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USING ECOLOGICAL NICHE MODELING TO PREDICT OCCURRENCE OF RARE FISH AND UNIONID MUSSELS IN EAST TEXAS

by

ASHLEY DUNITHAN

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science Department of Biology

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ABSTRACT

USING ECOLOGICAL NICHE MODELING TO PREDICT OCCURRENCE OF RARE FISH AND UNIONIDS IN EAST TEXAS

Ashley Dunithan

Thesis chair: Lance Williams, Ph.D.

The University of Texas at Tyler May 2012

Fish and Unionid mussels are important components of aquatic ecosystems and the population decline of these organisms has become a topic of concern. Currently, there are six species of concern and three state-threatened fish species and six statethreatened Unionid species that occur in East Texas. However, little information is known about the ecology of these species.

In this study, I used ecological niche modeling, the software package Maxent, and eleven abiotic environmental parameters to predict the probability of occurrence of rare fish and mussel species in East Texas.

We were unable to model the fish species; however, the models for the Unionids were statistically significant (AUC >0.75). We used ENMtools to determine if the Unionid species exhibited statistically significant ecological differences and concluded that the niche models were significantly different from one another. Through the use of this software, we were able to determine locations and quantities of similar habitat and geomorphology in east Texas to help describe the amount of available habitat for these species and predict their probability of occurrence.

CHAPTER 1: A COMPARISON OF ECOLOGICAL NICHE MODELING APPROACHES

INTRODUCTION TO ECOLOGICAL NICHE MODELING

Knowledge regarding geographic distribution of species is important for conservation biology and management of biodiversity (Margules and Pressey, 2000). Species distributions can be inferred through a variety of statistical methods used to create models that estimate and predict species' geographic distribution. Predictive models are an important technique used in analytical biology and have been applied to a variety of areas in ecology including conservation, invasive species management, and evolution (Yom-Tov and Kadmon, 1998; Corsi et al., 1999; Peterson et al., 1999; Welk et al., 2002). Ecological niche models provide information regarding potential geographic distributions of species by quantifying relationships between the species known distribution and environmental variables, both abiotic and biotic. Ecological niche models represent a species' ecological niche within a set of environmental dimensions (Rotenberry et al., 2006). A species' fundamental niche consists of the set of all conditions that allow for long-term survival; whereas, the realized niche is a subset of the fundamental niche that the species actually occupies (Hutchinson, 1957). The species' realized niche is often smaller than the fundamental niche, because of historical factors (dispersal limitations), biotic interactions (competition, predators), and realized environment (e.g. current conditions) (Pulliam, 2000; Anderson and Martínez-Meyer,

2004). Geographic areas that satisfy the conditions of a species' fundamental niche represent the potential distribution; whereas, the areas actually inhabited represent the realized distribution. Predictions of species distributions can provide a complete, finescale spatial coverage of the potential distribution, including areas where data are limited or unavailable. Predicted distributions can be used for further analysis, including assessing the quality of nature reserves, creating more efficient surveys, and determining the actual distribution of rare and endangered species (Yom-Tov and Kadmon, 1998). Predicted distributions are important for conservation because information regarding distributions is a necessary precursor for plans to mitigate decline or to create new populations through reintroduction (Martínez-Meyer et al., 2006). Ecological niche modeling has been used to facilitate the study of spatial patterns of animal diversity (Rosenzweg, 1995; Yom-Tov and Kadmon, 1998; Brown and Lomolini, 1998; Ricklefs, 2004; Graham et al., 2006). In addition to examining spatial patterns of animal diversity, ecological niche models have been used to identify unknown distributional areas and previously undiscovered species (Raxworthy et al., 2003; Bourg et al., 2005), determine potential impacts of climate change (Iverson and Prasad, 1998; Thomas et al., 2004; Thuiller et al., 2005a; Lawler et al., 2006), predict species invasions (Welk et al., 2002; Peterson and Shaw, 2003; Peterson and Shaw, 2003; Goolsby, 2004; Iguchi et al., 2004; Thuiller et al., 2005b), and to support conservation planning (Corsi et al., 1999; Araújo and Williams, 2000; Ferrier et al., 2002; Funk and Richardson, 2002; Rushton et al., 2004).

Ecological niche models have broad applications and are in widespread use. Therefore, multiple approaches have been developed. They utilize either regression

models or machine learning models (Hijmans and Elith, 2011). These approaches differ in their data requirements and statistical methods, and they often make different predictions about species' distributions (Guisan and Zimmerman, 2000; Elith and Burgman, 2003; Elith et al., 2006). Therefore, it is crucial to choose an appropriate approach to niche modeling for a particular situation, which depends on the assumptions one is comfortable making and on the type of data that is available.

REGRESSION MODELING METHODS

Regression modeling methods for niche modeling are either general linear models (GLMs; McCullagh and Nelder, 1989) or general additive models (GAMs; Hastie and Tibshirani, 1990). Regression modeling is the most appropriate when there is both presence and absence data available, and when the sampling regimen has been systematic and unbiased (Austin and Cunningham, 1981). Both GLMs and GAMs use regression analysis to model realized niches and are widely used because of the strong statistical component and accuracy in modeling ecological relationships (Austin, 2002). GAMs use non-parametric, data defined smoothers to fit non-linear functions, whereas GLMs fit parametric terms, usually some combination of linear, quadratic and/or cubic terms (Elith et al., 2006). GLMs offer a slightly more flexible modeling framework because they allow for the modeling of alternative distributions in the response variable and nonconstant variance functions (Guisan et al., 2002). GLM is one of the most established statistical frameworks for species distribution models (Austin and Cunningham, 1981); however, GAMs are able to model more complex ecological response shapes than GLMs (Yee and Mitchell, 1999). Statistical approaches require both presence and absence data; however, when absence data are unavailable the background pixels may be used as

pseudo-absences instead of true absences and the output is interpreted as the relative result of environmental suitability (Ferrier et al., 2002).

MACHINE LEARNING APPROACHES

As mentioned above, regression model approaches should ideally use absence data as well as presence data. But the validity of absence data is often questionable (Anderson et al., 2003) and in any event it is rarely available (Soberón, 1999; Ponder et al., 2001). Therefore machine learning approaches which are more robust to the lack of true absence data, are gaining in popularity (Elith et al., 2006). Commonly used machine learning modeling methods include classification and regression tree (CART; Brieman et al., 1984), Genetic Algorithm for Rule-Set Prediction (GARP; Peterson et al., 2002), and maximum entropy modeling (Maxent; Dudik et al., 2007).

Classification and Regression Trees

While GLMs describe general relationships between environmental variables and species distributions, CART uses an algorithm that repeatedly separates the multidimensional space into subsets based on the best predictor variable (Chambers and Hastie, 1992). Modeling with CART has provided advantages over regression-based approaches in describing relationships between environmental factors and species distributions in multiple studies (Iverson and Prasad, 1998; Vayssieres et al., 2000) because it is less restricted by parametric assumptions and has an improved ability to handle non-linear interactions (Brieman et al., 1984). CART, however, is not as effective as other modeling methods at predicting occurrence of rare species (Kintsch and Urban, 2002).

Genetic Algorithm for Rule-Set Prediction (GARP)

GARP uses a genetic algorithm, a search heuristic for binary classification, to produce a set of rules to describe a species' distribution (Stockwell and Noble, 1992). The rules are used to iteratively search for non-random correlations between presence and pseudo-absence data and environmental predictors to develop a final set of rules. The rules are produced after 1000 iterations or convergence is reached (Peterson and Kluza, 2003). The final output from GARP is stochastic resulting in different models, with a variation in results, produced from the same data (Anderson et al., 2003). Approximately 10 to 100 models should be retained, each rule set should be used to predict presence, and the proportion of models predicting presence for an observation, or pixel, should be interpreted as the probability of occurrence (Stockwell et al., 2006). Although GARP has been successful at predicting species distributions, this method tends to have higher omission errors than alternative modeling methods and is known to overpredict species distributions (Hernandez et al., 2006; Phillips, 2008; and Elith and Graham, 2009). *Maxent*

A more recently developed software package called Maxent (Dudik et al., 2007), is becoming the more commonly used modeling method to predict species distributions. Maxent is considered the most accurate modeling technique when presence-only information is available. In fact, Maxent actually outperforms statistical methods that use presence-absence information such as GAMs and GLMs (Elith et al., 2006). Maxent uses the statistical approach of maximum entropy to make predictions from occurrence localities and environmental variables corresponding to the geographic region of interest. The maximum entropy principle states that probability distributions with maximum

entropy (the most spread out, closest to uniform), taking into consideration the constraints (determined by the expected value of the distribution, which is estimated from the presence observations), is the best estimate of an unknown distribution because it agrees with everything that is known but avoids assuming anything that is unknown (Jaynes, 1990). Maxent models distributions directly by estimating the density of environmental variables conditional on presence of the species. The program starts with a uniform probability distribution and iteratively alters one environmental variable at a time to maximize the likelihood of the occurrence dataset. The algorithm is guaranteed to converge to the optimum probability distribution and because the algorithm does not use randomness, the outputs are deterministic (Hernandez et al., 2006). An important distinction between Maxent and regression models is that locations without species occurrence points are represented as background information in Maxent and not as absences (Franklin, 2009).

ADVANTAGES OF MAXENT

There are several advantages to using the Maxent approach compared to other modeling methods. Maxent provides a continuous description of habitat suitability by distinguishing between those with a sufficiently strong prediction versus those with increasingly stronger predictions allowing it to provide a more detailed output when compared with GARP (Phillips et al., 2006). This is likely the result of Maxent performing additively, the contribution of all environmental variables at each pixel (Elith and Graham, 2009). GLMs and GAMs are discriminative approaches which estimate the probability distribution over environmental variables given occurrence points directly while Maxent is generative which builds a probabilistic model for each environmental

variables and identifies which variable was most likely to have generated the occurrence point. The generative approach allows Maxent to produce better predictions when the amount of training data is small (small sample sizes) (Ng and Jordan, 2001). Because it uses a maximum entropy algorithm, Maxent appears to be less sensitive to sample sizes when compared to modeling methods such as GARP, GLMs, and GAMs; Maxent consistently outperform these methods at the smallest sample sizes (Wisz et al., 2008). Maxent had a higher accuracy (higher AUC values) with smaller datasets than GARP and produced accurate results in instances with low occurrence data (Hernandez et al., 2006). One study found high success rates and statistical significance in jackknife tests with sample sizes as low as five (Pearson et al., 2007), which is likely the result of the regularization process in Maxent that inhibits the over-fitting of models when occurrence data is limited (Phillips et al., 2006). The ability to provide significant results and accurate prediction with fewer occurrence points is useful when considering rare or specialist species that occupy limited geographic distributions and occur in relatively low numbers (Gaston, 1997). These advantages allow for the use of Maxent to predict distributions for rare and endangered species and helps elucidate the amount of potential habitat at larger spatial scales, or areas.

