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A semi-arid river in distress: Contributing factors and recovery solutions for three imperiled freshwater mussels (Family Unionidae) endemic to the Rio Grande basin in North America

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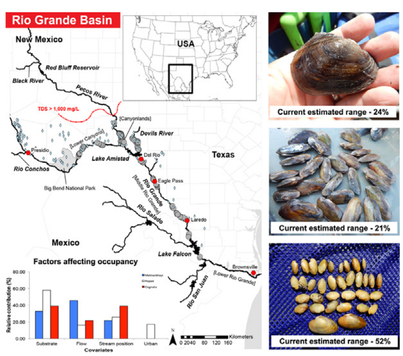
HIGHLIGHTS

- We assessed the conservation status of three rare mussel species in the Rio Grande basin.
- Actual and modeled occupancy of focal species was low indicating high level of imperilment.
- Modeled range reductions suggestive of human mediated water quantity and quality issues.
- Recommendations for water management and high value conservation reache to improve prognosis of focal species.

GRAPHICAL ABSTRACT



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ABSTRACT

Freshwater resources in arid and semi-arid regions are in extreme demand, which creates conflicts between needs of humans and aquatic ecosystems. The Rio Grande basin in the southwestern United States and northern Mexico exemplifies this issue, as much of its aquatic biodiversity is in peril as a result of human activities. Unionid mussels have been disproportionately impacted, though the specific factors responsible for their decline remain largely unknown. This is problematic because the Rio Grande basin harbors one federally endangered unionid mussel (*Popenaias popeii*, Texas Hornshell) plus two other mussel species (*Potamilus metnecktayi*, Salina Mucket; and *Truncilla cognata*, Mexican Fawnsfoot), which are also being considered for listing under the U.S. Endangered Species Act. To date, surveys for these species have not corrected for variability in detection so current range estimates may be inaccurate. Using single occupancy-modeling to estimate detection and occupancy at 115 sites along ~800 river kilometers of the Rio Grande in Texas, we found that detection probabilities were relatively high, indicating that our survey design was efficient. In contrast, the estimated occupancy was low, indicating that our focal species were likely rare within the Rio Grande drainage. In general, the predicted occupancy of our focal species was low throughout their respective ranges, indicating possible range declines. A comparison of currently occupied ranges to presumptive ranges underscores this point. The best-approximating models

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indicated that occupancy was influenced by habitat, water quantity and quality, and proximity to large-scale human activities, such as dams and major urban centers. We also discuss a series of conservation options that may not only improve the long-term prognosis of our focal species but also other aquatic taxa.

1. Introduction

Arid and semi-arid regions occupy ~40% of the world's surface area (Kingsford et al., 1998; Reynolds et al., 2007; Thomas, 2011) and rivers in these regions are under intense demand because they are the only exploitable surface water resource (Sheldon et al., 2002; Kibaroğlu and Schmandt, 2016). Perennial river systems that flow through arid zones are often sourced from snowmelt and rainfall, but depending on stream position, tributaries, groundwater resurgence and springs, may also contribute (Tooth and Nanson, 2011). These inputs, which vary in their duration and magnitude, combined with regional climate phenomena, result in a high degree of spatiotemporal habitat heterogeneity that over time leads to tightly coupled biotic and abiotic interactions. Human mediated impacts, which operate over both short and long temporal- and spatial-scales, disrupt these linkages and undermine the ecological integrity of these systems (Walker et al., 1995; Sheldon et al., 2002).

The Rio Grande is the 4th largest river in North America, draining a total of 870,236 km^2 within Colorado, New Mexico, and Texas in the southwestern United States and the states of Chihuahua, Coahuila, Nuevo Leon, and Tamaulipas in northern Mexico (Kammerer, 1990; Kibaroğlu and Schmandt, 2016). Throughout its length, the river flows through arid and semi-arid desert scrubland and grassland habitats (Dahm et al., 2005). The mainstem and its tributaries serve as a major water supply for communities that exist throughout the basin (Kibaroğlu and Schmandt, 2016); this demand for water has had negative consequences for aquatic biodiversity and ecosystem functioning within these systems (Contreras-Balderas et al., 2002; Hoagstrom et al., 2010; Karatayev et al., 2012). For example, 50% of the imperiled fishes in Texas are endemic to the Rio Grande drainage basin (Hubbs et al., 1991, 2008). Similarly, 25% of the freshwater mussel fauna in the Rio Grande drainage basin have either gone extinct or are in decline (Howells, 2001; Karatayev et al., 2012, 2015). Such losses have led conservationists to label the Rio Grande as one of the most imperiled rivers in North America (Wong et al., 2007).

Freshwater mussels (Bivalvia: Unionidae) are among the most imperiled faunas due to human impacts on water quantity and quality (Williams et al. 1993; Haag, 2012). The influence of stream flow, and presumably water quality, on mussels is pervasive because of the role stream flow plays in shaping mussel habitat and governing population endpoints, such as growth, survivorship and reproduction (Allen et al., 2013). Moreover, mussels provide important ecosystem services, such as biofiltration, nutrient cycling, and physical habitat modification, which are also influenced by water quantity and quality (Vaughn and Hakenkamp, 2001; Vaughn et al., 2008; Vaughn, 2018).

For many rivers, baseline data used to assess the status and distribution of species are missing or biased (NNMCC, 1998; Haag and Williams, 2014; FMCS, 2016; Holcomb et al., 2018). Biased survey data are often the result of survey designs that do not account for factors that can influence detection, which can include observer effects such as effort, life histories, and environmental conditions (Yoccoz et al., 2001; Martin et al., 2006). To date in the Rio Grande, monitoring programs for mussels have relied on haphazard sampling designs and survey methods that do not account for incomplete detection (Howells, 2001; Karatayev et al., 2012; Karatayev et al., 2015). As a result, inferences regarding a species status and long-term viability may be incorrect, which is problematic given that several mussel species (*Potamilus metnecktayi*, *Popenaias popeii*, *Truncilla cognata*) among others known to occur in this drainage basin have been petitioned for protection under the U.S. Endangered Species Act (ESA, 1973; USFWS, 2009; 2016). Thus, information on status and threats to mussels, in turn, could be used to support their management and protection (e.g., identifying stronghold populations and defining critical habitat), as well as provide additional information on the current condition of the aquatic biodiversity in the Rio Grande.

In this paper, we provide a case study on the threats to freshwater mussels in semi-arid rivers within the southwestern United States. We assessed the conservation status of three mussel species that are endemic to the Rio Grande basin. First, we use single-occupancy modeling to estimate the influence of survey and site-specific factors on occupancy and detection probabilities of *Popenaias popeii* (Texas Hornshell), *Potamilus metnecktayi* (Salina Mucket), and *Truncilla cognata* (Mexican Fawnsfoot). Second, we map the resulting predicted probabilities to evaluate range curtailment for these species within the Rio Grande. Third, we discuss factors that contribute to the decline of these species along with management implications and potential solutions.

2. Methods

2.1. Study area

The present study occurred across 4 sub-watersheds in the Rio Grande basin (Fig. 1). The uppermost sites were in the Lower Canyons of the Rio Grande Wild and Scenic River (upstream of Lake Amistad; hereafter, Lower Canyons), located in the Low Mountains and Bajada province of the Chihuahuan Desert ecoregion (Griffith et al., 2007). Flow within this portion of the Rio Grande is derived primarily from the Rio Conchos, spring inflows from the Edward-Trinity Plateau Aquifer, and historically spring snowmelt from Colorado and New Mexico (URGBBEST, 2012). Water infrastructure projects in the Rio Conchos and upper Rio Grande and introduction of the Giant Reed (*Arundo donax*), have reduced flow, leading to declines in mean and peak stream discharge.

The lowermost sites were in the middle Rio Grande between Lake Amistad and Falcon Reservoir (Fig. 1); these sites were located within the Rio Grande Floodplain and Terraces of the Southern Texas Plains ecoregion (Griffith et al., 2007). Flow in this portion of the Rio Grande is influenced by two large reservoirs (e.g., Lake Amistad in Del Rio, TX, and Falcon Reservoir, downstream of Laredo, TX), a number of small low-head dams, and the Maverick Canal, which is located downstream of Del Rio, TX. These projects have contributed to substantial daily variation in stream discharge and water depth. The middle Rio Grande is also urbanized relative to the other study reaches, and this land use along with agricultural and industrial activities have degraded water quality (Griffith et al., 2007; TCRP, 2013).

The remaining two sub-watersheds that were sampled in this study were located in the Devils River and the Canyonlands of the Pecos River (Fig. 1). The Devils River is a pristine tributary of the Rio Grande and lies within the Semi-arid Edwards Plateau province of the Edwards Plateau ecoregion (Griffith et al., 2007), which is a transition zone between central and western Texas. Flow in the Devils River is unregulated and is derived from groundwater seepage and springs (URGBBEST, 2012). The Pecos River is the largest northern tributary of the Rio Grande, and is located in the Chihuahuan Basins and Playas province of the Chihuahuan Deserts ecoregion and the Semi-arid Edwards Plateau province of the Edwards Plateau Region (Griffith et al., 2007); survey sites were located in the Canyonlands of the lower Pecos River. The flow in the Pecos River has been reduced from historical levels due to irrigation, flow-regulation, canal diversions and groundwater extraction, all of which have

