

THE ROLE OF LIFE HISTORY STRATEGIES AND DRYING EVENTS IN  
SHAPING MUSSEL COMMUNITIES: A MULTISCALE APPROACH

by

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## **ABSTRACT**

Life history strategies have long been used in ecological analyses and theories but have only recently been applied to frameworks for freshwater mussels, which are a highly imperiled group of organisms. One of the most severe threats for mussels in Texas is dewatering of their habitat brought on by increased frequency and intensity of droughts due to global warming together with increased anthropogenic water demand. Freshwater mussels are particularly sensitive to drying events because they are relatively sessile and cannot easily escape disturbance events. Therefore, the primary objective of this dissertation was to examine the role drying events and life history strategies play in structuring mussel communities by using a multi-scale approach spanning spatial, temporal, and organizational dimensions. Chapter 1 examined the connection between life history strategies and the individual responses of unionid freshwater mussels to drying events. This chapter proposed a life history-based framework for predicting responses of mussels to drying events. Chapter 2 assessed long-term changes in mussel community structure across multiple tributaries in the Colorado River basin, Texas after a severe drought event. This chapter showed that mussels declined post-drought, but the severity of decline depended on antecedent conditions in each tributary, including the most severe declines occurring in streams with the lowest discharge and highest estimated water temperatures. Chapter 3 combined spatially extensive surveys in the San Saba River and a life history approach to examine the factors driving the distribution of mussels at two spatial scales, including within and between river segments. The results

showed that mussels with different life history strategies exhibited patchy and predictable distributional patterns and suggested the importance of environmental control including hydrological disturbances. Chapter 4 provides a synthesis and a conceptual model that can be applied to predict the distribution and structure of mussel metacommunities in rivers subject to drying events based upon life history strategies and other selective forces.

# **I. MOVE ON OR TAKE THE HEAT: CAN LIFE HISTORY STRATEGIES OF FRESHWATER MUSSELS PREDICT THEIR PHYSIOLOGICAL AND BEHAVIORAL RESPONSES TO DROUGHT AND DEWATERING?**

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## **Abstract**

Freshwater organisms have developed different physiological, behavioral, and life history strategies to cope with drying events. Although freshwater mussels (Unionidae) are endangered and drought and dewatering events pose a major threat, especially in the southern US, little is known about their responses to such events and how physiology, behavior and life history strategies may be linked. Our goal was to examine whether and how behavioral responses to dewatering and physiological tolerances to desiccation are linked in five species of freshwater mussels (Unionidae) within Texas, including three state threatened species (*Cyclonaias petrina*, *Lampsilis bracteata*, and *Popenaias popeii*) and to explore how differences in responses relate to life history strategies. We measured horizontal and vertical movements under three dewatering rates and assessed desiccation tolerance by examining survival after emersion at 30 and 40°C with laboratory experiments. *Amblema plicata* and *C. petrina* had the lowest horizontal movement rates and the highest desiccation tolerances, whereas *L. bracteata* and *L. teres* were less tolerant to desiccation, but more mobile. *P. popeii* were intermediate in its responses.

Our results show that differences between species in their behavioral response to dewatering and physiological tolerance to desiccation tend to be associated with differences in life history strategies or may be explained by differences in adaptation to certain habitat conditions. We propose a life-history strategy-based framework for responses of mussels to drying events, which may be applicable to other taxa.

## **Introduction**

Physical disturbances, such as drought and anthropogenic dewatering (e.g. hydropower dam operation, excessive groundwater pumping), can be an important factor in structuring aquatic communities (Resh et al. 1988; Lake 2000). Stream drying events cause a decrease in habitat availability through streambed drying which leads to an increase in abiotic and biotic stressors (e.g. low dissolved oxygen, high water temperatures, increased predation) that can significantly reduce survival rates of aquatic organisms (Humphries and Baldwin 2003). Many places, such as the south-western United States, are expected to experience increases in drought events, both in magnitude and frequency, over the next few decades due to global climate change (Seager et al. 2007). Furthermore, the effects of drought on aquatic ecosystems will likely intensify due to an ever-growing water demand from humans (Alcamo et al. 2007). Organisms inhabiting hydrologically dynamic systems must possess behavioral or physiological adaptations to survive various disturbance events, for instance stream drying.

Survival adaptations to drying events can be largely categorized as either behavioral avoidance, physiological tolerance to drying, or adaptive life history traits such as dormancy (Williams 2006). Highly mobile organisms primarily use behavioral

avoidance to leave an area at the onset of drying to locate refuge habitats. For example, fish can swim to deeper pools (Detenbeck et al. 1992; Labbe and Fausch 2000) and many insect species (e.g. Coleoptera and Hemiptera) can fly away to nearby permanent water bodies to avoid being stranded (Fernando and Galbraith 1973). Organisms that are unable to locate refugia from drying disturbances have developed physiological adaptations (i.e. increased desiccation tolerance) to ensure survival including desiccation resistant eggs (e.g. Cladocerans and Mayflies), resistant nymph stages (e.g. Odonata), and in some cases resistant adult stages (e.g. tardigrades, amphibians, and lungfish) (Daborn 1971; Lehmkuhl 1973; Wilbur and Collins 1973). Although adaptations for surviving drying events are prominent in many organisms, the effectiveness of these adaptations can vary substantially depending on the species, habitat type, local environmental conditions, and duration of the disturbance event (Lake 2000; Magoulick and Kobza 2003; Williams 2006).

Unlike other freshwater organisms that seem to be well adapted to drying, unionid mussels are highly susceptible to the negative effects of drying events because they are largely sedentary and cannot easily escape disturbance events (Golladay et al. 2004; Haag 2012). Mortality associated with drying can cause significant declines in mussel abundance and substantial shifts in community structure (Haag and Warren 2008; Galbraith et al. 2010; Walters and Ford 2013). Additionally, these changes can lead to losses of rare species and mussel-provided ecosystem services (Haag and Warren 2008; Vaughn et al. 2015). At least two general responses by mussels to drying have been documented. First, mussels can move horizontally and at least some mussel species may track receding waters, such as in a drying pool within a stream (Gough et al. 2012) or

during a water-level drawdown in the Upper Mississippi River (Newton et al. 2015), although mussel movement has also been described as erratic in the absence of receding water (Schwalb and Pusch 2007). Second, mussels can burrow vertically into the substrate and survive desiccation during a drying event for a certain amount of time, especially if the water table can be still reached by the mussels. Desiccation tolerance seems to vary among species and except for a few (e.g., *Unio merus tetralasmus*, 699 days at 15°C and 100% relative humidity), most mussel species cannot survive desiccation for prolonged periods (> 1 week) (Holland 1991; Byrne and McMahon 1994; Bartsch Waller et al. 2000; Gough et al. 2012; Galbraith et al. 2015). Although mussels have evolved various adaptations for surviving (shorter) drying events, it is important to note that these strategies seem to be insufficient for rapid dewatering events due to anthropogenic influences (e.g. groundwater pumping, Galbraith et al. 2015, and dam operations, Newton et al. 2015).

Much of the previous research into the survival adaptations of mussels to dewatering have only focused on one of the two general responses of mussels, behavioral response (i.e. horizontal/vertical movement) (Bartsch et al. 2000; Gough et al. 2012; Newton et al. 2015; Galbraith et al. 2015; Table 1.1) or physiological tolerance (Holland 1991; Byrne and McMahon 1994; Bartsch et al. 2000; Johnson 2001; Golladay et al. 2004; Spooner and Vaughn 2008; Gough et al. 2012; Galbraith et al. 2015; Table 1.1). Gough et al. (2012) suggested a linkage between behavioral responses and physiological tolerances in mussels: species that burrowed when they became stranded had the greatest desiccation tolerance, (i.e., *Unio merus tetralasmus*) and species less tolerant to desiccation (*Pyganodon grandis*, *Lampsilis straminea*) tracked the receding water to a



greater degree.

Studies of other groups of organisms have shown that survival mechanisms employed by species during a disturbance event, such as dewatering can be related to differences in life history strategies (e.g., Hoffman and Parsons 1989; Facon et al. 2004). To the best of our knowledge, no study has examined this with mussels. Therefore, the goal of this study was (1) to examine whether and how behavioral responses to dewatering and physiological tolerances to desiccation, are linked in mussels, using the following species: *Cyclonaias petrina*, *Amblema plicata*, *Popenaias popeii*, *Lampsilis bracteata*, and *L. teres* and (2) to explore how differences in responses between species relate to differences in life history strategies with experiments (Table 1.2, Fig. 1.1).

It should be noted that *Cyclonaias petrina* and several other *Quadrula* species were recently reassigned from the genus *Quadrula* to *Cyclonaias* and we are referring to the new names from the recently revised list of freshwater mussels in this paper (Williams et al. 2017).

Mussels, similar to plants (C-S-R framework, Grime 2001) can be divided into three broadly different life history strategies based on differences in life history traits such as fecundity, body size, age at maturity and life span (Table 2, Haag 2012). Haag (2012) proposed how different strategies (opportunistic, equilibrium, and periodic) may dominate in different types of habitat (with different disturbance frequencies and intensities), and we propose that they may also respond differently to desiccation and dewatering (Fig. 1.1).

Opportunistic species likely have a lower tolerance to desiccation, as they already suffer a higher mortality as a “physiological consequence” of their early reproduction and

higher growth rates (Haag, 2012). Equilibrium species, on the other hand, are characterized by long life spans and low to moderate growth rates (Table 2), and many representative species are rather thick-shelled species with the ability to seal their shells tightly (e.g., Amblemini, Quadrulini, Haag, 2012), which may facilitate tolerance against desiccation (Byrne and McMahon 1994). Hence, we predict that equilibrium species should have the highest desiccation tolerance (Fig. 1.1). Periodic species, according to Haag (2012) are intermediate between opportunistic and equilibrium in their life history traits and the disturbance frequency of their habitat (e.g., more water level fluctuations). We therefore predict that they will also have an intermediate desiccation tolerance. Assuming a linkage between physiology and behavior as suggested by Gough et al. (2012), equilibrium species with the presumably highest desiccation tolerance should also have the lowest ability to track receding water and hence lowest mobility (Fig. 1.1). It is also assumed that they dominate in stable habitats (Haag 2012), where lower mobility may not be a disadvantage. In contrast, periodic species may experience more water level fluctuations in the headwaters where they tend to dominate, and we predict they should have the highest mobility (Fig. 1.1). Opportunistic species can dominate in highly disturbed habitats and their traits allow them to rapidly colonize such habitat, e.g., isolated lentic systems that can rapidly dry out, Haag 2012, Fig. 1.1). We predict their horizontal mobility to be intermediate between equilibrium and periodic species. In respect to burrowing behavior, studies have reported that the species with the higher desiccation tolerance tended to burrow deeper than more intolerant species (Gough et al. 2012; Galbraith et al. 2015; Newton et al. 2015). Accordingly, we predict that equilibrium species (with the assumed highest desiccation tolerance) will burrow deeper

than periodic or opportunistic species (Table 1.3).

In contrast to Gough et al. (2012), where two of the three species studied are known to occur in disturbed and ephemeral habitats, all of the five species we examined usually occur in permanent streams. According to Haag (2012) most *Lampsilis* species may have a periodic strategy, except for *L. teres* which is a typical opportunistic species. Little is known about the life history of *L. bracteata*, but it is a rather small species with relatively low fecundity and a long-term breeder (Seagroves 2017), matching traits for the periodic strategy (Table 1.2). The three remaining species (*A. plicata*, *C. petrina*, *P. popeii*) belong to the tribes Amblemini and Quadrulini, which mostly show traits consistent with the equilibrium strategy (Haag 2012, Table 1.2).

## **Methods**

### **Study Species**

Two of the five mussel species used in this study are considered state-threatened in Texas (*C. petrina*, *L. bracteata*) and one (*P. popeii*) is listed as federally endangered. *Cyclonaias petrina* and *L. bracteata* are endemic to central Texas, whereas *P. popeii* is native to the Rio Grande drainage in western Texas and New Mexico. The two common species used in this study, *A. plicata* and *L. teres* are widespread throughout much of the Mississippian region. All species were collected using visual and tactile search methods. All individuals collected were measured (mm), weighed (g), and uniquely tagged (Floy® Shellfish Tag). Mussels were collected from the Colorado (*C. petrina*, *L. bracteata*), Guadalupe (*A. plicata*), Brazos (*L. teres*), and Rio Grande (*P. popeii*) river basins, TX.

### **Dewatering Experiment**

*Cyclonaias petrina* (n = 30), *A. plicata* (n = 30), *P. popeii* (n = 30), *L. bracteata* (n = 18), and *L. teres* (n = 30), were collected and used to examine vertical and horizontal movement during a dewatering event. Experiments were carried out in six 3-m long insulated fiberglass tanks at the San Marcos Aquatic Resources Center (SMARC) of the United States Fish and Wildlife Service (USFWS). Our experimental and tank designs were similar to the one used by Galbraith et al. (2015). A sloping depth was created using purchased sand (median particle diameter D50 = 0.4 mm) where water depth ranges from 10 cm near the inflow of the tank and 50 cm near the outflow of the tank. Laboratory dewatering rates (no dewatering (control), slow, moderate, and fast) mimicked dewatering rates that could be experienced in central Texas rivers (e.g. San Saba River) due to agricultural pumping or dam operations (Hernandez 2016). Slow dewatering manipulation was set at 4 cm/day for 10 days, moderate at 8 cm/day for 5 days, and fast at 4 cm/hr for 10 hours. Dewatering experiments were done separately for each species so that species interaction did not affect mussel behavior. Temperature was held relatively constant (~22 °C) for all tanks during the study. Additionally, no aeration was used in the tanks during the experiment to mimic stagnant conditions during drying periods. Water quality measurements (temperature, dissolved oxygen, pH) were taken daily (slow and moderate rates) or hourly (fast rate) during experimental trials. Mussels were fed a 2:1 ml daily mixture of Shellfish Diet 1800 and Nanno 3600 (Reed Mariculture, Campbell, California, USA) at a concentration of ~300,000 cells/ml in each tank. Each trial included six tanks (3 control and 3 treatment tanks; 5 ind./tank except for *L. bracteata*: 3 ind./tank) with a single dewatering rate. Dewatering trials occurred in the same order for each species as follows: fast, moderate, and slow. Individuals were randomly selected and

placed into tanks before each dewatering trial. Since *L. bracteata* is only known from a limited number of populations and has shown poor survival after becoming stranded it was only used in the slow dewatering trial and in smaller numbers (see above).

Individuals were acclimated at the top of the slope behind a barrier in each experimental tank for 24 h before trials. Behavioral responses of mussels were recorded daily except for the fast dewatering rate, for which data were recorded hourly. Vertical movements were measured using pre-measured length of monofilament glued to the right valve of each mussel using LOCTITE epoxy putty (LOCTITE Henkel Corporation, Rocky Hill, CT, USA). The length of line remaining above the surface was measured and subtracted from the total length of the line to determine burrowing depth. If a mussel was not completely burrowed, the amount of exposed shell was measured and used to calculate the percentage of shell burrowed. Flags were used to mark mussel locations daily or hourly during each dewatering run. The tracks left in the sand were measured daily or hourly for each individual and added to quantify total horizontal movement. Occasionally, tracks could not be identified, and the linear distance between the individual and its past location was measured instead. The number of individuals that became stranded during each trial were recorded daily or hourly depending upon dewatering rate. Mussels were considered stranded after being fully emersed for at least one hour. Once this occurred, emersed individuals were removed from the experiment and placed into holding tanks and then returned to their respective collection sites.

Behavioral responses to dewatering were measured as mean horizontal movement, vertical movement (% shell burrowed), and percentage of individuals stranded. All statistical analyses were conducted using R 3.3.1 (R Core Team 2016). We

first used 2-way ANOVA to separately evaluate the effects of species, dewatering rates, and their interactions on horizontal movement, vertical movement, and percentage of individuals stranded. Assumptions of normality and homoscedasticity were tested using the Shapiro-Wilk and Levene's test, respectively. To better comply with these assumptions, horizontal movement values were  $\log_{10}(x+1)$  transformed and both % shell burrowed and % individuals stranded were normalized with a logit transformation (Warton et al. 2011). Individual differences for all ANOVA analyses were identified using Tukey's HSD post hoc test.

### **Desiccation Experiment**

We conducted a laboratory experiment to determine species-specific desiccation tolerances of four mussel species encompassing the three life-history strategies proposed by Haag (2012). Thirty individuals of each study species (*C. petrina*, *A. plicata*, and *L. teres*), except *L. bracteata* (n = 10), were collected, uniquely tagged, measured (mm), weighed (g), and transported to Texas State University. We used available data on desiccation tolerance of *P. popeii* (Morton 2017). Our lab experiment assessed the tolerance for each species in an emersed condition at two different temperatures (30 and 40 °C; 15 ind./spp./temp.; *L. bracteata*: 5 ind./temp.). These temperatures represent possible environmental conditions in a drying stream bed in the southern U.S. All mussels were held in tanks for at least 48 h to acclimate to trial temperature. Afterwards, mussels were randomly selected and placed onto individual petri dishes and placed into an incubator (VWR® Signature Diurnal Growth Chamber, Model 2015) with a relative humidity of  $24 \pm 2\%$  (Holland 1991). Mortality of individuals were monitored daily until the trials were complete.

Kaplan-Meier survival curves (Kaplan and Meier 1958) were developed for each species at both temperatures to estimate the mean survival times after emersion. Log-Rank statistic followed by Bonferroni multiple comparison test was used to test for differences among species survival curves within each temperature trial.

## Results

### Dewatering Experiment

Horizontal movement distances were highly variable within and among species with some mussels having no movement to a few individuals moving > 180 cm in one day. Aside from a few *L. teres* individuals, movement among mussels was erratic and did not clearly follow receding water levels. During dewatering dissolved oxygen levels was on average ~6 mg/l at the start of trials and decreased steadily until trials were completed, but never decreased below 2.1 mg/l in each tank, which has been documented to be above the minimum level needed by mussels for regulating oxygen consumption (Chen et al. 2001). Total mean horizontal movement was significantly affected by species ( $F_{4,60} = 40.98$ ,  $P < 0.001$ ), dewatering rate ( $F_{3,60} = 28.76$ ,  $P < 0.001$ ), and their interaction ( $F_{10,60} = 6.81$ ,  $P < 0.001$ ). As predicted, *L. bracteata* (periodic species) had the highest mean horizontal movements followed by the opportunistic species *L. teres* and *P. popeii* (one of the equilibrium species), whereas, the other equilibrium species, *A. plicata* and *C. petrina*, showed the lowest horizontal movement (Table 1.3; Fig. 1.2). Differences among species were evident within all dewatering rates (Reduced One-Way ANOVA; fast:  $F_{3,8} = 7.55$ ,  $P < 0.01$ ; moderate:  $F_{3,8} = 11.24$ ,  $P < 0.01$ ; slow:  $F_{4,10} = 42.79$ ,  $P < 0.001$ ; control:  $F_{4,34} = 5.48$ ,  $P < 0.01$ ; Fig. 1.2A-D). In addition, dewatering rates had a significant effect

on horizontal movement rates for all species ( $P < 0.01$  in all cases). Compared to movement rates in control tanks, *C. petrina*, *A. plicata*, and *P. popeii* showed a considerable increase (8-fold on average) during the moderate dewatering, but not during the slow dewatering. In contrast, both *L. bracteata* and *L. teres* showed considerably higher movement rates (2 to 6-fold respectively) during the slow dewatering compared to the control (Fig. 1.2). All species moved only short distances or not at all during the fast dewatering (Fig. 1.2).

All species showed little variation in vertical burrowing throughout the study. Most individuals only partially burrowed ( $\sim 40$ -60%) regardless of dewatering rate (Fig. 1.3A-D). A least few individuals ( $n = 7$ -16) depending on species from all species burrowed completely (100%) and were observed just below the surface. Nevertheless, vertical movement (% shell burrowed) was significantly different between species ( $F_{4,60} = 7.52$ ,  $P < 0.001$ ), and dewatering rates ( $F_{3,60} = 24.89$ ,  $P < 0.001$ ). The interaction between dewatering rate and species was also significant ( $F_{10,60} = 2.83$ ,  $P < 0.001$ ). The equilibrium species *A. plicata* and *C. petrina* had the largest average burrowing depth in the control tanks and during the moderate dewatering, but this was not significantly different to *L. teres* during moderate dewatering (Fig. 1.3, Table 1.3). No other differences in burrowing depths between species were detected. *Amblema plicata*, *P. popeii*, and *L. bracteata* burrowed significantly more in control tanks (14 -19% increase) than treatment tanks; whereas, *C. petrina* and *L. teres* showed little to no difference in burrowing among treatment and control tanks (Fig. 1.3).

All mussels became stranded during the fast dewatering trials (Fig. 1.4C). Additionally, a relatively high percentage of mussels became stranded at the moderate



and slow dewatering rates, except for *L. bracteata* (Fig. 1.4A-B). Percentage of mussels stranded was significantly influenced by species ( $F_{4,18} = 10.6$ ,  $P < 0.001$ ), dewatering rate ( $F_{1,18} = 4.78$ ,  $P < 0.05$ ), and their interaction ( $F_{3,18} = 4.26$ ,  $P < 0.05$ ). Percent of individuals stranded was similar among species at moderate dewatering rates. All species had a higher percentage of individuals stranded (46 – 100% increase) compared to *L. bracteata* during slow dewatering. *Popenaias popeii* was the only species that exhibited differences among dewatering rates with a higher proportion becoming stranded during moderate dewatering (100%) compared to slow dewatering (46%).

### **Desiccation Experiment**

Mussel survival was higher for all species at 30 °C compared to 40 °C (33-71% increase depending on species; Table 1.4). Both temperature treatments had significant differences in survival among species (30 °C: Log-Rank TS: 41.237, DF = 3,  $P < 0.001$ ; 40 °C: Log-Rank TS: 67.63, DF = 3,  $P < 0.001$ ). As predicted, the equilibrium species *C. petrina* and *A. plicata* had the highest mean survival rates, which was significantly higher compared to *L. teres* and *L. bracteata* at 30 and 40 °C ( $P < 0.001$ ; Table 1.3). In contrast to our prediction, *L. teres* had a slightly higher desiccation tolerance than *L. bracteata* ( $P < 0.05$ ; Table 1.4). Based on findings by Morton (2017) *P. popeii* would rank intermediate, being more desiccation tolerant than *L. bracteata* with median survival times of 1.1 and 5.6 days at 35°C and 25°C, respectively, but considerably less tolerant than *C. petrina* and *A. plicata*.

## Discussion

Our results show that differences between species in their behavioral response to dewatering and physiological tolerance to desiccation tend to be associated with differences in life history strategies or may be explained by differences in adaptation to certain habitat conditions (see below). In addition, the behavioral responses (especially horizontal mobility) of all five species studied here seem to be closely linked with their respective physiological (desiccation) tolerances, which supports previous findings for other species by Gough et al. (2012). Mussels that were most tolerant to emersion (*C. petrina* and *A. plicata*) had little horizontal movement during dewatering, whereas the more mobile *Lampsilis* species were considerably less tolerant to emersion. Based on our results and Morton (2017), *P. popeii* could be classified as ‘semi-tolerant’ due to its intermediate levels of horizontal movement and desiccation tolerance compared to our other study species. This linkage seems to be a general pattern in mussels, as seen in many insect species (Williams 2006).

Although it is more difficult to explore linkages with life history strategies, due to uncertainties in how to classify a species as life history information is often lacking, our experiments demonstrated that differences between species in behavioral and physiological responses were generally associated with life history strategies. The equilibrium species in our study (*A. plicata*, *C. petrina*) were indeed more tolerant to desiccation and became easily stranded, because of lower horizontal mobility. The opportunistic species (*L. teres* in our study) were as expected rather intolerant to desiccation, showed intermediate horizontal mobility, and thus became less easily stranded. The periodic species *L. bracteata*, was the only species not to become stranded

during the slow dewatering. Although the linkages between survival mechanism and life history during a drought event have not been directly examined by other studies, some data in the literature show similar relationships between behavioral and physiological responses and life history strategy to what we found in our study.

In general, previous studies support the idea that desiccation tolerance in mussels is closely linked with life history strategy. In 7 of 10 reported cases (including this study) involving six species, species considered (only as) opportunistic were intolerant of drying (Table 1.1). Conversely, 9 out of 12 reported cases involving eight species considered (only) equilibrium were tolerant of drying (Table 1.1). Periodic species appeared intermediate and were reported as intolerant in 11 out of 21 cases involving 13 species, whereas the remaining cases reported them as tolerant or semi-tolerant (Table 1.1). It is important to note that some species can be placed into more than one life history category depending upon local and regional factors impacting populations (Haag 2012; Table 1.1).

Considerably less data was available about movement behavior. Horizontal movement was high in both cases with opportunistic species for which data were available (Table 1.1). Only one other study reported on movement behavior of equilibrium species except for our study, finding low mobility, like our results (Newton et al. 2015; Table 1.1). The majority of studies (5 out of 8) reported high movement rates for periodic species (Table 1.1). Burrowing showed little difference between life history strategists with most species exhibiting moderate burrowing levels. In general, higher mobility appeared to be correlated with intolerance or semi-tolerance to desiccation (8 out of 9 cases), whereas lower mobility was mostly associated with higher tolerance to desiccation (6 out of 8 cases, Tables 1.1,1.3).

Differences between species could also be explained by differences in habitat use. For example, *L. teres* and *L. bracteata* having low tolerance to drying, will often be found in deeper pool and lentic microhabitats that are less likely to dry due to higher spring inputs in these types of habitat in central Texas rivers (Howells 2014; Morton et al. 2016). *Lampsilis bracteata* is endemic to extremely flashy headwater systems in central Texas (the region is called “Flashflood alley”, where a high proportion of bedrock in the watershed leads to quick increases in water levels after precipitation events). The high horizontal mobility of *L. bracteata* could be an advantage in such a system, where water levels may fluctuate rapidly, but temperature fluctuations are minimized by groundwater input in the headwaters (Wetzel 2001). The latter could explain the intolerance to desiccation. *Cyclonaias petrina* and *A. plicata* are largely found in stable shallow gravel run or riffle habitats in central Texas (Howells 2014), which are more prone to going dry, and a higher desiccation tolerance may be an advantage. *P. popeii* are found in a mix of habitats (e.g. riffles, crevices, pools) supporting its ability to both track water and burrow (semi-tolerant), similar to the responses predicted for periodic species. It seems that survival mechanisms used by various life history strategists may be affected by differential habitat use.

The higher mobility of the *Lampsilis* species tested here, is in accordance with other studies that have recorded higher rates of movement for Lampsilini species during a drying event compared to Quadrulini and Amblemini (Walleret al.1999; Gough et al. 2012; Newton et al. 2015). The *Lampsilis* species were also the only ones that showed a substantial effect of dewatering rate on movement in our study with substantially higher movement rates in the treatment compared to the control tanks (except for the fast

dewatering, see below).

Our results show that our study species are not well adapted to escaping rapid dewatering events and all species became stranded during the fast dewatering. Except for *L. bracteata*, a high proportion of individuals became stranded regardless of dewatering rate, which is consistent with findings by Galbraith et al. (2015). Thus, a large proportion of mussel populations can become stranded and experience high levels of mortality downstream of hydropower dams or intense agricultural pumping areas, where water can recede quickly (Sethi et al. 2004; Spooner et al. 2011; Newton et al. 2015).

Although burrowing behavior is thought to vary among species in the wild (Watters et al. 2001; Allen and Vaughn 2009) and in response to drought conditions (Gough et al. 2012) our study showed little difference in burrowing behavior among species, similar to another experimental study on dewatering by Galbraith et al. (2015), which suggested that this may be caused by the experimental set-up, not necessarily reflecting natural conditions. We used sand in our experimental set-up, which has been shown to facilitate burrowing compared to gravel (Hernandez 2016), but overall mussels seemed to burrow less in the experimental set-up compared to observations in the field in sandy habitat (ZM and ANS unpublished data).