RESEARCH OBJECTIVES

The objective of my thesis is to use landscape characteristics and the ecological niche modeling software, Maxent, to predict the probability of occurrence for rare fish and state-threatened mussel species in the Neches and Sabine rivers in east Texas, USA. Information regarding relationships between species and environmental variables will enhance knowledge of each species' ecology. Prediction and mapping of potential

suitable habitat for rare species may be used to assess impacts of disturbances and to guide management decisions and restoration efforts (Gaston, 1996).

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CHAPTER TWO: USING ECOLOGICAL NICHE MODELING TO PREDICT OCCURRENCE OF RARE FISH AND UNIONID SPECIES IN EAST TEXAS

INTRODUCTION

Information regarding geographic distributions of species is important for conservation and management of biodiversity (Margules and Pressey, 2000). The use of predictive models of species geographic distributions is an important technique in analytical biology and has been applied to a variety of areas of conservation and ecology (Corsi et al., 1999; Welk et al., 2002; Yom-Tov and Kadmon, 1998). Models and information regarding potential habitat may be used to assess impacts of disturbances and to guide management decisions and restoration efforts (Gaston, 1996). Landscape level characteristics can be used to predict smaller scale habitats associated with a particular species and will enhance knowledge of the species' ecology.

Spatially explicit methods that combine information regarding landscape characteristics and localities of known occurrence are useful for understanding the ecological processes driving species' distributions. A niche modeling approach known as maximum entropy distribution (Maxent Phillips et al., 2006) provides an understanding of habitat suitabilities of individual species on the landscape. Maxent models the specific environmental requirements for a species, or the realized niche (Hutchinson, 1957). Maximum entropy distribution modeling outperforms other machine-learning and regression modeling methods (Elith et al., 2006; Ortega-Huerta and Peterson, 2008) and

performs well at small sample sizes (Hernandez et al., 2006; Kumar and Stohlgren, 2009; Wisz et al., 2008). The ability to provide accurate predictions with fewer known localities is useful when considering rare or specialist species that occupy limited geographic distributions and occur in relatively low numbers (Gaston, 1997). Maxent produces a geographic model of habitat suitability by searching for the best solution comparing the distribution of the occurrence points to the predetermined environmental variables (i.e., ArcGIS layers) (Phillips et al., 2006). In ecological niche modeling, there are implicit ecological assumptions (Elith et al., 2011). Therefore selection of variables requires expert knowledge of the species' ecology. The environmental variables should coincide temporally with the occurrence localities (Anderson and Martínez-Meyer, 2004). The GIS maps of environmental parameters used should correspond to the years of data collection. Also, geographic extent should be taken into consideration when choosing environmental variables. Environmental variables should affect the species' distribution at the relevant scale (Pearson et al., 2004). Species' responses to environmental parameters is determined by the scale of the study area. Topographic and landcover variables likely influence species' distributions at meso- and topo-scales (Mackey and Lindenmayer, 2001). Maxent produces a map with a logistic score for each grid cell which can be interpreted as the degree of suitability of a particular location for the species, given the environmental attributes of that location (Phillips and Dudik, 2008). The resulting predictive models can be used as a conservation tool to predict patterns of species distributions across the landscape and aid in the development of recovery plans for imperiled fish and mussel species.

In lotic environments, biological patterns are influenced by abiotic conditions. Stream assemblages are structured through a hierarchical framework where landscapelevel features constrain and control local factors such as hydrology, sedimentation, nutrient dynamics, and channel morphology (Frissel et al., 1986; Tonn et al., 1990; Smiley et al., 2005). One of the most significant threats to riverine ecosystems is alteration of the natural flow regime (Dynesius and Nilsson, 1994; Nilsson and Berggren, 2000). Fragmentation of natural habitat and alterations of natural flow regime have been reported as the most significant threats to freshwater mussels and fishes of the southern United States (Williams et al., 1993; Warren et al., 2000; Vaughn and Taylor, 1999). Determining the impact river alterations may have on rare species can be accomplished with landscape-level knowledge of the availability and quality of habitat that currently exists in the watershed. In the state of Texas, there has been a dramatic increase in human population resulting in an increased demand for water. Depletion of groundwater resources places an increased demand on surface waters (Wurbs, 1985). Northeast Texas has become a prime site for reservoir development and commercial interest because of an abundance of water resources in the area. The Neches and Sabine River systems of east Texas are one focus of this increased demand for water resources and have planned reservoir projects.

Fishes are ecologically important components of lotic ecosystems (Holmlund and Hammer, 1999; Warren et al., 2000). Some of the richest fish faunas in North America occur in the southern region of the United States. Texas has a diverse fish fauna consisting of 247 species in 45 families with highest species diversity occurring in the eastern part of the state (Thomas et al., 2007). In the last three decades there has been a

consistent decline in diversity of fishes in east Texas because of human activities and alteration of lotic environments (Anderson et al., 1995). The number of fish species classified as imperiled in the south has increased by 75% since 1989 (Warren et al., 2000) and 20% of the fishes native to Texas are in need of conservation (Hubbs et al., 1991). In the eastern part of the state, six fish species are considered to be species of concern, *Anguilla rostrata*, American Eel; *Notropis atrocaudalis*, Blackspot Shiner; *Notropis chalybaeus*, Ironcolor Shiner; *Notropis sabinae*, Sabine Shiner; *Notropis shumardi*, Silverband Shiner; and *Erimyzon oblongus*, Creek Chubsucker, and three are considered state threatened: *Polyodon spathula*, Paddlefish; *Pteronotropis hubbsi*, Bluehead Shiner; and *Cycleptus elongatus*, Blue Sucker (Bender et al., 2005).

Along with fish species mentioned above, there are several species of mussels, whose life history is intertwined with fish (Howells et al., 1996), that are also imperiled in East Texas. Freshwater mussels belonging to the family Unionidae often occur in dense multispecies beds that perform functional ecosystem roles such as removing suspended organic matter, moving sediments, and providing habitat for other animals (Christian and Berg, 2000; Strayer et al., 1997; Vaughn and Hakencamp, 2001). Freshwater mussels are the most imperiled group of animals in North America. Over the last century, North American mussel populations have decreased with 35 species now considered extinct and approximately 50% imperiled (Shannon et al., 1993; Williams et al., 1993; Neves et al., 1997; Vaughn, 1997). Historically, freshwater mussels were abundant in riverine systems in the southeastern United States (Strayer et al., 1994; Parmalee and Bogan, 1998). There are approximately fifty species of Unionid mussels in the state of Texas, of which many have a distinct species composition in east Texas

(Neck,1982; Howells et al.,1996). Fifteen species in Texas are state-threatened with six of these occurring in east Texas: *Obovaria jacksoniana*, Southern Hickorynut; *Pleurobema riddellii*, Louisiana Pigtoe; *Lampsilis satura*, Sandbank Pocketbook; *Potamilus amphichaenus*, Texas Heelsplitter; *Fusconaia lananensis*, Triangle Pigtoe; and *Fusconaia askewi*, Texas Pigtoe. Additionally, one species is federally listed as endangered, *Arkansis wheeleri*, Ouachita Rock Pocketbook.

RESEARCH OBJECTIVES

I had two objectives in this study:

(1) Use ecological niche modeling to predict occurrence of rare fish and mussel species in east Texas.

(2) Determine which environmental variables (i.e., soil, vegetation, groundwater recharge, overland flow, etc.) are most important for rare species distribution.

METHODS

SAMPLING DESIGN

In 2010-2011, mussels and fish were surveyed in the Neches and Sabine Rivers of east Texas between April and October (Fig. 2.1). Biota were collected at five sites on the Neches River and nine sites on the Sabine River. The sampling locations were chosen to provide adequate coverage of the rivers in northeast Texas. Sites were sampled in a 200m reach containing as many geomorphic units as possible (i.e., riffle, pool, run) to be representative of the actual conditions. Fish were collected throughout each reach with a Smith-Root 2.5 generator powered pulsator (GPP) tote barge electroshocker. Studies have shown electrofishing to be the most effective technique for obtaining fish data in freshwater habitats (Yoder and Smith, 1999). Fish were identified to species, enumerated, and released except for voucher specimens. All difficult to identify specimens were preserved in formalin and keyed out in the lab. Mussels were sampled using one person hour tactile and visual searches in four 50m transects perpendicular to the channel at each site. Qualitative and quantitative methods have provided similar results for mussel species diversity, evenness, and richness values allowing for the use of visual surveys (Hornbach and Deneka, 1996). Living and recently dead mussels, indicated by the presence of tissue and shiny nacre, were identified to species, enumerated, and replaced except for voucher specimens. Long deceased mussels were not included in samples because stream flow can transport them from upstream locations

that are outside of the sampling area, which would provide inaccurate evidence of habitat suitability.

Additional mussel data were obtained from a database created by Bob Howells, (Appendix A). Lake Tawakoni, on the Sabine River, was the last reservoir constructed in the east Texas region and formation of the dam was finalized in 1980 allowing for mussel occurrence data dating back to the dam's construction to be incorporated into the models. Additional fish data were collected from Kevin Mayes, Texas Parks and Wildlife, and Matt Troia, University of Texas at Tyler (Appendix B).

