

# Conservation implications of late Holocene freshwater mussel remains of the Leon River in central Texas

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**Abstract** Zooarchaeology is the study of animal remains (bone, shell, antler, and other organic tissues) from archaeological sites, which can provide conservation biologists with data on human–environmental interactions with greater time depth than historical records. Such data are of interest because they can be used to study whether or not contemporary animal communities (in this case of freshwater mussels) have changed in terms of species composition or range as a result of human-induced changes to habitat, which is essential for determining a species' conservation status and formulating actions to protect remaining populations. This study considers whether or not the

taxonomic composition of the freshwater mussel community from the Leon River in central Texas differs between the late Holocene and today. Specifically, we analyzed two zooarchaeological assemblages and compared those results with recent surveys conducted within the Leon River. Three species proposed for listing under the Endangered Species Act are found in the zooarchaeological record, of which two are now extirpated from the river basin (*Truncilla macrodon* and *Fusconaia mitchelli*). The results of this study provide an example of how zooarchaeological data can be used to evaluate mussel community change through time and provide evidence of range curtailment for threatened mussel species.

**Keywords** Freshwater mussels · Conservation biogeography · Applied zooarchaeology · Range constriction · Conservation baselines

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## Introduction

As freshwater mussels (Family: Unionidae) provide many ecosystem services to the human populations reliant on rivers as a source of freshwater, their conservation is important for ensuring healthy rivers (Vaughn et al., 2015). These organisms are sensitive to anthropogenic changes to the natural flow regime of streams due to their sedentary adult and parasitic juvenile life stages, and thus have steadily declined (Vaughn & Taylor, 1999; Haag & Warren Jr., 2008;

Nobles & Zhang, 2011; Shea et al., 2013; Gates et al., 2015). Of the almost 300 species native to North America, approximately 10% are now considered extinct and 65% are imperiled (Haag & Williams, 2014). In Texas, there are currently 15 species listed as state threatened (Texas Administration Code, 2000, as amended) of which six are candidates for protection under the United States Endangered Species Act (hereafter ESA; Endangered Species Act, 1973, as amended). Of these six species, five are endemic to central Texas, making rivers in this region important for the conservation of unionid diversity in the state (Burlakova et al., 2011). This fact, coupled with realization that increasing human demands for water in central Texas (Wolaver et al., 2012) may impact remaining populations, has prompted state and federal agencies to identify mussel conservation goals and research needs (Neves, 1995; Haag & Williams, 2014; Freshwater Mollusk Conservation Society, 2016). Two of these goals center on the need for increased understanding of the geographic distribution of mussels and for more information on the status and trends of individual populations.

Knowledge about the geographic distributions of mussels, past and present, varies considerably by species and region. For states like Texas, where mussel conservation efforts are relatively new, the distribution of mussels is generally known, but detailed knowledge of the status of mussel populations within specific drainages or their historical distribution is lacking (Tsakiris & Randklev, 2016). Similarly, knowledge of the status and trends of individual populations are unknown, though this is not unique to Texas (see Haag & Williams, 2014). This paucity of information poses two major problems for mussel conservation efforts in Texas. First, a lack of species-distribution information means that inferences regarding the status of a given species, regardless of whether it is considered rare or common, may not be correct, which can then lead to flawed baselines for conservation and restoration efforts (Rick & Lockwood, 2013). Second, if population dynamics are unknown, then inferences regarding the stability or long-term viability of a population might be incorrect (Humphries & Winemiller, 2009).

Applied zooarchaeology is the study of faunal remains from archaeological sites to provide information relevant to conservation biology (Lyman, 1996; Cannon & Cannon, 2004; Peacock, 2005; Lyman,

2012; Peacock, 2012; Wolverson & Lyman, 2012a; Scharf, 2014; Dombrosky et al., 2016; Wolverson et al., 2016). Zooarchaeological data can be used to understand ecological processes that happen on ecological and evolutionary time scales (Landres, 1992; Swetnam et al., 1999; Scharf, 2014). Specifically, zooarchaeological data can be used to improve knowledge of the biogeographic distribution of mussels (Peacock et al., 2012; Wolverson & Randklev, 2016), but such data can also potentially provide evidence of mussel population dynamics such as maximum age and maximum growth (Christian et al., 2005; Weber, 2005; Randklev et al., 2009). In addition, historical and zooarchaeological data can inform conservation efforts with long-term data prior to industrial, post-industrial, and/or agricultural human-mediated impacts that occurred after the Euroamerican period began in North America (Alagona et al., 2012; Balaguer et al., 2014).

Applied zooarchaeology of freshwater mussel remains has informed conservation by providing evidence of taxonomic and/or community structure shifts and changes in the distribution of unionid populations. Since early research by Ortmann (1909), zooarchaeological specimens have been used as a reference for the prehistoric taxonomic composition of mussel communities in heavily impacted rivers (Parmalee et al., 1982; Parmalee & Bogan, 1986; Parmalee & Polhemus, 2004). Zooarchaeological data have been used to describe new species and explore prehistoric extinctions (Williams & Fradkin, 1999). Such data have also been used to address how unionid community structure has changed in river basins (Bogan, 1990; Miller et al., 2014; Mitchell & Peacock, 2014). More recently zooarchaeological unionid specimens have been used to discuss shifts in unionid ranges (Randklev et al., 2010b; Peacock et al., 2012; Randklev & Lundeen, 2012; Wolverson & Randklev, 2016). With this in mind, zooarchaeological data represent an under-utilized source of information for conservation and wildlife management in the southwestern United States.

The purpose of this applied zooarchaeological study is to evaluate whether or not the unionid community from the Leon River in central Texas changed between the late Holocene and today, thereby establishing a pre-Euroamerican baseline for community composition. Specifically, we analyzed mussel remains from site 41HM61 and multiple small

zooarchaeological assemblages surrounding Belton Lake on the Leon River in central Texas. The relative abundances of the resulting zooarchaeological analysis are reported. We discuss nominal-scale differences in taxonomic composition between the late Holocene zooarchaeological assemblages and the contemporary unionid fauna of this river. Although we discuss the broader mussel community in the Leon River, special attention is given to species that are of conservation concern.