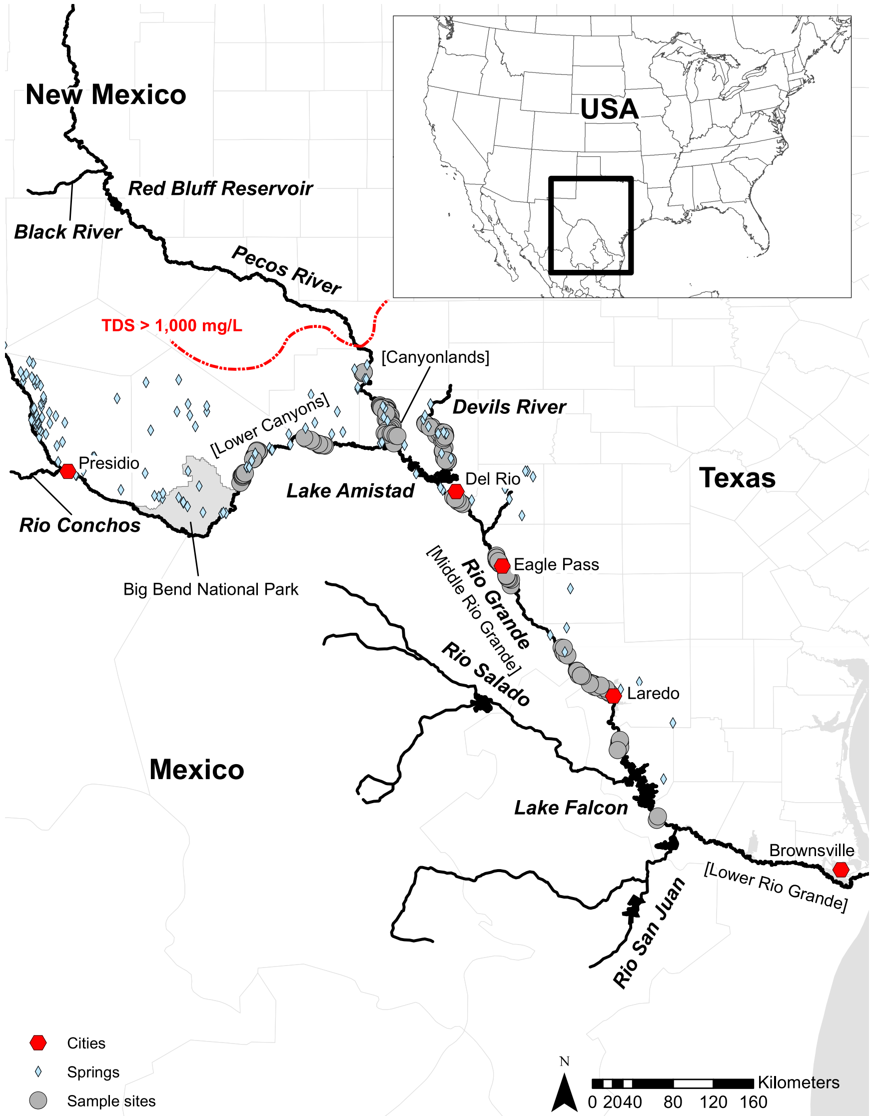

Fig. 1. Map of the study area showing locations of study reaches and sample locations.

led to increases in surface water salinity, particularly in the area upstream of the Canyonlands where freshwater spring inputs are now negligible (Miyamoto et al., 2008; URGBBEST, 2012).

2.2. Mussel species

The focal species of this study are *P. metnecktayi*, *P. popeii*, and *T. cognata*, all of which are endemic to the Rio Grande. *Potamilus metnecktayi* and *T. cognata* are considered state-threatened within Texas (TPWD, 2010) and are being considered for listing under the ESA (USFWS, 2009). *Popenaias popeii* is also state-threatened but is considered endangered under the ESA (USFWS, 2018). The historical range of *P. metnecktayi* in the Rio Grande is believed to include the area between the confluence with the Rio Conchos to Lake Falcon, in the lower Pecos near its confluence with the Rio Grande, and in tributaries of the Rio Grande in the northern part of Mexico (Metcalf, 1982; Neck and Metcalf, 1988; Johnson, 1999; Howells, 1999, 2001). To date, live collections of this species in the United States have been made between Big Bend National Park and the Lower Canyons (Karatayev et al., 2012); additionally, a shell of unknown age was documented in the middle Rio Grande near Laredo, TX (Karatayev et al., 2012).

In the US, *P. popeii* is thought to have occurred in the mainstem of the Rio Grande from downstream of its confluence with the Rio Conchos to Lake Falcon, in the Canyonlands of the lower Pecos River, and in Las Moras Creek, the Devils River, and the Black and North Spring rivers of New Mexico (Cockerell, 1902; Murray, 1975; Metcalf, 1982; Neck and Metcalf, 1988; Howells, 2001, 2010; Inoue et al., 2014). Currently, there are only four significant populations remaining in the U.S.: (1) Rio Grande near Laredo, TX; (2) the Lower Canyons of the Rio Grande; (3) Devils River, TX; and (4) the Black River, near Malaga, NM (Howells, 2001; Karatayev et al., 2012, 2015; Inoue et al., 2014).

Truncilla cognata historically ranged from portions of the Rio Grande that are now inundated by Lake Amistad to Lake Falcon, in the lower Pecos just upstream from its confluence with the Rio Grande, and in the Rio Salado of Mexico (Metcalf, 1982; Johnson, 1999; Howells, 2001). In the United States, populations of this species are known only to occur in the mainstem of the middle Rio Grande (Karatayev et al., 2012).

2.3. Sampling

Survey sites within the Rio Grande were selected following the methods outlined by Albanese et al. (2007). Ten-digit HUC watersheds and species occurrence data from previous sampling efforts were used to prioritize survey needs by focusing on areas that had not been surveyed or where past surveys failed to detect our focal species. For a subset of HUCs that met these criteria and were accessible using a motorized boat or canoes, we delineated the entire length of the river into 10-km reaches. Within each reach, sites were selected using a random sampling design with two strata: 1) river left or river right (except for midchannel habitats) and 2) mesohabitat: banks, backwater, midchannel, riffles, and boulder and bedrock (which include rock slabs and travertine shelves). It is important to note that in the Lower Canyons, boulder and bedrock habitat often includes canyon walls that extend above the river. Survey sites were 150 m^2 in area and we confined the search boundaries to the specific habitat type that was randomly selected. Sites within the mainstem of the Rio Grande were sampled from November 2014 to September 2015 and within the Pecos and Devils Rivers from September 2015 to May of 2016.

We performed timed searches in each randomly selected mesohabitat type to locate mussels. The timed-search method was chosen because it provides a more effective means of detecting rare species than quantitative sampling methodologies (Vaughn et al., 1997). Each site was surveyed tactilely by surveyors raking their fingers through the substrate, flipping rocks, and excavating crevices as well as visually by looking for mussel siphons (i.e., mantle aperture) or individuals laying at the surface. Sites were searched for a total of 4 person-hours (p-h), which was divided into 1 p-h searches (hereafter, search interval). During each search interval, surveyors were evenly distributed in the search area, and every effort was made to search all available microhabitats. At the end of each search interval, surveyors combined all live specimens into a mesh bag, which was kept submerged in water until the survey was complete. After completion of the survey, all live mussels from each search interval were identified to species, counted, measured and then returned to the river into the appropriate habitat. Snorkel and mask were used in shallow water and SCUBA was used at deeper sites where water depth exceeded 1.5 m.

2.4. Habitat measurements

The physical characteristics, relative stream position, and proximity to urban centers for each site were recorded to determine their effect on occupancy and detection of our focal species. Specifically, substrate composition was estimated using a modified Wentworth scale (see Gordon et al., 2004). Average current velocity was categorized as either slack water/perceivable or swift, as outlined in Wisniewski et al. (2013a). Wadeability was determined as the % of the site that was <1.5 m in depth. All visual estimates of habitat were made from within each 150 m^2 search area by the same persons (C. Randklev and M. Hart) (Table 1). Stream position and proximity to urban areas were calculated using ArcGIS 10.5 (Environmental Systems Research Institute, Redlands, California, USA). Effort per search interval (i.e., 1 p-h) was also examined to see if it affected detection.

2.5. Data analysis

Detection probability and site occupancy were estimated following Wisniewski et al. (2013a), using the single-season occupancy approach described by MacKenzie et al. (2002, 2006). Specifically, detection probability (p) is the probability of detecting our focal species (i.e., *P. metnecktayi*, *P. popeii*, *T. cognata*) within a single 1-h search interval (p-h), which was the combined catch of multiple surveyors, and site occupancy (ψ) is the proportion of sites occupied within the overall search area. We also calculated naïve occupancy, which is the number of sites observed as occupied relative to all sites sampled without accounting for detection (Wisniewski et al., 2013a). Occupancy and detection rates were generated separately for the Lower Canyons, middle Rio Grande, and the Devils River due to differences in flow, land use and habitat/substrate characteristics. Occupancy models were not developed for the Pecos River because only 3 live individuals from 2 of 42 sites were found during our surveys.

A set of candidate models was built using alternative parameterizations of the environmental covariates described in Table 1. Before fitting these models, we used Pearson correlation analysis to screen for multicollinearity, and we removed covariates with an $r > 0.50$. Variables representing linear distance from a specific point (e.g., cities) were examined as linear and quadratic terms. Model development consisted of considering various possible combinations of each covariate, though combinations of parameters were screened to ensure they made ecological sense. Parametric bootstrapping ($n = 10{,}000$) was performed to assess overdispersion ($\hat{c}$). The resulting candidate models were ranked based on sample-size adjusted Akaike's Information Criterion (AIC_c). AIC_c weights (w), which range from 0 to 1, were calculated, and the model with the highest weight was considered to be the best-approximating model (Burnham and Anderson, 2002). We considered models to be plausible if their $AIC_c \le 2$. For the best-approximating model, odds ratios were calculated to evaluate the effect of a given parameter estimate on detection and occupancy. We also calculated 95% confidence intervals for parameter estimates to assess their precision. Occupancy models were developed using R (R Development Core Team 2006 version 3.3.3) with the package "unmarked" version 0.12–2.

To visualize the output from the single-species occupancy analyses, we followed the methods presented in Randklev et al. (2015). Specifically, we first delineated the entire length of the Rio Grande and Devils River into 1-river-kilometer (rkm) intervals (hereafter, mapping segments) using ArcGIS. We then used the best-approximating model

Table 1
Covariates, and their data sources, included in candidate models for *Potamilus metnecktayi* (Salina Mucket), *Popenaias popeii* (Texas Hornshell), and *Truncilla cognata* (Mexican Fawnsfoot) occupancy (ψ) and detection (p) in the Rio Grande and Devils River, Texas. Scale refers to whether a covariate is a landscape or site-specific feature.

