The utility of zooarchaeological data to guide listing efforts for an imperiled mussel species (Bivalvia: Unionidae: Pleurobema riddellii)

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The utility of zooarchaeological data to guide listing efforts for an imperiled mussel species (Bivalvia: Unionidae: *Pleurobema riddellii*)

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**Abstract**

The status of species in freshwater systems shift over time due to natural and anthropogenic causes. Determining the magnitude and cause of these shifts requires a long-term perspective. This process is complicated when there are also questions about the taxonomic validity of a species. Addressing these issues is important because both can undermine conservation and management efforts if incorrect. *Pleurobema riddellii*, Louisiana Pigtoe, is under review for protection under the U.S. Endangered Species Act, but its status in the Trinity River basin, where the taxon was described, remains in doubt due to questions about its taxonomy and occurrence within this basin. To address these questions, we compared shell morphometrics of *P. riddellii* dating to the late Holocene with modern *P. riddellii*, late Holocene *Fusconaia* sp., and modern *Fusconaia* sp. using multivariate analyses to test associations between the putative morphotypes. Based on these analyses, we demonstrate that *P. riddellii* was likely present in the Trinity during the late Holocene, which indicates questions about its taxonomic validity or presence in this basin are unfounded. Our study further highlights the role zooarchaeological studies can play in status assessments and their utility in better understanding biogeographic patterns for rare species.

**KEYWORDS**

conservation, morphometrics, mussels, shifting baselines, Texas, zooarchaeology

1 | INTRODUCTION

The distribution and abundance of species in freshwater communities shift over time due to natural and anthropogenic causes. Determining the magnitude and potential causes of these changes requires a long-term perspective to disentangle natural variability from other trends (Lyman, 2012; Rick & Lockwood, 2013). Unfortunately, conservationists and natural resource managers often perceive faunal changes over relatively short-time scales, typically during the career length of individual biologists (Humphries & Winemiller, 2009). This short-
time scale is problematic because it can lead to shifting conservation baselines, wherein ideas of a “natural” baseline or reference point from which to measure biological change shift from one generation to the next due to changing cultural and scientific perceptions. As a consequence, benchmarks become a progressively less accurate target for the intended “natural” condition (Humphries & Winemiller, 2009; Papworth, Rist, Coad, & Milner-Gulland, 2009; Pauly, 1995), leading to incorrect conclusions regarding changes in species abundances, distributions, and assemblage composition. In turn, such conclusions can result in ineffective conservation and management actions (see discussions in Dromosky, Wolverton, & Nagaoka, 2016; Lyman, 1998; Peacock, Randklev, Wolverton, Palmer, & Zaleski, 2012; Popejoy, Randklev, Neeson, & Vaughn, 2018; Randklev, Wolverton, Lundeen, & Kennedy, 2010).