Our study showed that a proportion of a population of the most tolerant species (*C. petrina* and *A. plicata*) can survive emersion for a couple of weeks at 30 °C, however survival dramatically decreased for all species at 40 °C. Survival rates after emersion seem to primarily depend on shell morphology, temperature, and humidity levels (Holland 1991; Byrne and McMahon 1994; Haag 2012). Mussels with thicker shells (e.g., *A. plicata*) have the ability to seal their shell tightly and have therefore increased

emersion tolerance (Byrne and McMahon 1994), whereas both *Lampsilis* species tested in our study have thin shells and died relatively quickly. Additionally, survival rates after emersion tend to increase with decreasing temperatures and increasing humidity levels (Holland 1991; Byrne and McMahon 2000; Gough et al. 2014). Relative humidity levels in our study were ~25% in the environmental chamber used our desiccation experiment. It is likely that survival of our study species could dramatically increase with relative humidity levels of  $\geq 50\%$  (Holland 1991). Furthermore, the presence of groundwater beneath the stream bed surface could increase survival rates of burrowed individuals, by decreasing temperatures and increasing the humidity within the soil (Holland 1991; Gough et al. 2012). Hence, it is important for future field studies to examine the possible influence of the water table on the survival probability of stranded mussels.

Relating responses to drought and dewatering to life history strategies and habitat use may help to identify species with a higher risk to drying events. Equilibrium species, especially those with a thick shell, may be relatively tolerant of the immediate impacts of drying, but may become easily stranded when water levels fluctuate. Thinner shelled periodic species such as *L. bracteata*, may be less likely to become stranded, but seem to be highly susceptible to emersion during a drought and dewatering event. Future studies should also examine another important aspect in response to drought from our conceptual framework: the (re-) colonization potential. Opportunistic species like *L. teres* are intolerant to drying events but could have high colonization potential (Fig. 1.1) and reach previously dried habitats due to the high fecundity and the utilization of several host fish species. In contrast, both periodic and equilibrium species will likely have a lower colonization ability than opportunistic species due to traits such as lower fecundity and

lower growth rates. Whether equilibrium species have a higher colonization potential than periodic species (Fig. 1.1) may depend on the dispersal abilities of their host fish. Interestingly, a study on metacommunity structure of mussels in Ontario associated most of the mussels with presumably higher dispersal abilities as opportunistic and equilibrium species, whereas most of the mussels associated with periodic strategy were characterized as low dispersal mussels (Schwalb et al. 2015). Future studies investigating the impacts of drying events on mussels should test the predictions from our life-history based framework for the behavioral responses, physiological tolerances, and (re-) colonization potential of mussels during and after a drying event. It is important to note that species will exist along a gradient within this framework and could be placed anywhere in the triangle and not just within the three distinct groups.

Table 1.1. Data of desiccation tolerance and horizontal and vertical mobility of different species gathered in the literature of studies (including this study) examining the response of mussels to drying events. Life history strategies (Strategy) were assigned based on information provided in Table 6.3 in Haag (2012), which include opportunistic (O), periodic (P), and equilibrium (E) strategies. When species could be potentially grouped with different strategies, both strategies were listed (e.g., O/P). Tolerance refers to a species physiological ability to withstand negative impacts of drying events (e.g. high temps, emersion) and are classified as intolerant (I), semi-tolerant (S), and tolerant (T). Mobility (horizontal movement/ burrowing) was described as either high, moderate (mod), or low.

Species	Strategy	Tolerance	Mobility	Source
<i>Anodonta grandis</i>	O	I; Mean survival: 1.8 days at 35°C/ 0% RH	NA	Holland (1991)
	O	I; Mean survival: ~2 days at 35°C/ 5-95% RH	NA	Byrne and McMahon (1994)
<i>Lampsilis teres</i>	O	I; Mean survival: 2.27 days at 40°C, 5.07 days at 30°C	High horizontal: Mean ~10-35 cm/ind./day/ Moderate vertical: Mean % shell burrowed ~45-60	This study
<i>Pyganodon grandis</i>	O	I; Mean survival: 0.6 weeks at 35°C	High horizontal: Mean linear distance ~5 m over 3 weeks / Low vertical: Mean burrow depth ~4.8 cm	Gough et al. (2012)
<i>Pyganodon cataracta</i>	O	S; 25% mortality of study ind. over 10 day dewatering period at 22°C	High horizontal: Mean ~10-15 cm/ind/day / Low vertical: Mean % shell burrowed ~50%	Galbraith et al. (2015)
<i>Toxolasma parva</i>	O	I; Mean survival 1.75 days at 35°C/ 50% RH	NA	Holland (1991)
	O	I; Mean survival < 5 days at 35°C/ 5-50% RH	NA	Byrne and McMahon (1994)
<i>Truncilla truncata</i>	O	I; Thermally intolerant, decreased resource assimilation at 35°C	NA	Spooner and Vaughn (2008)
<i>Villosa lienosa</i>	O	T; 9% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
	O	T; Substantial numbers remain after drought; Stream flow: 0-32% of long-term mean	NA	Golladay et al. (2004)
<i>Villosa vibex</i>	O/P	T; 3% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
	O/P	T; Substantial numbers remain after drought; Stream flow: 0-32% of long-term mean	NA	Golladay et al. (2004)
<i>Villosa villosa</i>	O/P	S; Substantial numbers remain/lost after drought, site dependent; Stream flow: 0-32% of long-term mean	NA	Golladay et al. (2004)
<i>Alasmidonta heterdon</i>	P	I; 60% ind. w/ sustained gaping behavior 30 min. post emersion at 22°C	Moderate horizontal: Mean ~7-10 cm/ind/day/ Moderate vertical: Mean % shell burrowed ~35-50%	Galbraith et al. (2015)
<i>Alasmidonta marginata</i>	P	I; 92% mortality of study ind. over 10 day dewatering period at 22°C	No horizontal movement / Moderate vertical: Mean % shell burrowed ~35-55%	Galbraith et al. (2015)
<i>Alasmidonta varicosa</i>	P	I; 75% mortality of study ind. over 10 day dewatering period at 22°C	Moderate-High horizontal: Mean ~5-17cm/ind/day / Moderate vertical: Mean % shell burrowed ~35-45%	Galbraith et al. (2015)
<i>Lampsilis bracteata</i>	P	I; Mean survival: 1 day at 40°C, 3.4 days at 30°C	High horizontal: Mean ~5-40 cm/ind./day/ Moderate vertical: Mean % shell burrowed ~55-65	This study



Table 1.1. Continued

<i>Lampsilis cardium</i>	P	I; Thermally intolerant, decreased resource assimilation at 35°C	NA	Spooner and Vaughn (2008)
	P	S; 27% mean mortality over 4 months, mean temperature 23-26°C	High horizontal: Net distance moved ~5 m / Moderate-High vertical: 50-100% ind. Burrowed; Mean % shell burrowed: 50-100%	Newton et al. (2015)
	P	I; 82% total mortality over 9 weeks among sites, mean temperature 23-26°C	NA	MNDNR (2011)
	P	T; >90% survival probability 1 hr after emersion at 25°C/60% RH	NA/ High vertical: Est. probability to first uprighting ~90% at 2 days	Bartsch et al. (2000)
<i>Lampsilis straminea</i>	P	S; Mean survival: 1.6 weeks at 35°C	High horizontal: Mean linear distance ~5 m over 3 weeks / Moderate vertical: Mean burrow depth -2.9 cm	Gough et al. (2012)
	P	I; ~35% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
	P	I; Substantial decreases after drought among sites; Stream flow: 0-32% of long-term mean	NA	Galloday et al. (2004)
<i>Hamiota subangulata</i>	P	S; 28% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
	P	I; Substantial decreases after drought among sites; Stream flow: 0-32% of long-term mean	NA	Galloday et al. (2004)
<i>Medionidus pencilatus</i>	P	I; 50% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
<i>Obliquaria reflexa</i>	P	T; Thermally tolerant; increased resource assimilation at 35°C	NA	Spooner and Vaughn (2008)
<i>Strophitus undulatus</i>	P	I; ~50% mortality of study ind. over 10 day dewatering period at 22°C	High horizontal: Mean ~6-18cm/ind/day / Moderate vertical: Mean % shell burrowed ~55%	Galbraith et al. (2015)
<i>Toxolasma paulus</i>	P	S; 23% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
<i>Unio merus carolinianus</i>	P	T; 0% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
<i>Unio merus tetralasmus</i>	P	T; Mean survival: 14.3 weeks at 35°C	Low horizontal: Mean linear distance < 1 m over 3 weeks / High vertical: Mean burrow depth -3.2 cm	Gough et al. (2012)
	P	T; Mean survival: ~50 days at 35°C/ 5-95% RH	NA	Byrne and McMahon (1994)
	P	T; Mean survival: 51.4 days at 35°C/ 0% RH	NA	Holland (1991)
<i>Elliptio complanata</i>	P/E	S; ~30% mortality of study ind. over 10 day dewatering period at 22°C	Low-Moderate horizontal: Mean ~2-10 cm/ind/day / Moderate vertical: Mean % shell burrowed ~50%	Galbraith et al. (2015)
	P/E	T; 9% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
	P/E	T; Substantial numbers remain after drought; Stream flow: 0-32% of long-term mean	NA	Galloday et al. (2004)
<i>Elliptio crassidens</i>	P/E	I; 82% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
<i>Euryntia dilatata</i>	P/E	I; <10% survival probability 1 hr after emersion at 25°C/60% RH	NA/ Moderate vertical: Est. probability to first uprighting ~30% at 2 days	Bartsch et al. (2000)

Table 1.1. Continued

<i>Actinonaias ligamentina</i>	E	I; Thermally intolerant, decreased resource assimilation at 35°C	NA	Spooner and Vaughn (2008)
<i>Amblema plicata</i>	E	T; Thermally tolerant; increased resource assimilation at 35°C	NA	Spooner and Vaughn (2008)
	E	T; Mean mortality: 52% over 4 months, mean temperature 23-26°C	Low-Moderate horizontal: Net distance moved ~3 m/ High vertical: 78-83% ind. Burrowed, Mean % shell burrowed: 50-100%	Newton et al. (2015)
	E	T; 38% total mortality over 9 weeks among sites, mean temperature 23-26°C	NA	MNDNR (2011)
	E	T; Mean survival: 4.6 day at 40°C, 10.2 days at 30°C	Low horizontal: Mean ~1-9 cm/ind./day/ Moderate- High vertical: Mean % shell burrowed ~60-75	This study
<i>Cyclonaias petrina</i>	E	T; Mean survival: 6.67 day at 40°C, 9.93 days at 30°C	Low horizontal: Mean ~0-2 cm/ind./day/ Moderate vertical: Mean % shell burrowed ~50-60	This study
<i>Cyclonaias pustulosa</i>	E	T; > 90% survival probability 1 hr after emersion at 25°C/60% RH	NA/ Low vertical: Est. probability to first uprighing 20% at 2 days	Bartsch et al. (2000)
	E	I; Thermally intolerant; increased resource assimilation at 35°C	NA	Spooner and Vaughn (2008)
<i>Fusconaia flava</i>	E	T; Thermally tolerant; increased resource assimilation at 35°C	NA	Spooner and Vaughn (2008)
<i>Megalonaias nervosa</i>	E	T; Thermally tolerant; increased resource assimilation at 35°C	NA	Spooner and Vaughn (2008)
<i>Pleurobema pyriforme</i>	E	T; 15% mean weekly mortality under at 24-30°C, DO levels < 5mg/l, 0.1-18.6 cm/s over 5 months	NA	Johnson (2001)
<i>Popenaias popeii</i>	E	S; Mean survival: 1.1 day at 35°C, 5.6 days at 25°C	Moderate horizontal: Mean ~5-25 cm/ind./day/ Moderate vertical: Mean % shell burrowed ~40-60	This study/ Morton (2017)

Table 1.2. Life history strategies and their traits as proposed by Haag 2012 (see Table 6.3 in Haag 2012).

Traits	Opportunistic	Periodic	Equilibrium
Life span (years)	low ( $\leq 10$ )	moderate (8-30)	high ( $>25$ )
Age at maturity (years)	low (0-2)	low-moderate (1-3)	high ( $>3$ )
Fecundity	moderate-high	low-moderate (1-3)	variable; typically low, but broadcasters high
Max. adult size (mm)	moderate-large	small-moderate	moderate-large
Brooding strategy	long-term or multicyclic	mostly long-term	mostly short-term
Growth rate ( $K$ )	high	moderate-high	low-moderate

Table 1.3. Predicted and observed differences between species for horizontal movement rates, burrowing depth, and desiccation tolerance.

Predicted and observed differences between species	
Response variable	
Horizontal movement rates	<i>Predicted: L. bracteata &gt; L. teres &gt; P. popeii ~ A. plicata ~ C. petrina</i> <i>Observed: L. bracteata &gt; L. teres ~ P. popeii &gt; A. plicata ~ C. petrina</i>
Desiccation tolerance	<i>Predicted: L. teres &lt; L. bracteata &lt; P. popeii ~ A. plicata ~ C. petrina</i> <i>Observed: L. bracteata &lt; L. teres &lt; P. popeii &lt; A. plicata ~ C. petrina</i>
Burrowing depth	<i>Predicted: L. teres ~ L. bracteata &lt; P. popeii ~ A. plicata ~ C. petrina</i> <i>Observed: L. teres ~ P. popeii ≤ L. bracteata ≤ A. plicata ~ C. petrina</i>

Table 1.4. Mean  $\pm$  SE survival time (95% CI) for *Cyclonaias petrina* (Cp), *Amblema plicata* (Ap), *Lampsilis teres* (Lt), and *Lampsilis bracteata* (Lb) at 30 and 40 °C.

Species	Survival time	
	mean days $\pm$ SE (95% CI)	
	30°C	40°C
Cp	9.93 $\pm$ 1.53 (6.9 - 12.9)	6.67 $\pm$ 0.6 (5.4 – 7.9)
Ap	10.20 $\pm$ 0.76 (8.7 - 11.7)	4.6 $\pm$ 0.39 (3.8 - 5.4)
Lt	5.07 $\pm$ 0.35 (4.4 - 5.7)	2.27 $\pm$ 0.18 (1.9 - 2.6)
Lb	3.40 $\pm$ 0.25 (2.9-3.9)	1 NA

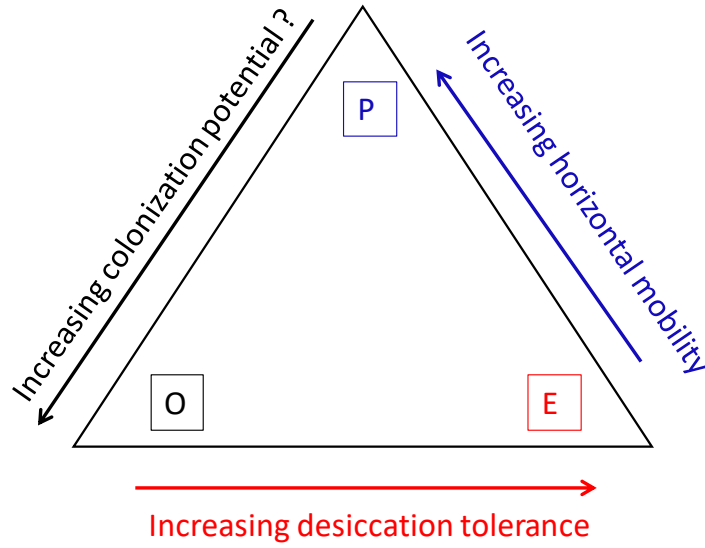


Figure 1.1. Conceptual life-history based framework for predicting behavioral responses, physiological tolerances, and (re-) colonization potential of mussels during and after a drying event. O: opportunistic, P: periodic, E: equilibrium life history strategy.

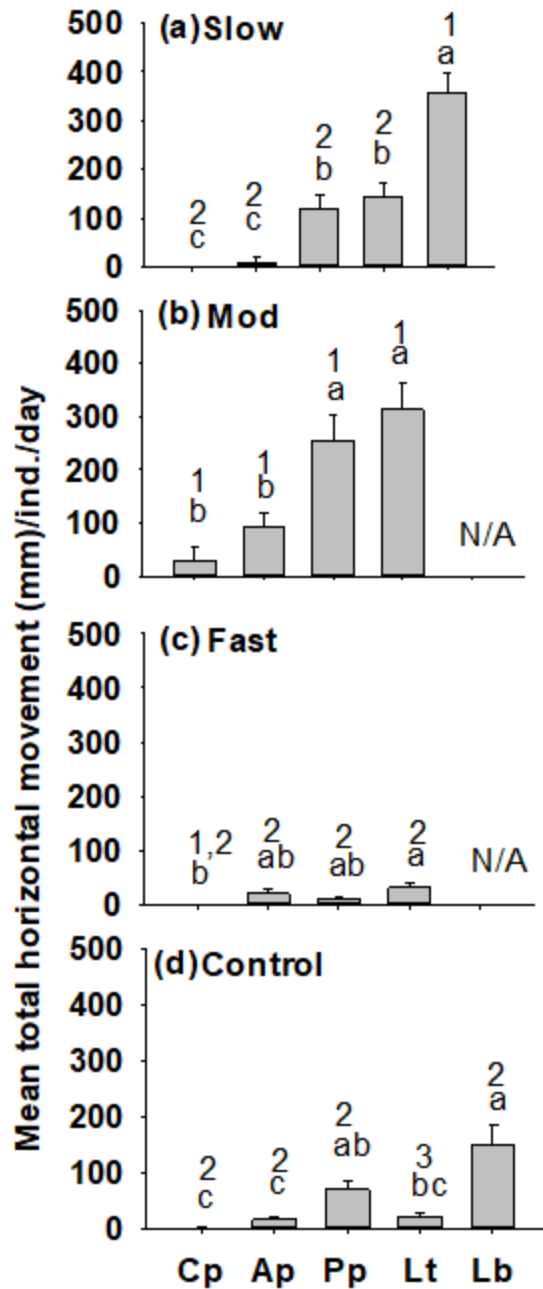


Figure 1.2. Mean ( $\pm$  SE) total horizontal movement for *Cyclonaias petrina* (Cp), *Amblema plicata* (Ap), *Popenaias popeii* (Pp), *Lampsilis teres* (Lt), and *Lampsilis bracteata* (Lb) under slow (A), moderate (Mod) (B), fast (C), and control (D) dewatering rates. Different lowercase letters denote significant differences ( $P < 0.05$ ) between species for a given dewatering rate. Different numbers denote significant differences ( $P < 0.05$ ) within a species between dewatering rates.

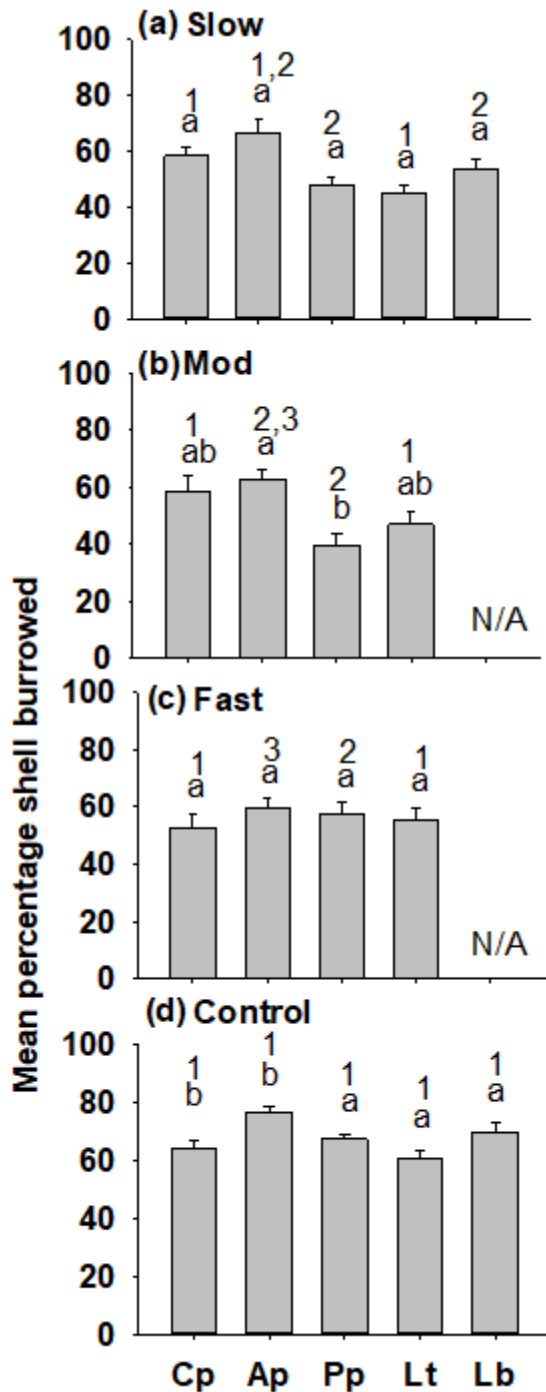


Figure 1.3. Mean ( $\pm$  SE) percentage of shell burrowed for *Cyclonaias petrina* (Cp), *Amblema plicata* (Ap), *Popenaias popeii* (Pp), *Lampsilis teres* (Lt), and *Lampsilis bracteata* (Lb) under slow (A), moderate (Mod) (B), fast (C), and control (D) dewatering rates. Different lowercase letters denote significant differences ( $P < 0.05$ ) between species for a given dewatering rate. Different numbers denote significant differences ( $P < 0.05$ ) within a species between dewatering rates.



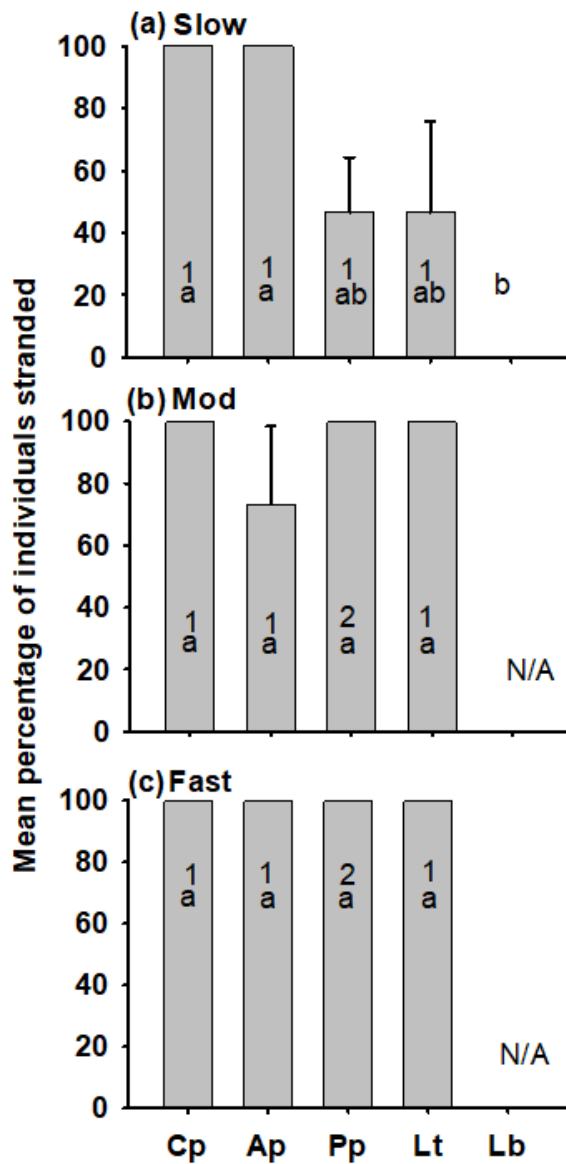


Figure 1.4. Mean ( $\pm$  SE) percentage of individuals stranded for *Cyclonaias petrina* (Cp), *Amblema plicata* (Ap), *Popenaias popeii* (Pp), *Lampsilis teres* (Lt), and *Lampsilis bracteata* (Lb) under slow (A), moderate (Mod) (B), and fast (C) dewatering rates. Different lowercase letters denote significant differences ( $P < 0.05$ ) between species for a given dewatering rate. Different numbers denote significant differences ( $P < 0.05$ ) within a species between dewatering rates.

## **II. CHANGES IN COMMUNITY COMPOSITION OF RIVERINE MUSSELS AFTER A SEVERE DROUGHT DEPENDS ON LOCAL CONDITIONS: A COMPARATIVE STUDY IN FOUR TRIBUTARIES OF A SUBTROPICAL RIVER**

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Changes in community composition of riverine mussels after a severe drought depend on local conditions: a comparative study in four tributaries of a subtropical river.

*Hydrobiologia*, 1-15.

### **Abstract**

The frequency and intensity of droughts are predicted to increase over the next few decades and understanding the impacts of drought on mussel populations is imperative for species conservation. Our objective was to examine the impacts of an exceptional drought in 2011 on mussel communities in four tributaries of the Colorado River basin in central Texas by testing hypotheses that post-drought community composition depends on 1) relative abundances pre-drought, 2) life history strategy of the mussels, 3) ability of sites to retain water, 4) changes in temperature and discharge. Surveys were conducted pre- (2005-2011) and post-drought (2017) and environmental conditions during the drought were examined using discharge data, satellite imagery, and water temperature estimations. No mussels were found at 9 out of 30 sites where mussel populations were present pre-drought. The most abundant species pre-drought tended to be the most abundant species post-drought and no significant difference between life

history strategies was found. There was no clear relationship with post-drought recovery and the ability of a site to retain water. The largest declines in species richness occurred in the tributaries with the lowest mean discharge and highest water temperatures, suggesting that mussels may be especially at risk in rivers with lower discharge.

## **Introduction**

Disturbances are often considered by stream ecologists to play a dominant role in structuring aquatic communities at multiple spatiotemporal scales (Resh et al. 1988; Lake 2000; Brown et al. 2011). Historically, researchers focused primarily on the impacts of high-flow disturbances (i.e. floods) on aquatic communities and gave relatively little attention towards low-flow events such as droughts (Lake 2000). In the past two decades an increasing number of studies have highlighted that droughts can often have more detrimental and longer lasting impacts on aquatic communities compared to floods, by causing significant decreases in habitat availability which lead to increases in biotic and abiotic stressors (Lake 2000; Humphries and Baldwin 2003; Magoulick and Kobza 2003). The negative impacts of droughts on aquatic ecosystems are a growing conservation concern because increasing frequency and intensity are projected to occur in many regions of the world in the coming decades due to global climate change (Lehner et al. 2006; Cayan et al. 2010; USGCRP 2018). Stream flows are further reduced by an increase in groundwater pumping due to growth in human population and intensification of agriculture, increasing the impact of droughts on aquatic communities (Alcamo et al. 2007; Atkinson et al. 2014; Randklev et al. 2018). The southwestern United States is highly susceptible to droughts and excessive water extraction and it is important to

understand their impacts on aquatic communities.

Freshwater mussels (order Unionoida) are considered one of the most imperiled faunal groups in North America (Haag and Williams 2014), with population declines linked to both long-term habitat loss (Strayer 2008; Downing et al. 2010) and drought-driven extinctions (Atkinson et al. 2014). Freshwater mussels are particularly sensitive to droughts because they are relatively sessile and cannot easily escape associated stream drying (Galbraith et al. 2015, Mitchell et al. 2018). Hence, freshwater mussels are good model species for investigating the impacts of droughts on stream communities. Droughts can increase mortality (directly, e.g. increased predation, Walters and Ford 2013; or indirectly), decrease mussel diversity (especially rare species), and change mussel community composition (Gagnon et al. 2004; Golladay et al. 2004; Haag and Warren 2008; Galbraith et al. 2010; Sousa et al. 2018), which can lead to losses in mussel provided ecosystem services (Vaughn et al. 2015). Several mussel species seem to have specialized strategies to increase their chances of survival during drought by either tracking receding water levels into deeper refuge pool habitats or by burrowing into the substrate and surviving desiccation for a given amount of time, although their survival quickly decreases at high air temperatures (Holland 1991; Byrne and McMahon 1994; Bartsch et al. 2000; Gough et al. 2012; Galbraith et al. 2015; Mitchell et al. 2018). Haag and Warren (2008) suggested that post-drought abundance is primarily a function of pre-drought abundance and that specialized drought survival strategies do not seem to be apparent in many mussel species. However, other studies have suggested that some mussel species are more sensitive to droughts than others and that the strategy and degree in which mussels react varies largely on species life history traits, habitat use, and

drought intensity (Gagnon et al. 2004; Golladay et al. 2004; Galbraith et al. 2010; Gough et al. 2012; Atkinson et al. 2014; Mitchell et al. 2018). Differences in the impact of drought may be explained by differences in local habitat conditions, however, to the best of our knowledge, no previous study has compared the impact of a severe drought on mussel communities in several sub-basins within a major river basin.