Scale	Variable	Definition	Data source[a]
	.	Constant, does not vary	
	Site specific (ψ)		
Landscape	City	Downstream distance (rkm) from Del Rio, Eagle Pass, or Laredo, depending on sample site location.	NID
	Stream position	Location of a given site (rkm) relative to the upstream boundary of a given study area. Lower Canyons = Presidio, TX; Middle Rio Grande = Amistad Dam; Pecos River = Independence Springs; and Devils River = Pecan Springs.	ESRI
Local	Swift water	Varies by presence of slow to moderate (0) or swift (1) flows	Survey
	Wadeable	% of site that was <1.5 m in water depth.	Survey
Local	% clay/silt	% Clay/silt within 150 m^2 search area.	Survey
	% sand	% Sand within 150 m^2 search area.	Survey
	% gravel	% Gravel within 150 m^2 search area.	Survey
	% cobble	% Cobble within 150 m^2 search area.	Survey
	% boulder and bedrock	% Boulder and bedrock within 150 m^2 search area.	Survey
	Survey specific (p)		
	Effort	Total search time (h) per survey interval.	Survey

Survey = site specific estimates.
[a] ESRI = Environmental Systems Research Institute; NID = National Inventory of Dams;

with variables that could be quantified using aerial imagery to determine the probability of occupancy per mapping segment, and the resulting values were mapped and color-coded. Covariates that could not be quantified using aerial imagery (i.e., survey specific covariates, see Table 1) were still included, but their input values were based on the average of the covariates across all sites occupied by a given species. For models that included only survey specific covariates, we model averaged the predictions across all models for a given sub-watershed with AIC_c values ≤2. We then calculated the proportion of mapping segments with predicted occupancy ≥0.5 to estimate the percentage of habitat remaining for our focal species.

To assess overall range decline, we first estimated the current range our focal species by calculating the total distance in rkms between the most upstream and downstream sites where live individuals of the species had been reported in either the Rio Grande or the Devils River. Recent records (2011–present) obtained from this study and those from Karatayev et al. (2012, 2015) and state and federal agencies were used. We then compared our estimation of the current range to the presumptive range, which we define as the known range based on live and shell records, excluding fossil records, irrespective of the date of collection (see *Mussel Species* in the Methods for details on data sources).

3. Results

A total of 448 p-h was invested surveying 112 sites located in the Rio Grande (38 sites in the Lower Canyons and 74 in the middle Rio Grande). Among these locations, we found 2060 live individuals of *P. popeii*, 213 of *T. cognata*, and 92 of *P. metnecktayi*. We found *P. popeii* at a total of 28 sites in the Rio Grande, 14 sites each in the Lower Canyons and the middle Rio Grande. *Potamilus metnecktayi* occurred at 22 sites but only in the Lower Canyons, whereas *T. cognata* was found at 30 sites but only in the middle Rio Grande. For the Devils and Pecos rivers, a total of 152 and 172 p-h were spent surveying 39 and 42 sites, respectively. *Popenaias popeii* was the only focal species found within either of these rivers. We found 127 live *P. popeii* among 15 sites in the Devils River and only 3 live individuals between 2 sites in the Pecos River.

Across all three species, a total of 84 candidate models were fitted with various combinations of site- and survey-level covariates for the Lower Canyons, middle Rio Grande, and Devils River. The total number of models per reach varied based on whether a given covariate was considered relevant to the waterbody in question. Based on the best-approximating model for each species, mean detection estimates ranged from 0.42 (95% CI: 0.29–0.56) to 0.82 (0.70–0.90; Table 2), and mean occupancy ranged from 0.20 (0.20–0.20) to 0.63 (0.58–0.87; Table 2). Species-specific estimates of mean occupancy and detection, the covariates associated with the best-approximating model, and the percentage of suitable habitat remaining in the Rio Grande are described below.

3.1. *Potamilus metnecktayi* (Salina Mucket)

Potamilus metnecktayi was only observed in the Lower Canyons of the Rio Grande. Estimated mean occupancy (ψ) was 0.63 (95% CI: 0.58–0.87), which was higher than our naïve estimate but within range of error so the two estimates may not be significantly different. The estimated mean detection (p) was 0.42 (95% CI: 0.29–0.56) (Table 2). The best-approximating model included detection as a constant and occupancy as a variable that changed with stream position, percentage of boulder and bedrock at a site, and water velocity (Tables 3 and 4). Odds ratios indicated that *P. metnecktayi* occupancy increased by a factor of 1.00 for each 1-rkm increase from Presidio, TX and was 1.08 times more likely to occur with every 1% increase in boulder and bedrock habitat (Table 4). *Potamilus metnecktayi* occupancy was also related to water velocity, as it was ~53 times more likely to occur in areas with low water velocity (Table 4). However, 95% CI for all modeled covariates overlapped with zero, indicating that our parameter estimates were imprecise. Merging the variables together by relative contribution using AIC weights shows that local scale factors (i.e., velocity, substrate type, and water depth) were most influential compared to landscape features (i.e., urban centers and dams; Table S1).

3.2. *Popenaias popeii* (Texas Hornshell)

Estimated mean occupancy (ψ) of *P. popeii* was 0.37 (95% CI: 0.37–0.47) in the Lower Canyons, 0.20 (0.20–0.20) in the middle Rio Grande, and 0.38 (0.38–0.49) in the Devils River, which were similar to naïve occupancy estimates (Table 2). Estimated mean detection (p) was 0.54 (95% CI: 0.40–0.67) for the Lower Canyons, 0.82 (95% CI: 0.70–0.90) for the middle Rio Grande, and 0.60 (95% CI: 0.46–0.72) for the Devils River (Table 2).

The best-approximating model for the Lower Canyons included detection as a constant and occupancy as a variable related to stream position and percentage of boulder and bedrock habitat (Tables 3 and 4). Odds ratios indicate that occupancy of *P. popeii* increased by a factor of 1.25 for each 1-rkm increase in distance from Presidio, TX. *Popenaias popeii* was also 1.35 times more likely to occur with every 1% increase in boulder and bedrock habitat (Table 4).

For the middle Rio Grande, the best-approximating model included detection as a constant and occupancy as a variable that was affected by the distance downstream from major urban centers and the percentage of boulder and bedrock (Table 3). Specifically, the occupancy of *P. popeii* increased by a factor of 1.07 for each 1-rkm increase in distance from either Del Rio, Eagle Pass, or Laredo, TX (Table 4). The occupancy

Table 2
Estimated mean detection (p) and occupancy (ψ) with 95% confidence intervals (CI) for best-approximating models and naïve occupancy (proportion of sites observed occupied without accounting for incomplete detection) of *Popenaias popeii* (Texas Hornshell), *Potamilus metnecktayi* (Salina Mucket), and *Truncilla cognata* (Mexican Fawnsfoot) in the Rio Grande and Devils River, Texas.

Model	p	95% CI	ψ	95%CI	Naïve ψ
Potamilus metnecktayi (Salina Mucket)					
Upper Rio Grande – lower canyons					
Boulder.bedrock + velocity + stream.position	0.42	0.29–0.56	0.63	0.58–0.87	0.58
Popenaias popeii (Texas Hornshell)					
Upper Rio Grande – lower canyons					
Boulder.bedrock + stream.position	0.54	0.40–0.67	0.37	0.37–0.47	0.37
Middle Rio Grande – Lake Amistad to Lake Falcon					
Boulder.bedrock + city	0.82	0.70–0.90	0.20	0.20–0.20	0.18
Devils river					
Clay.silt + wade	0.60	0.46–0.72	0.38	0.38–0.49	0.38
Truncilla cognata (Mexican Fawnsfoot)					
Middle Rio Grande – Lake Amistad to Lake Falcon					
Boulder.bedrock + velocity + stream.position	0.48	0.37–0.59	0.41	0.41–0.67	0.41

Table 3
Model selection results for examination of factors that affect occupancy (ψ) and detection (p) of *Potamilus metnecktayi* (Salina Mucket), *Popenaias popeii* (Texas Hornshell), and *Truncilla cognata* (Mexican Fawnsfoot) in the Rio Grande and Devils River, Texas.

Study Area	Model	AIC_c	ΔAIC_c	w_i	K
Potamilus metnecktayi (Salina Mucket)					
Upper Rio Grande – Lower Canyons					
p(.), ψ(%boulder.bedrock + velocity + stream.position)**		162.43	0.00	0.12	5
p(effort), ψ(%boulder.bedrock + velocity + stream.position)		163.34	0.91	0.08	6
p(.), ψ(%boulder.bedrock + velocity)		163.39	0.96	0.08	5
p(.), ψ(velocity + wade)		163.41	0.98	0.08	4
p(.), ψ(%boulder.bedrock + velocity + wade + stream.position)		163.67	1.25	0.07	6
p(.), ψ(%boulder.bedrock + wade)		163.96	1.53	0.06	4
Popenaias popeii (Texas Hornshell)					
Upper Rio Grande – Lower Canyons					
p(.), ψ(%boulder.bedrock + stream.position)*		98.50	0.00	0.76	4
Middle Rio Grande – Lake Amistad to Lake Falcon					
p(.), ψ(%boulder.bedrock + city)*		89.73	0.00	0.41	4
p(effort), ψ(%boulder.bedrock + city)		90.54	0.81	0.28	5
p(.), ψ(%boulder.bedrock + velocity + city)		91.64	1.91	0.16	5
Devils River					
p(.), ψ(%clay.silt + wade)**		120.02	0.00	0.16	4
p(.), ψ(%clay.silt)		120.38	0.36	0.13	3
p(.), ψ(%clay.silt + velocity)		120.57	0.55	0.12	4
p(.), ψ(%clay.silt + wade + stream.position)		120.85	0.82	0.11	5
p(.), ψ(%clay.silt + velocity + stream.position)		121.09	1.07	0.09	5
p(.), ψ(%clay.silt + stream.position)		122.00	1.97	0.06	4
Truncilla cognata (Mexican Fawnsfoot)					
Middle Rio Grande – Lake Amistad to Lake Falcon					
p(.), ψ(%boulder.bedrock + velocity + stream.position)**		246.55	0.00	0.13	5
p(.), ψ(stream.position)		247.01	0.46	0.10	3
p(.), ψ(%boulder.bedrock + stream.position)		247.15	0.60	0.09	5
p(.), ψ(%gravel + stream.position)		247.41	0.86	0.08	4
p(.), ψ(%cobble + velocity + stream.position)		247.66	1.11	0.07	5
p(.), ψ(%gravel + velocity + stream.position)		247.80	1.25	0.07	5
p(.), ψ(%sand + velocity + stream.position)		247.86	1.31	0.06	5

* Best-approximating model used to map occupancy.
** Model averaging used to map occupancy.

was also related to the percentage of boulder and bedrock such that it increased by a factor of 1.09 for every 1% increase in boulder and bedrock habitat (Table 4).