## Materials and methods

### Study area

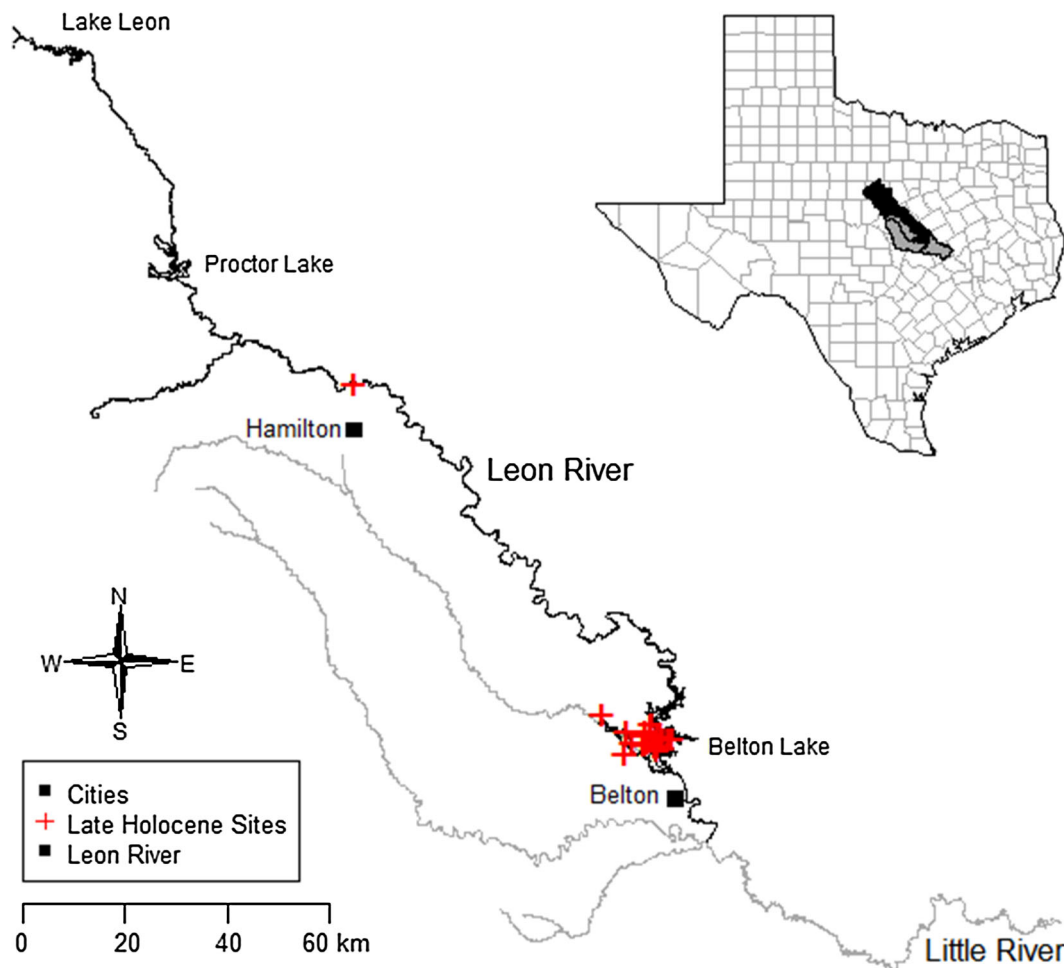
The Leon River is a tributary of the Brazos River in central Texas, located in the Great Prairie and Cross Timbers Forest ecoregions (Fig. 1; Tharp, 1939; Rose & Echelle, 1981). This region has a sub-humid climate, with hot, dry summers and cold, wet winters (Bomar, 1983). The Leon River is approximately 450 km long from its headwaters and has an average discharge of 0.396 m<sup>3</sup>/s at Hamilton (USGS 08100000) and 0.963 m<sup>3</sup>/s at Belton (USGS 08102500), though droughts are common in the summer months (June–September; United States Geological Service, 2015). The landscape surrounding the Leon River is dominated by agricultural and urban land, whose runoff has detrimental impacts on water quality (Randklev et al., 2013a). In 1996, the Leon River was listed in the State of Texas Clean Water Act Section 303(d) due to elevated levels of bacteria (Clean Water Act, 1972 as amended). Since then, a watershed protection plan has been developed to improve water quality for recreational use. Because freshwater mussels are sensitive to changes in hydrology and water quality, their presence and abundance in rivers is an indication of the river's ecological robustness or health (Strayer, 2008).

Recent studies on the Leon River have noted that mussel fauna appears to be declining in species richness due to river impoundments and poor water quality (Randklev et al., 2013a). Historically, the mussel fauna comprised sixteen species including *Fusconaia mitchelli* (Simpson in Dall, 1896), *Truncilla macrodon* (Lea, 1859), and *Quadrula houstonensis* (Lea, 1859), which are endemic to central Texas and are of conservation concern. Specifically,

*Q. houstonensis* and *T. macrodon* are candidates for listing under the ESA, while *F. mitchelli* is petitioned for listing (Table 1; Endangered Species Act, 1973, as amended; Texas Administrative Code, 2000, as amended; Randklev et al., 2013a; United States Fish and Wildlife Service, 2014). All three species historically occurred in the Colorado and Brazos River drainages with *F. mitchelli* also occurring in the Guadalupe drainage (Fig. 2; Howells et al., 1996; Howells, 2013). Recently *Q. houstonensis* has been found to be abundant and widely distributed in the lower Brazos River. *Fusconaia mitchelli* and *T. macrodon* were considered extirpated until populations were recently found in the Guadalupe and Brazos River basins (Randklev et al., 2010a, 2012, 2013c). Extant *F. mitchelli* populations are located in the San Saba (Colorado drainage), Llano (Colorado drainage), Guadalupe (downstream from Gonzales), and Little and San Gabriel Rivers (Brazos drainage; Randklev et al., 2012, 2013b; Sowards et al., 2013). New populations of *T. macrodon* have been recently found in the Colorado and Brazos Rivers (Randklev & Burlakova, personal communication). For the Leon River, to date, no live individuals or populations of *F. mitchelli* and *T. macrodon* have been found, but live individuals and shell material have been observed in the Little River, which the Leon River joins (Fig. 1; Randklev et al., 2012; Randklev et al. unpublished data). While there is a short historical record for the Leon River basin and a recent modern survey completed in 2011 (Randklev et al., 2013a), zooarchaeological data have received little attention and can provide a pre-Euroamerican baseline for mussel conservation efforts.