MODELING

We used the software package Maxent for our ecological niche modeling (Dudik et al., 2010). The analysis was limited to locations falling within east Texas, including the Trinity River as our western boundary and incorporating the Cypress, Sulphur, Sabine, Neches, and Angelina Rivers into our models. Habitat suitability models were built separately for each species. Species with less than five occurrence points were not modeled (Pearson et al., 2007). Eleven GIS layers were incorporated in the model, including infiltration excess and overland flow, groundwater recharge, soil type, vegetation type, sunlight, aquifers, spring source density, density of roads, density of dams, total nitrogen load, and landform. The sunlight layer provided information regarding solar radiation and mean annual cloud cover (Kriticos et al., 2012). Freshwater mussels are filter feeders and require a food supply rich in filamentous algae and other algae species which are photosynthetic organisms. We performed a kernel density function (Silverman, 1986), on the roads layer in ARCMap version 9.3 (ESRI Inc., 2008) to provide road densities. Density of roads provides information regarding anthropogenic activity in an area and information regarding urbanization. Reservoirs (Ruddy and Hitt, 1990) was obtained as a point coverage and we used a kernel density function to provide densities of the specified features. It has been reported that reservoir construction is the most significant factor influencing mussel populations (Neck, 1982). Landcover types were described in the vegetation layer (McMahan et al., 1984), major soil types were provided in the soil layer (Soil survey staff, 2006). The landform layer describes slope, local relief, profile type, percentage of area occupied by sand, ice and standing water, and patterns of major peaks (Hammond, 1964). In streams and rivers, habitat parameters including land use and landform characteristics are known to influence local habitat and biological diversity (Allan and Flecker, 1993; and Strayer, 2008). Landcover is a vital component in determining species endangerment "hot spots" in the United States (Flather et al. 1998). Soil type, vegetation, and land-use characteristics influence the hydrology and movement of water into a watershed. We also performed the kernel density function on the spring layer (Heitmuller and Williams, 2006). Hydrography features and the major aquifers were obtained from the aquifers layer (Hayes, 2006). The groundwater recharge layer provided the mean annual ground water recharge estimates (Wolock, 2003a). Information regarding infiltration excess and overland flow estimates were provided in the TopModel layer (Wolock, 2003b). River systems behave differently depending on the relative contribution of groundwater versus surface flow; therefore, alterations in overland flow and groundwater recharge result in variations in velocities which may select for individuals that are capable of surviving in modified flow regimes (Statzner et al. 1988). Sparrow modeling provided the estimate of total nitrogen loads in the

watershed (Smith et al., 1997) which influences the eutrophication of a system and may eliminate essential food supplies.

Most environmental data were obtained as raster files; vector data were converted to raster format in ArcMap with the Feature to Raster Conversion tool. Environmental layers were clipped in order to constrain the models to lotic habitats. We did this by adding a 1000m buffer around water features (ponds, streams, river, canals, and dams), obtained from an environmental layer called "NHDFlowline" obtained from the US Geological Survey (USEPA and USGS, 2005), and clipping the environmental layers to match the lotic buffer. The environmental data were projected in the Universal Transverse Mercator coordinate system North American Datum 1983 (XY coordinate system GCS_North_America_1983), and the cell sizes were equalized to a resolution of 0.014 arc-second resolution (approximately 4 m²). Once the environmental layers were processed in this way, they were converted to ASCII format for Maxent analysis.

In Maxent, we used the cross-validation option to assess predictive ability and usefulness as a model (Pearson et al., 2007); each species occurrence data point was used as the test data, in turn, while all the other occurrence points were used as the training data. In order to determine model fit for each species we used AUC and gain generated by the software. The area under the operator receiving curve, AUC (Fielding and Bell, 1997), measures the probability that a randomly chosen presence site will be ranked above a randomly chosen pseudoabsence site (Phillips and Dudik, 2008). Models with AUC > 0.75 are traditionally thought of as useful (Elith, 2002), but this cutoff is arbitrary (Elith et al., 2006; Lobo et al., 2008). Gain is the mean log probability of the occurrence samples, minus a constant that makes the uniform distribution have zero gain. In addition

to presenting the gain for the full model with all environmental variables, Maxent provides, for each environmental variable, gains for models created with only one environmental variable. We used the gains of each one-variable model and compared them to the gain of the full model, to determine what proportion of the total gain was accounted for by each variable. If an environmental variable's gain when modeled alone was less than five percent of the gain for the entire model, the variable was removed.

The niche identity test allows the user to test whether the habitat suitability scores generated by the ecological niche models from two species exhibit statistically significant ecological differences. It does this by pooling empirical occurrence points and randomizing their identities to produce two new samples with the same numbers of observations as the empirical data.

For niche models that had a good fit to the data (AUC > 0.75), we further tested whether they were significantly different from one another. We did this using ENMTools, a software package that allows one to test whether the habitat suitability scores generated by niche modeling for two species exhibit statistically significant ecological differences (Warren et al., 2010). Specifically, for every possible pair of species' niche models, we used the "niche identity test" module which asks whether niche models generated from two or more species are more different than expected if they were drawn from the same underlying distribution. It does this by pooling empirical occurrence points and randomizing (permuting) their identities to produce two new samples with the same numbers of observations as the empirical data (Warren et al., 2010). We repeated this procedure 100 times, generating niche similarity values based on the permutated data

from each run. This gave us our distribution under the null hypothesis of no difference in the niches of two species.

ENMtools output provides three different statistics to measure niche similiarity: Schoener's D (Schoener, 1968), the *I* statistic (Warren et al., 2008), and relative rank, RR (Warren and Seifert, 2011). All three metrics range from zero to one; zero indicating that species have completely different models and one meaning that the pair of species have identical models. The *I* and D statistic are calculated by taking the difference between the species suitability score at each grid cell, after the suitabilities have been standardized so that they sum to one over the geographic space being measured. The relative rank is an estimate of the probability that the relative ranking of any two patches of habitat is the same for the two models. Although the statistics emphasize different aspects of the data, we chose to use the *I* statistic because it has been shown that RR, *I*, and D metrics are highly correlated (Warren et al. 2008).

We calculated the five percent quantile of the null distribution of the *I* statistic using the R statistics software package (R Development Team, 2008). We considered two species to have significantly different niches if the observed *I* statistic was below the five percent quantile from the null distribution (corresponding to a 5% chance that two niche models would be that different if they were estimated from two species that actually had the same niche).

RESULTS

We did not obtain occurrence data for the Blackspot Shiner, Ironcolor Shiner, Silverband Shiner, Paddlefish, or the Bluehead Shiner. Only one occurrence point was provided for the American Eel and three for the Creek Chubsucker.

Six Blue Sucker and fifteen Sabine Shiner specimens were collected throughout east Texas (Appendix A). For the Blue Sucker model, the training AUC was 0.9986 and the test AUC was 0.4884. The model for Sabine Shiner had a training AUC of 0.998 and a test AUC of 0.36 indicating that the models did not perform better than random (Table 2.1).

The training AUC values for mussels ranged from 0.9898-0.9976 and test AUC values ranged from 0.7788-0.9097, indicating that all of the models are potentially useful (Table 2.2). As previously stated, environmental variables were only used if they contributed more than five percent to the full model (as measured by test gain when the model only included that particular environmental variable). The relative contributions of the different environmental variables to the niche models varied depending on the particular species. Out of the eleven environmental variables incorporated into this study, soil type contributed the most information to niche models of all mussel species. The only variable that contributed to the southern hickorynut model was soil type (Table 2.3). Aquifers, road density, landform, total nitrogen load, groundwater recharge, soil, annual mean cloud cover, Topmodel, and vegetation contributed more than five percent to the full model for Louisiana Pigtoe. The variables incorporated into the Texas Pigtoe model
were aquifers, spring density, landform, total nitrogen load, groundwater recharge, soil type, mean annual cloud cover, Topmodel, and vegetation. The environmental variables used for the Triangle Pigtoe were aquifers, reservoir density, landform, total nitrogen load, soil type, mean annual cloud cover, groundwater recharge, Topmodel, and vegetation. The Sandbank Pocketbook model incorporated aquifers, landform, total nitrogen load, groundwater recharge, soils, mean annual cloud cover, Topmodel, and vegetation. Finally, aquifers, reservoir density, spring density, landform, total nitrogen load, soils, Topmodel, and vegetation were incorporated in the Texas Heelsplitter model.

Each of the mussel species' niche models was significantly different from the other species' niche models, as indicated by the permutation tests (Table 2.4). Texas Pigtoe had the largest predicted distribution, including areas of the Trinity, Sabine, Neches, and Sulphur Rivers (Figure 2.2). The highest habitat suitabilities were predicted in the Sabine and lower Neches River, where a majority of the sampling efforts were concentrated. Louisiana Pigtoe and Triangle Pigtoe were both predicted to occur in the Neches and Angelina Rivers (Figure 2.3 and 2.4). Despite similarities between the potential distributions of these two species, Triangle Pigtoe showed higher habitat suitability in the Angelina River even though both the Louisiana Pigtoe and the Triangle Pigtoe have been found in the Angelina River. Sandbank Pocketbook was predicted to occur in the Sabine, Neches, Trinity, and Angelina Rivers with the highest habitat suitabilities occurring in areas of the Sabine and the lower Neches Rivers (Figure 2.5). The model for Texas heelsplitter predicted a sparse distribution in the Neches and Sabine Rivers (Figure 2.6). Southern hickorynut had the smallest predicted distribution, indicating occurrence only in the Neches River (Figure 2.7). The predicted distribution

for southern hickorynut corresponded with previous sampling efforts. A majority of occurrence localities for the Southern hickorynut occurred in the Neches River; however, one was found in the Sabine River in 1984 (Appendix B). The report of the southern hickorynut in the Sabine River may be caused by mistaken field identification providing an inaccurate distribution of this rare Unionid.

DISCUSSION

Ecological niche distribution patterns for the Blue Sucker and Sabine Shiner were unable to be modeled at this time. Two factors are known to inhibit predictive performance of the niche models of these species which are insufficient data of species occurrence and incorrect model specifications (e.g. environmental layers) (Barry and Elith, 2006). Our lack of occurrence data and choice of environmental layers may have contributed to our inability to successfully model the fish species.

Because fish are mobile organisms, various types of habitats might need to be included in each pixel to fulfill the different environmental requirements of the species (e.g., foraging and reproduction) (Mackey and Lindenmayer, 2001). To ensure that all habitat types are incorporated, it may be important to use larger pixels to account for larger portions of the landscape (Jaberg and Guisan, 2001). Fish also tend to utilize different habitats during specific life stages. Adult Blue Suckers utilize riffles and are often associated with swift flows (Morey and Berry, 2003) while shallow, slack water habitats are vital nursery areas for juveniles (Adams et al., 2006). Variation in habitat during a lifecycle would indicate the importance of fitting separate models for the various life stages (Guisan and Thuiller, 2005).