For researchers and conservationists who do employ a longer temporal perspective, the baseline chosen is typically the last 200 years. This phenomenon is described as the “Pre-1800 Dilemma,” and is based largely on the false notion that data for this period are: (a) more numerous and accessible compared to data from earlier periods; (b) more compatible with recently collected ecological data; and (c) provide a more appropriate baseline for contrasting between pre- and post-European settlement conditions, which are widely considered to be the catalyst of most, if not all, of today’s conservation issues (Szabo & Hedl, 2011). However, conservation targets based on benchmarks attuned to conditions within the last couple of hundred years may be problematic because communities change naturally on time scales that are much longer (Callicott, 2002; Landres, 1992), contributing to a shifting baseline problem. Thus, parsing the natural and anthropogenic drivers of biodiversity change requires long-term data that incorporate natural community changes (Magurran et al., 2010). Paleozoological data from archaeological and paleontological faunas offer greater time depth but are often dismissed for being too descriptive and imprecise, which is shown repeatedly not to be the case (Dietl & Flessa, 2011; Louys, Wilkinson, & Bishop, 2012; Lyman, 1998; Peacock, Randklev, Wolverton, Palmer, & Zaleski, 2012; Popejoy, Randklev, Neeson, & Vaughn, 2018). Anthropogenic alterations to freshwater environments have led to species loss comparable to mass extinctions during major transitions of geological time periods (Barnosky et al., 2011; Strayer & Dudgeon, 2010), and more freshwater mollusk extinctions have occurred in North American rivers than for any other region on Earth (Regnier, Fontaine, & Bouchet, 2009). Freshwater mussels (hereafter mussels) are among the most imperiled faunas in North America and have one of the highest extinction and imperilment rates globally (Haag, 2012; Haag & Williams, 2014; Williams, Warren, Cummings, Harris, & Neves, 1993). Natural resource managers and conservationists have attempted to mitigate these declines through a variety of strategies (FMCS (Freshwater Mollusk Conservation Society), 2016; NNMC (National Native Mussel Conservation Committee), 1998), including formal listing at state and/or federal levels (Earl et al., 2018). In Texas, located in the southwestern United States, similar efforts have resulted in the listing of 19 mussel species as state-threatened or endangered (TPWD (Texas Parks and Wildlife Department), 2010; 2020), of which 1 species (Popenaias popeii) is now listed as Endangered under the U.S. Endangered Species Act (ESA), 3 (Cyclonaias aurea, Cyclonaias houstonensis, Fusconaia lananensis) were excluded from ESA listing due to taxonomic revisions (Johnson et al., 2018; Pieri et al., 2018), 4 (Fusconaia askewi, Fusconaia chunii, Lampsilis satra, Potamilus streckersoni) have not been evaluated by U.S. Fish and Wildlife Service (USFWS), 1 (Obovaria arkansasensis) had a negative 90-day finding resulting in no USFWS action (USFWS, 2010), and 10 others are currently under review for protection under the ESA (USFWS, 2009a; 2009b; 2011; 2016; Table S1). The conservation status for these 10 species is being determined, in part, using knowledge of their historical and contemporary presumptive ranges and trends in distribution and abundance (Smith et al., 2018; TPWD, 2012). In both cases an assumption has been made, knowingly or unknowingly, that recent historical ranges for these species (since about late 1800s; e.g., Singley, 1893; Streeker, 1931) represent a “natural condition” to measure current change against.

*Pleurobema riddelii*, Louisiana Pigtoe, one of the ten species petitioned for listing by USFWS (2009b), is considered wide-ranging, occurring from central Texas, east into central Louisiana, and north into southeastern Oklahoma and southern Arkansas (Howells, 2010, 2014; Howells, Neck, & Murray, 1996). This species was originally described from the Trinity River at Dallas, TX (Lea, 1861) but since then researchers have commented on its precipitous decline in the Trinity River basin, starting in the early part of the 20th century, presumably due to poor water quality (Read, 1954; Read & Oliver, 1953;
have commissioned studies for *P. riddellii* to inform legislative protections by confirming the taxonomic validity of the species (i.e., identities; Inoue et al., 2018) and refining knowledge of its distribution throughout its presumptive range (Ford, Heffentrager, Ford, Walters, & Marshall, 2014; Khan, Smith, Inoue, Hart, & Randklev, 2018; Randklev, Inoue, Hart, & Pieri, 2017). The results of these efforts have painted a stark picture, thus corroborating earlier studies documenting the existence of only a few extant stronghold populations.

To further complicate matters, the type specimen of *P. riddellii* was described based on a single individual from the Trinity River near Dallas (Figure S1), and researchers have noted the external shell morphology of the type specimen is unlike genetically confirmed individuals collected throughout the remainder of the species presumptive range (Khan, Smith, Inoue, Hart, & Randklev, 2018). This is not entirely unexpected given that mussels can show a high degree of morphological plasticity due to large within-population variation and abiotic factors such as hydrology, local environmental conditions, and stream position (Graf, 1998; Hornbach, Kurth, & Hove, 2010; Ortmann, 1920; Peacock & Seltzer, 2008). However, live individuals of *P. riddellii* have not been reported from the Trinity River in decades despite exhaustive surveys in reaches where the mussel fauna has largely remained intact (Randklev, Inoue, Hart, & Pieri, 2017). These two factors, that is, its modern absence from the Trinity River basin and wide morphological variation, have led some to raise questions about its taxonomic validity and presence within the basin (Khan, Smith, Inoue, Hart, & Randklev, 2018).