For the Devils River, the best-approximating model included detection as a constant, and occupancy was related to the percentage of clay/silt at a site and the percentage of the site that was <1.5 m in water depth (Tables 3 and 4). Odds ratios indicate that *P. popeii* was 1.19 times less likely to occur for every 1% increase in silt/clay and was 1.03 times more likely to occur for every 1% decrease in water depth (Table 4). Relative contribution of important covariates across all three populations shows that local and landscape features were fairly equal in their influence on detection and occupancy (Table S1).

3.3. *Truncilla cognata* (Mexican Fawnsfoot)

Truncilla cognata was only observed in the middle Rio Grande between Lake Amistad and Lake Falcon. Estimated mean occupancy (ψ) was 0.41 (95% CI: 0.41–0.67), which was similar to our naïve estimate, and estimated mean detection (p) was 0.48 (95% CI: 0.37–0.59) (Table 2). The best-approximating model included detection as a constant and had occupancy varying with stream position, percentage of boulder and bedrock at a site, and water velocity (Tables 3 and 4). Odds ratios indicate that *T. cognata* occupancy increased by a factor of 1.01 for each 1-rkm increase from Amistad Dam and was 1.01 less likely to occur for every 1% increase in boulder and bedrock habitat (Table 4). *Truncilla cognata* occupancy was also related to water velocity, as it was 1.17 times more likely to occur in areas with high water velocity (Table 4). Parameter estimates for the percentage of boulder and bedrock habitat and water velocity were imprecise. Relative contribution of important covariates shows that local scale factors were most influential compared to landscape features (Table S1).

3.4. Occupancy maps

3.4.1. Comparing current range vs. presumptive range

Comparisons between the current and presumptive ranges indicate that all three species are experiencing a decline in their ranges. For *P. metnecktayi*, we estimated that it currently occupies 24% of its presumptive range within the United States, all of which is located within the Rio Grande between Big Bend and Lake Amistad; within this reach, *P. metnecktayi* occupies 46% of its range (Table 5). Similarly, we estimated that *P. popeii* currently occupies only 21% of its presumptive range within the United States, with the Devils (68%), Lower Canyons (27%) and Middle Rio Grande (25%) populations occupying the largest portions of their presumptive ranges within these reaches. Within the Pecos River, this species is close to extirpation, occupying only 5% and 0.6% of its presumptive range within the upper and lower Pecos River, respectively (Table 5). Finally, we estimated that *T. cognata* currently occupies 52% of its presumptive range within the United States, all of which is in the middle Rio Grande, where it occupies 60% of its presumptive range within this reach (Table 5).

3.4.2. Comparing predicted occupancy within the presumptive range

Application of the best-approximating models (Table 3) within the presumptive ranges of our three focal species shows the locations of high-priority reaches for conservation. The current range for *P. metnecktayi* is from the Rio Grande near Big Bend National Park to reaches located just upstream of Lake Amistad (Fig. 2a). Within the range, predicted occupancy was maximized in the Lower Canyons (i.e., predicted occupancy ≥0.5; Fig. 2b). This stretch of the river is approximately 132 rkms in length and represents 22% of the species' presumptive range within the lower Canyons sub-watershed and 12% of its total presumptive range within the United States. For *P. popeii*, the

Table 4
Parameter estimates (SE), lower and upper 95% confidence intervals (CL), and odds ratios for the best approximating models for occupancy (ψ) and detection (*p*) of *Potamilus metnecktayi* (Salina Mucket), *Popenaias popeii* (Texas Hornshell), and *Truncilla cognata* (Mexican Fawnsfoot) in the Rio Grande and Devils River, Texas.

Parameter	Estimate (SE)	Lower CL	Upper CL	Odds ratio
Potamilus metnecktayi (Salina Mucket)				
Upper Rio Grande – Lower Canyons				
p				
Intercept	−0.34 (0.29)	−0.92	0.23	
ψ				
Intercept	−7.29 (4.59)	−16.28	1.70	
%boulder.bedrock	0.08 (0.17)	−0.26	0.42	1.08
swift.water	−3.97 (5.87)	−15.48	7.54	52.98
stream.position	0.02 (0.01)	−0.4e-2	0.05	1.00
Popenaias popeii (Texas Hornshell)				
Upper Rio Grande – Lower Canyons				
p				
Intercept	0.15 (0.28)	−0.40	0.70	
ψ				
Intercept	−97.22 (33.47)	−162.83	−31.61	
%boulder.bedrock	0.30 (0.09)	0.11	0.48	1.35
stream.position	0.22 (0.08)	0.07	0.37	1.25
Middle Rio Grande – Lake Amistad to Lake Falcon				
p				
Intercept	1.49 (0.34)	0.84	2.15	
ψ				
Intercept	−14.08 (5.21)	−24.30	−3.87	
%boulder.bedrock	0.09 (0.03)	0.03	0.15	1.09
city	0.07 (0.03)	0.02	0.13	1.07
Devils River				
p				
Intercept	0.41 (0.28)	−0.15	0.96	
ψ				
Intercept	−0.06 (2.06)	−4.08	3.97	
%clay.silt	−0.17 (0.07)	−0.31	−0.02	1.19
wade	0.03 (0.02)	−0.01	0.07	1.03
Truncilla cognata (Mexican Fawnsfoot)				
Middle Rio Grande – Lake Amistad to Lake Falcon				
p				
Intercept	−0.08 (0.22)	−0.52	0.36	
ψ				
Intercept	−4.00 (1.14)	−6.23	−1.77	
%boulder.bedrock	−0.01 (0.01)	−0.03	0.01	1.01
swift.water	1.31 (0.75)	−0.16	2.79	1.17
stream.position	0.01 (0.4e-2)	0.01	0.02	1.01

current range is the Rio Grande mainstem from downstream of Big Bend National Park to Lake Amistad, Devils River, the lower reach of the Pecos River, a small reach of the Black River, and portions of the middle Rio Grande (Fig. 3a). Predicted occupancy shows a similar pattern (Fig. 3b) and was maximized in 150 rkm of the Lower Canyons (percentage of presumptive range within a given reach; 25%), 85 rkm of middle Rio Grande (18%), and 60 rkm of the Devils River (67%). Combined, these reaches represent approximately 295 rkms, or 17%, of the species' total presumptive range within the United States. The current range for *T. cognata* is from just upstream of Eagle Pass, TX to just upstream of Lake Falcon (Fig. 4a). Predicted occupancy shows a similar pattern to the current range of *T. cognata* (Fig. 4b), which represents 170 rkms, or 35%, of the species' presumptive range within the middle Rio Grande subwatershed and 31% of its total presumptive range within the United States.

4. Discussion

4.1. Single-occupancy modeling

Survey data play an important role in informing and guiding subsequent management and conservation decisions for rare species (Williams et al. 1993; Wisniewski et al., 2013a). As a result, it is important that survey designs account for incomplete detection to minimize biases caused by observer effects, species' life history, and environmental conditions at the time of sampling (Yoccoz et al., 2001; Martin et al., 2006). Survey designs that fail to account for variability in detection can result in underestimating a species' occupancy and thus potentially lead to inaccurate conclusions about the species' rarity and viability (Wisniewski et al., 2013a). In the case of mussels, most surveys assume that detection is perfect; however, our study along with others have shown this is not the case (Meador et al., 2011; Shea et al., 2013; Wisniewski et al., 2013a; Inoue et al., 2014; Holcomb et al., 2018). For example, Wisniewski et al. (2013a, 2014) used a single-occupancy modeling approach to assess the occurrence of mussels in a 119-km reach of the Flint River, Georgia. This study found low detection probabilities (≤0.30), indicating that a number of species had not been collected in their study area. In our study, occupancy was generally low for all species but detection was high (≥0.30), which suggests reductions in range we report are likely real and not a function of sampling bias. We attribute our high detection rates to the survey methodology, which confined surveyors to a fixed area for multiple search periods. This resulted in a target search rate of 0.625 m^2/min, which is higher than several published survey guidelines (i.e., 0.5 m^2/min) for endangered mussel species (Smith et al., 2001; Smith, 2006). We also found that detection varied within and across species, which has been observed for other mussel species in other river systems (Wisniewski et al., 2013a, 2014). Specifically, detection of *P. popeii* was 20% higher in the middle Rio Grande compared to the Devils River and Lower Canyons. This suggests that monitoring programs consider variability in detection across both species and survey sites when determining survey methods for rare mussel species. For occupancy, we found that in certain cases, naïve and estimated occupancy

Table 5
Percent of occupied range for *Potamilus metnecktayi*, *Popenaias popeii*, and *Truncilla cognata* in the Rio Grande basin. Estimated occupied stream length (rkm) and estimated presumptive range (rkm) are listed in parentheses. Estimated occupied stream length is based on the distance between the upper- and lower-most sites within a given reach where live individuals of our target species have been reported since 2011. Estimated presumptive range is based on a similar distance, though upper and lower bounds are based on historical and contemporary records of live individuals or shells, but not fossils or subfossils, from academic, state, and federal agencies.

Species	Rio Grande - mainstem			US: Rio Grande - tributaries				MX: Rio Grande - tributaries		Total - US	Total - US & MX
	Lower Canyons	Middle	Lower	Devils	Las Moras	Upper Pecos	Lower Pecos	Rio Salado	Rio San Juan		
Potamilus metnecktayi	46% (270/590)	0% (0/479)	0% (0/32)	N/A	N/A	N/A	0% (0/18)	0% (0/285)	0% (0/124)	24% (270/1119)	18% (270/1528)
Popenaias popeii	27% (158/590)	25% (119/479)	0% (0/32)	68% (61/90)	0% (0/48)	5% (14/294)	0.6% (1/166)	0% (0/394)	0% (0/123)	21% (353/1699)	16% (353/2216)
Truncilla cognata	0% (0/68)	60% (287/479)	N/A	N/A	N/A	N/A	N/A	0% (0/256)	N/A	52% (287/547)	36% (287/803)

were not the same (i.e., *P. metnecktayi* and *P. popeii* from the middle Rio Grande). Thus, had we not accounted for incomplete detection, predicted occupancy would be underestimated for both species. Wisniewski et al. (2013a) found similar results as naïve occupancy was, on average, 26% lower than estimated occupancy. Thus, our study along with previous studies further underscore the importance of accounting for incomplete detection when estimating occupancy and distributional range, especially for rare mussel species.

