



An interpretive framework for assessing freshwater mussel taxonomic abundances in zooarchaeological faunas



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ABSTRACT

Zooarchaeological freshwater mussel remains provide information about past environments, faunal communities, and human behaviors. However, one challenge of using archaeological assemblages of animal remains is differential preservation such that bones and shells of some taxa are more vulnerable to processes that destroy or remove them from the record over time. Thus, remains of some species of freshwater mussels may be underrepresented in terms of presence/absence data as well as abundance compared to the life or death assemblages. Evaluating the representativeness of assemblages before using such data to answer zooarchaeological and paleozoological research questions is common practice in archaeology, particularly for vertebrate remains. However, little research has focused on evaluating representativeness for molluscan assemblages. In this paper, three processes that potentially influence archaeomalacological data are addressed: mussel life history strategies, shell identifiability, and shell robusticity. Expectations about taxonomic abundances in unionid zooarchaeological assemblages are framed and assessed using two datasets from sites from the Leon River in central Texas. As expected, shell robusticity and identifiability influence zooarchaeological abundance data; differences in life history strategy can be used to interpret past stream environments. The expectations derived in this paper can be used as interpretive tools for understanding factors that influence archaeomalacological taxonomic abundance data.

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1. Introduction

Freshwater mussel (hereafter unionid) remains are prevalent in many zooarchaeological faunas and have been used to study past human behavior, environments, and animal ecology (Matteson, 1960; Klippel et al., 1978; Spurlock, 1981; Parmalee et al., 1982; Parmalee and Bogan, 1986; Bogan, 1990; Warren, 1991; Parmalee and Polhemus, 2004; Peacock, 2005, 2012; Williams et al., 2008; Randklev et al., 2009, 2010; Haag, 2012; Randklev and Lundeen, 2012; Miller et al., 2014). Paleozoological and zooarchaeological unionid presence/absence data are often used as evidence of shifts in human subsistence or biogeographic distributions of taxa during prehistory (Baker, 1936; Parmalee and Klippel, 1974; Warren, 1975; Peacock and Chapman, 2001; Peacock, 2012). Taxonomic abundance data from zooarchaeological assemblages can provide additional data with which to approach these types of questions

(e.g., studies of human behavior through foraging theory (Botkin, 1980; Mannino and Thomas, 2002; Braje et al., 2007; Morrison and Hunt, 2007; Singh and McKechnie, 2015)). Abundance data are also used in paleoenvironmental studies, for conservation purposes, or to assess environmental changes in species abundance as an alternative hypothesis to change in human subsistence (Matteson, 1960; Klippel et al., 1978; Casey, 1986; Peacock et al., 2005; Peacock and Seltzer, 2008; Randklev et al., 2010; Randklev and Lundeen, 2012; Miller et al., 2014; Campbell and Braje, 2015). Because taxonomic abundance data are used to address a wide variety of research and conservation questions, it is important to understand potential influences on the structure of such data.

Zooarchaeological data have been used to inform unionid conservation since 1909, when Ortman wrote, “The Destruction of the Fresh-Water Fauna in Western Pennsylvania”. Many studies since have discussed how zooarchaeological data can be used to improve mussel conservation (Matteson, 1960; Klippel et al., 1978; Spurlock, 1981; Parmalee et al., 1982; Parmalee and Bogan, 1986; Bogan, 1990; Warren, 1991; Randklev and Lundeen, 2012; Miller et al., 2014). While these studies set the groundwork for using

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zoarchaeological data for unionid conservation, many studies do not address shell preservation. Parmalee et al. (1982) notes *Anodonta* species were “well established locally in ... most of the reservoirs” but absent in zooarchaeological assemblages (pg. 87). Bogan (1990) addressed this lack of *Anodonta* species as a ‘cultural bias’ due to prehistoric peoples not sampling habitats other than riffles/shoals, which is a valid hypothesis. Parmalee and Bogan (1986) discussed difficulties associated with the identification of archaeological mussel valves, and cite sculpture as a diagnostic feature that improves identification. This paper seeks to add to this literature by addressing problems presented by Parmalee et al. (1982), Parmalee and Bogan (1986) and Bogan (1990) and by attempting to understand how three factors influence the presence and abundance of unionids in zooarchaeological assemblages.

Abundance data produced from zooarchaeological assemblages are influenced by many different forces, such as the interplay of abiotic and biotic factors at various spatial and temporal scales across the prehistoric landscape, differential preservation of shells, preferences of prehistoric people who incorporated unionids in their diets, and/or differential identifiability of some remains over others (Kidwell and Flessa, 1995; Poff, 1997; Kosnik et al., 2009; Wolverton et al., 2010; Peacock et al., 2012). These influences are alternative mechanisms that might drive patterns in taxonomic abundance and thus impact the results of zooarchaeological studies (Grayson, 1987; Lyman, 1994, 2012). Before burial, the cultural preferences of where prehistoric humans harvested mussels influenced the taxonomic composition of the deposited assemblage (Lyman, 1984; Peacock et al., 2012). After the shells are deposited in the lithosphere, differential diagenesis can influence abundance based on shell size, species, and soil moisture (Muckle, 1985). In addition, different types of excavation can influence the sample studied by zooarchaeologists (Nagaoka, 1994, 2005). The excavated assemblages from which zooarchaeological data are produced may pass through many filters prior to analysis, which includes aggregation into a deposited assemblage, time in the lithosphere, constraints on sampling, and analysis by zooarchaeologists, each potentially resulting in forms of data loss or addition (see Clark and Kietzke, 1967, p. 117; Meadow, 1980, p. 67; Lyman, 1994, pp. 12–40).

Three distinctive mechanisms that conceivably influence taxonomic composition and abundance data are addressed in this article: variable unionid life history strategies and their influence on population abundances, identifiability of shells, and preservation potential of shells from different unionid taxa. Life history strategies play an integral role in constructing ecological communities (Pianka, 1970, 1972; Southwood, 1977, 1988) and, thus, potentially influence taxonomic abundances in zooarchaeological data (Kidwell and Rothfus, 2010; Kidwell, 2013). In addition, differences in accuracy and precision of taxonomic identification can directly affect zooarchaeological mussel abundance (Gobalet, 2001); easily identified taxa are more likely to be accurately and precisely identified than hard-to-identify taxa. In addition to identifiability and abundance related to life history ecology, zooarchaeological taxonomic abundance data may be affected by differential preservation of shells from one taxon over another based on a species' shell phenotype (Wolverton et al., 2010). Together these factors have complex but predictable influences on zooarchaeological freshwater mussel taxonomic abundance data; thus, an interpretive framework that provides general expectations about which species ought to and ought not to be abundant can aid research in zooarchaeology and paleozoology that focuses on unionids. Rank order continua of life history strategy, identifiability (based on sculpture), and preservation potential are developed for taxa encountered in two zooarchaeological datasets from the Leon River of Texas and help frame expectations about aspects of taphonomy, ecology, and human behavior.