The uncertainty of whether or not *P. riddellii* is a valid taxon combined with questions about its existence in the Trinity River basin are significant knowledge gaps that could undermine ESA listing and conservation efforts for this species. For example, if the type is found to be invalid then a complete revision of its taxonomy would be required, which could delay or impede listing efforts. However, if the type is valid and *P. riddellii* is native to the Trinity River basin, then inferences about its overall viability are much more bleak than those based on the premise that it never occurred in the basin. To help address these questions, we used zooarchaeological data to test whether *P. riddellii* was present in the Trinity basin. To do this, we collected mussel data from the West Fork of the Trinity River from shells dating to the late Holocene (between 2,500 and 600 years before present). We then use contemporary reference shells to putatively identify *Pleurobema* and *Fusconaia*, the latter is commonly confused with *Pleurobema* using morphology but easily distinguished using genetics (Inoue et al., 2018). To test whether our putative identifications are correct we use a quantitative morphometric analysis to evaluate differences in shell shape between zooarchaeological and contemporary reference shells. Thus, we compare shell shape between validated modern specimens of *P. riddellii* and *Fusconaia* sp. to that of zooarchaeological specimens identified as belonging to either one of these taxa. We then use the resulting data along with our findings for other mussel taxa from the Trinity River drainage to discuss conservation and management implications.

## 2 | METHODS

### 2.1 | Study area

The Trinity River has an overall length of 579 km and encompasses approximately 46,539 km²; it is formed by the Clear, West, Elm, and East forks, flowing from just west of Dallas, Texas to the Gulf of Mexico (Kleinsasser & Linam, 1990). The Trinity basin is densely populated with approximately 6.9 million people as of 2010, the majority of which (~5.3 million) reside in the Dallas-Fort Worth metroplex (Perkin & Bonner, 2016), located near the river’s headwaters. Flow within the Trinity River has been heavily altered by flood control dams, reservoirs, wastewater discharges, and inter-basin water transfers. Land use ranges from agricultural and open rangeland to urbanized centers.

### 2.2 | Zooarchaeological data

Mussel data were collected from archaeological site 41TR198, which is located on the West Fork of the Trinity River, north of Fort Worth, TX (Figure 1). Radiocarbon dates from the site indicate a late Holocene age with dates ranging between 2,500 and 600 years before present (Peter & Harrison, 2011). Shell material from the site was analyzed at the University of North Texas, Laboratory of Zooarchaeology using modern reference samples housed there and at the Elm Fork Natural Heritage Museum and Texas A&M AgriLife Extension and Research Center in Dallas, TX.

### 2.3 | Morphometrics

Putative *P. riddellii* from the late Holocene were identified based on comparison of external morphology to contemporary reference shells of *P. riddellii* from throughout east Texas, but not from the Trinity River basin. Late Holocene *Fusconaia* sp. were also identified based on comparison of external morphology with modern *Fusconaia* sp. (Figures 2
and 3). \textit{Fusconaia} sp. includes sympatric \textit{Fusconaia chunii} (Trinity Pigtoe) and \textit{Fusconaia flava} (Wabash Pigtoe), which cannot be distinguished using external morphology (Pieri et al., 2018). \textit{Fusconaia} was included for comparison because members of this group are frequently confused with \textit{Pleurobema} when using morphology alone; therefore, identifications for all modern material were confirmed using genetics (Inoue et al., 2018).

