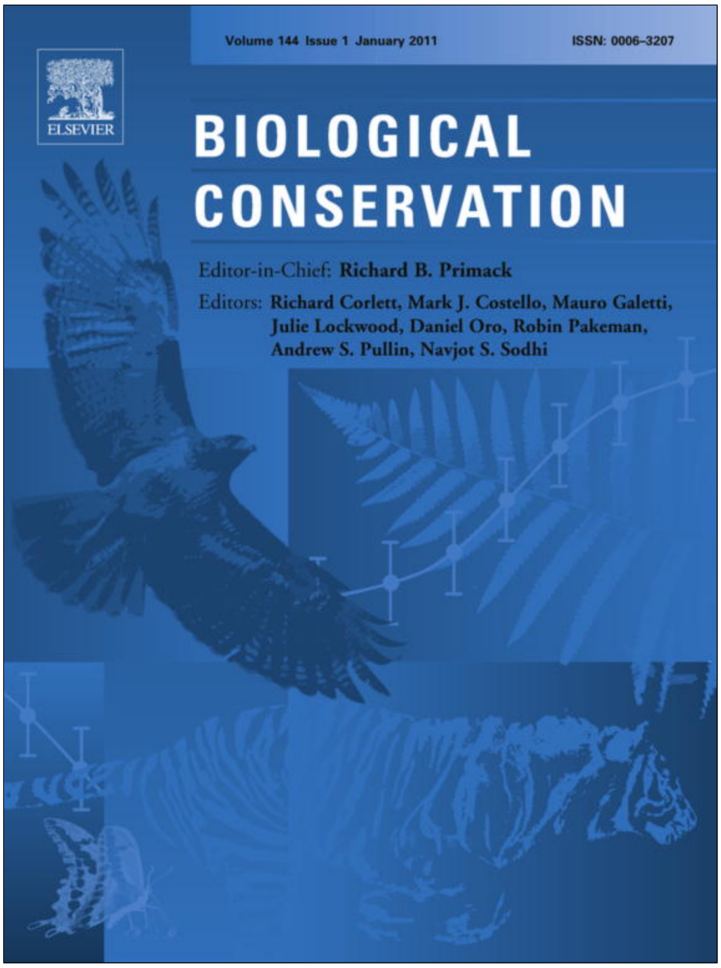
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Endemic species: Contribution to community uniqueness, effect of habitat alteration, and conservation priorities

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A B S T R A C T

The biodiversity crisis, particularly dramatic in freshwaters, has prompted further setting of global and regional conservation priorities. Species rarity and endemism are among the most fundamental criteria for establishing these priorities. We studied the patterns of rarity and the role of rare species in community uniqueness using data on freshwater bivalve molluscs (family Unionidae) in Texas. Due to the large size and gradients in landscape and climate, Texas has diverse and distinct unionid communities, including numerous regional and state endemic species. Analysis of the state-wide distribution and abundance of Unionidae allowed us to develop a non-arbitrary method to classify species rarity based on their range size and relative density. Of the 46 Unionidae species currently present in Texas, 65% were classified as rare and very rare, including all state and regional endemics. We found that endemic species were a critical component in defining the uniqueness of unionid communities. Almost all endemics were found exclusively in streams and rivers, where diversity was almost double that of lentic waters. Man's ongoing alteration of lotic with lentic waterbodies favors common species, and dramatically reduces habitat for endemics, contributing to homogenization of unionid fauna. We identified hotspots of endemism, prioritized species in need of protection, estimated their population size, and recommended changes to their current conservation status.

1. Introduction

Exponential human population growth is associated with a dramatic increase in pollution, habitat alteration, introduction of invasive species and other factors which have contributed to the sharp decline in biodiversity worldwide. As a result, many freshwater as well as terrestrial systems are inevitably going to be greatly simplified and homogenized (McKinney and Lockwood, 1999). This is especially true for freshwater ecosystems, which are among the most endangered on Earth, experiencing greater declines in biodiversity than many other ecosystems due to steeply rising human demands over the past century (Dudgeon et al., 2006; Revenga and Kura, 2003; Strayer and Dudgeon, 2010). More than half of the accessible continental runoff is now controlled and used by humans, and over half of world's major rivers are seriously polluted (Vörösmarty et al., 2005; World Water Commission, 1999). The biodiversity crisis that we are currently facing requires priority setting at global, regional, and local scales in order to concentrate limited resources on the most important conservation needs (Darwall and Vie, 2005; Groom et al., 2006; Knight et al., 2008; Mittermeier et al., 1998; Williams et al., 2002).

Species rarity, diversity, and endemism are among the most frequently cited criteria for establishing conservation priorities (Reid, 1998; Schmeller et al., 2008; Williams et al., 2002). High endemism is especially typical for freshwater habitats whose insular nature has led to the evolution of many species with small geographic ranges (reviewed in Strayer and Dudgeon, 2010). Habitat change,

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degradation, and destruction are the most important threats to endemics which are highly adapted to their specific environments. Rarity is the major determinant of a species' likelihood of extinction in both ecological and geological time (Gaston, 1994; Mace et al., 2008; Pimm, 1991), and species usually become rare before going extinct (Dobson et al., 1995). Therefore, endemic species that are characterized by limited spatial distribution (Anderson, 1994), and especially those that disperse poorly, can be expected to be the first candidates for extinction. Among the 62 extinct European taxa since 1500, only 11 were wide-ranging taxa, while all others were endemic to one country, or narrow-ranging endemics shared by two or three countries (Fontaine et al., 2007). Not surprisingly, endemism is an important criterion in most methods used to determine national conservation responsibilities (Schmeller et al., 2008). However, estimates of future extinctions are hampered by many factors, including limited knowledge of species' life history traits, niche, resource requirements, and location of hotspots of endemism, as well as the lack of suitable criteria to determine rarity (Kuussaari et al., 2009; Pimm et al., 1995).

Molluscs are among the most threatened group of animals on the planet: the number of mollusc extinctions worldwide is higher than the number of extinctions in all other taxa combined (Régnier et al., 2009). Freshwater bivalves in the order Unionoida are considered to be one of the most endangered groups of animals in North America (Bogan, 1993; Lydeard et al., 2004), with over 76% of the North American Unionidae and Margaritiferidae presumed extinct, threatened, endangered, or deemed of special concern (Williams et al., 1993). Among the main reasons for their decline are sensitivity to water and habitat quality, sedentary lifestyle, long life span, complex life cycle with parasitic larvae that require specific fish hosts, slow growth, and low reproductive rates (reviewed in Bogan, 1993; McMahon and Bogan, 2001; and Strayer et al., 2004, etc.).