### Mussel data-late Holocene

Freshwater mussel remains were analyzed from two assemblages: (1) 41HM61 in northern Hamilton county (Fig. 1) and 2) eighteen separate cave sites that surround Belton Lake (Fig. 1; Randklev, 2010). The Belton Lake assemblages are combined because they represent the same faunal community and many have low sample size (only three sites have more than 25 shells or shell fragments; Popejoy et al., 2016). The 41HM61 assemblage was deposited from 2700 BP to 1500 BP (Weinstein, 2015). For each assemblage, mussel shells were identified to species based on pseudocardinal teeth, umbo, shell shape, and sculpture



**Fig. 1** Map of the Leon River and nearby rivers in central Texas. The Leon River is depicted in black, with its watershed boundary shown in *black* within the state of Texas. *Red+* signs denote the locations of zooarchaeological assemblages

and then were tallied. State and regional taxonomic guides (Howells et al., 1996; Williams et al., 2008; Howells, 2013) as well as reference specimens housed at the University of North Texas Laboratory of Zooarchaeology were consulted for identification criteria. To be counted, a specimen (complete shell or fragment) must have included pseudocardinal teeth and umbo, which constitutes a non-repetitive element (NRE; Giovas, 2009; Harris et al., 2015). These characters are useful for quantification because they are present at all life stages, are the densest part of the shell and thus preserve well, and are taxonomically diagnostic, in many cases to genera or species. Specimens were identified to the lowest taxonomic category possible. Following guidelines by Driver

(41HM61 is located near Hamilton city, the Belton Lake assemblages are aggregated around Belton Lake). The modern unionid dataset was taken from field surveys conducted between Lake Proctor and the confluence of the Leon and Little River

(1992, 2011) and Wolverton (2013), all identifications were validated using a comparative collection with shells of species from the Brazos and its tributaries.

#### Mussel data-contemporary

Contemporary mussel data for the Leon River come from a longitudinal survey performed by Randklev et al. (2013a) between May and August 2011. The focus of the survey was to examine river-wide patterns of mussel diversity in the mainstem of the Leon River between Lake Leon and Belton Lake. Site selection was informal and based on the presence of potential mussel habitat (e.g., riffle, runs, woody debris, back-water, undercut banks) and whether the site was in an

**Table 1** Taxonomic abundances of freshwater mussels in the late Holocene and modern datasets

Tribe	Taxa	41HM61	Belton lake	Modern
Anodontini	<i>Arcidens confragosus</i> (Say, 1829)	0.3%	0.2%	0.2%
	<i>Pyganodon grandis</i> (Say, 1829)			1.0%
	<i>Utterbackia imbecillis</i> (Say, 1829)			0.3%
Lampsilini	<i>Cyrtonaiaa tampicoensis</i> (Lea, 1838)	0.6%	1.1%	
	<i>Lampsilis</i> sp.	11.8%		
	<i>Lampsilis hydiana</i> (Lea, 1838)	3.2%	2.7%	
	<i>Lampsilis teres</i> (Rafinesque, 1820)	10.8%	1.0%	5.6%
	<i>Leptodea fragilis</i> (Rafinesque, 1820)			11.1%
	<i>Potamilus purpuratus</i> (Lamarck, 1819)			0.3%
	<i>Toxolasma</i> sp. (Barnes, 1823)	0.6%		
	<i>Truncilla</i> cf. <i>macrodon</i> (Lea, 1859)*	1.6%		
	<i>Fusconaia mitchelli</i> (Dall, 1896)*	2.9%	7.2%	
Quadrulini	<i>Megalonaia nervosa</i> (Rafinesque, 1820)	5.1%	0.4%	4.3%
	<i>Quadrula</i> sp.	10.8%	0.2%	
	<i>Quadrula apiculata</i> (Say, 1829)	4.1%	3.8%	1.5%
	<i>Quadrula houstonensis</i> (Lea, 1859)*	6.4%	22.5%	30.6%
	<i>Quadrula verrucosa</i> (Rafinesque, 1820)	12.1%	2.5%	27.4%
	<i>Uniomereus tetralasmus</i> (Say, 1831)			0.0%
Amblemini	<i>Amblema plicata</i> (Say, 1817)	29.6%	58.5%	17.6%
	Total NRE	314	525	2072

Asterisk denotes species of conservation concern. Tribe according to Haag (2012). Percentages reflect total NRE identified to that taxa. Unidentified NRE are not included in this table. The 41HM61 assemblage has 85 unidentified specimen; the Belton Lake assemblages have 38 unidentified specimen

area that could be reached from a point of public access. The survey methodology followed that of Metcalfe-Smith et al. (2000), and was designed to provide guidance on the amount of effort needed to locate rare species by collecting as many individuals as possible during one or more search periods. Specifically, surveyors searched for mussels using visual and tactile (i.e., handpicking) techniques for a minimum of 1 person-hour (where 1 p-h = 60 min/number of surveyors). Additional 1 p-h searches were added until no new species were recorded. A total of 52 sites were surveyed, the size of the search area within each site ranged from 150 to 2132 m<sup>2</sup> (median = 818 m<sup>2</sup>), and the total amount of time spent surveying a site ranged from 1 to 26 person-hours (median = 2.5 person-hours). Relative abundance of mussels are calculated, from both the zooarchaeological and modern data, by dividing the number of mussels identified to a species by the total number of identified mussels in the data.