1.1. Unionid life history ecology

Life history strategies describe a species' differential allocation of energy based on the rate of population growth and reproductive ecology (Fisher, 1930; MacArthur and Wilson, 1967; Pianka, 1970). Life history should indirectly affect species abundance in zooarchaeological assemblages because reproductive ecological strategies influence their abundance in living communities (Southwood, 1977, 1988; Kidwell, 2001; Kidwell and Rothfus, 2010). Typically, Pianka's *r* versus *K* selection gradient is used to define life history strategies among different species (Pianka, 1970, 1972; Southwood, 1977, 1988). Although unionids are generally categorized as long lived and slow growing, they exhibit a wide range of variability in life history characteristics (Haag, 2012; Vaughn, 2012). In this study, unionid life history strategies are categorized into three types that are based on Winemiller and Rose's (1992) three endpoint continuum: opportunistic, periodic, and equilibrium strategies (see also Dillon, 2000; Grime, 2001; Haag, 2012). The opportunistic strategy is similar to Pianka's *r*-selection; such mussel species are characterized by a short life span, early maturity, and high fecundity (number of offspring). Equilibrium selected mussels live long and mature late, similar to Pianka's *K*-selection. Periodic selected mussels are “characterized by moderate to high growth rate, low to intermediate life span [low] age at maturity, and [low] fecundity” (Haag, 2012, p. 211). Periodic species are adapted to habitats that experience cyclical environmental variability, intermittently producing conditions conducive to successful reproduction (Winemiller and Rose, 1992; Haag, 2012). Stream position and habitat influence the abundance of different life history strategies in riverine biotic communities (Southwood, 1977, 1988; Haag, 2012; Mims and Olden, 2012). Haag (2012, p. 282) constructs a conceptual model that predicts the abundance of unionid taxa with different life history strategies based on biotic and abiotic factors for small, medium and large-sized rivers. Small, low order streams are predicted to experience high disturbance frequency and low habitat diversity and high competition for host fish and as result should be dominated by periodic and opportunistic species. Medium sized streams experience less disturbance and as a result have more habitat diversity, and competition for host fish is also reduced due to the fact that fish diversity increases with stream size. These factors cause higher relative abundance of periodic and equilibrium species. Large, high order rivers tend to be fairly stable in terms of disturbance and have high habitat diversity and very low potential for host competition as a result equilibrium species tend to proportionately more abundant in large order streams. Throughout the river, lentic mesohabitats (areas of still water such as pools, backwater or depositional areas along stream margins) should have high abundance of opportunistic species. Therefore, consideration of the type of stream, disturbance frequency, and potential habitat is important for understanding life history composition of faunal assemblages. For the small to medium sized Leon River, we expect periodic and equilibrium species to be most abundant, unless lentic mesohabitats were the focus of mussel gathering by prehistoric humans.

1.2. Identifiability

Differences in identifiability of shells between species relate to two factors: distinctiveness of shell morphology and preservation potential related to shell fragmentation. One way that zooarchaeologists account for differences in identifiability and also bolster confidence in data quality is to fully describe identification criteria (Driver, 1992, 2011; Wolverton, 2013). Zooarchaeological specimens are often fragmented and eroded, making identifications difficult, which is exacerbated by the fact that shell phenotype (e.g.,

shape and sculpture) is heavily influenced by hydrology and substrate type, which makes identifications problematic within and between species (Hornbach et al., 2010). Shea et al. (2011) evaluated the identification accuracy and precision of malacologists, and found that increased shell sculpture, size, and conservation status (listed as threatened by a government agency) led to higher identification rates of individual mussel taxa. Those species with sculptured shells tend to be more recognizable, those with conservation status tend to be better studied and thus more identifiable, and those of larger size also tend to be recognizable and easier to identify. Since shell sculpture, defined as the presence of plications, wrinkles, pustules, bumps, or ridges on a shell disk (see Fig. 1), often preserves well on shell fragments recovered from zooarchaeological contexts and is often diagnostic, it is used as a proxy for identifiability. Note that there are other shell characteristics that can be used for identification, such as hinge teeth and shell shape, but many of these characteristics depend on complete valves, which are not always available in zooarchaeological assemblages. Shea et al. (2011) also found that experience can reduce misidentification of freshwater mussels, but is dependent on the frequency of experience and shell being identified. Gobalet (2001) also noted that experience influences the identification of zooarchaeological specimen, though “despite educational attainment of terminal degrees and considerable experience [faunal analysts can exhibit] considerable difference of opinion on faunal identity”. While experience can influence misidentification, it is often unavoidable that a less experienced analyst will analyze archaeological faunas. In ecology it is intuitive that a greater level of experience leads to more precise taxonomic identifications; in zooarchaeology, the opposite tends to be true as experience with the limits of data quality tend to lead to more conservative identifications (e.g., Driver, 1992; Gobalet, 2001). Thus, regarding zooarchaeological mussel remains, sculpture is a better proxy for identifiability than experience because it occurs on the specimen itself and experience can be controlled through cross-examination and checks by other faunal analysts (Gobalet, 2001; Wolverson, 2013). Therefore in zooarchaeological assemblages, species that have sculpture should be identified with more taxonomic precision (e.g., to finer taxonomic levels) and more accurately (to the correct taxon) than those without sculpture if identifiability is driving taxonomic abundance.

Shell sculpture influences zooarchaeological data at the beginning (capture by prehistoric humans) and end (identification by zooarchaeologists) of the data recovery process (Klein and

Cruz-Urbe, 1984). Evaluation of modern sampling has revealed that tactile (searching stream sediment by hand), timed searches are likely to capture large, sculptured unionid species more often than small or unsculptured species (Hornbach and Deneka, 1996; Vaughn et al., 1997; Obermeyer, 1998). Because collection of prehistoric mussels by hunter–gatherers relied on tactile searches (Lyman, 1984, citing Spinden 1908 and Post 1938), it is appropriate to predict that taxa with sculptured shells would be harvested by prehistoric humans at a higher rate than those without shell sculpture. While this affects a different taphonomic stage of the faunal assemblage (the death assemblage instead of the sample assemblage after excavation (Lyman, 1994)), it is another way sculpture influences taxonomic abundances in zooarchaeological datasets. Based on differential harvest and differential identifiability, sculptured specimens are expected to be more abundant in zooarchaeological assemblages.