Texas experienced an exceptional drought in 2011 which persisted until mid-2012 and impacted over 80% of the state, including the Colorado River basin in central Texas (U.S. Drought Monitor 2011, [www.drought.gov](http://www.drought.gov)). A drought is classified as exceptional if it has a Palmer Drought Severity Index (PDSI) of -5 or less or if average weekly streamflow percentiles range from 0 to 2 (Palmer 1965; US Drought Monitor [www.drought.gov](http://www.drought.gov)). Streamflow declined well below average flow levels and some reaches even dried up in several parts of the Colorado River basin. Historically, these tributaries were home to approximately 20 species of freshwater mussel, several of which are currently candidate species for listing as endangered under the Endangered Species Act (Strecker 1931; USFWS 2011; Howells 2014; Appendix 2.1). It should be noted that taxonomy of several species from the *Cyclonaias* and *Quadrula* genera are currently under review and we are referring to the names from the recently revised list of freshwater mussels published by Williams et al. (2017), except for two species, *Cyclonaias pustulosa* (Lea) (formerly *C. houstonensis*; Johnson et al. 2018, Lopes-Lima et al. 2019) and *Quadrula quadrula* (Rafinesque) (formerly *Q. apiculata*; Lopes-Lima et al. 2019).

Our objective was to determine the impacts of an exceptional drought in 2011 on hydrologic and thermal conditions and mussel communities in central Texas rivers. We

developed two competing hypotheses to examine the responses of mussel communities to the drought: (H1) drought will impact all species similarly and post-drought relative abundance of mussels will correlate with pre-drought relative abundances or (H2) different life history strategists (developed by Haag 2012) with different desiccation tolerances will have varying responses during the drought (Table 2.1). Haag (2012) proposed how mussels with different strategies (opportunistic, equilibrium, and periodic) may dominate in different types of habitats (similar to Grime's CSR triangle for plants, Grime 2006). A recent study, in central Texas, extended this life-history based framework to behavioral responses to dewatering and physiological tolerances to desiccation (see Figure 1 in Mitchell et al. 2018). We expected all mussels to decline, but predicted the following changes in the relative abundance after the drought based on this framework: The relative abundance of equilibrium species (e.g. *Cyclonaias* spp.), should increase, because of their higher desiccation tolerances, whereas the relative abundance of periodic species (e.g. *Lampsilis bracteata*, Gould) should decline, because of their lower desiccation tolerance. The traits of opportunistic species (e.g. *Utterbackia imbecillis*, Say) allow them to rapidly colonize disturbed habitat, however they do suffer from relatively high mortality as a general physiological consequence of their fast growth and early reproduction (Haag 2012). We therefore predicted that opportunistic species should experience little change in their relative abundance (Table 2.1).

To better predict sensitive habitat for threatened species considering increasing drought intensity we also examined the relationship between drought response and local habitat conditions. We hypothesized that (H3) post-drought CPUE and species richness depends on the ability of the site to retain water (e.g., whether a site completely dried out,

had constricted flow (wetted channel width narrower than baseflow conditions), or retained water (across entire river channel), and that (H4) changes in CPUE and species richness of mussels in response to a drought depends on the degree of change in discharge and water temperature (Table 2.1). More specifically, we predicted decreases in species richness and CPUE would be significantly higher in sites that completely dried compared to sites that experienced constricted flows or retained water during the drought (H3). Furthermore, we predicted decreases in species richness and CPUE will be more severe within river sections that experienced lower mean annual discharge levels and increased water temperatures (H4, Table 2.1).

## **Methods**

### **Study area**

Mussels were surveyed both pre-drought (2005-2011) and post-drought (May-June 2017) at the same 30 sites from four tributaries within the middle Colorado River basin (103,340 km<sup>2</sup>) including Elm Creek (n = 4), Concho (n = 7), San Saba (n = 14), and Llano Rivers (n = 5; Fig. 2.1). The Concho River (~ 93 km) and Elm Creek (~20 km) primarily flow through rolling hills and semi-arid ranch land before meeting its confluence with the Colorado River. The San Saba River (~225 km) is the longest of the four tributaries in our study and is characterized as semi-arid ranch land in the middle and upper stretches, but more dominated by pecan orchards and row crop operations in the lower stretch. The Llano River (~169 km) is the most urbanized river compared to the other tributaries but still has substantial semi-arid ranch and farmland. Pre-drought surveys were conducted between 2005 and 2011 as part of a larger state-wide survey to

assess the distribution of freshwater mussels and were chosen based on access and in an attempt to cover the longitudinal gradient of the rivers (Burlakova and Karatayev 2012).

### **Assessing stream condition during drought**

In order to assess stream condition during the 2011/12 drought, summer 2012 National Agriculture Imagery Program (NAIP) imagery (near-infrared band) was used to map out wet vs. dry segments within the four tributaries (Fig. 2.1). NAIP imagery from 2011 was not available to assess stream condition, however 2012 imagery is appropriate to use because the drought was still in its exceptional stage at the time the images were taken. Additionally, NAIP imagery was used to determine if survey sites dried, experienced constricted flows (discharge below base flow levels causing parts of the channel to dry) or retained water during the drought. To assess secondary stressors on mussel communities we collected discharge and temperature (water and air) data within the study tributaries. Hourly temperature data from 2007 and 2010 were available through USGS for the Concho River and Elm Creek (lower reaches), but no water temperature data were available during the drought period because the USGS stream gages were inoperable. In addition, hourly temperature data (air and water) were collected for three months (July-September 2017) using HOBO temperature loggers at the Llano (mid-reach, Fig. 2.1) and San Saba Rivers (upper reach, Fig. 2.1). These data were used to construct simple linear regression models to estimate water temperatures, as a function of air temperature, during the 2011 drought within our study tributaries (Table 2.2). In general, air temperatures from July-September 2017 were similar or slightly higher (by 0.3 to 2.8°C) compared to those in September 2011, and maximum daily air temperatures differed by less than 2°C. Monthly average discharge levels were higher



during 2017 compared to 2011 in both the Llano ( $\sim 0.35 \text{ m}^3/\text{s}$  higher) and San Saba Rivers ( $\sim 1.4 \text{ m}^3/\text{s}$  higher), however both rivers exhibited similar discharge trends over time between the two years, and the relative difference in discharge did not change considerably. It should be noted that our estimates for water temperatures are rather conservative and may be underestimating the actual water temperatures during the drought.

### **Mussel sampling**

Mussels were sampled using a combination of timed searches and quadrat methods (only in lower San Saba and Concho rivers) during the pre-drought surveys (2005-2011; find details in Burlakova et al. 2011a, b) but only timed searches during the post-drought (2017) survey period since timed searches were used at the majority of sites pre-drought due to low mussel densities. Additionally, timed searches have been shown to be more effective at finding higher number of individuals and more rare species compared to quadrat methods (Strayer and Smith 2003), especially at sites in central Texas that had lower densities (Sanchez and Schwalb 2019). Search effort averaged 4.1 person-hours per site (range 0.25–12) during the pre-drought survey period, depending on site area. Pre-drought survey search effort was primarily chosen on expert opinion in the field that included the considerations of efforts to find new species. During post-drought surveys, each site was searched for a minimum of two person-hours with the addition of one person-hour afterwards until no new species were found, in average 2.4 ph. Effort was made to search all available mesohabitats within each site. All collected live mussels 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.

### **Data analysis**

Species richness and catch per unit of effort (CPUE; mussels/person-hour) were recorded for all sites during both survey periods. Normality and homogeneity of variance of the data were tested with the Shapiro–Wilk and Levene test, respectively, and data were  $\log(x + 1)$ -transformed to better meet the assumptions of all analyses. We examined changes in species richness and CPUE between pre- and post-drought survey periods using paired t-tests for all rivers combined and separately for the San Saba River and Elm Creek. Individual paired t tests were not conducted for the Llano (low sample size) and Concho rivers (no live mussels found post-drought). Species richness data were combined for analysis when multiple search methods (timed search and quadrat) were used at a specific site, whereas only timed search data were used to compare relative abundances among species. Pearson product moment correlation was used to test the hypothesis that post-drought relative abundances of individual species were associated with pre-drought relative abundances (H1). We used a oneway ANOVA to compare the change in relative abundances of species with different life history strategies between pre- and post-drought (H2). Life history strategies were assigned for each species based upon literature (see Table 6.3, Haag, 2012) and by our own judgment if there was a lack of life history information on a species (Table 3). Additionally, oneway ANOVA compared post-drought changes in species richness and CPUE among sites that experienced different flow conditions including those that completely dried, experienced constricted flows, or retained water during the drought (H3). Simple linear regression was used to examine the changes in species richness and CPUE among sites as a function of

mean daily discharge levels and mean estimated daily maximum water temperatures during the 2011 drought (H4).

To test whether an increase in sampling effort might result in an increase of the number of species or mussels collected, we tested relationships between post-drought timed search efforts and the log-transformed number of live species and total number of live mussels collected. Both regressions were non-significant (log total number of species collected live vs. timed search effort,  $R = 0.07$ ,  $P = 0.71$ , log total number of mussels collected vs. timed search effort,  $R = 0.15$ ,  $P = 0.42$ ), indicating no bias was introduced due to increased sampling effort. The same analyses were previously conducted for the pre-drought data as part of an unrelated state-wide project and found similar results.

## Results

A total of 999 live mussels from 11 species were collected during the pre-drought surveys and a total of 380 mussels from 9 species were collected post-drought (Table 2.3). *Amblema plicata* (Say) and *Potamilus purpuratus* (Lamarck) were found during the pre-drought but not post-drought surveys in the San Saba River. Overall species richness and CPUE of mussels were significantly lower post-drought for all sites ( $n = 30$ ) combined (Richness:  $t_{29} = 4.678$ ,  $P < 0.001$ ; CPUE:  $t_{21} = 2.612$ ,  $P < 0.01$ ). In the Llano River both surveys detected low densities of mussels with a total of 13 (1 species) and 8 (4 species) individuals found. A higher number of mussels were collected in the San Saba River during both survey periods. A total of 796 (11 species) and 364 (9 species) mussels were found during pre- and post-drought surveys, respectively (Table 3). Species richness and CPUE were significantly lower post-drought (Richness:  $t_{13} = 3.238$ ,  $P < 0.01$ ; CPUE:

$t_{12} = 1.742$ ,  $P < 0.05$ ), however species richness and CPUE increased post-drought at three sites in the upper reach, due to the increased presence of *Utterbackia imbecillis* (Figs. 2.1-2.2). A total of 93 and 97 mussels (5 species in both cases) were collected in Elm Creek and the Concho River during pre-drought surveys, respectively. Species richness and relative abundance decreased significantly post-drought in Elm Creek (Richness:  $t_3 = 3.83$ ,  $P < 0.05$ ; CPUE:  $t_3 = 3.35$ ,  $P < 0.05$ ) with only 8 mussels (4 species) being found and no live mussels were found post-drought at any of the Concho River survey sites (Table 2.3; Figs. 2.3-2.4).

Consistent with our **first hypothesis** (Table 2.1), relative abundances of species correlated between pre- and post-drought periods in all rivers where mussels were found post-drought (Elm Creek, Llano River, San Saba River,  $r = 0.89-0.99$ ,  $P < 0.05$  in all cases), indicating that species were affected similarly by the drought. Thus, the most abundant species pre-drought tended to be the most abundant post-drought and rare species pre-drought tended to be found in low abundance or were absent post-drought. For example, the most abundant species in Elm Creek pre-drought (*Cyrtonaias tampicoensis* Lea; periodic species) was the most abundant post-drought, whereas *Utterbackia imbecillis* (opportunistic species) was found in low abundances pre-and post-drought (Table 2.3).

Although the relative abundance of individual species varied, equilibrium species overall only slightly increased in their relative abundance in the San Saba River (from 79 to 84%) and Elm Creek (from 9 to 12.5%), whereas periodic species slightly declined (from 86 to 75% in Elm Creek and from 12 to 10% in the San Saba River, Table 3), providing weak support for our **second hypothesis**. Opportunistic species showed a slight

increase in Elm Creek (from 5 to 12.5%), but a slight decrease in the San Saba River (from 12 to 7%, Table 2.3). *Lampsilis bracteata* (periodic species) had the highest relative abundance pre- and post-drought in the Llano River, although three additional equilibrium species were found post-drought (but only 1 individual per species; Table 2.3; Figs. 2.1 and 2.5). Overall, changes in relative abundance between pre- and post-drought within our study rivers were similar between mussels with different life history strategies ( $F_{(2,24)} = 0.3$ ;  $P > 0.05$ ).

During peak drought conditions stream discharge levels decreased 77-96% below long-term average levels in all four study tributaries (Fig. 2.1). This resulted in drying, and the San Saba and Concho rivers had the largest number of dried reaches followed by Elm Creek and the Llano River, respectively (Fig. 2.1). In total, 67% of our survey sites experienced constricted flows (57%,  $n = 17$ ) or completely dried (10%,  $n = 3$ ) during the drought period (Figs. 2-5). Most sites (7 out of 9) where mussels were absent post-drought, but present pre-drought, experienced constricted flow (and presumably higher water temperatures; Figs. 2.1-2.3). This included all sites in the Concho River. Only three sites dried out completely (two in Elm Creek, one in the middle section of the San Saba River), and all experienced declines in species richness (33-100%). However, almost all sites (9 out of 10) that retained water (mostly located in the downstream section of the San Saba River, 1 site in Elm Creek) also experienced declines in species richness (25-100%). All but one site in the Llano River experienced constricted flows during the drought but only minor changes in species richness (Figs. 2.1 and 2.4). Contrary to our prediction (**hypothesis 3**), no significant differences in mean species richness ( $F_{(2,29)} = 0.44$ ,  $P = 0.65$ ) and CPUE ( $F_{(2,29)} = 1.1$ ,  $P = 0.34$ ) were found between sites that dried,

experienced constricted flows, or retained water during the drought (Table 2.1).

While no significant relationship was found between changes in CPUE and changes in discharge and water temperature for all sites combined as expected based on **hypothesis 4** (discharge:  $F_{(1,29)} = 0.04$ ,  $P = 0.84$ ,  $R^2 = 0.001$ ; temperature:  $F_{(1,29)} = 0.32$ ,  $P = 0.58$ ,  $R^2 = 0.01$ ), largest declines in species richness were detected at sites located in rivers (Elm Creek and Concho River) with lower annual discharge and higher estimated water temperatures compared to the other rivers (discharge:  $F_{(1,29)} = 4.6$ ,  $P = 0.04$ ,  $R^2 = 0.15$ ; temperature:  $F_{(1,29)} = 4.6$ ,  $P < 0.01$ ,  $R^2 = 0.31$ , Table 2.1). Elm Creek and the Concho River mean discharge during peak drought conditions were 0.4 and 0.38-0.43  $\text{m}^3/\text{s}$  (upper to lower Concho River), respectively, which was 83-96% below the mean annual discharge (based on years 1932-2018 for Elm Creek and 1915-2018 for Concho River; Fig. 2.1). Similarly, Elm Creek and the Concho River had the highest estimated number of days with temperatures reaching  $> 30^\circ\text{C}$  and the highest average water temperature compared to the Llano and San Saba rivers (Table 2.2). Elm Creek also had the longest period of consecutive days with water temperature  $> 30^\circ\text{C}$  followed by the Concho, Llano, and San Saba rivers, respectively (Table 2.2). In contrast, sites in the Llano River, which experienced only minor changes in mussel distribution and presence (Fig. 2.1), had the highest discharge and lowest average water temperatures. The mean drought discharge (upstream data from 1940-2018, midstream data from 1968-2018) was 1.76-1.90  $\text{m}^3/\text{s}$  (Figs. 2.1 and 2.4). The average water temperature for the Llano River during 2011 was  $21.5^\circ\text{C}$ , with a maximum estimated temperature of  $33.5^\circ\text{C}$  (Table 2.2). The San Saba River, where high mussel abundance and diversity were recorded during both survey periods, had intermediate levels of discharge (mean discharge 0.30-1.1  $\text{m}^3/\text{s}$ ;

data taken from 1916-2018) and water temperature (mean 2011 temperature: 23.9°C) during the drought compared to the other tributaries (Fig. 2.1; Table 2.2).

## **Discussion**

Our results show that mussels severely declined in the Colorado River basin post-drought, but the severity varied with conditions in each tributary, with the most severe declines occurring in tributaries with the lowest discharge and highest estimated temperatures (see below). In addition, our prediction for our first hypothesis was supported in three of our study tributaries because post-drought relative abundance seemed to depend largely on initial relative abundance with all species being impacted similarly by the drought, consistent with previous findings (Haag and Warren 2008). However, in the Concho River no mussels were found post-drought, so we could not analyze differences in relative abundance. Potential reasons for the disappearance of mussels in the Concho River are discussed below.

Increases in the relative abundance of equilibrium species and declines in periodic species in Elm Creek and San Saba River were in accordance with our second hypothesis, but these changes were only minor and not statistically significant. Additionally, as predicted, the relative abundance of opportunistic species remained relatively consistent between pre- and post-drought. It should be noted that the statistical power of our analysis of the second hypothesis was lowered significantly ( $\beta = 0.43$ ) by the low number of mussels found post-drought with different life history strategies, and low statistical power of mussel field studies is a general problem when trying to interpret ecologically meaningful patterns (Strayer and Smith 2003). In addition, species were placed in

general life-history categories based on the literature or our judgment, but neither tracking/burrowing behavior nor desiccation survival was tested or available in the literature for many of these species, potentially affecting the results. More studies are needed on biological traits of species that can aid in prediction of their survival during droughts.

While mussels with different life history strategies have been shown to respond differently to dewatering (Mitchell et al. 2018), these differences among species may become irrelevant during prolonged and extreme drought conditions under which all mussels experience high mortality rates. Although exceptions do exist, several studies have suggested that many mussels cannot survive desiccation for extended periods of time (>2 weeks), however survival could substantially increase if mussels have the ability to burrow into the sediment to seek thermal refuge, especially if groundwater is present (Holland 1991; Byrne and McMahon 1994; Bartsch et al. 2000; Gough et al. 2012; Galbraith et al. 2015; Mitchell et al. 2018), and if the sediment allows burrowing (e.g., not bedrock).

Surprisingly, in contrast to hypothesis 3, differences in CPUE and species richness were not impacted by whether sites completely dried, experienced constricted flows, or retained water during the drought. For example, large decreases in mussel richness and abundance were seen in the lower San Saba River at sites that retained water throughout the drought. As shown by other studies, low flow causes elevated temperatures and reduces oxygen levels, creating stressful conditions and increased mussel mortality (Johnson et al. 2001; Golloday et al. 2004; Haag and Warren 2008). Water temperatures > 30°C have been shown to significantly decrease survival and



physiological function of many freshwater mussel species, especially for early life stages, and even over short time periods (24 hr) (Pandolfo et al. 2010; Archambault et al. 2013; Ganser et al. 2013; Archambault et al. 2014; Ganser et al. 2015; Mitchell et al. 2018). Additionally, mussel species that are associated with the headwaters (e.g. *L. bracteata* in our study) or have relatively thin shells (e.g. *L. fragilis*) may be especially sensitive to increases in temperature (Mitchell et al. 2018).

Responses to drought clearly differed between tributaries and declines were most severe in tributaries with lower discharge and higher water temperatures (in terms of species richness, H4). However, no statistically significant relationship in changes in CPUE was found when sites were compared. This could be at least partly due to a lack of fine-scale measurements of discharge and temperature and several sites were assigned the same values. In addition, other factors may adversely affect mussels. For example, no mussels were detected in the Concho River, although none of the sites that previously contained mussels completely dried. Pre-drought mussel size distribution showed a prevalence of larger and presumably older individuals in the Concho River (mean shell length within sites  $\geq$  maximum adult lengths reported by Howells 2014) suggesting that a lack of recruitment may have led to local extinctions in the Concho River of the past decade. A lack of or limited dispersal due to barriers may have also contributed to the local extinctions. The Concho River ( $n = 17$ ) has the highest number of low-head dams (assessed by satellite imagery) compared to all other tributaries (Elm Creek ( $n = 2$ ), Llano ( $n = 3$ ), San Saba ( $n = 5$ )). Several studies have investigated the impacts of low-head dams on mussel populations and found that low-head dams can cause decreases in mussel species richness, relative abundance, and dispersal rates within rivers (e.g. Watters 1996;

Dean et al. 2002; Tiemann et al. 2016), however other studies have found increased mussel densities and faster growth rates immediately downstream of low-head dams (e.g. Gangloff et al. 2011; Singer and Gangloff 2011; Hornbach et al. 2014). There is a lack of studies on smaller barriers, such as low-water crossings, which are very abundant in Central Texas and could negatively impact species dispersal and alter natural flow regimes. However, small barriers may also have positive effects by creating refuge pools for mussels during droughts (Randklev et al. 2018) and the impact of barriers in a river may depend on their size (height and width), operation type, water outlet design, age, and the number of barriers within a watershed (Poff and Hart 2002).

We recognize several limitations in our study. Our site selection was restricted by available pre-drought data, which were collected as part of a larger and unrelated state-wide project. While the number of sites per tributary was relatively low (Appendix 2.2) and our surveys cannot provide a complete list of all species present in a tributary, it allowed us to compare responses to droughts in different tributaries. For example, despite a considerably lower number of sites compared to a recent study by Randklev et al. (2018), we also found that *Cyclonaias petrina*, *Tritogonia verrucosa*, and *C. pustulosa* were the most abundant species within the San Saba River post-drought and were primarily found in the lower reaches, whereas the upper and middle reaches of the San Saba River (classified as intermittent by Randklev et al. 2018) were primarily composed of a periodic species (*Lampsilis bracteata*) and an opportunistic pool species (*Utterbackia imbecilis*; Table 2.3).

Although relationships between timed search efforts and the number of live species and mussels collected were not significant, post-drought search effort was

sometimes considerably greater than during pre-drought surveys at certain sites (e.g. upper San Saba River), and some increases in species richness are likely due to increased search effort. However, we are confident that the decreases we detected in species richness reflect actual declines. Our post-drought surveys at sites with lower search effort pre-drought, failed to find any new species, apart from one site in the upper San Saba and Llano Rivers. Furthermore, sites were not sampled immediately post-drought, however the time between our sampling periods was similar or even shorter (depending on the site) compared to another study that examined the impacts of a severe drought on mussel communities in several streams in southeastern USA (Haag and Warren 2008). Due to the extended timeframe between sampling periods mussels could have recolonized a few sites, but we only found clear evidence of potential recolonization within two sites of our study area. We found one opportunistic species (*U. imbecilis*) in one middle San Saba site (classified as intermittent by Randklev et al. 2018) and two periodic species (*C. tampicoensis* and *L. bracteata*) in one Elm Creek site, both of which had completely dried during the drought. The presumably greater colonization potential and early maturation of the opportunistic species (*U. imbecilis*; Haag 2012; Mitchell et al. 2018) probably aided recruitment, via host fish, at both sites, whereas periodic species could have actively recolonized the Elm Creek site from another site within the river by utilizing its greater horizontal mobility (Mitchell et al. 2018).

It is important to consider that historically all rivers had a higher mussel species richness, and declines had already occurred before the drought in 2011 and did not reflect pre-settlement conditions. Additionally, it is important to note that the presence of smaller groups of individuals within our sites is not necessarily an indication of

functionally reproducing populations and thus may still be declining within the sites where they were sampled. Based on historical surveys, the Concho River had the highest documented species richness (20 species) followed by the San Saba (16 species) and the Llano rivers (14 species), with Elm Creek (9 species) having the least recorded species richness (Appendix 2.1). Our data suggests that the Llano River mussel communities were the least impacted by the recent drought, but the river has historically (several decades ago) suffered some of the greatest losses in terms of species diversity (70% decrease in species richness) compared to the other middle Colorado tributaries, except for the Concho River (100% loss within our study sites; Fig. 2.6, Appendix 2.1). The flow regime in the Llano River may have contributed to the greater historical decrease in species in the Llano River compared to the other study tributaries. The Llano River was substantially different in terms of flood magnitude, duration, and experienced much faster rise and fall rates and peak discharge levels during large floods (Table 2.4). Floods can pose serious problems for freshwater mussels, as they cannot seek refuge from high flows in a short amount of time, often leading to increases in mortality (Strayer 1999; Hastie et al. 2001).

Although we acknowledge the historical role of floods in structuring mussel communities (e.g., for the Llano River, see above) within central Texas, we think the 2011 drought, and not recent floods, played the dominant role in shaping mussel assemblages between our two survey periods. For example, if flooding were the cause of the local extirpation of mussels from the Concho River, we might expect to see a lack of mussel shell beds locally because they would be washed downstream. However, we found several historical “mussel beds” (composed of dead shells) at our Concho River

sites, even though no live individuals were found. Thus, it seems that in several of our study sites, mussels died from either direct or indirect mortality associated with drought and not washed out of the site by recent floods.

Compared to historical data Elm Creek and the San Saba River have lost 66% and 44% of species, respectively, however these changes seemed to have occurred more recently because most species from their historical assemblages were still found within these tributaries during the 1990s to early 2000s (Appendix 2.1; Fig. 2.6). The changes in historical mussel communities could have been caused by other human impacts. For examples, water quality degradation from urbanization and other land-use practices (e.g. cattle ranching) was identified as a concern for the Colorado River tributaries (TCEQ; [www.tceq.texas.gov](http://www.tceq.texas.gov)). Historically, the overall higher diversity of freshwater mussels found in the San Saba River is most likely due to the fact that it remained relatively undeveloped and largely maintained natural flow regime (TPWD 1974). However, in more recent years increased groundwater pumping has caused ~40 km of river (middle reaches) to dry up every year since the 2011 drought, regardless of drought condition (RPS Espey 2013; Geeslin et al. 2015). This poses a major threat for the mussels (Randklev et al. 2018). Excessive groundwater pumping can severely alter stream ecosystems and the aquatic biota within them, especially considering projections of high temperatures and water scarcity under future climate scenarios (Konikow and Kendy 2005; Falke et al. 2011; Inoue et al. 2014; Randklev et al. 2018). The annual drying of stream reaches within the San Saba River will not only lead to declines of adult mussels (Randklev et al. 2018), but the reaches that dry out could act as a sink habitat in which juveniles could be transported there via their host fish during fall-spring (e.g., *L.*

*bracteata*, Seagroves et al. 2019), when water is present, leading to high juvenile mussel mortality during the summer.

Based on our results it seems apparent that the 2011 exceptional drought had significant negative impacts on the mussel assemblages within the tributaries of the Colorado River basin. Smaller populations, increased disturbances, and dispersal barriers will likely make species recovery difficult in many areas within central Texas rivers, especially if human activities such as groundwater pumping are not properly managed. Our study highlights the importance of collecting long-term data on mussel assemblages and environmental conditions to understand more specifically which factors are impacting populations and to what degree.

Table 2.1. Hypotheses (H1-H4), predictions, and observed results of changes in mussel communities within central Texas after an exceptional drought. S = supported; PS = partly supported; NS = not supported.

Hypothesis	Prediction	Result
<b>H1</b>		
Drought affects all species similarly.	Relative abundances post-drought will correlate with pre-drought relative abundances.	S
<b>H2</b>		
Effects of drought differ between species with different life history strategies.	Increase in relative abundance of equilibrium, decline of periodic, opportunistic remains similar.	PS
<b>H3</b>		
Changes in species richness and relative abundance depend on whether a site completely dried, had constricted flows, or retained water during the drought.	Decreases in species richness and CPUE will be significantly higher at sites that completely dried, compared to sites that experienced constricted flows or retained water.	NS
<b>H4</b>		
Changes in species richness and relative abundance of mussels depends on changes in discharge and water temperature.	Decreases in species richness and CPUE will be more severe within river sections with lower mean annual discharge and increased water temperatures.	PS

Table 2.2. Estimated mean and maximum water temperatures during 2011, the number of days where temperatures reached >30°C (at some point during the day), and the longest period of consecutive days that temperatures reached >30°C at some point during the day for the four study tributaries during the 2011 drought derived from simple linear regression models.