Zooarchaeological shells are often fragmented and so we developed proxies (Figure 4) for measurements (i.e., shell length, width, and height) commonly used in morphometric analyses focused on delineating species boundaries for mussels (e.g., Johnson et al., 2018; Smith, Johnson, Inoue, Doyle, & Randklev, 2019). Specifically, umbo thickness (UT) captures width of the shell and is measured from the highest point of the umbo, dorsally, to the interdentum. Lateral tooth length (LTL) captures length of the shell and is measured from the anterior to posterior ends of the lateral teeth. Pallial line length (PLL) captures the height of the shell from the umbo to the ventral margin and is measured at the longest distance from the interdentum to the pallial line (Figure 4; Figures S2 and S3). We then used the following ratios of UT and PLL to LTL to convey differences in elongation and inflation among shells: PLL/LTL (elongation), UT/PLL (inflation), and UT/LTL (inflation). Ratios were then normalized using an arcsine-transformation.

2.4  |  Data analysis

A principal component analysis (PCA) was used to evaluate similarity and difference of shape using the ratios of
UT and PLL to LTL across the following putative morphotypes: (a) *Pleurobema* sp. from the late Holocene (n = 32); (b) modern *P. riddellii* from throughout east Texas (n = 24); (c) *Fusconaia* sp. from the late Holocene (n = 27); and (d) modern *Fusconaia* sp. from the Trinity basin (n = 41). Because PCA is an unconstrained ordination, we then used multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) to evaluate how well the PCA, using principal component (PC) scores, was able to distinguish the four morphotypes. A Bonferroni post-hoc test based on corrected values (i.e., raw $p$ values multiplied by the number of comparisons) was used to assess pairwise differences within and between *Pleurobema* and *Fusconaia* and $p$ values ≤0.05 were considered significant. We then calculated a cross-validated error matrix, using jackknife sampling, based on the DFA and presented percentages of correct group assignments to show the performance of classification of the four morphotypes using the PCA scores. In our PCA, we used a covariance matrix and only the first two components are considered significant based on the broken-stick rule (Legendre & Legendre, 1998).

The resulting components were then visualized using a distance biplot. The PCA was performed using the PRCOMP function in the STATS package, MANOVA using the MANOVA function in the MANOVA.RM package, and DFA using the LDA function in the MASS package in R version 3.02 (R Foundation for Statistical Computing, Vienna, Austria).

3 | RESULTS

The PCA yielded two distinct eigenvalues that described 100% of the total variation. The PCA biplot showed differentiation between *Pleurobema* and *Fusconaia* but not among late Holocene *Pleurobema* sp. and modern *P. riddellii* or between late Holocene *Fusconaia* or modern *Fusconaia* sp. (Figure 5). The results of the MANOVA corroborated differences observed in our PCA by showing significant differences between *Pleurobema* and *Fusconaia* (Wilk’s $\Lambda = 0.57$; $F_{6,238} = 12.98$; $p < 0.001$). Pairwise comparisons indicated significantly different morphologies between *Pleurobema* (late Holocene and
modern) and *Fusconaia* (late Holocene and modern), whereas pairwise comparisons did not show significantly different morphologies within *Pleurobema* or *Fusconaia* (Bonferroni corrected, \( p \leq 0.02 \); Table 1).

The DFA was able to successfully classify the various morphotypes but was better able to assign membership to the generic-level than to a specific morphotype, which mirrors our findings from the MANOVA and associated pairwise comparisons. For *P. riddellii*, the DFA assigned 81 and 71% of the individuals of late Holocene *Pleurobema* sp. and modern *P. riddellii* to *Pleurobema*, respectively (Table 2). For the late Holocene *Pleurobema* sp. the DFA correctly assigned 69.0% of the individuals, another 13% were assigned to modern *P. riddellii*, and the remaining 19% were classified as *Fusconaia* (Table 2). For modern *P. riddellii*, 21% of the individuals were correctly assigned, another 50% were classified as late Holocene *Pleurobema* sp., and the remaining 29% were assigned to *Fusconaia* (Table 2). For modern *Fusconaia* sp., the DFA correctly assigned 80% of the individuals, another 2% were assigned to late Holocene *Fusconaia* sp., and the remaining 17% were assigned to *Pleurobema* (Table 2). Thus, for both *Pleurobema* and *Fusconaia* the DFA was able to distinguish the two genera—that is, 81 and 71% of the late Holocene and modern individuals putatively identified as *Pleurobema* and 67 and 83% of the late Holocene and modern individuals putatively identified as *Fusconaia* were correctly classified to their respective genera. Finally, the DFA was less reliable in distinguishing modern vs. late Holocene morphotypes for either genera because of their near-exact morphological match.