1.3. Robusticity

In terms of shell morphology and differential preservation, shells from unionid species exhibit different shapes and structures (Wolverson et al., 2010), which can affect potential for preservation and thus the quantity or presence of a species in an assemblage. Wolverson et al. (2010) addressed differential preservation of shells from different species in zooarchaeological assemblages based on two physical shell characteristics: density and sphericity. Analyzing modern and zooarchaeological specimens from the Brazos and Trinity River, they determined that as a species' shell density increases (thicker, heavier shells), its preservation potential increases as well. As a species' shell sphericity increases (more globular and oval), its preservation potential also increases. We use Wolverson et al. (2010)'s conceptual model to assess how robusticity influences taxonomic abundance. If differential preservation is driving taxonomic abundance in zooarchaeological datasets, species with robust shells should exhibit greater abundance than those with comparatively fragile morphology.

2. Materials and methods

We analyze two late Holocene zooarchaeological datasets from the Leon River in central Texas to examine how the three processes described above affect taxonomic abundance data (Table 1). We employ non-repetitive elements (NRE) as a quantitative unit to count the number of mussels represented in each assemblage; each

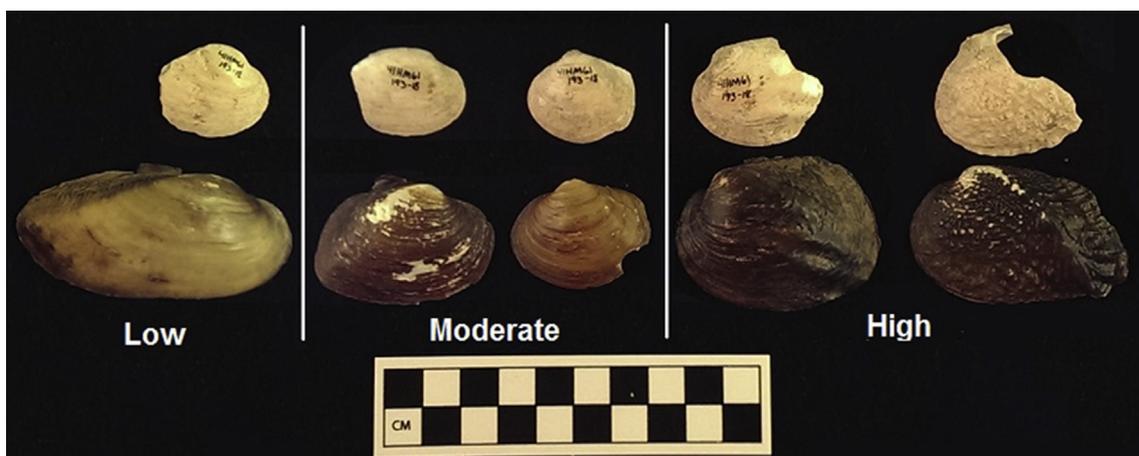


Fig. 1. Example of sculpture categories used in identifiability analysis. Species from left to right: *Lampsilis teres*, *Fusconia mitchelli*, *Quadrula houstonensis*, *Amblema plicata*, *Quadrula verrucosa*. Valves pictured are from the Leon River comparative collection at the University of North Texas. Subfossil valves are from 41HM61.

Table 1

Taxonomic abundances within the 41HM61 and Belton Lake assemblages. Missing values listed in the Belton Lake Assemblages indicate no specimens of that taxon were identified. * indicates a taxonomic category that includes a species of conservation concern (Texas Parks and Wildlife Department, 2009; U.S. Fish and Wildlife Service, 2014).

Taxa	41HM61		Belton Lake assemblages	
	NRE	Relative abundance	NRE	Relative abundance
<i>Amblema plicata</i>	93	23.3%	307	54.2%
<i>Arcidens confragosus</i>	1	0.3%	1	0.2%
<i>Cyrtonaias tampicoensis</i>	2	0.5%	6	1.1%
<i>Fusconaia mitchelli*</i>	9	2.3%	38	6.7%
<i>Lampsilis</i> sp.	37	9.3%		
<i>Lampsilis hydiana</i>	10	2.5%	14	2.5%
<i>Lampsilis teres</i>	34	8.5%	5	0.9%
<i>Megaloniais nervosa</i>	16	4.0%	2	0.4%
<i>Quadrula</i> sp.	34	8.5%	1	0.2%
<i>Quadrula apiculata</i>	13	3.3%	20	3.5%
<i>Quadrula houstonensis*</i>	20	5.0%	118	21.0%
<i>Quadrula verrucosa</i>	38	9.5%	13	2.3%
<i>Toxolasma</i> sp.	2	0.5%		
<i>Truncilla</i> cf. <i>macrodon*</i>	5	1.3%		
Unidentifiable umbo	85	21.3%	41	7.1%
Total NRE	399		566	

NRE represents a single umbo. NRE is appropriate because only one umbo is found on each valve (of which there are two on each unionid), represents the oldest and densest part of a shell and it is often diagnostic to a precise taxonomic level. For further discussion of NRE, consult [Giovas \(2009\)](#) (see also [Mason et al., 1998](#); [Claassen, 2000](#); [Glassow, 2000](#); [Harris et al., 2015](#)). The Belton Lake faunas come from 18 separate cave sites that surround the modern Belton Lake reservoir; these sites represent the Leon River close to its confluence with the Little River ([Randklev, 2010](#)). These assemblages were identified by Charles Randklev. The faunas comprise 525 NRE, and the fragmentation rate of shell remains from these rock shelter deposits is low. The second assemblage is from the 41HM61 site and represents an area upstream on the Leon River from Belton Lake. The 41HM61 assemblage was identified by Traci Popejoy, comprises 399 NRE, and is highly fragmented ([Popejoy, 2015](#)). The Leon River datasets represent similar faunal communities at a local spatial scale and similar temporal scale, but different preservation contexts. Our analyses use these assemblages as space- and time-averaged representations of the Leon River late Holocene unionid community.

Unionid species are categorized along ordinal continua that indicate their potential for either being high or low in abundance according to their life history ecology, identifiability, and preservation potential. These expectations are summarized in [Table 2](#). Taken together, in the mid-order Leon River an equilibrium species that produces a robust, sculptured shell has a higher probability of occurrence and high abundance in zooarchaeological assemblages

Table 2

Expectations for alternative mechanism discussed in this article. High abundance potential refers to the expectation that species with this trait will have higher abundances relative to the other species without this trait. Life history strategies abundance is dependent on stream type and position (see section 1.1).

Mechanism	High abundance potential	Low abundance potential
Life history strategy	Equilibrium and periodic strategy	Opportunistic strategy
Identifiability	Shells with sculpture	Shells with no sculpture
Preservation potential	Shells are spherical and dense	Shells are non-spherical and are less dense

than an equilibrium species with fragile, unsculptured shell morphology.