<b>River</b>	<b>Mean Temp °C</b>	<b>Max Temp °C</b>	<b>Days &gt;30°C</b>	<b>Con. Days &gt;30°C</b>	<b>Equation</b>	<b>R<sup>2</sup></b>
Llano	21.5	33.5	84	22	$Y = 9.338 + (0.577 * \text{Air})$	0.65
San Saba	23.9	33.8	71	21	$Y = 6.007 + (0.665 * \text{Air})$	0.58
Concho	23.9	36.8	125	73	$Y = 1.167 + (0.822 * \text{Air})$	0.80
Elm Creek	24.8	37.1	129	78	$Y = 3.114 + (0.783 * \text{Air})$	0.67



Table 2.3. Number of individuals (percent composition within tributary) by species and tributaries during pre- and post-drought survey periods (timed search and quadrat methods included) and percent change of species composition for each tributary between survey periods. Life history strategy for individual species is color coded as follows: Equilibrium (red), Periodic (blue), Opportunistic (black). Life history strategies were assigned for each species based upon the literature (see table 6.3, Haag, 2012) and by our own judgment if there was a lack of life history information available on a species.

River	Species	Pre-drought	Post-drought	% change
Elm Creek	<i>Quadrula quadrula</i>	8 (9)	1 (12.5)	3.5
	<i>Cyrtonaias tampicoensis</i>	77 (83)	4 (50)	-33
	<i>Lampsilis bracteata</i>	3 (3)	2 (25)	22
	<i>Leptodea fragilis</i>	1 (1)		-1
	<i>Utterbackia imbecillis</i>	4 (4)	1 (12.5)	8.5
Concho	<i>Quadrula quadrula</i>	60 (62)		-62
	<i>Cyclonaias petrina</i>	26 (27)		-27
	<i>Cyrtonaias tampicoensis</i>	2 (2)		-2
	<i>Potamilus purpuratus</i>	7 (7)		-7
	<i>Utterbackia imbecillis</i>	2 (2)		-2
San Saba	<i>Amblesma plicata</i>	10 (< 1)		-1
	<i>Quadrula quadrula</i>	2 (< 1)	2 (< 1)	1
	<i>Cyclonaias pustulosa</i>	230 (29)	65 (18)	-11
	<i>Cyclonaias petrina</i>	209 (26)	127 (35)	9
	<i>Cyrtonaias tampicoensis</i>	1 (< 1)	3 (1)	1
	<i>Lampsilis bracteata</i>	88 (11)	34 (9)	-2
	<i>Leptodea fragilis</i>	68 (9)	13 (4)	-5
	<i>Potamilus purpuratus</i>	4 (< 1)		-1
	<i>Tritogonia verrucosa</i>	174 (22)	110 (30)	8
	<i>Truncilla macrodon</i>	7 (< 1)	1 (< 1)	-0.7
	<i>Utterbackia imbecillis</i>	3 (< 1)	9 (2)	2
Llano	<i>Cyclonaias pustulosa</i>		1 (12.5)	12.5
	<i>Cyclonaias petrina</i>		1 (12.5)	12.5
	<i>Lampsilis bracteata</i>	13 (100)	5 (62.5)	-37.5
	<i>Tritogonia verrucosa</i>		1 (12.5)	12.5

Table 2.4. Median values of high flow conditions within the four study tributaries over time (Years) calculated from the Indicators of Hydrologic Alteration (IHA) analysis. High pulse count and duration (days) is the median number of high pulse events that occur each year on average. Large flood peak represents the median maximum discharge of large flood events within a river. Rise and fall rates ( $\text{m}^3/\text{s}/\text{d}$ ) represent the median of all positive (rise rate) or negative (fall rate) differences between consecutive daily values within the rivers. See TNC (2007) for further description of variables and IHA analysis methodology.

	<b>Llano River</b>	<b>San Saba River</b>	<b>Concho River</b>	<b>Elm Creek</b>
Years	1940-2017	1917-2017	1916-2017	1932-2017
High pulse count (#)	6.7	7.2	9.5	7
High pulse duration (days)	4	3.5	3	4
Large flood peak ( $\text{m}^3/\text{s}$ )	1,638	712	878	426
Large flood rise rate ( $\text{m}^3/\text{s}/\text{d}$ )	1,415	306	188	240
Large flood fall rate ( $\text{m}^3/\text{s}/\text{d}$ )	-44	-14	-19	-22

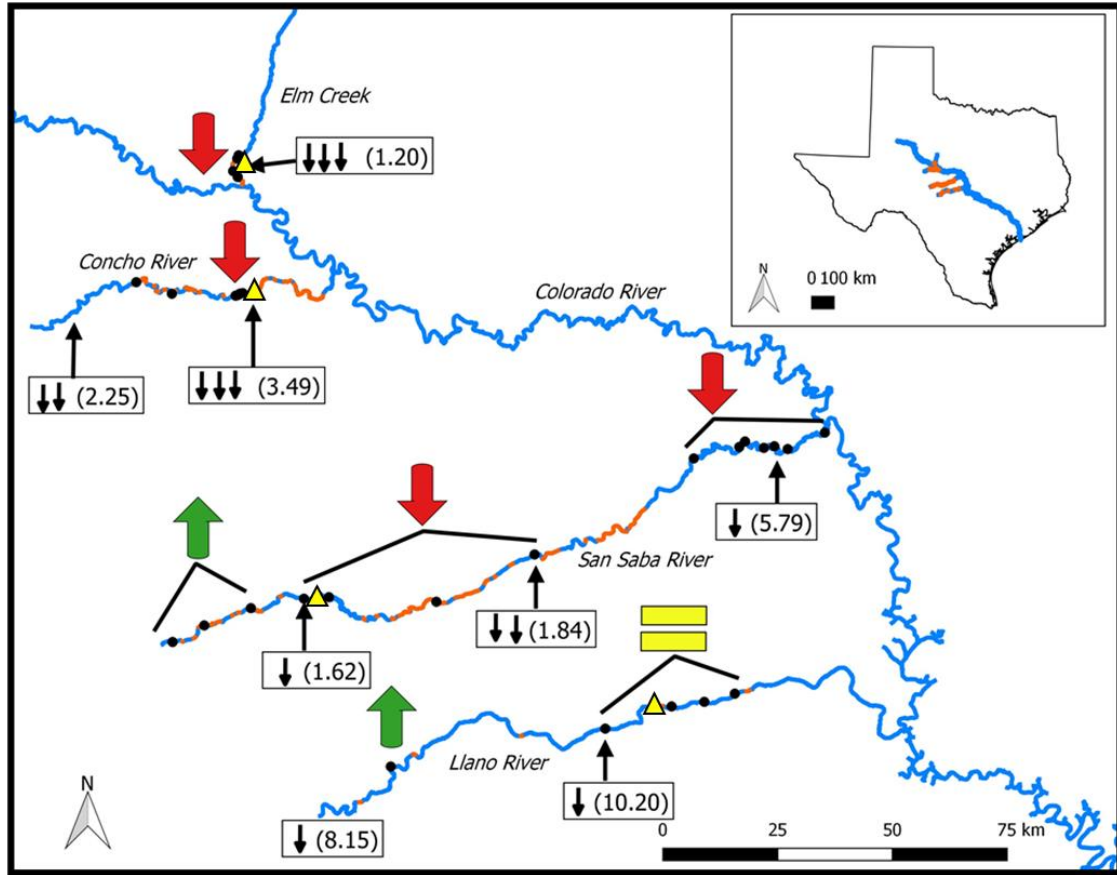


Figure 2.1. Site locations (black dots) for pre- and post-drought surveys in four tributaries of the middle Colorado River basin, Texas. Dry (orange) and wet (blue) segments within the study rivers of the Middle Colorado River basin, Texas using 2012 NAIP imagery. Boxes represent the percent decrease in discharge during 2011(long-term average  $m^3/s$ ) compared to the long-term average obtained from USGS gages within the study rivers. Three, two, and one arrows within boxes represent a decrease in mean discharge during 2011 of >87%, 82-86%, and 77-81%, respectively. Red arrows denote a general decrease in species richness and relative abundance, green arrows denote a general increase in species richness and relative abundance, and the yellow equal sign denotes little to no change at sites (see Figs. 2-5 for more site-specific changes). Yellow triangles denote temperature collection locations within each tributary.

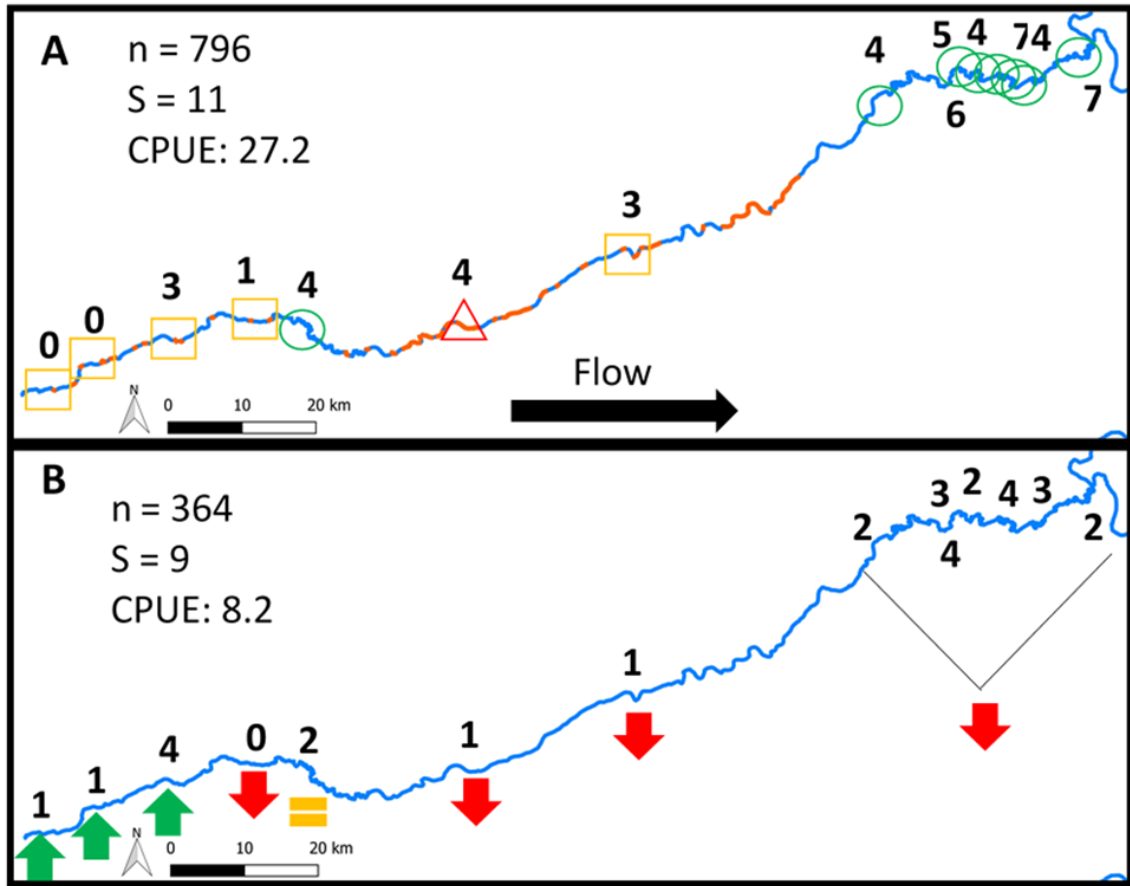


Figure 2.2. Comparison of pre- (A) and post-drought (B) sites within the San Saba River. For both survey periods,  $n$  denotes the total number of individuals sampled between all survey sites,  $S$  represents species richness from all sites combined, and CPUE is the mean relative abundance between sites. The bold numbers by each site represent site specific species richness during pre- and post-drought periods. For the pre-drought survey map (A), red triangles denote sites that dried during the drought, orange squares denote sites that experienced constricted channel flows, and green circles represent sites that retained water during the drought. For the post-drought map (B), red arrows denote a decrease in site specific CPUE over time, orange equal sign denotes no change in CPUE over time, and a green arrow denotes an increase in CPUE over time.

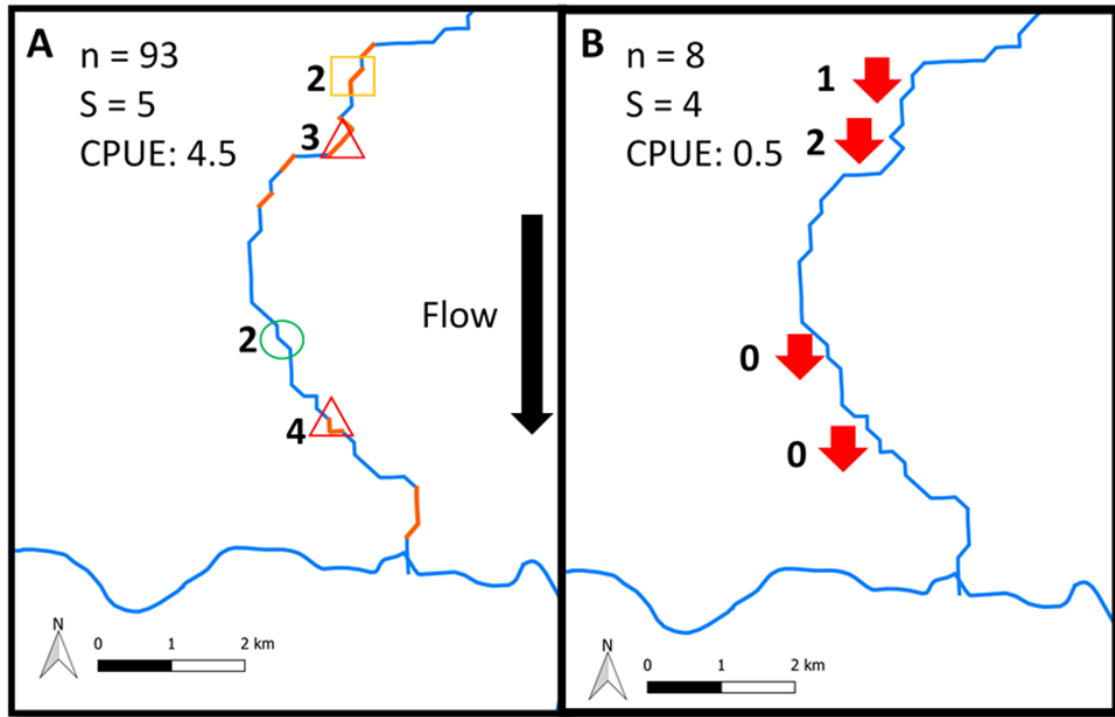


Figure 2.3. Comparison of pre- (A) and post-drought (B) sites within Elm Creek. See Fig. 2.2 for a description of symbols and labels.

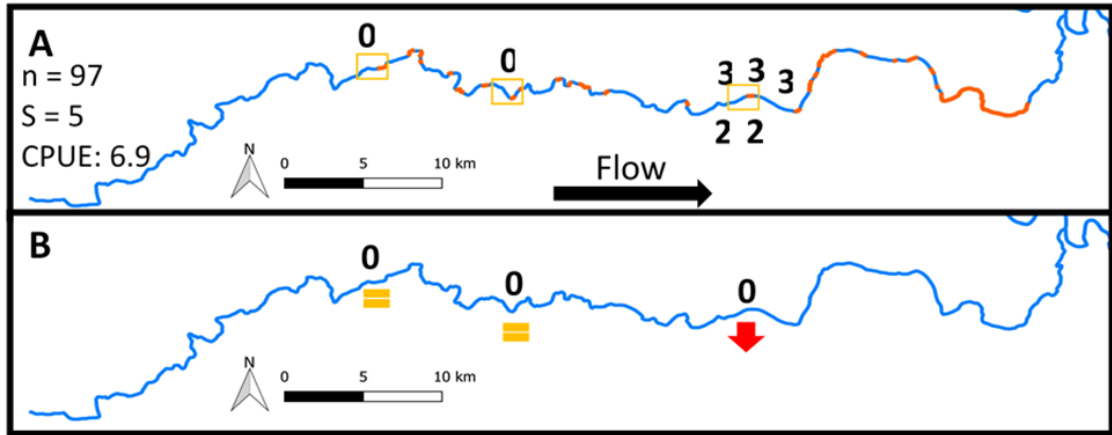


Figure 2.4. Comparison of pre- (A) and post-drought (B) sites within Concho River. See Fig. 2.2 for a description of symbols and labels.

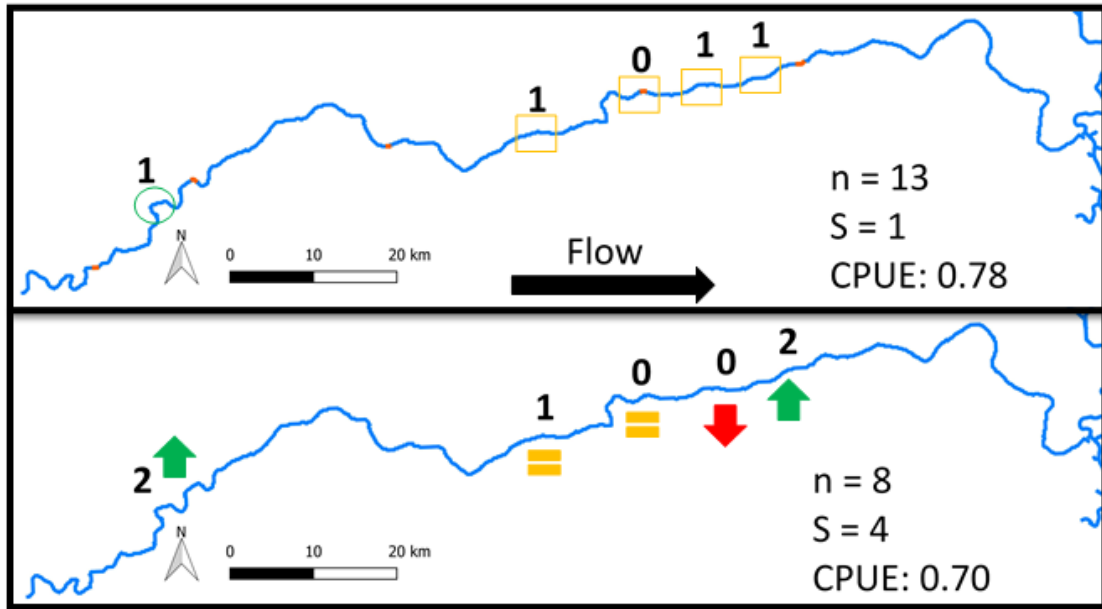


Figure 2.5. Comparison of pre- (A) and post-drought (B) sites within Llano River. See Fig. 2.2 for a description of symbols and labels.

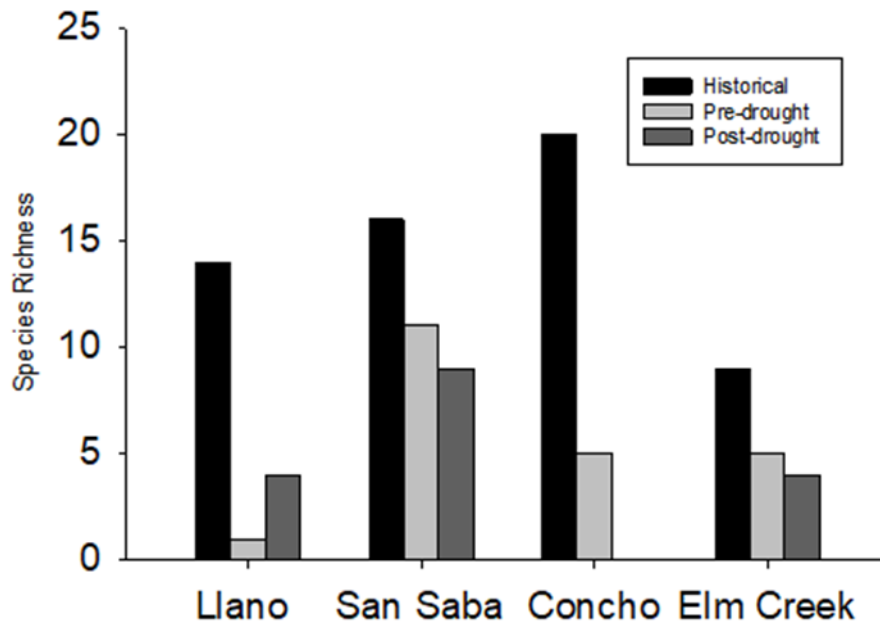


Figure 2.6. Species richness between historical (pre- 2005), pre- (2005-2011) and post-drought (2017) survey periods within study tributaries. See Table A1 for list of species from historical accounts and this study.



### **III. HOW DO THE ROLES OF LIFE HISTORY STRATEGIES AND ENVIRONMENTAL AND SPATIAL FACTORS FOR RIVERINE MUSSEL METACOMMUNITIES CHANGE ACROSS SPATIAL SCALES?**

#### **Abstract**

Examining metacommunity structure and underlying driving factors across multiple spatial scales and including a trait-based approach will help to gain a better understanding of metacommunity organization. This goal is crucial to eventually develop effective conservation strategies, especially for unionid freshwater mussels, which are one of the most imperiled groups of organisms in North America. The purpose of this study was to examine how the role of life history strategies and environmental and spatial factors for the distribution of riverine mussels change across spatial scales (segment and tributary). To gain an understanding of the spatial structuring of mussel metacommunities, we collected spatially extensive distribution data in three 20-km segments (upstream, midstream, and downstream) in the San Saba River, which is a tributary of the Colorado River, Texas. A variety of environmental and spatial variables were collected at each sampling site. A combination of RLQ-fourth corner, asymmetric eigenvector mapping, and variation partitioning analyses were used to model the relative importance of environmental and spatial factors in structuring mussels with different life history strategies. Our results showed that mussels with different life history strategies exhibited patchy and predictable distributional patterns along the longitudinal gradient of the San Saba River. The amount of variation explained by specific environmental and spatial factors in structuring mussels with different life history strategies depended on the

spatial scale (within vs. among segments) and differed between the upstream and downstream segment of the San Saba River. Additionally, our results suggested that mussels in the San Saba River are primarily structured by niche-based processes. Furthermore, our results showed that incorporating a life history strategy-based approach will yield similar patterns and increased community variation explanation compared to a taxonomic level approach.

## **Introduction**

A primary goal in stream ecology is to understand the distribution, abundance, and composition of organisms and communities in riverine environments. Ecological theory has long recognized that the distributions of organisms within streams are usually not random and that communities, subject to various selective forces, usually display various spatial patterns (Vannote et al. 1980; Thorp and Delong 1994; Poff et al. 1997; Leibold et al. 2004; Thorp et al. 2006; Humphries et al. 2014). Over the past two decades, metacommunity theory has been a valuable approach for predicting how local (environmental) and regional (dispersal) factors influence the distribution and community structure of riverine organisms at multiple spatiotemporal scales (Leibold et al. 2004; Brown et al. 2011; Altermatt 2013; Heino 2013; Tonkin et al. 2018a). Most studies conducted in riverine systems have found that local environmental filtering often plays a more important role in structuring communities than dispersal (spatial) processes, however, this may change depending on the specific taxa being considered and their location within the river network (Brown and Swan 2010; Grönroos et al. 2013; Heino et al. 2015; Schmera et al. 2018; Tonkin et al. 2018a). Additionally, incorporating a species

trait-based approach can vastly improve our understanding of metacommunity assembly processes for a wide variety of taxa to better inform conservation efforts (Leibold and Chase 2018).

Despite the benefits of the aforementioned approaches, no studies have wholly implemented a trait-based metacommunity approach to better understand the distribution and structure of freshwater mussel communities, despite their high degree of imperilment throughout the world (Lydeard et al. 2004; Downing et al. 2010; Haag and Williams 2014). Future conservation measures for mussels will benefit from a better understanding of how mussel life-history traits and environmental and spatial factors interact to determine species distributions at different spatial scales (Lopes-Lima et al. 2018; Ferreira-Rodriguez et al. 2019). A multi-scale approach for studying mussel distribution is highly important because factors influencing species abundances and community structures are often hierarchically nested (Allen and Starr 1982; Fausch et al. 2002; Wu 2013).

Historically, most studies investigating the distribution of mussels were conducted at a single spatial scale. For example, studies at the local (e.g. reach) scale (spatial scale  $10^{-1}$ - $10^2$  m) often found that near bed hydraulic variables, substrate type, and substrate stability were important in predicting mussel presence (e.g. Maio and Corkum 1995; Strayer 1999; Gangloff and Feminella 2007; Allen and Vaughn 2010), whereas larger (e.g. regional) scale studies (spatial scale  $10^5$ - $10^6$  m) commonly cite host-fish distributions, underlying geology, land use, and stream or catchment size as primary determinants for mussel presence (e.g. Vaughn 1997; Arbuckle and Downing 2002; McCrae et al. 2004; Poole and Downing 2004; Schwalb et al. 2013). However, there is a

scarcity of information regarding mussel distribution at more intermediate (e.g. segment) spatial scales ( $10^3$ - $10^5$  m), likely because collecting data at these scales is labor and cost intensive (Fausch et al. 2002). Only recently have researchers started to examine the distributional patterns of mussels at intermediate spatial scales (Inoue et al. 2014; Terui et al. 2014, Ries et al. 2016). However, these studies primarily described only the spatial patterns displayed by mussels at intermediate spatial scales and did not explicitly examine the relative importance of various environmental and spatial factors associated with those patterns.

A similar lack of studies exists on how life history traits influence mussel distribution and community structure. Recently, Haag (2012) provided the first conceptual framework (host-habitat continuum concept) to predict where mussel species with different life history strategies may dominate in different types of riverine habitats in response to various selective forces including disturbance frequency, competition (host, food, and space), habitat diversity, and predation (Fig. 3.1). The life history strategies (opportunistic, periodic, equilibrium) developed for this framework are like the CSR triangle theory developed for plants by Grime (1979) and the triangular continuum developed for fishes by Winemiller and Rose (1992). Opportunistic species can be characterized as fast growing with short life spans and moderate to high fecundity, whereas equilibrium strategists are long-lived slow growing species with relatively low fecundity (Table 3.1). Periodic species usually exhibit intermediate life history traits compared to opportunistic and equilibrium species (Table 3.1). Opportunistic species are predicted to have the highest relative abundance in areas of high disturbance such as isolated lentic habitats or in mainstem lentic microhabitats (Fig. 3.1; Haag 2012).

Periodic species are predicted to be more prevalent in small streams compared to other habitat types, whereas the relative abundance of equilibrium species is predicted to increase with stream size and lower disturbance levels (Fig. 3.1; Haag 2012). Although no formal assessment of the predictions from this framework have been conducted to date, a few recent studies have found some preliminary support for the host-habitat continuum concept (Daniel and Brown 2014; Chambers and Woolnough 2018; Hornbach et al. 2019). However, these studies did not provide specific details on the relationship between mussel life history strategies and individual environmental variables or incorporate other potentially important spatial factors to better understand the patterns of mussel metacommunity distributions.

Therefore, the primary objective of this study was to examine the role of life history strategies and environmental and spatial factors in the distribution of mussels along the longitudinal gradient of a semi-arid subtropical river located in central Texas, USA at two spatial scales (i.e. segment and tributary). To address our objective, mussel communities and a variety of environmental and spatial variables were sampled and measured within three 20 km segments (upstream, midstream, downstream) of the San Saba River. Specifically, we addressed the following questions: (1) Do mussel communities exhibit any spatial patterns (e.g. patchy, random, gradient) at intermediate spatial scales within our 20 km study segments? (2) Does the distribution of mussels with different life histories along the river gradient match the predictions of the host-habitat continuum concept proposed by Haag (2012)? (3) How does the relative importance of environmental and spatial factors for the distribution of mussels with different life history strategies change from upstream to downstream and between spatial scales (i.e. within

segments and between segments)? (4) How does incorporating a life-history strategy (functional) based approach compare to a species level (taxonomic) approach in understanding how environmental and spatial factors influence mussel communities at different spatial scales?

For question 1, we predicted that mussels would most likely exhibit a patchy distribution within our study segments, similar to the findings of Ries et al. (2016) who found that mussels, depending on age group, exhibited patchy spatial patterns in three out of four reaches (reach distance from 21-37 km) of the Upper Mississippi River. For question 2, following the prediction of Haag (2012) for small streams (Fig. 3.1), we predicted that the upstream San Saba River will be primarily composed of periodic species followed by opportunistic and equilibrium species, respectively. For the midstream segment, we predicted that the relative abundance of periodic and equilibrium species would be similar to each other and higher than opportunistic species (mid-sized streams, Fig. 3.1). Equilibrium species were expected to have the highest relative abundance in the downstream segment followed by periodic and opportunistic species, respectively (large stream mussel beds, Fig. 3.1). For question 3, following the network position hypothesis (Brown and Swan 2010; Schmera et al. 2018; Henriques-Silva et al. 2019), we predicted that both variation in community composition of mussels and life history strategies would show a stronger correlation with environmental factors in the upstream compared to the downstream segment. Additionally, we predicted that regional environmental variables would exhibit the strongest correlations with mussel life history strategists at the tributary scale. For question 4, we predicted that a functional approach would reveal similar patterns in explained variation of community structure compared to

a taxonomic approach at both spatial scales.