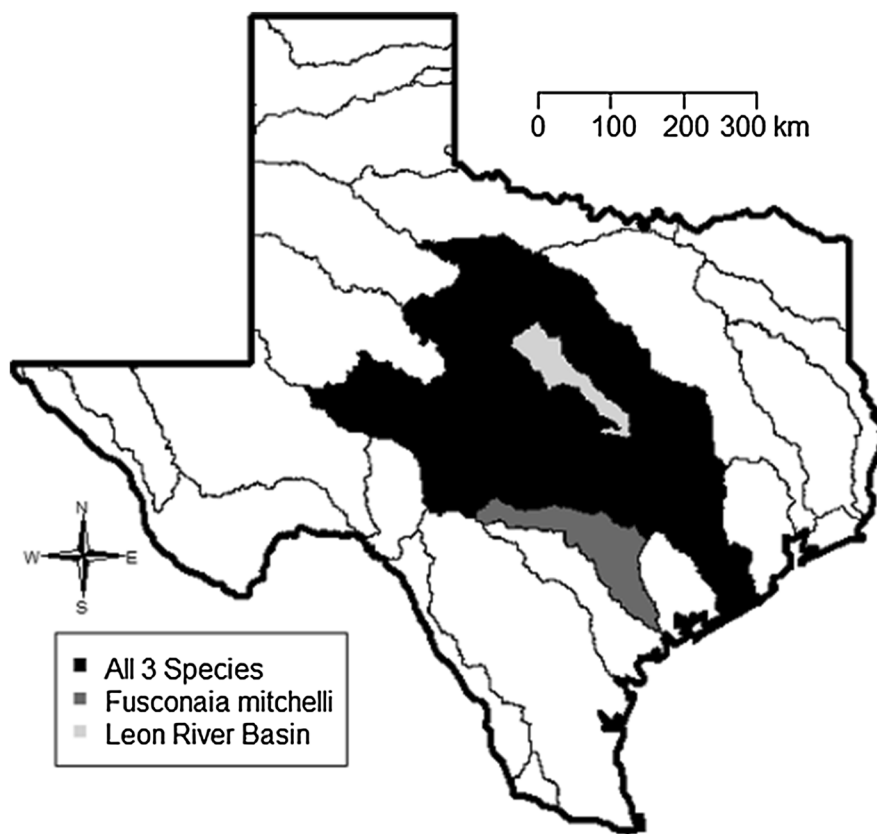
### Comparative analysis

The objective of this study was to determine if the unionid community in the Leon River has changed

between the late Holocene and today. We compared the taxonomic composition of the datasets to evaluate potential species extirpations and infiltrations. An interpretive tool that assesses whether unionid taxa are expected to be abundant or rare in zooarchaeological assemblages (based on a species' shell identifiability and robusticity) is used to evaluate missing unionid species (Wolverton et al., 2010; Popejoy et al., 2016). Considering only shell preservation, unionids that produce robust (dense and spherical) shells and sculpturing, which increases identifiability in fragmented specimens, should be more abundant in zooarchaeological assemblages than unionids that produce fragile, non-sculptured shells. The very fragile-shelled species unlikely to preserve in the zooarchaeological assemblages include: *Leptodea fragilis* (Rafinesque, 1820), *Pyganodon grandis* (Say, 1829), *Uniomereus tetralasmus* (Say, 1831), and *Utterbackia imbecillis* (Say, 1829). Use of this interpretive framework aids in determining if differences between the late Holocene and modern unionid assemblages are related to poor preservation of zooarchaeological shell.

While the robusticity/identifiability framework addresses preservation as a cause of mussel absence

**Fig. 2** Watersheds in which *F. mitchelli*, *T. macrodon*, and *Q. houstonensis* have been found historically. All three species are endemic to the Colorado and Brazos River basins. *Fusconaia mitchelli* is also found in the Guadalupe drainage. These polygons do not necessarily depict the range of these species. Watershed boundaries provided by National Hydrology Map (USGS, 2015) and mussel range definitions provided by Howells (2013)



from zooarchaeological assemblages, it does not eliminate the possibility of differential representation due to prehistoric cultural preference (based on mussel taste or collection habitat) or ecological change. However, these concerns should be treated as hypotheses and tested, rather than be assumed as limitations inherent to all zooarchaeological datasets. For example, Peacock et al. (2012) found, based on analysis of shell chemistry and nestedness, that shells from archaeological deposits typically derive, though not always, from waterbodies adjacent to those deposits, and thus concern about representativeness related to long distance transport of shell by prehistoric humans is unfounded. Similarly, Parmalee & Klippel (1974) demonstrated that mussels offer low caloric returns, which from an optimal foraging perspective suggests that prehistoric humans were likely collecting mussels from local streams not transporting them from distant waterbodies. A consideration with zooarchaeological data is differential representation of species due to prehistoric humans targeting mainly lotic habitats (e.g., riffle/shoals); therefore, species that primarily

occupy lentic environments (e.g., deep pools) may not have been collected (Haag, 2012). However, a more parsimonious explanation for the absence of lentic species from zooarchaeological assemblages is a difference in shell preservation between lotic and lentic species (Wolverton et al., 2010). Changes to river flow and substrate could result in disparities between zooarchaeological and modern unionid samples (Parmalee et al., 1982; Warren, 1991); it is difficult to assess whether these changes to river habitat are the result of natural or anthropogenic habitat change. To account for these possibilities, we focus on unionid species that are missing from the contemporary mussel community.

## Results

In total, seventeen unionid species were identified from the Leon River late Holocene assemblages. Site 41HM61 was the richest fauna with fourteen taxa (NRE = 314), whereas eleven taxa were identified



from the Belton Lake assemblages (NRE = 525; Table 1). For 41HM61, *Amblyma plicata* (Say, 1817; 30%), *Quadrula verrucosa* (Rafinesque, 1820; 12%), *Lampsilis teres* (Rafinesque, 1820; 11%), and *Q. houstonensis* (6%) accounted for almost half of the individuals identified from this assemblage. For the Belton Lake assemblage, *A. plicata* (59%), *Q. houstonensis* (23%), and *F. mitchelli* (7%) were the most abundant species. Comparing the two zooarchaeological assemblages, the Belton Lake assemblages comprise more species of conservation concern; the exception is *T. cf. macrodon*, which was only observed in 41HM61. The contemporary mussel fauna, based on Randklev et al. (2013a), comprises *Q. houstonensis* (31%), *Q. verrucosa* (27%), *A. plicata* (18%), and *L. fragilis* (11%), which differs from both of the late Holocene assemblages (Table 1).