Using this interpretive framework and its expectations ([Table 2](#)), it can be predicted which unionid species will be most and least abundant in the Leon River zooarchaeological datasets ([Table 3](#), [Fig. 2](#)). There is auto-correlation in this model (see section 2.1), thus *Amblema plicata*, *Quadrula apiculata*, and *Quadrula verrucosa* have high expected abundances since these species' shell exhibit two characteristics (high robusticity and high identifiability) likely to increase abundance. In contrast, *Lampsilis teres* and *Lampsilis hydiana* are expected to be least abundant in zooarchaeological assemblages as they exhibit two characteristics (low robusticity and low identifiability) predicted to have low abundance.

Table 3

Zooarchaeological taxonomic abundance expectations for the Leon River unionid community. Taxa are listed by alphabetical order. The robusticity category includes the expected three most abundant and three least abundant species. All taxa in the category with highest expected abundance (equilibrium and periodic species and highly sculptured) are included in this graph for the life history strategy and identifiability category.

Alternative mechanism	High abundance	Low/Rare abundance
Life history strategy	<i>Amblema plicata</i> <i>Quadrula apiculata</i> <i>Quadrula houstonensis</i> <i>Quadrula verrucosa</i> <i>Arcidens confragosus</i> <i>Cyrtonaias tampicoensis</i> <i>Toxolasma</i> sp.	<i>Lampsilis hydiana</i> <i>Lampsilis teres</i> <i>Truncilla</i> cf. <i>macrodon</i>
Identifiability	<i>Amblema plicata</i> <i>Arcidens confragosus</i> <i>Megaloniais nervosa</i> <i>Quadrula apiculata</i> <i>Quadrula verrucosa</i>	<i>Cyrtonaias tampicoensis</i> <i>Lampsilis hydiana</i> <i>Lampsilis teres</i>
Robusticity	<i>Amblema plicata</i> <i>Quadrula apiculata</i> <i>Quadrula verrucosa</i>	<i>Lampsilis hydiana</i> <i>Lampsilis teres</i> <i>Toxolasma</i> sp.

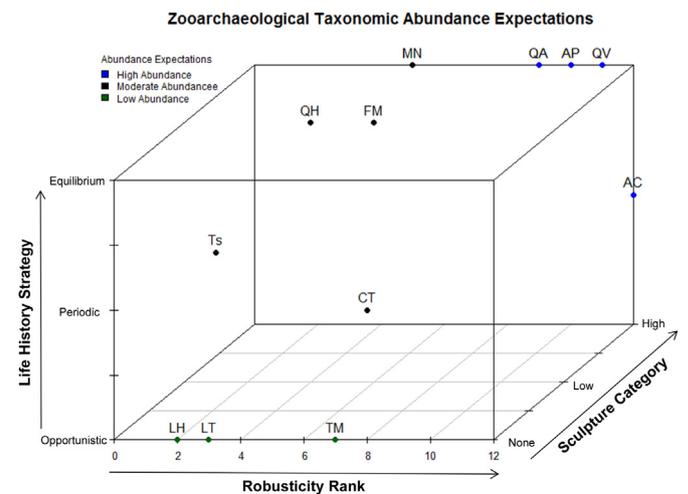


Fig. 2. Zooarchaeological taxonomic abundance expectations for the Leon River unionid community. A 3D scatterplot shows expected abundances for unionid species in the Leon River based on robusticity, identifiability and life history strategy. Arrows indicate which portion of the graph is expected to have high taxonomic abundance. Three categories of unionid species are illuminated: high, moderate, and low abundance expectations. These categories are defined in [Table 2](#), with species specific expectations listed in [Table 3](#). This diagram exhibits which species we expect to be abundant in the Leon River zooarchaeological assemblages based on robusticity, identifiability and life history strategy.

2.1. Limitations

Auto-correlation among life history strategy, sculpture, and robusticity possibly disrupts the interpretive value of this conceptual framework. Equilibrium species are likely to produce a more dense shell than opportunistic species because they tend to allocate energy toward growth rather than reproductive output (Haag and Rypel, 2011; Haag, 2012, 2013). Life history strategies are also possibly correlated with shell sculpture based on collinearity with habitat variables. Sculpture is a convergent evolutionary trait and relates to flow variability and predation pressure (Watters, 1994; Hornbach et al., 2010; Haag, 2012). As sculpture often reflects the habitat and flow regime of unionid species and life history strategies are influenced by habitat conditions, it is possible that these two factors are correlated (Pianka, 1970; Southwood, 1977, 1988). Despite these qualifications that aspects of life history ecology, preservation potential of shells, and sculpture can co-occur, each also potentially influences abundance independently. Developing expectations for each variable allows for clearer interpretation of zooarchaeological abundance data. In addition, since species' shell robusticity, shell sculpture and life history strategy can vary between mussel communities (Haag, 2012), consideration of these variables and expectations should be limited to use within the river basin represented by the zooarchaeological data.

2.2. Life history strategy categorization

Data from Haag's (2012, pp 180–214) description of unionid life history ecology are used to group mussels into the three categories: opportunistic, periodic, and equilibrium. When taxa are present in Haag's ordination of unionid life history strategy, that categorization is used. If a species is missing from Haag's ordination, phylogenetic and taxonomic relationships (often at the tribe level for Leon River mussels) are used to make assignments (see Table 4, Campbell et al., 2005; Haag, 2012).

Table 4

Robusticity and life history strategy values for Leon River zooarchaeological freshwater mussel assemblages. Highlighted cells indicate higher expected abundances if variable life history strategy, identifiability or robusticity influences taxonomic abundances. Robusticity mean values are found in Wolverson et al. (2010), which were calculated from a modern Brazos River assemblage. The shell sphericity and shell density values are summed to determine the ordinal rank of different species; note a high rank indicates high robusticity, and thus high expected abundance. ¹ indicates proximate values calculated for this article (sec. 2.4). Life history strategy is determined at a nominal scale using the figure from Haag (2012). Data Sources: ¹ Wolverson et al. (2010); ² Haag (2012); ³ Tribe rank – Howells (2013) and Haag (2012); ⁴ *Obliquaria reflexa* as a proxy – Haag (2012) and Campbell et al. (2005). Abbreviations that are used by the authors are listed below as well.