4.2. Habitat factors associated with occupancy

In addition to incomplete detection, occupancy was influenced by habitat, water quality, and proximity to urban centers. We found that the occupancy of *P. metnecktayi* and *P. popeii* in the Rio Grande and Pecos River increased in boulder and bedrock habitat. Historically, the Rio Grande above Lake Amistad is prone to flood flows exceeding ~900 m^3/s, but flash floods with discharge ranging from ~6 to 560 m^3/s are now more common due to impoundment of the Rio Conchos and the upper Rio Grande (URGBBEST, 2012). We attribute high occupancy for *P. metnecktayi* and *P. popeii* in boulder and bedrock habitat to the stability of the habitat, which protects mussels from scour during high flow events (Strayer, 1999; Hardison and Layzer, 2001; Morales et al., 2006). In the Devils River, *P. popeii* more frequently occupies riffles and clean-swept pools with bedrock. Boulder and bedrock habitat, which is typical of the Rio Grande, was also present in the Devils River but frequently covered in a silt-like calcium carbonate precipitate. Sedimentation with silt is known to be detrimental to mussel survival, growth, and reproduction (Brim Box and Mossa, 1999). Our results suggest that the difference in occupied habitat across populations represents an environmental shift from habitats that confer protection from scouring to

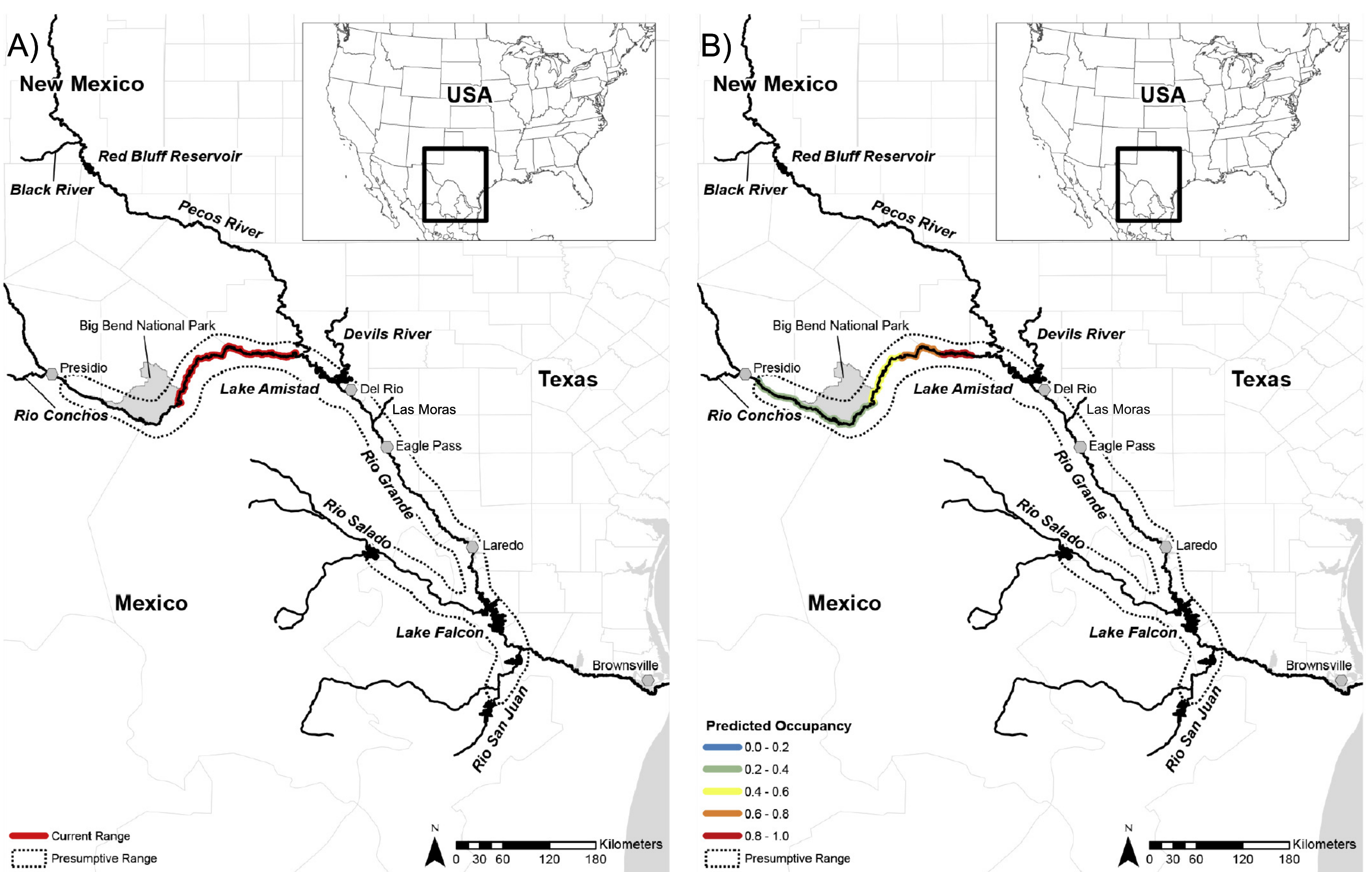

Fig. 2. Map comparing current range (A) and predicted occupancy (B) of *Potamilus metnecktayi*. Current range is based on known presence data of live individuals from 2011 to present. Data are from academic, state, and federal agencies. Predicted occupancy is based only on live individuals collected during this study using single-occupancy modeling.

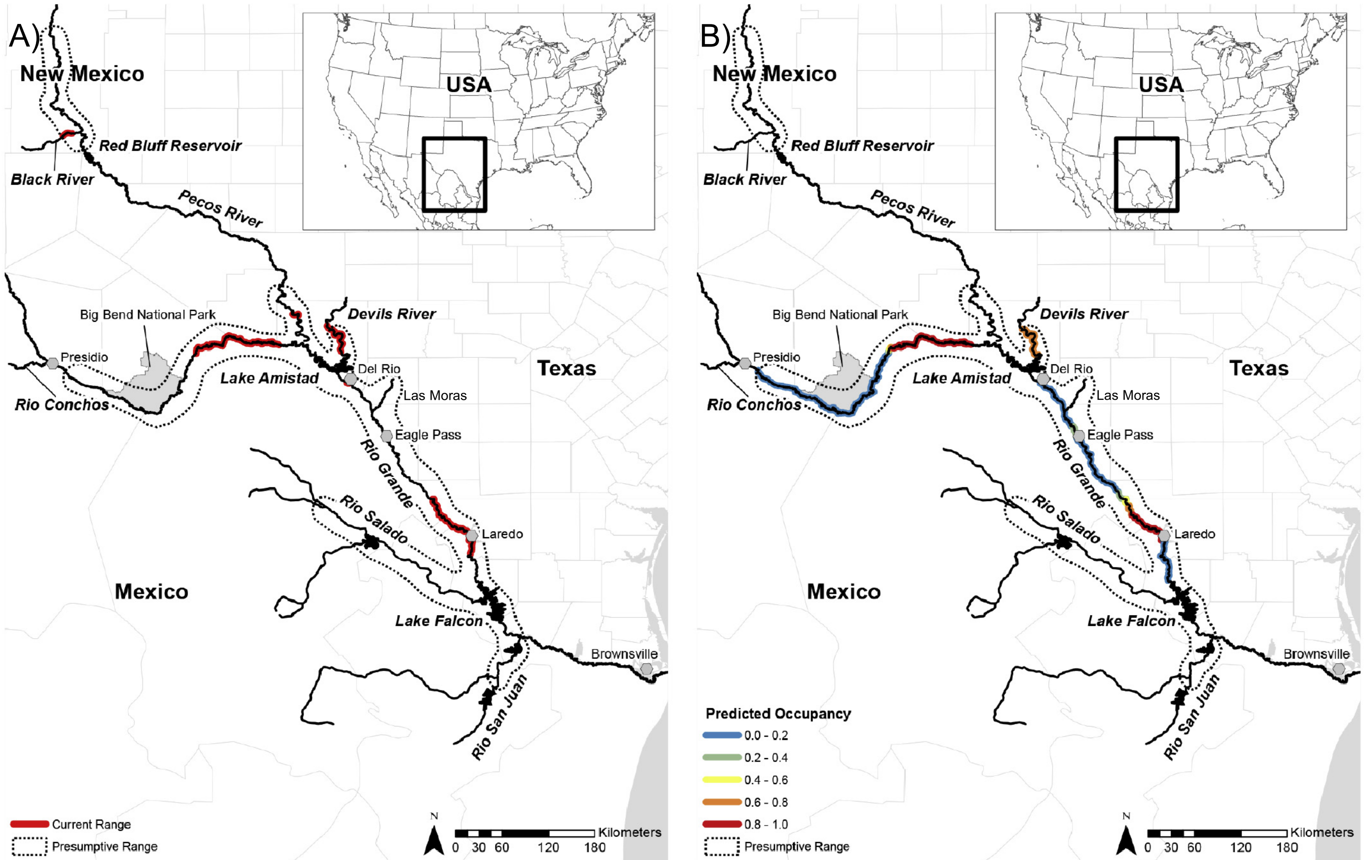

Fig. 3. Maps comparing current range (A) and predicted occupancy (B) for *Popenaias popeii* (B). Current range is based on known presence data of live individuals from 2011 to present. Data are from academic, state, and federal agencies. Predicted occupancy is based only on live individuals collected during this study using single-occupancy modeling.

those that are not impacted by sedimentation. Changes in the flow regime caused by climatic variability and associated drought likely underpin this shift.