We studied the patterns of rarity and the role of rare species in community structure using data on Unionidae in the state of Texas. Due to its large size, geographical location, and gradients in landscape and climate, Texas has diverse and distinct unionid communities, including numerous endemic species (Abell et al., 2000; Howells et al., 1996; Neck, 1984). Since 1800, over 1.2 million acres of artificial lakes have been created in Texas, including 200 major reservoirs and ~1000,000 small ponds, that have dramatically altered the hydrology of the state which historically had no natural lentic waters (Estaville and Earl, 2008; Masser and Schonrock, 2006). The purpose of this paper is to discriminate among common and rare Texas unionid species, determine the role of endemic species in community uniqueness, compare species composition in lotic and lentic environments, and prioritize species in need of protection.

2. Methods

2.1. Study area

We conducted a state-wide survey of unionids in Texas (latitudes 98°32–99°30, longitudes 102°08–93°31) from 2003 to 2009 (Fig. 1). This area encompasses several climate zones, from humid to arid, with mean annual precipitation decreasing from 140 cm on the east to less than 38 cm on the west (Estaville and Earl, 2008). There are 11,247 named streams and rivers in Texas that belong to two major drainage basins, the Mississippi River (Red River and Arkansas basins) and the Gulf of Mexico Coastal drainage basin (Dahm et al., 2005). Most East Texas watersheds are predominantly forested (>60% of total watershed area) with little urbanization (<8%). In contrast, Central Texas drainage basins are mostly rangeland (>50%) and very urban (up to 25%). Three quarters of the Rio Grande River drainage basin is scrubland and grassland (Dahm et al., 2005). Drastic differences in climate, soils, and landscapes contribute to differences among the rivers. Rivers flowing in the wet climate of East Texas are characterized by pine-covered banks and slow-moving currents. Central Texas rivers cut through hilly terrain and have steep gradients. Rivers in West Texas traverse extremely arid landscapes with high bluffs and canyons. Considering these differences, the studied areas were divided into four biogeographical regions (with regards to unionids) according to Neck (1982) (Fig. 1). Following Parmalee and Bogan (1998), we will refer to them as "provinces". Northern Texas, including the Canadian, Red, Sulphur, and Big Cypress Bayou river systems, is referred to as the Texoma Province – a part of Interior Basin, or Mississippian Province. The Sabine province includes the eastern part of Texas (Sabine, Neches, Trinity, and San Jacinto river basins). The Central Province includes the Brazos, Colorado, Guadalupe, San Antonio, and Nueces river basins, and coastal plain streams feeding into the Baffin Bay system (Neck, 1982). The Rio Grande Province consists of the Rio Grande River drainage basin.

2.2. Survey sites

Mussels were surveyed at 139 sites, distributed in 66 waterbodies, belonging to 11 major drainage basins of Texas (Fig. 1). Most of the sites were sampled once, however, 19 sites were sampled several times. Due to the prevalence of private land in Texas, where only 2% of the lands remain in public ownership (Texas Parks and Wildlife Department, 1974), survey sites were often selected within state parks, near public boat ramps, or based on accessibility from roads that either crossed or approached a waterbody. A Landowner Permission for wildlife research was acquired from each property owner before entering their property, if the land was private. The work was carried out with an appropriate Scientific Research Permit issued by the Texas Parks and Wildlife Department (TPWD).

Sampling was completed via hand collection of both live and dead mussels, by wading in low water, and by snorkeling. Due to poor visibility, tactile searches (running fingers over the sediment and checking up to 15 cm depths, depending on substrate) were used at all sites. Reconnaissance sampling (timed searches) was used to reveal the presence of mussels and species diversity (Strayer et al., 1997; Vaughn et al., 1997) at each site. If mussel assemblages were present, quantitative methods (randomly placed 0.25 m^2 quadrats, area searches, or systematic strip transects with a random start (Smith, 2006)) were used for assessments of density and population size (Dunn, 2000; Strayer and Smith, 2003). All collected live mussels and shells were taxonomically identified, counted, and measured with calipers to the nearest mm. Live mussels after measurements were carefully rebedded into the sediment from which they were taken. Shell condition of dead mussels was recorded for each specimen. Shells were considered recently dead if they contained tissue remains and/or internal and external colors were not faded. Shells with most or all of the internal coloration and gloss faded, shell epidermis absent, or aged and flaking, were considered long dead and were excluded from data analysis. Specimens were identified using published taxonomic keys and descriptions (Cummings and Mayer, 1992; Howells et al., 1996; Johnson, 1998; Oesch, 1995; Strayer and Jirka, 1997). Live specimens were preserved in 200 proof ethyl alcohol; dead shells were cleaned and dried. We deposited voucher specimens into the Great Lakes Center Invertebrate Collection (Buffalo State College, Buffalo, NY). Each specimen was labeled with a unique number, and cataloged in database with the following information: specimen number, species name, name of person who collected and identified the specimen, date of collection, and detailed site information. Specimens were also deposited in the North