## **Methods**

### **Study Area**

The San Saba River is a spring-fed river located in central Texas (Fig. 3.2). The mainstem of the river forms near Fort McKavett, TX in Menard County and flows east for approximately 225 km until its confluence with the Colorado River. The San Saba River is located within two ecoregions (level-IV). The upper three-quarters of the river is in the Edwards Plateau Woodland ecoregion and the remaining downstream section is in the Western Cross Timbers ecoregion. The up- and midstream mussel survey segments from our study (see below) are located in the Edwards Plateau Woodland ecoregion, whereas the downstream segment is located in the Western Cross Timbers ecoregion. The Edwards Plateau Woodland region supports grasslands and juniper/oak/mesquite savannas in relatively shallow soils underlain by limestone bedrock (Griffith et al. 2007; [tpwd.texas.gov](http://tpwd.texas.gov)). The Western Cross Timbers is a mix of savannah and woodlands on fine sandy loam soils with clay subsoils that retain water (Griffith et al. 2007; [tpwd.texas.gov](http://tpwd.texas.gov)). Land use is primarily characterized as semiarid ranch land in the middle and upper stretches, but more dominated by pecan orchards and row crop operations in the lower stretch. Mean annual precipitation in the San Saba River averages between 60-71 cm, with the upper reaches receiving less precipitation compared to downstream reaches ([twdb.texas.gov](http://twdb.texas.gov)). For the past decade the upper two-thirds of the San Saba River, particularly the midstream segment where several losing reaches are located (Slade et al. 2002), can experience seasonal flow intermittency and even stream bed drying

presumably due to unregulated groundwater pumping and diversions (RPS Espey, 2013; Geeslin et al. 2015).

### **Field Sampling- Mussel communities**

To examine fine-scale distribution of mussels in the San Saba River, spatially extensive surveys were conducted in three different river segments (upstream, midstream, and downstream; Fig. 3.2) during the summer and fall of 2018. Each segment was approximately 20 km in length (60 km total). Within the upstream and downstream segments, two surveyors kayaked downstream and conducted visual and tactile timed searches (0.5-person hours) every 100 m within each 20 km segment, totaling 200 sites per segment (400 sites total). Since the middle segment has been prone to extensive drying over the past decade and mussels are not likely to persist in those areas, only perennial pools (identified using aerial imaging) within the midstream segment were sampled for mussels. A total of 41 sites were sampled in the midstream segment. Each site consisted of a 10 m wide transect that extended from one riverbank to the other. All mussels were identified to species and counted before being placed back into the river at each site. Site coordinates, stream width (m), current velocity (m/s), mesohabitat type (pool, riffle, run), percentage of substrate type (silt, sand, gravel, pebble, cobble, boulder, bedrock), water quality parameters (temperature, dissolved oxygen, conductivity, pH), and percentage of emergent vegetation (0, 0-25, 25-50, >75) were measured at each sampling site (Appendix 3.1).

### **Field sampling- Fish communities**

In order to examine mussel host-fish distributions within our study area, fish communities were sampled using a multiple gear approach at three sites in each segment



where mussels were found during the continuous surveys. Fish collection sites were approximately 5-7 km apart in order to cover the longitudinal extent of each segment. At each site, three mini-fyke nets and one experimental gill net were set over night for approximately 12 hours. The nets were run the following morning and the fish that were captured were identified and counted before being released into the river. Afterwards, fish were sampled using pulsed-DC (60 Hz: 25% duty cycle) backpack electrofishing for one hour. Fish were stored in a live well until electrofishing was completed, identified to species, counted, and then released into the river. Effort was made to sample fish out of all available mesohabitats (i.e. pool, riffle, run) within each site.

### **Remotely Sensed Data**

Land cover data were extracted from the National Land Cover Database (USGS-NLCD 2019) and overlaid onto sample site locations using QGIS 3.12. Land cover data were summarized for each sampling site at three spatial scales including: (1) a reach scale that included a 100 m buffer on each side of the river that extended 1 km upstream, (2) a segment scale that included a 100 m buffer that extended 20 km upstream, and (3) a catchment scale that included land cover data for the entire watershed upstream of each sampling site. However, preliminary analyses showed that land cover variables were highly correlated between scales and thus only reach scale land cover data were used for data analysis (see below). The percentage of land cover data for each sample site were classified into seven categories: open water, developed, forest, shrub, herbaceous, agriculture, and wetlands. Ecoregions (level-IV) were downloaded from the EPA and overlaid onto site locations. Mean annual precipitation data (1981-2010) and the location of active groundwater wells (updated daily) were obtained from the Texas Water

Development Board. The number of groundwater wells within a 10 km buffer was recorded for each sample site.

### **Data Analysis**

Species per unit of effort (SPUE; species/person-hour) and catch per unit of effort (CPUE; mussels/person-hour) were recorded for each site during the survey period. We used a one-way ANOVA followed by a Tukey HSD post hoc test to examine differences in SPUE and CPUE between the three river segments. Normality and homogeneity of variance of the data were tested with the Shapiro–Wilk and Levene test, respectively, and data were  $\log_{10}(x + 1)$  transformed to better meet the assumptions of the analyses. We used permutational multivariate analysis of variance (PERMANOVA) to test for differences in host-fish communities within and between each river segment.

Similar to Ries et al. (2016; 2019), Mantel correlograms, using Moran's *I*, were developed to examine the potential intermediate scale spatial patterns (i.e. random, gradient, or patchy distributions) of freshwater mussel communities within the upstream and downstream segments. A random distribution pattern is identified by consistently low Moran's *I* values that fluctuate near zero regardless of the distance between sites. A gradient pattern is identified by a linear decrease in Moran's *I* values. A patchy distribution is identified by an exponential decline in Moran's *I* with increasing distance between sample sites. The degree of patchiness and the average patch size were estimated from the correlogram if the segment was determined to exhibit a patchy spatial structure. The degree of patchiness was obtained from the nugget (y-intercept) with increased values representing a higher degree of patchiness. The average patch size was estimated to be the distance at which spatial correlation values became nonsignificant. This analysis

was not conducted for the midstream segment due to a low number of sites containing few mussels.

To examine the relationship between mussel life history strategies and local and regional environmental variables, we used a combined RLQ and fourth-corner analysis developed by Dray et al. (2014) in the ‘ade4’ package in Program R (Dray and Dufour 2007; R Core Team 2019). Briefly, RLQ is an ordination method that examines the covariance matrix between species traits (e.g. life history strategies) and environmental factors weighted by species abundances (Doledec 1996), whereas the fourth-corner analysis tests multiple bivariate associations between species traits and environmental variables (Legendre et al. 1997; Dray and Legendre 2008). Three matrices were constructed for this analysis: R (environmental x site), L (species abundance x site), and Q (trait x species). Species traits were their respective life history strategy developed by Haag (2012): periodic, opportunistic, or equilibrium. These genus-level life history strategies were used instead of quantitative life history traits because these data are severely lacking for most mussel species, especially for endemic species in our study area. First, separate ordinations were conducted on each data matrix. We performed a correspondence analysis on the L matrix and a Hill-Smith analysis (Hill and Smith 1976) on the R and Q matrices. The RLQ analysis combined the three previous analyses and developed scores for sites, species, life history strategies, and environmental variables that were used to create an RLQ ordination plot to view the main structure of the data. Subsequently, we applied the fourth-corner analysis using two models (models 2 and 4 with 10,000 permutations; Dray et al. 2014) to evaluate the significance between mussel life history strategies and individual environmental variables. Model 2 tests the null

hypothesis that the distribution of species with fixed traits are not influenced by environmental factors, whereas the null hypothesis for model 4 states that species composition at sites with fixed environmental conditions are not influenced by species traits. The results of these models were combined to evaluate whether relationships between mussel life history strategies and environmental factors were significant (Dray et al. 2014). The false discovery rate was used to adjust P values for multiple testing in the fourth-corner analysis (Benjamini and Hochberg 1995). Significant associations identified by the fourth-corner analysis were overlaid onto the RLQ plot to visualize the associations (Dray et al. 2014). This analysis was conducted independently for the downstream and upstream segments and then again for all three segments combined. The RLQ and fourth corner analysis was not conducted independently for the midstream segment due to low sample size.

One drawback of the previous analysis is that it assumes all sites are independent of each other (i.e. the models do not take spatial dependence into account). This assumption is likely not being met as spatial autocorrelation is very common in ecological datasets (Koenig 1999). Recently, randomization procedures based on Moran's spectral randomization have shown to be useful to better account for spatial autocorrelation within trait-based analyses (Braga et al. 2018). However, this technique is limited to working with quantitative variables and cannot deal with categorical variables which are common in trait-based datasets, including this study. Thus, asymmetric eigenvector map (AEM) analysis was used to model the spatial structure of mussels with different life history strategies within the San Saba River. AEM analysis is a spatial modeling technique that was developed for ecosystems such as rivers, in which

directional physical processes (e.g. water currents) can asymmetrically affect the distribution of organisms (Blanchet et al. 2008a). Asymmetric eigenvectors were calculated using a life history strategy abundance response matrix. Additionally, eigenvectors were calculated using a downstream directional distance matrix accounting for the connectivity between sites. Edges of the connectivity matrix were weighted using water course distance in kilometers between sites. To evaluate spatial patterns at multiple scales, AEM variables were computed independently for the upstream and downstream segments (within segments) and then again for all three river segments combined (between segments). This analysis was not conducted separately for the midstream segment due to low sample size. A forward selection process was used for each set of AEM variables to reduce the number of spatial eigenvectors to predict the variation of community composition of mussels with different life history strategies (Blanchet et al. 2008b).

Variation partitioning based on redundancy analysis was used to determine the relative importance of environmental (identified using the RLQ-fourth corner analysis) and spatial (AEM) variables in explaining variation in community composition of mussels with different life history strategies within and between river segments. Additionally, variation partitioning compared the relative importance between local and regional (i.e. ecoregion, precipitation, and number of groundwater wells) environmental variables (identified by RLQ-fourth corner analysis) in explaining the distribution of mussels with different life history strategies. Prior to variation partitioning, environmental variables that were selected using the RLQ-fourth corner analysis were examined for multicollinearity. Any variable with a variance inflation factor  $> 10$  was

removed. Regional environmental variables and AEM variables were not included in the variation partitioning together because the two sets of variables were almost completely correlated. Furthermore, to evaluate the benefit of using a functional (life-history strategy) approach in explaining the variation in mussel distribution and community structure, we performed the same variation partitioning analyses mentioned above using a taxonomic (species abundance matrix) approach. All statistical analyses were conducted in Program R 3.6.1 (R Core Team 2019).

## **Results**

In total, 1,639 live mussels from 11 species were collected from the San Saba River (Table 3.2). Live mussels were found at 46% ( $n = 204$ ) of the survey sites (Fig. 3.2). The upstream segment contained the highest number of individuals ( $n = 862$ ) representing 9 species, whereas the midstream segment contained the fewest individuals ( $n = 22$ ) representing 4 species (Table 3.2). The downstream segment contained a similar number of individuals to the upstream segment ( $n = 755$ ) comprised of 9 species (Table 3.2). Average SPUE (range) for the upstream, midstream, and downstream segments was 0.92 (0-6), 0.24 (0-2), and 0.9 (0-5), respectively. The upstream and downstream segments had significantly higher average SPUE compared to the midstream segment ( $F_{2,438} = 7.35$ ,  $P < 0.001$ ; Tukey HSD:  $P = 0.001$ ). Mussel CPUE averaged (range) 8.6 (0-94), 1.1 (0-16), and 7.3 (0-96) for the upstream, midstream, and downstream segments, respectively. Mussel CPUE was significantly higher in the upstream and downstream segments compared to the midstream segment ( $F_{2,438} = 8.69$ ,  $P < 0.001$ ; Tukey HSD:  $P < 0.01$ ). There were no significant differences in SPUE or CPUE between the up- and

downstream segments (Tukey HSD:  $P > 0.05$  in both cases).

A total of 1,148 fish from 28 species were sampled within our study segments. All known host-fish species (see Ford and Oliver 2015), that are native to the San Saba River, for mussels that were sampled during the spatially extensive surveys were collected in our study segments. Fish communities were not significantly different within or between river segments (PERMANOVA;  $P > 0.05$  in all cases).

### **Question 1: Intermediate scale spatial patterns**

Following our prediction, mussel communities displayed a clear patchy spatial distribution (measured using nugget as a measure for the degree of patchiness) in the upstream (nugget: 0.11) and downstream (nugget: 0.03) segments indicated by significant positive short-range correlations (Fig. 3.3). The average patch size was 1,364 m and 324 m in the upstream and downstream segments, respectively (Fig. 3.3).

### **Question 2: Longitudinal distribution of mussel with different life history strategies**

As predicted, periodic species (*L. bracteata* and *Cyrtonaias tampicoensis*) had the highest relative abundance (51%) in the upstream segment followed by an opportunistic species (*U. imbecillis*; 34%) and equilibrium (15%) species (Table 3.2; Fig. 3.4A). Periodic and opportunistic species showed very similar distribution patterns in the upstream segment (Fig. 4B). Equilibrium species were primarily located in areas in which no other life history strategists was found (Fig. 3.4B). Unlike our predictions, the midstream segment was dominated by one opportunistic species (*U. imbecillis*, 69%) followed by periodic (22%) and equilibrium (9%) species, respectively (Table 3.2; Fig. 3.4A). The downstream segment was dominated by equilibrium species (e.g. *Cyclonaias petrina*, *C. pustulosa*, and *Tritogonia verrucosa*) as expected, although to a greater

degree, and comprised 96% of individuals (Table 3.2; Fig. 3.4A). Opportunistic and periodic species comprised 3% and 1% of mussel composition, respectively (Table 3.2; Fig. 3.4A). Equilibrium species were found throughout much of the downstream segment (Fig. 3.4D). Conversely, periodic species were located only in the upper section of the downstream segment and opportunistic were primarily found in the lower section of the downstream segment (Fig. 3.4D).

### **Question 3: Role of life history strategies and environmental and spatial factors- Within segments**

As predicted, there was a lower number of significant associations ( $n = 11$ ; Table 3.3; Fig. 3.5) between mussel life history strategies and local environmental variables in the downstream segment compared to the upstream segment ( $n = 22$ ; Table 3.4; Fig. 3.6). Additionally, the strength of association between life history strategies and environmental variables were higher in the upstream segment compared to the downstream segment (Tables 3.3-3.4). Equilibrium species were only associated with riffle mesohabitats in the downstream segment, whereas they were positively associated with riffle and run habitats with diverse substrate sizes (excluding bedrock) in areas with increased agricultural land cover in the upstream segment. In general, periodic species showed opposite environmental associations of equilibrium species within both segments, being found mostly in deeper sites (i.e. pools) with lower current velocities that contained softer (downstream segment) or bedrock (upstream segment) substrates (Tables 3.3-3.4; Figs. 3.5-3.6). Opportunistic species exhibited a relatively low number of associations with local environmental variables in both segments compared to other life history strategists. Opportunistic species were positively associated with riffle habitats in downstream



segment and with pool habitats in areas with increased land development and decreased shrub cover in the upstream segment (Tables 3.3-3.4; Figs. 3.5-3.6).

After forward selection, twenty AEM eigenvectors (Appendix 3.2) explained 84% of the variation of the composition of mussels with different life history strategies in the downstream segment. Three prominent spatial patterns were revealed in the AEM analysis (Fig. 3.7A). First, equilibrium species were found in consistent numbers throughout the downstream segment except for two areas (V4, Appendix 3.4), which had higher abundances of periodic or opportunistic species (Figs. 3.7A, Appendix 3.4). The opportunistic species (*Leptodea fragilis* and *Truncilla macrodon*) were found primarily in the lower section of the downstream segment (V16 and V70) in riffle habitats, whereas the periodic species (*C. tampicoensis*) were only found the upper regions (V72, V39, and V47) of the downstream segment where deeper pools were more prominent (Figs. 3.7A, Appendix 3.4).

A total of 29 AEM variables, of which 7 were notable, were selected in the upstream segment and explained 66% ( $P < 0.001$ ) of the variation of the composition of mussels with different life history strategies (Appendix 3.2; Fig. 3.7B). The distribution of opportunistic individuals was explained by larger spatial patterns (V1 and V2).

*Utterbackia imbecillis* were found in higher abundances in pool habitats throughout much of the upstream segment (Figs. 3.7B, Appendix 3.5). Periodic species exhibited similar distribution patterns compared to opportunistic individuals in the upstream segment (Figs. 3.7B, Appendix 3.5). However, periodic species were in highest relative abundance in one hotspot at the upper end of segment (V83) and at the lower quarter of the upstream segment (V33 and V14; Fig. Appendix 3.5). Equilibrium species were found in two

primary areas of the upper segment (V21 and V67; Fig. 3.7B, Appendix 3.5) in riffle and run habitats. The upper hotspot (V67) was primarily composed of *Tritogonia verrucosa*, whereas the lower hotspot (V21) contained a majority of *Cyclonaias* spp. and *Amblema plicata* (Fig. 3.7B; Appendix 3.5).

As expected, environmental factors (pure effects) explained more of the variation in mussel community composition in the upstream segment (15%,  $P < 0.01$ ) compared to the downstream segment (5%,  $P > 0.05$ ; Fig. 3.9A). However, pure spatial effects explained the largest amount of variation in community structure within both segments (upstream: 39%,  $P < 0.001$ ; downstream: 77%,  $P < 0.001$ ; Fig. 3.9A). The percentage of shared variation between environmental and spatial factors in the upstream and downstream segments was 12% and 2%, respectively (Fig. 3.9A).

### **Q3: Among segments (Upstream, midstream, and downstream)**

A total of 44 significant associations between mussel life history strategies and environmental variables were identified when data from all three river segments were combined (Table 3.5; Fig. 3.8). In general, life history strategists showed similar associations with local environmental variables at the tributary scale (between segments) as they did within segments. Equilibrium species exhibited fewer and contrasting environmental associations compared to opportunistic and periodic species (Table 3.5; Fig. 3.8). As predicted, regional variables (i.e. mean annual precipitation, ecoregion, and number of groundwater wells) had higher strengths of associations compared to most local environmental variables (Table 3.5; Fig. 3.8). The number of groundwater wells in the region had a strong positive association with equilibrium species. Periodic species were positively associated with the Edwards Plateau Woodland ecoregion and negatively

associated with mean annual precipitation, the number of groundwater wells, and the Western Cross Timbers ecoregion (Table 3.5; Fig. 3.8). Opportunistic species exhibited very similar associations to regional variables (except groundwater well numbers) compared to the periodic species, although the strength of the associations was generally lower (Table 3.5; Fig. 3.8).

After forward selection, 50 AEM variables explained 89% of the variation in the composition of mussels with different life history strategies (Appendix 3.2; Fig. 3.7C). However, the spatial structure of mussels was primarily driven by one largescale spatial variable (V1; Figs. 3.7C, Appendix 3.6) that separated the downstream segment from the upstream and midstream segments. The downstream segment was primarily composed of equilibrium species, whereas the upstream and midstream segments contained more periodic and opportunistic species (Fig. 3.7C), a pattern which was also highlighted in figure 3.4.

Spatial and local environmental variables explained more variation (89%,  $P < 0.001$ ) of mussel community composition with all segments combined compared to either segment individually (Fig. 3.9A). A substantial amount of variation (39%,  $P < 0.001$ ) was explained by pure spatial effects. Only a small fraction of the variation (2%,  $P > 0.05$ ) was explained by the pure environmental component. Not surprisingly, environmental variables were largely spatially structured at the tributary scale, accounting for 55% of the variation explained in mussel community composition (Fig. 3.9A). Variation partitioning between local and regional environmental variables (excluding AEM variables) did explain a significant amount of variation (57%;  $P < 0.001$ ) in mussel community composition at the river scale, however it was substantially less compared to

when AEM variables were considered (Fig. 3.9A).

#### **Question 4**

As predicted, the functional (life history strategy) approach revealed similar patterns, albeit at a greater magnitude, in explained variation of mussel community structure compared to the taxonomic (species level) approach at both spatial scales (Figs. 3.9A-B).

### **Discussion**

Our study was the first to combine spatially extensive surveys and a multiscale approach to examine patterns in community structure and life history strategies of freshwater mussels. The amount of variation explained by specific environmental and spatial factors in structuring mussels with different life history strategies depended on the spatial scale (within vs. between segments) and differed between the upstream and downstream segment of the San Saba River. Environmental variables explained significantly more of the variation in life history and species composition in the upstream compared to the downstream segment, however spatial variables explained the highest amount of variation at both spatial scales (within and between segments).

It is well known that mussels can display patchy distributions at both small and large spatial scales (Strayer et al. 2004; Newton et al. 2008; Haag 2012; Ries et al. 2016, 2019). However, few studies have quantified mussel patch sizes and distance between patches. The average patch size documented in this study was similar or smaller compared to average mussel patches in Upper Mississippi River (Ries et al. 2016; 2019). However, unlike our study, Ries et al. (2016; 2019) found that mussels, depending on age

group, were often randomly distributed (25-57% of cases). The increased randomness in mussel distributions documented in Ries et al. (2016; 2019) compared to our study could be due to differences in environmental heterogeneity. Patchy spatial patterns of mussels are most likely to occur in areas with increased environmental heterogeneity (Strayer et al. 2008). Ries et al. (2016; 2019) quantified mussel spatial patterns within navigational pools of the Upper Mississippi River, which are likely more environmentally homogenized (at least at larger scales) compared to our study segments, which contain no significant barriers capable of environmentally homogenizing our entire study segments.

In general, mussels within the upstream and downstream segments followed the predictions of the host-habitat continuum concept developed by Haag (2012). Similar to our results, Chambers and Woolnough (2018) found that equilibrium species (e.g. *Actinonaias*, *Amblema*, *Quadrula*) were proportionately more abundant in the lower portions of two central Michigan rivers, whereas the upper portions were primarily composed of periodic species (e.g. *Lampsilis*, *Lasmigonia*, *Strophitus*). In our study, periodic and opportunistic species were relatively abundant and distributed throughout much of the pools in the upstream segment. Equilibrium species were also found along the gradient of the upstream segment, but they did not dominate like they did in the downstream segment. It is possible, that periodic and opportunistic species dominate in the upstream segment, because they are better adapted to the flashier flow regime (i.e. increased disturbance) of the upstream segment (see below), whereas equilibrium species dominate in the downstream segment, because they may be superior competitors (Haag 2012). However, competition in mussels is not well understood (Strayer 2008; Haag 2012).

Contrary to our prediction, the midstream segment was primarily composed of opportunistic mussels, resembling the patterns predicted for highly disturbed lentic microhabitats and isolated lentic microhabitats (Figs. 3.1 and 3.4). Over the past decade the middle San Saba River has experienced intermittent flow conditions and often expansive streambed drying with isolated pools remaining, especially in locations with dams and groundwater inputs (Slade et al. 2002; RPS Espey 2013; Geeslin et al. 2015; Mitchell et al. 2019). These conditions explain well the high proportion of opportunistic individuals adapted to survive in isolated lentic habitats.

Hydrologic disturbance is known to play a key role in structuring riverine communities (Resh et al. 1988; Poff 1992; Lake 2000). Numerous studies have found that hydrological disturbance in the form of drought (e.g. Golladay et al. 2004; Haag and Warren 2008; Gough et al. 2012; Mitchell et al. 2019) or flood events (e.g. Tucker 1996; Strayer 1999; Hastie et al. 2001; May and Pryor 2016) can have substantial negative impacts on mussel communities. The decreased buffering capacity and the increased percentage of bedrock substrate results in a ‘flashier’ flow regime after rainfall events (e.g. more variable discharge levels, rise and fall rates, and reversals; Appendix 3.3) in the upstream segment compared to downstream. Thus, the flashier flow regime of the up- and midstream segments likely prevent equilibrium species from becoming dominant. Conversely, the softer substrates in the pool habitats in the downstream segment compared to the upstream segment are more likely to get washed out during flood events, thereby limiting the number of periodic and opportunistic species. This claim was supported by a recent translocation study conducted in the San Saba River (Hayes and Schwalb, in prep), in which opportunistic mussels (*U. imbecillis*), from the upstream

segment, that were transplanted to the downstream segment had significantly lower detection rates in downstream pools (40%) compared to upstream pools (100%) after six months, although no major flooding occurred during that period. Additionally, over the course of a year, an equilibrium species (*C. pustulosa*) had relatively high detection rates in downstream riffles (47-87%) compared to upstream riffles (20-50%) after larger flooding events.

In addition to environmental filtering, dispersal plays a major role in structuring metacommunities (Leibold and Chase 2018; Tonkin et al. 2018b). Significant spatial signals (pure effects) are often interpreted as species having either high levels of dispersal or being dispersal limited. For example, in our study, the same equilibrium species were found within the downstream and upstream segments, suggesting that they have efficient or high levels of dispersal to colonize areas throughout the San Saba River. Interestingly, a study on mussel metacommunity structure in Ontario found that the majority mussels classified as equilibrium and opportunistic species had presumably higher dispersal capabilities via their host fish compared to periodic species (Schwalb et al. 2015). It is likely that equilibrium species have high dispersal capabilities due to the high movement ability (lengths > 100 km) of their primary host fish group (Ictalurids; e.g. Dames et al. 1989; Fago 1999; Vokoun and Rabeni 2005). Conversely, with the exception of *C. tampicoensis*, different opportunistic and periodic species were found in the upstream and downstream segments, suggesting that some species may be either dispersal limited or habitat specialists adapted to more spring influenced reaches (upstream) or less flashy flow regimes (downstream). Absence of certain periodic and opportunistic species in both segments caused by dispersal limitation is unlikely because their host-fish species

(primarily Centrachidae and Sciaenidae) were widespread and abundant throughout the San Saba River and many species within these families are capable of movements from 15 to 161 km (e.g. Funk 1955; Gatz and Adams 1994; Richardson-Heft et al. 2000). Studies have often found weak relationships between host fish and mussel distributions at smaller spatial scales (Watters 1992; Lyons et al. 2007; Krebs et al. 2010; Cao et al. 2013; Daniel and Brown 2013). However, host fish distributions have been shown to be an important predictor of mussel distributions at larger spatial scales (Watters 1992; Vaughn and Taylor 2000; Burlakova et al. 2011; Schwalb et al. 2013; Daniel et al. 2018; Dascher et al. 2018). Genetic studies can be useful for examining dispersal limitations in mussels. For example, a population of *L. bracteata* (periodic species) in the San Saba River was found to be genetically different from a population in the Llano River, which is another tributary of the Colorado River (Inoue et al. 2020). Therefore, dispersal limitation for mussels likely plays a role at spatial scales larger than examined in our study (e.g. between sub-basins and basin).

At the tributary scale (between segments), most of the variation in mussel community structure was explained by pure spatial effects, which could reflect underlying environmental differences that were either unmeasured or that were better captured by AEM variables (Peres-Neto and Legendre 2010; Diniz et al. 2012; Leibold and Chase 2018). Thus, our results likely underestimated the role of environmental filtering in structuring mussels with different life history strategies in the San Saba River. For example, at the tributary scale, the primary spatial pattern that separated the up- and midstream segments from the downstream segment coincides with different ecoregions that have different flow regimes and underlying geologies that are likely structuring



mussel communities (see above). However, the short time span in which data were collected in our spatially extensive surveys could not accurately capture the temporal hydrologic variability between our study segments.

Our study showed that patterns at the taxonomic and functional level responded similarly to changes in environmental and spatial factors. However, there was a much greater amount of unexplained variation at the taxonomic level compared to the functional level, regardless of segment location or spatial scale. At least part of the higher amount of unexplained variation of community composition compared to life history strategies could be due to stochasticity. Especially between nearby patches with little or no environmental heterogeneity or differences in community composition will be largely the result of stochasticity of recruitment and demographic events (e.g., Chase 2007, 2010). However, studies that have critically evaluated the role of stochastic community assembly and ecological drift are very rare (e.g. Shinen and Navarrete 2014; Siepielski et al. 2010), and to the best of our knowledge none have been conducted on freshwater mussels. The differences in functionally distinct groups (e.g. mussel life history strategists) are more likely to be largely driven by deterministic and niche- and dispersal-based processes, whereas species composition is the results of niche, dispersal, and stochastic based processes.

