (2002) and post (2014) drought, **b** pre (2002) and post (2018) flooding, and **c** historical (2002) and more recent surveys (2018)

Table 3). Opportunistic Anodontini species [*P. grandis* and *Utterbackiana suborbiculata* (Say, 1831)] were only present in 2018 but contributed <2% to the total CPUE. Overall, CPUE per species was not significantly different between sampling events (paired *T*-test,  $T_{21} = 1.72$ ,  $P = 0.5$ ). A third (7 of 22) of the species declined or were not found in 2018, where 14 increased, but increases were fairly small (Table A2).

#### Relationship between abundance and occupancy

In accordance with hypothesis 1 and 3 previously widespread species occupied fewer sites and more species occupied a smaller fraction of sites post-drought and long term. A significant relationship was found between abundance (CPUE) and occupancy (proportion of sites mussels were found,  $R^2: 0.40\text{--}0.94$ ;  $P < 0.05$ ) in all surveys with abundance increasing exponentially with occupancy (Fig. 3). The relationship was weakest post-flood ( $R^2 = 0.40$ , Fig. 3). Post-disturbance the patterns of occupancy changed, and previously widespread species occupied fewer sites. The percentage of species occupying more than 60% of the sites declined from 35 and 44% to none post-drought and to 5% long-term respectively. Pre-flood only one species was widespread (>60% occupancy) and none post-flood. In addition, more species occupied a smaller fraction of sites post-drought and long term with the percentage of species occupying 20% of the sites or less increasing 39 and 33% post-drought and long-term respectively, but declining slightly post-flood (-7%, Fig. 3).

#### Relationship between changes in abundance and traits

Overall, species that were apparently extirpated tended to be smaller and those that increased significantly tended to be larger (see below), but size was not consistently correlated with changes in CPUE in any of the comparisons. There was also no significant relationship between changes in abundance of species and traits such as number of host fish, infection strategy or host specificity (Table 3, A1).

After the drought one of the species not found at any sites was one of the smallest (*P. riddellii*, 62 mm, equilibrium species). Similarly, the three species [*Leaunio lienosus* (Conrad, 1834), *O. arkansasensis*, and *Strophitus undulatus* (Say, 1817)] which were not found at any sites after the flood were somewhat smaller (ranging between 55 and 100 mm in length,

Table 3). Between 2002 and 2018 the five species that were not found or declined significantly were also smaller (62–80 mm max. shell length with the exception of *T. nobilis* (114 mm; Table 3)). In contrast, all species with increases in CPUE after the drought were >140 mm except for *Toxolasma* sp. (opportunistic) and *Obliquaria reflexa* (Rafinesque, 1820; periodic species, Table 3). Similarly, the species which increased considerably in CPUE (>10 p-H total CPUE) were larger (120–200 mm in length) post flooding and over the longer term except for *O. arkansasensis* (55 mm). It should be noted that small individuals were detected both in 2014 and especially in 2018, when the substrate was searched not only by tactile searches, but softer sediment was also rinsed through a mesh of 500  $\mu\text{m}$ .

#### Discussion

In contrast to other shorter-lived macroinvertebrates with higher mobility, the extreme disturbance events appeared to have long-lasting effects on the communities of the more sessile and longer-lived unionids in this study. The high intensity of the extreme climate events (most intense drought in 2011/2012 since the 1950s, most rainfall produced by any tropical hurricane in United States' history in 2017) likely contributed to the long-lasting effects. This is congruent with recent findings of an experimental study, that an increase in disturbance intensity (through global climate change) may pose a bigger threat to biodiversity than more frequent but less intense disturbances (Jaquet & Altermatt, 2020). Drought had the most detrimental impact leading to community-wide declines, whereas flooding led to shifts in community composition and spatial distribution. Over the long-term both large declines and significant community shifts occurred in accordance with our hypotheses.