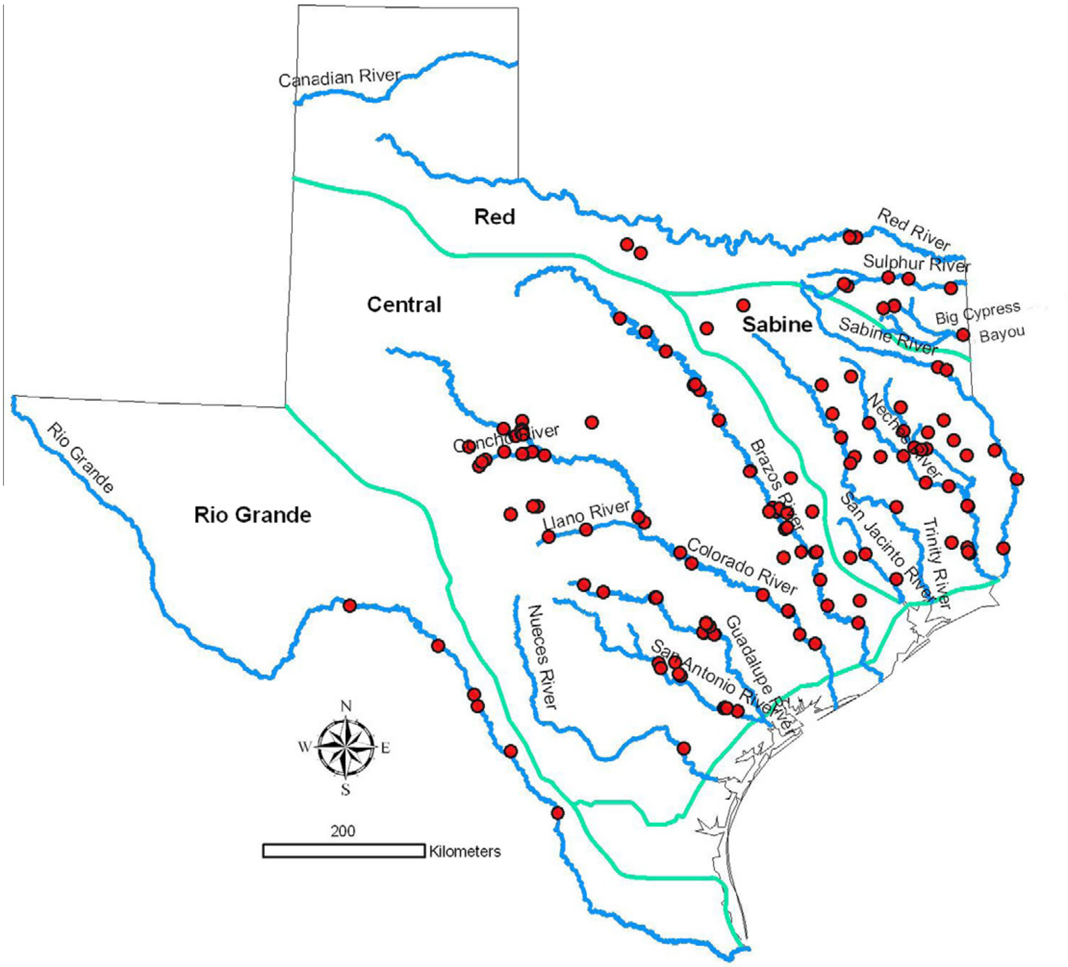

Fig. 1. Map of the state of Texas with sampling sites. Major surveyed Texas rivers and biogeographic provinces (Neck, 1982) to which they belong are outlined.

Carolina State Museum of Natural Sciences (Raleigh, NC), and the Invertebrate Zoology Collection of the National Museum of Natural History, Smithsonian Institution (Washington, DC).

2.3. Data analysis

We completed data analyses using relative density as catch-per-unit of effort data, i.e., the number of mussels per each species found live and recently dead per time search effort at each sampling site (mussels per man per hour, mussels mh^{-1}). According to Hornbach and Deneka (1996), quantitative and qualitative methods provide similar species richness, diversity, and evenness values and result in similar relationships between the number of mussels collected and the number of species found. Time search effort, calculated as the collective number of hours to survey a given site times the number of surveyors averaged 2.4 ± 0.1 mh among sites (mean ± standard error of the mean here and elsewhere unless noted) (median 2.0, max 8.0 mh). The number of species found in time search at the same sites was significantly higher than in quadrats at the same site (7.3 ± 4.0 mussels vs. 5.4 ± 3.6 in quadrats, $P = 0.011$, paired 2-tail t-test), indicating sufficient mussel recovery in time search. To check if an increase in sampling effort might result in an increase of the number of species or mussels collected, we tested the relationship between time search efforts and the number of species collected alive, total number of live mussels collected, and total number of species (live and dead) found at each sampling site. All the regressions were non-significant (log total number of species collected live vs. time search effort, $R = -0.015$, $P = 0.87$, log total number of live mussels collected vs. time search effort, $R = -0.035$, $P = 0.71$; log total number of mussels collected vs. time search effort, $R = 0.12$, $P = 0.12$). In addition, we found no correlation between the residuals of these relationships (e.g., between the log-transformed values of the number of species or mussels collected and the sampling effort) and time search efforts ($r = 0.00$) indicating no bias was introduced on account of increased sampling effort.

To rank species rarity based on their range size and abundance, we used species occurrence (proportion of waterbodies occupied by each species out of a total 59 waterbodies where molluscs were found) and their average relative density in the waterbodies. To reveal natural groupings in the relative density and occurrence data for each species sampled, we performed a Cluster analysis (using group average) on Euclidian distance resemblance matrix using PRIMER 6 software (Plymouth Routines in Multivariate Ecological Research, Version 6.1.6, Primer E-Ltd., 2006). Parameters were transformed (log transformation for occurrence data and fourth root transformation for the average relative density in the waterbodies, $P > 0.14$, Shapiro–Wilk's W test) and normalized prior to the analysis.

We followed Howells et al. (1996) and NatureServe Explorer (NatureServe, 2009) in distinguishing regional and Texas endemic species. Following Gaston (1994), we used a term "vagrant species" ("isolates at the edge of their range" (Main, 1984)) for taxons that were found only occasionally within the boundaries of Texas, which had, therefore, only a very small share of the global population of these taxa (Gardenfors et al., 2001).

Table 1
The mean relative density (in time searches, mussels mh^{-1}) and occurrence (%) of Unionidae calculated for 59 Texas waterbodies (excluding seven waterbodies where no mussels were found), 11 river basins, and four provinces. The rarity of mussels (last column) was assigned based on cluster analysis (Fig. 3B).

Species	Mean relative density by waterbody	% Occurrence by waterbody	% by basin	% by province	Rarity
Lampsilis teres	4.841	59.3	100	100	Very common
Amblema plicata	3.684	54.2	90.9	75	Very common
Pyganodon grandis	3.492	47.5	81.8	75	Very common
Quadrula apiculata	2.480	49.2	100	100	Very common
Cyrtonaias tampicoensis	1.437	28.8	54.5	50	Common
Quadrula mortoni	1.239	23.7	45.5	50	Common
Utterbackia imbecillis	0.548	35.6	81.8	100	Common
Potamilus purpuratus	0.712	30.5	72.7	75	Common
Toxolasma texasensis	0.657	30.5	81.8	75	Common
Leptodea fragilis	0.431	37.3	63.6	75	Common
Lampsilis hydiana	0.694	28.8	54.5	75	Common
Obliquaria reflexa	1.558	18.6	36.4	50	Common
Plectomerus dombeyanus	1.277	20.3	63.6	75	Common
Tritogonia verrucosa	0.523	22.0	81.8	75	Common
Megalonaias nervosa	0.328	27.1	72.7	100	Common
Quadrula quadrula	0.806	13.6	9.1	25	Common
Ligumia subrostrata	1.057	6.8	18.2	25	Rare
Quadrula aurea[a]	0.565	8.5	27.3	25	Rare
Fusconaia askewi[b]	0.523	8.5	36.4	50	Rare
Quadrula houstonensis[a]	0.357	10.2	18.2	25	Rare
Fusconaia lananensis[a]	0.346	6.8	9.1	25	Rare
Anodonta suborbiculata	0.301	6.8	27.3	50	Rare
Truncilla truncata	0.091	11.9	45.5	50	Rare
Potamilus ohiensis	0.254	6.8	27.3	75	Rare
Potamilus amphichaenus[b]	0.153	6.8	27.3	25	Rare
Uniomerus declivis	0.078	8.5	36.4	50	Rare
Lampsilis bracteata[a]	0.054	8.5	27.3	25	Rare
Quadrula nobilis	0.131	5.1	18.2	25	Rare
Arcidens confragosus	0.032	10.2	45.5	50	Rare
Pleurobema riddellii[b]	0.075	5.1	9.1	25	Rare
Glebula rotundata	0.144	3.4	18.2	25	Rare
Lampsilis satura[b]	0.036	6.8	18.2	25	Rare
Truncilla donaciformis	0.041	5.1	9.1	25	Rare
Toxolasma parvus	0.079	3.4	9.1	25	Rare
Quadrula nodulata	0.031	3.4	18.2	50	Rare
Truncilla macrodon[a]	0.023	3.4	18.2	25	Rare
Popenaias popeii[b]	0.048	1.7	9.1	25	Rare
Quadrula pustulosa	0.009	3.4	9.1	25	Rare
Potamilus metnecktayi[b]	0.029	1.7	9.1	25	Very rare
Quadrula petrina[a]	0.028	1.7	9.1	25	Very rare
Truncilla cognata[b]	0.027	1.7	9.1	25	Very rare
Lasmigona complanata	0.013	1.7	9.1	25	Very rare
Uniomerus tetralasmus	0.006	1.7	9.1	25	Very rare
Fusconaia flava	0.002	1.7	9.1	25	Very rare
Strophitus undulatus	0.001	1.7	9.1	25	Very rare
Quincuncina mitchelli[a]	0.000	1.7	9.1	25	Very rare