We recognize limitations in our study. Our classification of life history strategies for mussels collected in the San Saba River were based on Haag's (2012) broad genus-level classification, existing literature, and our own opinion, which aggregates the variety of life history strategies into three distinct life history groups. Because mussel life history traits can vary largely (between and within species and populations), it is important for

future studies to quantify specific life history traits (e.g. life span, fecundity, growth) of species within study systems to properly assign mussels to a life history strategy (Haag 2012). Our search time at each site likely did not allow to detect all rare species occurring there, which would most likely require a much higher search effort per site (Metcalf-Smith et al. 2000; Strayer and Smith 2003). However, the sampling design allowed us to track major changes in community composition, because those were detected by changes in the more abundant species. It is also important to note that each site was not considered one local community, but rather a subset of a local community. Hence several neighboring sites can be seen as a stratified sample of the same community since sampling occurred every 100 m and the average patch size was 324 and 1,364 m in the down- and upstream segments, respectively. In addition, the species richness and abundances found at our survey sites were comparable with a recent study in the San Saba River (Mitchell et al. 2019), which used considerably longer search times.

Spatially extensive surveys at the functional level allowed for a better understanding of how environmental and spatial variables interact to structure mussel communities within a river at multiple spatial scales. The techniques employed in this study can also be used to highlight mussel ‘hotspots’ that need protection, locate appropriate sites for mussel relocation projects, and to prioritize stream reaches for restoration projects. Moving forward, researchers should focus on more manipulative and controlled experiments (e.g. mussel translocation studies) to better tease apart the relative importance of environmental filtering, dispersal, and other neutral processes (i.e. ecological drift) in structuring mussel communities. Future studies should also examine how disturbance events shape the distribution of mussels with different life history

strategies at multiple spatial and temporal scales.

Table 3.1. Freshwater mussel life history strategies and their associated traits as proposed by Haag 2012 (see Table 6.3 in Haag 2012).

Traits	Opportunistic	Periodic	Equilibrium
Life span (years)	low ( $\leq 10$ )	moderate (8-30)	high ( $>25$ )
Age at maturity (years)	low (0-2)	low-moderate (1-3)	high ( $>3$ )
Fecundity	moderate-high	low-moderate (1-3)	variable; typically low, but broadcasters high
Max. adult size (mm)	moderate-large	small-moderate	moderate-large
Brooding strategy	long-term or multicyclic	mostly long-term	mostly short-term
Growth rate ( $K$ )	high	moderate-high	low-moderate

Table 3.2. The number of mussels with different life history strategies collected in different segments of the San Saba River.

Species	Segment			
	Downstream	Midstream	Upstream	Total
Periodic				
<i>Cyrtonaias tampicoensis</i>	11	0	104	115
<i>Lampsilis bracteata</i>	0	5	328	333
Opportunistic				
<i>Leptodea fragilis</i>	21	0	0	21
<i>Truncilla macrodon</i>	2	0	0	2
<i>Utterbackia imbecillis</i>	0	15	301	316
Equilibrium				
<i>Amblema plicata</i>	13	0	48	61
<i>Cyclonaias petrina</i>	347	1	13	361
<i>Cyclonaias pustulosa</i>	137	0	9	146
<i>Fusconaia mitchelli</i>	1	0	2	3
<i>Quadrula apiculata</i>	7	0	20	27
<i>Tritogonia verrucosa</i>	216	1	37	254
Total	755	22	862	1639

Table 3.3. Results from the fourth-corner analysis for the downstream segment of the San Saba River. Significant positive and negative associations are represented as red and blue squares, respectively. Nonsignificant associations are denoted by gray boxes. Significance of qualitative associations, derived from pseudo-F values, are represented by \* ( $P < 0.05$ ), \*\* ( $P < 0.01$ ), or \*\*\* ( $P < 0.001$ ). The strength of quantitative associations, derived from Pearson's  $r$ , are represented by + ( $r$ : 0-0.25), ++ ( $r$ : 0.26-0.50), +++ ( $r$ : 0.51-0.75), ++++ ( $r > 0.75$ ). Different categories of variables include mesohabitat (Meso), instream microhabitat features, and local landcover (LC). Codes for environmental variables are explained in Appendix 3.1.

LHS	Meso		Microhabitat features						LC
	rif	run	cv	dep	sil	san	grv	peb	for
Eq	**								
Op	*	*							
Per	**		+	+	+	+	+	+	+

Table 3.4. Results from the fourth-corner analysis for the upstream segment of the San Saba River. Significant positive and negative associations are represented as red and blue squares, respectively. Nonsignificant associations are denoted by gray boxes. Significance of qualitative associations, derived from pseudo-F values, are represented by \* ( $P < 0.05$ ), \*\* ( $P < 0.01$ ), or \*\*\* ( $P < 0.001$ ). The strength of quantitative associations, derived from Pearson's  $r$ , are represented by + ( $r$ : 0-0.25), ++ ( $r$ : 0.26-0.50), +++ ( $r$ : 0.51-0.75), ++++ ( $r > 0.75$ ). Different categories of variables include mesohabitat (Meso), instream microhabitat features, and local landcover (LC). Codes for environmental variables are explained in Appendix 3.1.

LHS	Meso			Microhabitat features						LC		
	pol	rif	run	cv	san	grv	peb	cob	bed	agr	dev	shb
Eq	***	**	*	++	++	+++	++	++	+++	++		
Op	**										+	+
Per	***	***	**	++	++	+++	++	++	+++			

Table 3.5. Results from the fourth-corner analysis for the San Saba River (all segments combined). Significant positive and negative associations are represented as red and blue squares, respectively. Nonsignificant associations are denoted by gray boxes. Significance of qualitative associations, derived from pseudo-F values, are represented by \* ( $P < 0.05$ ), \*\* ( $P < 0.01$ ), or \*\*\* ( $P < 0.001$ ). The strength of quantitative associations, derived from Pearson's  $r$ , are represented by + ( $r$ : 0-0.25), ++ ( $r$ : 0.26-0.50), +++ ( $r$ : 0.51-0.75), ++++ ( $r > 0.75$ ). Different categories of variables include mesohabitat (Meso), instream microhabitat features, and local landcover (LC). Codes for environmental variables are explained in Appendix 3.1.

LH	Meso			Microhabitat features										LC			Reg				
S	pol	ri f	ru n	cv	wid	co n	de p	sil	san	grv	peb	co b	be d	veg	agr	de v	shb	prec	wel	ep w	wct
Eq	** *	* *	** **								+	+	++						++ +		
	**			+	++	+	++	+		++	++	+	++	+	+	+	++	+++		***	** *
Per	**	* *	** **	++ +	++ +		++ +	+	++	++	+	++	++	+	+++	++	++	+++ +	++ +	***	** *



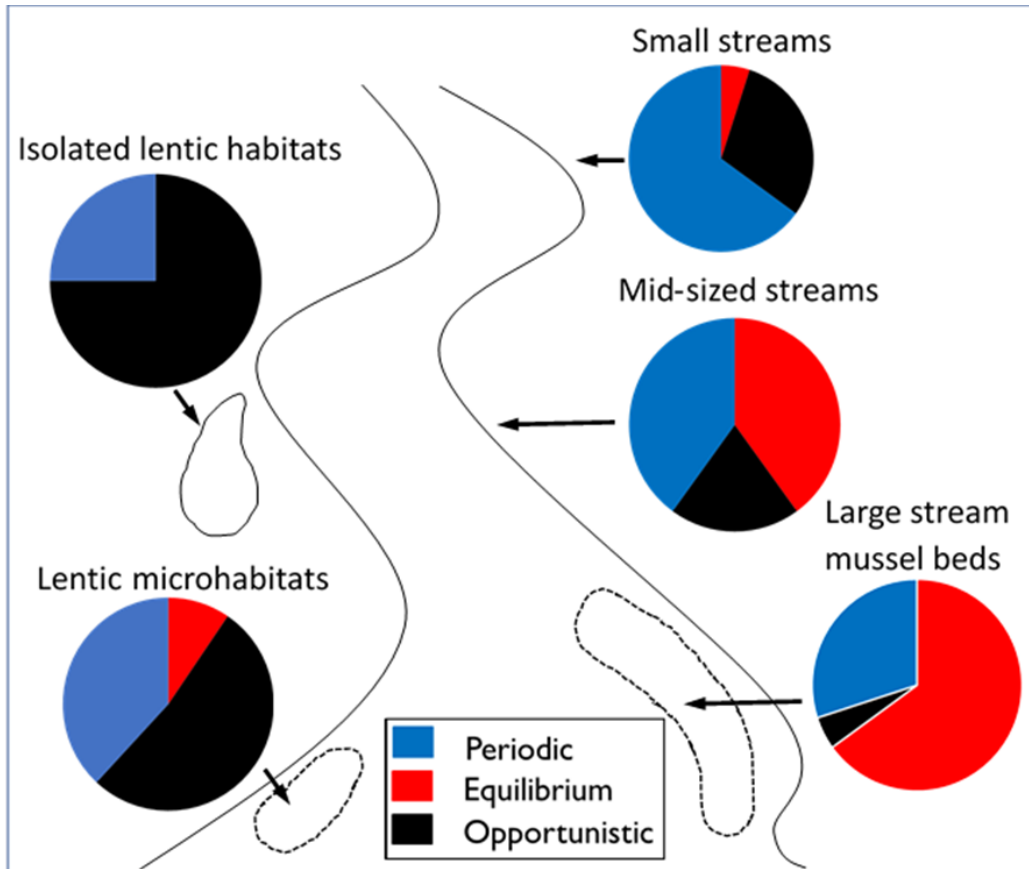


Figure 3.1. Predicted percentages of freshwater mussel life history strategists within different riverine habitats. Adapted from the host habitat continuum concept developed by Haag 2012 (see chapter 8; fig. 8.16 for more details; used with permission).

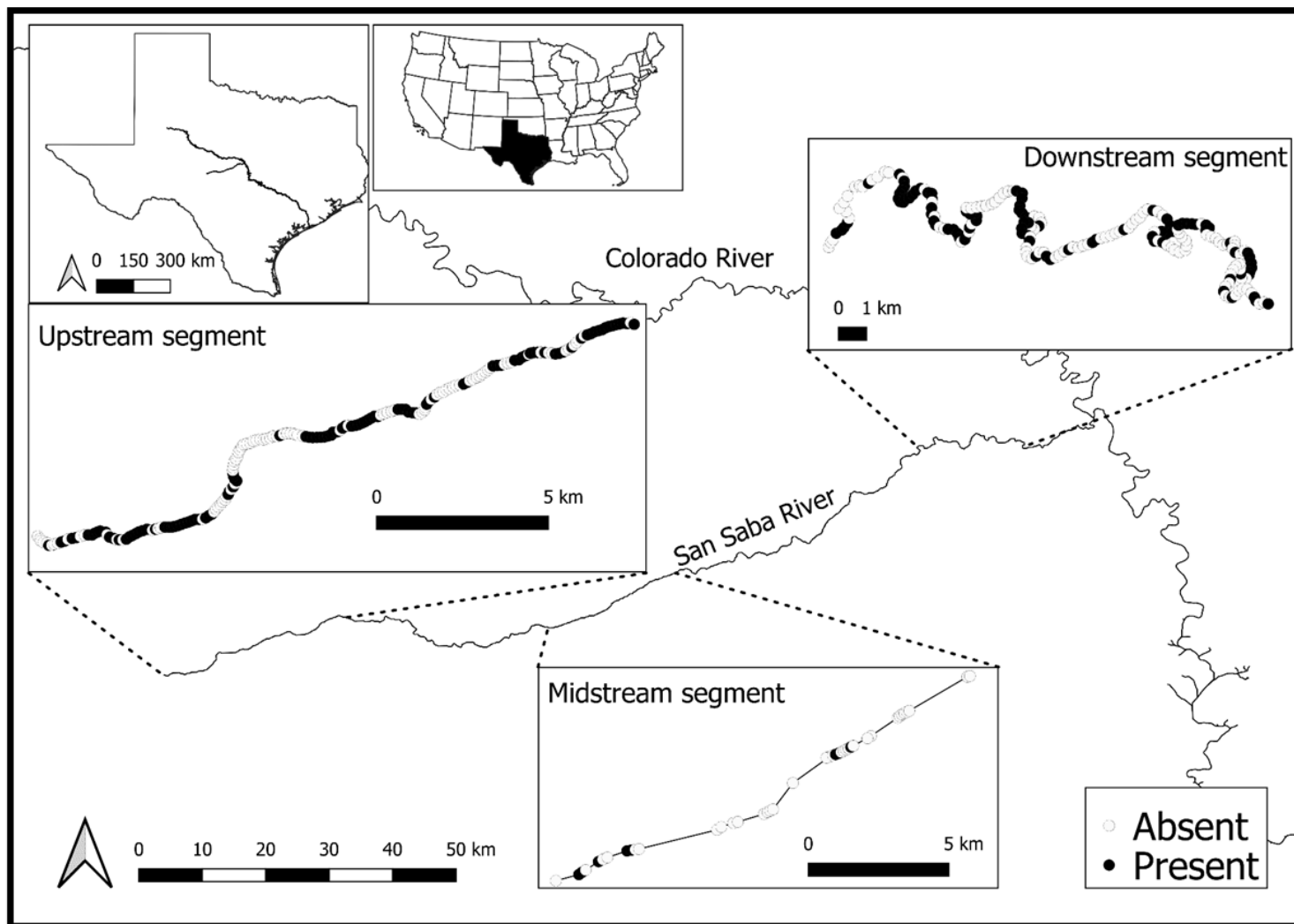


Figure 3.2. Segment locations within the San Saba River. Dots denote presence and absence of mussels at sample sites within segment.

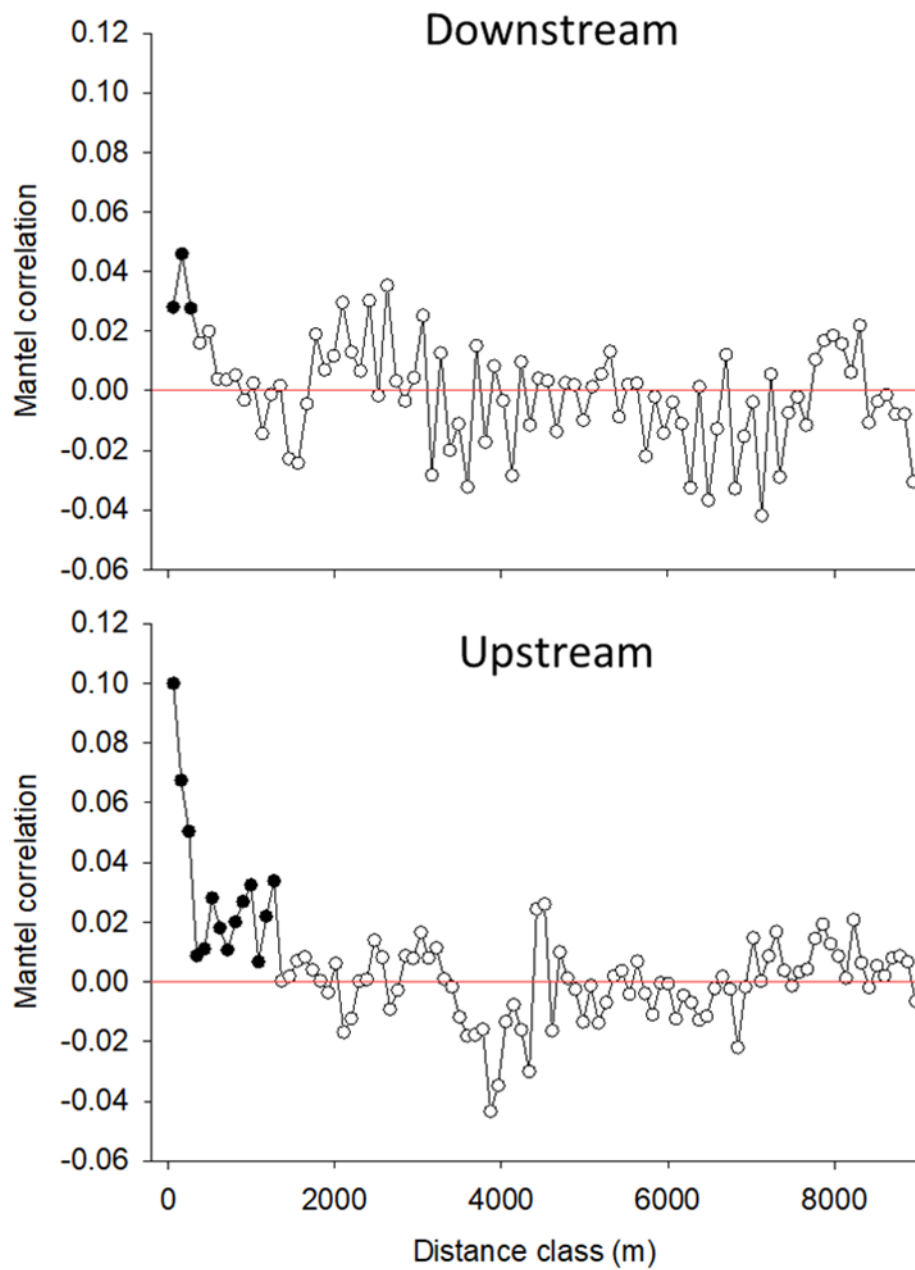


Figure 3.3. Mantel correlograms for the lower and upper segments of the San Saba River. Black and white squares represent significant and nonsignificant autocorrelation values, respectively.

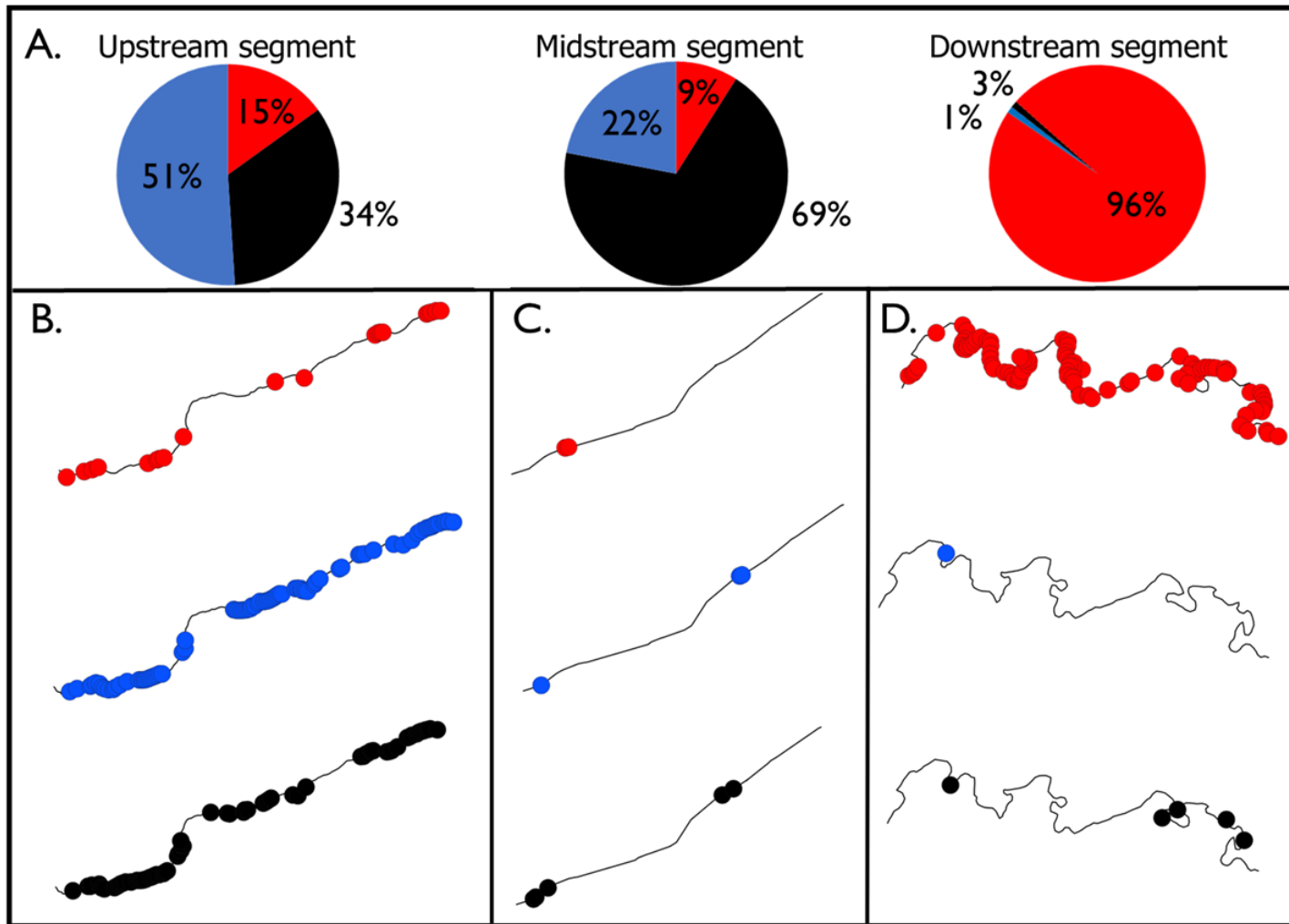


Figure 3.4. Observed percentages of freshwater mussel life history strategists in the upstream, midstream, and downstream San Saba River (A). Range maps for mussels with different life history strategies in the upstream (B), midstream (C), and downstream (D) San Saba River. Periodic, equilibrium, and opportunistic species are denoted by blue, red, and black dots, respectively.

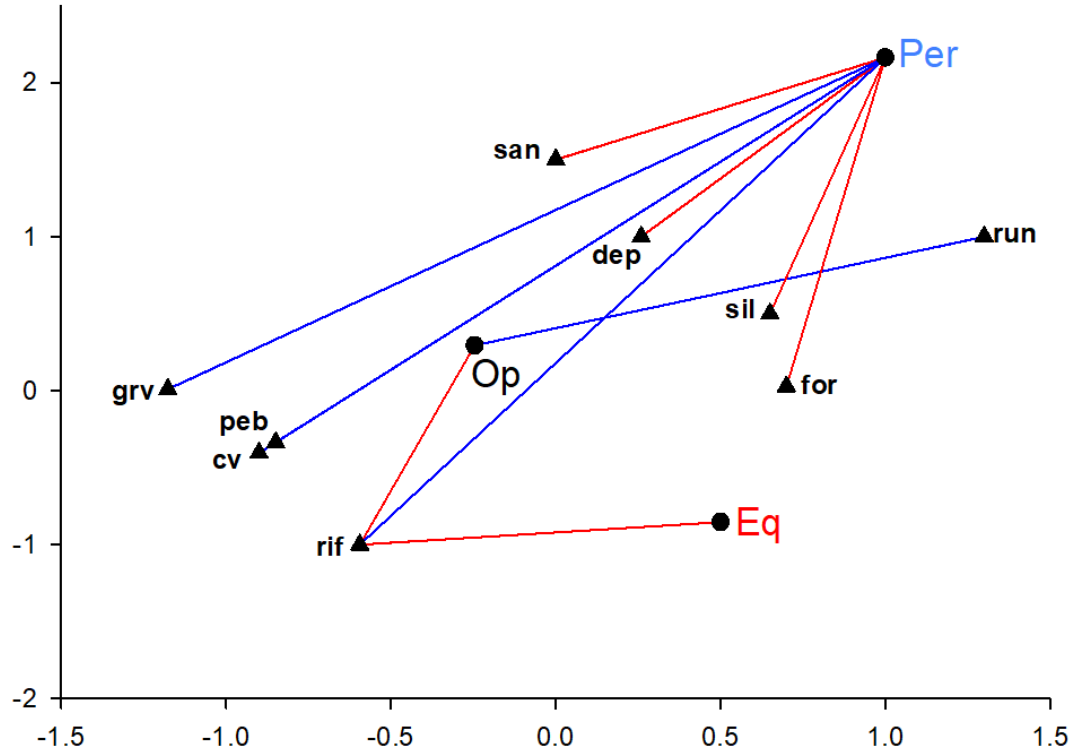


Figure 3.5. Significant associations, identified by the fourth-corner analysis and overlaid on the RLQ map, between life history strategies and environmental variables in the downstream segment of the San Saba River. Positive and negative associations are represented by red and blue lines, respectively. Only significant associations are shown. Environmental features are denoted by triangles and life history strategies are denoted by circles. Life history strategies include periodic (Per), equilibrium (Eq), and opportunistic (Op). Environmental variables are as follows: riffle habitat (rif), run habitat (run), water depth (dep), % silt (sil), % sand (san), % gravel (grv), % pebble (peb), current velocity (cv), % forest land cover (for), see Appendix 3.1.

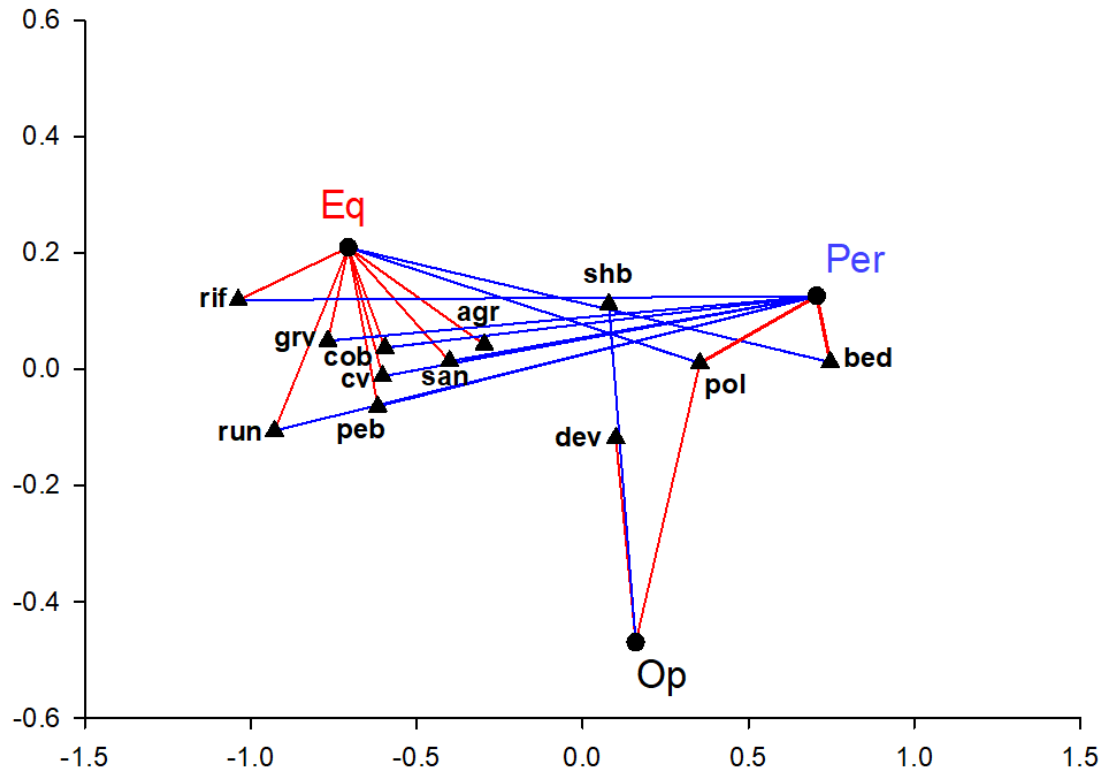


Figure 3.6. Significant associations, identified by the fourth-corner analysis and overlaid on the RLQ map, between life history strategies and environmental variables in the upstream segment of the San Saba River. Positive and negative associations are represented by red and blue lines, respectively. Only significant associations are shown. Environmental features are denoted by triangles and life history strategies are denoted by circles. Life history strategies include periodic (**Per**), equilibrium (**Eq**), and opportunistic (**Op**). Environmental variables are as follows: pool habitat (pol), riffle habitat (rif), run habitat (run), % sand (san), % gravel (grv), % pebble (peb), % cobble (cob), % bedrock (bed), current velocity (cv), % agricultural land cover (agr), % shrub land cover (shb), % developed land cover (dev), see Appendix 3.1.