A community shift was most obvious in the long-term dataset, where the dominance of equilibrium species (Pleurobemini and Quadrulini) shifted to mostly opportunistic and periodic species (Amblemini and Lampsilini), which is certainly not unique to freshwater mussels. Records of (long-term) shifts to more opportunistic species in response to human impact and climate change can be found from different types of ecosystems, for example, coral reefs (De Bakker et al., 2016), marine molluscs (Tomašových

et al., 2018), terrestrial ants (Leal et al., 2017) and freshwater mussels (Metcalfe-Smith et al., 1998). The more pronounced community shift in the longer-term data compared to immediately after flooding (survey in 2018 after flooding in 2017) was largely driven by increases of opportunistic and periodic species and not necessarily larger declines in equilibrium species. This can be explained by differences in a species' ability and speed to recover and colonize habitat, which will not be detectable soon after a disturbance as successful recruitment and growth into detectable adult stages (takes at least a few years) has not occurred yet. The increase of Amblemini, represented only by *A. plicata*, may have been facilitated by it being more thermally tolerant compared to other species (Atkinson et al., 2014; Galbraith et al., 2010).

Although some mussel species may evade high-flow events by burrowing into the substrate (Schwalb & Pusch, 2007), the effects of extreme flooding can be severe (Hastie et al. 2003). For example, Hastie et al. (2001) noted a total mortality of ~50,000 individual mussels, and some transects suffered a loss of at least 40% of the population. While we found a decline in unionids at some sites in response to the extreme flooding caused by Hurricane Harvey, we detected an increase at most sites in Pine Island Bayou which is a lower unit of the Big Thicket. Interestingly, mussels in Pine Island Bayou showed marks of physical damage, which may have occurred during downstream transport during the flooding, and the increased numbers could be the results of dispersal from upstream. Because of the protection of the BTNP, much of the floodplain and riparian area is heavily forested and undisturbed, and extreme flooding would most likely lead to more severe declines in rivers with more degraded habitat, as mussels are transported into unsuitable habitat, leading to population declines and reducing population recovery (Karatayev et al., 2020).

Structural heterogeneity may be important in buffering the impact of flooding at some sites and river sections by providing smaller (e.g., roots of trees) and larger-scale flow refuges (especially backwaters). For example, around the area of Village Creek State Park and downstream to the Neches River (sites 18, 21, 23–29, Fig. 1), the stream contained ample large woody debris and was well connected to the densely forested floodplain. These conditions likely decreased bed scour during the catastrophic flooding events and

dense patches of mussel beds were found post-flood. Woody debris may also be beneficial during stream drying by providing refuges for freshwater mussels (Golladay et al., 2004). Log-jams are often the only stable instream structures in Coastal Plain streams (Michener et al., 1998), and mussels have been found downstream of or in log-jams (especially the state listed *P. amphichaenus*, Tarter, 2019). Our post-hurricane survey also found 25 small unionids (ranging from <5 mm to <30 mm in length) in backwaters of the Lower Neches River, indicating signs of recent recruitment (see Tarter, 2019 for details). Backwaters are known to be important breeding ground for fish (e.g., Sheaffer et al., 1986); they also seem to be important recruitment habitat for freshwater mussels and need better protection.

One threat for these backwater habitats is severe drought. There is anecdotal evidence indicating that several backwaters and stream segments of the Big Thicket were dry or near dry during the extreme drought in 2011/12. During droughts, mussels can be subjected to thermal stressors and, as water levels decrease, can become stranded on dry land where they are exposed to terrestrial predation and desiccation (Bond et al., 2008; Walters & Ford, 2013; Archambault et al., 2014). Declines in mussel species richness, abundance and occupancy all suggested that the exceptional drought in 2011 led to large declines of mussel populations (overall > 50%). This has also been reported from other rivers in Texas (Mitchell et al., 2019) and elsewhere (e.g., Haag & Warren, 2008) and can lead to declines in the ecosystem services they provide (Vaughn et al., 2015; Vaughn, 2018). However, some long-term impacts may have also played a role as the pre-drought survey (2002) occurred several years before the extreme drought in 2011 and Hurricane Ike occurred in 2008. In contrast to flooding where flow refuge may dampen the negative impact on mussel communities in general, potential drought refuges that do not dry out, such as deeper pools, may still experience high temperatures detrimental to unionids and the lentic conditions may only support opportunistic species and probably some periodic species adapted to such conditions.