The spatial scale of the study should also be taken into consideration. The size of the geographic region of interest influences the importance of abiotic versus biotic factors: small scale studies have indicated a greater impact of competition and large scale studies have emphasized abiotic controls (Jackson et al., 2001). A higher variation in

biotic factors can be seen at the smaller scale than at a larger scale. A majority of variables in this study correspond to flow dynamics. Biotic variables relating to species interactions were not incorporated into our models. Recent analyses have shown that the predictive power of models can be increased significantly by incorporating variables representing the presence-absence of known competitors suggesting that competition might influence species distributions (Leathwick and Austin, 2001; Anderson et al,. 2002). Resource partitioning among fishes indicate that competition plays an important role in the organization of communities (Ross, 1986). Biotic interactions impact the geographic distribution of a species and must be taken into account when studying relationships between a species and its environment. We may be able to improve the prediction accuracy of the models for the fish species by incorporating biotic variables such as competition and predation.

Our study provides the first predicted niche distribution maps for rare mussels in east Texas. The models identify regions that have similar environmental conditions to where current populations are maintained. Also, soil type was the most important environmental parameter for all rare mussel species in our models. Landform and vegetation were also important variables for predicting mussel niche distributions. Previous research has shown that, species distributions may be influenced by habitat parameters including landform, watershed slope, soil composition, vegetation and landuse characteristics (Morris and Corkum, 1996; Brainwood et al., 2006). Because our models used landscape characteristics to map the fundamental niche of the species, the suitable habitat for these rare species may be overpredicted in some areas (Pearson 2007,

Murienne et al., 2009). However, the highest suitability scores appear to correspond to areas of occurrence.

State-threatened mussels were predicted to inhabit all major rivers in east Texas; however, our models predicted that all rare species modeled occur in the Neches River, one of the largest rivers in east Texas. This is likely a result of fewer alterations and an increase in habitat conservation efforts within the watershed including Davy Crockett National Forest, Big Thicket National Preserve, and the Neches River National Wildlife Refuge. The riparian corridor of the Neches watershed is considered to be bottomland hardwood forest floors, with piney woods vegetation and oak-hickory pine forest in the uplands (Fish and Wildlife Service, 1979). The vegetation of this region helps reduce the influence of impervious overland flow that would cause increased velocities which is more typical of urbanized areas. Recent studies have also shown that the Neches River has sections that are adequately connected to its floodplain (Troia, 2010). The lack of human alteration to the Neches watershed likely allows the mussels to remain in the substrate during seasonal flooding and inundation of the floodplain. The Angelina River is a major tributary of the Neches River and shares characteristics with the Neches River because of its close proximity.

The Sabine River is characterized by flat slopes and wide timbered floodplains. The upper reaches flow through prairie lands and contain deep sandy loam substrates. The lower portions of the Sabine River flow through flat terrain with hardwoods and forests consisting of hardwoods and conifers. Because of anthropogenic impacts, the Sabine River has low channel-floodplain connectivity (Phillips, 2008a). The Texas Pigtoe, Sandbank Pocketbook, and Texas Heelsplitter were predicted to occur in the

Sabine River and these species are known to occur in the Sabine River watershed (Howells et al., 1996).

The Trinity River is very different from other east Texas rivers with regards to soil and vegetation. The Trinity River basin is defined by gentle topography and mostly clay loam soils with cropland and rangeland as the dominant land cover. Research has shown that clay and loam soils impact surface water runoff and thus the addition of nitrogen in the Trinity River watershed (Chen et. al., 2000). Along with agricultural practices, urbanized areas are prominent throughout the Trinity River watershed including the cities of Fort Worth and Dallas. Anthropogenic impacts may influence the ability of rare mussels to survive in and inhabit the Trinity River watershed. However, the low habitat suitability scores we found in the Trinity River could be a result of the lack of sampling intensity in this portion of east Texas (Phillips, 2008b). Because the habitat in the Trinity River is drastically different from other east Texas rivers, correlations between mussel populations and environmental conditions in the Trinity River may not have been accurately portrayed. Three species had low habitat suitability scores (0.04) in the Trinity River (i.e., Texas Pigtoe, Triangle Pigtoe, and Sandbank Pocketbook). The Texas Pigtoe, Triangle Pigtoe, and Sandbank pocketbook are known to inhabit a majority of east Texas rivers; however, few specimens are reported in the Trinity River basin. The Sandbank Pocketbook has not been reported in the Trinity River basin (Howells, 1996) and the Triangle Pigtoe is considered an endemic of the Neches-Angelina drainage (Howells, 2011). The Texas Pigtoe has only recently been reported in the Trinity River (Appendix B).

CONCLUSIONS

In summary, I was able to successfully create niche models that predict the known presences of several imperiled mussel species in known areas, and that forecast other suitable areas of the area that may potentially contain the mussels as well or that may be suitable for reintroduction programs. On the other hand, I was unsuccessful at constructing niche models for two fish species that may serve as hosts for some of these mussels during their early life cycle stage. The inability to model the fish species is perhaps related to the fact that adult mussels are sedentary; whereas, fish are mobile and can inhabit different environments and different times. Furthermore, while our study focused on adult mussels, we did not distinguish adult fish from juveniles, which may have different habitat preferences. Future work on modeling of the fish distributions could provide information regarding habitat associations, life history information, and identify factors limiting populations for imperiled fish species. Fish distribution models could identify high priority habitat and link imperiled species sites with threats to address management options and guide restoration efforts.

Although several layers went into producing the potential geographic distribution maps, many factors influencing the dimensions of the realized niche were not taken into account, such as biotic interactions (e.g., predators, parasites and possible fish hosts). However, incorporating biotic components could improve the predictive accuracy of my models (Guisan and Zimmerman, 2000; Broennimann et al., 2007; Giovanelli et al., 2008). Fish are important components of Unionid distributions because Unionids

experience an obligate ectoparasitic larval stage called glochidia that attach to a fish or salamander host after release from the adult mussel. Some species of Unionidae are able to parasitize a taxonomically wide variety of fish species (Trdan and Hoeh, 1982) while others can use only a few closely related species (Zale and Neves, 1982; Yeager and Saylor, 1995). Integrating information regarding the presence of known fish host data through identification of potential glochidia-host relationships into our ecological niche models may provide a better understanding of the geographic distribution of east Texas Unionids and improve AUC test scores.

Along with the integration of biotic variables, future research should be directed at determining the reliability of ecological niche models to forecast the occurrence of rare mussels. The potential distribution maps produced from this study will provide a guide for ground truthing the models I created. Ground truthing will help determine whether Maxent and ecological niche models in general provide an adequate representation of the true spatial distribution of rare mussels in east Texas. The information provided in this thesis is timely and highly relevant given the potential threats to lotic habitats and to overall diversity in East Texas rivers. The information provided from the potential distribution maps may aid in field surveys and allocation of conservation resources by providing valuable biogeographical information that will help in planning land use management around existing populations, discovering new populations, identifying toppriority survey sites, or setting priorities to restore natural habitat (Kumar and Stohlgran, 2009; Raxworthy et al., 2003; Bourg et al., 2005).

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Figure 2.1. Points indicate locations of sampling reaches in the Upper Neches and Upper Sabine River.



Figure 2.2 Predicted potential suitable habitat for *Fusconaia askewi* in east Texas. The colorization scheme represents the predicted habitat suitability for the *F. askewi* with red being the most suitable habitat and blue indicating the least suitable habitat. The black points indicate occurrence locations.



Figure 2.3. Predicted potential suitable habitat for *Pleuroblema riddellii* in east Texas. The colorization scheme represents the predicted habitat suitability for the *P. riddellii* with red being the most suitable habitat and blue indicating the least suitable habitat. The black points indicate occurrence locations.



Figure 2.4. Predicted potential suitable habitat for *Fusconaia lananensis* in east Texas. The colorization scheme represents the predicted habitat suitability for the *F. lananensis* with red being the most suitable habitat and blue indicating the least suitable habitat. The black points indicate occurrence locations.



Figure 2.5. Predicted potential suitable habitat for *Lampsilis satura* in east Texas. The colorization scheme represents the predicted habitat suitability for the *L. satura* with red being the most suitable habitat and blue indicating the least suitable habitat. The black points indicate occurrence locations.



Figure 2.6. Predicted potential suitable habitat for *Potamilus amphichaenus* in east Texas. The colorization scheme represents the predicted habitat suitability for the *P*. *amphichaenus* with red being the most suitable habitat and blue indicating the least suitable habitat. The black points indicate occurrence locations.



Figure 2.7. Predicted potential suitable habitat for *Obovaria jacksoniana* in east Texas. The colorization scheme represents the predicted habitat suitability for the *O. jacksoniana* with red being the most suitable habitat and blue indicating the least suitable habitat. The black points indicate occurrence locations.

Table 2.1. Summary information for the individual fish species niche models. The AUC measures the probability that a randomly chosen presence site will be ranked above a randomly chosen presence site will be ranked above a randomly chosen pseudoabsence site; models with AUC > 0.75 are considered useful. Gain is the mean log probability of the occurrence samples, minus a constant that makes the uniform distribution have zero gain.

SPECIES	TRAINING AUC	TEST AUC	TEST GAIN
C. elongatus	0.9986	0.4884	-0.9524
N. sabinae	0.9749	0.6352	-0.1771

Table 2.2. Summary information for the individual mussel species niche models. The AUC measures the probability that a randomly chosen presence site will be ranked above a randomly chosen presence site will be ranked above a randomly chosen pseudoabsence site; models with AUC > 0.75 are considered useful. Gain is the mean log probability of the occurrence samples, minus a constant that makes the uniform distribution have zero gain.

SPECIES	TRAINING AUC	TEST AUC	TEST GAIN
P. riddellii	0.9927	0.899	0.9787
F. askewi	0.9898	0.8168	0.9766
F. lananensis	0.9941	0.9097	1.5025
L. satura	0.9927	0.8703	1.2138
O. jacksoniana	0.9969	0.7788	1.229
P. amphichaenus	0.9976	0.8141	1.4583

Table 2.3. Test gain values with only specified variables. The test gain value for the one-variable model provides the proportion of the total gain accounted for by each variable. The environmental variables were removed if the test gain of the one-variable model was less than 5% of the full model.