[b] Regional endemic.
[a] Texas endemic.

Differences in community structure were assessed with non-parametric multivariate statistical techniques on data matrices of the entire community, including all live and recently dead species and their relative densities. A square-root transformation was used to normalize relative densities for the analysis. Similarity of the community composition was summarized by calculating Bray–Curtis distances – a measure of similarity with values ranging from 0 (identical samples) to 1, which is not influenced by rare species as other indices (Bray and Curtis, 1957; Clarke, 1993). To visualize the differences among assemblages, we used Non-metric Multi-Dimensional Scaling (NMDS), which calculates a set of metric coordinates for samples, most closely approximating their non-metric distances. NMDS was found to be consistently reliable in a comparative study of ordination methods for community data (Clarke, 1993; Kenkel and Orlóci, 1986). In this analysis, we excluded sites where less than two species were collected.

Differences among communities were assessed by Analysis of Similarities (ANOSIM), a resampling technique that uses permutation/randomization methods on Bray–Curtis similarity matrices to identify differences among groups of samples, after which pairwise comparisons are conducted (Clarke, 1993). Large values of the test statistic (Global R) indicate complete separation of groups, and small values (close to 0) indicate little or no separation.

We used SIMPER ("Similarity Percentage") analysis to examine the contribution of each species to the average Bray–Curtis similarity among communities within each province. In addition, we determined the contribution of each species to the average Bray–Curtis dissimilarity between provinces. This analysis was done initially on the whole set of species, then repeated excluding endemic species, and finally, performed excluding very common and common species (categories of rarity are given in Section 3.1 and Table 1). Effects were considered statistically significant at $P < 0.05$.

3. Results

3.1. Species rarity

During the six years of our study we found 46 live and/or recently dead unionid species. There was a strong positive

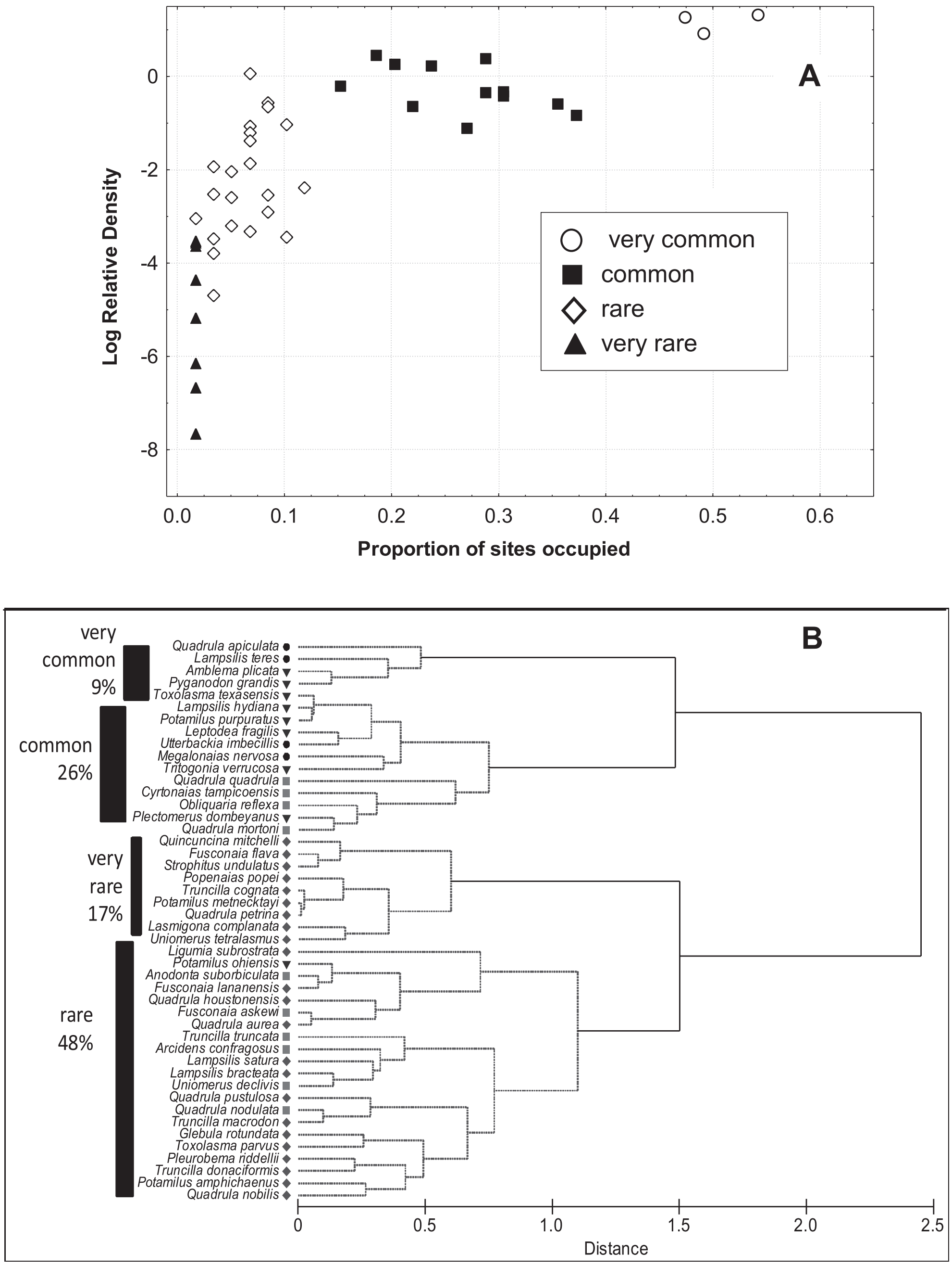

Fig. 2. The rarity classification of Texas unionid species. (A) Groups of rarity for species that found live and recently dead in 59 sampled Texas waterbodies. *Y* axis represents log-transformed average relative density (mussels mh^{-1}) of each species in the waterbodies, *X* axis – occurrence (proportion of waterbodies occupied). (B) Cluster analysis (group average) on Euclidian distance-based resemblance matrix built on normalized transformed data on occurrence and relative density of live and recently dead species. To satisfy the normality assumption we log-transformed the occurrence (as the ratio of occupied waterbodies from total surveyed), and used fourth root of average relative density calculated for 59 waterbodies. Clusters marked with solid lines are significantly different at $P = 0.001$ (SIMPER). The symbols represent unionid occurrence by province: diamond – 25%, rectangle – 50%, triangle – 75%, and circle – 100%.

relationship between the proportion of waterbodies where a species was observed, and its relative density (Pearson $r^2 = 0.76$, $P < 0.001$), indicating that species with wide occurrence were also more abundant.