Overall, the late Holocene assemblages lack fragile-shelled, lentic species that are found in the modern mussel fauna. Species such as *L. fragilis*, *P. grandis*, and *U. imbecillis* are present in the modern fauna but absent from the late Holocene assemblages (Table 2). This disparity is likely a result of poor preservation of shells of those species, though it could also be a function of increase in lentic habitat and loss or degradation of lotic habitat in the Leon River, or both. Shells of mussels missing from the modern assemblage, but present in the late Holocene datasets include *Cyrtornaias tampicoensis* (Lea, 1838), *F. mitchelli*, *Lampsilis hydiana* (Lea, 1838), and *T. macrodon* (Table 2). While *F. mitchelli* is moderately abundant in the late Holocene dataset, the other missing species are generally rare in the late Holocene assemblages. *Potamilus purpuratus* (Lamarck, 1819) is absent from both late Holocene datasets, which could be the result of poor preservation or of historical introduction to the river basin (Table 2). Shells of *P. purpuratus* exhibit moderate robusticity; thus, if present during the late Holocene, we would expect to find them in zooarchaeological assemblages (Wolverton et al., 2010). Both the late Holocene and the modern communities include *Arcidens confragosus* (Say, 1829; Table 2), which is absent in the historical record (Strecker, 1931; Howells, 2006). Since this species is typically rare, but widely distributed in Texas rivers (Howells et al., 1996), the zooarchaeological data confirm the presence of this species in the Leon River.

A taphonomic analysis of the 41HM61 and Belton datasets found that the assemblages were dominated

by species with moderately robust (dense and spherical) shells (Popejoy et al., 2016). Mussels with shells that have low-moderate robusticity and were present in the zooarchaeological assemblages are *L. hydiana*, *L. teres*, and *Megaloniaias nervosa* (Rafinesque, 1820). Shells of *T. macrodon* are not spherical, which decreases their probability of preservation, but were still identified in the zooarchaeological assemblages. When considering shell preservation in light of the implications of this paper, it is evident that despite differential preservation, the unionid community has changed in the Leon River since the late Holocene.

## Discussion

Our results show that the late Holocene unionid community differs from the modern unionid community. We found several species present in the zooarchaeological record that are not known to occur or are now absent in the Leon River. The patchy distribution of *L. hydiana* in central Texas has caused some malacologists to speculate that it was introduced into the Leon River during reservoir construction in the 1950s. Zooarchaeological evidence supports the historical account that *L. hydiana* is endemic to the Leon River and was historically “rather common” (Strecker, 1931, p. 39). The presence of *L. hydiana* in the zooarchaeological record provides evidence that range constriction has likely occurred for this species. Alternatively, this species may simply be exceptionally rare in the upper Leon and thus have not been recorded in contemporary surveys.

The zooarchaeological record contains shell remains of two extirpated species of conservation concern: *F. mitchelli* and likely *T. macrodon*. Specimens from the 41HM61 assemblage (*T. cf. macrodon*,  $n = 5$ ) are highly fragmented, which prevented positive identification, but they compare well with *T. macrodon* shells from nearby tributaries. Assuming the zooarchaeological specimens are from *T. macrodon*, the presence of shells of these species in the zooarchaeological assemblages and subsequent absence from the surveys in the Leon River in 2011 indicates that the distribution of *F. mitchelli* and *T. macrodon* in the Brazos River watershed has been reduced since the late Holocene. As more contemporary biogeographic data are produced, the distribution of these species will be better defined and the amount

**Table 2** Mussel community composition of the Leon River: Archaeological data through 2011

Tribe	Taxa	Late Holocene 750 BCE–450 CE	Strecker 1931 CE	TPWD 1994–2006 CE	Randklev et al. 2010b CE
Anodontini	<i>Arcidens confragosus</i>				
	<i>Pyganodon grandis</i>				
	<i>Utterbackia imbecillis</i>				
Lampsilini	<i>Cyrtonaias tampicoensis</i>				
	<i>Lampsilis hyadiana</i>				
	<i>Lampsilis teres</i>				
	<i>Leptodea fragilis</i>				
	<i>Potamilus purpuratus</i>				
	<i>Toxolasma</i> sp.				
	<i>Truncilla</i> cf. <i>macrodon</i> <sup>a</sup>				
Pleurobemini	<i>Fusconaia mitchelli</i> <sup>a</sup>				
	<i>Megalonaias nervosa</i>				
Quadrulini	<i>Quadrula apiculata</i>				
	<i>Quadrula houstonensis</i> <sup>a</sup>				
	<i>Quadrula verrucosa</i>				
	<i>Unio merus tetralasmus</i>				
Amblemini	<i>Amblema plicata</i>				

Dark cells represent the presence of that taxa in the dataset. Time period represented is listed below the dataset name. Time approaches the present as you move from left to right; BCE denotes Before Common Era, while CE denotes Common Era

<sup>a</sup> Species of conservation concern. TPWD represents surveys reported by Howells (2006). Tribes from Haag (2012). Data from Randklev et al. (2013a)

of range constriction within the Brazos River and its tributaries can be more carefully evaluated, informing potential ESA listing.

Analysis of freshwater mussel remains from zooarchaeological assemblages also have implications for understanding the river ecosystem—specifically the presence of host fishes. While fish remains are sometimes found and identified in zooarchaeological assemblages, records are more complete for fish with diagnostic jawbones, otoliths, vertebrae, or scales (Colley, 1990). Given the unionid taxa present in these zooarchaeological assemblages, we expect catfish (Ictaluridae), gar (Lepisosteidae), bass and sunfish (Centrarchidae), and minnows (Cyprinidae) to have been present in the late Holocene Leon River (Howells, 2013). Within the 41HM61 assemblage, the remains of gar, minnow, and finfish (Perciformes) were identified (Weinstein, 2015). By considering the host fish of the unionids present in the zooarchaeological assemblage, conservationists can evaluate whether host extirpation, loss of mussel habitat, or both, has contributed to mussel extirpations in the Leon River.

Zooarchaeological and historical data can be used to evaluate range constrictions/expansions, inform

species reintroductions, and to evaluate different stressors on freshwater systems (Humphries and Winemiller, 2009). Maps that incorporate zooarchaeological data can illustrate range constrictions/expansions and population refugia through time (Peacock, 2012). These maps can help focus future survey efforts and inform species reintroduction locations. For example, by consulting zooarchaeological data, malacologists were able to find remnant populations of *Plethobasus cyphus* (Rafinesque, 1820), a candidate for federal listing, within the Big Sunflower River in Mississippi (Jones et al., 2005; Peacock, 2012). For the Leon River, this study provides evidence that *F. mitchelli* and *T. macrodon* were present in the late Holocene. While extant populations of *F. mitchelli* and *T. macrodon* are present in the Little River, these populations cannot naturally recolonize the Leon River because of Lake Belton, which separates the two rivers, its host fish assemblage, and the mussel communities. If *F. mitchelli*, *T. macrodon*, or *Q. houstonensis* is listed under the ESA, our results provide an historical justification for the translocation of adults from extant populations or release of hatchery-propagated individuals into the Leon River above Lake Belton.