SPECIES	AQUIFER S	KERNEL DENSITY RESERVOIRS	KERNEL DENSITY ROADS	KERNEL DENSITY SPRINGS	LAND FORM	NITROGEN	GROUND WATER RECHARGE	SOILS	ANNUAL MEAN CLOUD COVER	TOP- MODEL	VEGETATION
P. riddellii	0.2447	-	0.3854	-	0.347	0.3529	0.3254	1.1133	0.2971	0.4258	0.894
F. askewi	0.2639	-	-	0.0601	0.1454	0.2772	0.301	0.955	0.2646	0.3026	0.7522
F. lananensis	0.2013	0.1871	-	-	0.4934	0.2155	0.1298	0.9054	0.2902	0.145	1.3643
L. satura	0.314	-	-	-	0.1954	0.233	0.2553	1.1697	0.2743	0.2043	0.3838
O. jacksoniana	-	-	-	-	-	-	-	1.229	-	-	-
P. amphichaenus	0.1006	0.087	-	0.0926	0.0988	0.1035	-	0.8804	-	0.1481	1.0568

 Table 2.4. Table for I values and 5% critical values. Two species were considered to have significantly different niches if the observed value was below the 5% critical value.

Species comparison	Observed value	5% critical value
L. satura Vs. P. riddellii	0.86	0.91
L. satura Vs. F. askewi	0.73	0.78
L. satura Vs. F. lananensis	0.68	0.91
O. jacksoniana Vs. P. riddellii	0.81	0.84
O. jacksoniana Vs. L. satura	0.78	0.82
O. jacksoniana Vs. P. amphichaenus	0.69	0.79
P. amphichaenus Vs. F. riddellii	0.61	0.86
P. amphichaenus Vs. L. satura	0.70	0.84
F. askewi Vs. P. riddellii	0.82	0.91
F. askewi Vs. P. amphichaenus	0.65	0.81
F. lananensis Vs. P. riddellii	0.78	0.87
O. jacksoniana Vs. F. askewi	0.77	0.79
O. jacksoniana Vs. F. lananensis	0.85	0.76
P. amphichaenus Vs. F. lananensis	0.49	0.86
F. askewi Vs. F. lananensis	0.75	0.84
O. jacksoniana Vs. P. riddellii	0.82	0.85

Species	Location	Drainage	Source	Date	Latitude	Longitude
Cycleptus elongatus	North of 271	Sabine	Williams and Dunithan	16-Aug-10	32.530388	-94.958797
C. elongatus	Hwy 59	Neches	Williams and Dunithan	21-Sep-10	31.137817	-94.8218833
C. elongatus	above SH 294 or L1	Neches	Troia 2010	Jul-Aug 2009	31.644950	-95.286780
C. elongatus	Below US 84	Neches	Troia 2010	Jul-Aug 2009	31.7859	-95.38458
C. elongatus	Above US 175	Neches	Troia 2010	Jul-Aug 2009	32.04528	-95.42312
C. elongatus	Downstream Hwy 190	Sabine	Kevin Mayes	18-May-06	30.730158	-93.608689
Notropis sabinae	3 miles NW of Hwy 79	Sabine	Ford and Dunithan	21-Jul-10	32.227133	-94.2478167
N. sabinae	1/8 mile West 149	Sabine	Ford and Dunithan	19-Aug-10	32.4123	-94.71338
N. sabinae	1/4 mile Upstream 43	Sabine	Ford and Dunithan	7-Oct-10	32.37211	-94.46267
N. sabinae	Hwy 79	Neches	Williams and Dunithan	24-May-11	31.89721	-95.43678
N. sabinae	below SH 294 L3	Neches	Troia 2010	Jul-Aug 2009	31.625430	-95.280270
N. sabinae	Bayou Anacoco	Sabine	Kevin Mayes	16-May-06	30.869428	-93.564325
N. sabinae	downstream of Hwy 190	Sabine	Kevin Mayes	17-May-06	30.730158	-93.608689
N. sabinae	Big Cow Creek FM 1416	Sabine	Kevin Mayes	18-May-06	30.605967	-93.79415
N. sabinae	Sabine River	Sabine	Kevin Mayes	18-Jul-06	30.33235	-93.757633
N. sabinae	East Fork San Jacinto River FM 945	Neches	Kleinsasser and Bradsby	19-Jul-99	30.425087	-95.124613
N. sabinae	Peach Creek at FM 1485	San Jacinto	Rosendale, J.	6-Aug-03	30.146956	-95.171224
N. sabinae	Caney Creek at FM 1485	San Jacinto	Rosendale, J.	13-May-03	30.148786	-95.192074
N. sabinae	Lake Creek	San Jacinto	Rosendale, J.	15-Oct-02	30.254882	-95.557934
N. sabinae	Bonita Creek	Neches	Linam, Jurgensen, Bowles	8-Aug-00	31.643	-94.662583
N. sabinae	Bonita Creek	Neches	Linam, Boles, Gibson	17-Oct-00	31.643	-94.662583

APPENDIX A: SITE DESCRIPTIONS OF OCCURRENCE LOCALITIES FOR FISH SPECIES.

Species	Location	Drainage	Source	Date	Latitude	Longitude
Pleuroblema	Angelina R., US 59 N of Lufkin & S of	Neches	USAO 4003	8-Aug-81	31.457670	-94.726370
riddellii	Nacogdoches					
P. riddellii	Angelina R., US 59 N of Lufkin & S of Nacogdoches	Neches	CMM 3375	8-Aug-81	31.457670	-94.726370
P. riddellii	Angelina R., US 59 N of Lufkin & S of Nacogdoches	Neches	Karatayev & Burlakova 2007	19-Aug-06	31.457670	-94.726370
P. riddellii	Big Sandy Creek, N of Segno (Village Creek drainage) Station 14	Neches	Bordelon and Harrel 2004	2001-2002	30.624770	-94.699980
P. riddellii	Neches R., SH 7 near Lufkin	Neches	N. Ford, pers. comm.	16-Sep-10	31.397160	-94.965970
P. riddellii	Neches R., below B.A. Steinhagen Reservoir (Town Bluff Dam B)	Neches	Howells 1997 MDS 144	17-Sep-96	30.792783	-94.167967
P. riddellii	Neches R., Big Slough (ScurlocksCamp), 7 mi NNE of Ratcliff	Neches	USAO 1727	14-Aug-82	31.486010	-95.110180
P. riddellii	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	CMM 2910-1	15-Aug-80	31.486010	-95.110180
P. riddellii	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	CMM 2937	15-Aug-80	31.486010	-95.110180
P. riddellii	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	CMM 2902	15-Aug-80	31.486010	-95.110180
P. riddellii	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	USAO 4734	16-Aug-84	31.486010	-95.110180
P. riddellii	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	CMM 3393	14-Aug-82	31.486010	-95.110180
P. riddellii	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	USAO 1727	14 Aug 1982	31.486010	-95.110180
P. riddellii	Neches R., Hickory Creek	Neches	USAO 1705	14 Aug 1982	31.484560	-95.110850

APPENDIX B: SITE DESCRIPTIONS OF OCCURRENCE LOCALITITES OF UNIONID SPECIES.

P. riddellii	Neches R., Hickory Creek	Neches	USAO 1706	14 Aug 1982	31.484560	-95.110850
P. riddellii	Neches R., near mouth Hickory Creek	Neches	USAO 1705	14-Aug-82	31.483910	-95.110910
P. riddellii	Neches R., SH 7 NW of Lufkin, SW of Pollok, E of Kennard	Neches	Karatayev & Burlakova 2007	7-Sep-07	31.396940	-94.965830
P. riddellii	Neches R., SH 94 NE Apple Springs (not Trinity R.)	Neches	CMM 2854	18-Aug-80	31.289090	-94.884020
P. riddellii	Neches R., SH 94, 7 mi NE Apple Springs, SW of Lufkin	Neches	CMM 2902	18-Aug-80	31.289400	-94.883980
P. riddellii	Neches R., SH 94, 7 mi NE Apple Springs, SW of Lufkin	Neches	CMM2854	18-Aug-80	31.289400	-94.883980
P. riddellii	Neches R., US 96, W of Evadale, E of Silsbee	Neches	USAO 6077	17 Aug 1990	31.357150	-94.093780
P. riddellii	Village Creek, FM 418	Neches	Howells (2006)	3-Sep-05	30.292783	-94.167983
P. riddellii	Village Creek, NE of Lumberton, Station 16	Neches	Bordelon and Harrel 2004	2001-2002	30.261960	94.17996
P. riddellii	Village Creek, near RR xing N of Creek Road N of Fletcher, Station 1	Neches	Bordelon and Harrel 2004	2001-2002	30.276060	94.18746
P. riddellii	Village Creek, SH 327	Neches	Howells (2006)	3-Sep-05	30.346933	-94.239217
P. riddellii	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW)	Neches	Howells (2006)	3-Sep-05	30.285083	-94.191467
P. riddellii	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW)	Neches	USAO 3526	15-Aug-86	30.285083	-94.191467
P. riddellii	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW), Station 3	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	2-May-02	30.285083	-94.191467

P. riddellii	Village Creek, Village Creek State Park	Neches	HMNS	18-Aug-80	30.255733	-94.170767
P. riddellii	Villlage Creek, off lower Village Creek Road NE of Lumberton, Station 2	Neches	Bordelon and Harrel 2004	2001-2002	30.255840	-94.172510
P. riddellii	Sabine R., US 271 at Gladewater	Sabine	USAO 1501	20-Aug-84	32.527590	-94.690170
P. riddellii	Sabine R., US 271 Gladewater	Sabine	USAO 3502	20 Aug 1984	32.527590	-94.690170
P. riddellii	Neches R., above US 75 (U2)	Neches	Troia 2010	Jul-Aug 2009	32.041670	-95.422920
P. riddellii	Neches R., above US 84 (M1)	Neches	Troia 2010	Jul-Aug 2009	31.784980	-95.394670
P. riddellii	Neches R., below US 84 (M2)	Neches	Troia 2010	Jul-Aug 2009	31.770530	-95.396690
P. riddellii	Neches R., below US 84 (M3)	Neches	Troia 2010	Jul-Aug 2009	31.764550	-95.400670
P. riddellii	Neches R., above SH 294 (D or L2)	Neches	Troia 2010	Jul-Aug 2009	31.639720	-95.283700
P. riddellii	Neches R., below SH 294 (D or L3)	Neches	Troia 2010	Jul-Aug 2009	31.625430	-95.280270
P. riddellii	Hwy 59	Neches	Ford and Dunithan, 2011	21-Sep-10	31.1378167	-94.8218833
P. riddellii	Hwy 7	Neches	Ford and Dunithan, 2011	16-Sep-10	31.3997	-94.9755
P. riddellii	Hwy 79	Neches	Ford and Dunithan, 2011	24-May-11	31.89721	-95.43678
P. riddellii	US 59 crossing	Angelina	Bennett, 2006	19-Aug-11	31.486933	-94.8236
P. riddellii	SH 327	Village Creek	Bennett, 2006	4-Sep-05	30.346933	-94.239217
P. riddellii	US 96	Village Creek	Bennett, 2006	5-Sep-05	30.285083	-94.191467
Lampsilis satura	Angelina R., SH 21 at Old Lindwood	Neches	USAO 2795	9-Aug-94	30.254210	-94.129810