Cluster analysis revealed four significantly different groups of unionid species (very common, common, rare, and very rare) based on their occurrence and relative density ($P < 0.001$, SIMPER; Global $R = 0.85$, $P = 0.001$, one-way ANOSIM) (Fig. 2B, Table 1). Only 16 species were very common and common in Texas, and four very common species were present at high densities in ~50% of all sampled waterbodies (Fig. 2, Table 1). Twenty-two rare species were found at low densities in 1–9 waterbodies and each of the eight very rare species were found in only one waterbody. Of the 30 rare and very rare species in Texas, 16 were vagrants common in other regions, and 14 were either regional or Texas endemics (Table 1). The distribution of Texas endemic species by provinces was not even ($\chi^2 = 11.8$, $P = 0.008$, Table 1), ranging from none in the Texoma and Rio Grande Provinces to six in Central Texas. In contrast, the number of regional endemics was higher in the Sabine Province bordering with the Mississippi (4) and in the Rio Grande Province adjoining the Panuco–Tamesi system (3). The Rio Grande and the Central Provinces had the highest percentage of very rare species relative to the total number of species in the province (25% and 16%, respectively).

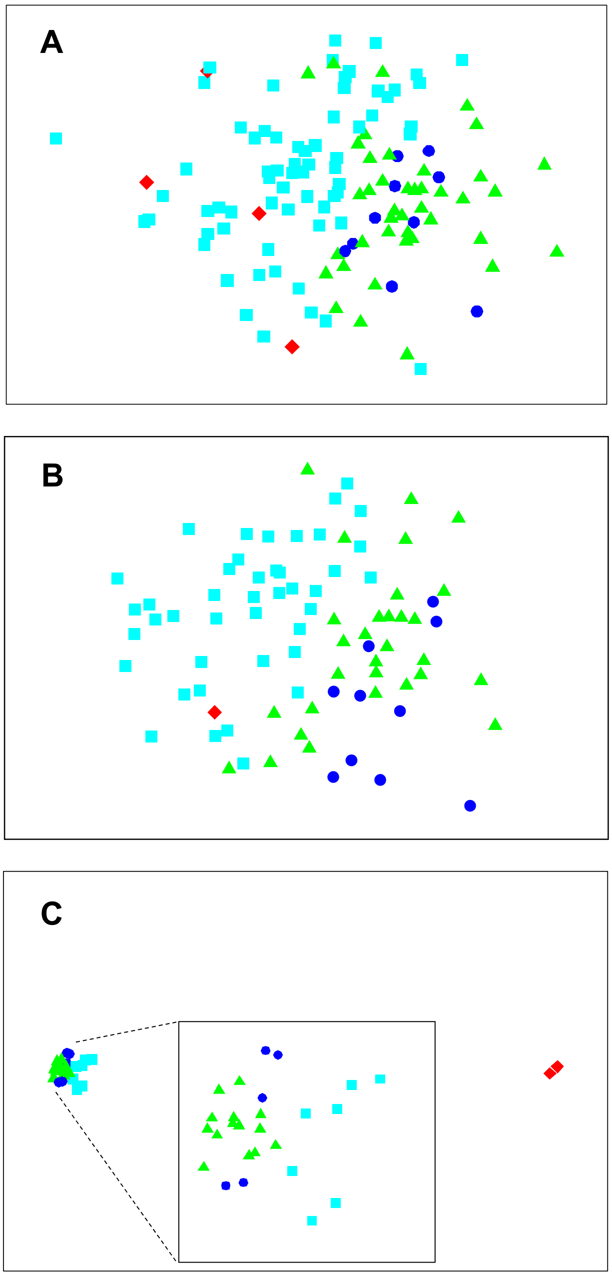

Fig. 3. Non-linear multidimentional scaling (NMDS) plots of unionid communities at all sampled sites (A), excluding endemic species (B), and excluding common and very common species (C). The sites are labeled by biogeographic provinces (Neck, 1982) (diamond – Rio Grande, rectangle – Central, triangle – Sabine, and circle – Texoma Province). Relative density data (mussels mh^{-1}) for live and recently dead molluscs collected at all sampled sites (excluding sites where less than two species were collected) were square-root transformed and converted to similarity matrix using Bray–Curtis similarity index. The insert on C shows enlarged cluster of sites in the Central, Sabine and Texoma Provinces. (A) 2D stress = 0.20, 3D stress = 0.15. (B) 2D stress = 0.24, 3D stress = 0.17; (C) 2D and 3D stress = 0.01.

3.2. Role of endemic species in community

To determine species responsible for similarity of communities within provinces, we examined the contribution of each species to the average Bray–Curtis similarity for each province. Several very common species contributed to greater than 50% of community similarity in most provinces, while rare endemic species contributed less than 5% except for the Rio Grande Province where one regional endemic (*Popenaias popeii*) was responsible for all of the similarity (Appendix A.1.1).

The largest contributors to the dissimilarity of unionid communities between the provinces were (1) the differences in relative densities of very common and common species shared between the provinces and (2) the absence of species from one of the provinces (Appendix A.1.2). The largest differences were found between communities of disjunct provinces sharing only a few common species (Sabine and Rio Grande: 96%, Texoma and Rio Grande: 98%, Appendix A.1.2).

Homogenization of communities due to the disappearance of rare endemic species is a possible scenario in the absence of conservation efforts. To explore possible changes in the structure of unionid communities, we tested for differences in community composition among provinces. All endemic species (seven Texas endemics and seven regional endemics) were excluded for this purpose from the analysis. We found that the exclusion of endemic species diminished the differences among provinces. Dissimilarities between communities in all provinces decreased on average by 6.4%, and the decline was larger for adjoining provinces with endemic species (e.g. 10% between Central and Rio Grande, Appendix A.2). Moreover, after excluding endemic species, the differences between several provinces became non-significant (Sabine and Rio Grande: $R = 0.453$, $P = 0.13$; Central and Rio Grande: $R = 0.257$, $P = 0.14$, Fig. 3A and B).