### 4 DISCUSSION

Using morphometric techniques, we were able to show that *Pleurobema* and *Fusconaia* were both present in the upper Trinity during the late Holocene, indicating these
genera are native to the Trinity River basin. Our data also show that *P. riddellii* is likely a valid taxon given its presence during the late Holocene, but molecular confirmation using a DNA barcoding approach of live specimens or ancient DNA from museum specimens or zooarchaeological shell is needed to confirm whether or not this is the case. It is possible that late Holocene individuals of *Pleurobema* are not the same species that occurs within the basin today. For example, Williams and Fradkin (1999) studying the mussel fauna from four pre-Columbian archaeological sites in the Apalachicola Basin of Alabama, Georgia, and Florida discovered a new unionid mussel, *Fusconaia apalachicola*, Apalachicola Ebonyshell, which appears to have gone extinct before modern malacologists or shell collectors could collect live or fresh shell. However, in our case, what we have identified as *Pleurobema* sp. from the late Holocene is a near-exact morphological match, in terms of shape and inflation, to that of modern *P. riddellii* collected from several river basins in east Texas. This would suggest its absence from the Trinity River basin today is likely in response to widespread environmental change (see discussion below), exacerbated by the fact that the periphery of a species’ range is often the area where organisms are most sensitive to environmental change (Johnson, McLeod, Holcomb, Rowe, & Williams, 2016; Polechova & Barton, 2015). Current distribution information for *P. riddellii* supports this hypothesis as stronghold populations are largely restricted to the Neches River basin (Howells, 2010, 2014; Howells, Neck, & Murray, 1996), which is in the center of its range (Figure S4).

The absence of *P. riddellii* from the Trinity River drainage today likely stems from ongoing issues with water quality and quantity throughout the basin. As early as the 1800s, journalists reported sewage pouring into the Trinity River (Dallas Daily Times Herald, 1891). By 1925, pollution had become so extreme the Texas Department of Health labeled the Trinity River the “mythological river of death” (Land et al., 1998). The passage of the National Environmental Policy Act in 1970 followed by the Upper Trinity Basin Comprehensive Sewerage plan in 1971 led to regulation of effluent discharges within the Trinity, which led to overall improvements in water quality (Perkin & Bonner, 2016). However, resuspension of residual benthic organic material, termed “black rises” from earlier pollution events resulted in elevated biochemical oxygen demand (BOD) leading to low dissolved oxygen that caused 13 major fish kills between 1970 and 1985 (Land et al., 1998; Perkin & Bonner, 2016).
Since the 1980s, researchers have noted a revitalization of the Trinity River fish assemblage (Perkin & Bonner, 2016) but similar improvements have not occurred for mussels (Randklev, Wolverton, Lundeen, & Kennedy, 2010; Randklev, Inoue, Hart, & Pieri, 2017; Wolverton & Randklev, 2016). The reason for this is that mussels as a group tend to be extremely sensitive to changes in water quality (Cope et al., 2008). Of particular concern is the presence of ammonia, primarily originating from regulated wastewater effluent and fertilizer applied to urban and agricultural lands (Land et al., 1998). Ammonia, specifically its un-ionized form, is toxic to mussels and can be lethal to juvenile mussels even at low concentrations (Newton, 2003; USEPA, 2013; Wang et al., 2007). Ammonia has been implicated in lack of recruitment and subsequent declines for mussel populations outside of Texas (e.g., Strayer & Malcolm, 2012) and preliminary water quality information from the Trinity River indicate this may also be the case for this system (Randklev, Inoue, Hart, & Pieri, 2017).