Zooarchaeological evidence can also help with corroborating species declines related to climate change and/or anthropogenic effects. For example, *Popenaias popeii* (Lea, 1857), Texas hornshell, inhabits the Rio Grande and Gulf Coast tributaries in Mexico and is a candidate for protection under the ESA (Howells, 2013). Recent genetic studies paired with ecological niche models of the remaining *P. popeii* indicate that the species experienced a population bottleneck during the Pleistocene era (Inoue et al., 2015). An analysis of available zooarchaeological data could be used to explicitly test this hypothesis and provide additional insight on *P. popeii*'s range in the Pecos River.

Zooarchaeological data provide useful baseline information that is rarely used by conservation biologists (Lyman, 2012; Wolverton & Lyman, 2012b), especially in areas less mussel-diverse than the Southeastern United States. This is unfortunate because the analysis of zooarchaeological datasets may lead to: (1) greater confidence in existing biogeographic hypotheses; (2) information on whether or not mussel community composition has changed over time; and (3) providing justification for and guidance of more intensive contemporary surveys and conservation efforts. Thus, zooarchaeological data like those presented in this study could play an important role in the United States Fish and Wildlife Service's species status assessments (a framework used for informing ESA decisions) and with guiding recovery activities for mussel species that become listed under the ESA. Regarding ongoing listing efforts in Texas, the absence of *F. mitchelli* and *T. macrodon* from the modern fauna, but their presence in both late Holocene assemblages, is evidence that both species are now extirpated from the Leon River. While the decision to list a species under the ESA is not solely based on range reduction, the extirpation of *F. mitchelli* and *T. macrodon* from the Leon River has undoubtedly affected both species' biological status by reducing their redundancy (i.e., ability to withstand catastrophic events such as those associated with climate change) and representation (i.e., genetic diversity that increases the probability that a species can adapt to environmental change). In turn, these reductions have likely decreased each species' overall viability and increased the likelihood of extinction for both in the near future. In summary, this article provides a case study on how zooarchaeological data

can be used for conservation biology and wildlife management and provides several recommendations for how these types of data can be used to support conservation activities for threatened mussel species.

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## References

- 31 Texas Administration Code § 65.175.
- Alagona, P. S., J. Sandlos & Y. F. Wiersma, 2012. Past imperfect: using historical ecology and baseline data for conservation and restoration projects in North America. *Environmental Philosophy* 9: 49–70.
- Balaguer, L., A. Escudero, J. F. Martín-Duque, I. Mola & J. Aronson, 2014. The historical reference in restoration ecology: re-defining a cornerstone concept. *Biological Conservation* 176: 12–20.
- Bogan, A. E., 1990. Stability of recent unionid (Mollusca: Bivalvia) communities over the past 6000 years. In Miller III, W. (ed.), *Paleocommunity Temporal Dynamics: the Long-Term Development of Multispecies Assemblies*. The Paleontological Society, Boulder: 112–136.
- Bomar, G. W., 1983. *Texas Weather*. University of Texas Press, Austin.
- Burlakova, L. E., A. Y. Karatayev, V. A. Karatayev, M. E. May, D. L. Bennett & M. J. Cook, 2011. Biogeography and conservation of freshwater mussels (Bivalvia: Unionidae) in Texas: patterns of diversity and threats. *Diversity and Distributions* 17: 393–407. doi:10.1111/j.1472-4642.2011.00753.x
- Cannon, K. P. & M. B. Cannon, 2004. Zooarchaeology and wildlife management in the greater yellowstone ecosystem. In Lyman, R. L. & K. P. Cannon (eds), *Zooarchaeology and Conservation Biology*. University of Utah Press, Salt Lake City: 45–60.
- Christian, A. D., J. L. Harris, W. R. Posey, J. F. Hockmuth & G. L. Harp, 2005. Freshwater mussel (Bivalvia: Unionidae) assemblages of the Lower Cache River, Arkansas. *Southeastern Naturalist* 4: 487–512.
- Clean Water Act, 1972. 33 United States Code §§1251–1387.
- Colley, S. M., 1990. The analysis and interpretation of archaeological fish remains. *Archaeological Method and Theory* 2: 207–253.
- Driver, J. C., 1992. Identification, classification and zooarchaeology. *Circaea* 9: 35–47.
- Driver, J. C., 2011. Identification, classification and zooarchaeology. *Ethnobiology Letters* 2: 19–39.
- Dombrosky, J., S. Wolverton & L. Nagaoka, 2016. Archaeological data suggest broader early historic distribution for blue sucker (*Cyprinus elongatus*, Actinopterygii, Catostomidae) in New Mexico. *Hydrobiologia* 771: 255–263.