Species	Abbreviation	Robusticity			Tribe ²	Life history strategy	Sculpture category
		Sphericity ¹	Density ¹	Summed Rank			
<i>Amblema plicata</i>	AP	0.56	2.02	2.58	10	Equilibrium ²	High
<i>Arcidens confragosus</i> [†]	AC	0.58	2.66	3.24	12	Periodic ³	High
<i>Cyrtonaias tampicoensis</i>	CT	0.54	1.92	2.46	8	Periodic ⁴	None
<i>Fusconaia mitchelli</i> [†]	FM	0.49	1.52	2.01	6	Equilibrium ³	Low
<i>Lampsilis hyadiana</i>	LH	0.51	1.13	1.64	2	Opportunistic ³	None
<i>Lampsilis teres</i>	LT	0.44	1.27	1.71	3	Opportunistic ²	None
<i>Megaloniais nervosa</i>	MN	0.48	1.52	2.00	5	Equilibrium ²	High
<i>Quadrula apiculata</i>	QA	0.61	1.90	2.51	9	Equilibrium ³	High
<i>Quadrula houstonensis</i>	QH	0.63	1.24	1.87	4	Equilibrium ³	Low
<i>Quadrula verrucosa</i>	QV	0.46	2.46	2.92	11	Equilibrium ³	High
<i>Toxolasma</i> sp.	Ts	0.60	0.34	0.94	1	Periodic ³	Low
<i>Truncilla macrodon</i> [†]	TM	0.45	1.80	2.25	7	Opportunistic ³	None

2.3. Identifiability categorization

Identifiability categorizations are based on sculpture on modern unionid shells from the Brazos River and its tributaries. Shell sculpture improves identification accuracy and precision in modern unionids (Shea et al., 2011). Shell sculpture has been quantified by

calculating the number of pustules per square centimeter (Peacock and Seltzer, 2008). In this study, sculpture is evaluated at an ordinal scale since fragmentation and erosion could affect the presence of sculpture on unionid specimens. Sculpture is categorized into three groups: shells with a high density of sculpture on its outer disk (>50%), shells with less dense sculpture on their outer disk (<50%), and shells without sculpture (Fig. 2). Unionids with highly variable shell sculpture, especially those that range from lightly sculptured or apostulose such as *Quadrula houstonensis* (with a telling common name: Smooth Pimpleback), are included in the less dense sculpture category. While beak sculpture (ridges on a valve's umbo) can be used to clarify the identification of unionids, it is not considered in this analyses as it is often eroded from zooarchaeological specimens.

Some unionid taxa have diagnostic pseudocardinal teeth (triangular knobs on the interior of the shell under the umbo/beak) that aid in their identification as dead or zooarchaeological specimens (e.g. *Fusconaia mitchelli*, *Quadrula* sp.). Pseudocardinal identifiability is not used to categorize shell identifiability in this study since it is highly variable and its use is contingent on the zooarchaeologist's expertise. Shell sculpture is morphologically variable as well, but is easily placed into types of sculpture (pustules versus plications), which can be diagnostic of different unionid taxa (Watters, 1994).

2.4. Taphonomic analysis based on robusticity

We assess robusticity by ranking taxa based on their summed mean shell density and mean shell sphericity (see Table 4). Ranking robusticity quantifies a taxon's preservation potential within a given zooarchaeological assemblage at an ordinal scale (Grayson, 1984). Shell sphericity is calculated as the ratio of shell length, width, and height. Shell density describes the structural strength of the shell and is measured through volume displacement. Shell sphericity and density were quantified by Wolverson et al. (2010)

for many taxa using modern shells from the Brazos River. Three species total, two of conservation concern (*Fusconaia mitchelli* and *Truncilla macrodon*) were not included in Wolverson et al.'s (2010) calculations because of sample size considerations. For this study, provisional data were collected for these species. For *Arcidens confragosus*, six right valves from the Sabine River, east Texas have

been measured to quantify shell sphericity and shell density. For *F. mitchelli*, six right valves from the Guadalupe River, central Texas are used to characterize this taxon's shell sphericity and shell density; for *T. macrodon*, five right valves from the Brazos River are used to quantify shell characteristics. These provisional data allow ranking the robusticity of the complete set of species from these datasets. A further analysis of taxonomic differential preservation in these data is conducted by constructing a 3D scatterplot to evaluate preservation based on shell density and sphericity independently following Wolvertson et al. (2010).

Histograms are used to evaluate how well abundance expectations match the relative abundance patterns in the zooarchaeological datasets. The x-axis in each histogram is arranged from expected high abundance to expected low abundance from left to right according to each of the three variables (life history strategy (Fig. 3)), identifiability based on sculpture (Fig. 4), and robusticity (Fig. 5).

3. Results

Life history strategy relates to taxonomic abundance within these zooarchaeological assemblages (Fig. 3). It was expected that for the Leon River, a small to medium sized stream, remains of equilibrium or periodic species would be more abundant than those of opportunistic species. The 41HM61 assemblage is dominated by equilibrium species, but contains a moderate proportion of opportunistic strategists. Both datasets have a low abundance of taxa that exhibit periodic life history strategies. The Belton Lake assemblages are dominated by equilibrium strategists, with only small proportional abundances of opportunistic taxa. That equilibrium taxa dominate both datasets, indicates that life history strategy in this mid-order stream likely influenced relative abundance.

Identifiability can influence abundance data generated from zooarchaeological assemblages (Fig. 4). It is expected that species with highly sculptured shells, such as *Quadrula verrucosa* and *Amblema plicata*, should exhibit higher relative abundances than species with unsculptured shells. Both the 41HM61 and the Belton Lake assemblages are dominated by species with sculptured shells, primarily *Amblema plicata*. *Q. houstonensis* has a high relative abundance in both datasets, but can be apustulose (without sculpture) and typically exhibits less sculpture than *Quadrula*

apiculata. While the abundance of some taxa appears to relate to the presence of sculpture (e.g., *A. plicata*), other taxa were identified based on other physical features, such as pseudocardinal teeth (e.g., *Q. houstonensis*). In general, identifiability, whether from sculpture or other morphological criteria, appears to influence taxonomic abundance in these zooarchaeological datasets.

Generally, species with more robust shells have a higher relative abundance in the zooarchaeological assemblages (Fig. 5). 3D scatterplots of shell density, shell sphericity, and taxonomic relative abundance are provided to assess how these shell characteristics independently influenced preservation (Fig. 6). By evaluating these robusticity characteristics independently, we remove undue influence from a large mean in one robusticity category; for example, while *Quadrula verrucosa* is ranked the second most robust species in the datasets, it actually exhibits low shell sphericity. From Fig. 6 it is evident that taxa with high shell sphericity (*Amblema plicata* and *Quadrula houstonensis*) are most abundant in the Belton Lake assemblages. The 41HM61 and Belton Lake datasets are dominated by robust taxa, but the presence of fragile taxa with moderate abundance indicates the taxonomic abundances in these datasets are not solely explained by differential preservation and thus may be representative of the late Holocene freshwater mussel community of the Leon River.