We found that habitat use by *T. cognata* was more general and was primarily influenced by its proximity to large dams and stream position. Large hydroelectric dams, such as Amistad, are known to alter the physical parameters of a river, and in turn, modify patterns and processes of ecosystems (Ward and Stanford, 1983). Recovery from dam-induced impacts can occur, but often only gradually and over long distances (Ward and Stanford, 1983; Poff and Hart, 2002). For mussels, river impoundment can negatively impact habitat quality, which can affect population performance (e.g., growth, survivorship and reproduction) and affect dispersal by impeding movement of their host fish. (Vaughn and Taylor, 1999; Haag, 2012; Allen et al., 2013; Randklev et al., 2016). Thus, the absence of *T. cognata* near Amistad Dam and the increased likelihood of their occurrence with distance from the reservoir is likely a consequence of river impoundment and its associated impacts. The same pattern was seen in *P. popeii*.

Water quality is known to impact mussel populations (Cope et al., 2008) and is degraded throughout much of the mainstem of the Rio Grande as a result of reduced flows and point and non-point source pollution (URGBBEST, 2012). For example, within the upper Rio Grande, water quantity and quality is impaired due to inputs from the Rio Conchos (URGBBEST, 2012). However, beginning near Big Bend National Park and culminating within the Lower Canyons, groundwater from springs and adjacent aquifers help to mitigate these impacts by augmenting flow (URGBBEST, 2012). Our results for *P. metnecktayi* and *P. popeii* follow this same pattern, as occupancy is reduced near the confluence with the Rio Conchos and maximized within the Lower Canyons. In the middle Rio Grande, water quality issues are more pervasive, especially near major urban centers, where elevated levels of organic and inorganic constituents were observed (TCRP, 2013). For example, maximum ammonia concentrations of ~1.34 to 3.36 mg/L, which reduce the viability of juvenile mussels (Wang et al., 2007), have been reported from the reaches (TCRP, 2013) where our focal species no longer occur or are reduced in numbers.

For the Pecos River, we were unable to model the occupancy of our focal species due to their extirpation or low prevalence, which is likely linked to reductions in water quantity and quality within this system. Specifically, reduced flows caused by human activities and underlying geology have increased the salinity level of the Pecos River to concentrations that are likely lethal to mussels (URGBBEST, 2012). Our survey results showed that *P. popeii* is still present in the Pecos River, but only in reaches where spring and groundwater contributions maintain salinity concentrations of ≤~2.0 ppt. Further upstream salinity concentrations range from 6 to 12 ppt in the upstream reaches and often exceed 30 ppt (URGBBEST, 2012). Recent studies have shown that salt concentrations as low as 0.1 ppt can cause sublethal stress in adults (Blakeslee et al., 2013) and reduce the viability of glochidia (Gillis, 2011). For *P. popeii*, salinity concentrations between 3 and 4 ppt are known to be lethal (M. Hart, unpublished data). Salinization of the Pecos River, along with the rivers underlying geology, has led to conditions that exacerbate Golden Algae (*Prymnesium parvum*) blooms, which has been responsible for high fish mortality in this river (URGBBEST, 2012). These algae blooms likely affect mussels because the toxins produced by Golden Algae (i.e., prymnesins) are harmful to most gill-breathing organisms. Finally, elevated water temperature may also be an issue for mussels in the Pecos River. During our survey of the Pecos River, live *P. popeii* were typically found at water depths exceeding 1.5 m. Generally, reductions in flow lead to a loss of thermal buffering, resulting in elevated water temperatures that could exceed thermal optima for various mussel life stages (Pandolfo et al., 2010; Galbraith et al., 2012; Ganser et al., 2013).

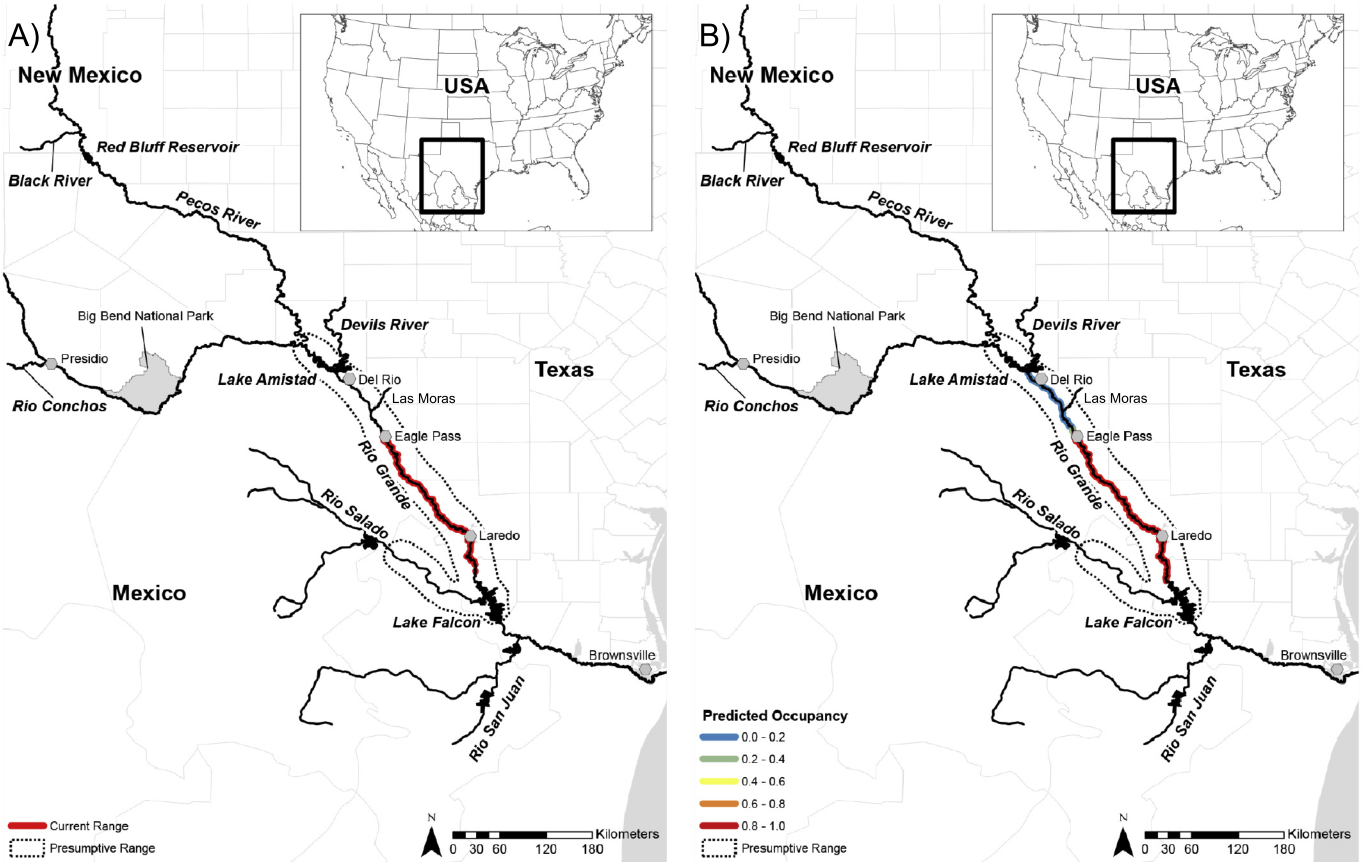

Fig. 4. Maps comparing current range (A) and predicted occupancy (B) for *Truncilla cognata* (B). Current range is based on known presence data of live individuals from 2011 to present. Data are from academic, state, and federal agencies. Predicted occupancy is based only on live individuals collected during this study using single-occupancy modeling.

Using the predicted occupancy and current range relative to the presumptive ranges, we were able to show substantial range declines for all three species. We found that the total area occupied by *P. metnecktayi* in the United States is only 24% of its presumptive range, which is confined to the Rio Grande above Lake Amistad. Within this reach, the current occupancy is estimated to be 46% but predicted high occupancy is only 22% of that range, all of which is located within the Lower Canyons where water quantity and quality are maintained by spring and groundwater inputs (URGBBEST, 2012). For *P. popeii*, our results show that this species has undergone a similar range reduction, as it currently occupies only 21% of its range within the United States. Current and predicted occupancy for the lower Canyons (27; 25%) and middle Rio Grande (25; 18%) mirrored this overall estimate, except for in the Devils River where occupancy, current and predicted, was almost 70%. The Devils River is considered one of the last pristine rivers in Texas (URGBBEST, 2012), so the fact that this species appears to be in better condition within this system makes ecological sense and underscores the challenges *P. popeii* faces in terms of water quality and quantity in the upper and middle Rio Grande. Finally, *T. cognata* appears to be the most resilient of our three focal species, as it currently occupies 52% of its range within the United States but this estimate is somewhat misleading given that its predicted occupancy is only 36%, and it only occurs in the middle Rio Grande, where water quality and quantity issues are pervasive.

4.3. Identifying conservation needs and recommended research

In semi-arid regions, rivers such as the Rio Grande are often the only exploitable surface water resource, and water sustainability within these regions has become an increasing issue for humans and wildlife. Complicating this issue is that the ecology of semi-arid streams is closely linked to the natural flow regime, and changes associated with water resource practices can cause long-term negative effects on aquatic biota (Walker et al., 1995; Pool and Olden, 2002; Sheldon et al., 2002). The results of our study show a mussel fauna in decline due to changes in water quantity and quality. These perturbations are forecasted to increase with growing human population and changing environment (Arthington, 2012; Kibaroğlu and Schmandt, 2016). Below we illustrate remaining research opportunities that could improve the long-term viability of not only the focal species but also other aquatic taxa within this drainage basin.

4.4. Water quantity and quality management

Water quantity and quality were the main factors influencing the occupancy of mussel species within the Rio Grande and several major tributaries. In Texas, there is a process, set forth by Senate Bill 3 in 2007, for the development of environmental flow standards that support a sound ecological environment by addressing water quantity and, to a lesser extent, quality issues. This legislative process is also informed by technical guidance from the Texas Instream Flow Program (TIFP, 2008). The upper Rio Grande and several major tributaries were included in this process (URGBBEST, 2012), but mussels were not explicitly considered and no standards were adopted for below Lake Amistad, and so flow recommendations developed as a result of this effort may not be adequate for ensuring their persistence within the Rio Grande.