- Endangered Species Act, 1973. 16 United States Code §1531–1544.
- Freshwater Mollusk Conservation Society, 2016. A national strategy for the conservation of native freshwater mollusks. *Freshwater Mollusk Biology and Conservation* 19: 1–21.
- Gates, K. K., C. C. Vaughn & J. P. Julian, 2015. Developing environmental flow recommendations for freshwater mussels using the biological traits of species guilds. *Freshwater Biology* 60: 620–635. doi:[10.1111/fwb.12528](https://doi.org/10.1111/fwb.12528)
- Giovas, C. M., 2009. The shell game: analytic problems in archaeological mollusc quantification. *Journal of Archaeological Science* 36: 1557–1564.
- Haag, W. R., 2012. *North American Freshwater Mussels: Natural History, Ecology and Conservation*. Cambridge University Press, Cambridge.
- Haag, W. R. & M. L. Warren Jr., 2008. Effects of severe drought on freshwater mussel assemblages. *Transactions of the American Fisheries Society* 137: 1165–1178.
- Haag, W. R. & J. D. Williams, 2014. Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels. *Hydrobiologia* 735: 45–60.
- Harris, M., M. Weisler & P. Faulkner, 2015. A refined protocol for calculating MNI in archaeological molluscan shell assemblages: a Marshall Islands case study. *Journal of Archaeological Science* 57: 168–179.
- Howells, R. G., 2006. *Statewide Freshwater Mussel Survey: Final Report*. Texas Parks and Wildlife Department, Austin.
- Howells, R. G., 2013. *Field Guide to Texas Freshwater Mussels*. BioStudies, Kerrville, TX.
- Howells, R. G., R. W. Neck & H. D. Murray, 1996. *Freshwater Mussels of Texas*. Texas Parks and Wildlife Press, Austin.
- Humphries, P. & K. O. Winemiller, 2009. Historical impacts on river fauna, shifting baselines, and challenges for restoration. *BioScience* 59: 673–684.
- Inoue, K., B. K. Lang & D. J. Berg, 2015. Past climate change drives current genetic structure of an endangered freshwater mussel species. *Molecular Ecology* 24: 1910–1926. doi:[10.1111/mec.13156](https://doi.org/10.1111/mec.13156)
- Jones, R. L., W. T. Slack & P. D. Hartfield, 2005. The freshwater mussels (Mollusca: Bivalvia: Unionidae) of Mississippi. *Southeastern Naturalist* 4: 77–92.
- Landres, P. B., 1992. Temporal scale perspectives in managing biological diversity. *Transactions of the North American Wildlife and Natural Resources Conference* 57: 292–307.
- Lyman, R. L., 1996. Applied zooarchaeology: the relevance of faunal analysis to wildlife management. *World Archaeology* 28: 110–125.
- Lyman, R. L., 2012. A warrant for applied palaeozoology. *Biological reviews of the Cambridge Philosophical Society* 87: 513–525.
- Metcalfe-Smith, J. L., J. Di Maio, S. K. Staton & G. L. Mackie, 2000. Effect of sampling effort on the efficiency of the timed search method for sampling freshwater mussel communities. *Journal of the North American Benthological Society* 19: 725–732.
- Miller, E. J., J. J. Tomasic & M. C. Barnhart, 2014. A comparison of freshwater mussels (Unionidae) from a late-Archaic archeological excavation with recently sampled Verdigris River, Kansas, populations. *The American Midland Naturalist* 171: 16–26.
- Mitchell, J. & E. Peacock, 2014. A prehistoric freshwater mussel assemblage from the Big Sunflower River, Sunflower County, Mississippi. *Southeastern Naturalist* 13: 626–638.
- Neves, R. J., 1995. Keynote address: A national strategy for the conservation of native freshwater mussels. *Conservation and Management of Freshwater Mussels II* 101: 1–10.
- Nobles, T. & Y. Zhang, 2011. Biodiversity loss in freshwater mussels: Importance, threats, and solutions. *Biodiversity Loss in a Changing Planet* 318: 17–162.
- Ortmann, A. E., 1909. The destruction of the fresh-water fauna in western Pennsylvania. *Proceedings of the American Philosophical Society* 48: 90–110.
- Parmalee, P. W. & A. E. Bogan, 1986. Molluscan remains from aboriginal middens at the Clinch River breeder reactor plant site, Roane County, Tennessee. *American Malacological Bulletin* 4: 25–37.
- Parmalee, P. W. & W. E. Klippel, 1974. Freshwater mussels as a prehistoric food resource. *American Antiquity* 39: 421–434.
- Parmalee, P. W. & R. R. Polhemus, 2004. Prehistoric and pre-impoundment populations of freshwater mussels (Bivalvia: Unionidae) in the South Fork Holston River, Tennessee. *Southeastern Naturalist* 3: 231–240.
- Parmalee, P. W., W. E. Klippel & A. E. Bogan, 1982. Aboriginal and modern freshwater mussel assemblages (Pelecypoda: Unionidae) from the Chickamauga Reservoir, Tennessee. *Brimleyana* 8: 75–90.
- Peacock, E., 2005. Environmental archaeology. *Journal of Alabama Archaeology* 51: 32–39.
- Peacock, E., 2012. Archaeological freshwater mussel remains and their use in the conservation of an imperiled fauna. In Wolverton, S. & R. L. Lyman (eds), *Conservation Biology and Applied Zooarchaeology*. University of Arizona Press, Tuscan: 42–68.
- Peacock, E., C. R. Randklev, S. Wolverton, R. A. Palmer & S. Zaleski, 2012. The “cultural filter,” human transport of mussel shell, and the applied potential of zooarchaeological data. *Ecological Applications* 22: 1446–1459.
- Popejoy, T., S. Wolverton, L. Nagaoka & C. R. Randklev, 2016. An interpretive framework for assessing freshwater mussel taxonomic abundances in zooarchaeological faunas. *Quaternary International*. doi: [10.1016/j.quaint.2015.09.101](https://doi.org/10.1016/j.quaint.2015.09.101)
- Randklev, C. R., 2010. Zooarchaeological analysis of the prehistoric mussel fauna from selected rock-shelters near Belton Lake: Belton County, Texas. Report for AMEC Earth & Environmental Inc, Bothell, WA.
- Randklev, C. R. & B. J. Lundeen, 2012. Prehistoric biogeography and conservation status of threatened freshwater mussels (Mollusca: Unionidae) in the upper Trinity River drainage, Texas. In Wolverton, S. & R. L. Lyman (eds), *Conservation Biology and Applied Zooarchaeology*. The University of Arizona Press, Tuscan: 68–91.
- Randklev, C. R., S. Wolverton & J. H. Kennedy, 2009. A biometric technique for assessing prehistoric freshwater mussel population dynamics (family: Unionidae) in north Texas. *Journal of Archaeological Science* 36: 205–213.
- Randklev, C. R., B. J. Lundeen, R. G. Howells & J. H. Kennedy, 2010a. First account of a living population of Texas fawnsfoot, *Truncilla Macrodon* (Bivalvia: Unionidae), in the Brazos River, Texas. *The Southwestern Naturalist* 55: 297–299.