Alternatively, when we removed common and very common species from the analysis we found that the contribution of regional and state endemics to the similarities within provinces increased. Thus, the contribution of *Fusconaia askewi* and *Fusconaia lananensis* to the similarity within the Sabine Province increased tenfold (from 4.6% to 41.3%), and Central Texas endemics (*Quadrula aurea*, *Quadrula houstonensis*, *Truncilla macrodon*, and *Quincuncina mitchelli*) comprised cumulatively over 96% to the similarity among communities in the Central Province (Appendix A.3.1). When excluding common species, the difference among provinces became more pronounced (Fig. 3C).

Endemic species also determined a large part of the dissimilarity in communities between provinces when common species were excluded. Endemic species combined were responsible for 38% of the dissimilarity between the Sabine and Texoma Provinces, 61% between the Sabine and Central Provinces, 48% between the Texoma and Central Provinces. Rio Grande and Central Texas endemics collectively contributed 97% to the dissimilarity between the Rio Grande and Central Provinces (Appendix A.3.2).

3.3. Habitat alteration and rare species

Naturally occurring lentic waters are not native to Texas. The massive construction of reservoirs during the last century has greatly altered freshwater habitats in the state (Dahm et al., 2005). We found that the total unionid diversity in lotic waterbodies (44 species) was substantially higher than in lentic waterbodies (26 species). Twenty species were found exclusively in streams and rivers (Appendix B.1). Species with a large contribution to the similarities of streams and rivers were mainly unionids with large, heavy and often sculptured shells (e.g., *Lampsilis teres*, *Amblema plicata*, *Cyrtonaias tampicoensis*, *Quadrula apiculata*, *Tritogonia verrucosa*, *Megalonaias nervosa*) that cumulatively comprised over 74% of total similarity of lotic communities (Appendix B.2). Lentic waters were different from lotic mainly due to the presence of Anodontinae: the most common species in reservoirs, *Pyganodon grandis*, alone contributed 38% to the total similarity of lentic waters. *P. grandis* and *Utterbackia imbecillis* were 24 and 4 times, respectively, more abundant in lentic than in lotic waterbodies (Appendix B.2). Another Anodontinae species, *Anodonta suborbiculata*, was found exclusively in reservoirs.

The relative abundance of species inhabiting lentic and lotic waters by rarity groups was significantly different ($F = 28.6$,

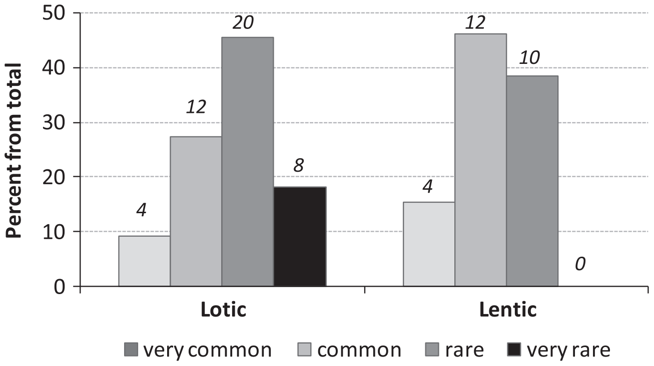

Fig. 4. Percent of rarity groups from total number of unionid species in lotic (streams and rivers, total 44 species found) and lentic (reservoirs, 26) waterbodies. Numbers above the columns represent the total number of species in each category.

$P < 0.0001$, Fisher's Exact Test, Fig. 4). All very common and common species were able to inhabit both lotic and lentic waters (Appendix B), and most of them were up to six fold more abundant in reservoirs than in rivers and streams. In contrast, none of the very rare species were found in standing waters (Fig. 4, Appendix B.1). Only one regional endemic, *Potamilus amphichaenus* and one Texas endemic, *Q. aurea*, were found in lentic waters (Table 2). All other endemic unionids were found exclusively in streams and rivers.

3.4. Conservation implications

Of the total 30 rare and very rare species in Texas, 16 were vagrants and may not be of the highest priority from a conservation perspective (Gardenfors et al., 2001; Gaston, 1994), because there are other geographical areas where their management will be far more effective. The remaining 14 species represented by state or regional endemics were selected as priority species for conservation. Only two of these 14 species are currently listed by the IUCN as critically endangered (*Q. mitchelli*, and *P. popeii*), two as endangered, six as near threatened, and four species were not evaluated (*Truncilla cognata, T. macrodon Quadrula petrina* and *Q. aurea*) (Table 2). Based on our estimates of former and current species range, population sizes and rates of decline, we suggest changes to the current IUCN conservation status for nine of these species (Table 2). We recommend transferring four species (*Lampsilis bracteata*, *Potamilus metnecktayi*, *T. cognata* and *Q. petrina*) to a higher risk category of critically endangered; three species (*T. macrodon*, *F. lananensis*, and *Pleurobema riddellii*) to the category of endangered and two species (*Q. aurea* and *Q. houstonensis*) to the category of vulnerable species.

4. Discussion

Analysis of contemporary data on the state-wide distribution and abundance of Unionidae in Texas allowed us to develop an original non-arbitrary method to classify the rarity of unionid species based on their range size and relative density. Based on this method, 46 unionid species currently present in Texas were recognized as very common, common, rare, or very rare. We found that all endemic species were rare, and were a critical component in defining the uniqueness of unionid communities. We also found that the ongoing replacement of lotic waterbodies with lentic ones largely favors very common and common species, and dramatically reduces habitat for endemic unionids. Finally, based on this study, we identified hotspots of endemism, prioritized species in need of protection and estimated their respective population size, and suggested relevant conservation measures.

4.1. Species rarity

There are many definitions of rarity, but most often rare species are regarded as having low abundance (density rarity) and/or small ranges (range-size rarity) (Gaston, 1994; Williams et al., 2002). One of the greatest advances to the study of rarity would be the establishment of recognized criteria for its identification, as currently, the cut-off points for abundances and range sizes are mostly chosen arbitrarily (Benkendorff and Przeslawski, 2008; Gaston, 1994). The advantage of our method was in applying cluster analysis to both continuous parameters of range-size and density rarity, thus allowing for a quantitative rather than arbitrary approach to determine species rarity. We found that all endemic unionids in Texas fell into the rare and very rare categories, and half of them were narrow endemics found only in few waterbodies in Texas. The merit of our classification was confirmed by the fact that all the 14 endemic species that we recommended as priority for conservation were recently added to the state's list of threatened species (Texas Register 35, 2010). Eleven of those species are currently under consideration for federal listing by the US Fish and Wildlife Service (*L. bracteata*, *Lampsilis satura*, *P. amphichaenus*, *Q. aurea*, *Q. houstonensis*, *Q. petrina*, *Q. mitchelli*, *T. cognata* and *T. macrodon* (74 FR 66261, December 15, 2009); and *F. lananensis* and *P. riddellii* (74 FR 66866, December 16, 2009).