Changes in water quantity within the basin is another issue that may have disproportionately impacted mussels due to their life history (i.e., long-lived, delayed maturity, slow growing, obligate parasitism). The Trinity River is one of the more highly regulated river systems in Texas, with eight major impoundments in its headwaters, one on its mainstem which effectively divides the river into two watersheds, and two more on adjacent tributaries located near the middle portion of the basin. Construction times of these dams started in 1914 and concluded with the final two impoundments in 1987 (Dowell & Breeding, 1967; Land et al., 1998). The result of these impoundments combined with urbanization of its headwaters and inter-basin water transfers have significantly impacted the natural flow regime. These changes have likely had not only strong negative consequences to the physical habitat for aquatic organisms in this basin but also to aquatic organisms themselves as biological adaptations (e.g., behavioral and physiological) to cope with intra- and interannual variation in hydrology are now mismatched with the current flow regime (Lytle & Poff, 2004; Poff et al., 1997). For mussels, human-induced changes to the flow regime have been implicated in declines for mussel populations in other river basins within the state and also outside of Texas (Gangloff, Siefferman, Seesock, & Webber, 2009; Gillis, 2012; Randklev et al., 2015).

Reconciling human versus natural changes to biogeographic patterns is important for accurately assessing the status of a species and also deriving recovery activities to
mitigate further declines. In this study, we show the distribution of P. riddellii differs from assessments that exclude data beyond the last couple hundred years, which underscores the pernicious effect of shifting baselines. In fact, other mussel species within this basin show similar patterns as it relates to pre- versus post-European contact. For example, Randklev, Wolverton, Lundeen, & Kennedy (2010) found that Plectomerus dombeyanus, Bankclimber, was more widely distributed in the Trinity during the late Holocene than today. Similarly, Lampsilis satura, Sandbank Pocketbook, was present during the late Holocene but now appears extirpated from the Trinity River basin (Wolverton & Randklev, 2016).

Natural resource management is often focused on the present and foreseeable future of a given resource. However, understanding the causes for the current condition of a resource requires a long-term historical perspective to place things within context. Our study emphasizes the need for long-term historical perspectives in conservation biology as our findings show that P. riddellii was likely present prior to widespread water quality degradation in the early 1900s. This finding will likely have profound implications for legislative protection for this species. From a broader conservation perspective, this study contributes to a growing body of literature (e.g., Peacoock, Randklev, Wolverton, Palmer, & Zaleski, 2012; Popejoy, Randklev, Neeson, & Vaughn, 2018; Popejoy, Randklev, Wolverton, & Nagaoka, 2018; Randklev, Wolverton, Lundeen, & Kennedy, 2010; Wolverton & Randklev, 2016) that emphasizes the need for conservationists and resource managers to utilize zooarchaeological data in their status assessments and recovery planning, particularly when trying to determine the extent and cause of faunal changes. Integrating these data will help minimize incorrect conclusions that could undermine listing decisions, and ultimately, contribute to effective conservation and recovery planning for imperiled species.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

ETHICS STATEMENT

All research was carried out in accordance with standard research practices.

DATA AVAILABILITY STATEMENT

All data are presented in the manuscript except the following information which is presented as supplementary files: (a) Figure showing right valve external views of P. riddellii, including its holotype (Appendix—Figure S1); (b) Figure showing the relationship between shell length and LTL, shell height and PLL, and shell width and UT for P. riddellii and Fusconaia sp. (Appendix—Figures S2 and S3); (c) Figure showing occurrence map for Pleurobema riddellii (Appendix—Figure S4); and (d) Word document providing Table S1 listing state and federal conservation status for mussel species of conservation concern in Texas. All supplemental information is available online and the authors are solely responsible for the content and functionality of these materials. This product (article, paper, supplement, etc.) has been peer reviewed and approved for publication consistent with USGS Fundamental Science Practices (https://pubs.usgs.gov/circ/1367/). Queries (other than absence of the material) should be directed to the corresponding author.

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SUPPORTING INFORMATION

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

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