L. satura	Angelina R., SH 7 crossing NE of Pollock	Neches	Karatayev & Burlakova 2007	7-Sep-06	30.255840	-94.172510
L. satura	Angelina R., US 59 N of Lufkin & S of Nacogdoches	Neches	USAO 4010	8-Aug-81	30.261960	-94.179960
L. satura	Neches R., below B.A. Steinhagen Reservoir (Town Bluff Dam B)	Neches	Howells 1995 MDS 119	3-May-93	30.268240	-94.179980
L. satura	Neches R., below B.A. Steinhagen Reservoir (Town Bluff Dam B)	Neches	Howells 1997 MDS 144	30-Jan-96	30.276060	-94.187460
L. satura	Neches R., below B.A. Steinhagen Reservoir (Town Bluff Dam B)	Neches	Howells 1997 MDS 144	17-Sep-96	30.285083	-94.191467
L. satura	Neches R., below B.A. Steinhagen Reservoir (Town Bluff Dam B)	Neches	McCullagh database	18-Jun-05	30.339790	-94.212190
L. satura	Neches R., below B.A. Steinhagen Reservoir (Town Bluff Dam B)	Neches	McCullagh database	18-Jun-05	30.369910	-94.265360
L. satura	Neches R., D-2, above FM 294	Neches	Troia 2010	2009	30.792783	-94.167967
L. satura	Neches R., D-3, below FM 294	Neches	Troia 2010	2009	30.792950	-95.167967
L. satura	Neches R., Hickory Creek	Neches	USAO 1688	14 Aug 1982	30.795630	-94.180110
L. satura	Neches R., M-1, above US 87	Neches	Troia 2010	2009	31.289400	-94.883980
L. satura	Neches R., M-3, below US 87	Neches	Troia 2010	2009	31.357150	-94.093780
L. satura	Neches R., near mouth Hickory Creek	Neches	USAO 1688	14-Aug-82	31.396940	-94.965830
L. satura	Neches R., SH 7 NW of Lufkin, SW of Pollok, E of Kennard	Neches	N. Ford, pers. comm.	16-Sep-10	31.397160	-94.965970
L. satura	Neches R., SH 94, 7 mi NE Apple Springs, SW of Lufkin	Neches	CMM 2846	18-Aug-80	31.457670	-94.726370
L. satura	Neches River, Evadale. US 96	Neches	Roback et al. 1980		31.483910	-95.110910

L. satura	Village Creek, E of Fletcher, Station 15	Neches	Bordelon and Harrel 2004	2001-2002	31.484560	-95.110850
L. satura	Village Creek, E of Kountze, Station 21	Neches	Bordelon and Harrel 2004	2001-2002	31.486010	-95.110180
L. satura	Village Creek, near RR xing N of Creek Road N of Fletcher, Station 1	Neches	Bordelon and Harrel 2004	2001-2002	31.625430	-95.280270
L. satura	Village Creek, SW of Silsbee, Station 19	Neches	Bordelon and Harrel 2004	2001-2002	31.627140	-95.281910
L. satura	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW)	Neches	USAO 3519	15-Aug-86	31.633300	-95.287680
L. satura	Village Creek, off lower Village Creek Road NE of Lumberton, Station 2	Neches	Bordelon and Harrel 2004	2001-2002	31.639720	-95.283700
L. satura	Sabine R., above US 69 (S of Mineola)	Sabine	N. Ford, pers. comm.	8-Jun-10	31.672490	-94.952730
L. satura	Sabine R., SH 149 S of Longview	Sabine	USAO 3595	14-Aug-81	31.674550	-95.400670
L. satura	Sabine R., SH 43, SW of Tatum	Sabine	Howells 1996 MDS 120	5-Jul-94	31.774530	-95.399080
L. satura	Sabine R., SH 43, SW of Tatum	Sabine	Howells (2006)	16-Aug-05	31.780520	-95.395540
L. satura	Sabine R., SH 43, SW of Tatum	Sabine	Howells (2006)	18-Aug-05	31.784980	-95.394670
L. satura	Sabine R., US 59	Sabine	Karatayev & Burlakova 2007	19-Aug-06	32.312740	-94.526490
L. satura	Neches R., above SH 294 (D or L2)	Neches	Troia 2010	Jul-Aug 2009	32.329310	-94.353910
L. satura	Neches R., below SH 294 (D or L3)	Neches	Troia 2010	Jul-Aug 2009	32.417500	-94.710050
L. satura	Neches R., below B.A. Steinhagen Reservoir (Town Bluff Dam B)	Neches	H. McCullagh, pers. comm.	11-Apr-00	32.613420	-95.487180

L. satura	Hwy 7	Neches	Ford, Dunithan	16-Sep-10	31.3997	-94.9756
L. satura	Hwy 79	Neches	Ford, Dunithan	22-Jun-11	31.89721	-95.43678
L. satura	1/2 Mile E of 149	Sabine	Ford, Dunithan	8/19/2010	32.418667	-94.705433
L. satura	1/8 Mile W of 149	Sabine	Ford, Dunithan	20-Jul-10	32.4123	-94.71338
L. satura	3 miles NW of Hwy 79	Sabine	Ford, Dunithan	21-Jul-10	32.227133	-94.2478167
L. satura	N of 271	Sabine	Ford, Dunithan	17-Aug-10	32.530388	-94.958797
L. satura	Downstream 59	Sabine	Ford, Dunithan	2-Jun-11	32.31485	-94.34042
L. satura	SR 7	Angelina	Bennett	Sep-7-06	31.457087	-95.726190
L. satura	US 59	Sabine	Bennett	18-Aug-06	32.327900	-94.352920
L. satura	CR 4400, Woodville	Neches	Bennett	28-Oct-05	30.792783	-94.167983
Obovaria jacksoniana	Neches R., Big Slough (ScurlocksCamp), 7 mi NNE of Ratcliff	Neches	USAO 1725	14-Aug-82	30.25584	-94.17251
0. jacksoniana	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	USAO 437	15-Aug-80	30.28508	-94.19147
O. jacksoniana	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	USAO 4735	16-Aug-84	30.33423	-94.20413
O. jacksoniana	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	USAO 1725	14 Aug 1982	30.33979	-94.21219
O. jacksoniana	Neches R., Hickory Creek	Neches	USAO 1694	14 Aug 1982	31.39716	-94.96597
O. jacksoniana	Neches R., near mouth Hickory Creek	Neches	USAO 1694	14-Aug-82	31.48391	-95.11091
O. jacksoniana	Neches R., SH 7 NW of Lufkin, SW of Pollok, E of Kennard	Neches	Karatayev & Burlakova 2007	7-Sep-07	31.48456	-95.11085

O. jacksoniana	Village Creek, Baby Galvez boat ramp area, Station 5	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	10-May-02	31.48601	-95.11018
O. jacksoniana	Sabine R., US 59 ca 18mi N of Carthage	Sabine	USAO 3453	19-Aug-84	31.76981	-95.39754
O. jacksoniana	Neches R., 1.3 km below US 84	Neches	Ford & Troia, In Press	9-Jul-09	31.77053	-95.39668
O. jacksoniana	Neches R., above US 84	Neches	Troia 2010	Jul-Aug 2009	31.78498	-95.39467
O. jacksoniana	Neches R., below US 84	Neches	Troia 2010	Jul-Aug 2009	32.32931	-94.35391
Potamilus amphichaenus	B.A. Steinhagen Reservoir, all sites combined	Neches	Howells 1997 MDS 144	27-30 Jan 1996	30.312140	-93.748000
P. amphichaenus	B.A. Steinhagen Reservoir, NE of US 190	Neches	Howells (2006)	24-Oct-05	30.840050	-94.168500
P. amphichaenus	B.A. Steinhagen Reservoir, S side Martin Dies State Park at PR 48	Neches	Howells (2006)	24-Oct-05	30.852200	-94.209560
P. amphichaenus	B.A. Steinhagen Reservoir, several sites combined	Neches	Howells 1995 MDS 119	29-Dec-93	30.852517	-94.173517
P. amphichaenus	B.A. Steinhagen Reservoir, SW corner reservoir, W side of dam	Neches	Howells (2006)	24-Oct-05	30.854300	-94.218130
P. amphichaenus	Neches R., SH 7 near Lufkin	Neches	N. Ford, pers. comm.	16-Sep-10	30.862583	-94.182800
P. amphichaenus	Sabine R., between FM 1804 & FM 13	Sabine	Howells (2006), N. Ford (pers. comm.)	1-2 Apr 2004	31.358603	-94.088117
P. amphichaenus	Sabine R., SH 43, SW of Tatum	Sabine	Howells (2006)	18-Aug-05	32.312740	-94.526490
P. amphichaenus	Sabine, Tawakoni to SH 19	Sabine	Ford et al. 2007		32.811330	-95.916080
P. amphichaenus	Neches R., US 96	Neches	H. McCullagh, pers. comm.	14-Apr-00	32.811580	-95.912030
P. amphichaenus	Neches R., below B.A. Steinhagen Reservoir (Town Bluff Dam B)	Neches	H. McCullagh, pers. comm.	11-Apr-00	32.909690	-95.999890