4. Discussion

4.1. Representativeness of taxonomic abundance

This study contributes to the zooarchaeological literature by exploring alternative mechanisms for the structure of unionid abundance data, which are used in many ways to answer archaeological questions: to understand human diet, paleoenvironmental conditions, and the paleoecology of mussel taxa. The interpretive framework presented in this article allows zooarchaeologists to evaluate the influence of life history strategies, identifiability, and robusticity on taxonomic abundance data. These alternative mechanisms address different stages the paleozoological fauna have passed through: the life assemblage, the death assemblage, the deposited assemblage, and the sample assemblage (Klein and Cruz-Urbe, 1984).

Life history strategies influence the abundance of different species on the landscape, which may influence the abundance of

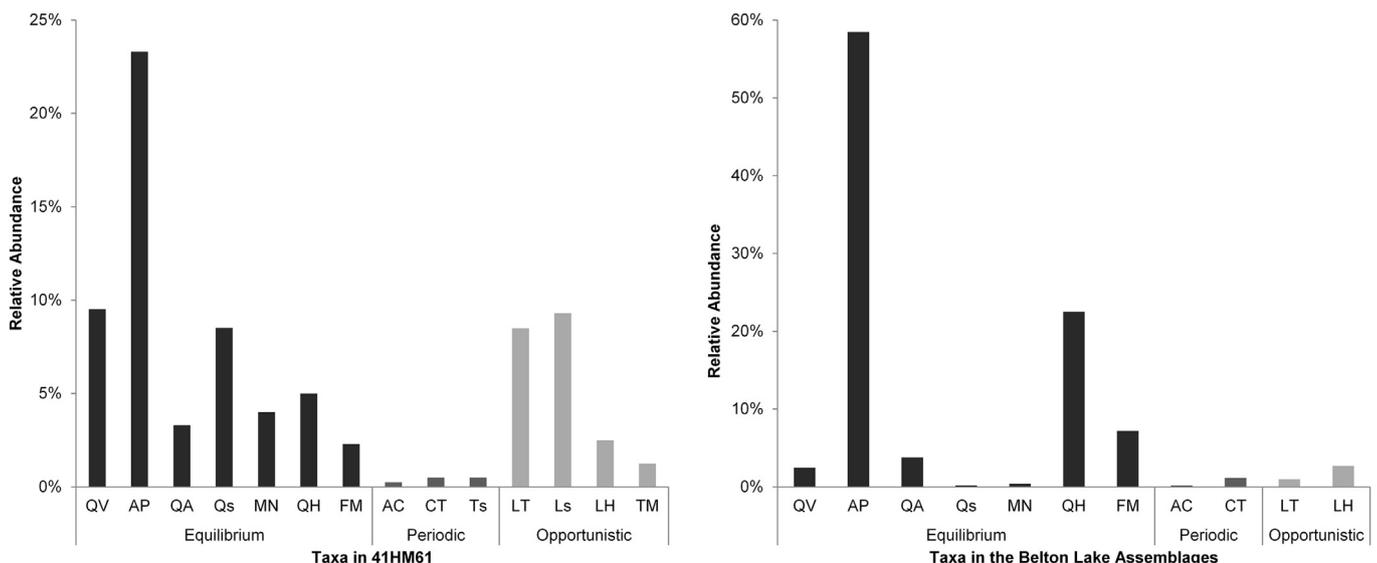


Fig. 3. Analysis of life history strategy's influence on taxonomic abundance in the 41HM61 and the Belton Lake assemblages.

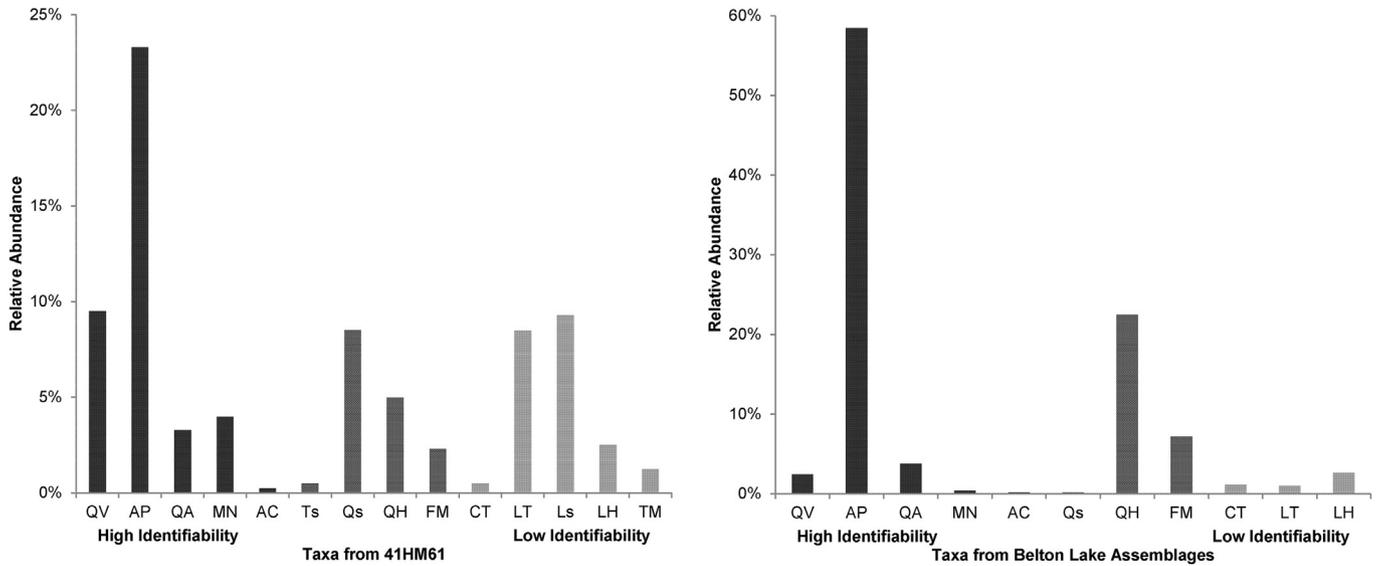


Fig. 4. Analysis of sculpture's influence taxonomic abundance in the 41HM61 and Belton Lake assemblages.