Thus, future conservation efforts in the Rio Grande and its associated tributaries could usefully examine whether current flows are sufficient to ensure long-term viability of the remaining aquatic fauna. The approach proposed by Maloney et al. (2012) successfully used hydraulic models that incorporate low- and high-flow stressors to quantify suitable habitat over a range of flows. Adopting this modeling approach, specific thresholds of hydraulic factors may be identified for the Rio Grande basin. These thresholds could be used to serve as targets for flow restoration strategies (Richter, 2016) being explored in Texas and could be used as conservation targets for state environmental flow efforts and in groundwater management (EARIP, 2012). Finally, regardless of whether mussel-flow targets are identified, managers could advantageously match the pattern of water demand to that of supply; this is often termed the “Simple Formula” (sensu Walker et al., 1995; Arthington and Balcombe, 2011). For the Rio Grande and its tributaries, this approach would mean protecting the hydrologic regime from excessive extraction during low flow periods, limiting extraction to certain conservative threshold flows during normal base flows, and maintaining unrestrained flooding to every extent possible without harming people and infrastructure.

The effects of organic and inorganic constituents on mussels have been increasingly studied (e.g., Cope et al., 2008). Recent studies showed that mussel sensitivity to waterborne contaminants could vary widely across species (Wang et al., 2007; Gillis et al., 2008). Thus, sensitivity of our focal species may not be well predicted by the toxic metrics of other mussel species. As a consequence, current state and federal water quality criteria may not be effective for protecting species in the Rio Grande. Research on species-specific sensitivity to ammonia and heavy metals, such as copper, in combination with temperature and dissolved oxygen, is required to narrow the potential water quality threats to mussel species within this basin. This information could be incorporated into hydraulic models used to provide guidance on environmental flows required by mussels (Maloney et al., 2012).

4.5. Establishing robust sampling and monitoring programs

There remain many segments of the Rio Grande and its tributaries that have yet to be formally surveyed using a robust design such as the one implemented in this study that accounts for incomplete detection. Managers could benefit from continued survey work, targeting areas that have not been well surveyed using the sampling methodology described in this study as a guideline, especially for large river mussel surveys. Widespread surveys coupled with strategically established long-term monitoring sites (e.g., Wisniewski et al., 2013b; Inoue et al., 2014) will facilitate a better understanding of how changes in flow, land use, and climate impact population endpoints, such as survival, growth, and reproduction. We define ideal long-term monitoring sites as 1) populations that have high abundance relative to other sampled locations (i.e., stronghold populations) and are likely self-sustaining (i.e., sign of active recruitments); and 2) habitat that has a high potential to support individuals and is conducive for successful reproduction. In our case, these sites are likely areas where estimated occupancy is ≥0.5 with the assumptions that high occupancy corresponds to suitable habitat and these sites are candidates for habitat restoration. The information gained from long-term monitoring programs will help evaluate population persistence and guide habitat restoration efforts. Finally, these monitoring sites could be used as a primer for developing conservation habitat units, similar to those used in the southeastern United States (i.e., Strategic Habitat Units and Strategic River Reach Units) to help prioritize and focus conservation activities for mussels and aquatic species and inform watershed restoration efforts (NEAT, 2006).

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References

(ESA) Endangered Species Act of 1973 (1973) Pub. L. No. 93-205, 87 Stat. 884, codified as amended at 16 U.S.C. §§1531–1544.
Albanese, B., Peterson, J.T., Freeman, B.J., Weiler, D.A., 2007. Accounting for incomplete detection when estimating site occupancy of bluenose shiner (*Pteronotropis welaka*) in southwest Georgia. Southeast. Nat. 6, 657–668.
Allen, D.C., Galbraith, H.S., Vaughn, C.C., Spooner, D.E., 2013. A tale of two rivers: implications of water management practices for mussel diversity outcomes during droughts. Ambio 42, 881–891.
Arthington, A., 2012. Environmental Flows: Saving Rivers in the Third Millennium. University of California Press, Berkeley and Los Angeles, California.
Arthington, A., Balcombe, S., 2011. Extreme flow variablity and the ‘boom and bust’ ecology of fish in arid-zone floodplain rivers: a case history with implications for environmental flows, conservation management. Ecohydrology 4, 708–720.
Blakeslee, C.J., Galbraith, H.S., Robertson, L.S., White, B.St. John, 2013. The effects of salinity exposure on multiple life stages of a common freshwater mussel, *Elliptio complanata*. Environ. Toxicol. Chem. 32, 2849–2854.
Brim Box, J., Mossa, J., 1999. Sediment, land use and freshwater mussels: prospects and problems. J. N. Am. Benthol. Soc. 18, 99–117.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer, New York.
Cockerell, T.D.A., 1902. Unio popeii. Lea. 16. The Natuilus, New Mexico, pp. 69–70.
Contreras-Balderas, S., Edwards, R.J., Lozano-Villano, M.L., García-Ramírez, M.E., 2002. Fish biodiversity changes in the lower Rio Grande/Rio Bravo, 1953–1966. Rev. Fish Biol. Fish. 12, 219–240.
Cope, W.G., Bringolf, R.B., Buchwalter, D.B., Newton, T.J., Ingersoll, C.G., Wang, N., Augspurger, T., Dwyer, F.J., Barnhart, M.C., Neves, R.J., Hammer, E., 2008. Differential exposure, duration, and sensitivity of unionoidean bivalve life stages to envronmental contaminants. J. N. Am. Benthol. Soc. 27, 451–462.
Dahm, C.N., Edwards, R.J., Gelwick, F.P., 2005. Gulf Coast Rivers of the Southwestern United States. In: Arthur, C.B., Colbert, E.C. (Eds.), Rivers of North America. Academic Press, Burlington, pp. 180–228.
Edwards Aquifer Recovery Implementation Program (EARIP), 2012. Habitat conservation plan. Final Report to the Steering Committee for the Edwards Aquifer Recovery Implementation Program, November, 2012 (444 p. plus appendices). http://www.eahcp.org/index.php/documents_publications/habitat_conservation_plan_and_appendices.
FMCS (Freshwater Mollusk Conservation Society), 2016. A national strategy for the conservation of native freshwater mollusks. Freshw. Mollusk Biol. Conserv. 19, 1–21.
Galbraith, H.S., Blakeslee, C.J., Lellis, W.A., 2012. Recent thermal history influences thermal tolerance in freshwater mussel species. Freshw. Sci. 31, 83–92.
Ganser, A.M., Newton, T.J., Haro, R., 2013. The effects of elevated water temperatures on native juvenile mussels: implications for climate change. Freshw. Sci. 32, 1168–1177.
Gillis, P.L., 2011. Assessing the toxicity of sodium chloride to the glochidia of freshwater mussels: implications for salinization of surface waters. Environ. Pollut. 159, 1702–2708.
Gillis, P.L., Mitchell, R.J., Schwalb, A.N., McNichols, K.A., Mackie, G.L., Wood, C.M., Ackerman, J.D., 2008. Sensitivity of the glochidia (larvae) of freshwater mussels to copper: assessing the effect of water hardness and dissolved organic carbon on the sensitivity of endangered species. Aquat. Toxicol. 88, 137–145.
Gordon, N.D., McMahon, T.A., Finlayson, B.L., 2004. Stream Hydrology: an Introduction for Ecologists. John Wiley and Sons, West Sussex.
Griffith, G., Bryce, S., Omernik, J., Rogers, A., 2007. Ecoregions of Texas. Texas Commission on Environmental Quality, Austin, TX.
Haag, W.R., 2012. North American Freshwater Mussels: Natural History, Ecology, and Conservation. Cambridge University Press, Cambridge, UK.
Haag, W.R., Williams, J.D., 2014. Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels. Hydrobiologia 735, 45–60.
Hardison, B.S., Layzer, J.B., 2001. Relations between complex hydraulics and the localized distribution of mussels in three regulated rivers. Regul. Rivers Res. Manag. 17, 77–84.
Hoagstrom, C.W., Remshardt, W.J., Smith, J.R., Brooks, J.E., 2010. Changing fish faunas in two reaches of the Rio Grande in the Albuquerque Basin. Southwest. Nat. 55, 78–88.
Holcomb, J.M., Shea, C.P., Johnson, N.A., 2018. Cumulative spring discharge and survey effort influence occupancy and detection of a threatened freshwater mussel, the Suwannee Moccasinshell (*Medionidus walkeri*). J. Fish Wildl. Manag. (In-Press). https://doi.org/10.3996/052017-JFWM-042.
Howells, R.G., 1999. Distributional surveys of freshwater bivalves in Texas: progress report for 1998. Management Data Series 161. Austin, TX, Texas Parks and Wildlife Department.
Howells, R.G., 2001. Status of Freshwater Mussels of the Rio Grande, with Comments on Other Bivalves. Texas Parks and Wildlife Department, Austin, Texas.
Howells, R.G., 2010. Texas hornshell (*Popenaias popeii*): summary of selected biological and ecological data for Texas. Biostudies. Report on file with Save Our Springs Alliance, Austin, Texas, Kerrville, Texas.
Hubbs, C., Edwards, R.J., Garrett, G.P., 1991. An annotated checklist of the freshwater fishes of Texas, with keys to identification of species. Tex. J. Sci. 43 (Supplement).
Hubbs, C., Edwards, R.J., Garrett, G.P., 2008. An Annotated Checklist of the Freshwater Fishes of Texas, with Keys to Identification of Species. Texas Academy of Science Available from:. http://www.texasacademyofscience.org/.
Inoue, K., Levine, T.D., Lang, B.K., Berg, D.J., 2014. Long-term mark-and-recapture study of a freshwater mussel reveals patterns of habitat use and association between survival and river discharge. Freshw. Biol. 59, 1872–1883.

Johnson, R.I., 1999. The Unionidae of the Rio Grande (Rio Bravo del Norte) system of Texas and Mexico. Occas. Pap. Mollusks 6, 1–65.

Kammerer, J.C. 1990. "Largest Rivers in the United States" http://pubs.water.usgs.gov/ofr87242. Accessed July 21, 2015.

Karatayev, A.Y., Miller, T.D., Burlakova, L.E., 2012. Long-term changes in unionid assemblages in the Rio Grande, one of the World's top 10 rivers at risk. Aquat. Conserv. Mar. Freshwat. Ecosyst. 22, 206–219.