P. amphichaenus	1/8 mi N 1794	Sabine	Ford and Dunithan 2011	22-Jul-11	32.293650	-94.335850
P. amphichaenus	1/8 mi E 1794	Sabine	Ford and Dunithan, 2011	22-Jul-11	32.281167	-94.325416
P. amphichaenus	Coal Company	Sabine	Neil Ford	27-Jul-11	32.397033	-94.500367
P. amphichaenus	Coal Company	Sabine	Neil Ford	25-Jun-11	32.394183	-94.497583
P. amphichaenus	Hwy 7	Neches	Ford, Dunithan	16-Sep-10	31.3997	-94.9756
P. amphichaenus	Hwy 79	Neches	Ford, Dunithan	22-Jun-11	31.89721	-95.43678
P. amphichaenus	N of Hwy 69	Sabine	Ford, Dunithan	8-Jun-10	32.6129	-95.48643
P. amphichaenus	Upstream of Hwy 14	Sabine	Ford, Dunithan	7-Oct-10	32.5631167	-95.2031833
P. amphichaenus	Downstream 59	Sabine	Ford, Dunithan	2-Jun-11	32.314850	-94.340420
P. amphichaenus	US 59	Sabine	Bennett	18-Aug-06	32.327900	-94.352920
P. amphichaenus	HWY 59	Sabine	Bennett	16-Aug-05	32.327900	-94.352920
P. amphichaenus	Hwy 43	Sabine	Bennett	16-Aug-05	32.390834	-94.441892
Fusconaia askewi	Big Cypress Bayou, 1 mi above US 59	Big Cypress	Shafer et al. 1992	Aug-Sep 1992	32.757760	-94.358890
F. askewi	Big Cypress Bayou, 1.2 km below Fort Sherman Dam	Big Cypress	Howells (2006)	4-Jun-06	33.092067	-95.014583
F. askewi	Angelina R., SH 7 crossing NE of Pollock	Neches	Karatayev & Burlakova 2007	7-Sep-06	31.397160	-94.965970
F. askewi	Angelina R., US 59 N of Lufkin & S of Nacogdoches	Neches	USAO 4000	8-Aug-81	31.457670	-94.726370
F. askewi	Angelina R., US 59 N of Lufkin & S of Nacogdoches	Neches	CMM 3374	8-Aug-81	31.457670	-94.726370
F. askewi	Beech Creek, Gore Store Road W of FM 92 (Village Creek drainage) Station 12	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	31-May-02	30.490533	-95.262400
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F. askewi	Turkey Creek, Hester Bridge, Village Creek State Park, Station 11	Neches	Howells 2003 MDS 214/Bordelon and Harrel 2004	28-May-02	30.551650	-94.332233
F. askewi	Village Creek, Baby Galvez boat ramp area, Station 5	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	10-May-02	30.334233	-94.204133
F. askewi	Village Creek, E of Fletcher, Station 15	Neches	Bordelon and Harrel 2004	2001-2002	30.268240	-94.179980
F. askewi	Village Creek, E of Kountze, Station 21	Neches	Bordelon and Harrel 2004	2001-2002	30.369910	-94.265360
F. askewi	Village Creek, FM 418	Neches	Howells (2006)	3-Sep-05	30.292783	-94.167983
F. askewi	Village Creek, FM 418, Station 8	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	20-May-02	30.292783	-94.167983
F. askewi	Village Creek, lower creek between northern-most tribs, Station 17	Neches	Bordelon and Harrel 2004	2001-2002	30.254210	-94.129810
F. askewi	Village Creek, lower creek, upstream of Neches R. and ponded area, Station 18	Neches	Bordelon and Harrel 2004	2001-2002	30.250660	-94.214760
F. askewi	Village Creek, NE of Lumberton, Station 16	Neches	Bordelon and Harrel 2004	2001-2002	30.261960	-94.179960
F. askewi	Village Creek, near RR xing N of Creek Road N of Fletcher, Station 1	Neches	Bordelon and Harrel 2004	2001-2002	30.276060	-94.187460
F. askewi	Village Creek, New FM 418 NE on Kountze, Station 20	Neches	Bordelon and Harrel 2004	2001-2002	30.398100	-94.264400
F. askewi	Village Creek, SH 327, Station 6	Neches	Howells 2003 MDS 214 /Bordelon and	14-May-02	30.346933	-94.239217

F. askewi	Village Creek, SW of Silsbee, Station 19	Neches	Bordelon and Harrel 2004	2001-2002	30.339790	-94.212190
F. askewi	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW)	Neches	USAO 3527	15-Aug-86	30.285083	-94.191467
F. askewi	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW)	Neches	Howells (2006)	3-Sep-05	30.285083	-94.191467
F. askewi	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW), Station 3	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	2-May-02	30.285083	-94.191467
F. askewi	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW), Station 4	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	8-May-02	30.285083	-94.191467
F. askewi	Villlage Creek, off lower Village Creek Road NE of Lumberton, Station 2	Neches	Bordelon and Harrel 2004	2001-2002	30.255840	-94.172510
F. askewi	Neches R., Big Slough (ScurlocksCamp), 7 mi NNE of Ratcliff	Neches	USAO 1726	14-Aug-82	31.486010	-95.110180
F. askewi	Neches R., Big Slough (ScurlocksCamp), 7 mi NNE of Ratcliff	Neches	USAO 4733	16-Aug-84	31.486010	-95.110180
F. askewi	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	CMM 2909	15-Aug-80	31.486010	-95.110180
F. askewi	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	CMM 2912-3	15-Aug-80	31.486010	-95.110180
F. askewi	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	CMM 2936	15-Aug-80	31.486010	-95.110180
F. askewi	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	CMM 3392	14-Aug-82	31.486010	-95.110180
F. askewi	Neches R., Big Slough, 7 mi NNE of Ratcliff	Neches	USAO 1726	14 Aug 1982	31.486010	-95.110180
F. askewi	Angelina R., SH 21 at Old Linnwood	Neches	USAO 2800	9-Aug-84	31.672490	-94.952730

F. askewi	Big Sandy Creek, N of Segno (Village Creek drainage) Station 14	Neches	Bordelon and Harrel 2004	2001-2002	30.624770	-94.699980
F. askewi	Hickory Creek, US 69 W of Hicksbourgh, Station 22	Neches	Bordelon and Harrel 2004	2001-2002	30.561520	-94.400070
F. askewi	Sabine R., Gladewater	Sabine	USAO 3500	20-Aug-84	32.527420	-94.960090
F. askewi	Sabine R., SH 43, SW of Tatum	Sabine	Howells 1996 MDS 120	5-Jul-94	32.312740	-94.526490
F. askewi	Sabine R., SH 43, SW of Tatum	Sabine	Howells (2006)	16-Aug-05	32.312740	-94.526490
F. askewi	Sabine R., SH 43, SW of Tatum	Sabine	Howells (2006)	18-Aug-05	32.312740	-94.526490
F. askewi	Sabine R., US 59	Sabine	USAO 2793	19-Aug-84	32.329310	-94.353910
F. askewi	Sabine R., US 59	Sabine	USAO 3454	19-Aug-84	32.329310	-94.353910
F. askewi	Sabine R., US 59	Sabine	Howells 1996 MDS 120	5-Jul-94	32.329310	-94.353910
F. askewi	Sabine R., US 59 N of Carthage	Sabine	CMM 3379	9-Aug-81	32.329310	-94.353910
F. askewi	Sabine R., US 59 N of Carthage	Sabine	USAO 6716	17-Aug-92	32.329310	-94.353910
F. askewi	Sabine R., between US 59 and Black Shoals	Sabine	Howells 1996 MDS 125	28-Jun-95	32.328430	-94.353890
F. askewi	Sabine R., US 59 up- and down-stream	Sabine	Howells (2006)	16-Aug-05	32.329310	-94.353910
F. askewi	Sabine R., US 59	Sabine	Karatayev & Burlakova 2007	19-Aug-06	32.329310	-94.353910
F. askewi	Sabine R., between FM 1804 & FM 14	Sabine	Howells (2006), N. Ford (pers. comm.)	1-2 Apr 2005	32.600060	-95.392470
F. askewi	Lake Fork Creek, US 80	Sabine	Howells 1996 MDS 120	11-Jul-94	32.632720	-95.353810

F. askewi	Neches R., below US 84 (M3)	Neches	Troia 2010	Jul-Aug 2009	31.764550	-95.400670
F. askewi	Neches R., above SH 294 (D or L1)	Neches	Troia 2010	Jul-Aug 2009	31.644950	-95.286780
F. askewi	Neches R., above SH 294 (D or L2)	Neches	Troia 2010	Jul-Aug 2009	31.639720	-95.283700
F. askewi	Neches R., below SH 294 (D or L3)	Neches	Troia 2010	Jul-Aug 2009	31.625430	-95.280270
F. askewi	Lake Fork Creek, Near Hawkins	Sabine	Texas Mussel Watch/ Ford and Ranklev	22-Oct-11	32.658332	-95.357437
F. askewi	Trinity	Trinity	Texas Mussel Watch	Summer 2011	32.763195	-96.8069718
F. askewi	1/8 mi N Hwy 43-upstream of coal shoal	Sabine	Ford, 2011	23-Mar-11	32.373083	-94.463417
F. askewi	1/8 mi N 1794	Sabine	Ford, 2011	22-Jul-11	32.291550	-94.334433
F. askewi	1/8 mi E 1794	Sabine	Ford, 2011	22-Jul-11	32.2811666	-94.325416
F. askewi	1/4 mi N 79	Sabine	Ford, 2011	1-Aug-11	32.2265833	94.23288333
F. askewi	Coal Company	Sabine	and Neil Ford	27-Jul-11	32.397033	-94.500367
F. askewi	Coal Company	Sabine	Neil Ford	25-Jun-11	32.394183	-94.497583
F. askewi	Coal Company	Sabine	and Neil Ford	26-Jul-11	32.390183	-94.484717
F. askewi	Coal Company	Sabine	Neil Ford	25-Jul-11	32.390183	-94.485583
F. askewi	Hwy 59	Neches	Ford, Dunithan	22-Sep-10	31.137817	-94.821883
F. askewi	Hwy 79	Neches	Ford, Dunithan	22-Jun-11	31.89721	-95.43678
F. askewi	1/2 Mile E of 149	Sabine	Ford, Dunithan	8/19/2010	32.418667	-94.705433
F. askewi	1/8 Mile W of 149	Sabine	Ford, Dunithan	20-Jul-10	32.4123	-94.71338