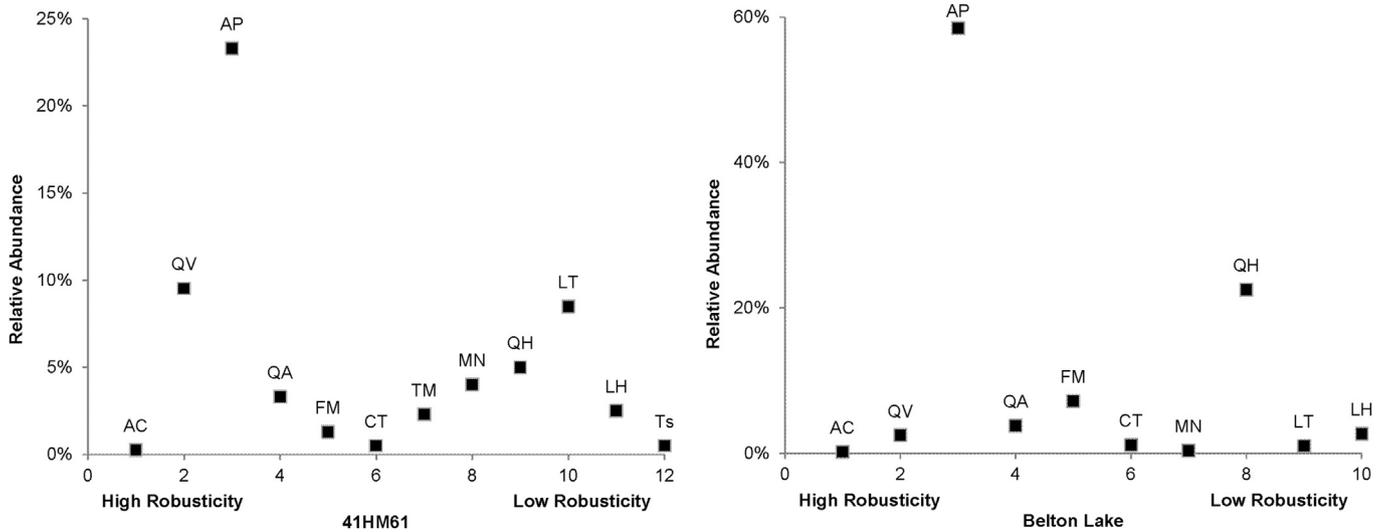


Fig. 5. The influence of shell robusticity on taxonomic abundance in the 41HM61 and Belton Lake assemblages.

taxa in the life assemblage (Southwood, 1977, 1988). Equilibrium life history strategists were commonly represented in the zooarchaeological assemblages, which may relate to stream size or sculpture and robusticity auto-correlating with life history traits. Equilibrium life history strategists are likely to invest more energy into phenotypic expression (Pianka, 1970, 1972; Geist, 1998), such as shell mass and complexity. In addition, robusticity to some extent may mediate identifiability as robust fragments tend to have better preserved shell morphology. The high abundance of equilibrium species in the zooarchaeological assemblages could also indicate that mesohabitats preferred by equilibrium strategists (riffles, mid-channel habitats) either were preferentially sampled by prehistoric humans, as suggested by Bogan (1990), or constituted a higher proportion of the prehistoric Leon River fauna (Howells et al., 1996; Haag, 2012; Howells, 2013).

The deposited assemblage is influenced by differential preservation due to variable shell robusticity among unionid taxa. By understanding factors that influence the deposited assemblage, zooarchaeologists and paleontologists further understand remains of which taxa are unlikely to survive to be recovered in the sample

assemblage, which can potentially explain the absence of important but missing taxa. Taxonomic identifiability directly influences the sample assemblage and influences data quality. Since “identification is the foundation on which all subsequent analysis rests”, it is important to understand how identifiability can influence taxonomic abundance in paleozoological data if we expect zooarchaeological studies to be as accurate and valid as possible (Lawrence, 1973, p. 397; Wolverson, 2013). A zooarchaeologist that understands how identifiability and shell robusticity influence abundance data can better interpret taxonomic patterns and further explain conclusions based on those patterns.

4.2. Interpreting paleoenvironmental studies and influence on human behavioral studies

Many paleoenvironmental studies use taxonomic abundances of unionid remains to understand the conditions of past stream environments by making inferences about mesohabitat preferences for taxa present in the zooarchaeological assemblage (Spurlock, 1981; Warren, 1991; Morey and Crothers, 1998; Peacock and



Fig. 6. Taphonomic analysis of the 41HM61 assemblage and the Belton Lake assemblages. Sphericity gradient and density gradient values are from Wolverson et al. (2010). The dark gray represents species with high preservation potential; these species have high shell density and high shell sphericity. The light grey represents species with low preservation potential; these species are less dense and less spherical.

Seltzer, 2008; Gulyás and Sümegei, 2012). Using the interpretive framework constructed in this article, paleozoologists can determine which taxa are likely to be absent or under-represented in zooarchaeological assemblages. Since “species characteristic of soft sediments ... have proportionally thin, nonsculptured shells” with reduced shell mass and high sphericity (Watters, 1994; Haag, 2012, p. 23), this interpretive framework indicates that some species characteristic of lentic mesohabitats are expected to be absent or underrepresented in paleoecological data, especially if taxa have low shell sphericity. While some lentic species have characteristically fragile and nondescript morphology, others are robust and easily identified (e.g. *Quadrula apiculata*). However, other lentic species exhibit high variability in their robusticity; larger shells of these taxa can be quite robust and should preserve in zooarchaeological assemblages (e.g. *Cyrtoneias tampicoensis* and *Potamilus purpuratus*). If lentic taxa characteristically exhibit low identifiability and low robusticity, they are more likely to be missing from zooarchaeological faunas and therefore, paleoenvironmental studies might have difficulty detecting the presence of lentic mesohabitats when relying on unionid taxonomic abundances (Haag, 2009). This is unlikely in the Leon River assemblages as a longitudinal modern survey indicates a low abundance (<15%) of fragile, nondescript species (Randklev et al., 2013), if prehistoric communities were similar to contemporary ones. Nonetheless, it is important for paleoecologists to evaluate the representativeness of faunal assemblages since differential preservation and identifiability can influence taxonomic abundances. This interpretive framework allows paleozoologists to predict if certain taxa, and therefore their mesohabitat preferences, are likely to be underrepresented in paleoenvironmental data.

4.3. Applied paleozoological data for modern conservation problems

Modern unionid populations are declining due to interruptions in river connectivity (i.e. impoundments), increased sedimentation, changes to water temperature, and influxes of urban and agricultural inputs (Galbraith et al., 2010; Nobles and Zhang, 2011; Haag,

2012; Haag and Williams, 2014). These anthropogenic impacts have caused decreases in unionid diversity and abundance as well as range constrictions (Galbraith et al., 2008; Randklev et al., 2010; Burlakova et al., 2011; Peacock, 2012; Randklev and Lundeen, 2012; Miller et al., 2014). By using zooarchaeological data, conservation biologists have access to local records of past unionid populations at extended time depths, which can be beneficial when local historical records are absent, imprecise, or from a highly altered landscape (Swetnam et al., 1999; Louys et al., 2012; Lyman, 2012; Randklev and Lundeen, 2012; Wolverson and Lyman, 2012). While paleoecological data provide insights about past ecosystems, the precision of these data is suspect due to taphonomic processes (Grayson, 1984; Lyman, 2008; Wolverson, 2013; Wolverson et al., 2014). The framework presented in the article is an interpretive tool that is helpful in understanding where a lack of precision confounds interpretation of zooarchaeological data.