Karatayev, A.Y., Burlakova, L.E., Miller, T.D., Perrelli, M.R., 2015. Reconstructing historical range and population size of an endangered mollusk: long-term decline of *Popenaias popeii* in the Rio Grande, Texas. Hydrobiologia https://doi.org/10.1007/s10750-015-2551-3.

Kibaroğlu, A., Schmandt, J., 2016. Sustainability of Engineered Rivers in Arid Lands: Euphrates-Tigris and Rio Grande/Bravo. The LBJ School of Public Affairs, The University of Texas at Austin, Texas.

Kingsford, R.T., Boulton, A.J., Puckridge, J.T., 1998. Challenges in managing dryland rivers crossing political boundaries: lessons from Copper Creek and the Paroo River, central Australia. Aquat. Conserv. Mar. Freshwat. Ecosyst. 8, 361–378.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier-Academic Press, San Diego, California.

Maloney, K.O., Lellis, W.A., Bennett, R.M., Waddle, T.J., 2012. Habitat persistence for sedentary organisms in managed rivers: the case for the federally endangered dwarf wedgemussel (*Alasmidonta heterodon*) in the Delaware River. Freshw. Biol. 57, 1315–1327.

Martin, J., Kitchens, W.M., Hines, J.E., 2006. Importance of well-designed monitoring programs for the conservation of endangered species: case study of the snail kite. Conserv. Biol. 21, 472–481.

Meador, J.R., Peterson, J.T., Wisniewski, J.M., 2011. An evaluation of the factors influencing freshwater mussel capture probability, survival, and temporary emigration in a large lowland river. J. N. Am. Benthol. Soc. 30, 507–521.

Metcalf, A.L., 1982. Fossil Unionacean Bivalves from three Tributaries of the Rio Grande. In: Davis, J.R. (Ed.), Symposium on Recent Benthological Investigations in Texas and Adjacent States. Texas Academy of Science, Austin, Texas, pp. 43–59.

Miyamoto, S., Anand, S., Hatler, W., 2008. Hydrology, Salinity, and Salinity Control Possibilities of the Middle Pecos River: a Reconnaissance Report. Texas Water Resources Institute (TR-2008-315).

Morales, Y., Weber, L.J., Mynett, A.E., Newton, T.J., 2006. Mussel dynamics model: a hydroinformatics tool for analyzing the effects of different stressors on the dynamics of freshwater mussel communities. Ecol. Model. 197, 448–460.

Murray, H.D., 1975. Melanoides Turberculata (Muller), Las Moras Creek, Brackettville. 43. Bulletin of the American Malacological Union, Inc, Texas.

NEAT (National Ecological Assessment Texas), 2006. Strategic habitat conservation. Final Report of the National Ecological Assessment Team. U.S. Fish & Wildlife Service and U. S. Geological Survey.

Neck, R.W., Metcalf, A.L., 1988. Freshwater bivalves of the lower Rio Grande, Texas. Tex. J. Sci. 40, 259–268.

NNMCC (The National Native Mussel Conservation Committee), 1998. National Strategy for the conservation of native freshwater mussels. J. Shellfish Res. 17, 1419–1428.

Pandolfo, T.J., Cope, W.G., Arellano, C., Bringolf, R.B., Barnhart, M.C., Hammer, E., 2010. Upper thermal tolerances of early life stages of freshwater mussels. J. N. Am. Benthol. Soc. 29, 959–969.

Poff, N.L., Hart, D.D., 2002. How dams vary and why it matters for the emerging science of dam removal. Bioscience 52, 659–668.

Pool, T.K., Olden, J.D., 2002. Taxonomic and functional homogenization of an endemic desert fish fauna. Divers. Distrib. 18, 366–376.

Randklev, C.R., Wang, H.H., Groce, J.E., Grant, W.E., Robertson, S., Wilkins, N., 2015. Land use relationships for a rare freshwater mussels species (Family: Unionidae) endemic to central Texas. J. Fish Wildl. Manag. 6, 327–337.

Randklev, C.R., Ford, N., Wolverton, S., Kennedy, J.H., Robertson, C., Mayes, K., Ford, D., 2016. The influence of stream discontinuity and life history strategy on mussel community structure: a case study from the Sabine River, Texas. Hydrobiologia 770, 173–191.

Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner II, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernandez, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lymna, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. Science 316, 847–851.

Richter, B., 2016. Water Share: Using Water Markets and Impact Investment to Drive Sustainability. Washington, D.C, The Nature Conservancy.

Shea, C.P., Peterson, J.T., Conroy, M.J., Wisniewski, J.M., 2013. Evaluating the influence of land use, drought, and reach isolation on the occurrence of freshwater mussel species in the lower Flint River Basin, Georgia (U.S.A.). Freshw. Biol. 58, 382–395.

Sheldon, F., Boulton, A.J., Puckridge, J.T., 2002. Conservation value of variable connectivity: aquatic invertebrate assemblages of channel and floodplain habitats of a central Australian arid-zone river, Copper Creek. Biol. Conserv. 103, 13–31.

Smith, D.R., 2006. Survey design for detetcting rare freshwater mussels. J. N. Am. Benthol. Soc. 25, 701–711.

Smith, D.R., Villella, R.F., Lemarie, D.P., 2001. Survey protocol for assessment of endangered freshater mussels in the Allegheny River, Pennsylvania. J. N. Am. Benthol. Soc. 20, 118–132.

Strayer, D.L., 1999. Use of flow refuges by Unionid mussels in rivers. J. N. Am. 18, 468–476.

TCRP (Texas Clean Rivers Program), 2013. Rio Grande Basin Summary Report. International Boundary and Water Commission, United States Section (206 pp.).

Thomas, D.S.G., 2011. Arid environments: their nature and extent. In: Thomas, D.S.G. (Ed.), Arid Zone Geomorphology: Process, Form and Change in Drylands, third edition John Wiley & Sons, Hoboken, NJ, pp. 1–16.

TIFP (Texas Instream Flow Program), 2008. Texas instream flow studies: technical overview. Texas Water Development Board Report 369:1–137. Texas Water Development Board, Austin, TX.

Tooth, S., Nanson, G.C., 2011. Distinctiveness and diversity of arid zone river systems. In: Thomas, D.S.G. (Ed.), Arid Zone Geomorphology: Process, Form and Change in Drylands, third edition John Wiley & Sons, Hoboken, NJ, pp. 1–16.

TPWD (Texas Parks and Wildlife Department), 2010. Threatened and endangered nongame species. Texas Register. 35, pp. 249–251.

URGBBEST (Upper Rio Grande Basin and Bay Expert Science Team), 2012. Environmental flows recommendations report. Final Submission to the Environmental Flows Advisory Group. Rio Grande Basin and Bay Area Stakeholders Committee and Texas Commission on Environmental Quality.

USFWS (U.S. Fish and Wildlife Service), 2009. Endangered and threatened wildlife and plants; 90-day finding on a petition to list nine species of mussels from Texas as threatened or endangered with critical habitat. Fed. Regist. 74, 66260–66271.

USFWS (U.S. Fish and Wildlife Service), 2018. Endangered and threatened wildlife and plants; endangered species status for Texas hornshell. Fed. Regist. 83, 5720–5735.

Vaughn, C.C., 2018. Ecosystem services provided by freshwater mussels. Hydrobiologia 810, 15–27.

Vaughn, C.C., Hakenkamp, C.C., 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshw. Biol. 46, 1431–1446.

Vaughn, C.C., Taylor, C.M., 1999. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. Conserv. Biol. 13, 912–920.

Vaughn, C.C., Taylor, C.M., Eberhard, K.J., 1997. A comparison of the effectiveness of timed searches vs. quadrat sampling in mussel surveys. In: Cummings, K.S., Buchanan, A.C., Mayer, C.A., Naimo, T.J. (Eds.), Conservation and Management of Freshwater Mussels II: Initiatives for the Future. Proceedings of a UMRCC symposium, 16–18 October 1995, St. Louis, Missouri. Upper Mississippi River Conservation Committee, Rock Island, Illinois, pp. 157–162.

Vaughn, C.C., Nichols, S.J., Spooner, D.E., 2008. Community and foodweb ecology of freshwater mussels. J. N. Am. Benthol. Soc. 27, 409–423.

Walker, K.F., Sheldon, F., Puckridge, J.T., 1995. A perspective on dryland river ecosystems. Regul. Rivers Res. Manag. 11, 85–104.

Wang, N., Ingersoll, C.G., Greer, E., Hardesty, D.K., Ivey, C.D., Kunz, J., Brumbaugh, W.G., Dwyer, F.J., Roberts, A.D., Augspurger, T., Kane, C.M., Neves, R.J., Barnhart, M.C., 2007. Chronic toxicity of copper and ammonia to juvenile freshwater mussels. Environ. Toxicol. Chem. 26, 2048–2056.

Ward, J.V., Stanford, J.A., 1983. The serial discontinuity concept of lotic ecosystems. In: Fontaine, T.D., Bartell, S.M. (Eds.), Dynamics of Lotic Ecosystems. Ann Arbor Science Publishers, Ann Arbor, pp. 29–42.

Williams, J.D., Warren Jr., ML., Cummings, K.S., Harris, J.L., Neves, R.J., 1993. Conservation status of the freshwater mussels of the United States and Canada. Fisheries 18, 6–22.

Wisniewski, J.M., Rankin, N.M., Weiler, D.A., Strickland, B.A., Chandler, H.C., 2013a. Occupancy and detection of benthic macroinvertebrates: a case study of unionids in the lower Flint River, Georgia, USA. Freshw. Sci. 32, 1122–1135.

Wisniewski, J.M., Shea, C.P., Abbot, S., Stringfellow, R.C., 2013b. Imperfect recapture: a potential source of bias in freshwater mussel studies. Am. Midl. Nat. 170, 299.

Wisniewski, J.M., Rankin, N.M., Weiler, D.A., Strickland, B.A., Chandler, H.C., 2014. Use of occupancy modeling to assess the status and habitat relationships of freshwater mussels in the lower Flint River, Georgia, USA. Walkerana 17, 24–40.

Wong, C.M., Williams, C.E., Pittock, J., Collier, U., Schelle, P., 2007. World's Top 10 Rivers at Risk. WWF International, Gland, Switzerland.

Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. Trends Ecol. Evol. 16, 446–453.