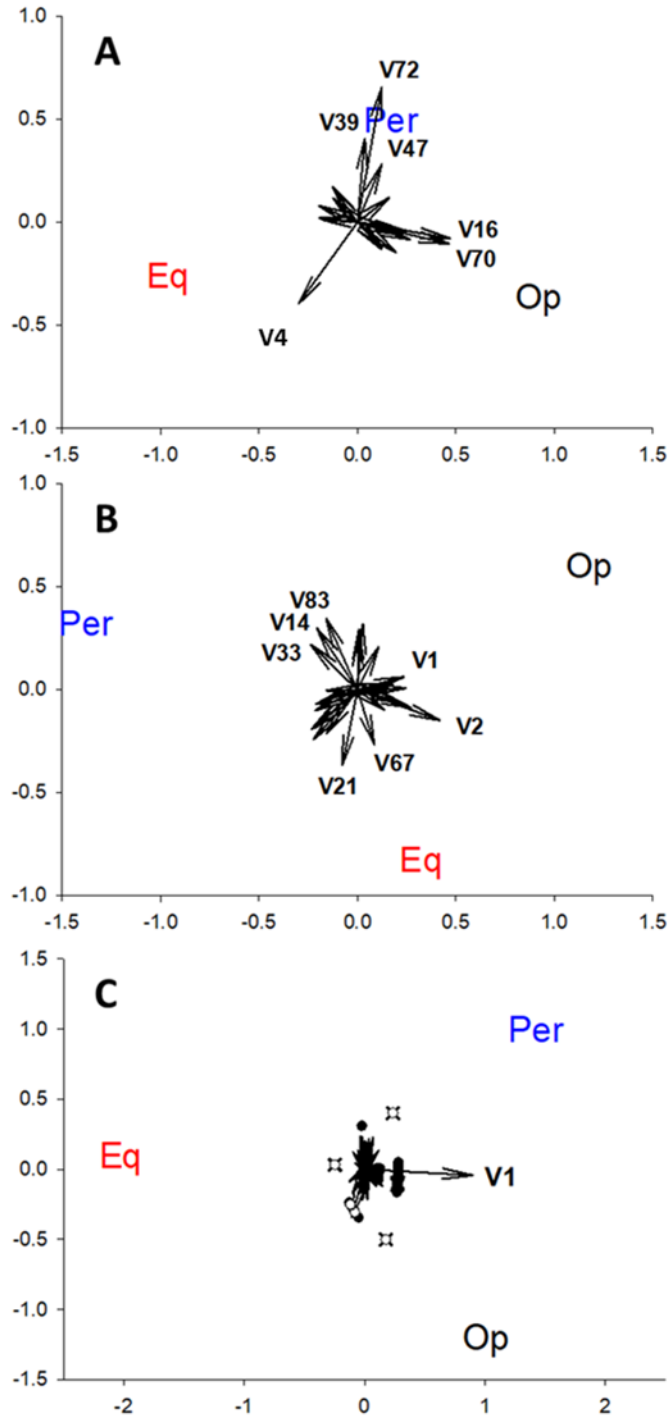


Figure 3.7. Redundancy analysis biplots for the downstream (A), upstream (B), and combined (C) segments of the San Saba River using life history abundance data. The arrows indicate significant AEM variables. Sites in panel “C” are as follows: black dots denote the upstream sites and white dots for the downstream sites, whereas the midstream segment sites are denoted by x. Life history strategies include periodic (Per), equilibrium (Eq), and opportunistic (Op). See Appendix 3.2 for a complete list of significant AEM variables within each segment.

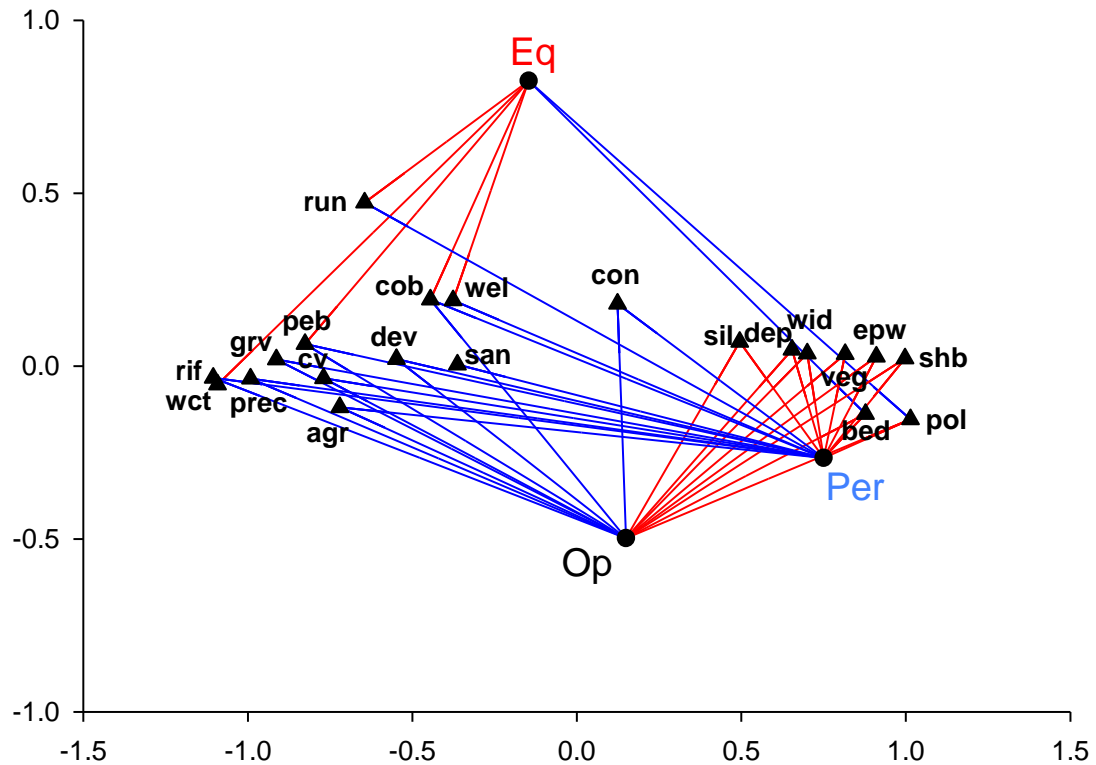


Figure 3.8. Significant associations, identified by the fourth-corner analysis and overlaid on the RLQ map, between life history strategies and environmental variables in the San Saba River (all segments combined). Positive and negative associations are represented by red and blue lines, respectively. Only significant associations are shown. Environmental features are denoted by triangles and life history strategies are denoted by circles. Life history strategies include periodic (**Per**), equilibrium (**Eq**), and opportunistic (**Op**). Environmental variables are as follows: pool habitat (pol), riffle habitat (rif), run habitat (run), water depth (dep), stream width (wid), water conductivity (con), % silt (sil), % sand (san), % gravel (grv), % pebble (peb), % cobble (cob), % bedrock (bed), % emergent vegetation (veg), current velocity (cv), % agricultural land cover (agr), % shrub land cover (shb), % developed land cover (dev), number of groundwater wells (wel), mean annual precipitation (prec), Edwards Plateau Woodland Ecoregion (epw), Western Cross Timbers (wct), see Appendix 3.1.



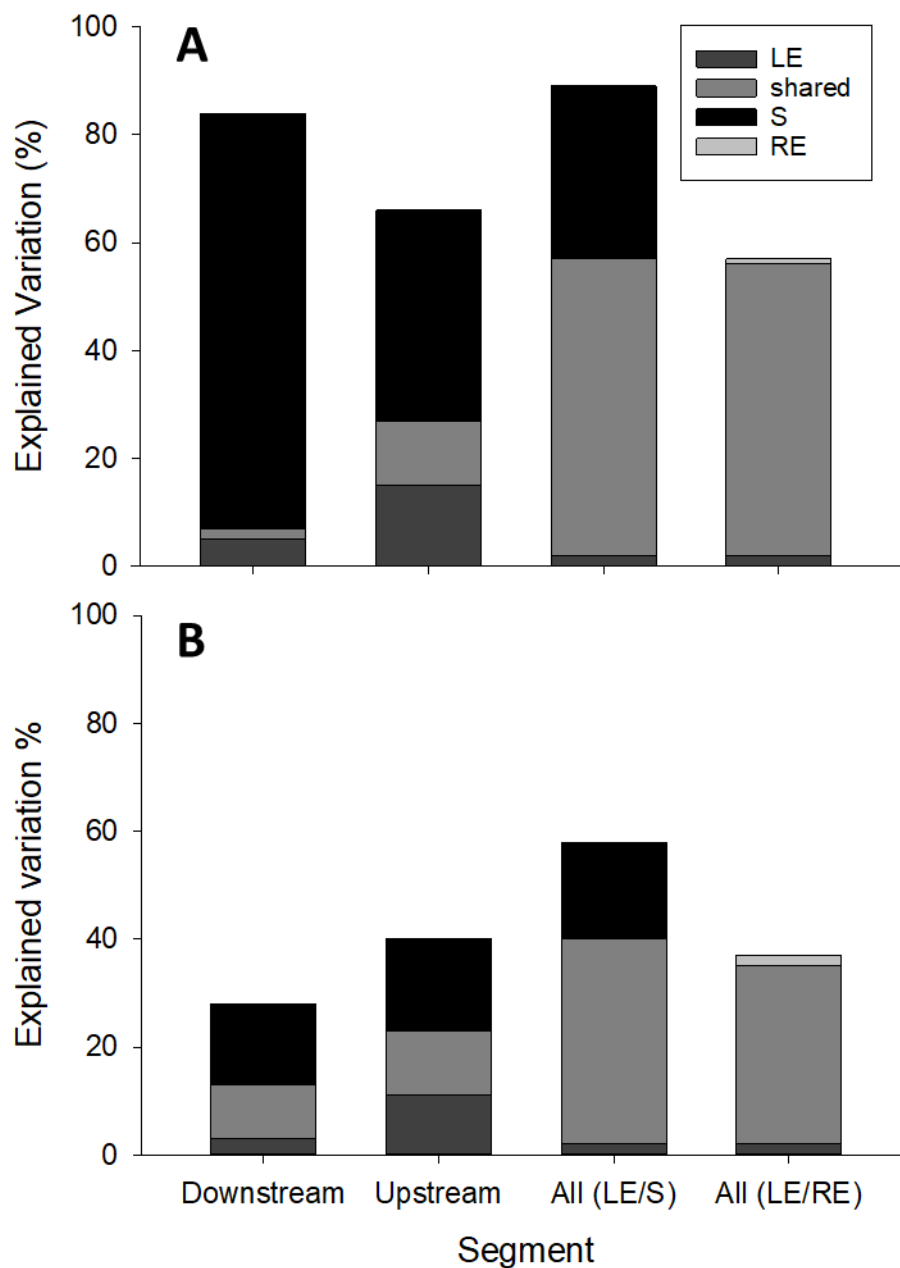


Figure 3.9. A) Percentage of variation in life history assemblages explained by local (LE) and regional (RE) environmental variables identified by the RLQ-fourth corner analysis, selected AEM variables (S), and their total shared variation (shared), B) Percentage of variation in species community composition explained by local (LE) and regional (RE) environmental variables identified by RDA following forward selection, selected AEM variables (S), and their total shared variation (shared).

#### **IV. CONCLUSION: THE ROLE OF LIFE HISTORY STRATEGIES AND DRYING EVENTS FOR MUSSEL COMMUNITIES AT MULTIPLE SPATIOTEMPORAL SCALES**

Metacommunity theory provides a useful framework to evaluate the relative importance of niche- and neutral-based processes in structuring ecological communities at multiple spatiotemporal scales (Leibold et al. 2004; Leibold and Chase 2018). Additionally, using a trait-based approach can help better understand the underlying mechanisms of metacommunity structure (Leibold and Chase 2018). Haag (2012) proposed this with his host-habitat continuum concept (HHC) that predicted that freshwater mussels with different life history strategies would dominate in different types of riverine habitats in response to various selective forces such as disturbance.

It is well established that hydrological disturbances (e.g. drought and floods) can have substantial impacts on aquatic community structure (Resh et al. 1988; Poff 1992; Lake 2000; Rolls et al. 2018). Although several studies have examined the impact of drying events on mussels (e.g. Holland 1991; Byrne and McMahon 1994; Bartsch et al. 2000; Gagnon et al. 2004; Golladay et al. 2004; Haag and Warren 2008; Sousa et al. 2018), most of them did not relate mussel responses to drought or dewatering events to differences in mussel life history strategies (but see Gough et al. 2012) and only focused on lab experiments to examine desiccation tolerances of mussels or on local site specific changes after a drought event. In general, there is a need for more studies with a multi-scale approach, because structuring forces are usually strongly scale dependent and driving factors may change across scales (Fausch et al. 2002). This research combined laboratory and field studies at multiple scales to examine whether variation in responses

(e.g., individual behavioral responses, changes in community composition) and patterns (e.g., spatial distribution) between species could be explained with differences in life history strategies.

To briefly recap the chapters, Chapter 1 focused on the smallest temporal (hours to days) scale (Fig. 4.1). It was the first study to examine the connection between life history strategies and the individual responses of unionid freshwater mussels, that usually occur in perennial streams, to drying events and proposed a life history-based framework for responses of mussels to drying events. Chapter 2 assessed long-term changes (decade), in mussel community structure across multiple tributaries after a severe drought event (Fig. 4.1). Chapter 2 showed that mussels severely declined in the Colorado River basin, Texas, post-drought, but the severity seemed to depend on conditions in each tributary, with the most severe declines occurring in tributaries with the lowest discharge and highest estimated water temperatures. Chapter 3 was the first study to combine spatially extensive surveys in the San Saba River and a life history approach to examine the factors driving the distribution of mussels at two spatial scales, within and between river segments (Fig. 4.1). The results showed that mussels with different life history strategies exhibited patchy and predictable distributional patterns and suggested the importance of environmental control including disturbances (drying and flooding).

The objectives of this chapter are 1) to examine the effectiveness of using life history strategies to explain responses (e.g., behavioral response to dewatering) and patterns (e.g., spatial distribution) in rivers subject to drought and dewatering; 2) to summarize how my study at a smaller scale (Ch. 1) informed the predictions and findings of the larger scale studies (Ch. 2 and 3); 3) to explore if relationships between mussel life

history strategies and mussel distributions observed within a tributary may scale up to larger spatial scales; 4) to propose that spatial patterns in the distribution of mussels with different life history strategies are primarily structured along gradients of hydrological disturbance and habitat heterogeneity; 5) to discuss the potential management applications of the results and relevance for metacommunity ecology; and 6) to identify future research needs.

The usefulness of life history strategies in explaining responses (e.g., behavioral response to dewatering) and patterns (e.g., spatial distribution) in rivers subject to drought and dewatering events was dependent upon the spatial and temporal scale of the study (Fig. 4.1). In addition, results of one chapter informed the predictions and interpretation of the findings of the others to better understand the factors that structure mussel communities. Life history strategies were a useful predictor for local short-term individual responses to drying events, at least in controlled environments (Ch. 1; Fig. 4.1). The life history-based framework for responses of mussels to drying events predicted that opportunistic species would have the lowest desiccation tolerance but would be able to recolonize previously dried habitats quicker compared to the other life history strategists. Equilibrium species were predicted to have the highest desiccation tolerance, but lowest mobility. Periodic species were predicted to have a lower desiccation tolerance compared to equilibrium species and the lowest recolonization potential into previously dried areas (Ch. 1).

Based on the framework developed in chapter 1, different long-term changes after a severe drought were predicted for mussels with different life history strategies (Ch. 2). Opportunistic species were predicted to experience little change in their relative

abundance since they would experience high mortality rates but would recover quickly with high recolonization rates. Periodic species were predicted to experience a higher decrease in relative abundance after a severe drought event compared to equilibrium species due to their lower desiccation tolerance and low recolonization potential. Equilibrium species were predicted to increase in relative abundance because of their higher desiccation tolerance. However, only partial support was found for life history strategies being useful predictors of long-term local changes in mussel community structure after a severe drought event (Ch. 2; Fig. 4.1). As predicted the relative abundance of opportunistic species remained similar post-drought. Although small increases in equilibrium species and decreases in periodic species were found as expected, they were not statistically significant. The results suggest that severe droughts override differential responses by inflicting high mortality on all mussels, which can be somewhat buffered by local conditions (Ch. 2).

In contrast, considering life history strategies showed to be effective when examining the spatial patterns of distribution of mussels in a river prone to flash flooding and drying. Differences in local habitat conditions were associated with differences in relative abundance of mussels with different life history strategies, which were also in accordance with the HHC (Ch. 3; Fig. 4.1). In general, periodic and opportunistic species preferred deeper pool habitats located in the upper San Saba River, whereas equilibrium species were more dominant in riffle habitats downstream (Ch. 3). These are patterns that could be expected based on the individual responses of mussels and the long-term community changes showed in chapters 1 and 2. For example, Ch. 1 suggested higher desiccation tolerance of equilibrium species which may allow them to persist in riffle

habitats, which are more likely to dry out during a drought event. Periodic and opportunistic species, on the other hand, may require the more thermally stable conditions in deeper pool habitats. Such responses to dewatering are not explicitly addressed in the HHC but may be especially relevant in rivers that experience drought. Additionally, the species with the highest relative abundance found within each river segment (i.e. upstream, midstream, and downstream) during the spatially extensive surveys (Ch. 3) were the same species that had the highest post-drought survival (Ch. 2) at survey sites within those river segments, which suggests that drying events (e.g., a severe drought event) can have long-term impacts on mussel community structure.

In general, the results from this dissertation showed that differences in life history strategies are important to understand the variation in individual responses and patterns in community structure at multiple scales. The distribution of mussels may be to a large extent the result of hydrological disturbances and could even be the most important driver in systems with high levels of disturbance (such as flash floods and drought in Central Texas). In contrast, mussel distributions in systems with low levels of hydrological disturbance may be more likely controlled by biotic interactions such as competition between species, predation, or host-fish distributions. A stronger role of environmental filtering in harsher environmental conditions may generally apply to aquatic communities. Indeed, recent metacommunity studies that examined the role of local environmental factors under varying levels of environmental harshness found that local environmental factors were better at explaining metacommunity structure under more stressful habitat conditions (e.g., in a drier and colder basin compared to a warmer and wetter basin (Vilmi et al. 2020), in intermittent compared to perennial stream reaches

(Valente-Neto et al. 2020), and in more polluted river ecosystems (Xiong et al. 2017; Peng et al. 2018). It is important to note that the degree of environmental harshness may depend on the spatial and temporal scale being studied, emphasizing the importance of a multiscale approach.

It is known that driving forces may vary across scales (Viana and Chase 2019), hence it would be interesting to determine if the observed relationships between mussel life history strategist distributions and hydrological disturbance (including low and high flow events) also occur at larger spatial scales than studied here (e.g. within mainstem rivers, between sub-basins). Preliminary work using mussel community and discharge data from 480 sites and 39 stream gages throughout the Colorado River basin showed that the patterns observed in the San Saba River (Ch. 3) resembled those at the larger spatial scale of the Colorado River mainstem (Fig. 4.2) and between sub-basins of different sizes within the Colorado River basin (Fig. 4.3). Opportunistic and periodic species were relatively more abundant in more isolated headwater sites and smaller streams, whereas equilibrium species were more dominant in more downstream sites and larger streams (Figs. 4.2 and 4.3). In general, opportunistic species were more strongly associated with low flow disturbance metrics (e.g. zero flow days, increased flow variability, extreme low flow frequency), whereas equilibrium species were more associated with high flow disturbance metrics such as large flood frequency and duration. Periodic species exhibited intermediate responses compared to the other life history strategists (Z. Mitchell, unpublished data).

Figure 4.4 provides a summary of the results from chapter 3 and preliminary results at larger spatial scales (see above) in respect to differences in the relative

abundance of different life history strategies. I propose that these patterns are primarily driven by the frequency and intensity of hydrological disturbance events and habitat heterogeneity. Thus, the predictions of the HHC, originally proposed for assemblage differences between small, mid-sized, and large streams (i.e. sub-basin scale), also seem to apply to smaller spatial scales (Fig. 4.4). At each spatial scale, for which data were available (not sub-basin), periodic and opportunistic species were found primarily in pool habitats, whereas equilibrium species were found predominantly in riffle and run habitats (Ch. 3; Fig. 4.4). Figure 4.4 also proposes that the relative influence of low flow disturbance events and flashy flow regimes in structuring mussel communities decreases in the downstream direction and with increased stream size (Fig. 4.4). Conversely, habitat heterogeneity is expected to increase with spatial scale (Fig. 4.4). Dispersal limitation may also increase with spatial scale, but this was not addressed here. At even larger spatial scales, i.e., between basins (not shown in figure 4.4), other factors, such as differences in host fish communities and historical colonization patterns will start to play a bigger role in determining the functional composition of mussels (e.g., Haag 2010; Burlakova et al. 2011; Schwalb et al. 2013; Dascher et al. 2018). Climatic differences may also drive larger scale differences in flow regimes and disturbance frequency and intensity (Dascher et al. 2018). For example, an increased abundance of periodic and opportunistic species might be expected in more arid rivers of west Texas that are more likely to experience low flow disturbance events, whereas a higher percentage of equilibrium species could be expected in east Texas rivers which receive substantially more rainfall. More data will need to be collected from other river basins throughout Texas to examine the validity of the HHC at the basin scale and to identify the driving



factors of the functional composition of mussels at larger spatial and temporal biogeographic scales.

The results of this research are also relevant for conservation efforts, because it shows the importance of considering life history strategies when making management decisions such as identifying species most at risk and the threats they are facing (e.g., drought or excessive groundwater pumping). Additionally, it is often costly to collect spatially extensive data across large regions to delineate communities. As part of future research efforts, data from this project will provide managers information on whether data collected at isolated sites (often bridge crossings) are useful to monitor mussel communities in central Texas. The extensive datasets collected in this project can also be used to identify mussel hotspots in need of protection, areas in need of stream restoration, and locate appropriate sites for mussel relocation projects.

While metacommunity research has mostly focused on short-lived, and passively dispersing organisms in aquatic habitats (Logue et al. 2011, Soininen 2014), freshwater mussels have received little attention (e.g., Schwalb et al. 2015). To some extent this may be because freshwater mussels are not as routinely monitored as fish and macroinvertebrates and they are relatively long-lived, hampering experimental approaches. By combining a multiscale approach that involved both experimental and field-based methods and focusing on life history strategies, this study was able to show that despite potential differences between individual species, the same patterns of changes in the relative dominance of different life history strategies (functional composition) in response to differences in environmental conditions (e.g. hydrological disturbance, local habitat conditions) were observed at different spatial scales within a

river basin. Mussels in different river basins are usually disconnected and differences in community composition at such a biogeographic scale are likely driven by other factors (see above). However, within a river basin, at a metacommunity scale where mussels are at least potentially connected via movement of their host fish, similar driving factors (e.g. hydrological disturbance events, and local habitat conditions) may result in similar patterns of distribution of life history strategists at different spatial scales, even though species composition can change drastically within a river basin. The similarities in patterns between mussel community composition and environmental factors between spatial scales would not have been evident with a taxonomic approach.

Although this dissertation was focused on freshwater mussels in a river basin in central Texas, the findings may apply to other river systems that experience similar levels of disturbance or to other taxa, especially for other relatively sedentary organisms. Several gaps in knowledge need to be addressed to gain a better understanding of factors structuring mussel communities 1) quantifying mussel life history traits, 2) examining how other types of disturbances (e.g. floods and anthropogenic barriers) influence mussel distributions throughout a river network, 3) using manipulative field studies (e.g. translocation studies) to better tease apart the relative importance of niche- and neutral based processes in structuring mussel communities, and 4) assessing the validity and relative importance of other community structuring factors (e.g. competition, predation).

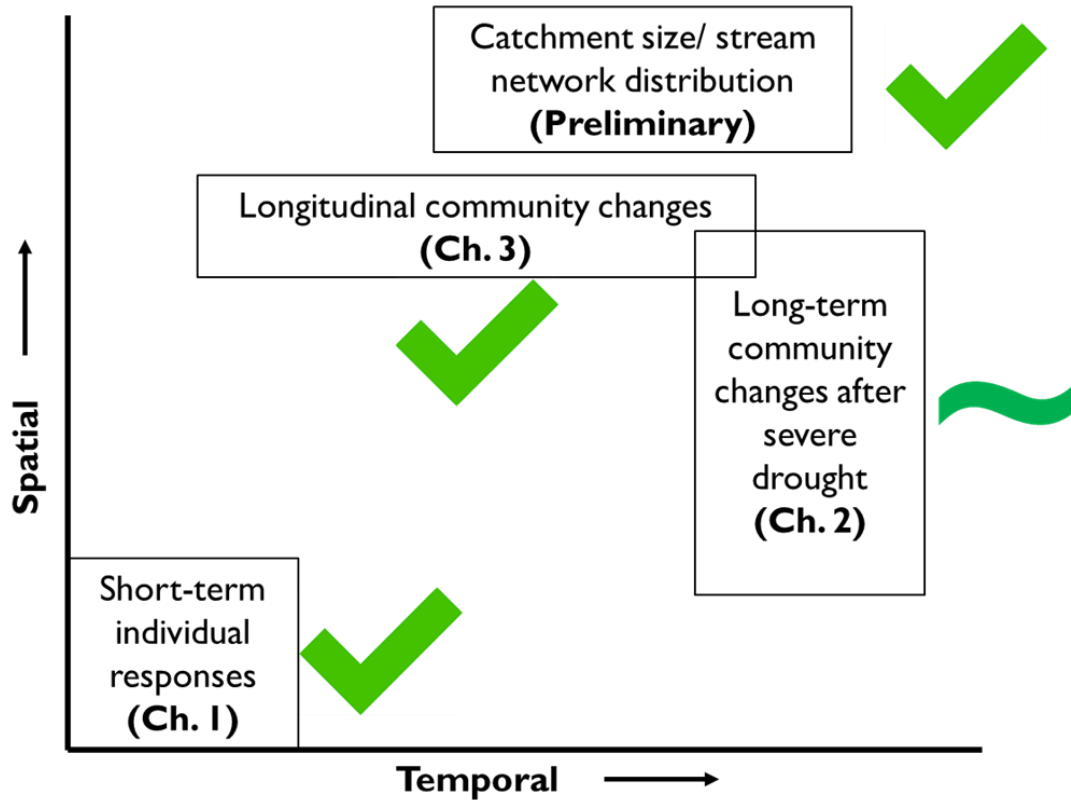


Figure 4.1. Conceptual diagram describing the effectiveness of life history strategies to predict the distribution of mussel communities at multiple spatiotemporal scales. Green check marks denote that life history strategies were useful predictors at a given scale and a green tilde denotes partial support.