For example, we apply our interpretive framework to understand how robusticity and identifiability influence the interpretation of zooarchaeological data for conservation biologists. Four biogeographic/taphonomic groups are used to interpret taxonomic abundance patterns in the 41HM61 and Belton Lake datasets shown in a 3D scatterplot (Fig. 7). These groups are similar to those used by Wolverson et al. (2010). “Taphonomically important taxa” generally produce fragile shells and include *Lampsilis* sp., *Lampsilis teres*, and *Toxolasma* sp. Evidence of these taxa in faunal assemblages indicates good preservation and high identifiability of remains. “Taphonomically important, but extirpated taxa” reveal species that are absent from the river (or extirpated) and thus important for conservation biology and that are likely to be underrepresented in zooarchaeological data. This category includes *Cyrtoneias tampicoensis*, *Fusconaia mitchelli*, *Lampsilis hydianna* and *Truncilla* cf. *macrodon*. The presence of these taxa in zooarchaeological assemblages often provides evidence of range reduction. Taxa that are “more abundant today than in the past” potentially reveal shifts in the unionid community through time and include *Quadrula verrucosa* and *Quadrula houstonensis*. Using these interpretive groups, it is evident that *Cyrtoneias tampicoensis*, *Fusconaia mitchelli*, *Lampsilis hydianna* and (potentially) *Truncilla macrodon*

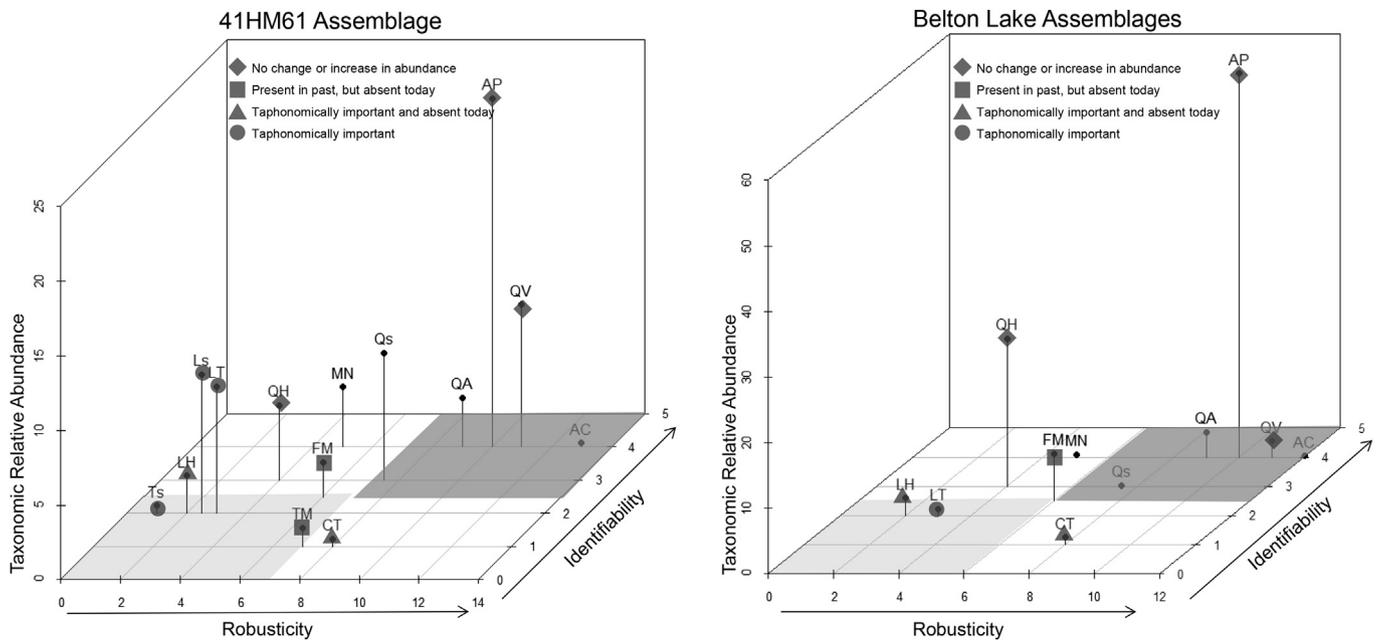


Fig. 7. Interpretive use of this conceptual model reveals biogeographic and taphonomic information about these assemblages. Four groups are used to understand the interpretive value of this zooarchaeological data: no change or increase in abundance, present in past but absent today, taphonomically important but extirpated today, and taphonomically important. The dark area of the figure represents taxa that have high expected abundance. The light grey area represents taxa that have low expected abundance.

have experienced range constrictions since the late Holocene. Two of these extirpated species are of conservation concern: *Truncilla macrodon* is a candidate for federal listing, *Fusconaia mitchelli* is petitioned for federal listing, and both are listed as threatened by the state of Texas (Texas Parks and Wildlife Department, 2009; U.S. Fish and Wildlife Service, 2014). *Truncilla cf. macrodon* provides an interesting example, as *T. macrodon* is unrecorded today in the Leon River, but historically found in the Little River and Brazos River. The robusticity values indicate that *Truncilla macrodon*'s shell is not spherical and unsculptured indicating low preservation and identifiability potential (Figs. 4 and 5). This could explain the poor preservation and absence of *Truncilla macrodon* in the Leon River datasets and historical records (which includes recently dead shell material). Since evidence of range constriction is indicative of population decline and essential for listing species at the federal level, these zooarchaeological data are useful and important for unionid conservation efforts in Texas.

5. Conclusions

The goal of this study has been to assess how life history ecology, shell identifiability, and shell robusticity influence taxonomic abundance in paleozoological datasets. While life history ecology did not influence zooarchaeological data as expected, shell robusticity and identifiability influence taxonomic abundances in unionid assemblages. As such, it is important to consider alternative hypothesis (specifically shell robusticity and identifiability) when interpreting unionid zooarchaeological data. Two examples are provided highlighting how the implementation of this framework can improve the interpretation of unionid zooarchaeological data for paleoenvironmental studies and applied zooarchaeology for conservation.

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