Mussels in general recover slowly after a disturbance (Haag, 2012). It is possible that some recovery occurred after the drought at least for some species and led to a somewhat smaller decline (overall -53% of CPUE) in the long-term dataset compared to

post-drought in 2014 (overall -65% of CPUE). Protection of mussels from the additional impact of flooding in 2017 in the backwaters (see above) may have facilitated such a recovery.

More focus on backwater habitat sampling in 2018 and misidentification of species in the historical dataset may have contributed to some apparent changes in mussel communities, as species with similar morphology [e.g., *Quadrula quadrula* (Rafinesque, 1820) and *T. nobilis*] can be difficult to differentiate and identification in this study (2018 sampling) was enhanced by genetic analysis of tissue samples. However, it is unlikely that misidentification affected the major patterns we observed. We also acknowledge that the analysis of different disturbance effects included a different set of sites (Table 4), but data from the same sites were used for each analysis.

Although there was no clear relationship with size, species that were apparently extirpated tended to be smaller and species that increased in abundance tended to be larger. A relationship between body size and conservation status with smaller species being more imperiled has been found by previous studies (Strayer, 2008; Schwalb et al., 2011). Larger species with sculpturing may be less likely to be dislodged during flooding compared to thinner and smooth shelled species (Watters, 1994; Levine et al., 2014), although burrowing behavior may also play a role (Schwalb & Pusch, 2007; Troia & Ford, 2010). Differences in search methods can also lead to differences in the detection of differently sized mussels (Sanchez and Schwalb, 2021). However, all surveys used in this study used the same tactile methods and searched the substrate. If there is a bias, it should be toward smaller individuals in 2018 as sieves were also used to detect recruitment. Hence an increase in larger species in 2018 should reflect an actual increase and not a sampling bias.

In addition to the extreme disturbance events, other human impacts may have also affected mussels in the study area. For example, near the most upstream site in Little Pine Island Bayou, surface dissolved oxygen levels as low as 2.17 mg/L have been recorded during high temperature events (Kleinsasser & Linam, 1987) and Pine Island Bayou is considered an impaired waterway not meeting criteria for aquatic life due to continued reports of low dissolved oxygen (TCEQ, 2020). However, water quality in this part of the Neches River Basin is not a new threat but was

already a problem before our historical comparison (pre 1970s), when regulations started to improve water quality in that area (Harrel & Hall, 1991). The impacts of infrastructure and oil and gas operations in the region should also be carefully evaluated.

An important impact of climate change for coastal areas is saltwater intrusion, which is driven by sea level rise, storms and tides, droughts, ground and surface water extraction withdrawals and hydrologic connectivity (Tully et al., 2019). The construction of a ship channel through Sabine Lake in the early 1900s, along with innumerable pipeline canals, has promoted saltwater intrusion in the Big Thicket (White & Tremblay, 1995). As few unionid species can tolerate high levels of salinity (e.g., opportunistic species such as *Sagittunio subrostratus* (Say, 1831), *P. grandis*, and *U. suborbiculata*), survey sites were restricted to the stream reaches upstream of the saltwater barrier in the Neches River. Interestingly, in 2018 (post-flood), *G. rotundata*, a species known to be tolerant of brackish water (Johnson et al., 2018), was the most abundant species in the Pine Island Bayou sub-basin. Similar increases in *G. rotundata* were found in the Pearl River in Louisiana after Hurricane Katrina in 2005 (Brown et al., 2010). In addition, some smaller individuals of *Rangia cuneata* (Sowerby, 1832), an estuarine bivalve species that requires saline water to complete transformation through the larval stage (Hopkins et al., 1973), were noted in this reach in 2018, but not 2014, which may indicate a recent spread triggered by saltwater intrusion.

The synergistic effects of interior wetland subsidence and shoreline erosion have caused the Neches River Basin to be subject to the most extensive loss of contiguous coastal wetlands in the state, including those of the Lower Neches River (White & Tremblay, 1995). These wetlands compose the backwater refuges in the Big Thicket where rare and threatened species (along with signs of recruitment) were predominantly found in this study. Backwaters and wetlands may act as crucial refuges for extreme climatic events, not just for mussels, but also fish and other riverine organisms, and need to be protected as part of a management plan to mitigate the impact of climate change in subtropical rivers.

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**Data availability** Data are available from the authors upon reasonable request.

#### Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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