By definition, endemism is the restriction of the natural range of a taxon to a defined area (Anderson, 1994; Gaston, 1994; Laffan and Crisp, 2003; Williams et al., 2002): species are endemic to an area if they occur exclusively within that area. However, endemism does not necessarily imply rarity, because narrowly endemic species may be abundant within their range and rare species may be geographically widespread (Cron et al., 2009; Gaston, 1994; Williams et al., 2002). A strong positive relationship between the proportion of Texas waterbodies where a species was found and its relative density indicated that species with narrow geographical ranges were also less abundant. Local rarity increases vulnerability and the likelihood that demographic and environmental stochasticity will wipe out populations, as a restricted distribution means that all or most individuals will probably experience adverse conditions simultaneously (Gaston, 1998; Lawton et al., 1994). The positive relationship between local abundance and geographical distribution means that, with regard to risk of extinction, species will tend to face a "double jeopardy" (Gaston, 1998), as higher extinction rates are correlated particularly with species with restricted ranges and low density (Gaston, 1994; Groom et al., 2006).

4.2. Role of endemic species in community uniqueness

Excluding rare species from community analyses is a common procedure because they are often considered unimportant components of communities that contribute little to analyses and add noise to statistical solutions (reviewed in Cao et al., 2001, 1998; and Gaston, 1994). We found that endemic species determined a large part of the disparity in community composition among the provinces, and their exclusion diminished this distinction to the degree that the differences between adjacent provinces became non-significant. In contrast, exclusion of common species amplified the differences among provinces and revealed the role of endemic species in community structure. Therefore, rare and endemic species are critical components of community structure, and their loss will ultimately lead to homogenization and simplification of communities and the forfeiture of their uniqueness. Our results agree with Goodall (1954), who observed that the inclusion of rare species helped to recognize a unique community in PCA ordination, and with other studies showing that the exclusion of rare species led to a serious underestimation of the differences in species rich-

Table 2
Status of rare species in Texas (excluding vagrant species), including number of significant populations, total number of live individuals (or estimated population size) (*N*), and their distribution in Texas (data from our 2003–2009 surveys). Classification of threat for each species is given according to the current IUCN status, and suggested changes to the status based on this study.

Species (TE – Texas endemic, RE – regional endemic)	# Populations found	*N*	Locations: waterbody	Current IUCN (2010) status[a,b]	Suggested IUCN status
Group 1 – priority for surveys					
Quincuncina mitchelli (TE)	None	1 (relatively recently dead[c])	San Marcos River	CR (A1c)	CR (possibly extinct)
Truncilla cognata (RE)	None	5	Rio Grande River	NE	CR (A2c, B2a, B2biii, B2biv)
Lampsilis bracteata (TE)	None	13 (+3 very recently dead[d])	Guadalupe, San Saba, Llano rivers, Live Oak Creek, and Elm Creek	NT	CR (A2c, C1)
Potamilus metnecktayi (RE)	None	15	Rio Grande River	EN (A1ce)	CR (A2c, C1)
Popenaias popeii (RE)	None	12	Rio Grande River, Devils River (T. Miller, personal communication)	CR (A1c)	No change
Group 2 – priority for protection of known populations					
Quadrula petrina (TE)	1	4030 ± 498 (95% CI)	Concho River	NE	CR (A2c, B2a, B2biii, B2biv)
Truncilla macrodon (TE)	2	2794 ± 1379 (95% CI)	Colorado River Brazos River (our data; Randklev et al., 2010)	NE	EN (C1)
Fusconaia lananensis (TE)	4	157	Angelina River, Attoyac Bayou, Sandy and Village creeks	NT	EN (B2a, B2biii, B2biv; C1)
Potamilus amphichaenus (RE)	4	5 (+61 very recently dead)	Sabine and Trinity rivers, B.A. Steinhagen Reservoir (Neches River), Lake Livingston (Trinity River)	EN (B1 + 2c)	EN (B2a, B2bi; C1)
Pleurobema riddellii (RE)	3	57	Neches and Angelina rivers, Village Creek	NT	EN (C1)
Quadrula houstonensis (TE)	6	103	Brazos, Navasota, Little Brazos, Little, Colorado rivers, Yegua Creek	NT	VU (B1)
Quadrula aurea (TE)	4	779	Guadalupe, lower San Antonio, lower San Marcos rivers, and Lake Corpus Christi (Nueces River)	NE	VU (A2c, B1)
Lampsilis satura (RE)	4	16 (+3 very recently dead)	Neches, Sabine, Angelina rivers, Village Creek	NT	No change
Fusconaia askewi (RE)	5	395	Village Creek, Neches, Sabine, Angelina rivers, Big Cypress Bayou	NT	No change

[a] IUCN Categories: critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), not evaluated (NE).

[b] IUCN (2010) criteria: (A) – population reduction. A1: population reduction (>90% (CR), >70% (EN), >50% (VU)) observed, estimated, inferred, or suspected in the past, where the causes of the reduction are clearly reversible and understood and ceased based on and specifying any of the following: (c) a decline in area of occupancy, extent of occurrence and/or habitat quality; (e) effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites). A2: population reduction (>80% (CR), >50% (EN), >30% (VU)) observed, estimated, inferred, or suspected in the past, where the causes of reduction may not have ceased or may not be understood or may not be reversible. (B) – geographic range in the form of either B1 (extent of occurrence: <100 km^2 (CR), <5000 km^2 (EN), or <20,000 km^2 (VU)) or B2 (area of occupancy: <10 km^2 (CR), <500 km^2(EN), <2000 km^2 (VU)), and two of the following: (a) severely fragmented or number of locations equal to: 1 (CR), $\leqslant$5 (EN), or $\leqslant$10 (VU); (b) continuing decline in (i) extent of occurrence (ii) area of occupancy, (iii) area, extent and/or quality of habitat, (iv) number of locations or subpopulations and (v) number of mature individuals; (c) extreme fluctuations in any of (i) extent of occurrence, (ii) area of occupancy, (iii) number of locations or subpopulations, and (iv) number of mature individuals. (C) – small population size and decline measured in the number of mature individuals (<250 (CR), <2500 (EN), or <10,000 (VU)), and C1 (an estimated continuing decline of at least: 25% in 3 years or 1 generation (CR), 20% in 5 years or 2 generations (EN), or 10% in 10 years or 3 generations (VU), up to a maximum of 100 years) (IUCN, 2010). To qualify for listing in any of the threat categories, a species needs to meet any one of the five criteria A through E at that level (Mace et al., 2008).

[c] External colors of the shell were not faded.

[d] Soft tissue remained attached to the shell.

ness and can damage the sensitivity of community-based methods to detect ecological changes (reviewed in Cao et al., 2001, 1998).