- Randklev, C. R., S. Wolverton, B. J. Lundeen & J. H. Kennedy, 2010b. A paleozoological perspective on unionid (Mollusca: Unionidae) zoogeography in the upper Trinity River basin, Texas. *Ecological Applications* 20: 2359–2368.
- Randklev, C. R., M. S. Johnson, E. Tsakiris, S. Rogers-Oetker, K. J. Roe, J. L. Harris, S. E. McMurray, C. Robertson, J. Groce & N. Wilkins, 2012. False spike, *Quadrula mitchelli* (Bivalvia: Unionidae), is not extinct: first account of a live population in over 30 years. *American Malacological Bulletin* 30: 327–328.
- Randklev, C. R., M. S. Johnson, E. Tsakiris, J. Groce & N. Wilkins, 2013a. Status of the freshwater mussel (Unionidae) communities of the mainstem of the Leon River, Texas. *Aquatic Conservation: Marine and Freshwater Ecosystems* 23: 390–404.
- Randklev, C. R., E. Tsakiris, R. G. Howells, J. Groce, M. S. Johnson, J. Bergmann, C. Robertson, A. Blair, B. Littrell & N. A. Johnson, 2013b. Distribution of extant populations of *Quadrula mitchelli* (false spike). *Ellipsaria* 15: 18–21.
- Randklev, C. R., E. Tsakiris, M. S. Johnson, J. A. Skorupski, L. E. Burlakova, J. Groce & N. Wilkins, 2013c. Is false spike, *Quadrula mitchelli* (Bivalvia: Unionidae), extinct? First account of a very recently deceased individual in over thirty years. *The Southwestern Naturalist* 58: 247–250.
- Rick, T. C. & R. Lockwood, 2013. Integrating paleobiology, archeology, and history to inform biological conservation. *Conservation Biology* 27: 45–54.
- Rose, D. R. & A. A. Echelle, 1981. Factor analysis of associations of fishes in Little River, central Texas, with an interdrainage comparison. *The American Midland Naturalist* 106: 379–391.
- Scharf, E. A., 2014. Deep time: the emerging role of archaeology in landscape ecology. *Landscape Ecology* 29: 563–569.
- Shea, C. P., J. T. Peterson, M. J. Conroy & J. M. Wisniewski, 2013. Evaluating the influence of land use, drought and reach isolation on the occurrence of freshwater mussel species in the lower Flint River basin, Georgia (USA). *Freshwater Biology* 58: 382–395.
- Sowards, B., E. T. Tsakiris, M. Libson & C. R. Randklev, 2013. Recent collection of a false spike (*Quadrula mitchelli*) in the San Saba River, Texas, with comments on habitat use. *Walkerana* 16: 63–67.
- Strayer, D. L., 2008. *Freshwater Mussel Ecology: A Multifactor Approach to Distribution and Abundance*. University of California Press, Berkeley.
- Strecker, J. K., 1931. *The Naiades or Pearly Freshwater Mussels of Texas*. Baylor University Museum, Waco, TX.
- Swetnam, T. W., C. D. Allen & J. L. Betancourt, 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9: 1189–1206.
- Tharp, B. C., 1939. *The Vegetation of Texas*. Anson Jones Press, Houston.
- Tsakiris, E. T. & C. R. Randklev, 2016. Structural changes in freshwater mussel (Bivalvia: Unionidae) assemblages downstream of Lake Somerville, Texas. *American Midland Naturalist* 175: 120–127.
- United States Fish and Wildlife Service, 2014. Federal register: endangered and threatened wildlife and plants; Review of native species that are candidates for listing as endangered or threatened; Annual notice of findings on resubmitted petitions. Annual description of progress on listing actions 79: 72450–72497.
- United States Geological Survey, 2015. National Water Information System data available on the World Wide Web (USGS Water Data for the Nation), <http://waterdata.usgs.gov/tx/nwis/si>. Accessed 1 January 2015.
- Vaughn, C. C., C. L. Atkinson & J. P. Julian, 2015. Drought-induced changes in flow regimes lead to long-term losses in mussel-provided ecosystem services. *Ecology and Evolution* 5: 1291–1305.
- Vaughn, C. C. & C. M. Taylor, 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conservation Biology* 13: 912–920.
- Warren, R. E., 1991. Freshwater mussels as paleoenvironmental indicators: A quantitative approach to assemblage analysis. In Purdue, J. R., Klippel, W. E., & B. W. Styles (eds), *Beamers Bobwhites and Blue-Points: Tributes to the Career of Paul W. Parmalee*. Illinois State Museum: 23–66.
- Weber, E., 2005. Population size and structure of three mussel species (Bivalvia: Unionidae) in a northeastern German river with special regard to influences of environmental factors. *Hydrobiologia* 537: 169–183.
- Weinstein, R. A., 2015. Archaeological and geological test excavations at site 41HM61, Hamilton County, Texas: Middle Archaic through late prehistoric occupation in the Leon River valley of central Texas. Environmental Affairs Division of the Texas Department of Transportation.
- Williams, J. D. & A. Fradkin, 1999. *Fusconaia apalachicola*, a new species of freshwater mussel (Bivalvia: Unionidae) from pre-Columbian archaeological sites in the Apalachicola basin of Alabama, Florida, and Georgia. *Tulane Studies in Zoology* 31: 51–62.
- Williams, J. D., A. E. Bogan & J. T. Garner, 2008. *Freshwater Mussels of Alabama and the Mobile Basin in Georgia, Mississippi, and Tennessee*. The University of Alabama Press, Tuscaloosa.
- Wolaver, B., C. Cook, B. Scanlon & M. Young, 2012. A hydrologic-characterization approach for Texas aquatic species studies. *Gulf Coast Association of Geological Societies Transactions* 62: 645–651.
- Wolverton, S., 2013. Data quality in zooarchaeological faunal identification. *Journal of Archaeological Method and Theory* 20: 381–396.
- Wolverton, S. & R. L. Lyman, 2012a. *Conservation Biology and Applied Zooarchaeology*. University of Arizona Press, Tucson.
- Wolverton, S. & R. L. Lyman, 2012b. Introduction to applied zooarchaeology. In Wolverton, S. & R. L. Lyman (eds), *Conservation Biology and Applied Zooarchaeology*. University of Arizona, Tuscan: 1–22.
- Wolverton, S. & C. R. Randklev, 2016. Archaeological data indicate a broader late Holocene distribution of the sand-bank pocketbook (Unionidae: *Lampsilis satura* Lea 1852) in Texas. *American Malacological Bulletin*, New York.
- Wolverton, S., L. Nagaoka & T. C. Rick, 2016. *Applied Zooarchaeology: Five Case Studies*. Elliot Werner Publications Inc, New York.
- Wolverton, S., C. R. Randklev & J. H. Kennedy, 2010. A conceptual model for freshwater mussel (Family: Unionidae) remain preservation in zooarchaeological assemblages. *Journal of Archaeological Science* 37: 164–173.