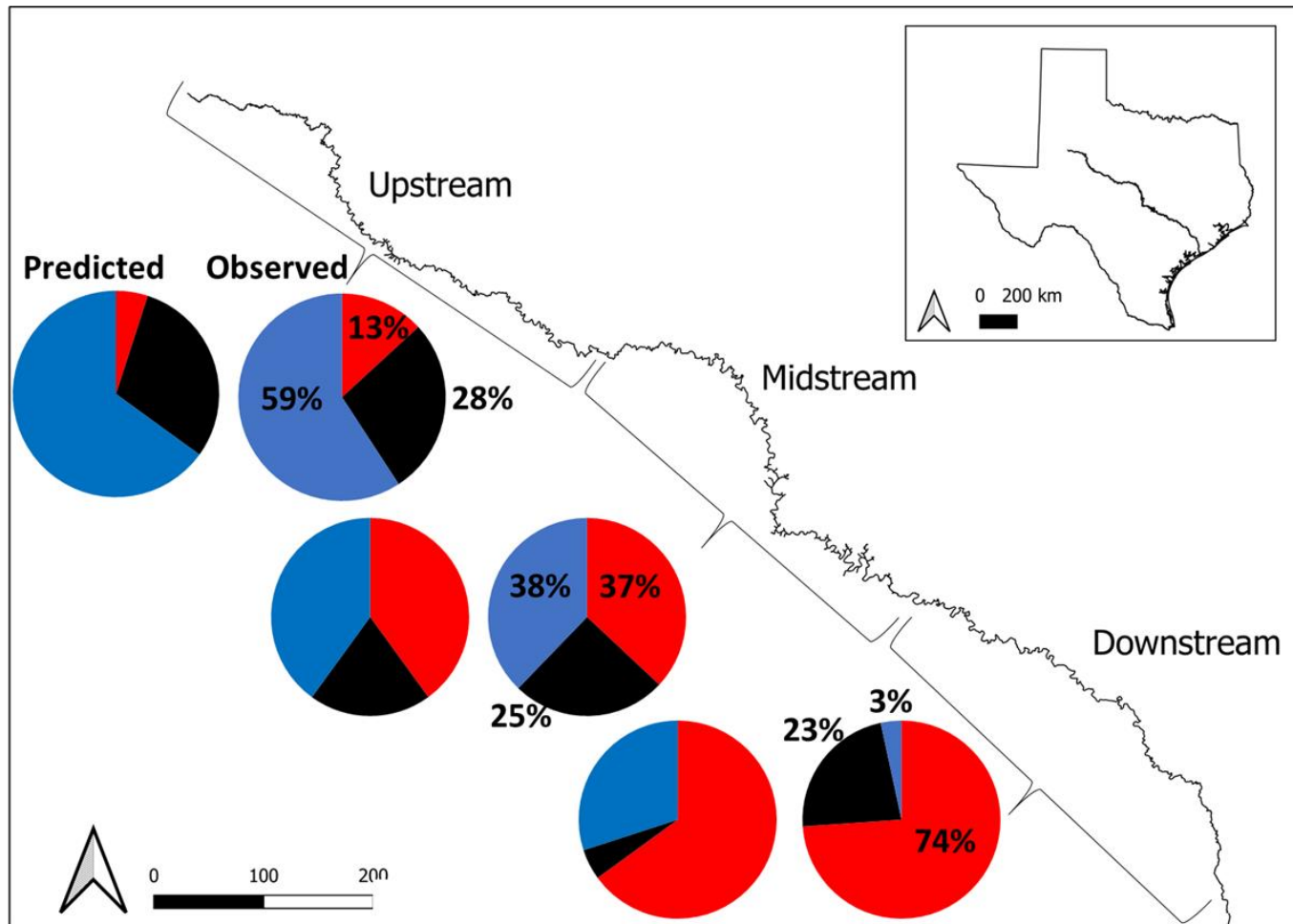


Figure 4.2. Predicted and observed percentages of freshwater mussel life history strategists in the upstream, midstream, and downstream Colorado River, Texas. Periodic, opportunistic, and equilibrium species are denoted by blue, black, and red, respectively. Data on mussel distributions were obtained from this study; Howells (1992, 1993, 1994, 1995, 1996, 1998, 1999, 2004); Bonner et al. (2018).

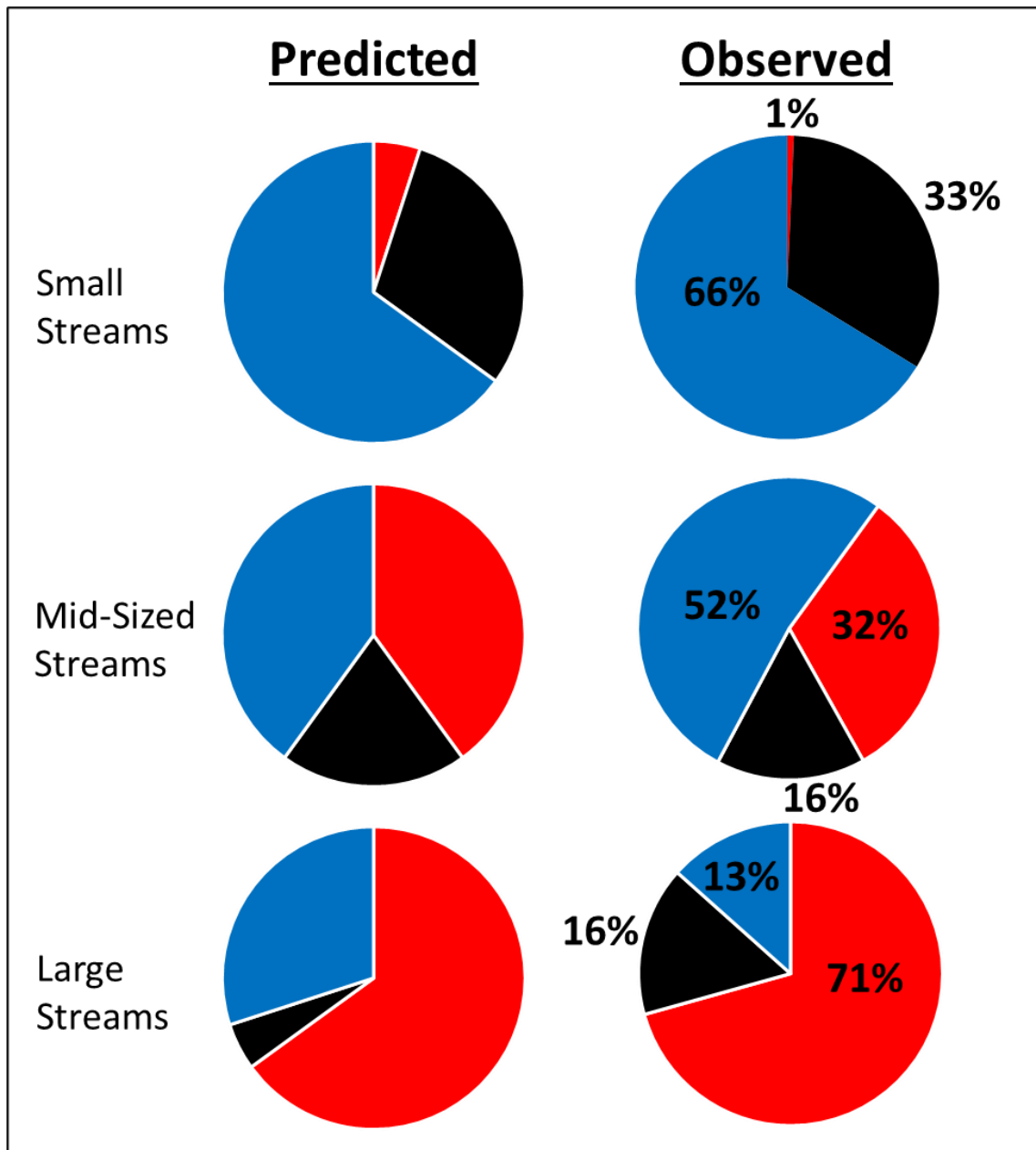


Figure 4.3. Predicted and observed percentages of freshwater mussel life history strategists for different size streams in the Colorado River basin, TX. Catchment sizes for small, mid-sized, and large streams were  $< 500 \text{ km}^2$ ,  $500\text{-}10,000 \text{ km}^2$ ,  $> 10,000 \text{ km}^2$ . Periodic, opportunistic, and equilibrium species are denoted by blue, black, and red, respectively. Mussel distribution data collected from this study; Howells (1992, 1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000, 2002, 2003, 2004); Bonner et al. (2018); Randklev et al. (2018); Seagroves et al. (2018).

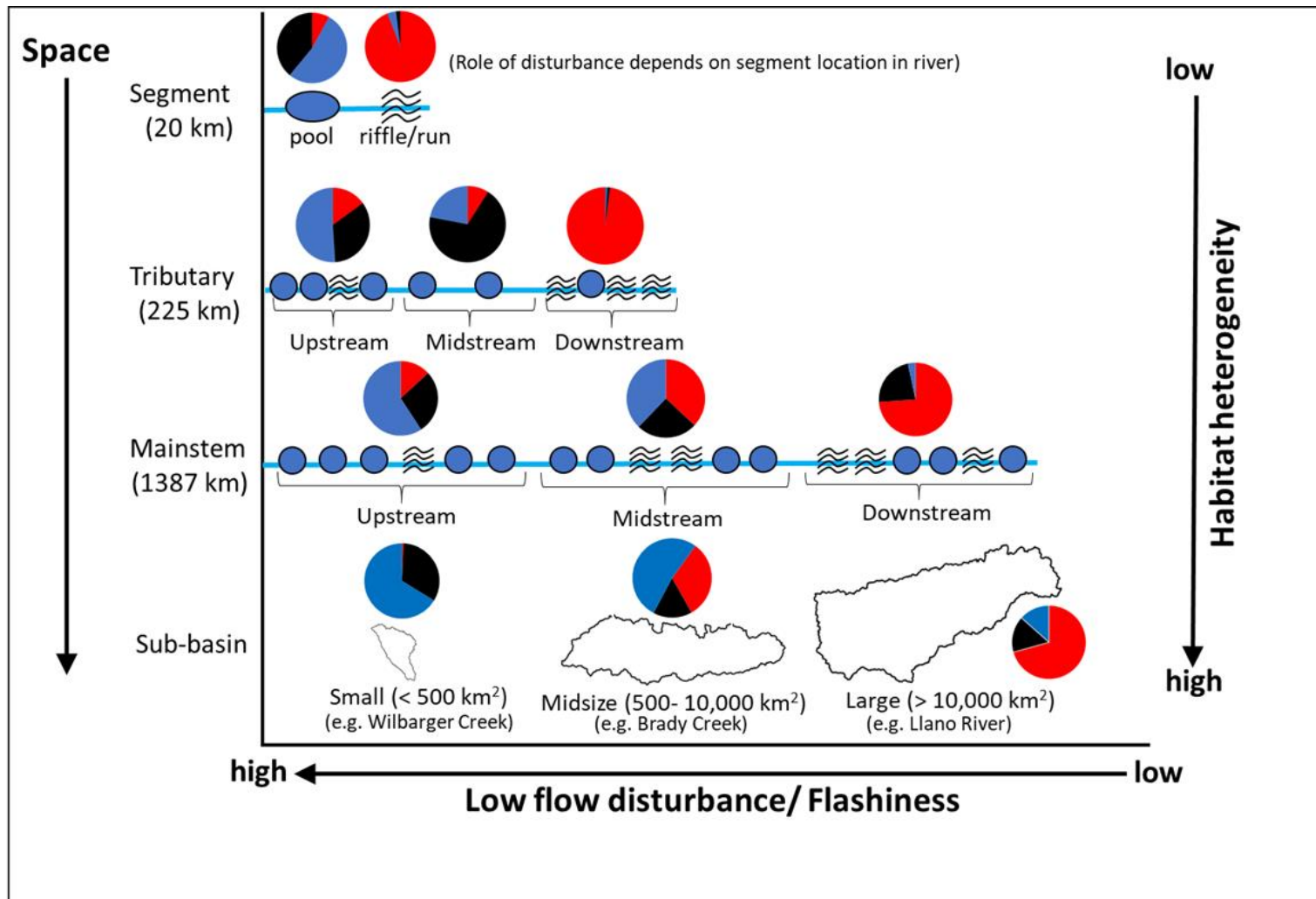


Figure 4.4. Observed percentages of freshwater mussel life history strategists in their observed mesohabitats at various spatial scales in the Colorado River basin along predicted gradients of hydrological disturbance and habitat heterogeneity. Periodic, opportunistic, and equilibrium species are denoted by blue, black, and red, respectively.

## APPENDIX SECTION

Appendix 2.1. Historical and current records of live unionids from four tributaries (Llano, San Saba, Concho, and Elm Creek) of the middle Colorado River. An X denotes species presence during each of the three time periods: Historical (data collected from Strecker 1931, Howells<sup>a-i</sup>), Pre-drought, 2005-2011 (this study; Burlakova et al. 2011a,b; Burlakova and Karatayev 2012), and Post-drought (this study, 2017).

River	pre-1950	1950-2004	Pre-drought	Post-drought
Llano River				
<i>Amblema plicata</i>	X			
<i>Quadrula quadrula</i>	X			
<i>Cyclonaias petrina</i>	X	X		X
<i>Cyclonaias pustulosa</i>	X			X
<i>Cyrtonaias tampicoensis</i>		X		
<i>Fusconaia mitchelli</i>	X			
<i>Lampsilis bracteata</i>	X		X	X
<i>Lampsilis teres</i>	X			
<i>Potamilus purpuratus</i>	X			
<i>Pyganodon grandis</i>		X		
<i>Strophitus undulatus</i>	X			
<i>Toxolasma parvus</i>	X			
<i>Tritogonia verrucosa</i>	X			X
<i>Utterbackia imbecillis</i>		X		
San Saba River				
<i>Amblema plicata</i>	X	X	X	
<i>Quadrula quadrula</i>		X	X	X
<i>Cyclonaias pustulosa</i>		X	X	X
<i>Cyclonaias petrina</i>	X	X	X	X
<i>Cyrtonaias tampicoensis</i>		X	X	X
<i>Fusconaia mitchelli</i>	X			
<i>Lampsilis bracteata</i>	X	X	X	X
<i>Lampsilis teres</i>	X	X		
<i>Leptodea fragilis</i>		X	X	X
<i>Potamilus purpuratus</i>	X	X	X	
<i>Pyganodon grandis</i>		X		
<i>Strophitus undulatus</i>	X			
<i>Toxolasma parvus</i>	X			
<i>Tritogonia verrucosa</i>	X	X	X	X
<i>Truncilla macrodon</i>			X	X
<i>Utterbackia imbecillis</i>		X	X	X

## Appendix 2.1. Continued

### Concho River

<i>Amblema plicata</i>	X	X		
<i>Quadrula quadrula</i>	X	X	X	
<i>Cyclonaias pustulosa</i>	X			
<i>Cyclonaias petrina</i>	X	X	X	
<i>Cyrtonaias tampicoensis</i>		X	X	
<i>Fusconaia mitchelli</i>	X			
<i>Lampsilis bracteata</i>	X	X		
<i>Lampsilis teres</i>	X	X		
<i>Leptodea fragilis</i>		X		
<i>Megalonaias nervosa</i>		X		
<i>Potamilus ohioensis</i>	X			
<i>Potamilus purpuratus</i>	X	X	X	
<i>Pyganodon grandis</i>		X		
<i>Strophitus undulatus</i>	X			
<i>Toxolasma parvus</i>	X			
<i>Toxolasma texasiensis</i>		X		
<i>Tritogonia verrucosa</i>	X			
<i>Truncilla macrodon</i>		X		
<i>Uniomerus declivis</i>		X		
<i>Utterbackia imbecillis</i>		X	X	

### Elm Creek

<i>Quadrula quadrula</i>		X	X	X
<i>Cyclonaias petrina</i>		X		
<i>Cyrtonaias tampicoensis</i>		X	X	X
<i>Lampsilis bracteata</i>		X	X	X
<i>Lampsilis teres</i>		X		
<i>Potamilus purpuratus</i>		X		
<i>Leptodea fragilis</i>		X	X	
<i>Uniomerus declivis</i>		X		
<i>Utterbackia imbecillis</i>		X	X	X

Note: Find the following articles at: [https://tpwd.texas.gov/publications/fishboat/fish/fisheries\\_management/mds\\_inland.phtml](https://tpwd.texas.gov/publications/fishboat/fish/fisheries_management/mds_inland.phtml)

<sup>a</sup>Howells RG (1994) Distributional surveys of freshwater bivalves in Texas: progress report for 1992, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 118.

<sup>b</sup>Howells RG (1995) Distributional surveys of freshwater bivalves in Texas: progress report for 1993, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 119.

<sup>c</sup>Howells RG (1996) Distributional surveys of freshwater bivalves in Texas: progress report for 1995, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 125.

<sup>d</sup>Howells RG (1997) Distributional surveys of freshwater bivalves in Texas: progress report for 1996, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 144.

<sup>e</sup>Howells RG (1998) Distributional surveys of freshwater bivalves in Texas: progress report for 1997, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 147.

<sup>f</sup>Howells RG (2000) Distributional surveys of freshwater bivalves in Texas: progress report for 1999, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 170.

<sup>g</sup>Howells RG (2001) Distributional surveys of freshwater bivalves in Texas: progress report for 2000, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 187.

<sup>h</sup>Howells RG (2002) Distributional surveys of freshwater bivalves in Texas: progress report for 2001, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 214.

<sup>i</sup>Howells RG (2005) Distributional surveys of freshwater bivalves in Texas: progress report for 2004, Texas Parks and Wildlife Department, Austin, Texas. Management Data Series No. 222.



Appendix 2.2. Search effort in person-hours for each tributary (N denotes number of sites) during pre- and post-drought survey periods.

<b>River</b>	<b>N</b>	<b>Period</b>	<b>Effort (p-h)</b>
Elm Creek	4	pre	19.5
		post	12
Concho	7	pre	14
		post	19
San Saba	14	pre	52
		post	31
Llano	5	pre	20
		post	11
Total	30	pre	105.5
		post	73

Appendix 3.1. Local and regional variables, and associated codes, that were collected at each sample site in the San Saba River.

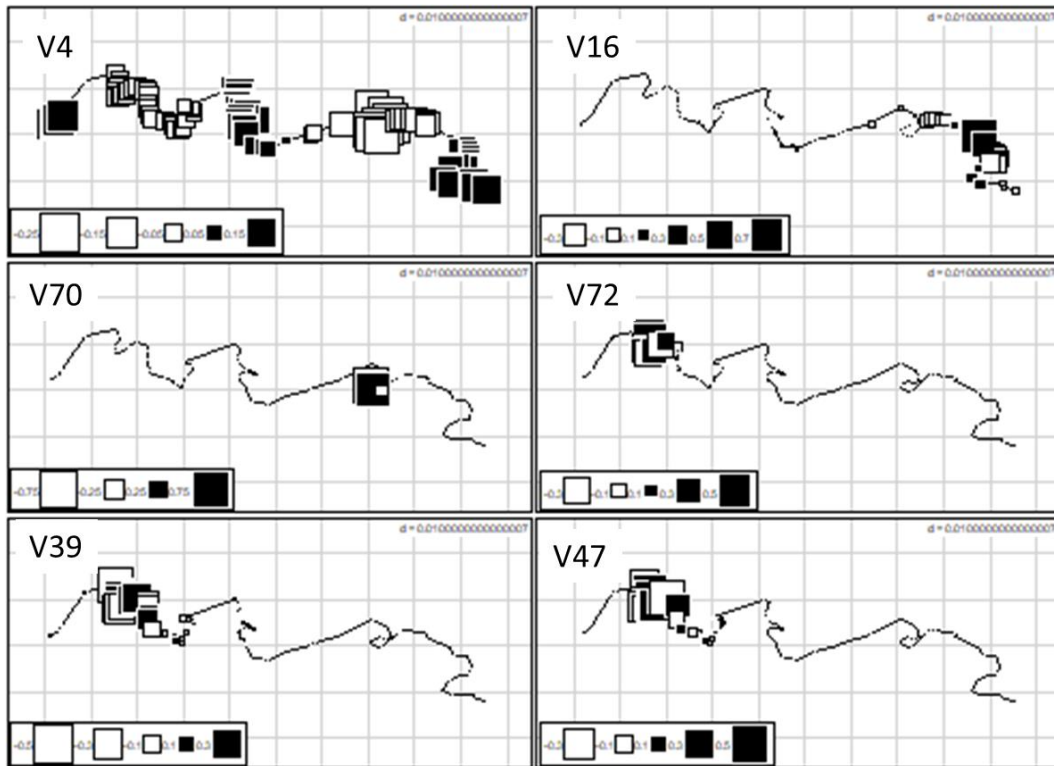
<b>Category</b>	<b>Variable</b>	<b>Code</b>
Local environmental	Mesohabitat:	
	riffle	rif
	run	run
	pool	pol
	Stream width (m)	wid
	Current velocity (m/s)	cv
	Dissolved oxygen (mg/l)	do
	Dissolved oxygen (%)	dop
	Conductivity (uS/cm)	con
	Specific conductivity (uS/cm)	scon
	Water Temperature (°C)	temp
	Mean water depth (m)	dep
	Percent silt substrate (%)	sil
	Percent sand substrate (%)	san
	Percent gravel substrate (%)	grv
	Percent pebble substrate (%)	peb
	Percent cobble substrate (%)	cob
	Percent boulder substrate (%)	bld
	Percent bedrock substrate (%)	bed
	Percent emergent vegetation (%)	veg
Local land cover	Percent open water (%)	wat
	Percent developed (%)	dev
	Percent forest (%)	for
	Percent shrub (%)	shb
	Percent herbaceous (%)	herb
	Percent agriculture (%)	agr
	Percent wetlands (%)	wet
Regional environmental	Ecoregion:	
	Edwards Plateau Woodland	epw
	Western Cross Timbers	wct
	Mean annual precipitation (cm)	prec
	Groundwater wells within 10 km	wel

Appendix 3.2. Significant AEM variables, after forward selection, in different segments of the San Saba River. Variables are listed in the order they were selected.

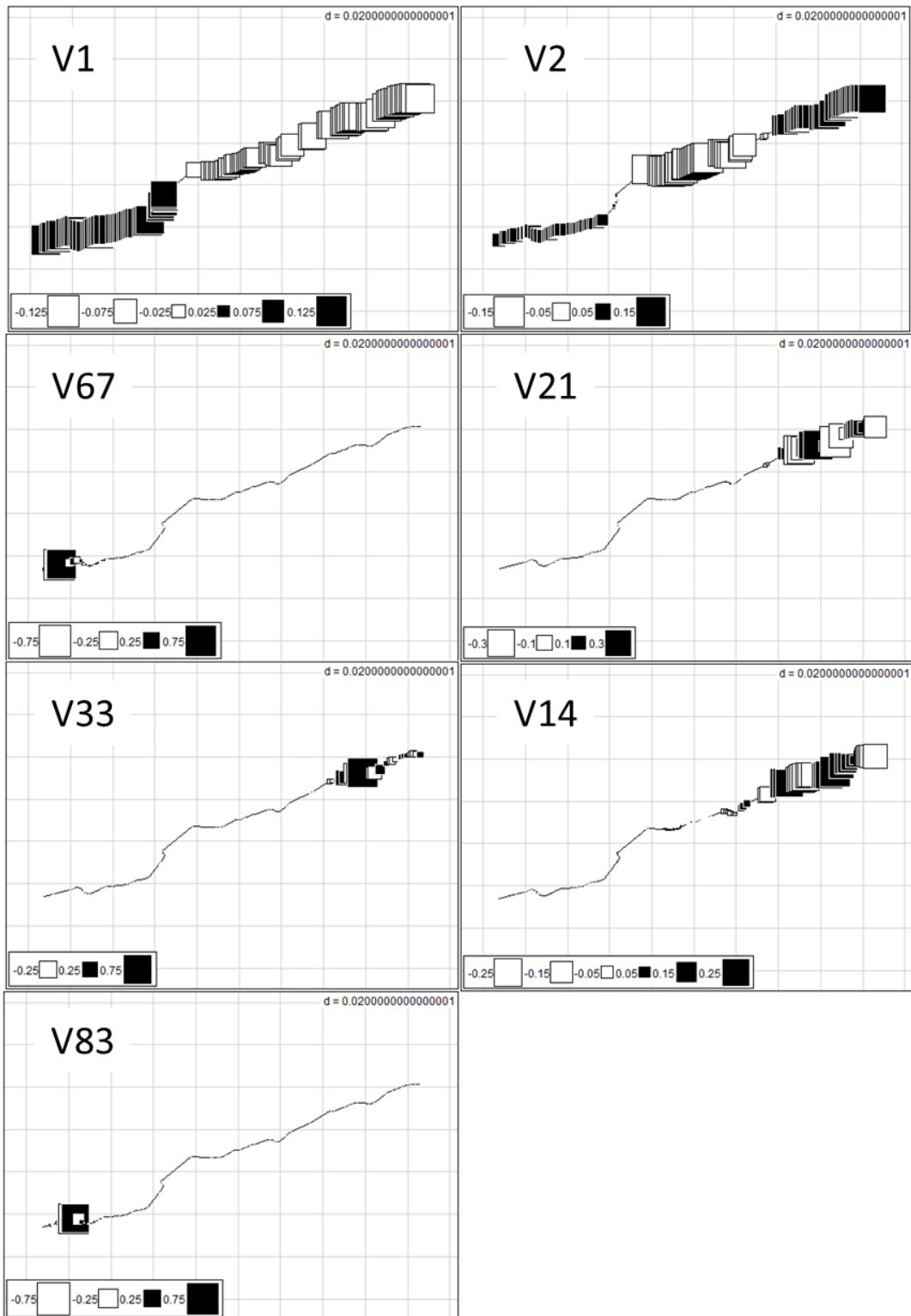
<b>Segment</b>	<b>Selected AEM variables</b>
Downstream	4,16,70,72,39,47,68,29,36,45,8,28,14,85,23,1,60,78,88,71
Upstream	1,2,67,21,33,14,83,20,37,3,74,40,1,41,7,101,22,16,8,67,23,28,11,6,66,9,5,72,80
Combined	1,6,17,46,32,80,74,10,165,50,151,89,3,19,90,37,21,52,154,35,2,54,193,150,14,39,4, 26,139,64,22,13,28,138,146,161,160,23,99,183,59,63,125,143,124,117,60,177,140,11

Appendix 3.3. Coefficient of variation values for mean annual flow, mean rise and fall rates, and the number of reversals for the up- and downstream segments of the San Saba River (2000-2019). Values were derived from the Indicators of Hydrologic Alteration. See The Nature Conservancy (2009) for more details on how variables were calculated.

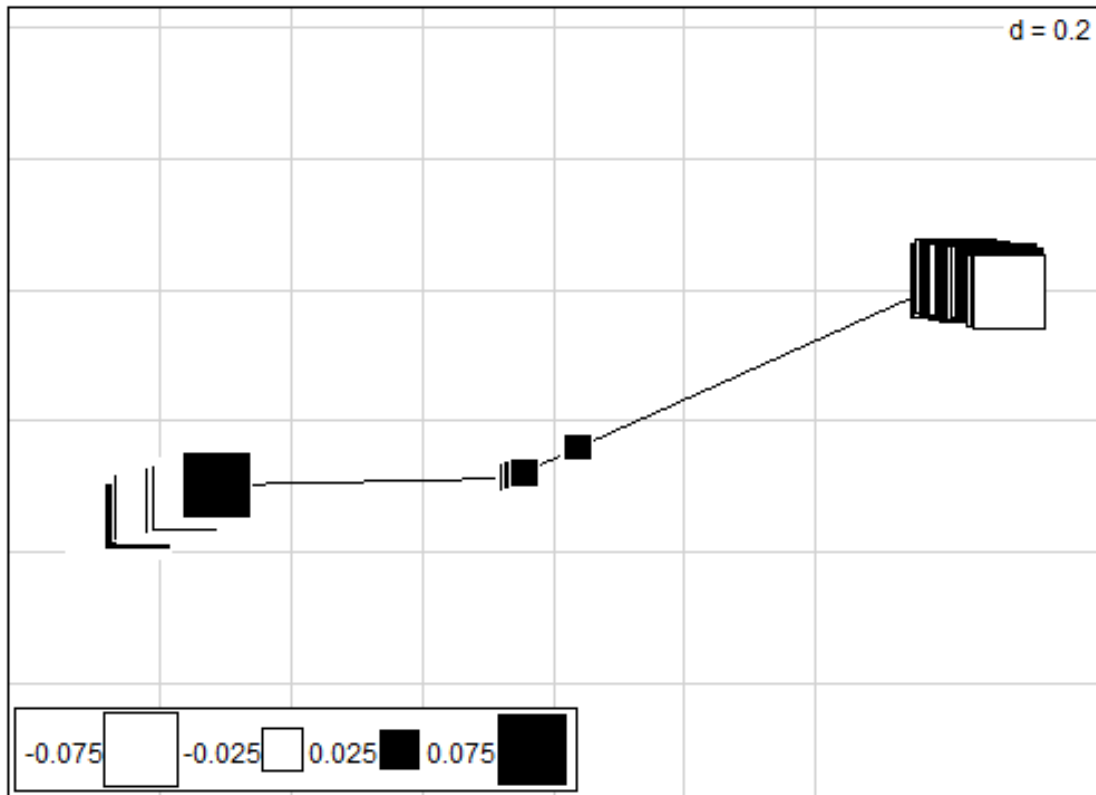
	Upstream	Downstream
Annual flow	8.03	4.1
Rise rate	2.16	1.21
Fall rate	-2.04	-1.24
Reversals	0.3	0.16



Appendix 3.4. Notable AEM variables for the downstream segment in the San Saba River.



Appendix 3.5. Notable AEM variables for the upstream segment in the San Saba River.



Appendix 3.6. Primary AEM variable for the San Saba River (all segments combined).

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