4.3. Habitat alteration and endemic species

The intensive alteration of Texas hydrology since the late 19th century was associated with the massive construction of reservoirs and the disappearance of hundreds of streams and springs. Dams and impoundments change the hydrologic regime of rivers, resulting in reduced water flows and habitat diversity, increased water level fluctuations, accumulation of silt, interrupted fish and mussel life cycles and dispersal, and the reduction in freshwater fauna (Petts, 1984; Vaughn and Taylor, 1999; Watters, 2000). In contrast to natural lakes, long periods of flooding in reservoirs alternate with short periods of exposure, drastically reducing the abundance and diversity of aquatic macrophytes and benthic animals in the drawdown zone (Baxter, 1977; Burlakova and Karatayev, 2007; Richardson et al., 2002; Watters, 2000). We found that the ongoing habitat alteration had a very strong effect on endemic species and the unionid community at large. With the exception of two species, all endemics were found exclusively in streams and rivers. None of the very rare unionids were found in reservoirs. The total unionid diversity in streams and rivers was almost double that of reservoirs. The population of Texas is expected to double by 2060, increasing water demand (Estaville and Earl, 2008), which will lead to the construction of new reservoirs. In the absence of conservation actions, this may result in further homogenization and simplification of unionid communities, as well as the loss of rare endemic species.

4.4. Conservation priorities

This study has shown that all state and regional endemic unionids in Texas are of the highest priority for conservation. Application of the IUCN, 2010 criteria (Gardenfors et al., 2001; IUCN, 2010; Mace et al., 2008) demonstrated that these endemic species require immediate conservation efforts (Table 2). Assessment of species under the IUCN Red List categories represents the first critical step in setting priorities for conservation actions, but the category of threat is not sufficient to determine priorities for conservation action (IUCN, 2010). We suggested two different approaches for protection of these endemic species: (1) priority for surveys and (2) priority for protection of known populations. The first group includes five species that we qualified as critically endangered (*L. bracteata*, *P. popeii*, *P. metnecktayi*, *Q. mitchelli,* and *T. cognata*). During our study, not a single large subpopulation was discovered for any of these species that could be protected. Therefore, we suggest that extensive surveys are of the highest priority for this group. For example, less than 300 specimens of the very rare Texas endemic *T. macrodon* have been documented since it was described in 1859 (Howells et al., 1997; Randklev et al., 2010). However, in May 2009 we found a population of *T. macrodon* in the Lower Colorado River, which allowed us to move this species into the second group (Table 2). This group included species for which at least one sustainable population is known (*F. askewi*, *F. lananensis*, *L. satura*, *P. riddellii*, *P. amphichaenus*, *Q. aurea*, *Q. houstonensis*, *Q. petrina*, and *T. macrodon*, Table 2). Conservation plans for these species should involve the development of strategic planning, including an assessment of current and anticipated threats, and the development of conservation goals and objectives (IUCN/SSC, 2008). Another important aspect is to conduct phylogenetic systematic studies of some of these species and their populations, to assess their genetic diversity and isolation (Lydeard and Roe, 1998; Lydeard et al., 2004).

To minimize the research–implementation gap in conservation planning (Knight et al., 2008), we are currently working with TPWD personnel to prioritize sites for conservation based on species endemism and diversity. The scale of conservation efforts should be broad – from specific sites to entire watersheds (Higgins et al., 2005). The protection of freshwater ecosystems is the ultimate conservation challenge as they are often hotspots for human activities (Dudgeon et al., 2006). Molluscs are among the selected priority taxonomic groups which act as reliable biodiversity indicators and, therefore, their protection will also ensure conservation of other freshwater taxa (Darwall and Vie, 2005), including fish hosts necessary to complete their life cycle. Due to the connected nature of aquatic systems, the protection of sites of aquatic diversity often requires consideration of areas far beyond the borders of the target site. The maintenance of a natural flow regime within a river or stream may be much more important to the biodiversity of a site than direct protection of the site itself (Darwall and Vie, 2005). However, water pollution and especially residual contamination of sediments may also prevent population recovery due to the greater sensitivity of juveniles to contaminants, especially to sediment-bound contaminants that are more persistent and occur at higher concentrations than in the overlying water (Yeager et al., 1994). Restoration of habitat, including management of water and sediment quality and the prevention of further alteration are all very important steps for freshwater taxa conservation. Texas endemic *Q. petrina*, according to our surveys, has most likely only one remaining population left. This population is currently under direct threat due to restrained water release from several upstream reservoirs, recent drought, and urban and agriculture runoff (Table 2, Appendix C). Only prompt, basin-wide, conservation measures can save this population. Similarly, the conservation of Rio Grande endemic species greatly depends on the overall health of the river, which is one of the World's top 10 rivers at risk (Wong et al., 2007).

The first priority for conservation among the biogeographic provinces in Texas are the Central and Rio Grande Provinces, characterized both by a high number of endemics, and by high percentages of very rare species. Many environmental and anthropogenic factors contributed to the degradation of unionid fauna in these parts of Texas. Central Texas suffers from acute droughts, and the recent drought of 2007–2009 was the most severe since the all-time record drought of the 1950s (Lower Colorado River Authority, 2010). The lack of forests and overgrazing contribute to excessive runoff in Central Texas rivers during heavy, short rainfall (Texas Parks and Wildlife Department Report, 1974). In addition, this area is heavily populated, hosting several large cities (e.g., San Antonio, Austin) and counties that saw the highest population growth in the last decades (Texas Almanac, 2010–2011).

Selecting hotspots of rarity or narrow endemism is a popular approach for selecting priority areas for the conservation of biodiversity (Reid, 1998; Williams et al., 2002). An area of endemism is recognized by the coincident restrictedness of two or more taxa (Harold and Mooi, 1994; Laffan and Crisp, 2003), and a hotspot of endemism is determined as an area including more endemics than expected in comparison to the surrounding landscape (Laffan and Crisp, 2003; Williams et al., 1996). According to the Ramsar Convention Rules (Hails and Peck, 2007), if at least 10% of fish are endemic to a wetland, it should be recognized as an internationally important system. By these criteria, the Central Texas watersheds of the Colorado, Guadalupe, and San Antonio rivers could be recognized as internationally important hotspots for endemism with Central Texas as the priority region for national conservation.

During the last 110 years, one unionid species *Quadrula couchiana* has most likely gone extinct in Texas (Howells et al., 1996), and another species may be on the verge of extinction (the last live *Q. mitchelli* was found before 1950 (Wurtz, 1950). Unionid species with long generation times and populations near their extinction threshold are most likely to have an extinction debt. Even with no further habitat loss, many species are doomed to become locally or regionally extinct. However, as long as the species predicted to become extinct persist, there is still time for conservation measures (Kuussaari et al., 2009).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.08.010.

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