F. askewi	3 Miles NW of Hwy 79	Sabine	Ford, Dunithan	21-Jul-10	32.227133	-94.2478167
F. askewi	N of 271	Sabine	Ford, Dunithan	17-Aug-10	32.530388	-94.958797
F. askewi	Upstream Hwy 14	Sabine	Ford, Dunithan	21-Jun-10	32.5631167	-95.2031833
F. askewi	Downstream 59	Sabine	Ford, Dunithan	2-Jun-11	32.31485	-94.34042
F. askewi	SR 7	Angelina	Bennett	Sep-7-06	31.457087	-95.726190
F. askewi	US 59	Sabine	Bennett	18-Aug-06	32.327900	-94.352920
F. askewi	Fort Sherman Dam Road	Big Cypress	Bennett	4-Jun-06	33.080767	-94.999267
F. askewi	Texas 43	Sabine	Bennett	18-Sep-05	32.369733	-94.457767
F. askewi	US 59	Sabine	Bennett	16-Aug-05	32.327900	-94.353930
F. askewi	SR 43	Sabine	Bennett	16-Aug-05	32.547383	-94.589800
F. askewi	FM 418	Hardin	Bennett	3-Sep-06	30.2927833	-94.168
F. askewi	US 96	Hardin	Bennett	Sep-5-05	30.285083	-94.191500
F. askewi	HWY 59	Sabine	Bennett	16-Aug-05	32.547383	-94.589800
F. askewi	Hwy 43	Sabine	Bennett	16-Aug-05	32.369733	-94.457800
Fusconaia lananensis	Angelina R., SH 7 crossing NE of Pollock	Neches	Karatayev & Burlakova 2007	7-Sep-06	31.48629	-94.82364
F. lananensis	Angelina R., US 59 N of Lufkin & S of Nacogdoches	Neches	Karatayev & Burlakova 2007	19-Aug-06	31.45767	-94.72637
F. lananensis	Beech Creek, Gore Store Road W of FM 92 (Village Creek drainage) Station 12	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	31-May-02	30.4905333	-94.2624

F. lananensis	Turkey Creek, Hester Bridge, Village Creek State Park, Station 11	Neches	Howells 2003 MDS 214/Bordelon and Harrel 2004	28-May-02	30.55165	-94.3322333
F. lananensis	Village Creek, Baby Galvez boat ramp area, Station 5	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	10-May-02	30.334233	-94.2041333
F. lananensis	Village Creek, E of Fletcher, Station 15	Neches	Bordelon and Harrel 2004	2001-2002	30.26824	-94.17998
F. lananensis	Village Creek, E of Kountze, Station 21	Neches	Bordelon and Harrel 2004	2001-2002	30.36991	-94.26536
F. lananensis	Village Creek, FM 418	Neches	Howells (2006)	3-Sep-05	30.292923	-94.165258
F. lananensis	Village Creek, lower creek between northern-most tribs, Station 17	Neches	Bordelon and Harrel 2004	2001-2002	30.25421	-94.12981
F. lananensis	Village Creek, Nature Conservancy area downstream of FM 418	Neches	Karatayev & Burlakova 2007	3-Jun-07	30.3962	-94.26629
F. lananensis	Village Creek, NE of Lumberton, Station 16	Neches	Bordelon and Harrel 2004	2001-2002	30.26196	-94.17996
F. lananensis	Village Creek, near RR xing N of Creek Road N of Fletcher, Station 1	Neches	Bordelon and Harrel 2004	2001-2002	30.27606	-94.18746
F. lananensis	Village Creek, New FM 418 NE on Kountze, Station 20	Neches	Bordelon and Harrel 2004	2001-2002	30.3981	-94.2644
F. lananensis	Village Creek, SW of Silsbee, Station 19	Neches	Bordelon and Harrel 2004	2001-2002	30.33979	-94.21219
F. lananensis	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW)	Neches	Howells (2006)	3-Sep-05	30.2850833	-94.1914666
F. lananensis	Village Creek, US 96 between Lumberton (NE) & Silsbee (SW), Station 3	Neches	Howells 2003 MDS 214 /Bordelon and Harrel 2004	2-May-02	30.2850833	-94.1914666

F. lananensis	Villlage Creek, off lower Village Creek Road NE of Lumberton, Station 2	Neches	Bordelon and Harrel 2004	2001-2002	30.25584	-94.17251
F. lananensis	Attoyac Bayou, FM 138 SW of Stockman	Neches	Karatayev & Burlakova 2007	5-Jun-07	31.768386	-94.426159
F. lananensis	Attoyac Bayou, CR 392 (New Hope xing) upstream of SH 21	Neches	Howells (2006)	2-Sep-05	31.543207	-94.306867
F. lananensis	Big Sandy Creek, N of Segno (Village Creek drainage) Station 14	Neches	Bordelon and Harrel 2004	2001-2002	30.62477	-94.69998
F. lananensis	Attoyac Bayou, CR 392 (New Hope xing) upstream of SH 21	Neches	Howells 1996 MDS 120	25-Jul-94	31.543133	-94.30691
F. lananensis	Sandy Creek (Attoyac Bayou drain.), CR 2913	Neches	Howells (2006)	2-Sep-05	31.6868833	-94.38345
F. lananensis	US 59 crossing	Angelina	Bennett, 2006	19-Aug-05	31.486933	-94.8236
F. lananensis	SR 7	Angelina	Bennett, 2006	7-Sep-06	31.457087	-94.72619
F. lananensis	FM 138	Attoyac Bayou	Bennett, 2006	5-Jun-06	31.768386	-94.426159
F. lananensis	Nature Conservancy	Village Creek	Bennett, 2006	27-Jun-06	31.646732	-94.268492
F. lananensis	CR 392	Attoyac Bayou	Bennett, 2006	2-Sep-05	31.5432833	-94.3069833

APPENDIX C: TEST GAIN VALUES FOR MODELS WITH ONLY THE SPECIFIED VARIABLE. THE VARIABLES WERE REMOVED IF THE TEST GAIN VALUES FOR THE ONE-VARIABLE MODELS WERE LOWER THAN THE TEST GAIN FOR THE FULL MODEL.

SPECIES	TRAINING AUC	TEST AUC	TEST GAIN
P. riddellii	0.992	0.8777	0.9652
E askovi	0.0001	0.8107	1 1208
r. uskewi	0.9901	0.8197	1.1398
F. lananensis	0.995	0.8676	1.2273
L. satura	0.9934	0.852	1.2518
O. jacksoniana	0.9973	0.7284	0.4746
P. amphichaenus	0.9975	0.8131	1.3045

SPECIES	AQUIFERS	KERNEL DENSITY RESERVOIRS	KERNEL DENSITY ROADS	KERNEL DENSITY SPRINGS	LAND FORM	NITROGEN	GROUND WATER RECHARGE	SOILS	ANNUAL MEAN CLOUD COVER	TOP-MODEL	VEGETATION
P. riddellii	0.2474	0.0383	0.3789	-0.0935	0.3611	0.3508	0.3242	1.0709	0.2978	0.4279	0.9962
F. askewi	0.2545	-0.0092	0.028	0.0683	0.1423	0.2674	0.2884	1.1119	0.2593	0.2819	0.7483
F. lananensis	0.1996	0.1841	0.0309	-0.0861	0.4882	0.2111	0.1263	0.9318	0.2753	0.1428	1.3975
L. satura	0.316	0.007	-0.0569	-0.0159	0.2046	0.2442	0.2682	1.3018	0.2856	0.2216	0.3872
O. jacksoniana	-0.067	-0.0124	-0.0149	0.0061	-0.3216	-0.0252	-0.0113	1.1951	-0.0183	-0.023	-0.1671
P. amphichaenus	0.1048	0.0723	0.0488	0.0839	0.0918	0.0788	0.0431	0.9232	0.023	0.1392	0.9084

APPENDIX D: SCHOENER'S D OBSERVED AND 5% CRITICAL VALUES. TWO SPECIES WERE CONSIDERED TO HAVE SIGNIFICANTLY DIFFERENT NICHES IF THE OBSERVED VALUE WAS BELOW THE 5% CRITICAL VALUE.

Species comparison	Observed value	5% critical value
L. satura Vs. P. riddellii	0.66	0.73
L. satura Vs. F. askewi	0.61	0.70
L. satura Vs. F. lananensis	0.37	0.70
O. jacksoniana Vs. P. riddellii	0.52	0.55
O. jacksoniana Vs. L. satura	0.49	0.57
O. jacksoniana Vs. P. amphichaenus	0.43	0.51
P. amphichaenus Vs. F. riddellii	0.37	0.57
P. amphichaenus Vs. L. satura	0.45	0.60
F. askewi Vs. P. riddellii	0.59	0.71
F. askewi Vs. P. amphichaenus	0.39	0.56
F. lananensis Vs. P. riddellii	0.51	0.61
O. jacksoniana Vs. F. askewi	0.48	0.49
O. jacksoniana Vs. F. lananensis	0.47	0.58
P. amphichaenus Vs. F. lananensis	0.23	0.61
F. askewi Vs. F. lananensis	0.51	0.59
O. jacksoniana Vs. P. riddellii	0.52	0.57

APPENDIX E: OBSERVED AND 5% CRITICAL RELATIVE RANK VALUES. TWO SPECIES WERE CONSIDERED TO HAVE SIGNIFICANTLY DIFFERENT NICHES IF THE OBSERVED VALUES WERE BELOW THE 5% CRITICAL VALUES.

Species comparison	Observed value	5% critical value
L. satura Vs. P. riddellii	0.76	0.77
L. satura Vs. F. askewi	0.73	0.78
L. satura Vs. F. lananensis	0.62	0.77
O. jacksoniana Vs. P. riddellii	0.03	0.62
O. jacksoniana Vs. L. satura	0.03	0.64
O. jacksoniana Vs. P. amphichaenus	0.03	0.59
nichaenus Vs. F. riddellii	0.53	0.63
P. amphichaenus Vs. L. satura	0.60	0.70
F. askewi Vs. P. riddellii	0.70	0.77
F. askewi Vs. P. amphichaenus	0.53	0.59
F. lananensis Vs. P. riddellii	0.63	0.72
O. jacksoniana Vs. F. askewi	0.03	0.55
O. jacksoniana Vs. F. lananensis	0.02	0.62
P. amphichaenus Vs. F. lananensis	0.42	0.68
F. askewi Vs. F. lananensis	0.646	0.647
O. jacksoniana Vs. P. riddellii	0.03	0.63